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Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean

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ABSTRACT: Ecosystems are fundamentally structured in space and time. The identification and quantification of scales of variability has occupied a central place in ecology for several decades. This paper examines spatial changes in the diversity of calanoid copepods and its regional dependence in the North Atlantic Ocean at diel, seasonal and interannual scales. Point cumulative semi-variograms, initially proposed for geological purposes, are described and intensively used to understand the relationships between diversity and its spatial scales of variability. A map of the mean spatial dependence in calanoid diversity is then proposed and diel and seasonal changes examined. This shows that diversity changes at small spatial scales over the European shelf seas. In oceanic areas, diversity changes at large spatial scales in both the subarctic and the northern boundary of the subtropical gyres. Low spatial scales of variability are detected in the Gulf Stream extension, in the path of the North Atlantic Current and west of Europe. A negative relationship between diversity and its spatial dependence is found in almost all the oceanic regions. This relationship is constant at all temporal scales. At an annual scale, relationships between diversity, spatial dependence and climatic indices have been investigated. Some links have been detected but both the intensity and the sign of these relationships vary greatly in space. The regime shift that took place in the North Sea after 1988 involved a sharp change in the diversity of calanoid copepods and a significant strengthening in the contrast between the neritic and oceanic spatial dependence.

KEY WORDS: Spatial scale of variability · Point cumulative semi-variograms · Calanoid copepods · Pelagic diversity · Continuous Plankton Recorder (CPR) survey

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INTRODUCTION

Ecosystems are fundamentally structured in space and time (Margalef 1979, Frontier & Pichot-Viale 1993, Lundberg et al. 2000), and the identification and the quantification of scales of variability has been a topic of great importance in ecology for several decades (e.g. Levin 1992, Mann & Lazier 1996, Haury & McGowan 1998, Beaugrand et al. 2001). Haury et al. (1978), by the use of a 3-dimensional time-space plot (Stommel 1963), estimated the spatial and temporal structure of zooplankton biomass variability. At all spatial scales, physical features often represented important factors

involved in the control of spatial and temporal patterns of biomass variability. Similar conclusions have been subsequently found (e.g. Platt & Sathyendranath 1994, Mann & Lazier 1996, Haury & McGowan 1998, Beaugrand et al. 2002, this issue).

Many techniques are available to quantify and analyse the temporal variability of biological variables (e.g. Diggle 1990, Ibañez & Etienne 1991, Legendre & Legendre 1998). For example, Colebrook (1981, 1982, 1985, 1991) and Colebrook & Taylor (1984) applied maximum entropy spectral analysis to determine the characteristic frequency of the long-term change in the abundance of plankton around the United Kingdom. One-dimensional spectral analysis has also been applied to examine spatial scales of variability of

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biological variables such as chlorophyll fluorescence and copepod abundance (Tsuda et al. 1993) or physical variables (Yoder et al. 1993). Moran's (1950) or Geary's (1954) spatial autocorrelation coefficients can also be used to assess the scales of variability involved in the changes of organism abundance. Semi-variograms, proposed for the first time by Matheron (1962), are also often applied to identify spatial behaviour of a biological variable at different spatial scales (e.g. Planque 1996, Grioche et al. 1997). For example, Planque (1996) used experimental semi-variograms to examine the spatial scale of variability of *Calanus finmarchicus* and *C. helgolandicus* for different months across the North Atlantic Ocean.

However, the application of these techniques to assess the spatial variability of a variable is limited. For example, classical experimental semi-variograms are highly sensitive to the non-regularity of the distribution of observations inside a given spatial domain (Sen 1989, Wackernagel 1995). Sampling by many monitoring programmes such as the Continuous Plankton Recorder (CPR) survey is irregular in space, and thus an unbiased estimation of experimental semi-variogram is not possible. Moreover, the choice of distance classes in the building of the experimental semi-variogram is quite arbitrary and may highly influence the shape of the curve (Sen 1989). These drawbacks led Sen (1989) to propose a new way to evaluate the spatial dependence of observations for geological purposes.

This method, known as the point cumulative semi-variogram, has been applied in this paper to evaluate the spatial dependence of the diversity of calanoid copepods in the North Atlantic Ocean at 3 temporal scales of variability: diel, seasonal and annual scales. Firstly, as this technique has never been used in oceanography, a full description of its potentialities is given. Secondly, this method is used to characterise the mean spatial variability of the diversity of calanoid copepods at diel, seasonal and annual scale over the North Atlantic Ocean. Thirdly, the mean spatial relationships between the diversity and its spatial dependence are investigated. Finally, Sen's point cumulative semi-variogram is applied to study annual and long-term changes in the diversity and its spatial dependence in relation to climatic indices such as the North Atlantic Oscillation (NAO), the northern hemisphere temperatures and the regime shift in the North Sea marine ecosystems (Reid et al. 2001a).

MATERIALS AND METHODS

Biological data. Biological data used in this study were collected from the CPR survey. This biological monitoring programme has sampled plankton on a

monthly basis over the North Atlantic and adjacent seas since 1946 (Warner & Hays 1994). Samples are collected by a high-speed plankton recorder towed behind voluntary merchant ships at a standard depth of about 6.5 m (Hays 1994). Plankton is retained by a continuously moving band of silk, which has an average mesh size of 270 μm , corresponding to approximately 3 m^3 of filtered seawater (Hays 1994). One CPR sample represents 10 n miles of tow. A complete description of this programme is given by Colebrook (1960, 1975) and Warner & Hays (1994). In the present study, data of 108 copepod taxa, corresponding to the sampling period 1958 to 1999, were extracted from the CPR database.

Climatic data. Two climatic indices were used to assess the relationships between diversity, its spatial dependence and climatic factors. Temperature anomalies for the northern hemisphere from 1958 to 1998 were provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office, London. The winter NAO index (Hurrell 1995) for the period 1958 to 1999 was obtained from the Internet site: www.met.rdg.ac.uk/cag/NAO/index.html. The NAO is a basin scale alternation of atmospheric mass over the North Atlantic between the high pressures centred on the Azores and low pressures around Iceland (Dickson & Turrell 2000). The index used here is based on the differences in normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864 (Hurrell 1995).

Geostatistical analyses. All analyses presented in this study have been performed on the total number of calanoid copepod species or taxa per CPR sample (Beaugrand et al. 2000, 2001). This index represents a reliable indicator of the diversity for the CPR data (Beaugrand & Edwards 2001). This will be referred to as calanoid diversity thereafter. Experimental semi-variograms and point cumulative semi-variograms were then calculated at diel, seasonal and annual scales.

Calculation of geographical distances: The locations of all CPR samples are recorded as latitudinal and longitudinal points. Before the calculation of semi-variograms and point cumulative semi-variograms, longitude and latitude of each sampling site were converted into geographical distances (Step 1 in Fig. 1) using:

$$h_{i,j} = \arccos(\sin \varphi_i \sin \varphi_j + \cos \varphi_i \cos \varphi_j \cos g) \quad (1)$$

$$d(i,j) = 6377.221 \times h_{i,j} \quad (2)$$

$d(i,j)$ is the distance (in km) between i and j . φ_i is the latitude (in radians) at point i and φ_j the latitude at point j ; and g is the difference in longitude between i and j . The constant in Eq. (2) is the Earth radius in km.

The experimental semi-variogram: The experimental semi-variogram (Matheron 1962), γ_d , is based on the

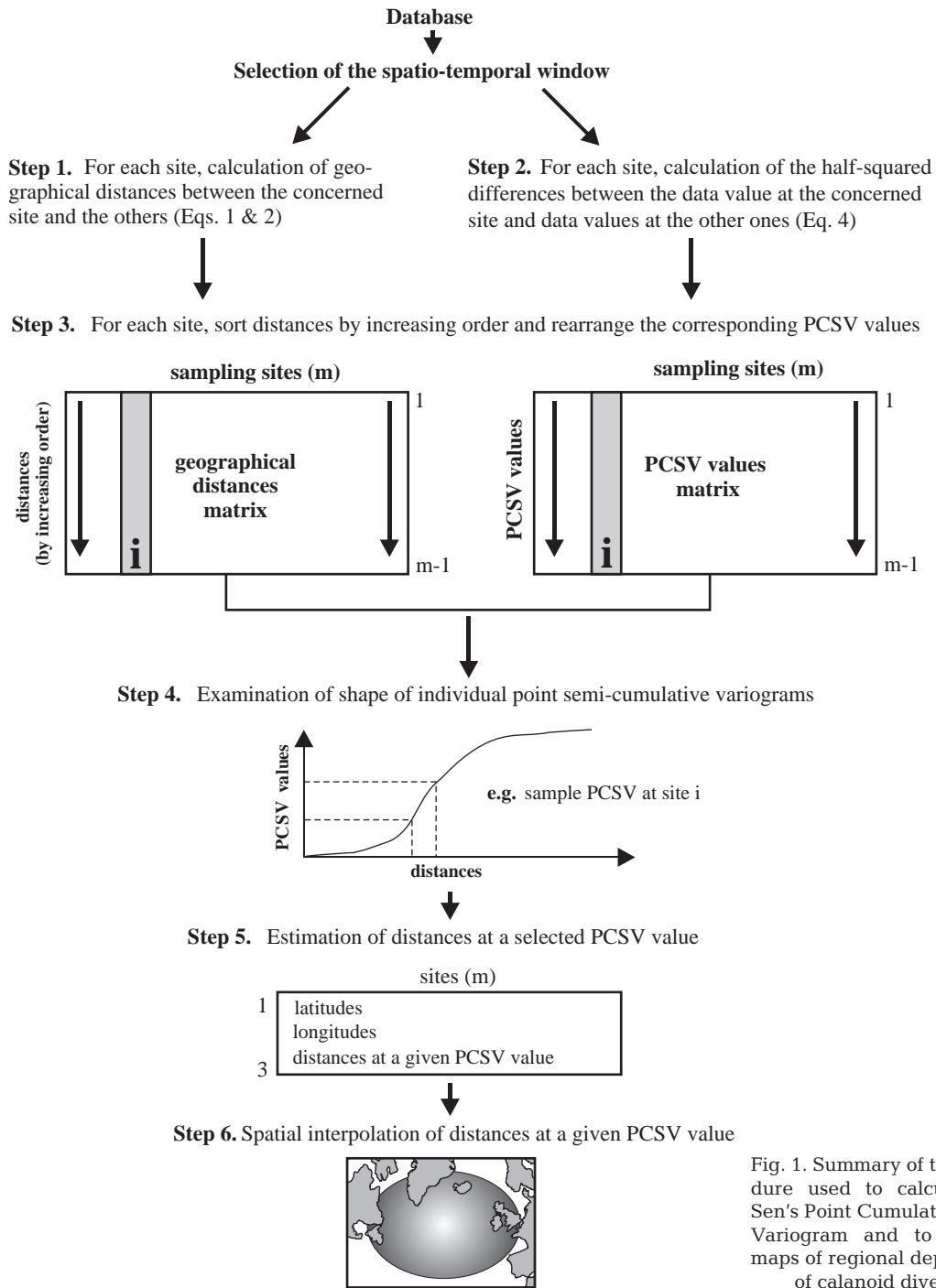


Fig. 1. Summary of the procedure used to calculate the Sen's Point Cumulative Semi-Variogram and to produce maps of regional dependence of calanoid diversity

calculation of half-squared differences of all pairs of values of a measured variable (Wackernagel 1995). The plot of dissimilarities γ_d against the spatial separation of sample pairs defined a variogram cloud. As cloud variograms are often highly variable at short distances, the variogram has been calculated by averaging values of all half-squared differences inside

predefined distance classes (Journel & Huijbregts 1978). This leads to the following formula:

$$\gamma_d = \frac{1}{2n_d} \sum_{i=1}^{n_d} (Z_i - Z_{i+h})^2 \quad (3)$$

where γ_d is value of the semi-variogram for each distance class defined by vector \mathbf{d} . n_d is the number of

possible dissimilarities inside the distance class \mathbf{d} . z_i and z_{i+h} are the 2 measured variables separated by a distance h , with $h \in$ distance class \mathbf{d} .

Sen's point cumulative semi-variogram (PCSV): The general procedure used to calculate this function and to exploit potentialities of the model in this study is summarised by Fig. 1. In contrast to the experimental semi-variogram, a point cumulative semi-variogram (PCSV) (Sen 1989, 1998) is performed for each sampling site inside a spatial domain. This model is based on the same dissimilarity measure involved in the calculation of the experimental semi-variogram (Step 2 in Fig. 1). However, for each site, distances calculated between the concerned site and the other ones are sorted in an ascending order and the corresponding dissimilarities are progressively pooled (Step 3 in Fig. 1). This can be formulated as follows:

$$\gamma_{(d_i)} = \frac{1}{2} \sum_{j=1}^{m-1} (Z_c - Z_j)^2 \quad (4)$$

where d_i is the i th site at which the PCSV is calculated between the measured variable Z_c at the concerned site and variables Z_j of site j ; m is the total number of sites (or sampling points). There are, therefore, as many cumulative semi-variograms as samples. This allows the spatial dependence of the regional variable to be locally examined (Sen 1989, 1998). Here, spatial dependence is defined as the distance (in km) for a given PCSV value. If this distance is relatively small, the dependence between observations is more local, which means that the regional variable varies at a low spatial scale. If the distance is higher for the same PCSV value, the spatial dependence between observations is more regional, which means that the regional variable changes at a larger spatial scale.

General procedure used to map the spatial dependence of calanoid diversity: The heterogeneity of the regional variable can be evaluated by plotting PCSV values against geographical distances (or other type of distances) for each site (Step 4 in Fig. 1). However as there are as many experimental PCSVs as points, the spatial heterogeneity of the regional variable can also be assessed numerically by determining the distance at a fixed PCSV value for each site (Step 5 in Fig. 1) and then interpolating and representing these distances on a map (Step 6 in Fig. 1). This gives an indication of the local behaviour of the variability of the regional variable. For example, anisotropic behaviour can be easily detected by simple examination of the map. The PCSV is selected by trial and error. Elevated PCSV values may be less reliable as the number of samples decreases with the distance from which the experimental cumulated semi-variogram is calculated. On the other hand, the selection

of too small a PCSV value may just reflect a noisy signal or a variability related to the sampling instrument.

To determine the distance at a fixed PCSV level, a weighted mean of the superior and inferior distances was calculated. These distances were then mapped using the inverse squared distance method (Lam 1983) on latitudes and longitudes converted in Lambert coordinates to avoid a strong alteration of distances on the map (Planque et al. 1997, Beaugrand et al. 2000, Beaugrand et al. 2001). These analyses were programmed in MATLAB.

Mapping of the mean spatial dependence of calanoid diversity. To produce a map representing the average spatial dependence of calanoid diversity, the same procedure used by Beaugrand et al. (2000) to map the diversity (1958 to 1997) of this same taxonomic group was applied. Maps of diversity and spatial dependence (see Fig. 1) were produced for each year and each season (December to February, March to May, June to August, September to November) for daylight and dark periods from 1958 to 1999. A PCSV value of 100 was fixed by trial and error. The inverse squared distance method was used to interpolate spatially the distances. Search radius was fixed to 250 n mile and the number of neighbours was constant and equal to 10. The size of the pixels was equal to 50 n mile². The size of the pixel was selected by trial and error but also corresponds with the size used by Planque & Fromentin (1996) for the same kind of dataset. This represents a good compromise between the spatial size of a CPR sample (10 n mile) and the spatial density of the CPR sampling. Then, values of each pixel for different periods were averaged to produce a map for each season for daylight and dark periods. The function described by Beaugrand et al. (2001, their Fig. 1) was used to produce maps of spatial dependence for daylight and dark periods.

To examine the relationships between diversity and spatial dependence, a method based on the Merriam & Sondergard (1988) Reliability Index procedure was used. This method consists of calculating correlation in a moving window centred on each possible pixel for 2 maps of identical dimensions. This procedure allows regional relationships between 2 maps to be visualised. Selected by trial and error, a window of 11 pixels (along longitudes) \times 11 pixels (along latitudes) was used. The Pearson correlation coefficient was then calculated between all possible pairs of values ($11^2 = 121$) if the number of non-missing data was superior or equal to 70. Probability maps of the values of the correlation coefficient will not be displayed as with the spatial interpolation procedure, data are not spatially independent.

Annual maps of diversity and spatial dependence.

From 1958 to 1999, annual maps of diversity and spatial dependence were built by averaging 8 base maps produced for each year (4 seasons for daylight and dark periods). Correlation analyses (Pearson linear correlation coefficient) were performed for each pixel to try to establish if there were any relationships between diversity, spatial dependence and climatic indices. Probabilities were calculated with and without the consideration of autocorrelation. Box-Jenkins (1976) autocorrelation function modified by Chatfield (1989) was used in each pixel. Then, the correction using the Chelton's (1984) formula was applied as Pyper & Peterman (1998) showed that this type of correction gave better results than the Garret-Petrie (1981) method and more stable results than the Kope & Botsford (1990) method.

Differences in the diversity of calanoids and its spatial dependence between the period 1958–1987 and 1988–1999. Reid et al. (2001a,b) have recently suggested that a regime shift in the North Sea ecosystems took place circa 1988. To test this hypothesis and to examine its geographical extent, the annual diversity and its spatial dependence was grouped into 2 periods: 1958 to 1987 and 1988 to 1999. The mean diversity and spatial dependence values were then calculated and a Kruskal-Wallis test was performed between years of the 2 different periods for each pixel to assess the probability of observed changes.

RESULTS

Sample point cumulative semi-variograms

In order to illustrate Sen's PCSV model, data were firstly selected in the North Atlantic Ocean from 1960 to 1980 for August, using only night data (Fig. 2a). The regional experimental semi-variogram (Fig. 2b) calculated from these data shows that the diversity of calanoid copepods is spatially dependent up until about 1200 km where the semi-variogram levelled off. A sill (the value of the variogram at the distance from which the variance ceases to increase) of approximately 8 was identified corresponding to the range of 1200 km. A nugget effect (the value of the variogram for distance 0) of about 2.25 was detected, which indicates sampling-related variance or variability at a small spatial scale.

Fig. 2c–f displays the experimental PCSVs for 4 selected samples in the North Atlantic Ocean. The shapes of the 4 PCSVs are different, which reflects the presence of at least 4 regions of distinct pattern of spatial variability in the diversity of calanoids and indi-

cates that the selected region is spatially heterogeneous (Sen 1989, 1998). All experimental PCSVs have a small portion where the PCSV values are weak or equal to 0 for a distance ranging between 0 and 100 to 250 km. This means that a small (or no) change in the diversity of calanoid copepods occurs around this range and thus that a physical process may be responsible for homogenisation of the diversity in these areas. Curvature portions present in all sample PCSVs indicate a spatial dependence of value of diversity for calanoid copepods while the straight lines following these portions indicate that calanoid diversity becomes spatially independent. Flattened portions at large distances (Fig. 2c) may sometimes occur because of a scale effect on the curve. It should also be noted that the last portion of PCSVs only contains a few points indicating that caution should be taken with the interpretation.

While it is difficult to interpret the experimental semi-variogram in Fig. 2c, the sample PCSV clearly shows a strong spatial dependence around the station concerned until at least 1200 km in the Atlantic Arctic Province (Longhurst 1998). The sample PCSVs (Fig. 2d) at a site located in the northern part of the North Atlantic Drift Province (Longhurst 1998) has a similar shape to the former PCSV. However, the spatial dependence around the site is 50% weaker at the PCSV cut-off of 1000. Using the local semi-variograms performed for each site, this difference, easy to identify by the examination of sample PCSVs, is difficult to detect by looking at the corresponding experimental semi-variograms.

The sample PCSV in the northern part of the subtropical gyre (Fig. 2e) exhibits successive curvature portions which means that the spatial variability in the diversity of calanoids is controlled by different physical processes which act at different spatial scales. Off Newfoundland (Fig. 2f), the PCSV is similar to the former with a 50% decrease of the spatial dependence at a PCSV value of 1000. Here also, this difference would have been difficult to detect by examination of the sample semi-variograms at the 2 sites.

Mapping of the spatial dependence

In practice, as there are as many PCSVs as sites, it is not possible to examine all graphics. However, the spatial dependence can be assessed by fixing a PCSV value and numerically determining the corresponding distances for all plots. Interpolation methods can be then used to map the spatial dependence of the regional variable. At a given site for a fixed PCSV value, the smaller the distances are, the more

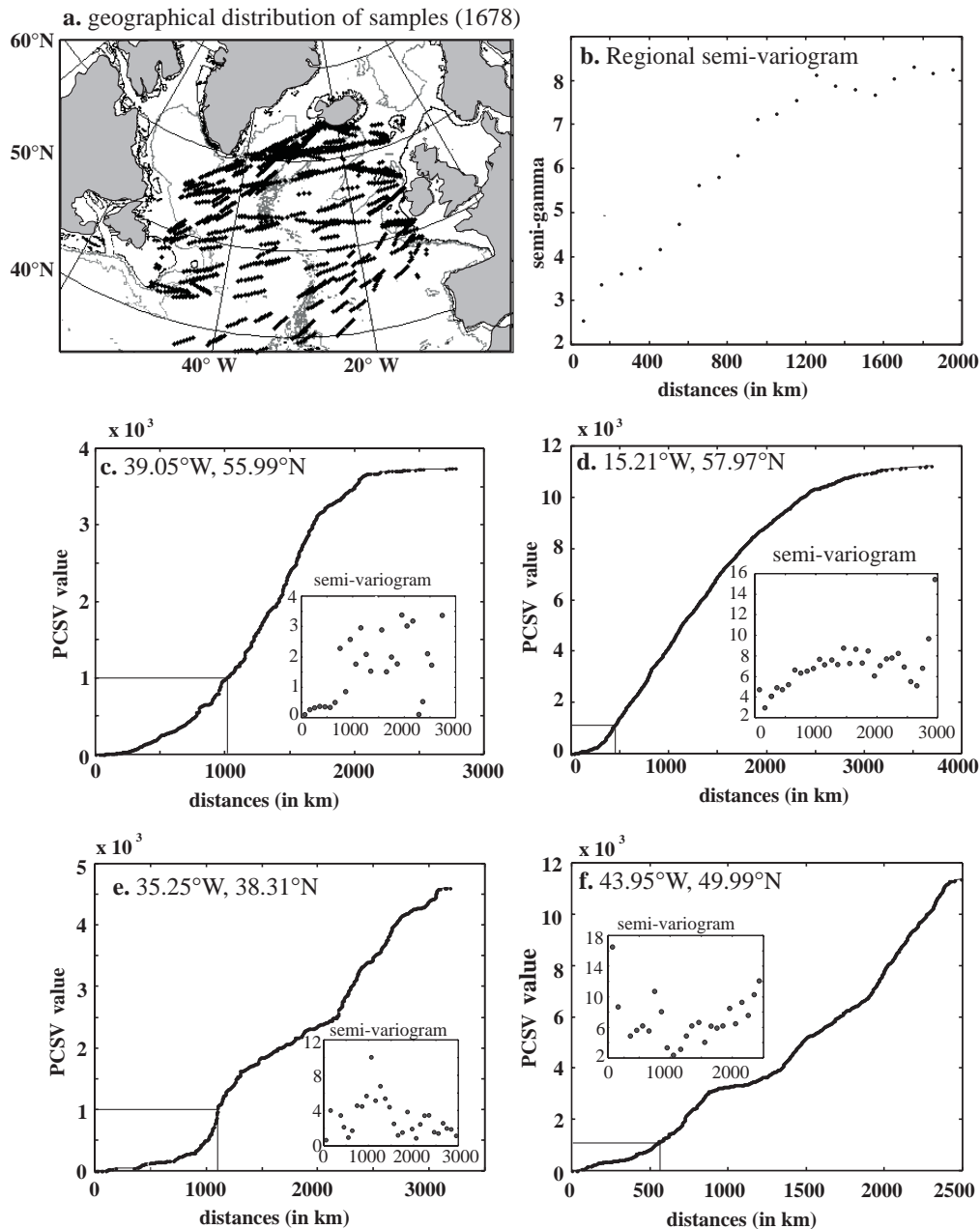


Fig. 2. Experimental semi-variograms and PCSVs calculated in the northern North Atlantic Ocean in August for the period 1960 to 1980 (1678 samples collected during dark periods). (a) Geographical distribution of samples. (b) Regional experimental semi-variogram of the diversity of calanoid copepods. (c to f) Experimental PCSVs and local semi-variograms of the calanoid diversity at some sites. Dark periods were selected using the function presented in Beaugrand et al. (2001, their Fig. 1)

local the variability, and the more regional the spatial dependence between observations (large-scale variability).

Fig. 3 shows the results of this procedure for 3 PCSV values (200, 500 and 1000). Results in the 3 maps are similar. The spatial dependence is high in the subarctic and subtropical gyres. At the PCSV threshold of 200, calanoid diversity (as the mean number of taxa per

CPR sample) varies at about 500 and 600 km on average in both gyres. Between these gyres, an area of lower-scale spatial variability is detected, which highly corresponds with the path of the North Atlantic Current west of the mid-Atlantic ridge (Beaugrand et al. 2001). Another area of lower-scale spatial variability is found in the northern part of the North Atlantic Drift Province (Longhurst 1998).

Mean spatial dependence of the diversity of calanoids in the North Atlantic Ocean

Using all CPR samples from the period 1958 to 1999 in the North Atlantic and adjacent seas, the same procedure described above to assess the spatial dependence was applied for each season for daylight and dark periods. Diversity of calanoids was also calculated for the same periods. Fig. 4a shows the calanoid diversity in subsurface waters for dark periods. This map is very similar to that produced by Beaugrand et al. (2000) for the period 1958 to 1997 and there is no need to comment on it here. Fig. 4b displays the mean spatial dependence of calanoid diversity for dark periods. In oceanic regions, both subtropical (northern part) and subarctic gyres have the strongest spatial dependence. A more local variability is detected between the 2 gyres and west of Europe. A gradient between oceanic and neritic regions is quite visible on both sides of the North Atlantic Ocean.

In general, the correlation between each pixel of both the diversity and spatial dependence maps is negative ($r = -0.61$, $df = 1169$). The probability is highly significant ($p < 0.0001$). However as the use of spatial interpolation involves a high spatial autocorrelation, the probability should be considered with caution. Calculation of the local correlation coefficient (using a spatial window of 11 pixels \times 11 pixels) indicates that the relationships between diversity and its spatial dependence are negative throughout nearly all the regions (Fig. 4c). This means that the smaller the scale at which the spatial variability changes, the higher the diversity is. This relationship is weaker over the European shelf edge and in the Bay of Biscay. A positive relationship is detected over the Grand Banks, south of Greenland and in the North Sea.

Spatial dependence at diel and seasonal scales

Maps of the spatial dependence of diversity of calanoids for daylight and dark periods (not shown) show similar spatial patterns but diversity spatially changes at

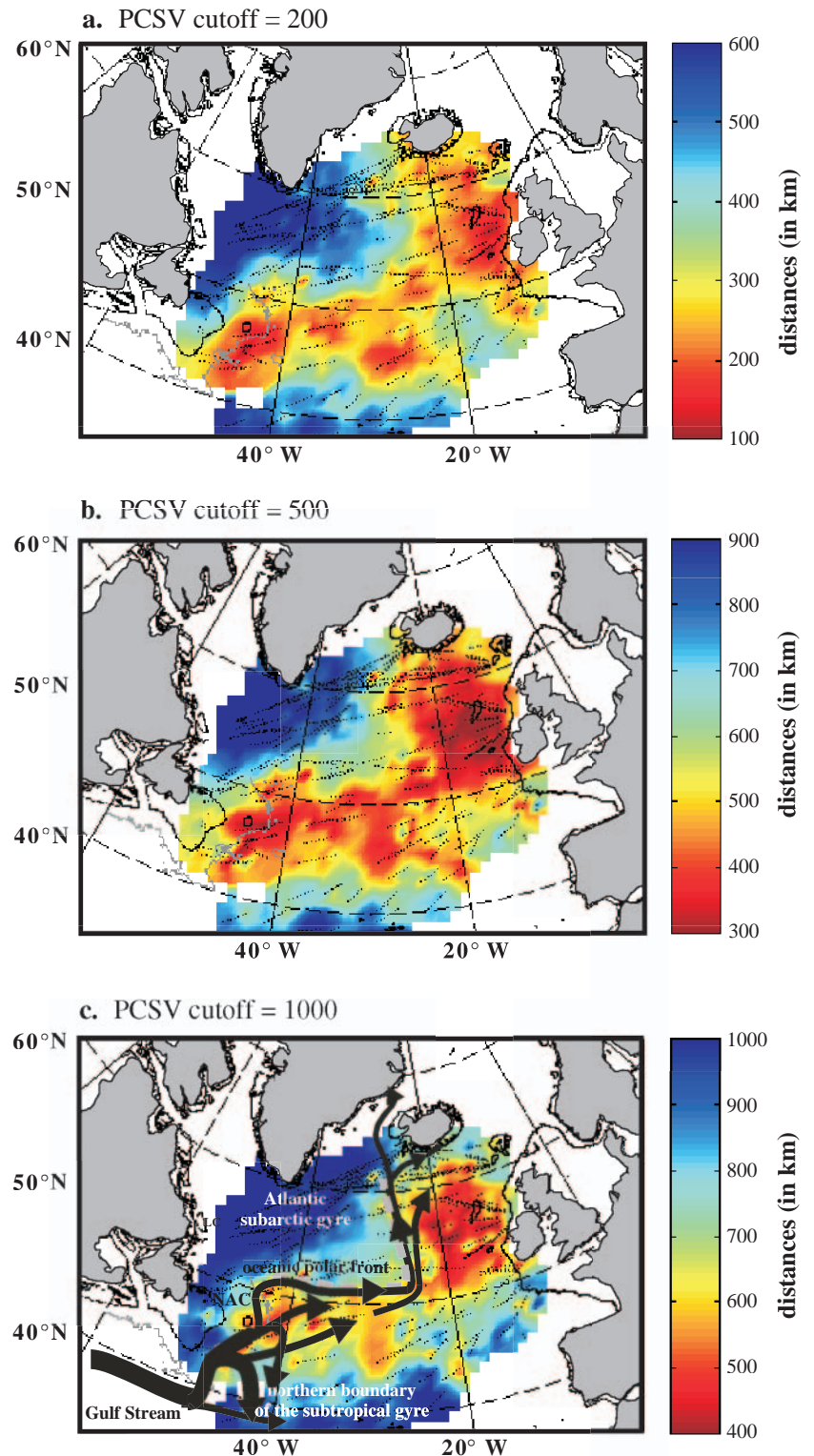


Fig. 3. Maps of the mean regional dependence of the calanoid copepod diversity in the North Atlantic Ocean in August (dark data) for the period 1960 to 1980. (a) PCSV level of 200. (b) PCSV level of 500. (c) PCSV level of 1000. The path of the North Atlantic Current is superimposed (Beaugrand et al. 2001)

a smaller scale at night. At a seasonal scale (Fig. 5), patterns of spatial scale of change in the diversity between different seasons are stable overall. Spatial variability in calanoid diversity occurs at a higher scale in winter. From spring, spatial variability is lower and reaches a minimum in autumn. A stronger seasonal change is detected in the north-eastern part of the North Atlantic province (Longhurst 1998).

Diversity, spatial dependence and climatic indices

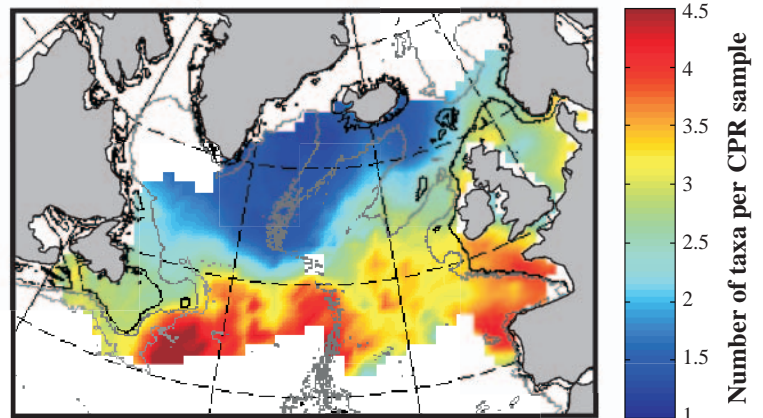
Annual maps of calanoid diversity and its regional variability were produced. Fig. 6a,b shows the correlations between annual changes in calanoid diversity and the winter NAO index, and between calanoid diversity and northern hemisphere temperatures. Significant negative correlations are detected in the oceanic areas while positive relationships are found in the north-eastern part of the North Sea. Positive correlations between diversity and northern hemisphere temperatures seem to occur in the north-eastern part of the North Sea. However, probabilities become insignificant when the temporal autocorrelation is corrected.

Fig. 6c,d displays the correlation maps between spatial dependence and winter NAO index, and between regional dependence and northern hemisphere temperatures. A significant positive link is detected between regional dependence in the diversity of calanoids and the NAO in oceanic areas west of the British Isles. In other areas, the correlations are more negative. The same pattern is seen when the correlations between spatial dependence and northern hemisphere temperatures are examined. However, the contrast between both regions is emphasised. Again, when the autocorrelation is considered, this pattern becomes insignificant.

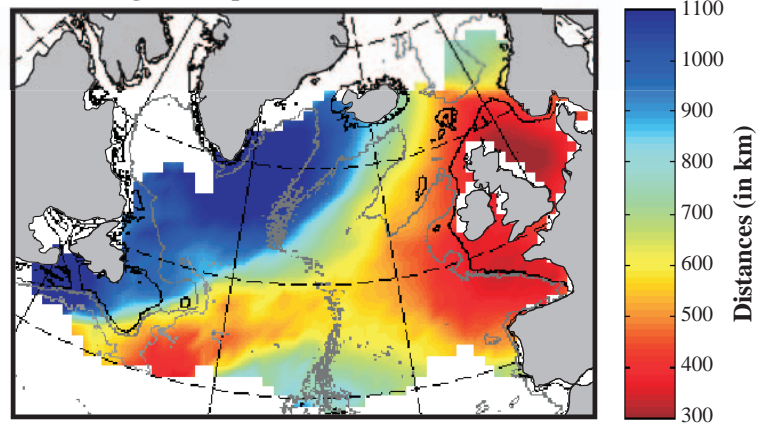
Influence of the regime shift of the North Sea on the calanoid diversity and its spatial dependence

Annual maps of calanoid diversity and spatial dependence have been grouped into 2 periods: 1958 to 1987 and 1988 to 1999. A clear shift in the spatial distribution of diversity occurred after 1987 (Fig. 7a). Diversity decreased considerably in the west European basin and west of the British Isles after 1987. A clear increase

a. Mean diversity



b. Mean regional dependence



c. Correlations

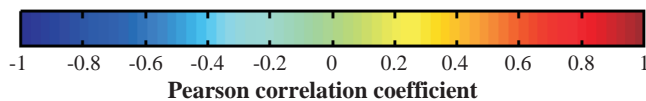
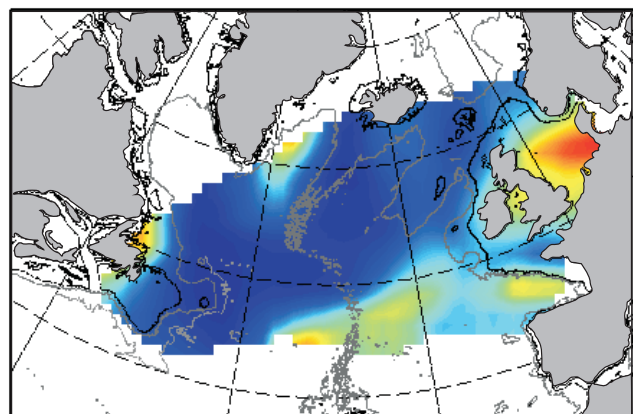


Fig. 4. Mean maps of the diversity of calanoid copepods (a) and its regional dependence (b) in the North Atlantic Ocean and adjacent seas. These maps represent the mean of 8 maps of the regional dependence of diversity produced for each season for daylight and dark periods at a PCSV level of 100. Similarly to Fig. 3, several PCSV levels were tried and gave similar conclusion. c represents the sliding 2-dimensional Pearson correlation between a and b

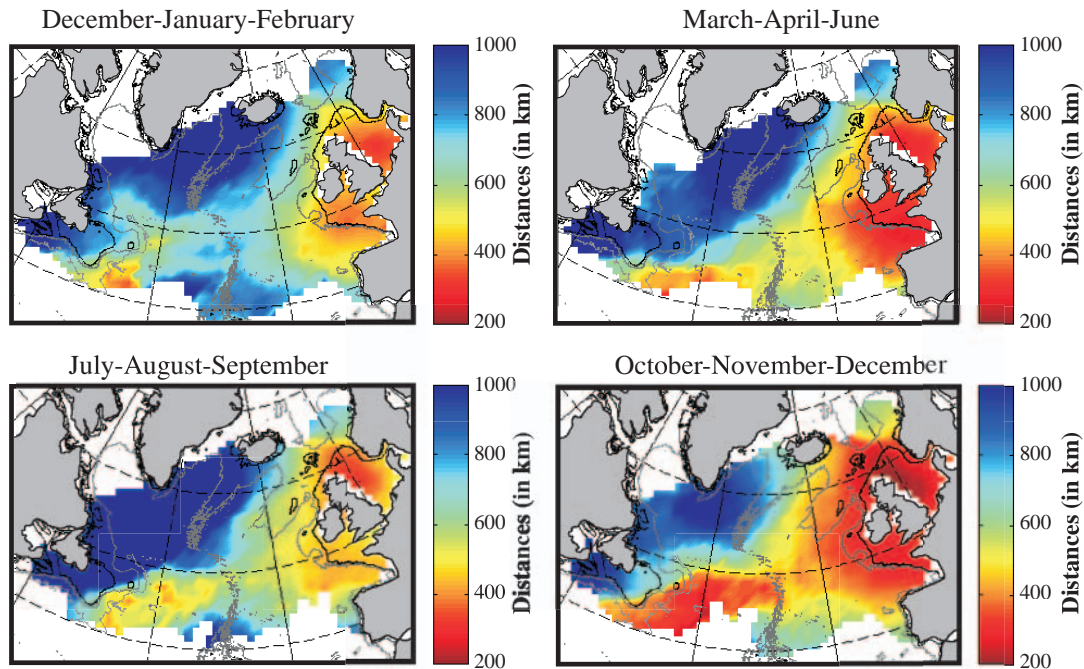


Fig. 5. Seasonal changes in the regional dependence of the diversity of calanoids. Dark periods were only used according to the same procedure utilised by Beaugrand et al. (2001, their Fig. 1)

occurred during the second period in the NE North Sea. Diversity is still high over the southern part of the European shelf edge. A Kruskal-Wallis test performed for each pixel clearly demonstrates that these changes are significant with the exception of coastal areas and the southern North Sea. The spatial dependence of calanoid diversity has significantly increased west of British Isles and decreased over the European shelf and the west European basin (Fig. 7b). Sliding 2-dimensional correlations between diversity and its spatial dependence calculated for both periods (not shown) indicate that the positive relationship in the North Sea has moved northwards since 1987. The positive relationships seen in the southern part of the Bay of Biscay became negative for the period 1988 to 1999.

DISCUSSION

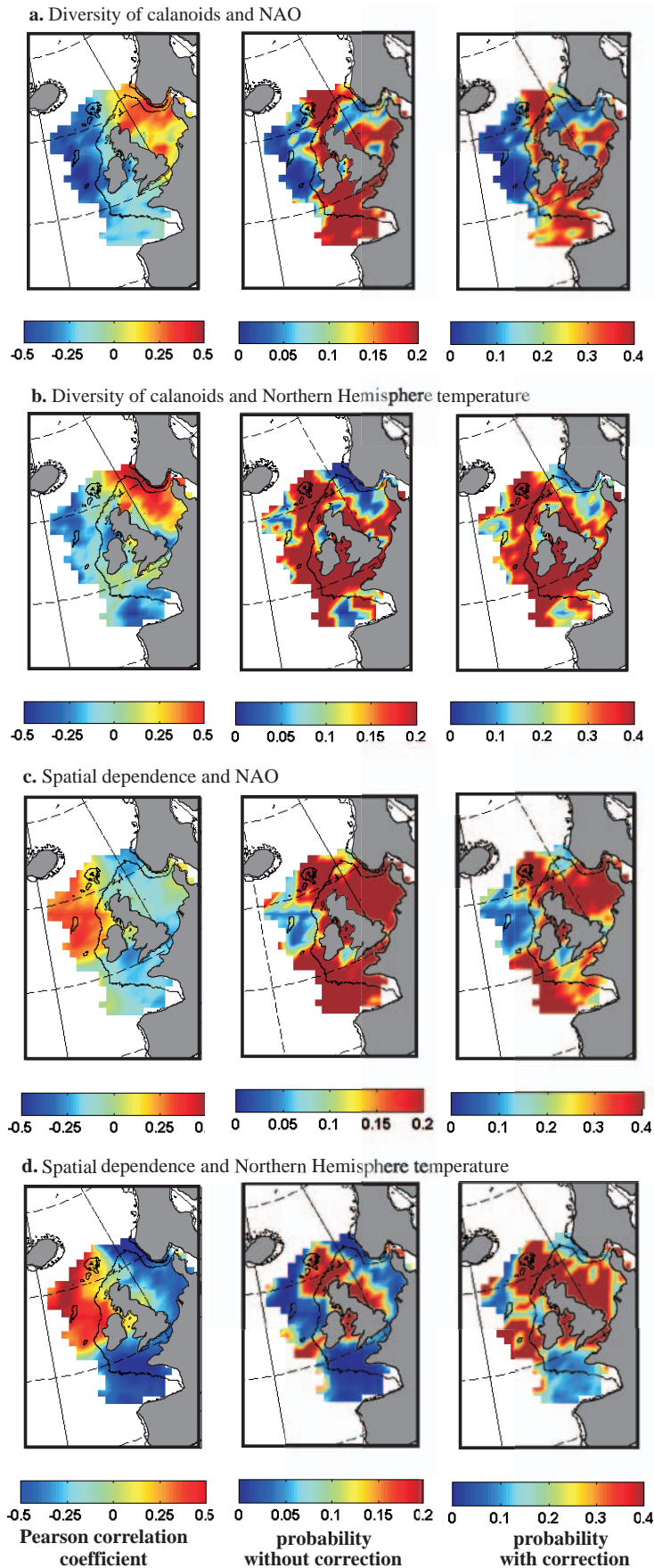
Sen's point cumulative semi-variogram

Sen's point cumulative semi-variogram allowed local behaviour of the regional variable to be examined and its spatial heterogeneity to be assessed (Sen 1989). This represents a great advantage in comparison with the classical semi-variogram, which only examines the regional variable globally. Local semi-variograms, greatly variable, are clearly not adapted for this purpose and Fig. 2 showed that in most cases, they were not interpretable.

The mapping of distances for a fixed PCSV value is of great interest. Local variability and anisotropic behaviour of the regional variable can be visualised and quantified. The selection of the PCSV value is important and results may slightly vary from one threshold to another (Fig. 3). It is highly recommended to use several thresholds. Sen (1989, 1998) discussed other technical advantages of this method.

Diversity and spatial dependence of calanoids at diel and seasonal scale

Mapping of the spatial dependence of the calanoid diversity showed that diversity varies at a smaller spatial scale in neritic than in oceanic regions. At a PCSV fixed to 100, European shelf sea diversity changes during dark periods for distances ranging from 300 to 450 km (Fig. 4b). Canadian continental shelf sea diversity varies at a greater scale, more than twice the rate in European seas. In oceanic regions, diversity is spatially stable in the Atlantic Arctic province (Longhurst 1998), about 1000 km at a PCSV = 100 and in the northern boundary of the subtropical gyre (on average about 800 km at a PCSV = 100). Lower-scale spatial patterns in calanoid diversity are observed in the Gulf Stream extension (as defined by Beaugrand et al. 2001), in the path of the North Atlantic Current west of the mid-Atlantic ridge and west of Europe.



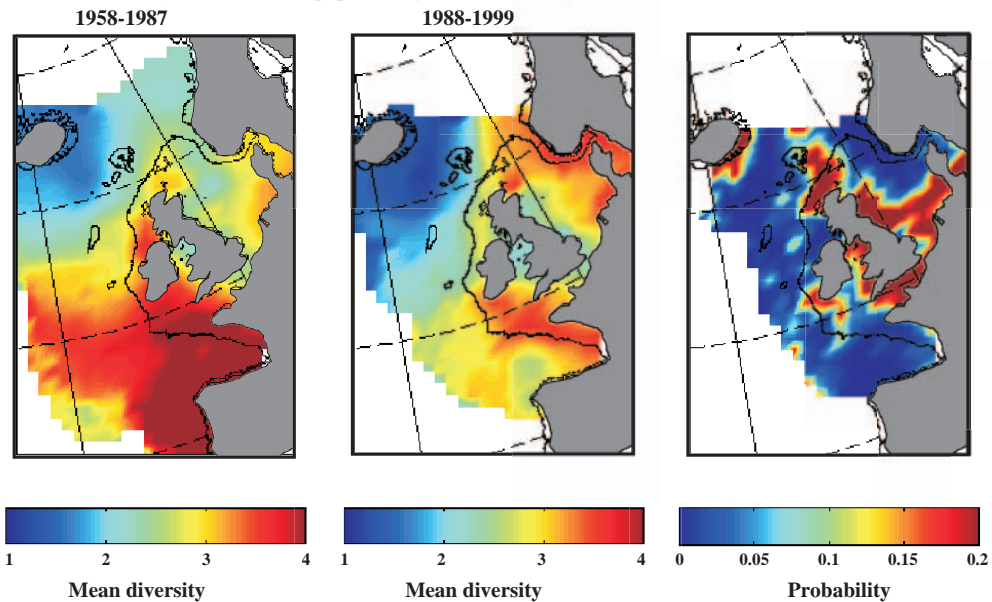
Spatial distribution of eddy kinetic energy and occurrence is strongly heterogeneous in the ocean (Stammer & Böning 1996, see Fig. 16 in Pingree et al. 1999). Maximum variability is often found in the path of major oceanic surface currents such as the Gulf Stream (Stammer & Wunsch 1999). Close correspondence exists between the lower-scale spatial variability observed in the Gulf Stream extension and in the path of the North Atlantic Current west of the mid-Atlantic ridge (Fig. 3) and maps of eddy kinetic energy produced by Wunsch & Stammer (1995), Stammer & Böning (1996), and Ducet et al. (2000). Eddy activity related to the path of the North Atlantic Current and the Oceanic Polar Front is likely to explain the low scale of spatial variability observed between the sub-arctic and the northern boundary of the subtropical gyre.

In oceanic areas west of European seas and east of about the mid-Atlantic ridge, diversity also changes at a low spatial scale (Figs. 3 & 4). Even though eddy energy is weaker in oceanic regions west of Europe, mesoscale eddy activity has been reported in this area (Stammer & Böning 1996, Read & Pollard 2001). During the North Atlantic Bloom Experiment (Ducklow & Harris 1993), spatial changes in chl *a* and temperature were investigated in regions along the 20°W meridian near 48 and 60°N between 26 April and 3 June 1989 (e.g. Watson et al. 1991, Robinson et al. 1993, Yoder et al. 1993). Temperature and chl *a* concentrations were found to be significantly positively correlated providing evidence that physical processes, attributed by the authors to upwelling and mixing, affect the spatial distribution of phytoplankton biomasses.

Two main processes are seen to be important in the generation, energy, frequency and longevity of eddies. First, the presence of eddies west of the British Isles has been ascribed to the path of the North Atlantic Current (White & Heywood 1995, Bersch et al. 1999, Read & Pollard 2001). Secondly, it has also been demonstrated that winds are involved in the generation of the mesoscale eddy field (Stammer & Böning 1996, Stammer &

Fig. 6. Pearson correlation between the mean annual calanoid diversity and (a) winter NAO index and (b) northern hemisphere temperature. Pearson correlation between the mean annual spatial dependence of calanoid diversity and (c) winter NAO index and (d) northern hemisphere temperatures. In each case, the corrected and not corrected probability for temporal autocorrelation is indicated (see 'Materials and methods')

a. Mean diversity of calanoid copepods (night observations)



b. Mean regional dependence of calanoid diversity in November-December (night observations)

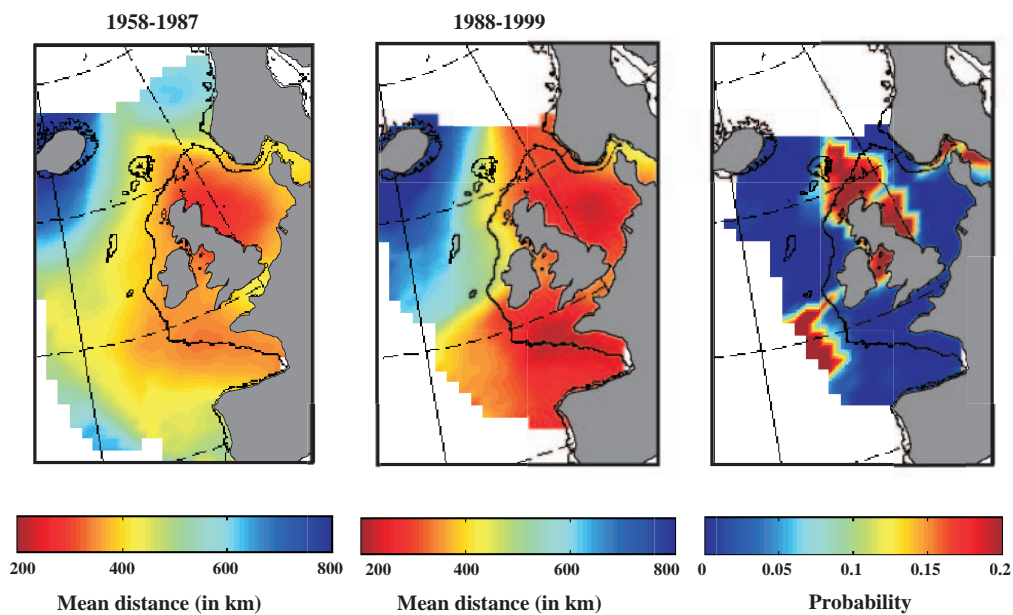


Fig. 7. Mapping of (a) diversity of calanoids and (b) its regional dependence for the periods 1958 to 1987 and 1988 to 1999. A Kruskal-Wallis test was performed in each pixel to examine where the differences between the 2 periods were significant. The resulting probabilities are also plotted

Wunsch 1999). Seasonal charts of eddy variability produced by Stammer & Wunsch (1999) show that the strongest production of eddies occurs during autumn. This corresponded with seasonal changes in wind forcing west of the European continental shelf, which also coincides with the maximum low-scale variability in calanoid diversity found in this study (Fig. 5). However, eddy kinetic energy is still elevated in winter in their

charts while spatial variability in diversity is at its highest annual level. This result may be explained by the low diversity during this period. Other factors such as the topography (Martin et al. 1998) and the seasonal development of the pycnocline (maximum influence in late summer, Strass et al. 1992) are suspected to also influence the production of eddies, particularly west of the British Isles.

Relationships between diversity and spatial dependence

A negative relationship was found between diversity and its spatial dependence in almost all areas. The robustness of this relationship is difficult to assess in the present study as data are spatially autocorrelated because of the use of spatial interpolations. However, the same relationships between diversity and its spatial dependence were detected for each season, at the scale of the North Atlantic Ocean and European seas, which is a good indication of its validity. This indicates that the more local the spatial changes in diversity are, the higher the diversity is. However, this result should not be extrapolated to the whole ocean or considered as a primary factor that explains regional differences in diversity. Examination of a global scale map of planktonic foraminera diversity (Rutherford et al. 1999) and maps of eddy kinetic energy (Stammer & Wunsch 1999, Ducet et al. 2000) does not visually show a strong link in subtropical and equatorial areas. The central gyre of the North Pacific, which is characterised by high diversity (McGowan & Walker 1985, McGowan 1990), has a low average eddy kinetic energy (Ducet et al. 2000). Thus, the link between diversity and eddy kinetic energy is not likely to be true at a global scale but may be a characteristic of the northern North Atlantic Ocean pelagic ecosystems. Furthermore, the negative relationship between diversity and spatial dependence seems to become positive in the northern boundary of the subtropical gyre (Fig. 4c). A large area in the North Sea also exhibits a positive link between diversity and its spatial dependence.

Beaugrand et al. (2001) have emphasised the importance of local physical processes in the regulation of spatial distributions of pelagic diversity in the northern North Atlantic. Beaugrand et al. (2000) demonstrated a pronounced local as well as an east-west asymmetry in the diversity of calanoids in the same area. The warm North Atlantic and European shelf edge currents were seen to be strongly involved in this spatial pattern (Beaugrand et al. 2001, 2002). This study strengthens this hypothesis and introduces more elements which improve interpretation of spatial changes in the pelagic diversity in this area. Factors implied in the spatial regulation of the diversity are primarily physical in the region of interest. Biological factors such as competition (Pianka 1966) and predation (Paine 1966) do not seem to play an important role. Rohde (1992) reviewed major hypotheses to explain changes in diversity from the poles to the tropics. He concluded in his review and other subsequent papers (e.g. Rohde et al. 1993, Rohde 1997) that energy was the main factor responsible for this difference, although other authors argued that this pattern could be explained by the area

(Rosenzweig 1995, Rosenzweig & Sandlin 1997), the history (Crame & Clarke 1998) or a mid-domain effect (Colwell & Lees 2000). Transposing Rohde's (1992) view to the regulation of diversity at the scale of our spatial area, in agreement with Beaugrand et al. (2001, 2002), we think that energy, its intensity (temperature or hydrodynamics) and frequency (seasonal and annual fluctuations in temperature and/or hydrodynamics) is strongly involved in the spatial control of diversity in the North Atlantic Ocean.

Annual and long-term changes in diversity, spatial variability and climatic indices

Diversity was found to be positively correlated with the winter NAO index in the northern North Sea and negatively correlated in oceanic regions west of the British Isles. Positive correlations were also found between northern hemisphere temperatures and diversity in the northern part of the North Sea while negative correlations were detected in some oceanic regions such as the Bay of Biscay. The significant change in probability, when the correction to account for the autocorrelation is applied, indicates that northern hemisphere temperature signals and/or spatial dependence time series are serially correlated.

Beaugrand et al. (unpubl.) have recently shown that a significant biogeographical shift in the whole community of calanoid copepods has been occurring at the scale of the North Atlantic Ocean. In Europe, the mean number of warm-water pseudo-oceanic, oceanic and neritic species moved northwards, while the mean diversity of colder-water species has significantly decreased in their southern range of spatial distribution. Significant correlations were found between these biogeographical changes, the NAO and northern hemisphere temperatures. The consistency of these results provides evidence that the low-frequency plankton variability in this region may have been governed by climatic warming (Intergovernmental Panel on Climate Change 2001) since at least the end of the 1970s. This was particularly strong in the northern part of the European shelf edge and in the North Sea. However, the global increase in temperature may not only act directly on plankton physiology or phenology, but may also manifest itself through existing hydroclimatic channels such as the NAO, which in turn influences the spatial distribution of plankton. Our results are in agreement with these findings for the northern part of the North Sea, but the use of the diversity index failed to detect these changes throughout the European shelf edge.

The relationship between spatial dependence in calanoid diversity and both climatic indices is positive

in oceanic areas west of the British Isles. This means that during a high NAO, the spatial variability in diversity changes at a higher scale in the ocean. This is slightly negatively correlated elsewhere with the NAO index, although this is not statistically significant. A greater negative correlation is observed for northern hemisphere temperatures, although also not statistically correlated when the correction to account for autocorrelation is applied. At this stage, it is difficult to propose a reasonable mechanistic explanation which may link spatial dependence to temperatures and the NAO. The positive phase of the NAO, possibly influenced by the global increase in temperatures (Hurrell et al. 2001), has emphasised the contrast between oceanic and neritic regions with the notable exception of the Bay of Biscay. This has increased the spatial scale of variability over the ocean and has decreased it over shallow regions and in the Bay of Biscay. Processes such as the path of currents, wind direction and intensity and change in pycnocline depth may also play a role, but the sequence seems to differ from that involved at a seasonal scale.

Many changes in the biological composition of the North Sea marine ecosystems were detected at the end of the 1980s (e.g. Lindley et al. 1990, 1993, Greve 1994, Reid et al. 1998). For example, the doliolid *Doliolum nationalis*, the dinoflagellate *Ceratium extensum* and the siphonophore *Muggiaea atlantica*, usually found in oceanic water, were detected in the central North Sea in 1987 (Lindley et al. 1990, Greve 1994). Reid et al. (1998) also reported a sharp change in an indicator of phytoplanktonic biomass in the North Sea after 1987. This cascade of biological events has been named a 'regime shift' by Reid et al. (2001a). This has been attributed to an exceptional inflow of oceanic water due to an increase in the shelf edge current, possibly mediated by the recent persistent positive phase in the North Atlantic Oscillation (Reid et al. 2001b, Reid & Beaugrand in press). Our results clearly show the consequence of this regime shift on calanoid diversity with a significant increase in diversity that occurred in the northern and central North Sea. In contrast, a clear decrease is detected in the oceanic areas while the diversity is still high over the European shelf edge. A significant change in the scale of spatial variability has occurred since 1987 (Fig. 8).

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