



In Collaboration with
the Netherlands Institute for Sea Research

**JOURNAL OF
SEA RESEARCH**

Journal of Sea Research 45 (2001) 63–77

www.elsevier.nl/locate/seares

Identification of global and local components of spatial structure of marine benthic communities: example from the Bay of Seine (Eastern English Channel)

Konstantinos Ghertsos^a, Christophe Luczak^{a,b,*}, Jean-Claude Dauvin^a

^aStation Marine de Wimereux, CNRS UPRES A 8013 ELICO, 28 Avenue Foch, BP 80, 62930 Wimereux, France

^bIUFM, Centre de Gravelines, 40 Rue Victor Hugo, BP 129, 59820 Gravelines, France

Received 17 March 2000; accepted 16 August 2000

Abstract

Data from samples of the macrobenthic *Abra alba*–*Pectinaria koreni* community of the eastern Bay of Seine (English Channel) collected in winter 1986 are analysed to illustrate the advantages of a novel method of multivariate analysis of spatial patterns described by Thioulouse et al. (Environ. Ecol. Stat., 2 (1995) 1–14), consisting of local and global approaches. Multivariate ordination procedures are applied that take spatial components into account explicitly through the construction of a neighbourhood graph between closely placed sampling sites, which is then used to weight the data. The result is a decomposition of spatial structure on local and global scales. This method is for the first time applied to macrobenthic data of this region. It shows the underlying importance of spatial scaling in analysis and proves to offer more information than classical ordination methods such as correspondence analysis, which may confuse the two different spatial scales. Global analysis is proposed as a powerful tool to define species assemblages and local analysis as an additional instrument to define partitions resulting from biological interactions. Additionally, this method appears capable of incorporating rare species (which influence classical analyses, often resulting in their elimination from datasets) by minimising their effects on the global scale and conversely maximising them on the local scale. This analysis demonstrates the importance of explicitly incorporating spatial information into the detection and interpretation of patterns in a macrobenthic community. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Benthic communities; English Channel; Global and local components; Spatial constraint; Neighbourhood graph; Geary and Moran statistics; Bay of Seine

1. Introduction

Recent research on the macrobenthos has demonstrated the important role that spatial scales of observation play in the description of benthic community structure and more generally in the spatial distribution of marine invertebrates (Thrush, 1991; Luczak, 1996).

A number of classical ordination techniques have been extensively used in benthic ecology. Lately new methods of a more sensitive and refined nature have been developed. These methods are capable of incorporating environmental parameters and spatial information into the analysis of ecological data (Ter Braak, 1986; Méot et al., 1993; Borcard et al., 1992; Clark and Warwick, 1994; Dolédec and Chessel, 1994; Thioulouse et al., 1995).

Ordination under spatial constraint is a paradoxical subject (Chessel et al., 1997). Most ecological

* Corresponding author.

E-mail address: christophe.luczak@univ-lille1.fr (C. Luczak).

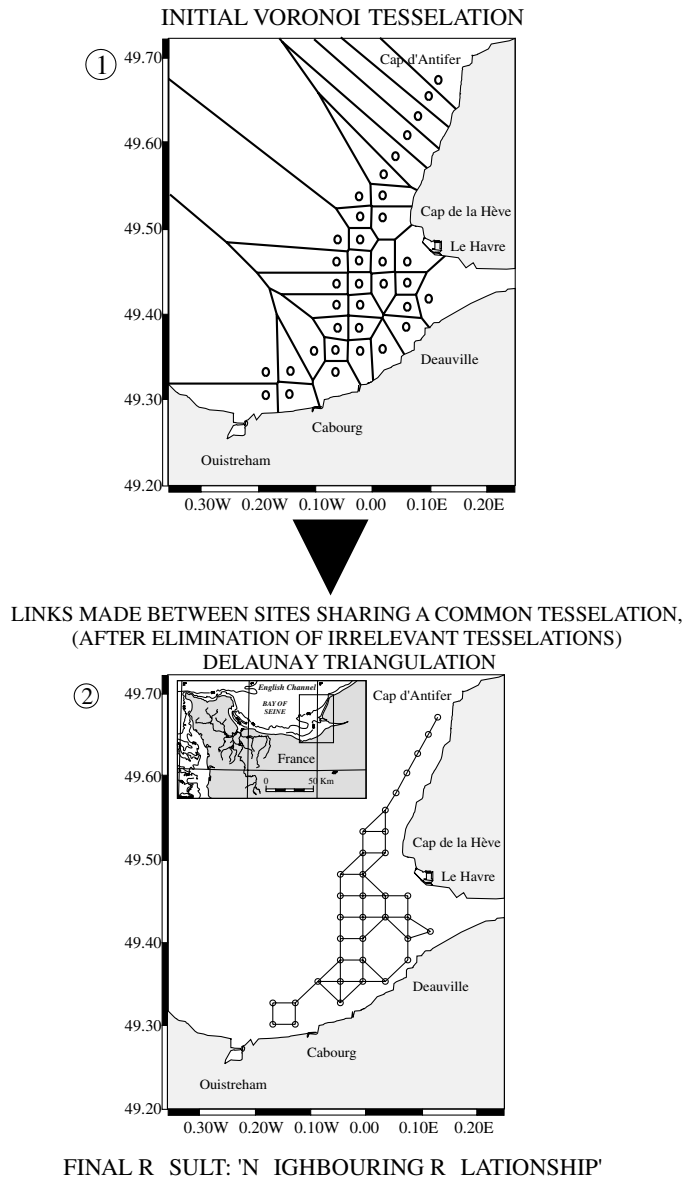


Fig. 1. Maps showing the steps leading to the creation of a neighbouring relationship between sites (circles) with (1) all initial Voronoi tessellations and (2) Delaunay triangulations resulting from the linkage of sites sharing common tessellations (after elimination of irrelevant tessellations, for example, those situated at extremities of the sampling grid), from the 1986 sampling.

observations are made with respect to space and time. The paradox is that spatial information is rarely incorporated into the analysis explicitly, while at the same time appearing in the interpretation of many studies (Chessel et al., 1997). Hatheway (1971), for example, using correspondence analysis, displays

factorial co-ordinates on maps. Hill (1974) and Estève (1978) display factorial co-ordinates along a transect, as Dessier and Laurec (1978) display them with respect to time, constituting the usual approach in benthic community analysis (Thiébaud et al., 1997). In all these cases, the structure of observations

(sampling sites on a map, points along a transect, sampling over time) is never introduced into the analysis.

When incorporated into the analysis explicitly, space is most often used in the form of a polynomial of geographical co-ordinates of sampling sites (Legendre, 1990) or as a geographical distance matrix (Legendre, 1993). One other option, introduced by Lebart (1969), consists in integrating spatial information after creating and subsequently using a neighbourhood graph. An appropriate connection network is used to link sites to one another and then this information is translated into a contiguity matrix. This graph weights the data structure and gives increased importance to neighbouring sites and the contrary for more distant ones. For example, if Delaunay triangulation is used, by definition two points are neighbours if their corresponding Voronoi polygons have at least one side in common.

One of the advantages of a neighbourhood graph resides in its capacity to incorporate the existence of environmental constraints and barriers. Additionally, this technique remains one of the simplest in terms of spatial integration (Thioulouse et al., 1995). Effectively, the presence in a study area of physical structures inaccessible to scientists may be incorporated directly into the neighbourhood graph. For example, two points may be very close geographically but subjected to very different conditions. This justifies the choice that they may not have to be considered as neighbours (Gaertner, 1997; Gaertner et al., 1998).

The method used here and developed by Thioulouse et al. (1995) consists of decomposing total variance of the data into local and global components achieved after the incorporation of a neighbourhood graph into a multivariate analysis.

This paper has two objectives. First, an ecological objective, in analysing spatial structure of the macrobenthic community taking explicitly into account hierarchical structure on two scales: global and local. Second, a methodological objective, in examining the efficiency of this technique for benthic community ecology in terms of simplicity and derivation of additional information when compared to the use of classical techniques such as correspondence analysis (CA), although this may also apply to principal components analysis (PCA).

2. Materials and methods

2.1. Data and sampling sites

The data come from the ongoing study of the Bay of Seine, eastern English Channel (Fig. 1). This section with a network of 40 sampling sites has been extensively investigated over several years. The sites are situated in the *Abra alba*–*Pectinaria koreni* community (Cabioch and Gentil, 1975; Gentil, 1976). Sampling was carried out once every winter prior to the recruitment of many of the species. Data for 1986 were examined for the application of this technique. A detailed description of the sampling procedures may be found in Thiébaud et al. (1997). Two replicate samples were collected per site using a Hamon grab (Dauvin, 1979), which samples approximately 0.25 m² of sediment. Samples were sieved with a mesh size of 2 mm and then fixed with 4% neutralised formaldehyde before being sorted and identified down to species level.

The hydrodynamic conditions of this bay ensure larval retention (Thiébaud et al., 1992) maintaining a certain degree of stability (Gentil et al., 1986; Thiébaud et al., 1997). Dominating species here have benthic-pelagic life cycles. Coupling hierarchical classification with correspondence analysis, Thiébaud et al. (1997) were able to demonstrate that although the benthic species in most of the Bay of Seine were stable, more variable species assemblages were apparent off the mouth of the Seine. Of the 40 sites sampled, four were devoid of fauna and therefore could not be used. Analysis was performed on the remaining 36 sites.

2.2. Method

The method is described briefly here. An in-depth description is found in Thioulouse et al. (1995). This method decomposes total variance into global and local components. The technique allows for the visualisation of information on two different spatial scales.

The proximity between sampling sites is defined by the neighbourhood graph (Cliff and Ord, 1973). This graph is created from the map of the sampling sites in order to designate neighbours. We used a connection network, known as Delaunay triangulation. First a Voronoi tessellation was made on the sampling sites

based on a matrix of X - Y co-ordinates. Then separations between sites deemed irrelevant were eliminated such as tessellations at the extremities of the sampling site grid and those between sites separated by a distance greater than 3.5 km (corresponding to the mean site-site distance). Finally, sites sharing at least one side of their respective Voronoi polygons were linked. This is the basis of Delaunay triangulation. Sites were thus linked to one another on the basis of their geographical proximity (Fig. 1). Sites linked together in this way were designated as neighbours.

Mathematical Notations for the creation of the neighbourhood graph (taken from Thioulouse et al., 1995; Gaertner, 1997):

Supposing $\mathbf{X} = [x_{ij}]$ matrix n, p containing data (p variables and n sites) \mathbf{X}^t is the transposition of \mathbf{X} $\mathbf{x} = [x_i]$ vector x_i (column vector of X). The neighbouring relationship between sites is introduced by the square matrix of sites $\mathbf{M} = (m_{ij})$ where $m_{ij} = 1$ if sites i and j are neighbours and $m_{ij} = 0$ for the contrary case. $\mathbf{P} = [p_{ij}]$ matrix deducted from \mathbf{M} by $p_{ij} = (1/2m)m_{ij}$ where $m =$ total number of neighbourhood pairs, so $\sum_{ij} p_{ij} = 1$. $\mathbf{D} =$ diagonal matrix of neighbourhood weights $p_i = 1/2m \sum_j m_{ij}$.

This matrix forms the basis of this spatial analysis as it allows greater importance to be given to sites with many neighbours as opposed to those with few, such as sites situated at sampling grid extremities (Thioulouse et al., 1995). The analysis on the global scale identifies the similarities between neighbouring sites whereas the analysis on the local scale concentrates on the differences between these neighbours. (See Appendix A for mathematical details on the analysis.)

The decomposition is related to two principal indices of autocorrelation: the index of Moran (1948) for the global scale and the Geary (1954) index for the local scale. Either PCA (principal components analysis) or CA (correspondence analysis) may be used as multivariate complements to this method. PCA concentrates on abundances, whereas CA searches for similarities between species–site abundance profiles. However, in this study, data were dominated by species occurring in large numbers but also containing numerous zeros. The Chi squared metric preserved in CA is an asymmetrical coefficient that does not take into account double zeros in estimating similarities, which is not the case

in the euclidean distance metric preserved in PCA (Legendre and Legendre, 1998). Additionally, CA which maximises the variance of conditional means follows well the ecological theory of the niche (Ter Braak, 1986, 1987; Thioulouse and Chesssel, 1992). CA is recommended for use in reduced space ordination of species abundance data containing numerous zeros (Gauch et al., 1977; Legendre and Legendre, 1998) and therefore CA was used in this study. According to Gamito and Raffaelli (1992) in a study comparing the performance of a different range of ordination methods on the same data, CA was argued to have performed best overall.

The initial step in the technique described in this article is termed the total analysis and differs from classical analyses in that the values per sampling site are weighted according to their corresponding number of neighbours deduced from the neighbourhood graph. This method may be applied to either CA or PCA. Thus the only difference with these analyses is that for the total analysis increased weights, and consequently importance, are assigned to sites with a larger number of neighbours and the contrary for those with fewer.

The resulting total variance is decomposed using the properties of CA of maximisation of the variance between neighbouring sites for the analysis of local structures (smaller scale) and maximisation of the covariance between neighbouring sites for global structures (larger scale). Total variance mathematically is a sum of global variability and local variances. More specifically, local analysis searches a linear combination of initial variables that maximises the variance between neighbouring sites (thus differences between neighbours) and this relies on the Geary (1954) index. Global analysis searches a linear combination of initial variables that maximises the covariance between neighbouring sites (thus similarities between neighbours) and rests upon the Moran (1948) index of autocorrelation. Further mathematical details of this analysis may be found in Méot et al. (1993), Thioulouse et al. (1995), Gaertner (1997) and Gaertner et al. (1998) and in the Appendix A.

The identity of the results between global and local analyses equal to classical CA is not a mathematical artefact but proof that the structure is adherent to ecological order as shaped by environmental patterns (Chesssel et al., 1997). The representation of species in

Table 1
Top 10 dominant species of the *Abra alba*–*Pectinaria koreni* community in February 1986 from Thiébaud et al. (1997)

Ten dominant species	Zoological taxon	Mean abundance (ind. m ⁻²)
<i>Owenia fusiformis</i>	Polychaeta	425.4
<i>Cultellus pellucidus</i>	Mollusca	123.2
<i>Acrocnida brachiata</i>	Echinodermata	122.8
<i>Pectinaria koreni</i>	Polychaeta	35
<i>Magelona mirabilis</i>	Polychaeta	28.8
<i>Abra alba</i>	Mollusca	26.8
<i>Echinocardium cordatum</i>	Echinodermata	8.6
<i>Nephtys hombergii</i>	Polychaeta	8.6
<i>Lanice conchilega</i>	Polychaeta	6.8
<i>Ophiura texturata</i>	Echinodermata	5.6

local and global factorial space may be used to identify those playing important roles in the structuring of the sites at each respective spatial scale. This technique was developed by Thioulouse et al. (1995) for detecting spatial patterns in bird ecology. It was further employed by Gaertner (1997) in a study of fish of the NW Mediterranean, but to our knowledge it has never been applied to benthic community analysis.

This method was applied using the ecological package ADE version 4 (Thioulouse et al., 1994, 1995) available on the internet at the address <http://pbil.univ-lyon1.fr/ADE-4/>.

3. Results

Owenia fusiformis, the tube-dwelling polychaete, dominated most of the area numerically (Table 1), followed by other key species of other taxa. For a

Table 2
Data characteristics before and after rare species elimination

Data	Number of species	Number of sites
Raw data	74	40
Removal of 4 sites devoid of fauna	74	36
Removal of species present exclusively in one site	52	36
Removal of species present in only two sites	40	36

detailed description of the community, see Thiébaud et al. (1997).

To limit the influence of rare species, Thiébaud et al. (1997) eliminated species present in less than 5% of the samples (= species present in only two sites). In this example, species present in one site only were eliminated from the dataset even though, as shown later in Fig. 6, this step is not really necessary in the case of the method of Thioulouse et al. (1995). A synopsis of these eliminations is presented in Table 2.

Fig. 2 displays the resulting eigen value inertia distributions after analysis in order to select the number of axes to be retained. Eigen value inertias decrease axis by axis; the point at which a significant decrease is found is often used as the criterion for axis number retention (Lebart et al., 1995). The eigen values of the global analysis display negative values corresponding to negative spatial correlations. These values have no meaning in terms of mapping and do not offer any additional spatial information (Chessel et al., 1997). Calculation shows that the sum of eigen values of global and local analyses is equal to the sum of the eigen values of total analysis. This fact confirms the decompositional nature of this analysis. Information that can be derived from Fig. 2 indicates that axis retention ought to have been fixed at 1 axis for the total analysis, 2 or 4 axes for the local analysis and 3 axes for the global one, but instead the choice was standardised and the first three axes were thus retained for each analysis.

3.1. Analysis of the sampling sites

The analysis of the sampling sites (Fig. 3) displays factorial values of sites on a map with white squares corresponding to negative values and black circles to positive values with the relative sizes being proportional to the values concerned. This depiction has the advantage that gradients or partitions may be distinguished more easily.

These results show that for 1986, total, global and local structures are not completely identical. Structures evident in total analysis appear to be heavily influenced by global structures, but are also somewhat influenced by local structures. This confirms that the data represent spatial partitions and not pure gradients because if that was the case structures would be

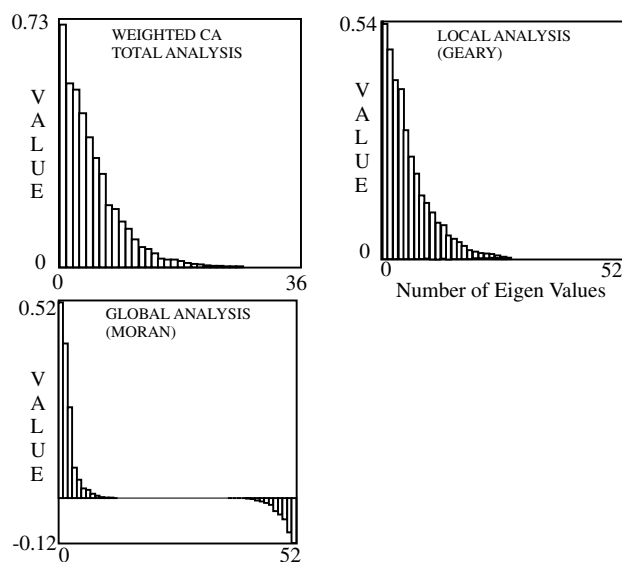


Fig. 2. Graphs displaying the eigen value distributions resulting from total, global and local analyses after implementation of the method of Thioulouse et al. (1995).

identical in local global and total analyses (Thioulouse et al., 1995).

Global analysis illustrates four partitions. The first axis displays oppositions between sites at the mouth of the estuary (negative values) and seaward sites (positive values). The second axis shows oppositions between northerly (negative) and southerly (positive) sites. The third axis illustrates the isolation of a group of sampling sites situated seaward of the estuary mouth (negative values). This information allows the distinction of these four sites.

- *Group 1* 'at the mouth of the estuary' (negative on axis 1, positive on axis 2, slightly positive on axis 3).
- *Group 2* 'seaward of the estuary' (positive on axis 1, negative on axis 2, negative on axis 3).
- *Group 3* 'northerly' (positive on axis 1, negative on axis 2, positive on axis 3).
- *Group 4* 'southerly' (positive on all three axes).

Local analysis showed that on a smaller spatial scale at the mouth of the estuary (group 1) a high spatial heterogeneity existed on the first axis, perhaps as a result of the more extreme nature of this highly unstable environment. Axis 2 concentrated more seaward of the estuary (group 2) and the third axis

mixed the estuarine region as a whole with the northern transect. These results show that while groups 1 and 2 separate themselves in global analysis, important fluctuations on a local scale may also be observed.

To understand which species were responsible for these different partitions of sampling sites on different spatial scales, an analysis on the species level must be carried out.

3.2. Analysis on the species level

The principal species assemblage descriptors from Thiébaud et al. (1997) as well as species found at the extremities of the groups distinguished from Fig. 4 were plotted according to their factorial scores. These additional species appear to play a major role in structuring the assemblages on a global scale and were not previously considered as assemblage descriptors. The other less important species were removed to clarify the figure and to stress the importance of global analysis as a powerful tool in the definition of species assemblages. Thus the above defined group 1 corresponds to the *Pectinaria koreni* assemblage with the addition of *Macoma balthica*, *Nephtys hombergii* and *Nephtys cirrosa*; group 2 to the *Cultellus pellucidus*–*Chaetozone setosa* assemblage with the addition of *Eteone longa* and *Magelona mirabilis*;

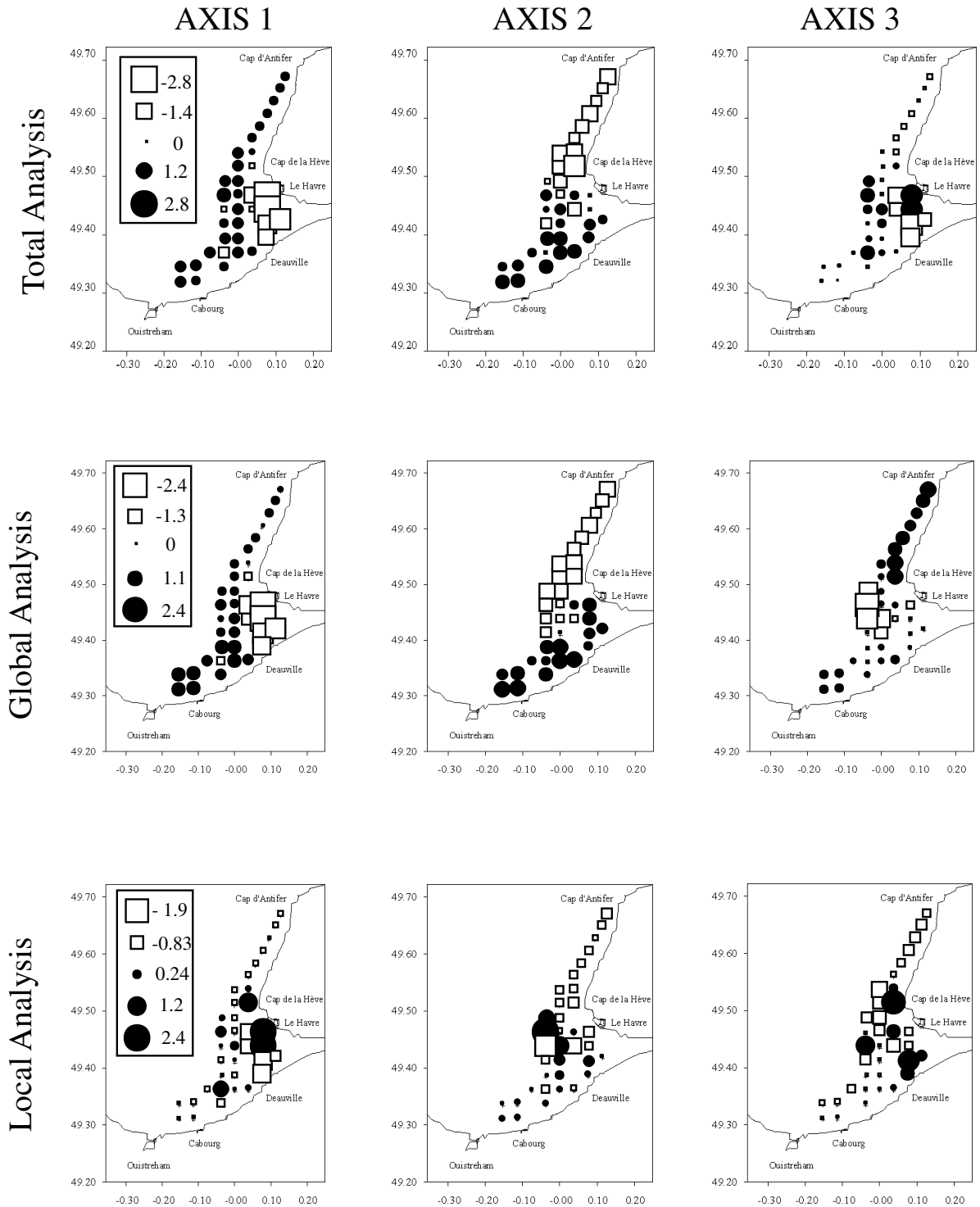


Fig. 3. Maps of factorial scores for sampling sites, for the first three axes of each analysis, total, global and local, after using the method of Thioulouse et al. (1995).

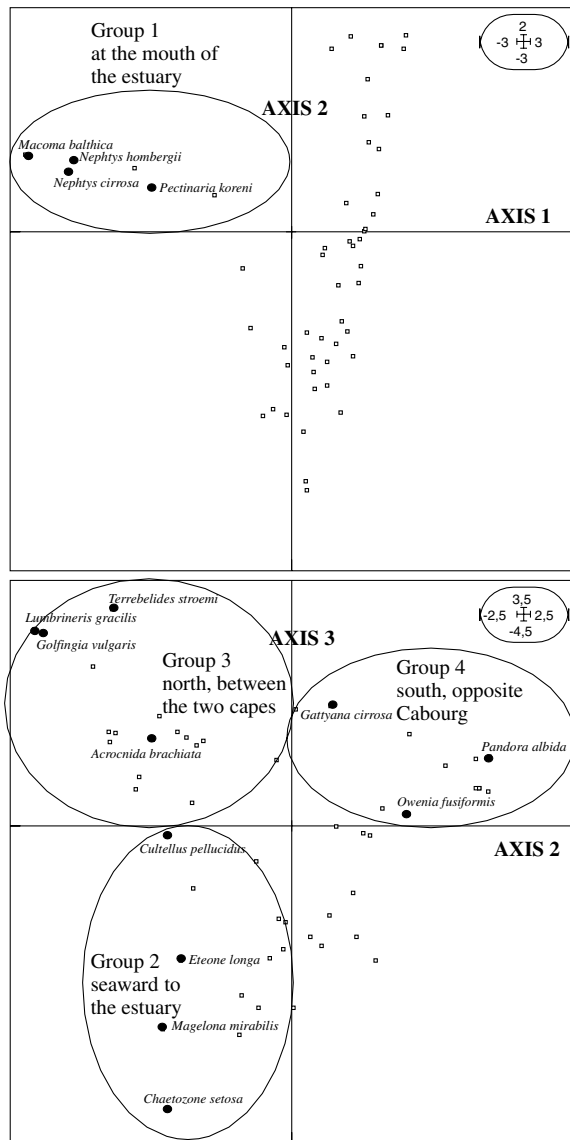


Fig. 4. Factorial scores for the first three axes of global analysis for species using the method of Thioulouse et al. (1995).

group 3 to the *Acrocnida brachiata* assemblage with the addition of *Terrebelides stroemi*, *Lumbrineris gracilis* and *Golfingia vulgaris*, and group 4 corresponds to the *Owenia fusiformis* assemblage with the addition of *Gattyana cirrosa* and *Pandora albida*. These assemblages were all initially described by Thiébaud et al. (1997), but the importance of the additional species had not been noted so far. These results

are generally in agreement with Thiébaud et al. (1997) as far as assemblage descriptors are concerned but some confusion arises as to the exact spatial extent of each assemblage.

The first axes of both global and local analyses are displayed simultaneously in Fig. 5 to show the extent to which some species structure the macrobenthos on these two different spatial scales. At the same time, the real abundance distribution is illustrated for some of the species situated at the extremities of the axes. As stated, local analysis, conducted on a smaller spatial scale, illustrated strong spatial heterogeneity at the mouth of the estuary (groups 1 and 2). In simple correspondence analysis (CA), this spatial scale dependent distinction may not have been possible. This type of representation is not, however, restricted to only the first axes of both analyses (global and local) since the combinations possible are numerous. The species found at the extremities of the axes show the greatest weights in the two analyses and consequently are those that structure the sampling sites most on these two different scales.

Locally, an opposition exists between the species *Nephtys cirrosa*, *Nephtys hombergii* (with positive values on the local analysis axis) and *Macoma balthica*, *Arenicola marina* and *Pectinaria koreni* (with negative values on the global analysis axis). This opposition is of interest as these two groups belong to two different trophic groups, the *Nephtys* spp. being carnivores and the others deposit feeders. At the same time, the polychaete species *Pectinaria koreni* appears to structure the community on both local and global scales.

A simple correspondence analysis was carried out on three datasets (the complete data with all species, data with species present in one site only removed and lastly a dataset with species present in one and two sites only removed). For the complete dataset, local influences (patch of *Cerastoderme edule*) hindered any immediate conclusion on global assemblage structures. These structures appeared later after removal of some of the rarer species and were similar to those identified in global analysis. However, the assemblage separations were not as sharply opposed to neighbouring sites as in the results of global analysis. Also no ideas are given on the confusions existing between different scales.

The analysis of Thioulouse et al. (1995) was carried

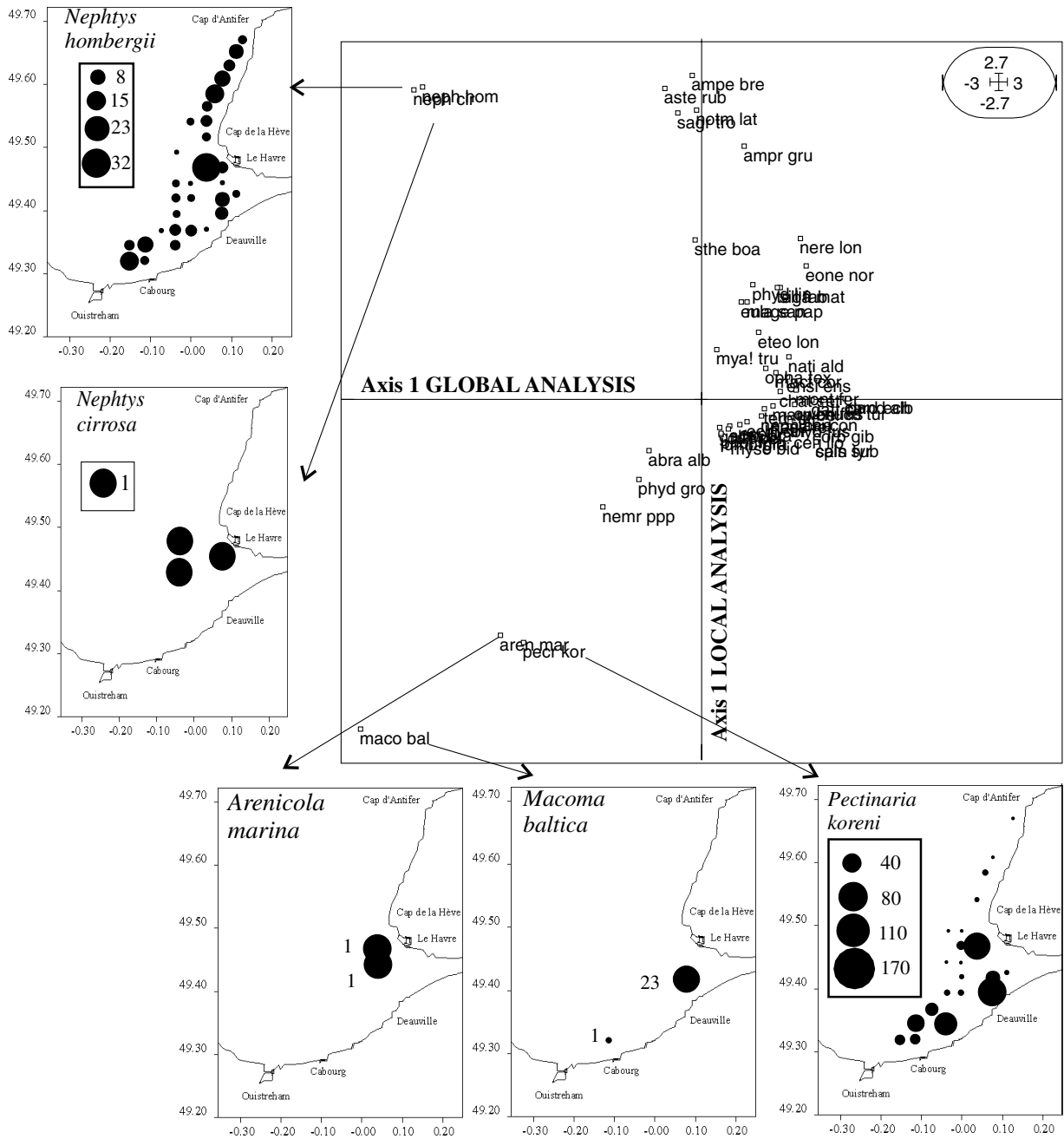


Fig. 5. Factorial scores for the first axis of global versus the first axis of local analysis for species using the method of Thioulouse et al. (1995).

out on the three different datasets used in Fig. 6. Notably, major changes are only seen in the local analysis; the global analysis remains relatively unperturbed. This method can include rare species while at the

same time decreasing their importance when observations on larger scales are considered. This pattern was not apparent with the simple CA of Fig. 6. In the case of the complete dataset one can see that the ‘patch’

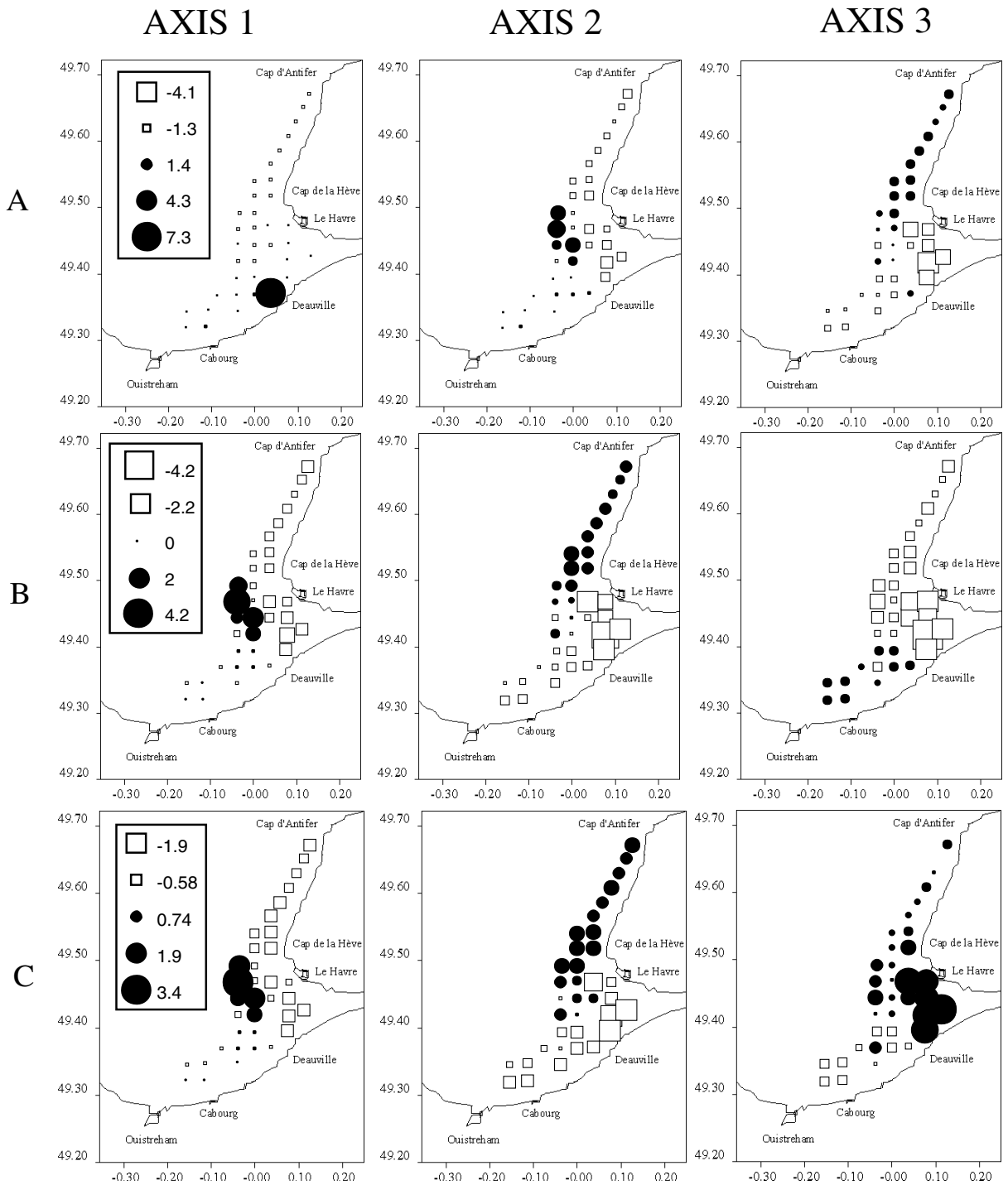


Fig. 6. Maps of factorial scores of sampling sites for the first three axes of simple correspondence analysis, using datasets with a progressive elimination of rare species: A: Complete dataset 74 species over 36 sampling sites; B: Dataset with species present exclusively in one site removed, 52 species remaining in total; C: Dataset with species present exclusively in one and two sites removed, 40 species remaining in total.

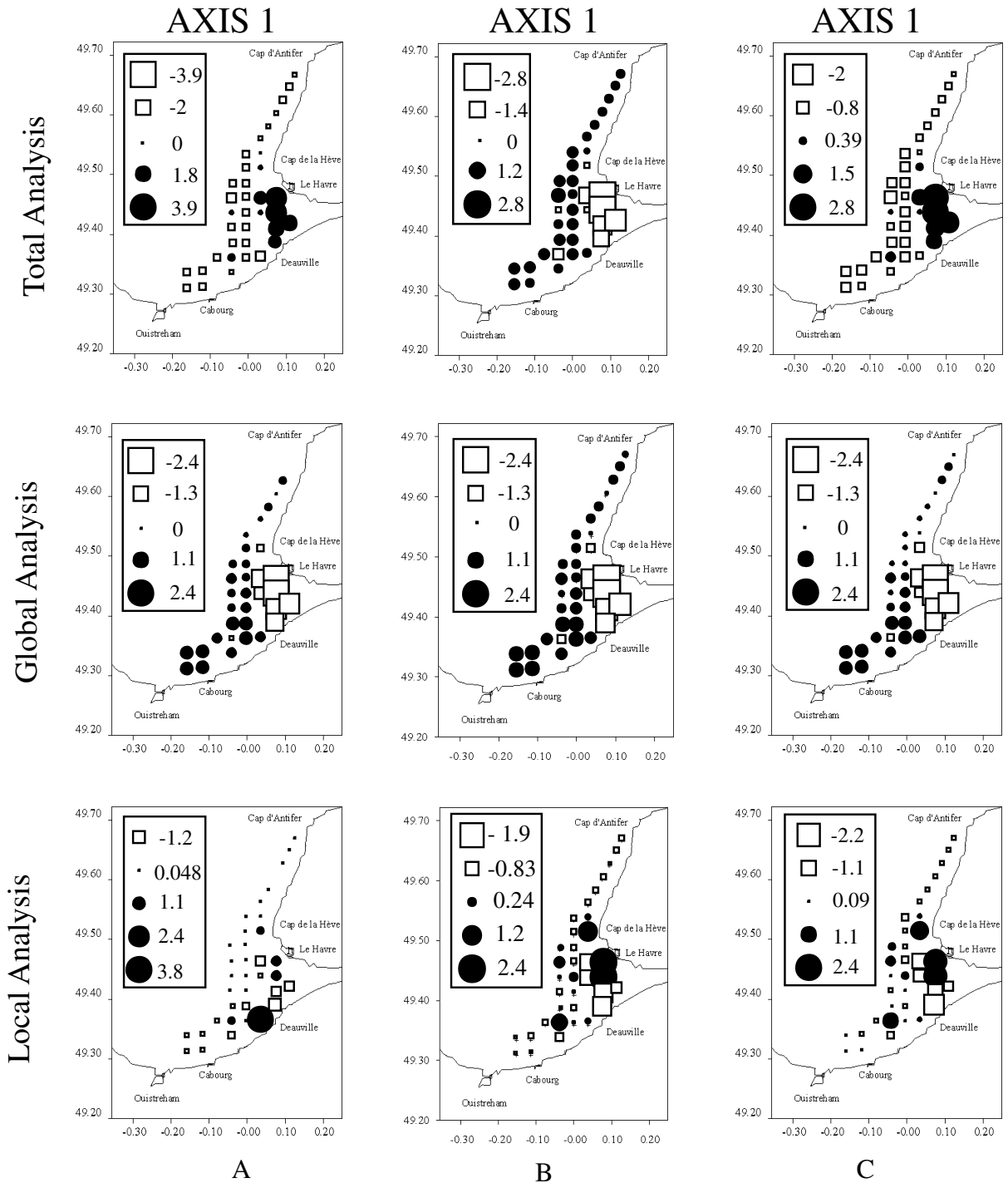


Fig. 7. Maps of factorial scores of sampling sites, for the first axis of each analysis of the method of Thioulouse et al. (1995), using datasets with a progressive elimination of rare species: A: complete dataset, 74 species over 36 sampling sites; B: dataset with species present exclusively in one site removed, 52 species remaining in total; C: dataset with species present exclusively in one and two sites removed, 40 species remaining in total.

dominating the CA in Fig. 6 is decomposed in the local analysis of Fig. 7 for the same dataset.

4. Discussion

Generally, more information may be derived from the use of this local and global approach than from classical methods because space is taken into account explicitly. A certain elasticity of this method results in the choice and construction of the neighbourhood graph. Other geometrical manipulations also exist that can be carried out on the sampling site distribution in order to construct the neighbourhood graph. This means that spatial information in the form of environmental constraints can more easily be introduced so that the method in itself presents an added advantage. However, it still relies largely on the initial sampling strategy. As always, the sampling strategy must be conceived with a suitable area per individual sample, distance between sampling sites and over a sufficiently long period and extensive and varied geographic area, in order to detect patterns or changes pertaining to the initial ecological question. Some subjectivity in the structure of the neighbourhood graph may at first seem a weakness, but it should be

considered a strength because frequently methods are not elastic enough to offer customised adaptations. For example, any geographical obstacles occurring on the sampling grid (in terrestrial ecology a river for example) may be taken into account. If samples are positioned in an irregular manner, the minimal spanning tree (or Gabriel graph) technique may also be used to decide on the neighbourhood of sites (Legendre and Legendre, 1998).

The assemblage distribution of Thiébaud et al. (1997) is displayed in Fig. 8. Similarities exist but the distributions in Thiébaud et al. (1997) are not identical to the groups resulting from Fig. 4 in the global analysis. The illustrations of Thiébaud et al. (1997) display smaller structures especially towards the mouth of the estuary. As stated, local analysis showed that on a smaller scale high spatial heterogeneity occurred at the mouth of the estuary. This may confirm that CA coupled with hierarchical classification here presented a mosaic of both global and local scales leading to the descriptions in Thiébaud et al. (1997). The use of the method of Thioulouse et al. (1995) separated the two scales giving explanations for the patchy assemblage distributions at the mouth of the estuary. Global analysis may provide a powerful tool in species assemblage description for the macrobenthos. The assemblage descriptions of Thiébaud et al. (1997) demonstrate that although the benthic species in most of the Bay of Seine were stable, more variable species assemblages were apparent off the mouth of the Seine. The only difference is that in this study a spatially explicit approach is adopted giving further explanations as to the macrobenthic spatial structure of this community.

Ecologically, however, this analytical method has interesting results. Thiébaud et al. (1997) define four assemblages; our results show the same four assemblages but with two (groups 1 and 2) highly heterogeneous ones on a local level. Moreover, additional species appear to structure the global scale with more weight than the numerically dominant species used in the previous assemblage classifications. The third axis of global analysis (Fig. 3) interestingly shows an underlying gradient stretching from the northern to the southernmost sites (positive values) in opposition to the patch (group 2) seaward of the estuary. One may actually question whether ‘assemblages’ is a good term to use here because the available information

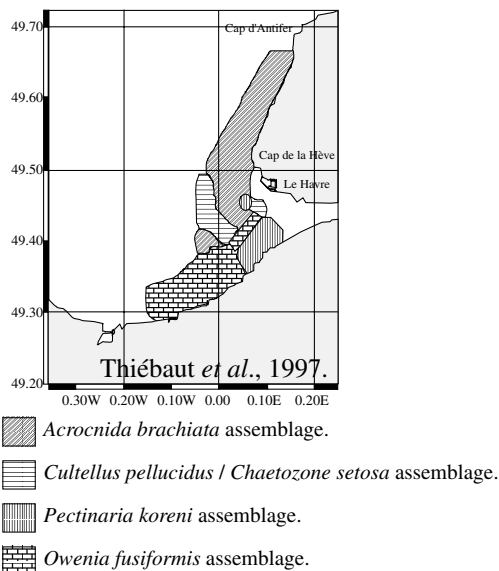


Fig. 8. Map showing assemblage distributions for 1986 resulting from correspondence analysis coupled with hierarchical clustering, redrawn from Thiébaud et al. (1997).

points to a gradient-type situation gradually changing from north to south, with a particular zone in between caused by the Seine estuary. Axis 2 of global analysis further displays this point with the southernmost part linked to the eastern part of the estuary mouth (group 1) and the northernmost part linked to the western part of the estuary mouth (group 2). Thus this estuarine zone (groups 1 and 2) may either be considered a separate zone in a steady north–south gradient, as shown by local analysis, or a zone of contact between the northern part and the southern part through the areas distinguished by groups 1 and 2 of global analysis. This additional information was not available after using classical CA and displays a complementary ecological utility of this method.

On local scales, some feeding status partitions were noted and on global scales previously described assemblages were redefined. A large number of methods have been developed to distinguish and separate structures resulting from biological interactions from physical forcing. In this case, local analysis may be useful in defining potential biological partitions existing on smaller spatial scales, which is of interest in contemporary marine ecology. However, local and global scales depend on the initial spatial scale of observation, in other words, the distance between sampling sites. Following Thioulouse et al. (1995), the results showed that the data did not conform to a pure gradient on all scales since total, global and local structures were not equal.

In future, this method may be used for time series analysis where the neighbourhood graph can be constructed simply by giving added weight to sampling dates before or after the given set. Thus for example monthly data may be used to look at monthly fluctuations on a local scale or to look at either seasonal or annual fluctuations on a global scale. Additionally, no geometrical manipulation will be required as time is uni-dimensional, so the graph would link each month to its preceding and following months and therefore would be simple to construct. A neighbourhood graph may also be constructed with respect to an environmental gradient such as depth, sediment type or temperature in the same way as space was used in this example. The possibilities are numerous and display the potential that this technique may offer in its various applications.

Lastly, as a result of its decompository nature this technique offers the added advantage that it may take into account the presence of rare species occurring on smaller spatial scales in local analysis. Such rare species are often eliminated from datasets because they may influence and hinder a correct analysis, as in our example of simple CA in Fig. 6. The question arises as to why they are rare (or ‘accidental’) and whether they were adequately sampled. If such questions cannot be concretely answered we think it best to include a maximum of data. This is a positive point because although rare species may influence the analysis, their removal may involve considerable loss of information. Such elimination appears to contradict the very essence of ecology, and this technique removes the need to eliminate or alter the data.

Acknowledgements

This work contributed to the ‘GDR Manche’ study under the PNDR programme under the co-ordination of Dr Louis Cabioch and Professor Christian Retière. The authors would like to thank the crew of NO ‘Pluteus’ and J.C. Lorgere and B. Brouazin for participating in the sea missions. Eric Thiébaud is gratefully acknowledged for his help in the database creation and maintenance. The authors would also like to thank Dr Simon Thrush and other anonymous referees for their useful guidance in the manuscript’s completion. C. Conforti is gratefully acknowledged for her aid with the English.

Appendix A. Definition of total variance, local variance and global variability (after Thioulouse et al., 1995; Gaertner, 1997)

The mean of variable x with the weights \mathbf{D} gives:

$$\bar{x}_D = \sum_i p_i x_i = \mathbf{x}^t \cdot \mathbf{D} \mathbf{1}_n$$

The variance is equal to the *total variance*:

$$\text{Var}_{(x)} = \sum_i p_i (x_i - \bar{x}_D)^2$$

If x is \mathbf{D} -centred (the mean of x with weights \mathbf{D} is equal to 0) results in a matrix form of:

$$\text{Var}_{(x)} = \mathbf{x}^t \cdot \mathbf{D} \mathbf{x}$$

Local analysis searches a linear combination of the initial variables, which maximises the variance between neighbouring points. This analysis thus concentrates on the differences between neighbouring points. It maximises the local variance of the variable $x(VL_{(x)})$.

$$VL_{(x)} = \sum_i \sum_j p_{ij}(x_i - x_j)^2$$

Under the matrix form of:

$$VL_{(x)} = x^t \cdot (\mathbf{D} - \mathbf{P}) \cdot x = x^t \cdot \mathbf{D} \cdot (\mathbf{I}_n - \mathbf{D}^{-1} \cdot \mathbf{P}) \cdot x$$

The reference to the Geary index arises from the fact that this index rests upon the relationship $VL_{(x)}/Var_{(x)}$.

Global analysis searches a linear combination of initial variables, which maximises the covariance between neighbouring points. This analysis concentrates on the similarities between neighbouring points. It maximises $VG_{(x)}$, the global variability (spatial autocovariance) of the variable x

$$VG_{(x)} = \sum_i \sum_j p_{ij}(x_i - \bar{X}_D)(x_j - \bar{X}_D)$$

if x is \mathbf{D} -centred:

$$VG_{(x)} = \mathbf{x}^t \cdot \mathbf{P} \mathbf{x} = \mathbf{x}^t \cdot \mathbf{D} \cdot (\mathbf{D}^{-1} \cdot \mathbf{P}) \cdot x$$

References

- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Cabioch, L., Gentil, F., 1975. Distribution des peuplements benthiques de la partie orientale de la Baie de Seine. *C.R. Acad. Sci. Paris* 280, 571–574.
- Chessel, D., Thioulouse, J., Champely, S., 1997. Autocorrélation et composantes cartographiables. ADE-4 thematic document 7.3. <ftp://pbil.univ-lyon1.fr/pub/mac/ADE/ADE4/DocThemPDF/Thema73.pdf>.
- Clark, K.R., Warwick, R.M., 1994. Change in marine communities, an approach to statistical analysis and interpretation. NERC, UK, 144 pp.
- Cliff, A.D., Ord, J.K., 1973. Spatial Autocorrelation. Pion, London (178 pp.).
- Dauvin, J.-C., 1979. Recherches quantitatives sur le peuplement des sables fins de la Pierre Noire et sur sa perturbation par les hydrocarbures de l'Amoco Cadiz. Thèse doctorat 3ème cycle, Univ. Paris 6, 251 pp.
- Dolédéc, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshw. Biol.* 31, 277–294.
- Dessier, A., Laurec, A., 1978. Le cycle annuel du zooplancton à Pointe-Noire (RP Congo), description mathématique. *Oceanol. Acta* 1, 285–304.
- Estève, J., 1978. Les méthodes d'ordination: éléments pour une discussion. In: Legay, J.M., Tomassone, R. (Eds.). *Biométrie Ecologie*. Société Française de Biométrie, Paris, pp. 223–250.
- Gaertner, J.-C., 1997. Organisation des assemblages démersaux dans le golfe du Lion: structures spatiales et stabilité temporelle Thèse de doctorat, Université de la Méditerranée, Observatoire des Sciences de l'Univers, Centre d'Océanologie de Marseille.
- Gaertner, J.-C., Chessel, D., Bertrand, J., 1998. Stability of spatial structures of demersal assemblages: a multitable approach. *Aquat. Liv. Resour.* 11, 75–85.
- Gamito, S., Raffaelli, D., 1992. The sensitivity of several ordination methods to sample replication in benthic surveys. *J. Exp. Mar. Biol. Ecol.* 164, 221–232.
- Gauch Jr., H.J., Whittaker, R.H., Wentworth, T.R., 1977. A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.* 65, 157–174.
- Geary, R.C., 1954. The contiguity ratio and statistical mapping. *Inc. Stat.* 5, 115–145.
- Gentil, F., 1976. Distribution des peuplements benthiques en Baie de Seine. Thèse 3ème cycle, Université Paris VI.
- Gentil, F., Irlinger, J.P., Elkaim, B., Proniewski, F., 1986. Premières données sur la dynamique du peuplement macrobenthique des sables fins envasés à *Abra alba* de la Baie de Seine orientale. *Actes de Colloques IFREMER* 4, 409–420.
- Hatheway, W.H., 1971. Contingency table analysis of rain forest vegetation. In: Patil, G.P., Pielou, E.C., Waters, W.E. (Eds.), *Statistical Ecology. III Multi-Species Population Ecosystems and Systems Analysis*. Pennsylvania University Press, University Park and London, pp. 271–314.
- Hill, M.O., 1974. Correspondence analysis: a neglected multivariate method. *Appl. Stat.* 23, 340–354.
- Lebart, L., 1969. Analyse statistique de la contiguïté. Publication de l'Institut de Statistiques de l'Université de Paris 28, 81–112.
- Lebart, L., Morineau, A., Piron, M., 1995. *Statistique Exploratoire Multidimensionnelle*. Dunod, Paris.
- Legendre, P., 1990. Quantitative methods and biogeographic analysis. In: Garbary, D.J., South, G.R. (Eds.), *Evolutionary Biogeography of the Marine Algae of the North Atlantic*. NATO, ASI series, vol. G22. Springer, Berlin, pp. 9–34.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673.
- Legendre, L., Legendre, P., 1998. *Numerical Ecology*. Elsevier, Amsterdam (853 pp).
- Luczak, C., 1996. Dynamique du recrutement au sein du peuplement *Abra alba* dans la baie sud de la Mer du Nord: Approche Systémique, Thèse de doctorat. Université des Sciences et Technologies de Lille 1.
- Méot, A., Chessel, D., Sabbatier, R., 1993. Opérateurs de voisinage et analyse des données spatio-temporelles. In: Lebreton, J.D., Asselain, B. (Eds.), *Biométrie et Environnement*. Masson, Paris, pp. 45–71.

- Moran, P.A.P., 1948. The interpretation of statistical maps. *J. R. Stat. Soc. (B)* 10, 243–251.
- Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- Ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69, 69–77.
- Thiébaud, E., Dauvin, J.C., Lagadeuc, Y., 1992. Transport of *Owenia fusiformis* larvae (Annelida: Polychaeta) in the Bay of Seine. I. Vertical distribution in relation to water column stratification and ontogenic vertical migration. *Mar. Ecol. Prog. Ser.* 80, 29–39.
- Thiébaud, E., Cabioch, L., Dauvin, J.C., Retière, C., Gentil, F., 1997. Spatio-temporal persistence of the *Abra alba*–*Pectinaria koreni* muddy-fine sand community of the eastern Baie of Seine. *J. Mar. Biol. Assoc., UK* 77, 1165–1185.
- Thioulouse, J., Chessel, D., 1992. A method for the reciprocal scaling of species tolerance and sample diversity. *Ecology* 73, 670–680.
- Thioulouse, J., Dolédec, S., Chessel, D., Olivier, J.M., 1994. ADE software: multivariate analysis and graphical display of environmental data. In: Guariso, G., Rissoli, A. (Eds.), *Software per l’Ambiente*. Patron Editore, Bologna, pp. 56–72.
- Thioulouse, J., Chessel, D., Champely, S., 1995. Multivariate analysis of spatial patterns: a unified approach to local and global structures. *Environ. Ecol. Stat.* 2, 1–14.
- Thrush, S.F., 1991. Spatial patterns in soft-bottom communities. *Trends Ecol. Evol.* 6, 75–79.