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Long-term variations of four macrobenthic community structures

Macrobenthos
Community structure
Species abundance model
Long-term survey
English Channel-North Sea

Macrobenthos
Structure
Modèle de distribution
d'abondance
Suivi à long terme
Manche - Mer du Nord

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ABSTRACT

This study examines whether meso-scale meteorological events, in particular the alternation of cold and mild periods, influenced the structure of four *Abra alba* communities, sampled from 1977 to 1992 on the northwest French coast. We propose a new numerical procedure to describe temporal variations in the structure of each assemblage, using some niche-oriented models recently developed by Tokeshi (1993). The description of the temporal changes in the structure of each community was summarized into a 2D-plot of an ordination, performed on observed and simulated patterns. Results showed that important changes occurred in these four assemblages, which were not directly related to the meso-scale climatic events, but mainly to the local environmental factors and biotic interactions. Furthermore, it appears that stable environmental conditions would favour more stable structures, but do not determine the precise type of the structure.

RÉSUMÉ

Variations structurelles à long terme de quatre assemblages macrobenthiques.

L'objet de ce travail est l'influence des changements climatiques à méso-échelle, en particulier l'alternance de périodes chaudes et froides, sur la structure de quatre assemblages macrobenthiques, échantillonnés de 1977 à 1982 sur les côtes nord-ouest de la France.

Une nouvelle méthode est proposée pour décrire les variations structurelles au cours du temps, basée sur quatre modèles de distribution d'abondance développés par Tokeshi (1993). A la différence des modèles déterministes classiques (Motomura, Preston, Mandelbrot), ces modèles sont stochastiques et reposent uniquement sur une partition donnée de la niche totale. Projetés dans une ordination avec les échantillons réels, ils permettent d'identifier les types de structure entre lesquels l'assemblage a fluctué au cours du temps. Les résultats mettent en évidence une importante variabilité structurelle qui n'est toutefois pas liée au « déterminisme » climatique à méso-échelle ; les variations structurelles semblent plutôt résulter de facteurs hydroclimatiques locaux (vent, courants, quantité de matière organique), de perturbations d'origine anthropique (pollution par les hydrocarbures), et de facteurs biotiques (relations interspécifiques, ponte, recrutement). Les résultats montrent également que la stabilité des conditions environnementales locales favorise la stabilité des structures, sans pour autant en déterminer le type.

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INTRODUCTION

Long-term variations in species abundances of four fine and muddy/fine sand macrobenthic communities of the northwest French coast were related to meso- scale climatic events, in particular the alternation of cold and mild years (Fromentin *et al.*, in press). This influence was especially marked on the northern sites where no important local event took place. The study raised the question: do these meso-scale meteorological features also influence the structure of macrobenthic communities? If so, it would be desirable to evaluate the extent of variability induced by changes in metorological conditions. If not, what are the main causes of the temporal variations in the structure of these benthic communities? Answering such questions involves detection and description of temporal changes within these communities.

Since Motomura (1932), the patterns of relative abundance (or biomass) of species have often been considered to reflect the structure of natural communities. These patterns are usually interpreted through different graphical representations (Frontier, 1976; Gray and Pearson, 1982; Lambshead *et al.*, 1983). In the present study, the four macrobenthic communities were sampled on 38, 77, 81 and 117 occasions, respectively, during the periods of the surveys. Thus, the graphical solution would lead to more than three hundred plots. An alternative involves comparing the different data sets, using some species abundance models. The common objective of using such models, e.g. geometric series, log-normal or Mandelbrot models, is to fit data sets to a model in order to summarize the structure of the community with a few statistical parameters (Fisher *et al.*, 1943; Frontier, 1977, 1985; Mandelbrot, 1977; May, 1972; Motomura, 1932; Pielou, 1975; Preston, 1948; Preston, 1962). However, our purpose is different and is oriented towards the description of temporal variability in structure of benthic communities. In view of recent criticisms of these classical deterministic models (Hughes, 1985; Hughes, 1986; Tokeshi, 1993), we employed some stochastic and niche- oriented models, recently developed by Tokeshi (1990; 1993). Description of the temporal fluctuations of the structure of each community is summarized into an ordination plot performed on the observed and simulated patterns.

MATERIALS AND METHODS

Study sites and sampling

The four sites belong to the same infralittoral *Abra alba* community, occurring along the English Channel and the southern part of the North Sea. Their main characteristics are given briefly in Table 1 (for more details see Dauvin *et al.*, 1993*b*).

Table 1

Mean density, species richness and diversity for one sample, and total species richness (total number of species found since the beginning of the survey) at the four sites.

Densité, richesse spécifique et diversité moyennes pour un échantillon, et richesse spécifique totale (nombre total d'espèces trouvé depuis le début du suivi) dans les quatre sites.

	Pierre Noire	**Rivière de Morlaix**	**Baie de Seine**	**Gravelines**
Mean density	7545	3320	5380	5080
Total species richness	420	308	130	154
Mean species richness	102	60	38	33
Mean diversity (Shannon index)	3.8	2.9	3.2	2.4

The Gravelines station is located in the southern part of a large fine-sand *Abra alba* community distributed along the coast from Calais to Belgium in the southern part of the North Sea, and is dominated by bentho-pelagic species. This site is characterized by strong currents, under the influence of tides and wind directions, and by low pollutant discharges without recognizable effects on the fauna (Dewarumez *et al.*, 1986). The Baie de Seine station is part of the largest isolated muddy/fine-sand *Abra alba* community (400 km^2) of the French English Channel coast. Most of the dominant species have also a pelagic larval cycle. Hydrodynamic conditions depend on tide, horizontal gradients of density and wind (Cabioch, 1986), but this bay shows an important retention capacity involving low dispersion of the larvae (Thiébaut *et al.*, 1992). The two stations of the Baie de Morlaix: Pierre Noire and Rivière de Morlaix are located in a fine and a muddy/fine-sand *Abra alba* community (6 and 2 km^2 respectively). Rivière de Morlaix is dominated by bentho-pelagic species, whereas amphipods (direct development) and some polychaetes with a reduced pelagic phase are the dominant species at Pierre

Noire. This bay, under the influence of Atlantic waters, was polluted in March 1978 by the Amoco Cadiz oil spill, Pierre Noire being the most affected of the two sites (Dauvin, 1984; Dauvin and Ibanez, 1986; Ibanez and Dauvin 1988). Dauvin (1990) showed that most of the species at these two sites had one limited recruitment period (in summer or autumn). The time lag between settling of species and the sampling of juveniles varies from no delay to one year, but this time lag is about three months for most of the dominant species.

Details on sampling are given in Dauvin *et al.* (1993*b*). Briefly, a Smith-McIntyre grab was used with a sieve of 1 mm mesh size. Pierre Noire station was sampled 117 times between April 1977 and December 1992 (twelve samples per year from 1977 to 1981 and five samples per year from 1982 to 1992); Rivière de Morlaix, 77 times between October 1977 and December 1992 (five samples per year); Baie de Seine, 38 times between October 1983 and January 1993 (about four samples per year); and Gravelines, 81 times between April 1978 and October 1992 (five samples per year).

Species abundance models and numerical procedure

The four models considered in this work were presented in detail in Tokeshi (1990; 1993).

The first three - the Random Fraction model (RF), the Dominance Pre-emption model (DP) and the Dominance Decay model (DD) - are niche-apportionment models. Assuming that an assemblage consists of species with similar resource requirements within the same niche space, the process of niche apportionment can be described as a unit mass or stick (in the sense of Mac-Arthur, 1957; 1969), sequentially divided into several pieces. Thus, the RF model involves a sequential division of the niche in a random fashion (Fig. 1*a*). The total niche is first divided into two pieces at random, then one of these is randomly chosen and divided into two at random, and so on. There is no dominance hierarchy in this model, a newly colonizing species is supposed to occupy an arbitrary proportion of the niche. The DP model stresses dominance (Fig. 1*b*). Here, the first species takes more than a half of the total niche, the second, more than half of the remaining niche, and so on. This process guarantees the dominance of one species over all the subsequent ones. In contrast, the DD model denies dominance (Fig. 1*c*). The total niche is first divided into two pieces at random and the largest piece is chosen and divided at random. The largest piece is always chosen for the following breaks which leads to an equitable abundance distribution.

In the fourth model, the Random Assortment model (RA), species are considered without interactions, or with independent variations. This concept considers that the total niche does not remain constant in size and is not saturated (in contrast to the three other models). This could occur in a variable environment where there is not enough time to develop fully competitive interactions. In the calculation of this model pattern (Fig. 1*d*), the first species would be

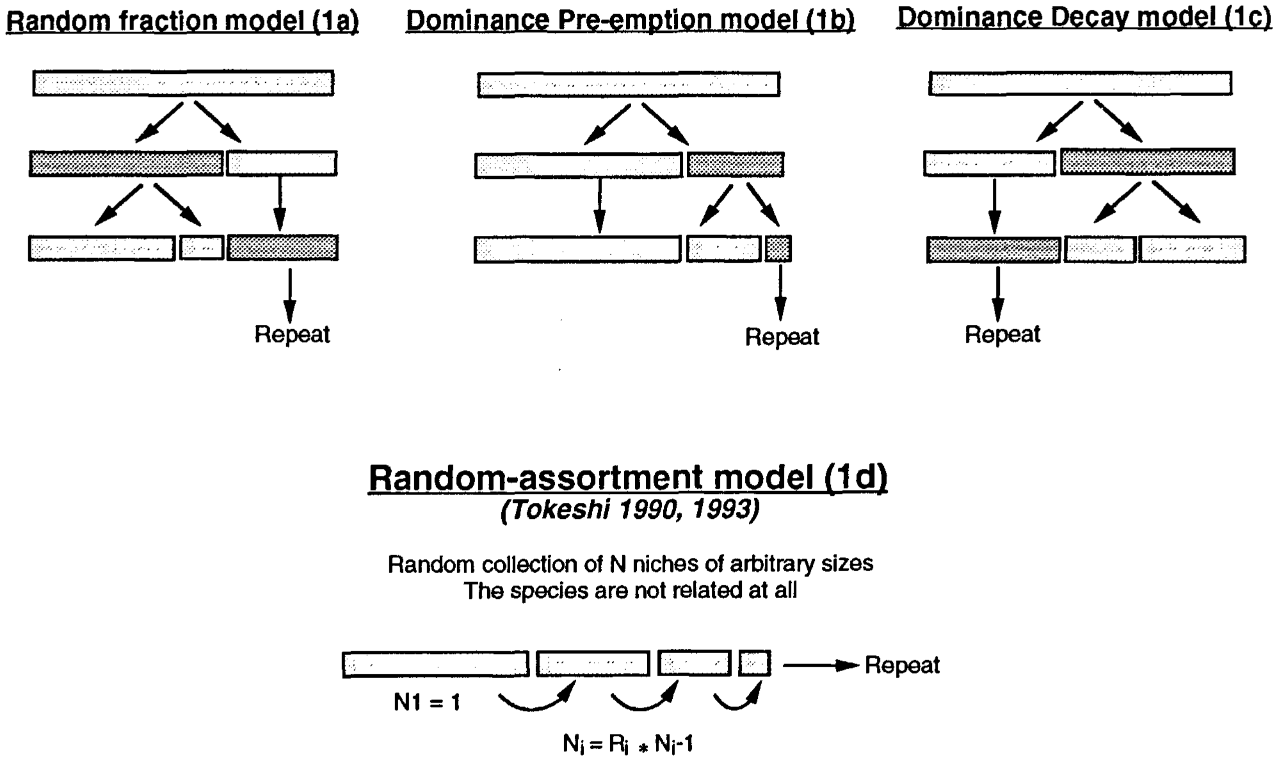


Figure 1

Schematic procedures for the Random Fraction model (1a), Dominance Pre-emption model (1b), Dominance Decay model (1c) and Random Assortment model (1d).

Procédures pour les modèles : Random Fraction (1a), Dominance Pre-emption (1b), Dominance Decay (1c) and Random Assortment (1d).

assigned a value of one. The second species will be a random fraction (between zero and one) of the the first one. The third will be a random fraction of the second, and so on.

All these four models are stochastic, and the expected patterns were derived from 10,000 simulations. An example of these four patterns is shown (Fig. 2) with a total of 15 species. The DP model has the steepest slope and the DD model the shallowest. The RF model is closer to DD than DP, whereas the RA model leads to an unequitable distribution between the DP and the RF models.

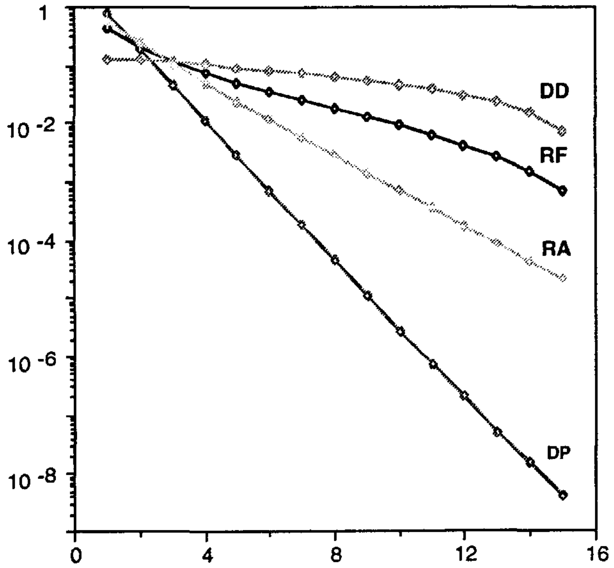


Figure 2

Rank-abundance patterns simulated from the four models, considering 15 species (semi-log representation). RF: Random Fraction, DP: Dominance Pre-emption, DD: Dominance Decay, RA: Random Assortment.

Diagrammes rang-fréquence simulés à partir des quatre modèles, en considérant 15 espèces (représentation semi-log). RF : Random Fraction, DP : Dominance Pre-emption, DD : Dominance Decay, RA : Random Assortment.

In the present study, rather than fitting each observed pattern to these models, we have projected both simulated and observed patterns into the same space of an ordination, as in Amanieu *et al.* (1981). The numerical procedure is summarized in Figure 3:

– Step 1: Observed patterns are obtained from the raw data, by calculating a rank abundance pattern for each chronological sample. Simulated patterns are derived from the four models.

– Step 2: The two matrices of observed and simulated patterns are gathered (observed and simulated patterns being calculated for the same number of species). Hellinger distances are calculated between all the patterns.

– Step 3: An ordination and a classification are computed on this Hellinger matrix. Results of these two analyses are represented on the same plot, which contains the observed patterns (S_j) and the four simulated patterns. Envelope boundaries correspond to the different groups distinguished by the classification.

MDS-ordination (non-metric multidimensional scaling) was chosen because this method can summarize distances between objects in a smaller number of dimensions than PCA or CA (Legendre and Legendre, 1984). Here, one MDS-ordination was performed at each site on a Hellinger distances matrix between observed and simulated patterns. Hellinger distance between two patterns a and b, considering n species is:

$$D_{a,b} = \sum_{j=1}^{n} |\sqrt{f_{j,a}} - \sqrt{f_{j,b}}|^2$$

where $f_{j,a}$ is the frequency of the species j in the pattern a, $f_{j,b}$ is the frequency of the species j in the pattern b.

Hellinger distance was chosen rather than the euclidean distance or the dissimilarity between k dominance curves (Clarke, 1990), because of its higher power of discrimination. Interpretation of the temporal fluctuations of the structure can be directly read on a single 2-D plot, by examining the distances between observed patterns and between observed and simulated patterns.

Variations in the number of species from one sample to another leads to a problem. Following Tokeshi (1990), the decision was made to only keep the most abundant species along the survey. According to previous studies (Ibanez and Dauvin, 1988, Ibanez *et al.*, 1993), this took two parameters into account. Firstly, the relative abundance, RA, which is defined as:

$$RA(j) = \frac{\sum_{j=1}^{N} A(i, j)}{\sum_{i=1}^{P} \sum_{j=1}^{N} A(i, j)}$$

where N is the number of samples and P the number of species

$A(i, j)$ is the abundance of species (i) in the sample (j).

Secondly, the presence/absence ratio, PAR:

$$PAR(i) = \frac{N(i)}{N}$$

where $N(i)$ is the number of samples where species (i) is present.

Species that were present in more than 50 % of the samples and had a relative abundance (0.001 were retained, except for Pierre Noire where an important species in the two last years (*Ampelisca tenuicornis*) was added. We retained 49 species which accounted for 96.8 % of the total abundance at Pierre Noire; 34 species at Rivière de Morlaix (97.1 % of the total abundance); 32 species at Baie de Seine (97.6 % of the total abundance); and 27 species at Gravelines (96.1 % of the total abundance). It is reasonnable to consider that these species, accounting for 96.1 % to 97.6 % of the total abundance, represent the major part of structures in these communities (the remaining species showed some very low relative abundances, and only appeared in the lower end of a rank-abundance pattern).

Seasonal variations in abundance of these benthic species are mainly related to the recruitment phases. At the Baie

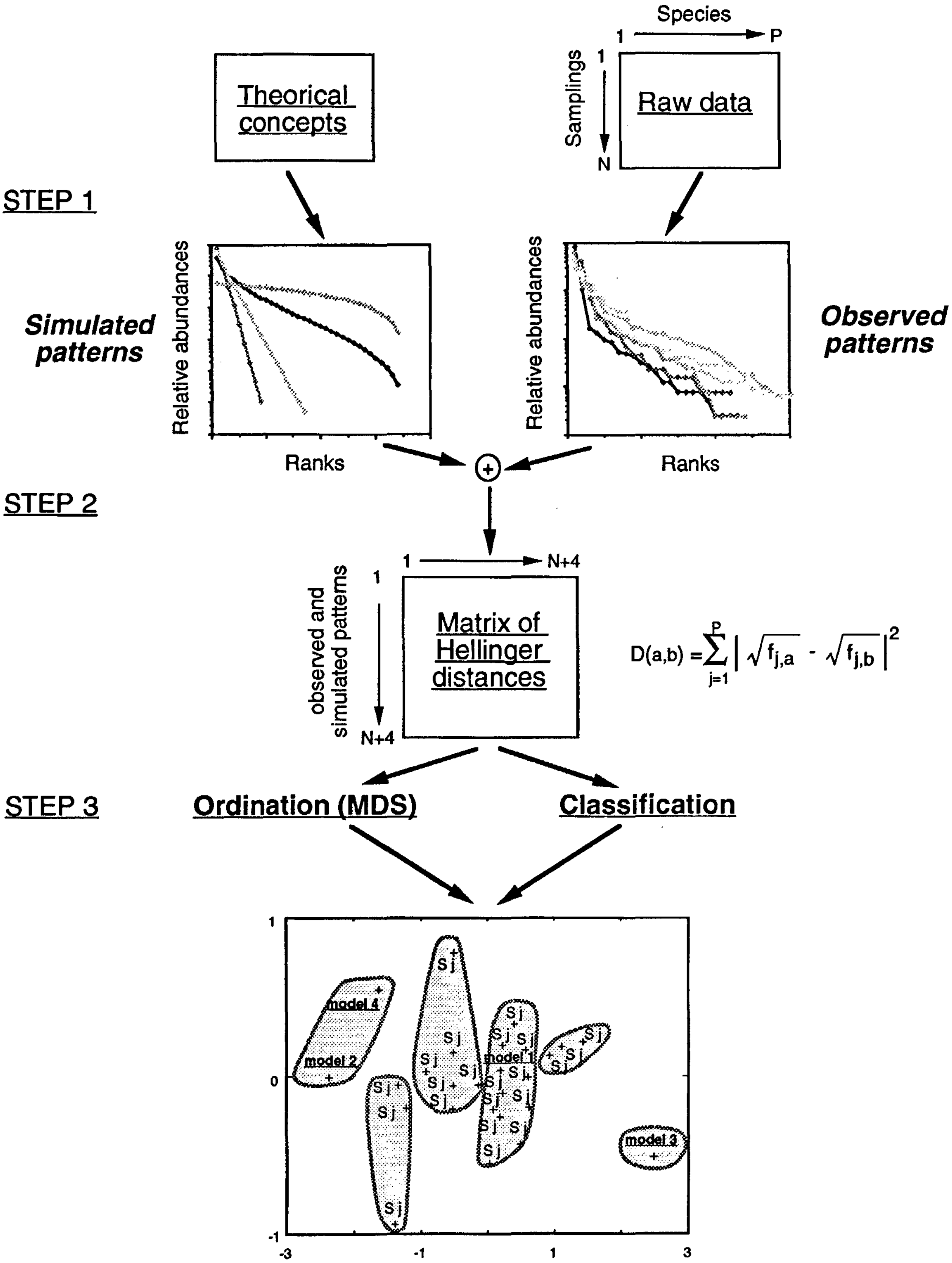


Figure 3

Numerical procedure performed for each species assemblage. The final 2-D plot results from the MDS (non metric multidimensional scaling) computed on the Hellinger matrix. Envelope boundaries correspond to the different groups distinguished by the classification, which was also calculated on the Hellinger matrix.

Procédure numérique opérée sur chaque assemblage d'espèces. La figure finale résulte de la MDS (cadrage multidimentionnel non métrique) calculée à partir de la matrice de distances de Hellinger. Les enveloppes délimitent les différents groupes obtenus par la classification, calculée sur la même matrice de distances.

de Morlaix sites, there is one major recruitment period (in summer or at the beginning of autumn) and generally two recruitment periods at the two other sites (in spring and at the beginning of autumn). During winter, the community ages and species composition and abundance change little. Therefore, samples collected from April to October during the same year were treated as a single entity (symbol "*r*" in the MDS plot), and samples collected from November to March as another entity (symbol "*w*" in the MDS plot). This type of treatment, previously applied by Tokeshi (1990), allows us to concentrate on the interannual variability component, by taking into account the main seasonal variability.

The problem of using the number of individuals to define species patterns still remains. Considering niche-apportionment models, the number of individuals seems an unsatisfactory measure because of differences in size among the species (Tokeshi, 1993). Biomass should reflect resource requirements more accurately than do numbers. Having no complete biomass information on the Gravelines and Baie de Seine sites, a complete analysis could only be made in terms of number. However, information on both biomass and number of individuals is available at the Pierre Noire and Rivière de Morlaix sites and a comparison between the two measures is presented.

RESULTS

The comparison between rank-abundance patterns and rank-biomass patterns was made on the five samples collected at Pierre Noire in 1992 (Fig. 4). Differences between these two kinds of pattern are less important than we might have expected, even if biomass patterns are generally more straightforward than abundance ones. These two kind of patterns were also projected in a MDS-ordination and it appeared that differences beween biomass and abundance patterns are very low compared with seasonal ones. These results indicate that biomass or species number patterns have synchronized changes.

Results from a previous work (Fromentin *et al.*, in press) showed that temporal variations in the abundance of some species of the Gravelines and Baie de Seine communities were related to the alternation of cold and mild years. At Gravelines, this result may be summarized by a MDS plot of the observations performed on the annual means of abundances (Fig. 5*a*). The species abundances observed in 1990 and 1989 are clearly separated from those of 1986, and secondly from those of 1978, 1980, 1985 and 1987. This roughly corresponds to the alternation of cold and mild years; 1989 and 1990 being the warmest years of the series, whereas 1985 and 1986 are the coldest ones (1978 and 1987 also being rather cold years). Clearly different results were obtained with the annual rank-abundance patterns (Fig. 5*b*). In this plot, 1979 and 1981 are distinct from 1978, 1980, 1984, 1985 and 1990. This separation does not correspond to the alternation of cold and warm periods as in the previous case; mild and cold years are on the contrary very close, e.g. 1989 and 1986. Thus, there is no obvious impact of the meso-scale climatic events when rank-abundance patterns are considered instead of annual means of abundances. A similar conclusion was obtained from the Baie de Seine data.

The final stress of configuration of the four MDS-ordinations, performed on the '*r*' and '*w*' patterns of each year, is low (between 0.04 and 0.06), and indicates a good fit in two dimensions. The interannual variability of the Pierre Noire community structure clearly demonstrates the impact of the Amoco Cadiz oil spill in March 1978 (Fig. 6*a*). Before the pollution event (G1), the community was close to the dominance hierarchy DP model. Decimation of *Ampelisca* (amphipod) populations, which were dominant, led to a pattern with lower dominance (G3). The structure was then characterized by the RF model, and remained stable for ten years. It became slightly more equitable in 1981 and during the recruitment periods in 1980, 1985 and 1986 (G4). Since 1989 the structure of this community has been closer to its initial state, but remained at a lower level of dominance. This change coincided with the reappearance of the populations of *Ampelisca* in 1988-1989 (Dauvin *et al.*, 1993*a*). The separation of the data point for the 1992 recruitment period from the rest seems to be due to the appearance of a third dominant species of amphipods (*Ampelisca tenuicornis*). Besides interannual variability, seasonal variations of the structure were low, except in 1982 when a temporary proliferation of *Polydora pulchra* occurred.

Recent history of the Rivière de Morlaix community structure (Fig 6*b*) reveals a clear trend from a strong dominance hierarchy in 1978-1979 (G1) to a random distribution since 1984 (G4). The group G3 covering the intermediate period, from 1979 to 1983, is a transition between these two states. Changes occuring in 1978 and 1979 problably resulted from the Amoco Cadiz oil spill (Dauvin, 1984), inducing a drop in dominance, as at Pierre Noire. However, the Rivière de Morlaix community has remained more equitable since 1984, and thus showed a lower stability and resilience than at Pierre Noire (Frontier and Pichod-Viale, 1993; Holling, 1973). Besides this strong tendency towards a more equitable structure, the seasonal variability is low, except during the 1985 and 1987 winter periods, which were characterized by a sudden rise in dominance.

The Baie de Seine community structure can be roughly characterized by the RF model (Fig. 6*c*). Interannual and seasonal fluctuations always centred around this model, except during the 1988 and 1985 winter periods (G1), which were characterized by a higher dominance hierarchy. This suggests that the structure of this community is relatively stable.

Temporal variability in the Gravelines community can be divided into four groups (Fig. 6*d*). The first group contains the recruitment periods from 1979 to 1983 (except 1980) and the winter period 1982, and is characterized by a strong dominance hierarchy, as demonstrated by its proximity to the DP model. The second group, including the 1988 and 1990-1992 periods, is close to the RA model, typical of an unequitable distribution. The third and fourth groups, which include 1978, 1980, 1984-1987 and 1989 periods, are

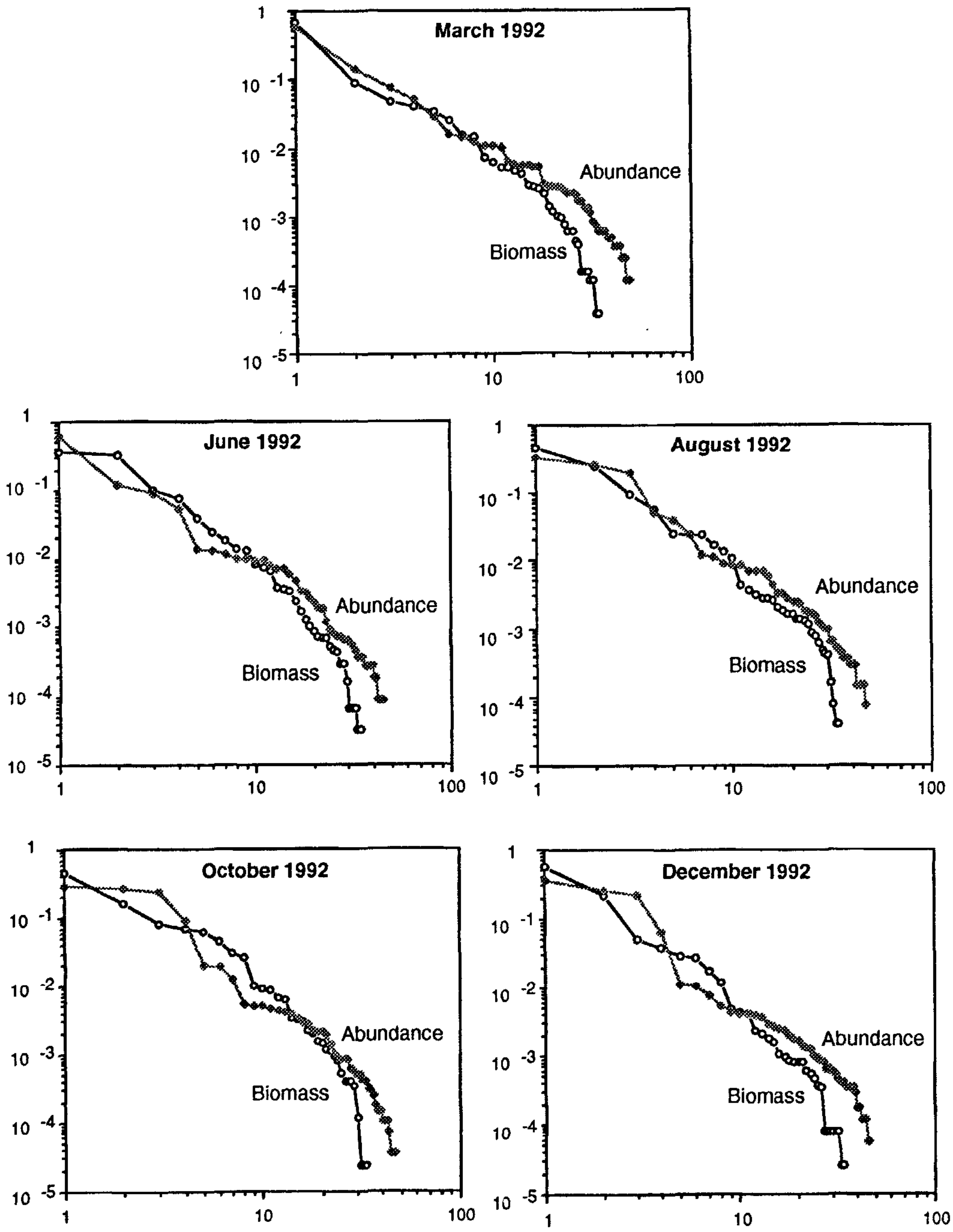


Figure 4

Comparison between rank-abundance patterns and rank-biomass patterns for the five temporal samplings colllected at Pierre Noire in 1992.

Comparaison des diagrammes rang-fréquence calculés sur les abondances et sur les biomasses pour les cinq prélèvements de 1992 effectués à Pierre Noire.

characterized by a random fraction pattern, as is indicated by their proximity to the RF model. In the Gravelines site, important seasonal variations also occurred, recruitment periods being often more dominated than winter periods. However, these seasonal changes did not occur with the same amplitude. They were particularly strong in 1979, 1981, 1983, 1990, but much weaker in 1984, 1985, 1987, 1989. The deterministic causes of these changes are not obvious: a rather equitable structure during the winter can as well be followed by important changes during the recruitment period, as by none; and a dominant structure during the recruitment period can as well be followed by a more equitable one during winter, as by none. The seasonal variability of the Gravelines community seems complex but as large as the interannual one.

These results also show that temporal changes in the structures of these four macrobenthic communities always occurred between the DP model and the RF model, and were least related to the DD model (typical of equitable distributions). There was no synchronized change in the structure, each community had its own temporal feature. The Baie de Seine community was the most stable one, whereas the Gravelines community showed larger and more frequent changes. It is interesting to note that this community, which was not polluted, showed greater

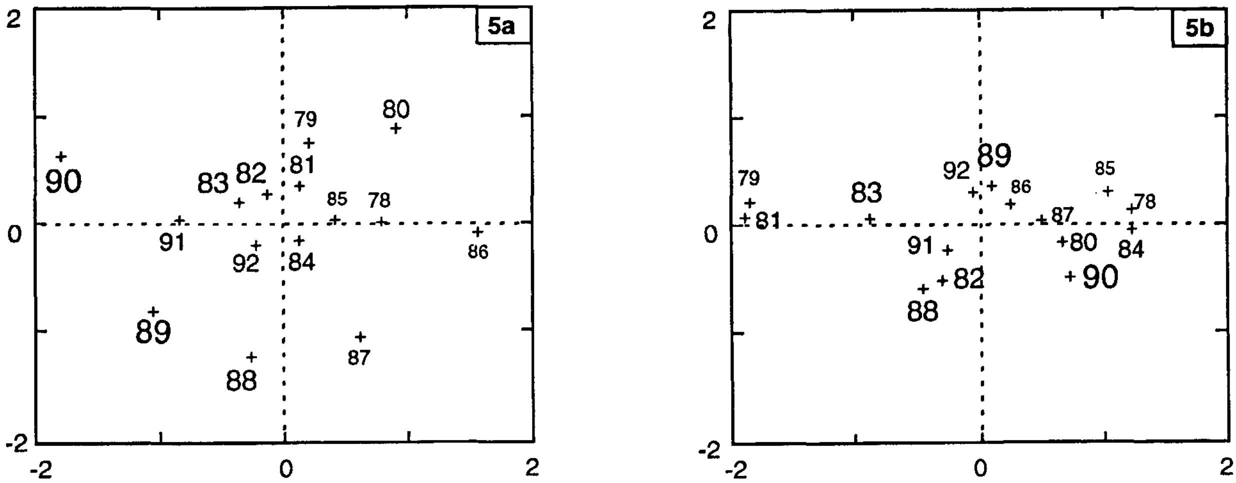


Figure 5

The MDS plots are performed on the data collected at Gravelines during the 1978-1992 period, to ordinate the different years of the survey in a 2-D plot. Plot (5a) is calculated on the annual means of the species abundances; plot (5b) on the annual rank-abundance patterns. The size of the symbols is proportional to the degree of warmth (the warmer the year, the larger the size).

Les graphes des MDS sont obtenus à partir des données du site de Gravelines échantillonnées de 1978 à 1992, afin de projeter les différentes années dans un espace à deux dimensions. Le graphe (5a) est calculé sur les abondances annuelles des espèces, le graphe (5b) sur les distributions d'abondance annuelle des espèces. La taille des symboles est proportionnelle à la température (plus chaude est une année, plus grosse est la taille du symbole).

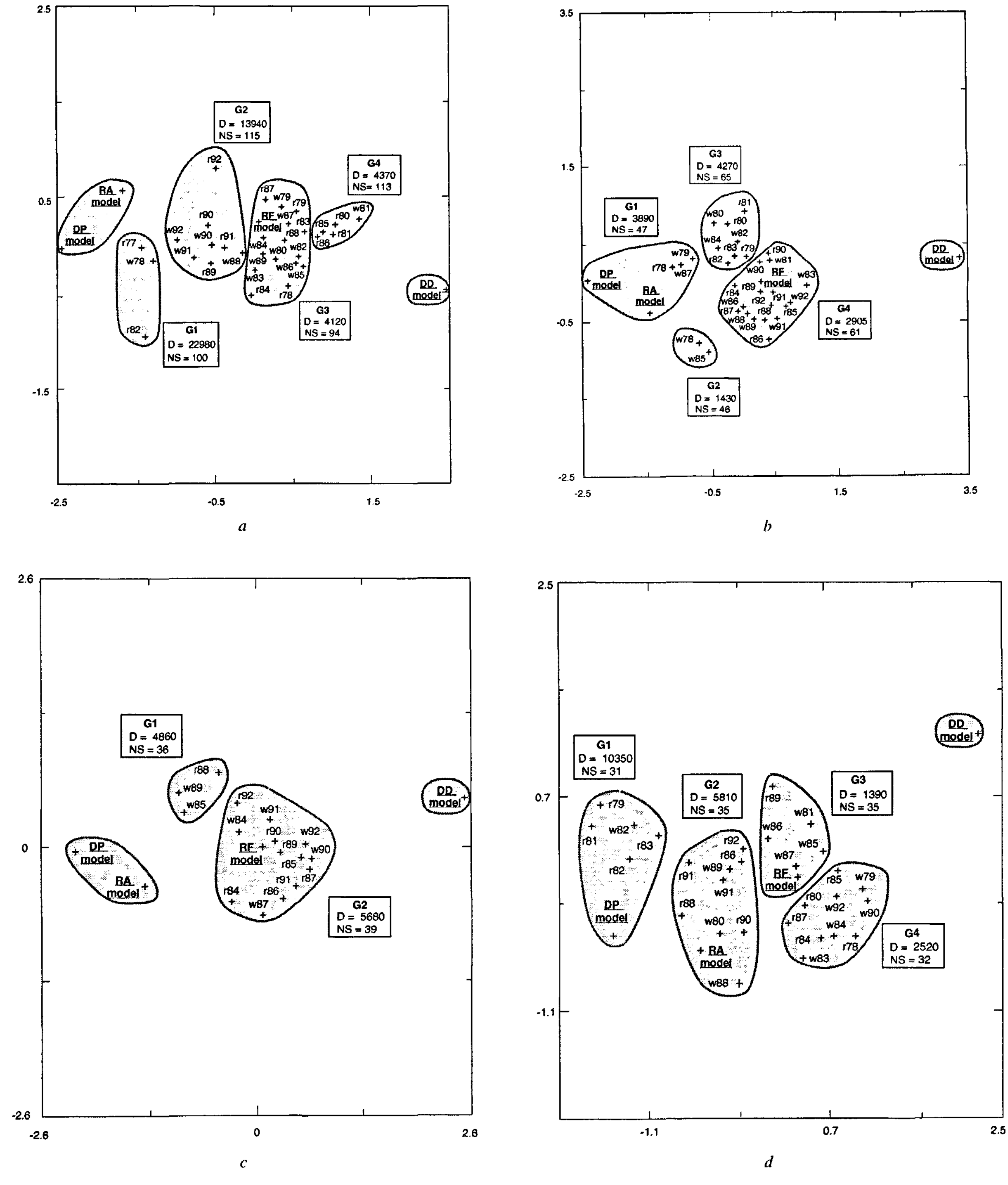
variations in its structure than the two communities which were impacted by the Amoco Cadiz oil spill.

DISCUSSION-CONCLUSION

Analysis of the MDS-ordinations performed on the rank-abundance patterns and species abundances suggests no obvious effects of the alternation of cold and mild years on the structure of the Gravelines assemblage. No significant difference was seen either between cold and mild winters, or between cold and warm recruitment periods. Differences between recruitment and non-recruitment periods cannot be related to meteorological conditions. Furthermore, structure stability seems also to be independent of the alternation of cold and mild years. However, climatic impact was clear on the Gravelines and the Baie de Seine communities in term of species abundances (Fromentin *et al.*, in press). This suggested the possible existence of some indicator species of meteorological conditions, which become more abundant during certain climatic conditions, e.g. *Abra alba* at Gravelines (Fromentin and Ibanez, 1994). As the community structure did not change in relation to these meteorological changes, we hypothesize that species changed their place in the hierarchy of the community in relation to meteorological conditions, but that these changes did not directly affect the whole community structure.

One meso-scale event, the eutrophization of the North Sea and the Skagerrak-Kattegat areas, has probably led to important and synchronous changes in different benthic assemblages (Austen *et al.*, 1991; Josefson *et al.*, 1993). Our work shows that the meso-scale climatic events did not induce such consequences and that temporal variations in the structure of these four assemblages seem more dependent on local conditions. Variations in the Pierre Noire community were mainly due to the effects of the Amoco Cadiz oil spill, which induced some successions of different dominant species. However, these successions cannot explain variations in the structure of the three other assemblages. Indeed, the Rivière de Morlaix community which was rather different in 1978 and after 1984, was nevertheless dominated by the same two species of polychaetes: *Chaetozone setosa* and *Melinna palmata*. The situation was more complex at Gravelines, where different species occurred as dominants. The community was mainly dominated by the polychaete *Lanice conchilega*, and secondly by the bivalves *Abra alba, Tellina fabula*, and the polychaete *Spiophanes bombyx* from 1978 to 1985; then mainly by *Spiophanes bombyx* from 1986 to 1988, by *Abra alba* in 1989; *Lanice conchilega* again becoming the most dominant species since 1990. These changes did not correspond to the changes in the community structure. Two years dominated by the same species, e.g. 1978 and 1979, may be typical of different structures, whereas two years dominated by different species, e.g. 1988 and 1991, may be characterized by some close species distribution.

The community structures of these sites seem more dependent on the intensities of recruitment than on the identity of dominant species. The hypothesis linking intensity of recruitment with density in winter cannot be supported either. At Gravelines very low densities in some winters, e.g. 1978, 1979, 1981 or 1985, were followed by some either strong or weak recruitments. However, we can neither ignore the possible importance of the biological control on the community structure (which will involve another study), nor neglect the local environmental factors, such as wind, current, tides, quantity of organic matter, and anthropogenic pollutions etc. Indeed, our results suggest that the Amoco Cadiz oil spill explains most of the variations in the Pierre Noire community structure.



a

b

c

d

Figure 6

MDS plots performed on the rank-abundance patterns during the recruitment period ('r') and winter period ('w') of each year and on the four simulated patterns, at Pierre Noire (6a), Rivière de Morlaix (6b), Baie de Seine (6c) and Gravelines (6d). Envelope boundaries correspond to the four to five groups distinguished by the classification calculated in each assemblage. For each group, the mean density (D, number of individuals per m²) and the mean number of species (NS) are given.

MDS calculées sur les rang-fréquence des périodes de recrutement ('r') et hivernales ('w') de chaque année ainsi que sur les quatre modèles à, Pierre Noire (6a), Rivière de Morlaix (6b), Baie de Seine (6c) et Gravelines (6d). Les enveloppes délimitent les quatre à cinq groupes obtenus par la classification, calculée pour chaque assemblage. Pour chaque groupe, la densité moyenne (D, nombre d'individus par m²) et le nombre moyen d'espèces (NR) sont donnés.

Furthermore, it is very interesting to note that Gravelines site, which was subject to highly variable environmental conditions, was the only one to yield some data conforming to the RA model. This might also confirm the possible importance of local environmental factors, underlining the fact that the RA model is theoretically defined for an assemblage of species unrelated to each other, as might be the case in a stochastically variable environment (Tokeshi, 1993).

The hypothesis that the high variability of Gravelines community may be related to some highly variable environmental conditions refers to the old stability/diversity controversy. The question of stability was first considered as a result of biotic interactions, one salient problem being the link between complexity, connectance and equilibrium (De Angelis, 1975; Gardner and Ashby, 1970; May, 1972; McNaughton, 1978; Rejmanek and Stary, 1979; Zaret, 1982). Noting that populations do vary more in climatically unpredictable systems, Pimm (1984) suggested that extrinsic factors may govern variability (or stability) more than intrinsic ones. More recently, De Angelis and Waterhouse (1987) have proposed that both extrinsic and intrinsic factors could control variability. For these authors there is a spectrum from stable equilibrium systems to non-equilibrium systems. The former are structured primarily by biotic interactions, such as interspecific competition (Hughes, 1985, 1986), whereas the latter are controlled more by environmental variations. Pierre Noire community seems typical of the former system, its structure results mainly from biotic relations, e.g. the effects of destruction and re-apppearance of *Ampelisca*. In contrast, Gravelines community seems more typical of the latter system under an external control.

In conclusion, it appears that: 1) three of the four communities did not reach any kind of climax during the periods of the surveys, their structures continuously changing through time (only Pierre Noire seems close to a climax situation, characterized by a high dominance of amphipods); 2) changes were not related to the alternation of cold and mild years, but to local environmental and biological factors; 3) when dominance was high, so was density; 4) stable communities seem to be structured by biotic interactions, whereas unstable ones seem more under the control of environmental factors. In this study, we focused mainly on the comparison of four macrobenthic communities in relation to meso-scale and local events. Clearly, further investigation of the biological processes of the main dominant species and the biotic interactions is needed.

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