Long-term variability of the *Abra alba* community in the southern bight of the North Sea

Long-term trends
Time series
Multivariate methods
Benthos

Tendances à long terme
Séries chronologiques
Méthodes multivariées
Benthos

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ABSTRACT

The *Abra alba* community from the Gravelines area has been studied since 1976. During this period, sudden and unpredictable variations of the species composition have been observed. These important changes affect a limited number of species without changing the bionomical structure of the community. The species in question are found to be characteristic of this community, and are the more abundant ones.
Multivariate statistical methods were used to study quantitative data on the benthic population collected from 1978 to 1992. This analysis was performed in association with air temperature data.
Results showed the existence of a six- or seven-year cycle, and this is confirmed by the observation of two complete periods. This cycle, which is found to be related to variations in climatic conditions, is generated by characteristic species of the community. Nevertheless, the species mainly responsible for the two "maxima" phases of the cycle are not the same. A different situation emerges during the years 1991-1992, with a new incoming species, *Ensis directus*, and modification of the nature of the sediment.
The study of the community performed without the representative species, taking into account less abundant and less frequent species, shows a different kind of trend.

RÉSUMÉ

Variabilité à long terme du peuplement à *Abra alba* dans la baie sud de la Mer du Nord.

Le peuplement à *Abra alba* de la région de Gravelines fait l'objet d'un suivi à long terme depuis 1976. Pendant cette période, des fluctuations brutales et imprévisibles de sa composition spécifique ont pu être mises en évidence. Ces profondes altérations intéressent un nombre restreint d'espèces dites « caractéristiques du peuplement », en fait les plus abondantes, sans remettre en cause la structure bionomique du peuplement.
Le travail porte sur le traitement statistique multivariable des données quantitatives recueillies de 1978 à 1992 sur le peuplement benthique d'une station. Ce traitement est réalisé en relation avec des données climatologiques.
Les résultats obtenus ont permis de mettre en évidence l'existence d'un cycle de six ou sept années, confirmée par l'observation de deux périodes complètes.

Ce cycle, qui a pu être mis en relation avec des variations des conditions climatiques, est généré par les espèces caractéristiques du peuplement. Les espèces principalement responsables des deux phases « maxima » du cycle ne sont cependant pas les mêmes. Les années 1991-1992 présentent une situation différente, marquée par l'apparition d'*Ensis directus* et par la modification des caractéristiques granulométriques du site.
Une étude du peuplement réalisée sans les espèces caractéristiques, en prenant en compte les espèces moins abondantes ou plus rares, montre une évolution différente.

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INTRODUCTION

Benthic communities along the French coast, in the southern bight of the North Sea, have been studied for nearly twenty years. This area is affected by severe anthropogenic perturbations: dense maritime traffic; industrial complexes; harbour installations. It is exposed to particular natural conditions: the proximity of the Dover Strait induces powerful hydrodynamic processes. Gradients of reduced current strength create several macrobenthic assemblages, which are distributed according to the nature of the sediment (Souplet *et al.*, 1980; Davoult *et al.*, 1988; Prygiel *et al.*, 1988; Dewarumez *et al.*, 1991, 1992). The present study examines temporal variations of the *Abra alba* community. This muddy fine sand community exists along the entire coast, at a depth no greater than 10 m, from Cape Blanc Nez to the Scheldt estuary and beyond (Dewarumez *et al.*, 1978; Dewarumez, 1979; Belgrano *et al.*, 1990).

The purpose of this paper is to detect the existence of cyclical trends or long term cycles in the changes of the benthic community in question, and to relate these changes to variations of global effects, such as climatic conditions. Several studies have pointed to the importance of long-term changes in meteorological features, and especially temperature, on the changes of benthic communities (Glémarec, 1979; Gray and Christie, 1983; Dauvin *et al.*, 1993; Ibanez *et al.*, 1993; Fromentin and Ibanez, 1994). Numerical methods to display these developments and their inter-relationships are proposed.

In this first part of the study, the complete data set was used. As in most quantitative studies of benthic time series, the analysis takes mainly into account the more abundant species, and accords less importance to less abundant and rare species. But the organization of a community shows different levels, and less abundant species can reveal a different pattern of development than the more abundant ones (Frontier and Viale, 1993). The second part of the study focuses on these less abundant but not necessarily rare species, and analyses the evolution of the community without its more representative species.

MATERIAL AND METHODS

Study area and sampling

The study area is located in the southern part of the North Sea, off the French coast, between Calais and Dunkirk (Fig. 1). Samples were taken in the *Abra alba* community, at a station near Gravelines, situated 1.5 sea miles distant from the mouth of the Aa river, at a depth of 8 metres. Data are quantitative; samples were collected with a Smith McIntyre or a Van Veen grab (10 replicates of 0.1 m). Values are expressed in density: number of individuals/m^2.

The data relate to the macrobenthic population sampled between 1978 and 1992. During this period, 81 samples were taken, in which a total of 151 species or taxa was described. There were important changes in the frequency of sampling from year to year (from 10 to as few as 4 samples), and sampling was irregularly spaced in time.

Data analysis

Correspondence Analysis (or Reciprocal Averaging) on the contingency table crossing samples and species (or taxa) was performed to study the temporal evolution of the community (Benzecri *et al.*, 1973; Hill, 1973; Legendre and Legendre, 1984; Leprêtre, 1988).

The aim of the study is to determine the long-term evolution, *i.e.* inter-annual variations. As already stated sampling was irregular in time, and there was an important heterogeneity in the number of samples collected per year. The first difficulty lay in equilibrating years, in such a way that they were all represented in the the same fashion in the correspondence analysis.

In order to do this, we assumed each sample to be representative of a period of time, and weighted data of each of the samples with the length of the period. We used the month as time unit, and the origin t_0 was set in January 1978. For a series of samples observed at times $t_1, t_2, \ldots, t_n$, the weight w_i associated with the sample taken at time t_i was:

$$w_i = \frac{t_i + t_{i+1}}{2} - \frac{t_{i-1} + t_i}{2}$$

Values in the sample taken at t_i were multiplied by w_i.

Correspondence analysis was performed on the weighted data. We added the annual and monthly means of samples as supplementary variables in the analysis (*i.e.* not active in the analysis). To calculate these mean values, missing samples were replaced by the nearest collected sample in time.

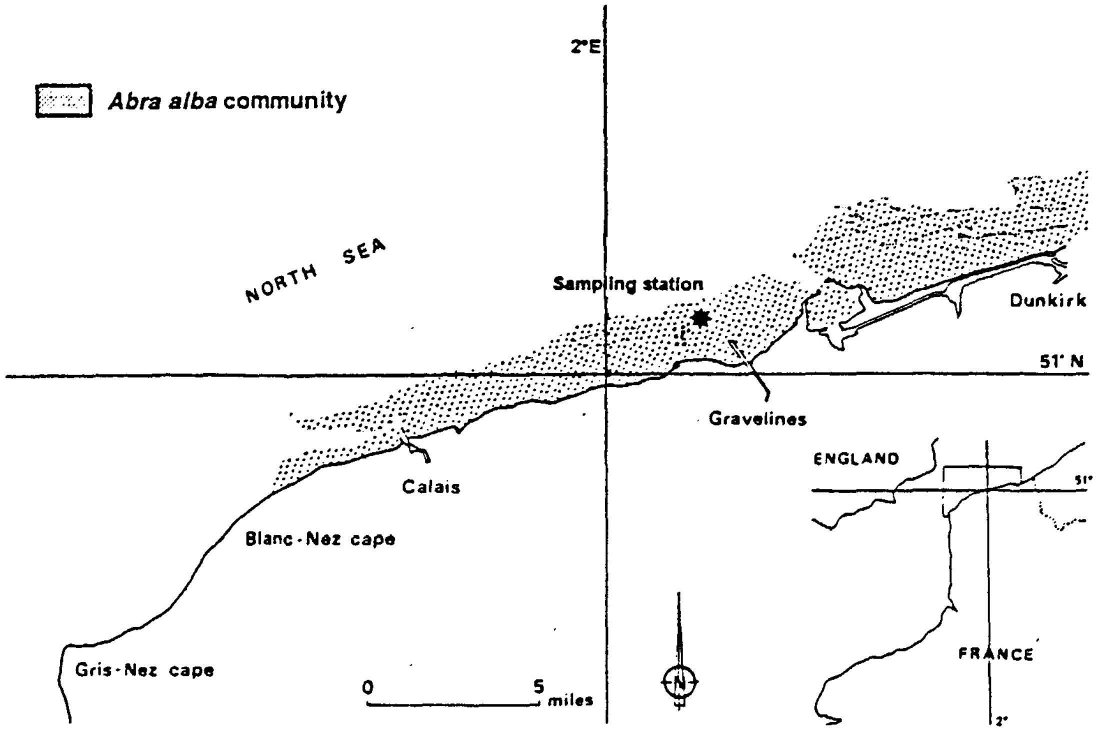


Figure 1

Study area.

Interpreting multivariate analysis with a large collection of data is difficult, especially in the case of time series. The presentation of results on a factorial plane is often confused, and a trajectory does not permit a clear indication of long-term trends.

We propose two different methods of presenting the results obtained from the correspondence analysis in order to demonstrate the evolution of the community in a chronological manner. Co-ordinates on a limited number of axes from the correspondence analysis are used to calculate distances between samples.

In the first method, we used co-ordinates on the most significant axes of samples and mean values for each month (added as supplementary variables in the correspondence analysis). For each sample, the distance between the sample and the mean of the month corresponding to the sample is calculated. Then we have an expression in time of the difference between collected samples and a mean situation, unaffected by seasonality.

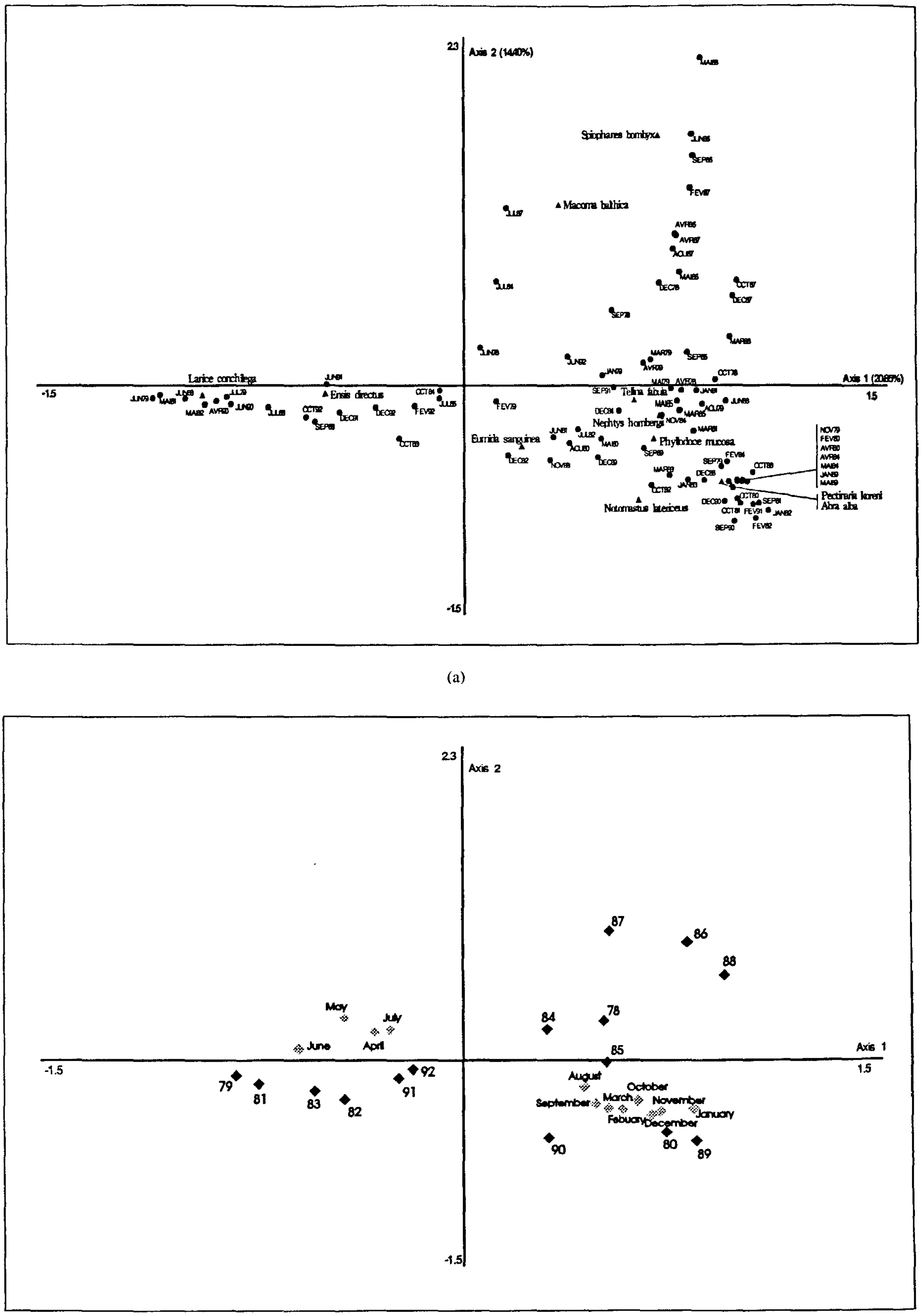
For the second method, we first calculate the distance between two successive samples and the distance between the means of the months corresponding to the two samples. Then we express the ratio between these two distances as a function of time. The purpose here is to show when, in the succession of samples, the difference between two samples is higher (or lower) than the mean difference that should have been observed. This can reveal when unusual, short-time scale events occur rather than showing up a long-term trend.

RESULTS

Analysis of the complete data set

First, the correspondence analysis performed on the total set of data shows that species strongly contributing to the first inertia axes are characteristic species of the community. Ordination in the plane of axes I (20.85% of total inertia) and II (14.40%) shows a main group of samples characterized by *Abra alba, Tellina fabula, Pectinaria koreni, Nephtys hombergii, Phyllodoce mucosa, Eumida sanguinea* and *Notomastus latericeus* (Fig. 2*a*). Two subgroups may be distinguished, opposing *Abra alba* and *Pectinaria koreni* to *Tellina fabula* and *Nephtys hombergii.* The first axis separates from this main group samples collected in 1979 and from 1981 to 1983, associated with *Lanice conchilega.* The second axis isolates samples from 1986 to 1988, associated with *Spiophanes bombyx* and *Macoma balthica.* Most of the samples of the two groups were taken in spring and summer, during the period from April to September. Years 1991 and 1992 are characterized by the appearence of *Ensis directus,* a North-American species, observed for the first time in this area in June 1991 (Luczak *et al.,* 1993). The third axis (11.0%) opposes 1980 to the main group, associated with *Pectinaria koreni, Mya truncata* and *Cerastoderma edule.*

Mean years and mean months are projected as supplementary variables on the axes of this first analysis. Projection on plane I-II of the mean years confirms the inter-annual trend (Fig. 2*b*). The community departs from its original position in 1978. It stays away during the period 1979-1983 (1980



(a)

(b)

Figure 2

– Ordination of samples and species in the plane of axes I and II from the C.A. performed on the complete data set. (2a).
– Projection in this plane of mean years and mean months as supplementary variables (2b).

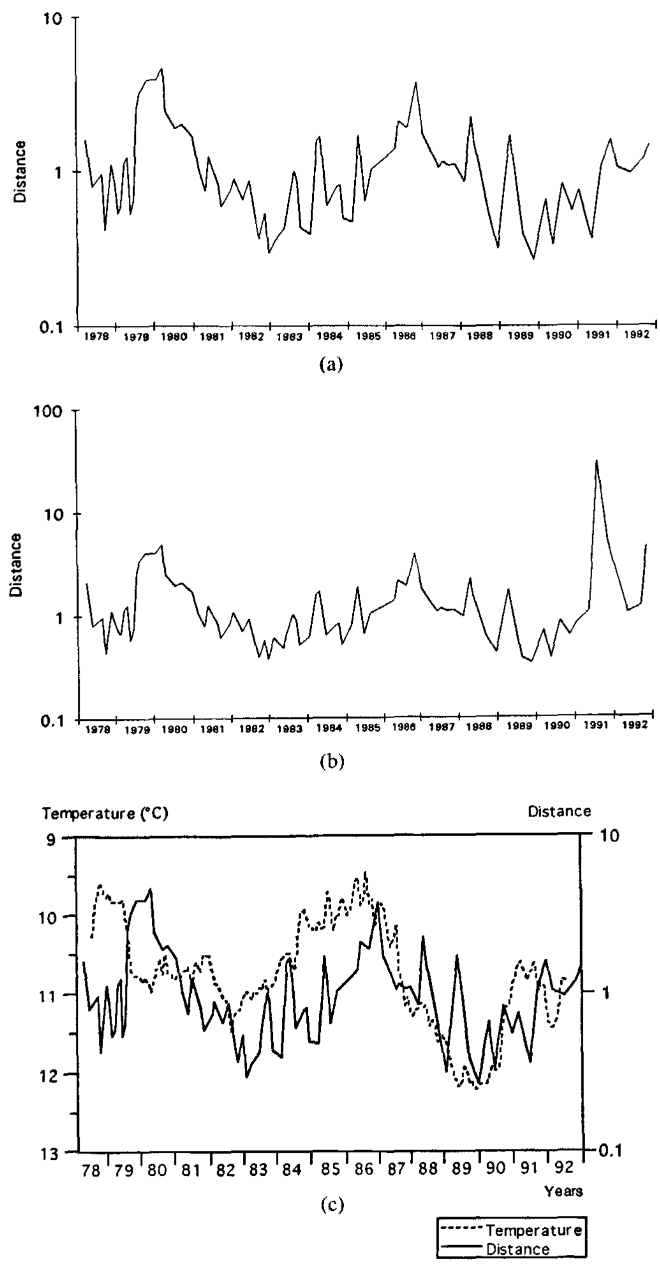


Figure 3

– Distance to mean month calculated from the first 3 axes of the C.A. (3a).
– Distance to mean month calculated from the first 5 axes of the C.A. (3b).
– Distance to mean month from first 3 axes of the C.A. (solid line) and 12-term moving average performed on monthly temperatures (dotted line) (3c).

marks a departure from the original situation on the third axis) and then returns in 1984 and 1985. It moves away a second time from 1986 to 1988 and returns to the original situation in 1989-1990. It then shows the special nature of the years 1991 and 1992. Projection of the mean months (as supplementary variables) distinguishes the April to July period from the remainder of the year, and shows that this late spring and early summer period, when recruitment occurs, is determinant for the evolution of the site.

The distance to the mean month calculated from the first three axes of the correspondence analysis shows a cyclical variation of the community (Fig. 3*a*). An important seasonal variation can also be observed. Performing the calculation on the first five axes shows, in addition, the discontinuity of years 1991-1992 (Fig. 3*b*). Maximum deviations from the mean situation, found from the end of 1979 to 1981 and from 1986 to 1987, correspond to changes in climatic conditions. A twelve-term moving average is performed on the monthly temperature measured at Dunkirk in order to remove seasonality and to assess the inter-annual trend. The distance calculated on the first three axes follows with a delay of almost one year the temperature variation (Fig. 3*c*): high distances correspond to low temperatures. A correlation analysis was performed between distance and smoothed temperature data with different time lags. The optimal negative value for Spearman's rank-order correlation coefficient is obtained for a 9-month delay. This negative correlation keeps large values for lags from 4 to 12 months (Table 1).

The ratio of distance between successive samples and distance between mean months shows numerous peaks, especially in the first years of the study (Fig. 4). Two major discontinuities appear in 1980 and at the beginning of 1987.

Analysis without characteristic species

The cyclical evolution revealed by the complete data set analysis is due to a few species which are the more abundant ones. A group of 19 species accounts for more than 95% of the contributions to inertia of the five first axes of the correspondence analysis. To determine whether or not less abundant species share the same evolution, we applied the same methodology to a reduced data set. Species with contributions to the inertia of the first five axes of the correspondence analysis higher than the mean of all contributions were removed. To avoid the effects of excessively sporadic species, species appearing less than ten times in the 81 samples were also removed. Forty species were finally retained.

The first axis of the correspondence analysis performed on these data was generated by only one species, *Venerupis*

Table 1

Spearman's rank-order correlation of distance vs. moving average smoothed temperature with different time lags.

Lag (months)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Spearman's r_s	–0.29	–0.36	–0.39	–0.45	–0.50	–0.53	–0.52	–0.54	–0.60	–0.57	–0.51	–0.42	–0.30	–0.22	–0.17	–0.08
Proba ($\rho_s = 0$)	< 5%	< 1%	< 1%	< 1‰	< 1‰	< 1‰	< 1‰	< 1‰	< 1‰	< 1‰	< 1‰	< 1%	< 5%	n.s	n.s	n.s

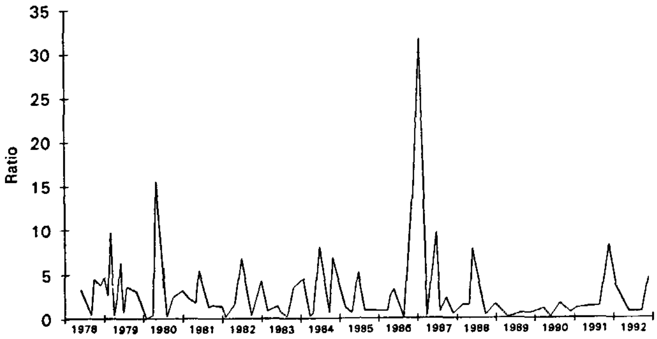


Figure 4

Ratio of distance between two successive samples and distance between the corresponding mean months calculated from the first 3 axes of the C.A.

pullastra, very abundant in 1982 and 1983. This species was then removed and a second analysis was performed. Ordination in plane I-II with the projection of mean years shows a first group from 1978 to 1983. Years 1984 and 1985 become isolated from this group, associated with *Mysella bidentata* (Fig. 5). Year 1986 returns to the first group. From 1987 to 1992, years separate from the main group, without any homogeneity between them.

Distance to the mean month is calculated from co-ordinates on the first five axes of the correspondence analysis (Fig. 6). Results do not show clearly a cyclical variation as does the analysis with all species. In the first part, until 1985, the variation of the distance appears to show a slight opposition to the variation due to main species: a "low" phase in 1981 and a "high" one in 1984-1985. But from 1987, distance seems to increase, following a continuous, regular drift. The ratio of distance between successive samples and between mean months only shows an important discontinuity at the beginning of 1985 (Fig. 7).

CONCLUSION-DISCUSSION

The methods of calculating distance to a reference with results from a correspondence analysis proposed here permit the demonstration of changes in a community as a function of time. This method may be easier to read than a factorial plane, and facilitates the establishment

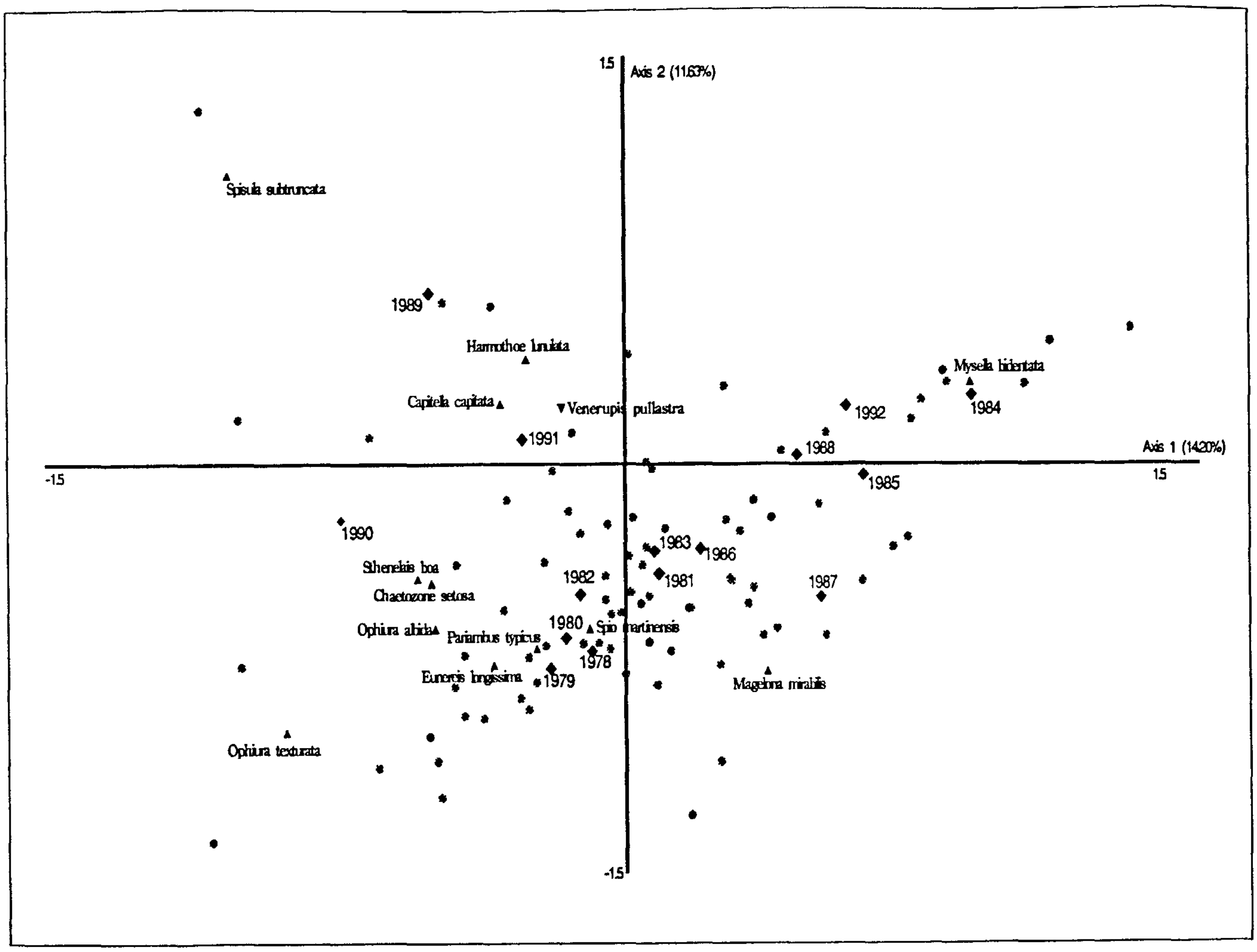


Figure 5

Ordination of samples and species in the plane of axes I and II from the C.A. performed without characteristic species. Mean years are added as supplementary variables.

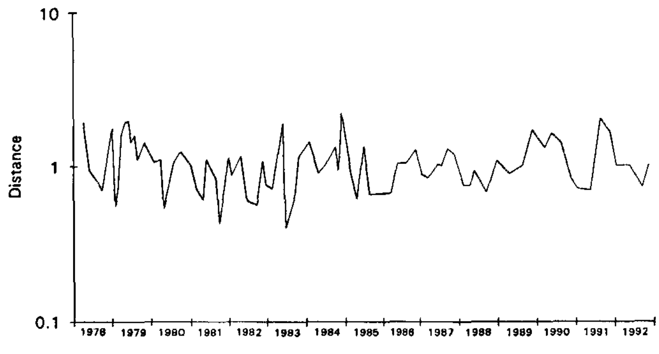


Figure 6

Distance to mean months calculated from the first 5 axes of the C.A.

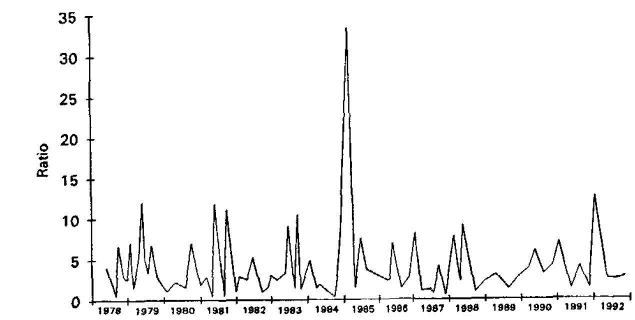


Figure 7

Ratio of distance between two successive samples and distance between the corresponding mean months calculated from the first 5 axes of the C.A.

of a relationship with environmental data. Distance to the mean month confirms the existence of a periodic modification of this *Abra alba* community, strongly related to temperature. Following cold years, one or a very few species have high densities, and dominate the community. However, the cyclical variation of the community does not correspond to a cyclical variation of the species, considered separately each from the other. The pattern of change of the community is not the same as the patterns of change of the representative species of this community. During the fifteen years of the study, two cold periods induce a deviation of the community from is basic state, but the main species involved in the different periods of this variation are not the same: *Pectinaria koreni, Mya truncata* (1980) and *Lanice conchilega* (1981) for the first period; and *Spiophanes bombyx* and *Macoma balthica* for the second period (1986-1987).

This cyclical variation is generated by a limited number of species, representative of the community, which show great abundances and often have chaotic dynamics. Most of them are opportunistic, and will react by an important increase in their densities to small, favourable changes in environmental conditions (Dauvin *et al.*, 1993; Dewarumez *et al.*, 1978, 1991, 1992). Species less abundant but with a more balanced population dynamic will certainly be able to reveal more profound changes of the ecosystem. This hypothesis appears to be confirmed by results of the second analysis, performed with strongly contributing species in the analysis of complete data removed. This trend, although it appears less obvious, can be opposed, in a first time, to the cycle due to representative species. A second part of the data, from 1987 to 1992, shows a regular drift of the community from its original state, but not in the direction of any stable situation. This evolution may be related to changes in the sediment composition. In the first years, equally blended middle and fine sand (about 52% of middle sands and 42% of fine sands) characterize the granulometric structure. During the final years, up to 1991, a dominance of fine sands (20% of middle sands and 71% of fine sands) is observed, and the silt content of the sediment appears to show a slight increase (from 4% up to 7.5%).

The particular nature of years 1991 and 1992 is due to the coincidence of two factors: the first recorded presence on the French coast of *Ensis directus*, a North American species colonizing the North Sea from the German Bight since the end of the 1970s; and a change in the nature of the sediment. Probably after a storm in summer 1991, the granulometric structure of the sediment around the sampling area changed a from muddy fine sands to coarse-middle sands (from 1.5% of coarse sands before summer 1991 up to 55% in late 1991). This was followed by the disappearance of most of the macrofauna. Only 15 species and a total of 91 ind./m^2 were found in September 1991, as compared with a mean density of 5080 ind./m^2 and a mean species richness of 32 species. The community appears to have rapidly recovered a normal state in 1992, due to an increase of silt content and despite the high content of coarse sand.

Important discontinuities in the variation of this community have been observed over the period of fifteen years. The influence of short spatio-temporal scale events is obvious and is confirmed by observations (or non-observations) of events on neighbouring sites. Numerous hydroclimatic processes are capable of inducing high variability in the community. But the retrievial of information about such local conditions from historical data is not an easy matter, and a local interpretation of the drastic changes of the community remains to be performed. In addition, periodic changes in the community are associated with different species, and the factors determining which of the latter will take over during the cold periods will have to be related to a finer scale.

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