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SHAPE ANALYSIS OF TEMPORAL ECOLOGICAL PROCESSES: LONG-TERM CHANGES IN ENGLISH CHANNEL MACROBENTHIC COMMUNITIES

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Abstract: Long-term benthic times series data reflect the impact of anthropogenic or hydroclimatic factors, as well as biological behaviour strategies. A numerical method known as 'typology of shapes of series' (TSS) can be used to clear up this complexity. The method is illustrated using macrobenthic data set from the western part of the English Channel (48 species, regularly sampled from 1977 to 1992). TSS is based on the concept that the shape of temporal variation in species abundance gives precise information on responses to environmental variables at different scales, and on reproductive strategy. Shape is characterised by four indices that describe the intensity of year to year and seasonal variations, and the degree of intermittence of the series. 12 groups of similar shapes were detected from the 48 species. Separate analyses were made on groups of species with strong long-term trends, regular seasonal variations, and those of sporadic occurrence. Species abundances were affected by the 1978 'Amoco Cadiz' oil spill, as well as by variation of hydro-climatic parameters.

Introduction

The study of temporal change in coastal macrobenthic communities is now relatively common (see Bachelet et al. 1997). In macrobenthic data sets there are a number of common characteristics: (1) a high number of species, most of which are rare; (2) wide fluctuations in species abundance over time, with periods of recruitment producing high abundance followed by periods of a high mortality; and (3) high between-species differences in maximum abundance. The detection of patterns amongst biological variables is therefore particularly difficult, as the most abundant species will tend to monopolise the information contained in the data. Transformation of the raw data (logarithms, double root) is therefore necessary, to down-weight the importance of the very abundant species before statistical or multivariate analyses (Field et al. 1982, Clarke & Green 1988). The retention of rarer species may strongly distort the results when classification or ordination methods are used. Selection of the most representative benthic species is thus an essential preliminary step in data treatment. Examples include using species that make up more than a fixed percentage of the total abundance in at least one sample (Pearson 1975), detecting the main changes in the slope of the curve representing the number of species against the percentage of zero (Ibanez et al. 1993a), or identifying different categories (rare, intermediate or dominant species) based on a probabilistic model (Manté et al. 1995, 1997). These methods are based on distribution properties, not on ecological concepts. Clarke & Warwick (1998) extracted the most representative species from a set of chronological series by stepwise randomisation. These representative species produced a similar ordination of the samples that was similar to that obtained using all species. An objective selection of sensitive species indicative of pollution was proposed by Pearson et al. (1983). At each sampling point in a time series, plots are drawn with the percentage number of species on the ordinate and the number of individuals per species (in geometric classes) on the abscissa. The shapes of the distributions allow recognition of the species which account for the trends in the data set.

Typology of shapes of series (TSS) had been proposed as a method that is more informative than raw or transformed data in describing temporal variation in macrobenthic communities (Ibanez & Fromentin 1997). The basic assumption is that the shape of a species abundance curve is characteristic of its behavioural patterns or demographic strategy. The method is used to help ecologist visually recognise species with continuous vs. seasonal vs. discontinuous trends. With additional ecological knowledge, each pattern of variation may be related to a specific type of reproductive strategy, or to different sensitivities to environmental factors, at various scales. TSS is a semi-objective method that allows a classification of the graphs defined by species time series. Three steps are involved in TSS: (1) definition of the shape characteristics; (2) classification of species into groups with common shape characteristics; (3) separate analysis of each species group to relate their responses to underlying environmental variation. TSS is a numerical analysis that is dependent on the similarity of shapes of temporal change in species. Similarity does not correspond to a global comparison, but is instead based on overall temporal patterns.

In this study, we illustrate the TSS method using long-term (1977-1992) time series data on macrobenthic species abundance in the western English Channel. The method is used to characterise groups of species with similar temporal shapes. Each group is then analysed separately to identify ecological responses related to underlying environmental factors.

Material and methods

Sampling and Data

To test the method, we used an available macrobenthic time-series having a large number of collected species and a relatively large number of observations. It is an *Abra alba-Hyalinoecia bilineata* community from the Bay of Morlaix, which was regularly sampled over 16 years (1977-1992). The main characteristics of the sampling of abiotic and biotic conditions are described elsewhere (Dauvin 1984; Dauvin & Ibanez 1986) and are only summarised here. The Pierre Noire station is located in the eastern part of the Bay of Morlaix (48°42,50' N, 3°51,96' W, 17 m depth). The sediment was fine sand (median particle size, 148-204 m). The bottom water temperature varied between 8°C in March and 15.5°C in September, and salinity between 34.5 in winter and 35.3 at the beginning of autumn. During the survey (April 1977 to December 1992), 117 samples were collected. 12 observations were made in each annual cycle from April 1977 to March 1982, and five observations per year between 1982 and 1992. A Smith-McIntyre grab was used. Ten samples were taken at each sampling date, giving a total area of 1m^2. After collection, the sediment was sieved (1 mm circular mesh) and the retained material fixed using 10% buffered formaldehyde. A second sorting was done after staining with 10% Rose Bengal. Species were identified and counted for each grab, then their densities were pooled together and expressed as number of individuals/m^{-2}.

The station was impacted by a hydrocarbon spill from the Amoco Cadiz in spring 1978, resulting in local extirpation of the dominant *Ampelisca* populations (Dauvin 1984, 1998, Dauvin & Ibanez 1986). Of the 220,000 tons of oil spilled into the sea, between 10,000 and 92,000 tons (according to different authors) was trapped in subtidal sediments (Dauvin 1984). The presence of hydrocarbons in the subtidal bottom sediments of the Morlaix bay was evident in April 1978, just two weeks after the wreck (Cabioch et al. 1978). At Pierre Noire, the levels of hydrocarbons in the sediments, as measured by infrared spectro-photometry, increased to 200 ppm in the summers of 1978 and 1979, but did not exceed 50 ppm after the winter of 1981 (Dauvin 1984). After 1981, the sediments were recolonised by species whose populations were locally extirpated by the oil spill (Dauvin 1987, 1991, 1998).

Species Selection

Based on previous studies (Ibanez & Dauvin 1988, Ibanez et al. 1993a, Fromentin et al. 1997), only the most representative species were selected by taking into account two parameters. The first is relative abundance:

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

where N is the number of samples, P the number of species and A(i,j) the abundance of the ith species in jth sample. The second is the presence/absence ratio (PAR):

$PAR_i = N_i/N$

where N_i is the number of samples in which species *i* is present.

Forty eight species were selected, corresponding to the species which were present in at least 50% of the samples and had a relative abundance > 0.001.

Numerical Methods

A flowchart of the methods is presented in Fig. 1. The numerical procedures are summarised below.

Step 1. Species abundances are represented as an irregular series of samples over 16 years. The 'area method' (Fox & Brown 1965), previously used in marine ecology by Ibanez et al. (1993a) and Fromentin et al. (1997), was used to regularise the series as one observation for each of four seasons: January, April, July and October. The area method is a weighted average of the data according to the distance between their dates and the reference dates. Sixty-three time periods for the 48 species were obtained, from July 1977 to October 1992.

Step 2. Extract the general trend from the multiannual series. Given the paucity of observations per year, classical polynomial adjustment or moving averages could not be used. Instead, the 'eigenvector filtering method' (EVF; Colebrook 1978) was employed, using the PASSTEC package (Ibanez & Etienne 1998). This method uses principal component analysis (PCA) in a weighting and moving average process. An important properties of the method is that it eliminates all frequency bands equal to or higher than the annual cycle. Unlike most other methods, no observations are lost at the boundaries of the series, and no arbitrary choice is required regarding the shape of the trend. Taking a series Z_t varying between 1 and N, one first constructs a matrix of data Z corresponding to m differentiated series. Eigenvalues and eigenvectors are then extracted from the m x m autocovariance matrix to compute principal components. Judicious choice of the number m of the shifted series may be estimated by the lag of the zero of the autocorrelation function of Z_t (Takens 1981; Ibanez & Etienne 1992).

The first component is the portion of variation common to all the m series, and is therefore similar to the general trend of the series Z_t. The second component corresponds to residual information after removing this common component. If a seasonal cycle is present, it will be associated with the second component. The corresponding eigenvalues indicate the explained variability of components.

The product of an eigenvector and its corresponding component defines a predicted table Z. Since Z contains the same observation several times, it is necessary to average the homologous elements in order to reconstruct a unique smoothed time series F_t. Elements located between positions m and N-m+1 are averaged m times, while the others are only represented m-1, m-2... times following their location from the boundaries.

The first and second eigenvalues/components are used in estimating the filtering variable F1 and F2. These smoothed series correspond to the principal trends of the original series (Colebrook 1978). Although principal components themselves are linearly independent, the averaging procedure allows

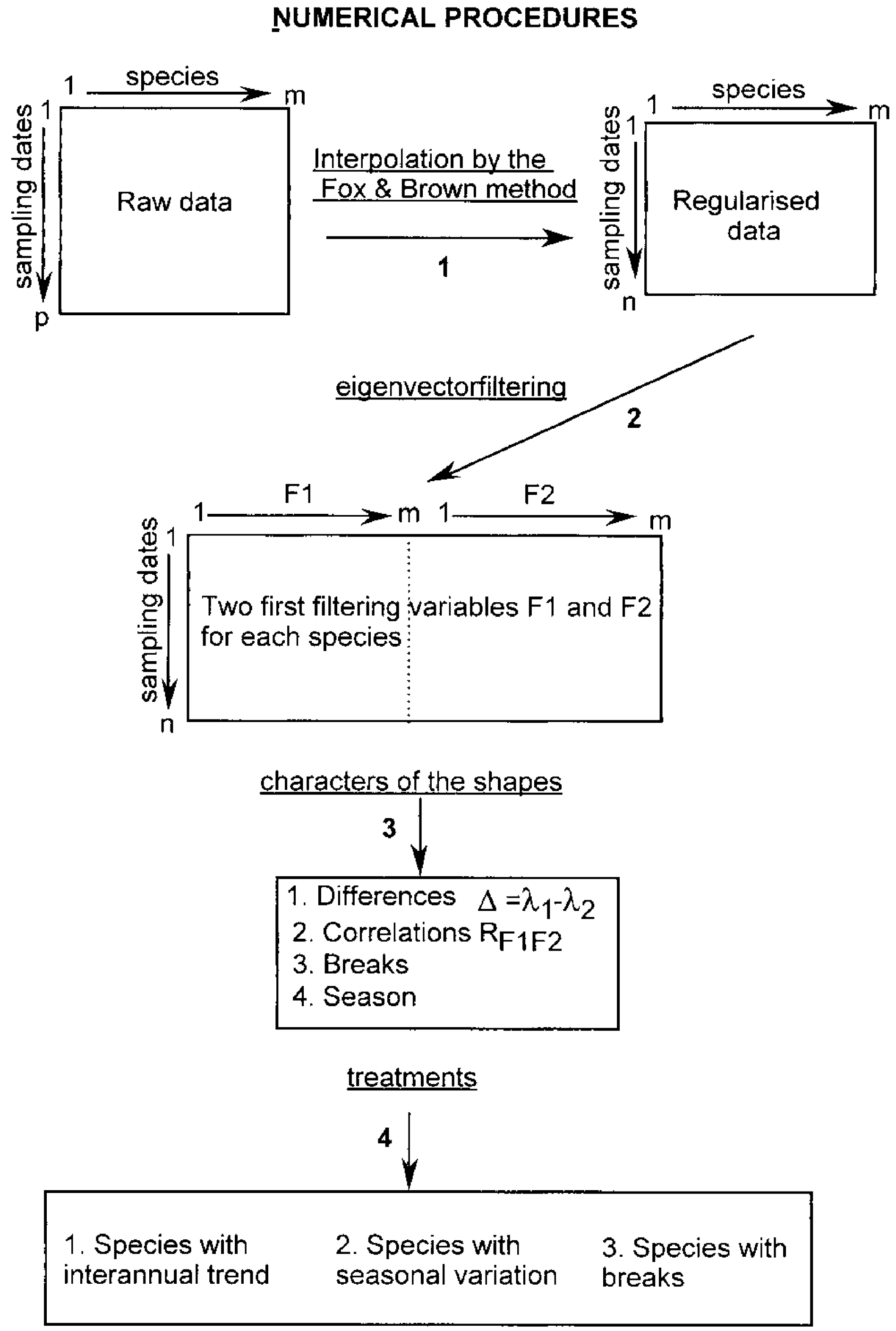

Figure 1. Flowchart summary of the numerical procedures used on each biological data set.

the F values to be correlated. This property is more realistic than a rough independency, because the seasonal variation in the data curves is correlated with average trend values.

Step 3. The interpretation of filtering variables is made using times series simulations (Ibanez & Etienne 1992), and by empirical treatment of benthic data (Souprayen et al. 1991; Ibanez et al. 1993a; Fromentin et al. 1997). In our example (four collections per year), the best choice for the order m of the covariance matrix is four (Ibanez & Etienne 1992). By using this, F1 corresponds to the inter-annual trend and F2 to the seasonal variation (if it exists).

The difference Δ between the corresponding latent roots λ_1 and λ_2 is indicative of the relative importance of inter-annual and seasonal variations. Three cases are recognised:

1. If Δ is large, only year to year variation is important.

2. If Δ is very low and the correlation between F1 and F2 (R_{F1F2}) is high, only seasonal variation is present (Ibanez & Etienne 1992).

3. If Δ takes on an intermediate value, an inter-annual trend exists but an additional test is necessary to determine whether seasonal variation (S) is present. This is done using ANOVA, followed by a regression between F2 and a cycle of four observations.

Another characteristic of the temporal series is the presence of breaks (B): some species are rare or absent over several years. An empirical method can be used to detect breaks (Ibanez & Fromentin 1997), in which a threshold is fixed as:

$$T= [\mathrm{MIN}\ \log(F1) + \mathrm{MAX}\ \log(F1)]/2$$

The degree of intermittence of a series will be the maximum number (log values) of successive observation below T.

In order to define a limited group of species with similar shapes, only two states were considered. The main discontinuity of the ranked distribution for Δ and B, for all species, is useful in finding the limit between states. Test values (at a significance probability of 5%) were used for the correlation R and seasonal variation S. Given the strong dependence between successive observations, rigorous tests with random permutations could have been performed. However, we only obtained rough estimates of an index without further confirmation.

Step 4. Classify species into groups of similar shape. Three data treatments were used:

(1) Analysis of species with dominant pluri-annual trends. The simple use of cumulative functions of F1 is presented. The mean of each F1 was removed for each observation, and a new series was cumulated giving a cumulated histogram. A positive slope of the curve indicates that the local mean is above the general mean, a negative the inverse situation. This method allows recognition of the local trend of the series. Curves identifying the changes were compared to those for environmental variables (Ibanez et al. 1993b).

(2) Analysis of species showing annual trends and/or seasonal variation. These trends are indicated by variable F2. A simulation was performed to characterise the season of each of species. Eight series of ones and zeros, with the size of the observed series, were simulated : the first with ones only in April, the second only in July, the third in October and the fourth in January. Then series with ones only in April and July, July and October, October and January, January and April, April and October, July and January were examined. A correlation between these binary simulated series and the values of F2 can be estimated by the formula (Grandjouan 1982):

$$R = \frac{P \times Q}{P+Q} \times \frac{\bar{X1} - \bar{X0}}{\sqrt{\sum_{i=1}^{n} (X_i - \bar{X})^2}}$$

where P and Q represent respectively the frequencies of the values 1 and 0 of the binary variable, X the values of the quantitative variable, and the mean of X when (simultaneously) the binary variable is 1 or 0.

In order to test the fit between the binary seasonal model and F2, 2000 correlations were simulated by reordering the values of F2. The percentage of simulated correlations greater than the observed value indicates the probability of rejecting the null hypothesis of no similarity between series.

(3) Analysis of breaks in the series. These indicate strong changes in abundance, which may reflect the effects of competition, the impact of environmental variables, and human disturbances such as oil spills. The width and the length of the breaks give important information on temporal changes in the ecosystem. For example, species having breaks greater than 5 years are represented by F1, and the values within the periods of breaks change by its minimum value.

Results and discussion

Groups of Species with Similar Shapes

The values of characters Δ, R, S and B for the 48 species are summarized in Table 1. The ordered distribution for Δ shows a major discontinuity between the 24th and 25th species (Fig. 2a). The 25th to 48th species were thus considered to have significant long-term trends. For the correlation R_{F1F2}, only eight species showed significant deviation from random ($p < 0.05$). For the seasonality character S, the threshold for the percent of explained variable of the sinusoidal regression is 20.33. 21 species exceeded this value. For the index of intermittence B, the discontinuity t_1 in the ordered distribution appears between the 23th and the 24th species (Fig. 2b), which corresponds to a maximum gap of <3 years. Another discontinuity, t_2, is located between the 37th and 38th species. The last eleven species have gaps of up to 5 years.

Let Δ_0, R_0, S_0, B_0 be the first (low) states of the characters, and Δ_1, R_1, S_1, B_1 the second (high) states. Twelve species group combinations of these characters were found:

G1: Δ_0, R_0, S_0, B_0: Four species, including the polychaetes *Lanice conchilega* (22) and *Spio decoratus* (44: Fig. 3), and the amphipods *Megaluropus agilis* (28) and *Perioculodes longimanus* (39). These

Table 1. Values of the four characteristis of shape for the 48 species. Δ: difference between the first two eigenvalues λ_1 and λ_2 extracted from each eigenvector decomposition. R: correlations between the first two filtering variables F1 and F2. S: percent of variance explained by a sinusoidal function with a seasonal period. B: number of successive observations corresponding to poor abundance. Δ and R are multiplied by 1000.

Species	Δ	R	S	B
1. Abra alba	469.86	100.19	24.05	32
2. Abra prismatica	151.93	87.69	26.33	15
3. Ampelisca armoricana	439.62	269.6	8.37	36
4. Ampelisca brevicornis	206.1	60.13	27.61	13
5. Ampelisca sarsi	545.02	12.82	18.34	10
6. Ampelisca typica	39.93	88.02	30.85	13
7. Ampharete acutifrons	169.58	29.52	31.63	7
8. Aricidea cerrutii	542.04	73.39	10.41	17
9. Aricidea fragilis	152.06	7.12	10.85	23
10. Aricidea minuta	232.76	119.99	18.44	17
11. Bathyporeia elegans	176.02	41.7	29.93	10
12. Bathyporeia tenuipes	495.51	70.83	28.96	11
13. Chaetozone setosa	617.87	153.87	14.55	17
14. Euclymene oerstedii	515.43	7.94	37.42	19
15. Phaxas pellucidus	390.41	63.09	8.54	11
16. Diplocirrus glaucus	484.8	24.04	8.51	6
17. Eteone longa	190.02	63.91	26.06	6
18. Eumida sanguinea	59.32	32.63	27.02	11
19. Exogone hebes	129.73	125.31	21.36	26
20. Heterocirrus alatus	168.23	419.11	4.52	44
21. Hyalinoecia bilineata	632.04	45.99	11.82	29
22. Lanice conchilega	226.5	175.5	6.7	9
23. Clymenura clypeata	702.01	8.09	13.71	8
24. Leucothoë incisa	64.61	158.66	27.39	8
25. Magelona alleni	612.81	54.6	21.3	18
26. Magelona filiformis	313.13	190.88	7.19	34
27. Marphysa bellii	77.59	96.58	22.8	17
28. Megaluropis agilis	78.98	225.97	15.09	9
29. Myriochele oculata	158.67	167.35	9.87	13
30. Nephtys hombergii	303.23	113.25	21.97	9
31. Notomastus latericeus	26.16	875.91	25.52	2
32. Nucula hanleyi	482.12	7.15	15.74	19
33. Nucula turgida	471.24	4.03	18.61	19
34. Odontosyllis gibba	114.6	85.68	34.97	9
35. Ophiura albida	207.18	27.43	24.35	11
36. Owenia fusiformis	343.22	78.12	10.85	7
37. Paradoneis armata	482.8	23.4	19.6	46
38. Pariambus typicus	32.81	315.7	20.89	7
39. Perioculodes longimanus	54.71	134.49	13.8	10
40. Phyllodoce groenlandica	19.22	822.25	10.16	2
41. Polydora flava	398.69	272.9	5.16	14
42. Polydora pulchra	55.88	404.27	8.5	19
43. Scoloplos armiger	546.73	123.29	15.86	34
44. Spio decoratus	183.21	211.94	19.75	11
45. Spiophanes bombyx	867.17	7.11	8.49	26
46. Thyasira flexuosa	624.54	306.88	3.98	28
47. Urothoë pulchella	655.79	26.7	26.34	10
48. Venus ovata	521.64	97.57	37	10

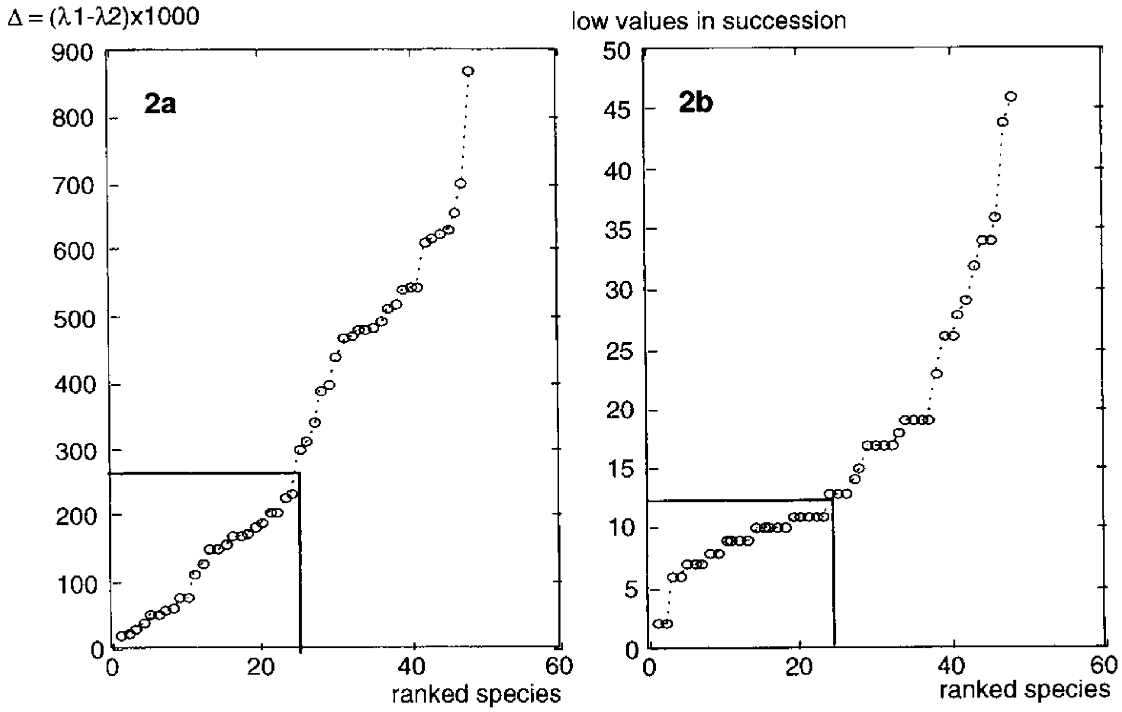

Figure 2. (a) Ranked differences Δ between the two first latent roots λ_1 and λ_2 of the auto-covariance matrix of the descriptors. The order of the auto-covariance matrix is four, since 4 shifted series were considered. A threshold between the 24th and 25th species is marked by a strong change of the slope of the curve, separating species with a low long-term trend (1 to 24) from those with important year to year variation (25 to 48). Species names correspsonding to these numbers are given in the text. (b) Ranked lengths of the gaps of the series of densities. A threshold t_1 between species 23 and 24, associated with a strong change of the slope of the curve, was retained. This separates 23 species with a maximum gap less than 12 observations (3 years) from the remaining rarer ones. Analyses were performed on species having a gap up to 20 observations (5 years). A strong change of the curve, t_2, (between the 37 and 38th species) corresponds to a 5-years break.

are well-represented species with irregular temporal shapes, characterised by local trends but no strong long-term or seasonal trends.

G2: Δ_0, R_0, S_0, B_1: Three species, including the polychaetes *Aricidea fragilis* (9: Fig. 3), *Aricidea minuta* (10) and *Myriochele oculata* (29). Temporal series are similar to G1, but breaks are present.

G3: Δ_0, R_0, S_1, B_0: Seven species, including the polychaetes *Ampharete acutifrons* (7), *Eteone longa* (17), *Eumida sanguinea* (18: Fig. 3), and *Odontosyllis gibba* (34), the amphipods *Bathyporeia elegans* (11) and *Leucothoe incisa* (24), and the ophiurid *Ophiura albida* (35). These species display seasonal variation, but inter-annual trends are not important.

G4: Δ_0, R_0, S_1, B_1: Five species, including the polychaetes *Exogone hebes* (19) and *Marphysa bellii* (27), the amphipods *Ampelisca brevicornis* (4) and *Ampelisca typica* (6), and the bivalve *Abra prismatica* (2: Fig. 3). These species show strong breaks in the temporal series, but show annual cycles when present.

G5: Δ_0, R_1, S_0, B_0: One species, the polychaete *Phyllodoce groenlandica* (40: Fig. 3). This species has similar F1 and F2 values and displays irregular changes over time.

G6: Δ_0, R_1, S_0, B_1: Two species, including the polychaetes *Heterocirrus alatus* (20: Fig. 3) and *Polydora pulchra* (42). These species shows extremely erratic changes in abundance over time, and had identical F1 and F2 values.

G7: Δ_0, R_1, S_1, B_0: Two species, the polychaete *Notomastus latericeus* (31: Fig. 3) and the amphipod *Pariambus typicus* (38). These two species show strong seasonal variation.

G8: Δ_1, R_0, S_0, B_0: Five species, including the polychaetes *Diplocirrus glaucus* (16), *Clymenura clypeata* (23), and *Owenia fusiformis* (36),the amphipod *Ampelisca sarsi* (5: Fig. 3), and the bivalve *Phaxas pellucidus* (15). These species show strong inter-annual trends but no seasonal changes (F2 having only irregular local variations).

G9: Δ_1, R_0, S_0, B_1: Nine species, including the polychaetes *Aricidea cerrutii* (8), *Chaetozone setosa* (13), *Hyalinoecia bilineata* (21), *Magelona filiformis* (26), *Paradoneis armata* (37: Fig. 3), *Scoloplos ar-*

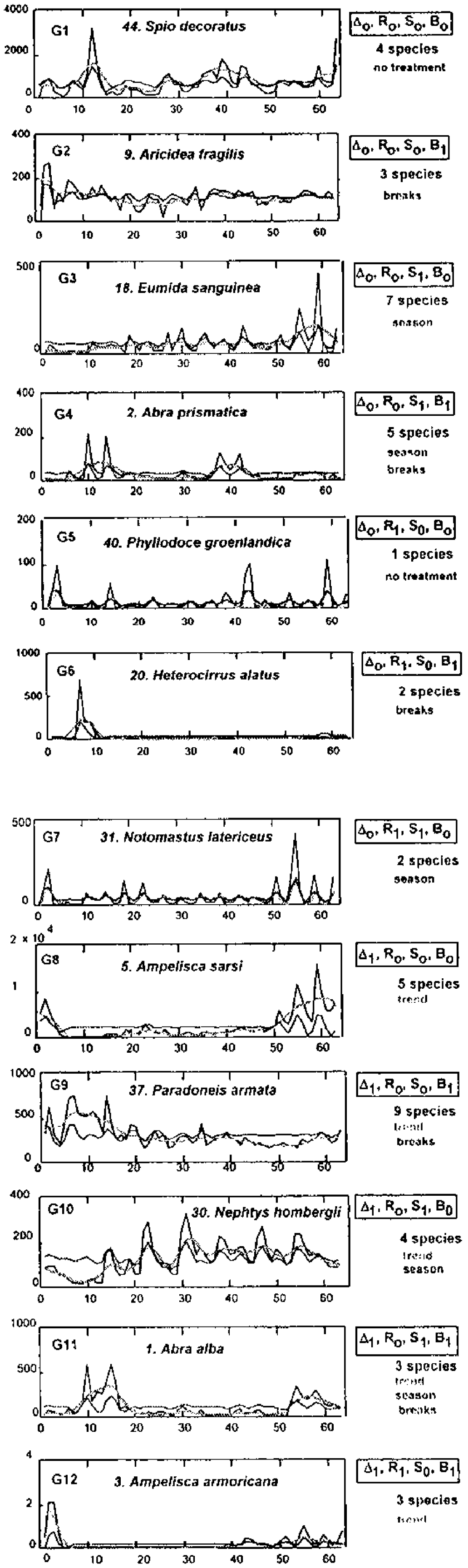

Figure 3. Representative series for species in each of the 12 selected 'characteristic shape' groups. Observed densities are represented by a thin line, the filtering variable by a thick gray line, and F2 by a thick black line. States of the shapes characters are also shown: D, difference between the eigenvalues λ_1 and λ_2; R, correlation between F1 and F2; S, fit to the seasonal variation; B, length of the maximum break in the series. 0 and 1 associated to these characters correspond to a partition into two states, low and high. The number of species within each group, and the main distinctive properties of the graphs, are also shown.

miger (43), *Spiophanes bombyx* (45) and the bivalves *Nucula hanleyi* (32) and *Nucula turgida* (33). These species are characterised by a strong general temporal trend and low abundances. For these species, F2 was not interpretable.

G10: Δ_1, R_0, S_1, B_0: Four species, including the amphipods *Bathyporeia tenuipes* (12) and *Urothoe pulchella* (47), the polychaete *Nephtys hombergii* (30: Fig. 3), and the bivalve *Timoclea ovata* (48). These species display both inter-annual (F1) and seasonal (F2) changes.

G11: Δ_1, R_0, S_1, B_1: Three species, including the bivalve *Abra alba* (1: Fig. 3), and the polychaetes *Euclymene oerstedii* (14) and *Magelona alleni* (25). These species show high variability at both the inter-annual and seasonal scales, but in addition have large breaks.

G12: Δ_1, R_1, S_0, B_1: Three species, including the amphipod *Ampelisca armoricana* (3: Fig. 3), the polychaete *Polydora flava* (41), and the bivalve *Thyasira flexuosa* (46). These species show erratic changes in abundance over time, but with a long-term trend corresponding to large periods of rare abundance. F2 was not interpretable.

Of the 16 possible combinations, only 12 had been identified. No species showed the four last possibilities:

(i) Δ_0, R_1, S_1, B_1: This is a series with seasonal changes, breaks, and low F1 that is correlated with F2. This corresponds to an unlikely series, in which F1 follows both seasonal variation and breaks.

(ii) Δ_1, R_1, S_0, B_0: In such a series, F1 and F2 are correlated and there is an absence of seasonal change. A series cannot have F1 and F2 describing the sole long-term trend.

(iii) Δ_1, R_1, S_1, B_0: This corresponds to a high F1 correlated with F2, and seasonal change. In this case both the long-term and seasonal trends must be represented by F1 and F2, an impossible case.

(iv) Δ_1, R_1, S_1, B_1: This corresponds to a high F1 that is correlated with F2, seasonal changes, and presence of breaks. This is unexpected, since F1 and F2 would have to represent both the seasonal trend and breaks.

Table 2. Correlation between the filtering variables F2, for species presenting seasonal variation, with binary models of annual cycles. Tests obtained with 2000 random permutations of the vector of species abundance. * and ** represent the 5% and 1% level of statistical signification, only for indicative information.

Species	Jan	July	Oct	Ju-Oc	Oc-Ja	Ja-Ap
12. Bathyporeia tenuipes	.27*					
38. Pariambus typicus		.41**				
18. Eumida sanguinea			.53**			
31. Notomastus latericeus			.50**			
19. Exogone hebes			.35**			
24. Leucothoe incisa			.51**			
1. Abra alba				.27*		
14. Euclymene oerstedii				.65**		
30. Nephtys hombergii				.51**		
35. Ophiura albida				.48**		
2. Abra prismatica				.65**		
4. Ampelisca brevicornis				.50**		
6. Ampelisca typica				.56**		
27. Marphysa bellii				.44**		
48. Timoclea ovata					.57**	
7. Ampharete acutifrons					.56**	
17. Eteone longa					.46**	
11. Bathyporeia elegans						.61**
34. Odontosyllis gibba						.67**
47. Urothoe pulchella						.36**

Species with Seasonal Change

Seasonal changes are identified by the filtering variable F2. Of the twelve groups, five showed significant seasonal variations: G3, G4, G7, G10 and G11, for a total of 21 species. Results of the simulations of year cycles are presented in Table 2.

Only *Magelona alleni* (G11) had no significant correlation: the long absence of this polychaete at the beginning of the 1980's was probably the reason for this lack of correlation. In the same group G11, *Abra alba* showed a probability of only 5%, as did *Bathyporeia tenuipes* (G10). The shape of F2 for both species was especially irregular. The 18 remaining species showed a level of probability less than 1%.

Three main seasonal changes were identified:

1. Species showing maximal abundance in winter (January), or in winter and spring (January-April). Included here are three amphipods species, *Bathyporeia elegans*, *Bathyporeia tenuipes* and *Urothoe pulchella*, which are known to migrate from the intertidal zone to the subtidal zone at the end of autumn and return to the intertidal zone in spring. Also included here is the polychaete *Odontosyllis gibba*, which has an autumnal recruitment (Dauvin 1984, 1987, 1989).

2. Species showing maximal abundance in summer or autumn. Thirteen species showing high summer recruitment fall into this category. In temperate waters such as the Bay of Morlaix, seasonal changes in environmental factors such as sea temperature and light occur, with the result that period of reproduction of macrobenthic species occur during the most favourable season (Dauvin, 1989).

3. Species with maximal abundance towards the end of the year. This group includes three species. *Eteone longa* has late recruitment at the end of summer, while *Ampharete acutifrons* and *Timoclea ovata* have prolonged periods as temporary meiobenthos, are small in size and grow slowly (Dauvin 1989).

Species with Inter-Annual Trend

Three groups showed evidence of inter-annual variation: G8, G9, G10, G11, G12, which together include 24 species. Eight species showed significant periods (> 5 years) of disappearance or low abundance: *Abra alba*, *Ampelisca armoricana*, *Hyalinoecia bilineata*, *Magelona filiformis*,

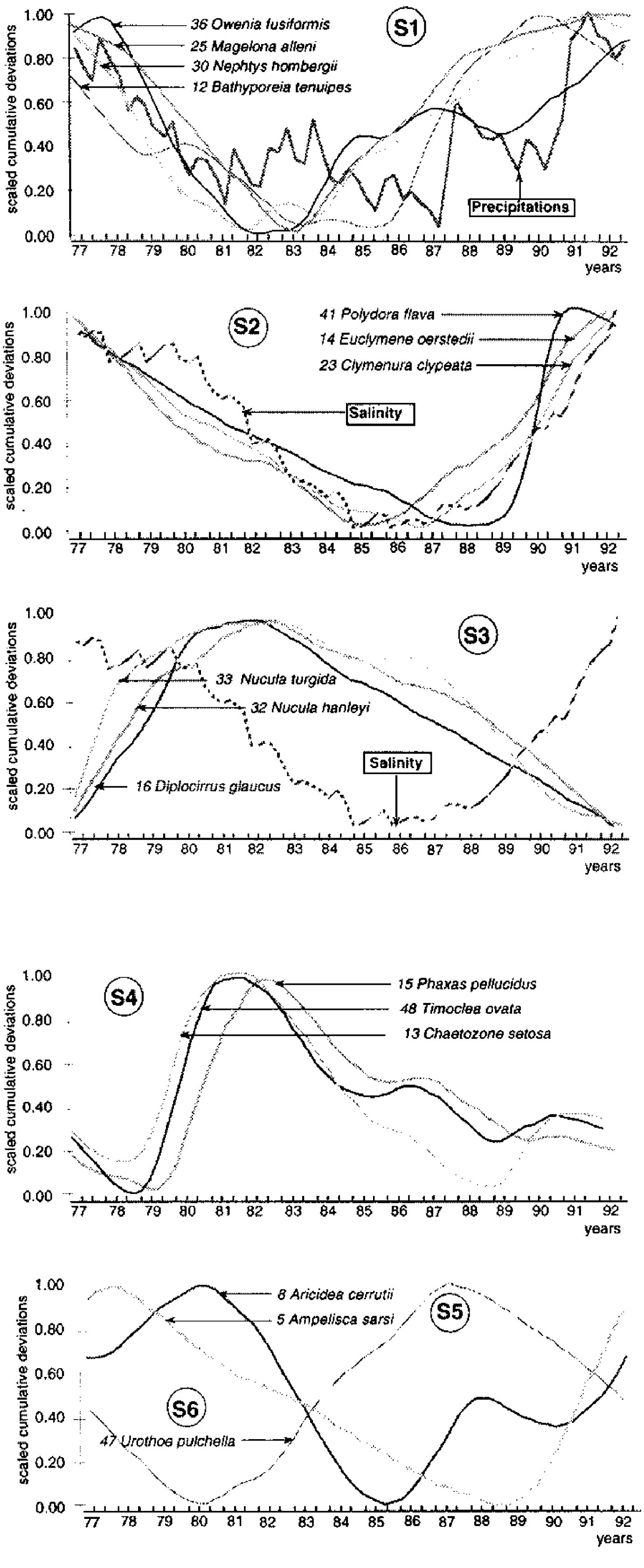

Figure 4. Cumulative sums of the filtering variable F1 for the six groups of species showing the greatest year to year variation. Cumulative sums for precipitation and salinity are represented with groups S1, S2 and S3. An increasing slope of the curve indicates values up to the mean of the data, while decreasing values correspond to values below the mean. For a clear visualisation, ordinates are scaled for all the curves to a minimum of zero and a maximum of 1. This scaling does not change the values of the correlation coefficient.

Table 3. Correlation between the cumulative sums of the filtering variable F1, for species with long term trend, with the cumulative sums of environmental variables. Given the strong auto-correlation of the cumulative sums, any tests can be performed.

Species	Pressure	Air T°	Precipitations	Water T°	Salinity
S1. *Bathyporeia tenuipes* (12)	0.17	-0.01	0.54	0.34	0.32
S1. *Magelona alleni* (25)	-0.13	0.02	0.61	0.38	0.39
S1. *Nephtys hombergii* (30)	-0.05	0.10	0.63	0.32	0.22
S1. *Owenia fusiformis* (36)	0.10	0.16	**0.65**	0.40	0.40
S2. *Euclymene oerstedii* (14)	0.42	0.29	0.86	0.76	0.88
S2. *Clymenura clypeata* (23)	0.50	0.33	0.80	0.81	**0.95**
S2. *Polydora flava* (41)	0.59	0.41	0.75	0.79	0.88
S3. *Diplocirrus glaucus* (16)	-0.04	-0.14	-0.69	-0.39	-0.74
S3. *Nucula hanleyi* (32)	-0.16	-0.20	-0.76	-0.50	-0.68
S3. *Nucula turgida* (33)	-0.12	-0.19	-0.67	-0.42	**-0.80**
S4. *Chaetozone setosa* (13)	0.40	0.10	-0.31	-0.03	0.07
S4. *Phaxas pellucidus* (15)	0.05	-0.09	-0.55	-0.54	**-0.60**
S4. *Timoclea ovata* (48)	0.16	-0.07	-0.49	-0.36	-0.31
S5. *Ampelisca sarsi* (5)	0.60	0.31	0.52	0.65	**0.87**
S5. *Aricidea cerrutii* (8)	0.20	0.00	0.30	0.49	0.79
S6. *Urothoë pulchella* (47)	-0.46	-0.20	-0.11	-0.48	**-0.69**

Paradoneis armata, Scoloplos armiger, Spiophanes bombyx and *Thyasira flexuosa*. Their changes were therefore analysed as species with breaks.

Figure 4 shows The cumulated function (Ibanez et al. 1993b) for the first filtering variable F1 of the 16 remaining species illustrates a remarkable succession of species (Fig. 4). Correlations between the trends F1 and the cumulative sums of environmental factors, atmospheric pressure, air temperature, precipitation, water temperature and salinity are summarised in Table 3. No statistical test is proposed, since there is strong autocorrelation present in the cumulative sums. Even random simulations with permutations of the values of one series will not give a correct estimation: the experimental correlation will be mostly higher than the simulated ones, since auto-correlation is lower in the latter. Six groups were detected:

(S1) Four species (*Bathyporeia tenuipes, Magelona alleni, Nephtys hombergii, Owenia fusiformis*) showed a decreasing trend until the middle of the 1980s. Changes in abundance were strongly correlated (between r = 0.65 for *O. fusiformis* and r = 0.54 for *B. tenuipes*) with changes in precipitation, as represented by a cumulative sum (Ibanez & Fromentin 1997).

(S2) Three species (*Euclymene oerstedii, Clymenura clypeata, Polydora flava*) declined in abundance until 1985, and then increased after 1989. This trend is highly correlated with changes of salinity (represented by a cumulative sum), from r = 0.95 for *C. clypeata* to r = 0.87 for *A. sarsi*.

(S3) Three species (*Diplocirrus glaucus, Nucula hanleyi, Nucula turgida*) were characterised by low abundance in 1977, followed by a peak in abundance in the early 1980s and declining abundance thereafter. This trend is negatively correlated with the salinity (represented by the cumulative sum): r = -0.80 for *N. turgida*, and r = -0.74 for *D. glaucus*).

(S4) Three species (*Chaetozone setosa, Phaxas pellucidus, Timoclea ovata*) decreased in abundance until 1979 (two years after the 'Amoco Cadiz' oil spill), increased from 1979 to peak in the early 1980s, and then declined again. A small increase is apparent at the end of the series.

(S5) *Ampelisca sarsi* and *Aricidea cerrutii* showed unique responses. *A. sarsi* behaved similarly to the second group (2), but increased in abundance in the first few years of the survey (correlation with changes in salinity r = 0.79). *A. cerrutii* also increased in abundance during the first few years, and declined from 1981 to 1986. It increased again towards the end of the series, with a weak decline in 1989 and 1990. This correlated highly (r = 0.87) with salinity (represented by the cumulative sum).

(S6) *Urothoe pulchella* showed a particular and relatively periodic behaviour of approximately seven years: it decreased until 1981, increasing until 1988, and decreased again after 1988.

These species trends should be explained by natural environmental factors: e.g. sea temperature, salinity, precipitation. They varied within the season, but also showed long-term trend within climatic changes (Fromentin & Ibanez 1994). The Amoco Cadiz oil spill was an important factor for explaining the trends of sensitive species like amphipods and especially the dominant species *Ampelisca* which was destroyed by hydrocarbons. The pollution off the Brittany coast also provoked an increase in sediment organic matter during the first years following the event (1979-1980; Dauvin 1984). There were also biotic factors which occurred in relation to the disappearance and the low recolonisation of the dominant *Ampelisca* species. There was a succession of abundant of species over time: i) Species which were abundant at the beginning and at the end of the series (*Nephtys hombergii, Euclymene oerstedii, Ampelisca sarsi,...*). Changes of *A. sarsi* were due to the pollution: high decrease of abundance in 1978, low recolonisation, and high increase of the population until 1990. ii) Species with low abundance at the beginning and at the end of the series, which showed maximum abundance from 1980 to 1982 in relation with the secondary effect of the oil spill (increasing of organic matter): *Chaetozone setosa*, iii) Species with low abundance at the beginning and at the end of the series, which showed a maximum of abundance from 1980 to 1985 (*Nucula hanleyi, N. turgida, Diplocirrus glaucus*). iv) *Urothoe pulchella* which showed changes opposite to those of *Ampelisca* species: low abundance when *Ampelisca* dominated, and maximum abundance when *Ampelisca* showed low abundance.

Species with Breaks

Eleven species displayed breaks of at least five years duration (Fig. 5): *Aricidea fragilis* (G2), *Exogone hebes* (G4), *Heterocirrus alatus* (G6), *Spiophanes bombyx* (G9), *Hyalinoecia bilineata* (G9), *Magelona filiformis* (G9), *Scoloplos armiger* (G9), *Paradoneis armata* (G9), *Abra alba* (G11), *Thyasira flexuosa* (G12), *Ampelisca armoricana* (G12).

The population of *A. armoricana* was locally extirpated in 1978 when the sediment had been polluted by the hydrocarbons from the Amoco Cadiz spill. The species was absent for ten years before recolonisation began in 1987. By 1992, colonisation was still incomplete (Dauvin et al. 1993a). *A. fragilis* showed a similar shape with some erratic peaks of abundance from 1979 to 1992, and an important

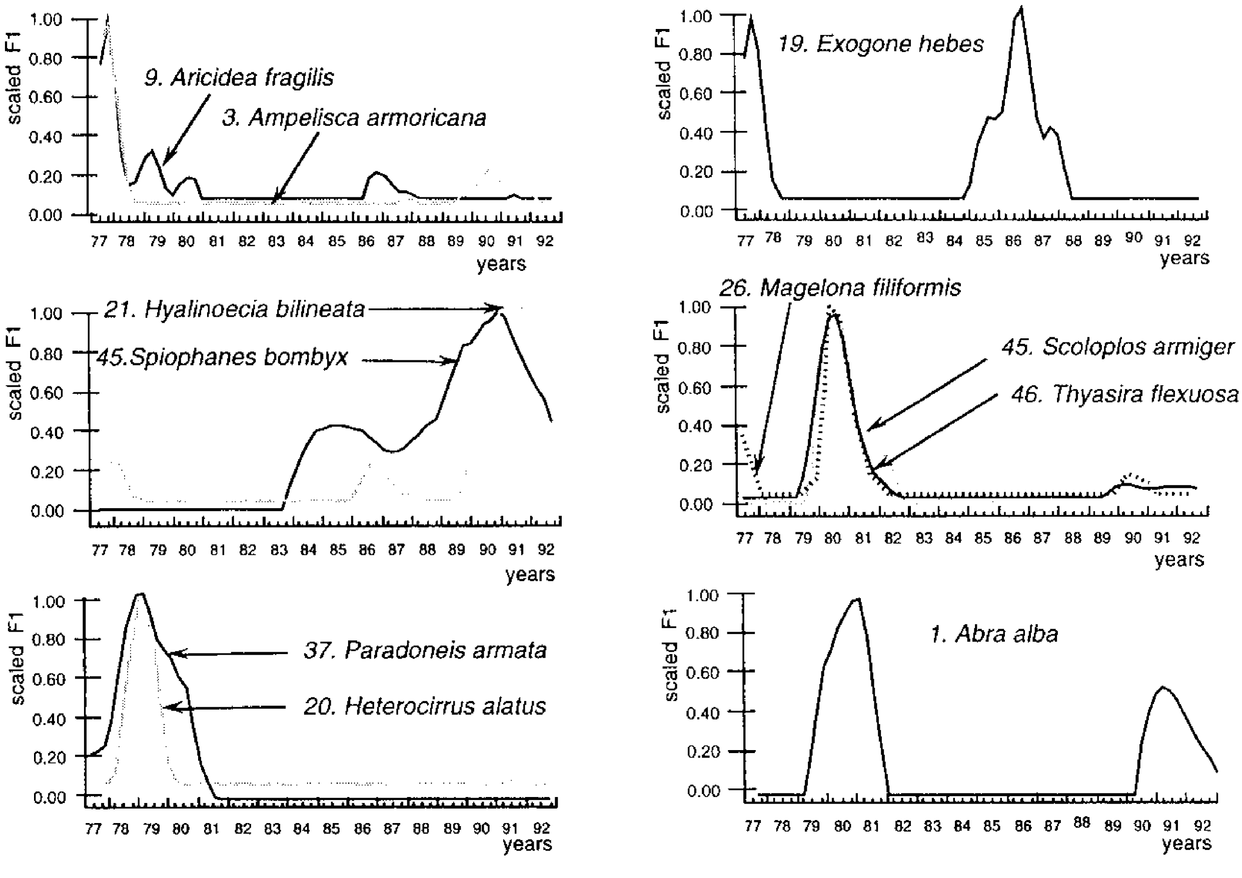

Figure 5. Variation of the filtering variable F1 for the eleven species with gaps up to 5 years. The periods of breaks were represented by the minimum of the data. The ordinate is rescaled (minimum 0, maximum 1).

decrease in 1978 that may be attributable to the oil spill. By contrast, the polychaetes *Paradoneis armata* and *Heterocirrus alatus* increased in abundance in 1978-79 following the spill, then declined and showed very low abundance along the rest of the series (Dauvin 1984). The polychaetes *H. bilineata* and *S. bombyx* appeared in the community only at the end of the series. *S. bombyx* colonisation began in 1984, and *H. bilineata* in during the 1990's (low peak of abundance in 1986-1987, and a rapid increase in 1990). Five species (*E. hebes, H. alatus, M. filiformis, S. armiger, A. alba*, and *T. flexuosa*) showed peaks of abundance with an interval of ten-eleven years : in 1977-1978 and 1986-1987 for *E. hebes*, and in 1980-1981 and 1990-1991 for the four other species. In the case of *A. alba*, such a ten-year cycle of abundance was also observed in the Bay of Seine, but northerly in the southern Bay of the North Sea in the Gravelines area (Dauvin et al. 1993b) a cycle of 7-8 years (correlated with temperature) was observed. The two peaks of abundance were similar for *E. hebes* and *A. alba*, but for *Scoloplos armiger, Magelona filiformis* and *Thyasira flexuosa*, the first peak that occurred just after the Amoco Cadiz spill was greater than the second in 1990. These three species were probably stimulated by the increase in organic matter following the spill.

Discussion

Ambiguity in Interpretation of Benthic Series using Classical Data Analysis Methods

Numerous data analysis methods have been proposed for the treatment of a collection of observations in time or space. Stochastic process analysis (Kendall 1976, Box & Jenkins 1976) and geostatistics (Matheron 1971, Wackernagel 1995) are focused on the type of dependence between successive observation. This fundamental property is not taken into account by statistical multivariate data analysis. Unfortunately, the estimation of characteristic latent stochastic processes (e.g. autoregressive, moving average), and estimating a stable model for the variogram, are problematic when analyzing heterogeneous and short benthic data series.

Initially, numerical analyses such as classification and ordination seemed to be more adapted to the interpretation of benthic time series: (i) Classifications with different distances (Lance & Williams 1967) with the constraint of temporal connectiveness (Legendre et al. 1985); (ii) Global approach in species or observation spaces, i.e. simple ordination methods such as principal component analysis and correspondence analysis (Saporta 1992); (iii) Multivariate analysis at the global and local scales, i.e. structures considering nearer observations (Dolédec & Chessel 1994); (iv) Ordinations in biological spaces with physical and/or spatio-temporal information as covariates: redundancy analysis and canonical correspondence analysis (Borcard et al. 1992, ter Braak 1986).

These techniques involve multivariate analysis models: decomposition of the variance, orthogonal functions, linear combinations of attributes, partial correlation, metric or semi-metric distances. The chief property of such analyses is that they summarise the data: clustering of sites by time and species. Scaling techniques (ordinations) reduce the dimensionality of the data. The results are represented in a mathematical space that may be difficult to interpret: axes are combinations of variables, resulting in simultaneous projection of variables of different types (e.g. species and environmental factors) or of observations and descriptors. It may be difficult to find a clear ecological description of this information. In order to eliminate the redundancy in multivariate time series, Clarke & Warwick (1998) proposed finding the descriptors that best reproduces an MDS ordination of the samples based on the entire data set: an example is presented in this paper. This method allows consideration of a few biological categories that best represents functional groups of species. Nevertheless, times series characteristics (inter-annual and seasonal variations), and improvement of the significance of the ordination axes, remain problematic.

Classical statistical parameters such as the mean and variance are inadequate descriptors of series marked by large gaps (Fromentin et al. 1993). Since these parameters are usually performed over all the species, ambiguous situations might occur: for example, high correlation can occur between a species with an increasing monotonic trend and a rare species with only a single strong peak at the end of the series. Thus, classical classifications will be spurious with respect to the true ecological models of temporal variation in species. Also, without prior detection of the patterns, the ordination synthesis will be a mixture of species with different ecological behaviours. Two species may be very far apart in ordination space, not only because their trend is opposite, but possibly because their shape of variation is different. On the other hand, two species could be very close in ordination space if they have simultaneous large gaps, even if their high values are never concomitant. Thus, it seems more adequate to make a preliminary classification based on the shape of the curve, as is done by the TSS method. We propose that the choice of interpretative treatment should be made after the nature of the species response is known.

Pattern Recognition as a Tool for Time Series Interpretation

Before applying TSS, a few examples of analysing shapes of series were tested. In a first approach, pattern recognition was performed in order to compare continuous plankton transect data (Pigeau 1986, Ibanez 1990). In this approach, a time series is viewed like a 'sentence'. At each point, a vector of quantitative or qualitative attributes can be introduced (the words of the sentences, corresponding to the precise description of local shape of the curve). An inferential syntactic algorithm allows comparison of sentences, e.g. to estimate the difference between the underlying patterns. This procedure is much more precise than the classical metrics of (classical) distance or similarity, because supplementary information is added to the signal prior to comparison.

Consideration of the shape of benthic series had appeared during the treatment of benthic European data (COST 647 program of the European Commission, 1988-1991). An obstacle was the comparison of series with unequal sample numbers and dates. In order to decide if the differences were significant at a certain probability level, a test of difference between the shapes of the series was performed, starting from the equations of the polygonal regression (De Carolis 1976, Ibanez 1991). Each series, fitted by a polygonal line, was defined by a distribution of coefficients. The distributions of such coefficients were then compared using various non-parametric tests (Siegel 1956). Two series were deemed to be homogeneous if none of these tests rejected the null hypothesis ($p < 0.05$).

As with classical multivariate analysis, TSS aims to summarise information. The utility of TSS lies in finding a simple classification of the data prior to multivariate analysis, since the shapes of density fluctuations are meaningful for the ecologist and questions asked will be different in each case:

(i) For very erratic species with large gaps, consideration is given to sampling effort variability, or in the case of occasional species, invasion from a contiguous area.

(ii) Series with a gap may correspond to an opportunistic species, a stressed environment, a succession of latent and trend periods (suggesting a dynamic interaction of opportunistic species), or the impact of an anthropogenic event. Models describing punctual events such as 'superposed epoch analysis' (Prager & Hoenig 1989) should be performed.

(iii) A monotonic trend in species abundance reveals the establishment of continuous favourable or unfavourable conditions, and no regular seasonal recruitment. A comparison with climatic changes is obvious. Such species may be sensitive to macro-scale physical phenomena (warming, atmospheric pressure changes). Modelling may be appropriate.

(iv) Species may display seasonal variation, corresponding to a regulation of factors with a constant k-strategy of reproduction. Appropriate questions include: why does recruitment occur one or two times per year, and why does it occur at a given season? Trophic competition factors, local variability of environment have to be considered.

(v) When general and seasonal trends are present, stability but sensitivity to one or more factors is suggested. There may be an alternation in r and k strategies.

An advantage of TSS is the use of the EVF decomposition, as this systematically detects the main movements of the series even if they are very irregular (see Fig. 3). The decomposition does not lead to orthogonal components, as F1 and F2 may be correlated. The used filtering corresponds to a classical multiplicative model of decomposition: $Z_t = T_t \cdot S_t \cdot R_t$, where Z_t is the original series, T_t the trend, S_t seasonal movement, and R_t residuals.

In fact, a series (usually) shows that seasonal variation occurs, but with a large variance during periods where the trend follows a steep gradient. So EVF must be applied to the raw data, without transformation. F1 and F2 correspond to smoothed series. This smoothing reinforces the homogeneity more than does a log-transformation. Since further treatments utilize F1 and F2, there is no problem of stabilisation of the variances. By simulation, it was demonstrated that PCA ordination on the F1 extracted from raw times series increases the similarities between descriptors. Also, the time contiguity of the observations is respected in the factorial planes (Ibanez 1991). The remaining part of the signal (breaks, residuals obtained by the difference between the series and the sum of F1 + F2, unusual peaks), has to be specifically treated; e.g. test of noise, periodicity detection, and interpretation of anomalies.

The variance of the filtering variables F1 and F2 allows estimation of the degree of representativity of the series, not only on the basis of amplitude of variation, but also by their ecological kinetics. Only the choice of the number of shifted series, which is necessary for the filtering algorithm, may be arbitrary. However, the lag corresponding to a zero auto-correlation function gives a precise indication for this choice (Ibanez & Etienne 1992; Ibanez et al. 1993a).

The presented definition of 'groups' could be improved using rigorous agglomerative classification algorithms. However, the statistical 'truth' may be too detailed (e.g. detection of many 'significant' groups of shapes) since the shapes form a continuum. The aim of TSS is only to sort the species prior to other treatments.

In this study, the proposed treatments following TSS were not particularly sophisticated (e.g. correlation, cumulated histogram). The aim was not to 'rediscover' results already published, and no representations were made in any mathematical space. However, the results are meaningful enough to characterise the communities sensitive to large-scale trends of climate and hydrology, to recognise the main types of seasonal variation, and to detect the specific responses of the organisms to the pollution oil spill of 1978.

Conclusion

In benthic ecology, it is always a handicap to interpret the temporal changes of multiannual series of species, since only a few species quantitatively dominate the community. Changes are often described from temporal evolution of the dominant species, and never for species with low abundance. Such an approach is very useful for the rapid examination of long-term changes of dominant species in the community, e.g. identification of periods of presence or absence of species, and periods of maximum abundance. By contrast, the TSS method permits to comparison of temporal trends between species having very different abundances. For the Pierre Noire community, four main trends could be identified:

1. Species that disappeared immediately following the 1978 Amoco Cadiz spill, and recolonised the com-

munity at the end of the observation period, e.g. *Ampelisca* species.

2. Species that proliferated immediately following the 1978 Amoco Cadiz spill, e.g. *Heterocirrus alatus*, indicating a positive response to increased organic matter.

3. Species that showed separated periods of abundance, e.g. *Abra alba*.

4. Species that showed systematic fluctuations in abundance over time, e.g. *Paradoneis armata* and *Nephtys hombergii*. Some species showed regular recruitment throughout the study, and the method revealed for these species an annual cycle. Others showed very irregular erratic changes that were more difficult to interpret. Temporal changes for several species groups could be correlated with climatic variation (e.g. precipitation and salinity). In the case of the amphipod *Urothoe pulchella*, its trend could be the result of competition with amphipods of the genus *Ampelisca*.

For benthic studies, the TSS method should be useful in comparing trends of different communities along a large biogeographical gradient, as was done within the framework of the COST 647 coastal benthic ecology project (Souprayen et al. 1991). The number of benthic surveys has increased over the past few decades (Bachelet et al. 1997), making it absolutely necessary to promote new synthetic methods for comparing results of benthic changes at meso- or global scales.

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Literature cited

Bachelet, G., J. Castel, J.C. Dauvin, F. Ibanez, and P. Nival (editors) 1997. Long-term changes in marine Ecosystems. Oceanologica Acta 20: 1-329.

Borcard, D., P. Legendre and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Box, E.P. and G.M. Jenkins. 1976. Times series analysis: forecasting and control. Holden-Day, New York.

ter Braak, C.J.F. 1986. Canonical correspondence analysis a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Cabioch, L., J.C. Dauvin and F. Gentil. 1978 Preliminary observations on pollution of the sea bed and disturbance of sub-littoral communities in northern Brittany by oil from the 'Amoco Cadiz'. Mar. Poll. Bull. 9: 303-307.

Clarke, K.R. and R.H. Green. 1988. Statistical design and analysis for a 'biological effect' study. Mar. Ecol. Prog. Ser. 46: 213-226.

Clarke, K.R. and R.M. Warwick. 1998. Quantifying structural redundancy in ecological communities. Oecologia 113: 278-289.

Colebrook, J.M. 1978. Continuous plankton records: overwintering and annual fluctuations in the abundance of zooplankton. Mar. Biol. 84: 261-265.

Dauvin, J.C. 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz. Thèse de doctorat Etat, ès sciences, Université de Paris VI.

Dauvin, J.C. 1987. Evolution à long terme (1978-1986) des populations d'Amphipodes des sables fins de la Pierre Noire (Baie de Morlaix, Manche Occidentale) après la catastrophe de l'Amoco Cadiz. Mar Envir Res 21: 247-273.

Dauvin, J.C. 1989. La méiofaune temporaire d'un peuplement subtidal de sédiment fin de la Manche occidentale. Echantillonnnage, composition qualitative et quantitative. Ann. Inst. Océanogr. Paris 65: 37-55.

Dauvin, J.C. 1991. Effets à long terme de la pollution de l'Amoco Cadiz sur la production de deux peuplements subtidaux de sédiments fins de la baie de Morlaix (Manche Occidentale). In: Elliot, M. & J.P. Ducrotoy (eds.). Estuaries and coasts: spatial and temporal intercomparisons. Proc. 19th ECSA Symposium. Pages 349-358. Olsen & Olsen, Fredensborg, Denmark.

Dauvin, J.C. 1998. The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Mar. Poll. Bull. 36: 669-676.

Dauvin, J.C. and F. Ibanez. 1986. Variations à long terme (1977-1985) du peuplement des sables fins de la Pierre Noire (Baie de Morlaix, Manche Occidentale): analyse statistique de l'évolution structurale. Hydrobiologia 142: 171-186.

Dauvin, J.C., D. Bellan-Santini and G. Bellan. 1993a. Les genres *Ophelia* et *Ampelisca* de la région de Roscoff: exemples d'allotopie et de syntopie dans les communautés marines de substrat meuble. Cah. Biol. Mar. 34: 1-15.

Dauvin, J.C., JM. Dewarumez, B. Elkaim, D. Bernardo, J.M. Fromentin and F. Ibanez. 1993b. Cinétique de *Abra alba* (Mollusque-Bivalve) de 1977 à 1991 en Manche Mer du Nord. Relation avec les facteurs climatiques. Oceanologica Acta 16: 413-422.

De Carolis, L.V. 1976. Osservazioni statistiche sull'impliego di polygonali continue nelle analisi degli elettrocardiogrammi. Metron 34: 129-141.

Dolédec, S. and D. Chessel. 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. Freshwater Biol. 31: 277-294.

Field, J.G., K.R. Clarke and R.M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8: 37-52.

Fox, W.T. and J.A. Brown. 1965. The use of time-trend analysis for environmental interpretation of limestones. J. Geol. 73: 510-518.

Fromentin, J.M., F. Ibanez and P. Legendre. 1993. A phytosociological method for interpreting plankton data. Mar. Ecol. Progr. Ser. 93: 285-306.

Fromentin, J.M. and F. Ibanez. 1994. Year to year changes in meteorological features of the French coast area during the last half-century. Examples of two biological responses. Oceanologica Acta 17: 285-296.

Fromentin, J.M., F. Ibanez, J.C. Dauvin, J.M. Dewarumez and B. Elkaim. 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. J. Mar. Biol. Ass. U.K. 77: 287-310.

Grandjouan, G. 1982. Une méthode de comparaison statistique entre les répartitions des plantes et des climats. Thèse de doctorat Etat, ès sciences, Université Louis Pasteur, Strasbourg.

Ibanez, F. and J.C. Dauvin. 1988. Long-term changes in a muddy fine sand *Abra alba-Melinna palmata* community from the Western

English Chanel: multivariate time-series analysis. Mar. Ecol. Prog. Ser. 49: 65-81

Ibanez, F. 1990. Interprétation des structures spatio-temporelles en écologie planctonique. Actes du Colloque "Biomètrie et Océanographie". Société de Biomètrie, n6. Lille. Publié par l'IFREMER. 33-64.

Ibanez, F. 1991. Treatment of the data deriving from the COST 647 project on coastal benthic ecology: the within-site analysis. In: Keegan, B.F. (ed.). Space and time series data analysis in coastal benthic ecology. Pages 5-43. COST 647 Project on Coastal Benthic Ecology, Commission of the European Communities .

Ibanez, F. and M. Etienne. 1992. Le filtrage des séries chronologiques par l'analyse en composantes principales des processus (ACPP). J. Rech. Océanogr. 16: 66-72.

Ibanez, F., J.C. Dauvin and M. Etienne. 1993a. Comparaison des évolutions à long terme (1977-1990) de deux peuplements macrobenthiques de la baie de Morlaix (Manche occidentale). Relations avec les facteurs hydroclimatiques. J. Exp. Mar. Biol. Ecol. 169: 181-214.

Ibanez, F., J.M. Fromentin and J. Castel. 1993b. Application de la méthode des sommes cumulées à l'analyse des séries chronologiques. C. R. Acad. Sci. 316: 7545-748.

Ibanez, F. and J.M. Fromentin. 1997. Une typologie à partir de la forme des séries chronologiques (TFS). Oceanologica Acta 20:11-25.

Ibanez, F. and M. Etienne. 1998. PASSTEC: Programme d'Analyse des Series spatio-Temporelles en Ecologie Côtière. Manuel d'utilisation. Brochure éditée par l'Observatoire Océanologique de Villefranche sur Mer. 150 pages.

Kendall, M. 1976. Time-series. Griffin, London.

Lance, G.N. and W.T. Williams. 1967. A general theory of classificatory sorting strategies. I. hierarchical systems. Computer J. 9: 373-380.

Legendre, P., S. Dallot and L. Legendre. 1985. Succession of species within a community: chronological clustering, with applications to marine and freshwater zooplankton. Am. Nat. 125: 257-288.

Manté, C, J.C. Dauvin and J.P. Durbec. 1995. Relative abundance of species, a new method for time series analysis: application to long term changes of macrobenthic communities from the Bay of Morlaix. Mar. Ecol. Prog. Ser. 120: 243-250.

Manté, C., J.P. Durbec and J.C. Dauvin. 1997. Analyse de l'évolution temporelle de communautés macrobenthiques à partir des probabilités de présence des espèces. Oceanologica Acta 20: 71-79.

Matheron, G. 1971. La théorie des fonctions aléatoires intrinsèques généralisées. Publication n N-252, Centre de Géostatistique, Ecole des Mines de Paris, Fontainebleau.

Pearson, T.M. 1975. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. IV. Changes in the benthic fauna attribuable to organic enrichment. J. Exp. Mar. Biol. Ecol. 20: 1-41.

Pearson, T.H., J.S. Gray and P.J. Johannessen. 1983. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. 2. Data analyses. Mar. Ecol. Prog. Ser. 12: 237-255.

Pigeau, F. 1986. Interprétation de l'échantillonnage en continu par l'analyse syntaxique. Mémoire DEA, Univ. Paris VI.

Prager, M.E. and J.M. Hoenig. 1989. Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel . Trans. Am. Fish. Soc. 118: 608-618.

Saporta, G. 1990. Probabilités analyse des données et statistique. Editions Technip.. Paris.

Siegel, S. 1956. Non-parametric statistics. McGraw-Hill, New York.

Souprayen, J., J.C. Dauvin, F. Ibanez, E. Lopez-Jamar, B. O'Connor and T.H. Pearson. 1991. Long-term trends of macrobenthic communities: numerical analysis of four north-western European sites. In: Keegan, B.F. (ed.). Space and time series data analysis in coastal benthic ecology. Pages 265-438. COST 647 Project on Coastal Benthic Ecology, Commission of the European Communities.

Takens, F. 1981. Detecting strange attractors in turbulence. In: Warwick, R.M., D.A. Rand & L.S. Young (eds.). Dynamic systems and turbulence. Pages 366-381. Springer Verlag, New York.

Thiébaut, E., L. Cabioch, J.C. Dauvin, C. Retière and F. Gentil. 1997. Spatio-temporal stability of the *Abra alba - Pectinaria koreni* muddy fine sand community from the eastern part of the bay of Seine (English Channel). J. Mar. Biol. Ass. U.K. 77: 1165-1185.

Wackernagel, H. 1995. Multivariate geostatistics. Springer, Berlin.