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Fractal properties of spatial distribution of intertidal benthic communities

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Abstract We studied the spatial distribution of intertidal macrozoobenthos, microphytobenthos (diatom algae) and sediments at scales from decimeters to kilometers using an index of spatial homogeneity, D_I. Sediments were found to be randomly distributed, making up a mosaic of silty and sandy sites. On the contrary, the estimated spatial variability of macrofauna within all the scales up to 5500 m depended upon neither extent (total area covered) nor grain (finest spatial resolution) but only their ratio. We treat this as evidence of statistical self-similarity (fractal property) of the pattern. For diatoms, spatial heterogeneity of community structure was also self-similar in the range from 0.25 to 75 m (within a single bight). At larger scales, microalgae showed a combination of patchy structure with pronounced gradient along the shoreline from brackish-water to marine flora. Thus, fractal properties of both groups became manifested at scales corresponding to their mean body size. The ranges of fractal patterns were approximately equal to 10^3–10^5 if measured in body size units. We suggest that fractal-like spatial structures may be a general feature of communities, and speculate on the nature of such patterns.

Introduction

The interplay between pattern and scale is now recognized as a key problem in ecological studies (Turner et al. 1991; Holling 1992; Azovsky and Mokievsky 1996). One such phenomenon which has been intensively studied on a number of scales is spatial heterogeneity of communities (Kotliar and Wiens 1990; Milne 1991).

Spatial distributions are traditionally described in terms of such basic types as uniform, random (mosaic), patchy or clinal (gradient) (Greig-Smith 1983). Each of these patterns, however, describes an extreme case and fails to represent the real continuum of intermediate forms. Patchiness is the most common pattern recognized, and studies of spatial heterogeneity are often focussed on identification of patch size (or distance between patches) as the only *characteristic* scale of the structure (Galiano 1983; Turner et al. 1991). Thus, the actual complexity of patterns is reduced to several levels of patchiness. However, distinct patches can rarely be identified in real spatial patterns. Instead, complex and often uncertain patterns have been found at all scales studied (Findlay 1982; Palmer 1988). This situation is quite usual for marine benthos (Tufail et al. 1989; Ardisson et al. 1990; Fleeger et al. 1990; Saburova et al. 1995; Underwood and Chapman 1996). In general, the wider the range of scales considered, the more levels of patchiness are found in some hierarchical regularity (Korepanov 1991; O'Neill et al. 1991). This suggests more complicated spatial structures than implied in the ordinary patch model. Moreover, different species may perceive environmental variability at different scales and thus exhibit different patterns (Wiens and Milne 1989).

Lately the idea of scale-dependent hierarchy of biotic and environmental structures has undergone considerable inquiry (O'Neill et al. 1986; Palmer 1988; Kolasa and Pickett 1989; Holling 1992; Azovsky and Mokievsky 1996). The hierarchical concept of patchy patterns (Kotliar and Wiens 1990) implies several levels of nested patches. Only the smallest patches can be considered homogenous, and their boundaries clearly identified. Furthermore, changes in scale may lead to changes in the patterns observed. Both scale parame-

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ters, *extent* (the size of the study area) and *grain* (the finest spatial resolution), may affect an observed pattern in different ways (Milne 1991; Azovsky and Chertoprood 1997). If some properties of species distribution remain the same along many scales we can classify the pattern as *fractal* – a special case of spatial structure.

Fractals are, by definition, structures heterogeneous at all spatial scales, with a scale-dependent self-similarity (Mandelbrot 1983). At every scale of observation, new details are revealed, yet these details are reminiscent of details elsewhere in the fractal object or in the same part of the object, but on a different scale. In our case a fractal pattern implies hierarchically nested patches of different size but of the same contrast (average distinction between smaller patches within the larger patch) and aggregation (sensu Kotliar and Wiens 1990), i.e. a pattern looks equally heterogeneous at all scales. Patterns of this kind correspond generally to the hierarchical patchiness concept, but they are the only structures in which spatial variability is scale-invariant, i.e. remains constant while extent and grain change.

In most methods commonly used to study spatial patterns, only one scaling parameter is usually varied; traditionally it is *grain* (usually considered as sample size) in landscape ecology and *extent* in benthic ecology. More advanced methods, based either on blocking techniques or autocorrelation, consider long sequences of adjacent or equally spaced samples (Turner et al. 1991; Cullinan 1992). But they require rather extensive sampling effort to examine a wide range of scales, and therefore are hardly applicable to benthic research. Furthermore, these methods are oriented to identify patterns of only one particular type, namely, the patchiness or gradients. An alternative approach was recently suggested by Loehle and Wein (1994). Developing their approach further we proposed a method of identification of *different* spatial patterns and verified the method by means of computer simulations (Azovsky and Chertoprood 1997, 1998). The goal of the present research was to test the above method on benthic intertidal communities. The main questions of the research were: (1) How does the spatial heterogeneity of littoral sediments and biota change with a scale of observation (in terms of its grain and extent)? (2) Do organisms that differ in body size exhibit similar spatial patterns, and, if so, at which scale?

In answer to these questions the distribution of two groups of species of extremely dissimilar size (microalgae and macroinvertebrates) were studied at scales ranging from decimeters to kilometers – the typical scope of benthic research. In the present study we focussed on the variations of the whole community structure rather then on the distribution of separate species. It should be noted that, in terms of community structure, we use the term *patch* to indicate an area of uniform species composition rather than uniform abundance of certain species.

Materials and methods

Study area and sampling design

The study was carried out on a 5.5 km section of the silty-sand, middle intertidal zone on the southern shore of the Chernaja Bight (Kandalakscha Bay, White Sea, 66°30′N; 33°E, Fig. 1A) in the period from 17 July to 23 August 1995. The shoreline is characterized by a lace-like sequence of bays (so-called *scallops*); the bays are 200 to 400 m long and separated by rocky ledges. Each bay consists of several (usually three) smaller bays, about 70 to 100 m long (Fig. 1B).

The hierarchically nested, unequally spaced sampling program (Underwood and Chapman 1996) was used to cover a maximum scope of scales (changing the extent and grain). The program consisted of three parts (Fig. 1). (1) Sampling plots of 1 × 1 m were grouped together in triplets at a distance of 2.5 m from each other, so that each triplet covered an 8 m shore segment. These triplets were set, in turn, in groups of three, 25 m apart. Each group of nine plots thus covered 74 m of shoreline (a single scallop) (Fig. 1C). Nine sample groups (81 plots in 9 successive scallops) covered about 3 km. (2) Five 1 m^2 plots were chosen in one of the scallops

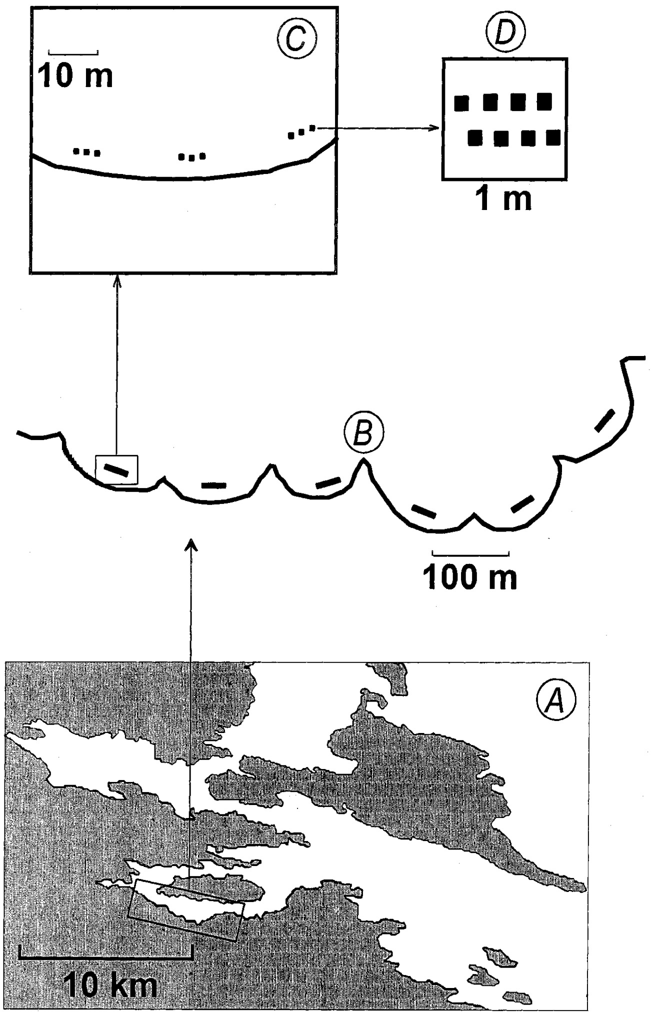

Fig. 1 Area of study and sampling design. **A** Kandalaksha Bay, White Sea, Russia; **B** shoreline profile and arrangement of sample groups; **C** arrangement of sampling plots in the groups; **D** 1 m^2 plot (single sample or eight microscale samples)

to study the microscale distribution. Eight 10 × 10 cm samples were taken from each plot (Fig. 1D). Each of these samples were treated separately. Thus 4 *large-scale* and 40 *small-scale* samples were taken within the 74 m segment of shoreline. (3) Along the adjacent 2.5 km section of shoreline, three 1 m^2 plots spaced in 2.5-m intervals were sampled in each of the six scallops (in total 18 samples).

In all, there were 134 quantitative samples of benthos taken from 94 (76 + 18) 1 m^2 plots and forty 10 cm^2 plots. This sampling program allowed us to vary both the extent (considering segments of various total length) and the grain size (averaging the data within appropriate groups of samples). To increase grain size, several adjacent but spatially separated samples were pooled together and then considered as a single, combined sample. Thus we consider *grain* as the *overall length of the shoreline* covered by a single block of samples, but not as the number of samples or their total size. For instance, eight small samples from each microscale plot were grouped to obtain a data set with 1 m grain. Then, averaging the data from triplets (three neighboring samples of 1 m^2 each) we derived the grain of 8 m, and so on. To examine the largest extents, Series 1 and 3 were merged, and three central plots were considered in each of 15 scallops. This *zoomed window blocking* technique (Turner et al. 1991) allowed us to examine various combinations of extents (ranging from 25 cm to 5.5 km) and grains (from 10 cm to 2 km).

Collections of macrobenthos were made by box samplers (four 25 × 25 cm boxes for large-scale samples or one 10 × 10 cm box for small-scale ones) up to 30 cm depth and then passed through a 0.5 mm sieve. Animals were identified and counted under stereomicroscope and weighed. Wet weight was determined; mollusks were weighed with shells but without pallium water. Simultaneously, diatom algae (Bacillariophyta) were sampled at the same sites. Five random subsamples were collected from each plot by pipe sampler (1 cm^2 area). Diatoms were fixed by eosin-ethanol, then extracted by stirring up and precipitating, and counted in a Goryaev chamber under light microscope. Permanent slides were made for identifying species (using both light and SEM microscopy) and measuring cell volumes (Saburova et al. 1995).

The following characteristics of sediments were measured at each site: dry weight contents of four size fractions (> 1 mm, 1 to 0.5 mm, 0.5 to 0.1 mm, < 0.1 mm), organic matter content (as weight loss of dried samples after combustion at 350 °C), the thickness of modern deposits and the particle size (mean value and variance).

Methods of data analysis

Relative metabolic rate (as respiration rate, R) was estimated for the macrofauna by the equation:

$$R = k \times N^{0.25} \times B^{0.75} \ , \tag{1}$$

where N and B are the species' abundance and biomass per unit area, and k the taxon-specific respiration intensity corrected for shell weight for mollusks (Alimov 1979). This value reflects the species' abundance better than number or biomass do (Schmidt-Nielsen 1984). For diatoms, the biomass per square centimeter values were calculated.

An ordination of samples by principal components analysis (PCA) was carried out to obtain a general representation of the spatial variability of the whole community. Correlation matrices for sediments and covariances for the biological data were used. The factor scores of the samples for the first PCA axes (in some cases – second ones as well) were used as univariate markers (representatives) of habitat or community structure at the site. The PCA scores are well suited to our purpose since they are additive, i.e. the overall value for a set of pooled samples could be calculated as the mean of a single sample's scores (Zar 1984).

Earlier we proposed the measure of spatial heterogeneity for multi-species systems, D_I, as the diversity of the profile of ordination scores (Azovsky and Chertoprood 1997). Briefly, the procedure was the following. Original sample scores were power-transformed to base 10 to circumvent dealing with negative values and then were normalized to the unit sum:

$$Z_i^* = 10^{Zi} \ , \tag{2}$$

$$P_i = Z_i^* \Big/ \sum_{i=1} Z_i^* \ , \tag{3}$$

where Z_i is the position of the i-th sample (or set of pooled samples) on the ordination axis. The evenness of the transformed scores based on the Shannon diversity index was used as the homogeneity measure:

$$D_I = \left(- \sum_{i=1}^{N} P_i \log P_i \right) \Big/ \log N \ , \tag{4}$$

where N is the total number of points (pooled samples of the given grain) within an area of given extent. Here D_I measures deviation from uniformity, with the following behavior. For a totally uniform pattern, $D_I = 1$. The more heterogeneous the spatial structure is, the more diverse the samples' scores and the lower the D_I value. We calculated D_I for various combinations of extent and grain choosing appropriate data sets and then estimated the scale-dependence of D_I by multiple log-linear regression analysis (MANOVA) in the form:

$$D_I = a + b \times \log(\text{extent}) + c \times \log(\text{grain}) \ , \tag{5}$$

where a is a regression constant and b and c are the effects of extent and grain, respectively.

Computer simulations have shown the essential distinctions in D_I scale-dependence for different patterns (Azovsky and Chertoprood 1998). For *random mosaics*, the evenness of the structure increases linearly with an increase of both grain and (to a lesser degree) extent, i.e. in terms of Eq. 5, $c > b > 0$ (Fig. 2a). In the case of *gradient*, on the contrary, D_I values decline rapidly as either grain or extent increase ($b < 0$; $c < 0$; Fig. 2b). Simple *patchy structures* exhibit more complicated non-monotonous behavior with a peak at the extent equal to mean patch size, while the minimum occurs at the patch-sized grain (Fig. 2c). Thus, scale-dependence of D_I for patchy structures does not fit the linear approximation well, but does allow us to estimate the patch size. Finally, for *fractal patterns* (Fig. 2d), the positive effect of grain and the same negative effect of extent turn out to compensate for each other ($b = -c$). As a result, D_I remains constant (i.e. spatial heterogeneity actually remains invariable) at all scales if extent and grain change proportionally. Hence the form of scale-dependence of the index (expressed in terms of the regression coefficients) indicates the type of spatial pattern, and the condition $b = -c$ could be used as a criterion of self-similarity, which could be tested directly by F-statistics for a general linear model (Draper and Smith 1981).

Data processing was carried out by SYSTAT 6.0 statistical package (SPSS, Chicago).

Results

General description of communities and PCA results

Sediments

Sediments were formed by poorly sorted silty sands. The mean modal size of particles was 0.2 mm, mean aleuropelits content was 66.6% and mean content of organic matter was 4.6% of dry weight. Silt content varied from 42.4 to 88.7% and organic matter ranged from 0.1 to 23.6%. PCA was done on eight abiotic variables (weight content of four size fractions and organic matters,

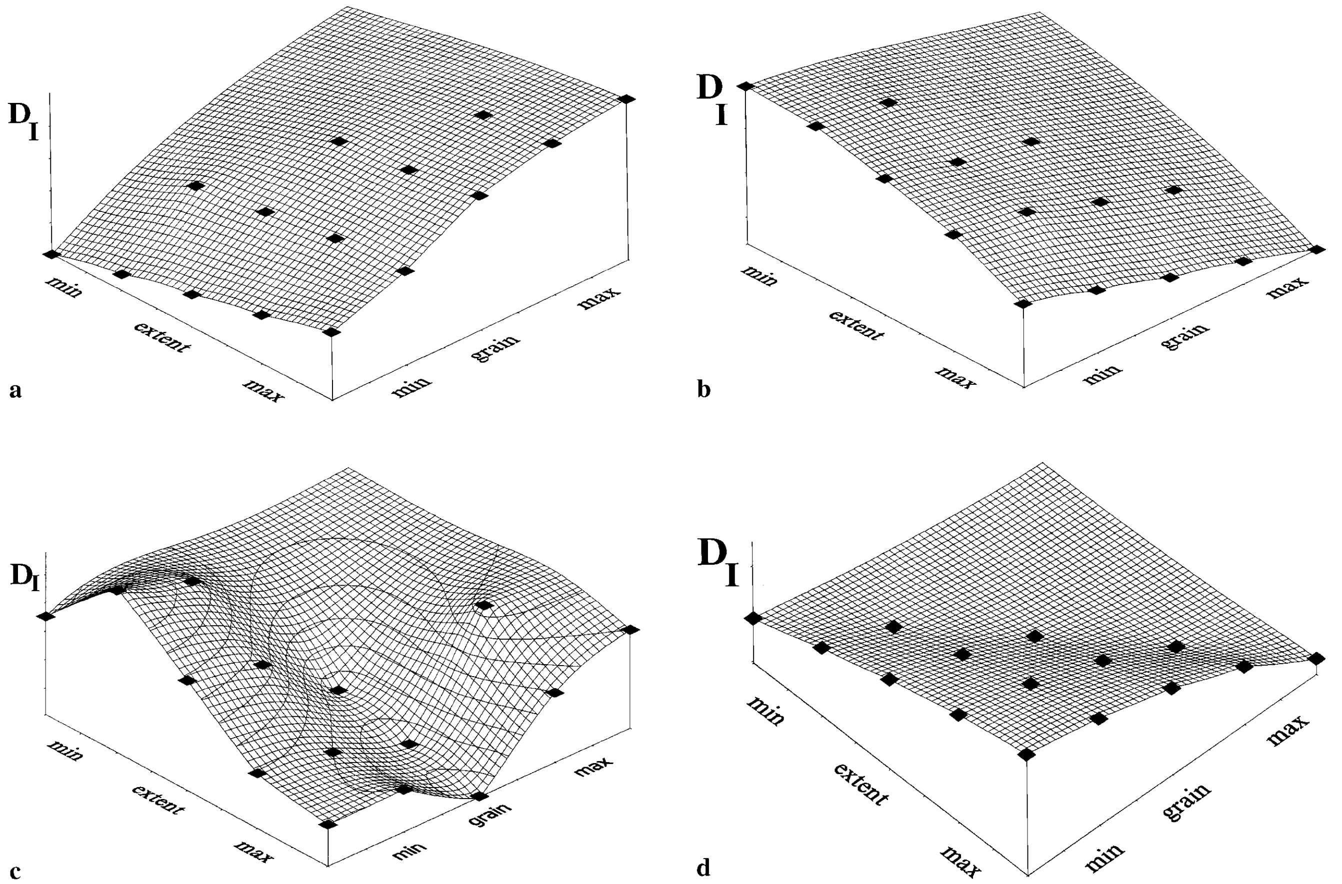

Fig. 2 Model examples of scale-dependence of D_I for different spatial patterns: **a** random mosaic, **b** gradient, **c** patches, and **d** fractal pattern

thickness of modern deposits, mean particle size and variance). The first two components were used for further analysis. The first one accounted for 50% of total samples' variance and reflected sediment granulometry, particularly silt/sand ratio. The second component (19% of total variance) was most strongly correlated to deposits' thickness and organic versus large-particle content and could be interpreted as associated with the degree of local water movement.

Macrozoobenthos

A total of 34 macroinvertebrate species was found at the study site. The prosobranch *Hydrobia ulvae* and the bivalve *Mya arenaria* prevailed (on average 50.2% and 19.7% of total community respiration, respectively). Although both mollusks were rather abundant in most samples, their peaks did not coincide, resulting in quite a complicated pattern, with either species alternately dominating. No obvious correlations between the dominant and other species or grouping of any species in well-pronounced combinations were found.

The first principal component accounted for 65.1% of total variance in macrobenthic structure. *Hydrobia ulvae* and *Mya arenaria* had the most significant loadings. Hence, this component reflected mainly the abundance ratio of the two dominant species. The second component was determined by overall abundance of the three subdominant species: *Macoma balthica, Mytilus edulis* and *Peloscolex benedeni*. It accounted for as little as 17.7% of total variance.

No significant correlations between macrobenthos (abundances of top ten species or the first two PCA score values) and sediment characteristics of single samples were found. After averaging the data over triplets of nearest samples (8 m grain size) a few correlations became statistically significant. In particular, *Mytilus edulis* turned out to be positively correlated to both principal components' values for sediments ($r = +0.75$ and $+0.66$, respectively; both correlations are significant at the 95% level). This suggests that mussels tended to avoid well-sorted sandy sites with high water activity. Nevertheless macrobenthos and sediments were found to be distributed in general almost independently at scales of meters to hundreds of meters.

Microphytobenthos

Unlike macrobenthos, the diatom flora was quite diverse (129 species), with no obvious dominance. Data of the 30 most-abundant species (over 95% of total biomass) were used for the PCA ordination. The analysis was done separately for the whole data set and then for a microscale subset (44 samples from 74 m shoreline segment). By ordination of the complete data set (full range of scales), the first component accounted for 34.9% of total variance. Two algal complexes could be distinguished on the basis of PCA loadings. The first one included mostly fresh- and brackish-water forms (*Navicula canalis, N. cryptocephala, N. hungarica* var. *luneburgensis, Nitzschia paleacea*), whereas the other complex consisted of marine species, mainly *Navicula radiosa* var. *tenella, N. halophila, N. capitata* var. *luneburgensis, Diploneis vacillans* and *Nitzschia apiculata*. Relative abundance of either of the two complexes determined the greater part of the total spatial variability of the microalgal distribution.

Analysis of scale-dependence of spatial heterogeneity

Using the PCA scores, the spatial homogeneity index D_{I} was calculated for various combinations of extent and grain. The form of D_{I} scale-dependence (results of regression analysis by Eq. 5) was used to determine the type of spatial pattern at different scales and to test the hypothesis of self-similarity (see "Materials and methods" for details on data analysis).

Sediments

Similar behavior of the sediments' spatial homogeneity index was found for both principal components (Table 1). There was no obvious scale-dependence for the whole data set. For the extents up to 2.5 km both effects of grain and extent were positive, but the influence of grain was twice as strong as the effect of extent. This pattern corresponds well to the random mosaic model without any homogeneous areas exceeding single-sample size. So the results suggest a random-like local distribution of littoral sediments without pronounced patchiness or any self-similarity.

Macrozoobenthos

The first principal component scores were used to determine the spatial distribution of macrofauna. The community showed high variability of structure in a wide range of spatial scales, without any well-defined patches. Two examples of principal component profiles (ordination scores plotted along the shoreline transect) are presented in Fig. 3 to illustrate the spatial variability. The areas with dominance of either *Mya arenaria* (positive scores) or *Hydrobia ulvae* (negative scores) alternate with each other on every scale, so the patterns look distinctly similar despite on almost tenfold difference in both grain and extent. The pattern's

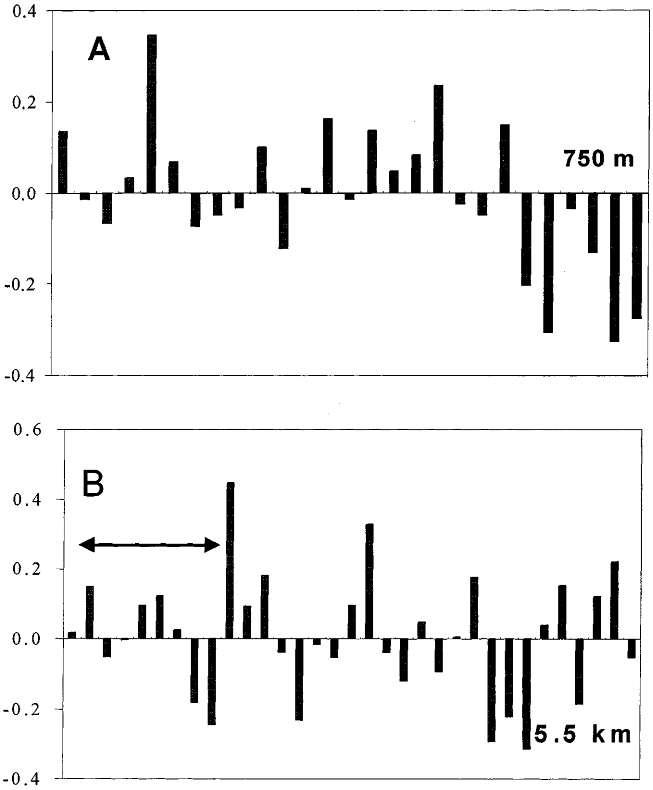

Fig. 3 Principal component profiles of macrobenthos. Bars are the ordination scores of sample blocks of given grain arranged along a shoreline segment of given extent (horizontal scale is arbitrary). Negative and positive values correspond to the dominance of *Hydrobia ulvae* or *Mya arenaria*, respectively. **A** Extent 750 m, grain 1 m; **B** extent 5500 m, grain 8 m (*horizontal arrow* marks the location of samples shown in Panel A).

Table 1 Scale-dependence of spatial homogeneity index, D_{I} (results of regression analysis) for sediments (first and second PCA axes) [significance levels: *ns* not significant, *95%, **99%, values in parentheses are standard errors; self-similarity hypothesis test (*F*-statistics): – rejected, + accepted at 95%; ++ accepted at 99%, *NP* not performed]

Range of extents (m) involved in analysis	Regression coefficients		Multiple correlation, *R*	Test for self-similarity ($b = -c$)
	log(grain) *b*	log(extent) *c*		
First principal component (granulometry)				
8–5500	−0.088 (0.045)$^{\mathrm{ns}}$	0.046 (0.033)$^{\mathrm{ns}}$	0.481	NP
8–2500	0.081 (0.005)**	0.037 (0.006)**	0.988	–
Second principal component (water activity)				
8–5500	−0.011 (0.033)$^{\mathrm{ns}}$	−0.071 (0.045)$^{\mathrm{ns}}$	0.528	NP
8–2500	0.028 (0.011)*	0.014 (0.013)$^{\mathrm{ns}}$	0.677	–

homogeneity measure (D_I) increased with grain and decreased with extent (Table 2). When the data on the overall range of studied extents (8 to 5500 m) were considered, the effect of grain only slightly and insignificantly exceeded the effect of extent. When the analysis was restricted to smaller areas (up to 2500 m), absolute values of the regression coefficients became still closer (hypothesis of self-similarity was confirmed at the 99% significance level). Hence the effects of simultaneous change in grain and extent reciprocally compensated for each other so that D_I values remained constant. Thus, spatial heterogeneity of macrofauna proves to be dependent upon neither total sampled area nor grain size but only upon their ratio. This is evidence of statistical self-similarity (fractal properties) of the pattern within a scale range up to 2500 m. The slightly greater effect of grain in comparison to extent (especially pronounced for large areas) may be attributed to the elements of randomness.

In fact, for areas over 1 km considered separately, the grain effect was strengthened and the extent effect became slightly positive (Table 2), just as in the case of random mosaics. However we should note that the expansion of area from 2500 to 5500 m was accomplished by adding 18 samples only – too few to be sure about patterns found on this scale.

Microphytobenthos

Diatom algae differed considerably from macrofauna in behavior of the spatial homogeneity index. If the total data set was examined at a whole range of scales, D_I values significantly correlated with neither grain nor extent (see Table 3). Hence we reconsidered the data separately on large and small scales.

On a large scale (over 75 m), the influence of grain size almost disappeared, but the negative effect of extent became significantly stronger. As was shown previously (Azovsky and Chertoprood 1998), such behavior corresponded to a pattern combination of gradient and large-scale patchiness, with patch size exceeding most of the grain values. Actually the PCA score values gradually increased along the shore (Fig. 4C); this indicates the progressive replacement of the brackish-water complex by marine species from bay to bay from the Chernaja River estuary toward the open sea. The small peak of brackish-water that forms at the right end of the transect was apparently caused by a brook flowing into the sea at that location.

In contrast, both regression coefficients, while low, were positive on a microscale (under 75 m). In general a random-mosaic distribution seemed to appear, but precise comparison between microscale samples on the basis of ordination of the whole data set was complicated somewhat by their high similarity. Therefore, the ordination procedure was repeated for 44 microscale samples taken within a single bay. The results supported the high variability of diatom distribution. The pattern looked equally heterogeneous on both a scale of meters (Fig. 4A, extent/grain ratio: 80) and a scale of dozens of meters (Fig. 4B, extent/grain ratio: 75). For this data set, the scale-dependence of D_I was found to be similar to that of macroinvertebrates: the distribution became more homogeneous (D_I increased) as the grain increased, while the opposite effect of extent was a bit weaker (Table 3). On the smallest scales (under 8 m), the absolute values of regression coefficients became all the more similar, i.e. the ten-

Table 2 Scale-dependence of spatial homogeneity index, D_I, for macrobenthos (first PCA axis) (symbols as in Table 1)

Range of extents (m) involved in analysis	Regression coefficients		Multiple correlation, R	Test for self-similarity ($b = -c$)
	log(grain) b	log(extent) c		
8–5500	0.075 (0.009)**	−0.046 (0.013)*	0.914	+
8–2500	0.053 (0.007)**	−0.043 (0.009)**	0.940	++
8–1000	0.027 (0.008)**	−0.022 (0.007)*	0.900	++
1000–5500	0.080 (0.010)**	0.050 (0.077)^{ns}	0.954	–

Table 3 Scale-dependence of spatial homogeneity index, D_I, for microphytobenthos (first PCA axis) (symbols as in Table 1)

Range of extents (m) involved in analysis	Regression coefficients		Multiple correlation, R	Test for self-similarity ($b = -c$)
	log(grain) b	log(extent) c		
Ordination for all the samples				
0.25–5500	−0.040 (0.023)^{ns}	−0.025 (0.022)^{ns}	0.725	NP
75–5500	−0.007 (0.017)^{ns}	−0.089 (0.024)*	0.857	–
0.25–75	0.009 (0.005)^{ns}	0.011 (0.004)*	0.881	–
Ordination for 44 "microscale" samples only				
0.25–75	0.060 (0.024)*	−0.038 (0.017)*	0.677	+
0.25–8	0.047 (0.016)*	−0.032 (0.012)*	0.750	++

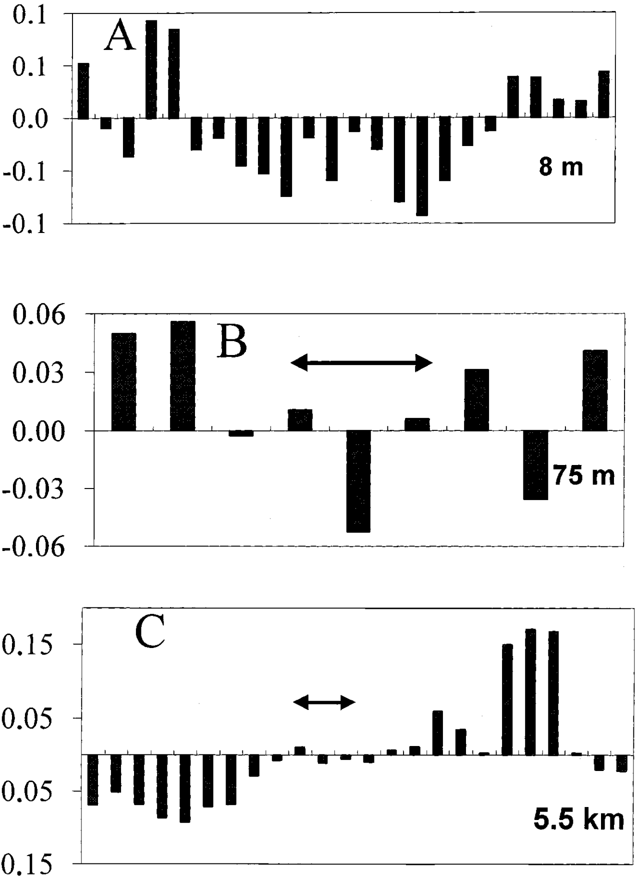

Fig. 4 Principal component profiles of diatom algae. Negative and positive values correspond to the dominance of "brackish-water" or "marine" complexes, respectively. **A** Extent 8 m, grain 10 cm; **B** extent 75 m, grain 1 m; **C** extent 5500 m, grain 8 m (*horizontal arrows* mark the location of samples shown on panel directly preceeding)

dency of reciprocal compensation grew more evident and was highly significant. Thus, the microalgal community also demonstrated statistical self-similarity of spatial variability, but only on a microscale (within a single bay). Further, the combination of a regular gradient with bay-sized patches was found on a scale of hundreds of meters to kilometers (Fig. 4C).

Discussion

We examined spatial variability of intertidal micro- and macrobenthos in relation to scaling parameters (extent and grain) ranging from decimeters to kilometers by using the spatial homogeneity index D_I. Our analysis was not specially designed to estimate the characteristic scale of species variability. Instead, we tried to reveal a *general type* of pattern in a range of scales. Both communities showed, within a certain range of scales, a rather peculiar spatial pattern. It is not a random mosaic pattern, due to its evident autocorrelation: on average, neighboring samples are more similar to each other than to all others, though they can vary considerably. It rather looks like weakly pronounced patchiness, especially if observed at a certain, fixed scale. However, the patches are distributed neither randomly nor regularly, but form larger aggregations. These second-order patches become clearly perceptible at an increasing grain size (pooling samples within first-order patches). They, in turn, also form aggregations (patches of the next order), etc. Moreover, the contrast (sensu Kotliar and Wiens 1990), i.e. average distinction between smaller patches within the larger patch, remains constant at every scale, thus providing statistical self-similarity of the pattern. Thus, such *fractal* spatial structure of community could be described as the hierarchy of nested patches of various sizes but of similar contrast. Observed heterogeneity of these structures does not depend on the scale of observation as long as the extent/grain ratio does not change. In our case, it means that a kilometer-long littoral section divided by 100-m segments looks as heterogeneous (in respect to distribution of benthos) as a 10-m plot divided by 1-m pieces. Though such structures are not *pure* fractals in the strict sense of the word, but they possess the main properties of fractals – scale-invariance and fractional dimension. Any formal estimation of fractal dimensions was beyond the scope of our study, though such estimations are possible in principle (Feder 1988).

Multiscale analysis of heterogeneity: advantages and restrictions

There are several methodically important conclusions that can be drawn from our data. The point is that fractal and patchy structures are not effectively distinguished by commonly used methods applied to a narrow range of scales. Furthermore some methods may also yield obscure results if only one scaling parameter is varied. For instance, the widely used, block-size procedures (Greig-Smith 1983; Cullinan 1992) demonstrate more or less monotonous decrease of variance with increasing grain for both fractal and non-fractal patterns. Fractal structure is not identified if studied at a fixed scale because of its, by definition, multiscaled nature. At the same time one would vainly look for any *characteristic* patch size in such a pattern: there will always be more or less homogeneous areas, no matter whether samples are taken over 1 or 100 m. Only the comparison of multiscaled data allows reliable identification of fractal distribution.

Many authors have described diffuse patches of various sizes concealed by random mosaics (Tufail et al. 1989; Ardisson et al. 1990; Fleeger et al. 1990; Saburova et al. 1995). Could they have actually been dealing with fractal patterns? The following observation suggests this hypothesis: the wider the range of scales examined, the more levels of patchiness are generally discovered, and the more likely the researcher will point out the complex nature of heterogeneity. Korepanov (1991), for example, found a regular increase of patch sizes in accordance with the studied area of storage ponds. Burkovsky et al. (1996) also noted that aggregations of psammophilous ciliates presented the entire spectrum of possible sizes. In particular, a similar pattern of species distribution has recently been described by Gudimov (1994) for the *Portlandia arctica–Nuculana pernula* biocenosis in the eastern part of the White Sea. Areas of dominance of one of these two bivalve species alternated on different spatial scales. This *scale-invariant alternation* (Gudimov 1994) was considered to be evidence of fractal distribution, however, without any statistical proof.

Probably the complex mosaics of patches of assorted sizes so often described for benthos were, in fact, more complicated, polydominant cases of fractal distribution. Unlike the traditional models that consider a *single fractal object in empty space*, this situation supposes that the *entire* space is occupied with several intertwined fractal objects, each including elements of the others instead of void spaces.

The problem in analyzing these *multifractal* ecological structures is the difficulty of finding a simple description. The existing methods are designed mainly to describe univariate distributions and can only provide information on the space-filling properties of single-type patterns (Feder 1988; Plotnick et al. 1993; Loehle and Wein 1994). Actually, however, a community is characterized by numerous variables, i.e. abundances of species. As general approaches to studying spatial structure of multicomponent objects are poorly developed (in particular, there are no methods for estimating their fractal dimension), one has to reduce the multispecies data to a single common characteristic. For this purpose various ordination procedures are usually used; we have applied the PCA method.

The validity of further analysis therefore depends on (and is limited by) the reliability of the ordination procedure: we can consider only a part of the structural variability, i.e. that described by the chosen axis. This is quite enough for an acceptable description of the simplest cases. For macrobenthos, for example, more than two-thirds of the overall variability are described by one component only, the *Hydrobia ulvae*/*Mya arenaria* ratio. In fact, we consider the distribution of these dominant species to be representative of the whole community's structure. In more complicated situations, a certain degree of information is lost, as in the case of diatom algae. Some other mathematical shortcomings of the approach have previously been discussed (Azovsky and Chertoprood 1998).

Spatial limits of fractality and size of organisms

Distribution of benthic communities does not retain its self-similarity at all the scales studied. For macrobenthos, the distribution over the whole 5.5 km area was nearly mosaic; for diatom algae, fractal properties already disappear on a scale of hundreds of meters (beyond a single bay). The mere fact of limitation is not surprising. Many natural objects are neither self-similar at all scales nor geometrically exact in structure. Their scale-invariant properties are always limited to a finite range of scales (Burrough 1981; Milne 1991). These boundaries are of particular interest, as either structure-generating processes or environmental limitations also change at these critical scales (Frontier 1987; O'Neill et al. 1991).

From this standpoint, it is most interesting to note that fractal properties of each group are manifested at scales corresponding to their typical body size. In fact, macrobenthic organisms are, on average, several millimeters in size, and their fractal distribution is manifested from dozens of meters to kilometers; diatom cell sizes are dozens of micrometers, and their fractal structure ranges from decimeters to dozens of meters. Thus, the range of fractality for both groups is approximately equal (three to five orders of magnitude) if measured in their own units – mean body size. This confirms our earlier assumption (Burkovsky et al. 1994; Azovsky and Mokievsky 1996) that organisms of different sizes may generate similar spatial patterns but on different scales.

Nature of fractality: where does it come from?

The most intriguing but obscure question is: what are the possible reasons for the scale-invariance discovered for biotic heterogeneity? Patchiness or a gradient pattern could be explained by the influence of numerous factors, and usually the explanations are quite obvious; even the mosaic pattern can be explained by the absence of significant interactions and stochastic environmental effects. Fractal distribution, as such, is much more complicated, though it is found in an outwardly homogenous environment. Two hypotheses could be proposed to explain its origin, both raising more questions than providing answers.

First, distribution of species could reflect a distribution of some abiotic factors presenting a *template* upon which organisms and ecological systems operate (Milne 1991). If so, in our case the template should be fractally organized. Indeed, many environmental parameters do display statistical self-similarity over a certain range of scales (Burrough 1981). Moreover, the scalloped structure of the studied coastline shows some evident features of self-similarity. Fractal patterns are often generated by processes operating in transition zones such as the marine intertidal flat (Mandelbrot 1983; Bradbury et al. 1984; Pennycuick and Kline 1986). Superposition of several environmental gradients acting on different scales could result in rather complex spatial patterns of biota (Azovsky et al. 1998). However, neither fractality in the distribution of sediments, nor significant correlations between the biota and the measured sediment properties were found. Thus, we can only guess at what factor could form such a template. Could it be circulating tidal currents, microrelief or sediment chemistry?

We would also like to point out that macro- and microbenthos have different ranges of fractality. Different organisms should have different scales of perception of the physical environment, exhibiting patterns of different types upon one and the same template. Therefore, the properties of habitats are not just a function of the landscape pattern, but also the ability of the organisms to perceive this pattern (Wiens and Milne 1989; Azovsky and Mokievsky 1996).

In accordance with another hypothesis, a fractal spatial pattern is the result of community self-organization, which is then transformed into other structures (fixed patches or gradients) under the evident external (environmental) influences. If so, fractals may be a universal way of biota's self-organization and filling up the space.

It is known that fractal structures arise from certain diffusion-and-growth processes in a random environment (Mandelbrot 1983; Sander 1986). These processes could be of various natures but what all them have in common is their localization in some *active growth points*. But distribution of benthos is also related to the seasonal processes of population growth and expansion. Development of microbenthic communities begins with spring colonization and expansion from initial aggregations (on a scale of centimeters to meters). In an earlier paper we pointed out an analogy between the colonization dynamics and a diffusion process (Azovsky 1988). For the most macroinvertebrates, the migration and settlement of planktonic larvae is of fundamental importance (Butman 1987; Burkovsky et al. 1997). In addition, the *Hydrobia ulvae* adults could also migrate with tidal currents and redistribute in the range from tens to hundreds of meters (Armonies and Hartke 1995). Both processes are regulated by local near-shore circulations and tidal currents, which are turbulent, i.e. fractal, in a range of scales (Mandelbrot 1983).

It seems natural that any developing system (including a community of live organisms) tends to increase its internal structuring (heterogeneity) as long as its size permits. Any increase in size adds new structural elements – this is the way some macroalgae, trees, clouds and many other fractal objects grow (Mandelbrot 1983; Sander 1986). Fractal properties have recently been shown for the spatial distribution of terrestrial vegetation (Turner et al. 1991) and of marine plankton (Tsuda 1995). But why and how biological communities realize this type of organization is still a puzzle. Other authors (O'Neill et al. 1986; Kolasa 1989; Holling 1992) have proposed similar concepts of fractal-like ecosystem organization, but the reasons behind this pattern remain a matter of further investigation.

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