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Mesoscale spatial structures of soft-bottom macrozoobenthos communities: effects of physical control and impoverishment

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ABSTRACT: The recognition of the nature of spatial and temporal variability within ecosystems is crucial for understanding the processes that maintain species diversity and ecological stability. In the present study, mesoscale spatial structures of soft-bottom macrobenthic communities were explored at sites with contrasting disturbance regimes and benthic diversities. Two sites in a glacial Arctic fjord were selected: the Inner site, where sediments are inhabited by an impoverished community composed of a few species resistant to large-scale, chronic physical disturbance by glacial sedimentation, and the Outer site, where diverse fauna is structured by biological interactions among populations of species of different sizes and functional groups. Samples were taken at 6 stations (4 van Veen grabs collected per station) located along a 1 km transect separated by 0 (samples collected at the same station), 200, 400, 600, 800, and 1000 m. Spatial variation at the Inner site was apparent only in changes in relative abundances among a few numerically dominant species (explored using untransformed data), and the fauna was homogenous with respect to species composition (based on presence/absence data). The spatial heterogeneity in the Outer site community was evident both in species composition and in relative abundances of dominant species populations. The significant autocorrelation peaks on a correlogram of Bray-Curtis similarities of untransformed data indicated a successive sequence of homogenous patches of a minimum 200 m radius, separated by 600 m. Spatial patterns of species composition similarity varied among species groups of different mobility: sedentary fauna did not exhibit a mesoscale patchiness, while clear patchiness was documented for motile and discretely motile organisms. The current study demonstrates that the spatial structure of benthic biota is related to the diversity and the perturbation level of the studied communities. It also supports the recommendation for spatial separation of replicate samples in soft-bottom macrobenthic surveys.

KEY WORDS: Spatial patterns · Scale · Soft bottom · Macrofauna · Diversity · Disturbance

INTRODUCTION

The term 'distance similarity decay' was introduced by geographers and was later adopted by macroecologists to define the decrease of similarity between 2 observations as the distance between them increases (Nekola & White 1999). On smaller scales the relationship between distance and the commonality of species composition in ecosystems is usually not simple or monotonic; instead, hierarchical mosaics of patches of decreasing size (i.e. areas differing from the surroundings that can be detected at smaller scales nesting within patches detectable at larger scales) are observed (Kotliar & Wiens 1990). The recognition of the nature of spatial and temporal variability within ecosystems is crucial for understanding the processes that maintain species diversity and ecological stability (Legendre & Fortin 1989). The spatial variability of natural communities also has significant practical implications. The rate of similarity decay is of crucial impor-

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tance for sampling procedures and statistical analyses of ecological data: autocorrelation of data (significant relationships between the measured value and the positions of the stations) can result in the inaccurate estimation of variance among replicates if sampling stations are too close together (Somerfield & Gage 2000).

In the marine benthic ecological literature 2 aspects of species distribution are often referred to as 'spatial variability': (1) intensity of spatial patterns within a group of samples collected in a particular area (but without reference to the exact positioning of stations) explored with use of mean:variance relationships for univariate measures or by index of multivariate dispersion (IMD) for multivariate data (Warwick & Clarke 1993) and (2) spatial structure, i.e. how species and communities are distributed in space, taking the geographical positions of the stations into account and exploring how measures vary with distance between samples (Somerfield & Gage 2000). The intensity of spatial patterns has often been reported as one of the possible indicators of benthic disturbance (e.g. Warwick & Clarke 1993, Włodarska-Kowalczuk et al. 2005), while the issue of the relationship between (1) the benthic community spatial structure and (2) the species richness and perturbation level of the community has not been addressed.

A substantial number of articles address the spatial distribution patterns of individual species on different scales, while comparatively few studies explore the spatial structure of whole benthic communities (Kendall & Widdicombe 1999, Somerfield & Gage 2000). Heterogeneity in the distribution of benthic species has usually been ascribed to spatial heterogeneity in physical environmental settings, most often to bottom substrate characteristics (e.g. variability in sediment grain size composition) or the occurrence of small-scale seafloor morphological features that form the so-called 'benthoscape' (Zajac 1999). Benthoscape structures, as well as the faunal variability, can be studied at different scales and were classified by Zajac (1999) into (1) large-scale (i.e. tens of km^2), (2) mesoscale (hundreds of m^2 to km^2) and (3) small-scale (tens of m^2 and less) phenomena. That spatial configurations of particular species distributions can be related to behavioral and functional characteristics has been shown on a small scale by Reise (1979). Spatial patterns of species distribution are produced by an interplay of spatial and temporal environmental variability as well as biological processes and can be modified by natural and anthropogenic disturbances (Caswell & Cohen 1991); thus, a mosaic of biological patches can form even in areas that are homogenous in terms of basic physical characteristics. Kendall & Widdicombe (1999), Somerfield & Gage (2000), and Parry et al. (2003) described the spatial structure of macro- and megabenthic communities within patches of apparently homogenous sediments.

The present study was conducted in a west Spitsbergen glaciated fjord (Hornsund). Previous studies in similar areas documented clear differences in both the physical regimes and benthic communities of the inner and outer fjordic basins. In the outer basins the low level of physical disturbance results in the development of a biologically accommodated, diverse community composed of animals from a wide range of size and functional groups, presumably exploiting a range of resource niches and creating complex food webs (Syvitski et al. 1987, Włodarska-Kowalczuk et al. 2005). In the glacier-proximal inner basins the physically controlled and impoverished benthic community consists of only a few species belonging to 1 functional guild (usually small, motile detritus-feeders) and well adapted to resist disturbance (Włodarska-Kowalczuk et al. 1998, Włodarska-Kowalczuk & Pearson 2004). Kendall et al. (2003) reported the very homogenous distribution of benthic species in the glacier-proximal, inner basin of Kongsfjord (Spitsbergen). In the current study, 2 sites were selected that had contrasting disturbance regimes and different benthic characteristics (highly diverse/undisturbed outer fjord and impoverished/physically controlled inner fjord) to explore the patterns of change of among sample similarity as the distance separating the geographical locations of the samples increased. We were also interested to see if differences in spatial configurations of species of different functional traits (observed for individual species, e.g. by Reise 1979) would be expressed in multivariate patterns produced by groups of species. We focused on meso-scale (according to the classification of Zajac 1999) spatial structures and hypothesized that: (1) the spatial heterogeneity of macrobenthic composition will be more evident in a biologically accommodated/diverse outerfjord community and (2) spatial structure will vary among groups of species of different mobility.

MATERIALS AND METHODS

Study area. Hornsund is a wide, open (no sill) fjord located on the southwest coast of Spitsbergen (at 76 to 77° N). Despite its high northern location, the western coast of Spitsbergen has a relatively warm Atlantic character due to the influence of the West Spitsbergen Current, an extension of the North Atlantic Current. The banks of the Hornsund inner basin, Brepollen, are almost entirely formed by the cliffs of 5 tidal glaciers (Storbreen, Hornbreen, Svalisbreen, Mendelejevbreen and Chomjakovbreen). The glacial or glaciofluvial inflows transport large amounts of mineral suspensions and produce steep gradients of water turbidity and mineral sedimentation along the fjord axis. The fjordic sediments are composed of glacio-marine deposits, which are mostly silt and clay (M. Zajączkowski pers. comm.). The sediment accumulation rate in Brepollen can reach 35 cm yr^{-1}, while in the outer parts of Hornsund it is as low as 0.1 cm yr^{-1} (Görlich et al. 1987). Longer persistence of fast ice cover and high water turbidity in the inner basins of Hornsund reduces primary production in the water column, and organic matter sedimenting to the bottom is diluted by the high inorganic sediment load (Görlich et al. 1987).

Sampling and laboratory analyses. Sampling took place in July 2005 from aboard the RV 'Oceania'. Two localities were selected for sampling (Fig. 1): (1) Inner, located in Brepollen, a glacial bay at the fjord head (15.34° E, 76.55° N), and (2) Outer, located at the fjord entrance near the southern bank of the fjord (16.30° E, 77.01° N). The selected sampling areas were as uniform as possible with regard to both sediment granulometry and depth. At each locality, samples were taken at 6 stations positioned along a 1 km transect. The neighboring stations were separated by 200 m. At each station 4 samples were collected using a van Veen grab (0.1 m^2). Thus, a hierarchical structure of the spatial distribution of samples was achieved: there were a number of sample pairs separated by 0 (collected at the same station), 200, 400, 600, 800 and 1000 m. Of course, the samples collected at the same station were not separated by exactly 0 m. The ship was positioned at a certain point and replicate grabs were collected. Samples collected in this way were separated by a few meters, but to simplify the presentation of results we named them as 'separated by 0 m'. The scale of sampling in each locality was defined by a grain of 0.1 m^2, a lag of 200 m and an extent of 1000 m (after the terminology of Thrush et al. 1999). Station depths varied from 100 to 120 m on the Inner transect and from 100 to 115 m on the Outer transect. The sediment samples for granulomeric and total organic carbon (TOC) content analyses were taken at each station with a box-corer. At both sites the sediments were composed mostly of silt and clay fractions (<0.0063 mm) with sand admixtures varying from 1.4 to 2.9% at the Inner site and from 6.8 to 15.1% at the Outer site (W. Szczuciński unpubl. data). The TOC content in the sediments ranged from 1.83 to 1.89% at the Inner site and from 1.61 to 1.84% at the Outer site (W. Szczuciński & G. Schetter unpubl. data). The van Veen grab was lowered gently to the sea bottom to minimize the bow-wave, which can wash away the surficial sediments (Blomqvist 1991). Recovered sediments were sieved aboard ship using a 0.5 mm mesh sieve. The samples were fixed in formalin aboard ship, and all the animals were sorted, identified to the lowest possible taxonomic level and enumerated in the laboratory. All the samples collected at Stn 4 and 1 sample collected at Stn 5 on the Inner transect were improperly preserved and thus excluded from the analyses.

Data analyses. The diversity of the 2 localities was assessed on sample and whole-transect scales. Sample diversity was expressed by the number of species (S) per sample and by the Hurlbert rarefaction index ($ES_{[n]}$), an estimate of the number of species in a subsample of n individuals, which was developed to facilitate comparisons of the sample diversity comprised of different numbers of individuals (Hurlbert 1971). The $ES_{[n]}$ was calculated for n = 100. Differences in sample density (D), S, and $ES_{[100]}$ between 2 locations were identified using 1-way ANOVA. The normality of distribution was tested with the Shapiro-Wilks test and the homogeneity of variance with the Brown-Forsyth test.

Species accumulation curves described the number of observed species (S_{obs}) as a function of the number of samples. They permitted the comparison of the diversity of faunal assemblages at comparable levels of sampling effort. Species accumulation curves with 95% confidence intervals (CI) were computed using the formulae by Colwell et al. (2004). The computation of CI allowed for the statistical comparison of species richness of 2 data sets, i.e. the differences were not significant at $p < 0.05$ if the 95% CI overlapped (Colwell et al. 2004).

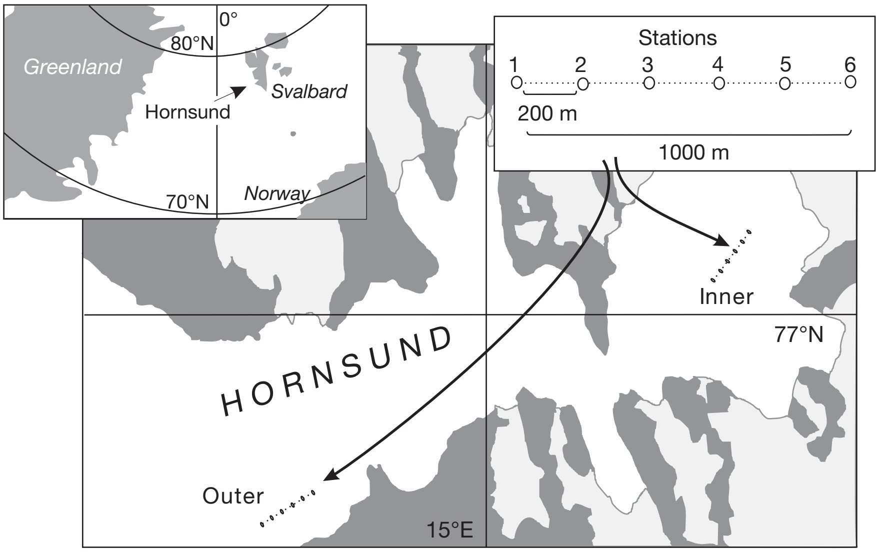

Fig. 1. Spatial configuration of sampling stations on transects and location of the 2 transects (Inner and Outer) in Hornsund. Light grey areas indicate glaciers

Frequency of occurrence (percentage of samples in which a species was found in the total number of samples) and dominance (percentage of individuals of a particular species in the total number of all animals found in all samples) were calculated for all species at each site. The diversity of functional groups (guilds) was also described. All species were classified by their feeding mode and comparative mobility according to Fauchald & Jumars (1979), Feder & Matheke (1980), Kuznetsov (1980) and other publications and unpublished observations. Following Fauchald & Jumars (1979), guilds representing combinations of 5 feeding types (carnivores, herbivores, suspension-feeders, surface detritus-feeders and subsurface detritus-feeders, or burrowers) and 3 mobility types (sessile, discretely motile and motile) were considered. The number of guilds and percentage of each functional group in the total number of organisms at each site was calculated.

The BIO-ENV procedure was applied to examine the relationship between biotic data and environmental factors including depth, sand (fraction >0.063 mm) and TOC content in sediments. The environmental data were normalized prior to the analysis. The Spearman rank correlation (R_S) was calculated between the biotic Bray-Curtis similarity matrix and abiotic matrices including all possible combinations of the considered environmental factors (Clarke & Warwick 1994).

The Bray-Curtis index was used to explore the patterns of spatial configurations along the transects. The biotic similarity among samples was calculated using: (1) untransformed data and (2) presence/absence data. The analyses of presence/absence data describe patterns in species composition. The Bray-Curtis index computed on untransformed species abundance data reflects similarities in the abundance of dominant species and strongly underestimates the importance of less abundant species (Clarke & Warwick 1994). The Bray-Curtis similarities were calculated for both untransformed and presence/absence data for each sample pair within a transect. In addition to sample similarity matrices, a matrix containing spatial distances separating each sample pair was constructed.

Spatial autocorrelation analysis, in which measures of spatial distance are a part of the analysis, was applied to analyze spatial configurations of biotic similarities. Relationships between the similarities and spatial separation of samples was examined using R_S, computed between corresponding elements of the biotic similarity and spatial distance matrices (Somerfield & Gage 2000). Correlation significance was determined with a Monte Carlo permutation procedure using the RELATE routine of the PRIMER program (Clarke & Warwick 1994). The spatial patterns of biotic similarities were explored using multivariate correlograms. Biotic similarities within sample groups separated by the same distance were compared to the similarities of all other samples. The relationships between the similarity matrix and 'model' matrices were tested with R_S. 'Model' matrices were created by coding the sample similarities separated by the relevant distance as 1 and all the other similarities as 0. The computed correlation coefficients were plotted against the relevant spatial distances (Somerfield & Gage 2000). Significant positive autocorrelation occurred when $p < 0.025$, while significant negative autocorrelation occurred when $p > 0.975$ (Somerfield & Gage 2000). The alternation of positive and negative autocorrelation values were an indication of patchiness (Legendre & Fortin 1989). The significant autocorrelation minimum on a correlogram was used to indicate the extent of a patch of similar fauna (Legendre & Fortin 1989). If a significant autocorrelation maximum was detected at a sample separation distance larger than that of the minimum, then the distance between patches of similar composition were defined (Legendre & Fortin 1989, Parry et al. 2003). The last correlation coefficient was not interpreted because it was based on too few pairs of samples (Legendre & Fortin 1989).

The analyses of spatial patterns (as described above) of species composition (examined using the Bray-Curtis index of similarity of presence/absence data) were conducted separately for different mobility groups at the 2 transects. Three mobility types were considered: (1) sedentary, no post-settlement movement, (2) discretely motile, stationary during feeding but capable of moving from place to place and (3) motile, feeding while in motion and moving relatively frequently or continuously. Multivariate correlograms were constructed only for discretely motile and motile species on the Outer transect, as only in these cases was the significant correlation between sample similarities and spatial separation documented.

Species accumulation curves and the Bray-Curtis similarities were computed using EstimateS (v. 7.5, R. K. Colwell, available at: purl.oclc.org/estimates). $ES_{[n]}$ and R_S were calculated, and the BIO-ENV analysis was conducted, using the PRIMER package.

RESULTS

Density and diversity of benthic communities

The mean density (D) of macrofauna was much higher in samples collected on the Outer transect (mean ± SD, 913.3 ± 135.7 ind. 0.1 m^{-2}) than on the Inner transect (327.1 ± 83.9 ind. 0.1 m^{-2}) (Fig. 2a). There was a significant difference between the number of animals per sample between the 2 localities (1-way ANOVA, $F = 271.4$, $p < 0.0001$). Similarly, S and

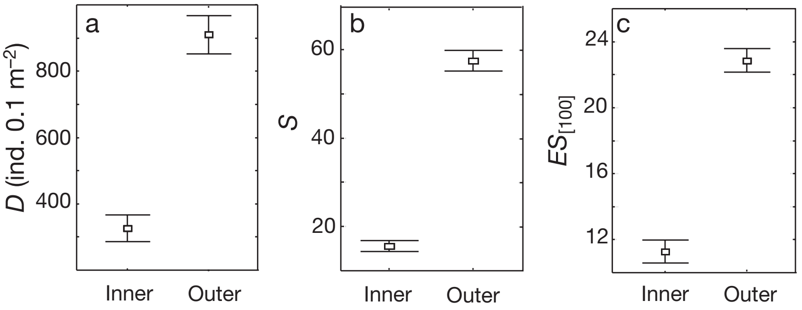

Fig. 2. Mean ± 0.95 confidence intervals (CI) (a) density (D), (b) number of species per sample (S), and (c) Hurlbert index ($ES_{[100]}$) in samples taken on the Inner and Outer transects

$ES_{[100]}$ were significantly higher at the Outer site (mean ±SD, 58.2 ± 5.4 and 22.8 ± 0.8, respectively) than at the Inner site (16.3 ± 2.6 and 11.3 ± 1.5, respectively) (Fig. 2b,c). The significant differences in S and $ES_{[100]}$ were identified using 1-way ANOVA ($F = 941.9$, $p < 0.0001$ and $F = 562.5$, $p < 0.0001$, respectively).

The total observed number of macrobenthic species was 40 at the Inner site and 168 at the Outer site. The species accumulation curve representing the Inner locality stabilized towards asymptotic values, while the Outer curve was quite steep and showed no signs of leveling off (Fig. 3). The Outer curve lay over the Inner curve at all accumulation levels. The 95% CI for S_{obs} never overlapped indicating that there were significant differences between the curves of the 2 sites at $p < 0.05$.

Dominant species, functional groups and relations to environmental factors

Small, motile detritus-feeding polychaetes of 2 species, *Aphelochaeta* sp. and *Cossura longocirrata*, made up more than 80% of all animals collected in samples from the Inner transect (Table 1). Those 2 species were also abundant on the Outer transect but were accompanied by large numbers of the carnivorous polychaete *Lumbrineris* sp. and tube-building polychaetes *Apistobranchus tulbergi* and *Maldane sarsi,* discretely motile and sedentary, respectively (Table 1).

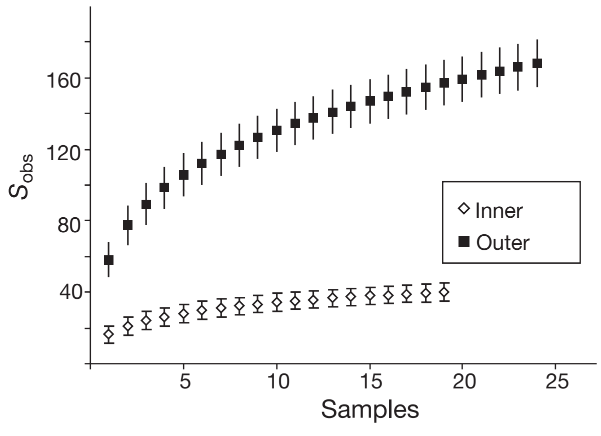

Fig. 3. Species accumulation curves for the Inner and Outer transects. The curves are plotted along with 95% CI

Five functional groups were found in the Inner transect samples (Table 2). Motile detritus-feeders (either surface or subsurface) made up almost 90% of all animals collected at this site. On the Outer transect, 12 functional groups were discriminated (Table 2). Motile surface detritus-feeders made up 44% of all animals. The distribution of fauna among the other groups was more even than on the Inner transect (Table 2).

The BIO-ENV analysis showed that at both sites the species distribution patterns could not be explained by the environmental variables considered in the present study. The correlations between the individual factors or combinations of factors and the biotic data were very weak (ranging from 0.01 to 0.40, Table 3).

Spatial patterns of whole communities

No evidence of spatial patterns of similarity estimated with the presence/absence data was observed

Table 1. Dominant species on the Inner and Outer transects. D: dominance; F: frequency of occurrence. Ten most abundant species are presented for each site

Inner	D (%)	F (%)
Inner		
Aphelochaeta sp.	51.0	100
Cossura longocirrata	31.4	100
Polycirrus arcticus	3.8	100
Chone paucibranchiata	2.4	100
Euchone sp.	2.3	100
Chaetozone setosa	3.2	95
Aglaophamus malmgreni	1.5	100
Heteromastus filiformis	0.8	89
Thyasira dunbari	0.7	63
Levinsenia sp.	0.4	68
Outer		
Aphelochaeta sp.	31.0	100
Lumbrineris sp.	9.3	100
Cossura longocirrata	8.2	100
Apistobranchus tullbergi	8.1	100
Chaetozone setosa	7.5	100
Leitoscoloplos mammosus	7.3	100
Maldane sarsi	5.9	100
Eteone flava/longa	1.4	100
Heteromastus filiformis	1.4	100
Melita formosa	1.2	50

Table 2. Percentages of functional types in total number of animals on the Inner and Outer transects. Functional group codes: first letter/s, feeding type — f: suspension-feeders, s: surface detritus-feeders, b: subsurface detritus-feeders, c: carnivores; last letter, mobility type — m: motile, d: discretely motile, s: sedentary; u: unknown functional type

Functional group	Inner	Outer
bs	–	6.1
ss	–	2.5
fs	2.6	0.5
sd	4.1	8.9
fd	–	0.2
f/sd	2.4	0.3
bm	33.0	18.5
cm	–	12.9
c/sm	–	1.4
sm	55.4	43.7
fm	–	0.1
f/sm	–	0.4
u	1.5	4.6

Table 3. BIO-ENV analysis: Spearman rank correlations (R_S) between biotic and abiotic similarity matrices on the Inner and Outer transects. Abiotic matrices include all combinations of environmental variables (*k*): sand: >0.063 mm fraction of sediment; TOC: total organic carbon in sediment; D: depth. Values in bold indicate the highest correlation

k	Variable	R_S	
		Inner	Outer
1	Sand	**0.40**	0.27
	TOC	0.01	**0.39**
	D	−0.01	−0.24
2	Sand, TOC	0.29	0.30
	Sand, D	0.20	0.27
	TOC, D	0.03	0.26
3	Sand, TOC, D	0.20	0.31

along the Inner transect. The spatial autocorrelation analyses between similarity and spatial distance matrices showed a homogenous distribution of species. The significant negative autocorrelation of Bray-Curtis similarity of untransformed data at the Inner transect occurred at a distance of 800 m indicating the possible presence of patches with a minimum radius of 800 m (Fig. 4).

Spatial patterns of similarity of untransformed data were evident along the Outer transect, although the relationship between similarity and distance was not simple or monotonic. The multivariate correlograms showed that the studied spatial patterns were patchy. On the correlogram of Bray-Curtis similarities of untransformed data at the Outer transect there were 2 significant negative autocorrelation minima, at 200 and 800 m, and 1 autocorrelation maximum. This may indicate a sequence of patches, homogenous patches of a minimum radius of 200 m and successive patches of similar composition separated by 600 m. One significant negative autocorrelation minimum at 800 m was detected on the correlogram of untransformed data at the Outer transect.

Spatial patterns in mobility groups

Four sedentary, 6 discretely motile and 22 motile species were recorded in samples collected on the Inner transect. Forty sedentary, 14 discretely motile and 93 motile species were found at the Outer locality.

The distribution of species of all mobility groups was homogenous at the Inner site: there was no significant Spearman's correlation between the presence/absence data similarity and distance matrices. In addition, no spatial structures were observed in the distribution of sedentary species at the Outer locality. The spatial configurations of discretely motile and motile species on the Outer transect were very similar. Both groups exhibited positive Spearman correlations of similarity and distance matrices indicating that samples taken close together were more similar than samples collected further apart (Table 4). Significant negative autocorrelation minima at multivariate correlograms indicated the occurrence of patches with a minimum radius of 800 m in distribution of both motile and discretely motile species (Fig. 5).

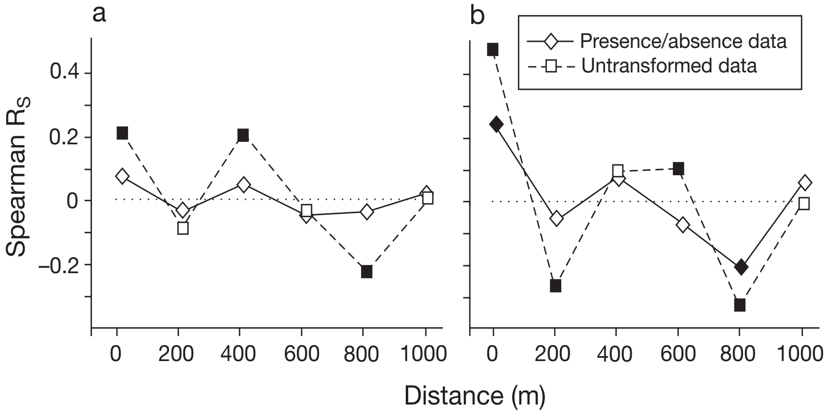

Fig. 4. Multivariate correlograms produced for Bray-Curtis similarities computed on untransformed and presence/absence data for samples collected on the (a) Inner and (b) Outer transects. Black symbols: significant autocorrelation values ($p < 0.025$ or $p > 0.975$); white symbols: non-significant values ($0.025 < p < 0.975$)

Table 4. Spearman rank correlations (R_S) between corresponding elements of sample Bray-Curtis index similarity matrices (based on untransformed and presence/absence data) and sample distance matrices on the Inner and Outer transects. Only presence/absence data were used in the analysis of mobility groups. *$p < 0.05$

	Inner		Outer	
	R_S	p	R_S	p
All species, presence/absence data	0.044	0.243	0.192	0.007*
All species, untransformed data	0.215	0.018*	0.257	0.004*
Sedentary species	–0.126	0.989	–0.003	0.504
Discretely motile species	0.003	0.433	0.165	0.013*
Motile species	0.082	0.160	0.201	0.004*

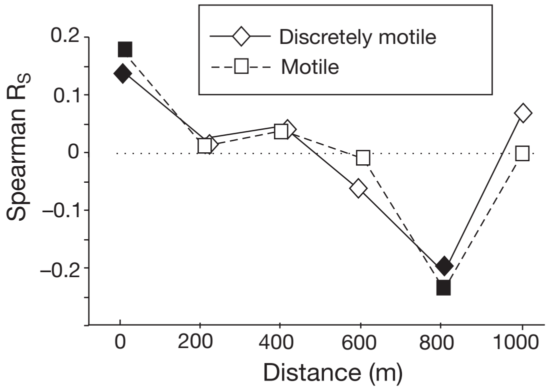

Fig. 5. Multivariate correlogram of Bray-Curtis similarities of motile and discretely motile species composition in samples (based on presence/absence data) collected on the Outer transect. Black symbols: significant autocorrelation values ($p < 0.025$ or $p > 0.975$); white symbols: non-significant values ($0.025 < p < 0.975$). No significant correlation between sample similarities and spatial separation was found for sedentary species

DISCUSSION

There was a strong spatially-related structure in benthic species composition in the biologically accommodated outer fjord community, while the physically controlled fauna of the inner fjord was very homogenous within the extent of the present study (1 km). The variation of species composition in samples from the Inner site (estimated using presence/absence data) was not related to distance between samples on a scale of hundreds of meters. The spatial variation in the glacial bay macrofauna was apparent only in changes in relative abundances among a few numerically dominant species (expressed by Bray-Curtis index similarities computed on untransformed data). A similar spatial pattern (consistent species pool and variations in numbers of dominant species) was also reported for glacier-proximal sediments in Kongsfjord (West Spitsbergen) (Kendall et al. 2003). The glacier-proximal benthic communities are structured by the chronic physical disturbance produced by the sedimentation of mineral materials transported by glacial melt waters (Włodarska-Kowalczuk et al. 1998, Włodarska-Kowalczuk & Pearson 2004, Somerfield et al. 2006). Only species resistant to continuous burial by sedimenting mineral particles and able to dwell in unstable, frequently resuspended and redeposited sediments can survive in glacier-proximal areas (Syvitski et al. 1987). The sample species richness was 3-fold lower in the Hornsund glacial bay (Inner locality) than in the Outer locality. The species pool in the glacial bay was very low, as the species accumulation curve started to level off after as few as 10 samples collected. Apparently, there are fewer species available for possible variation among samples in the Inner site community than in the Outer site community. The glacial bay community is impoverished not only in terms of species numbers but also with regard to functional group diversity; the fauna is almost entirely composed of 1 functional group: small, motile detritus-feeders. The biological interactions among species are limited due to the simplicity of the community structure, low densities of benthic populations and overwhelming effects of physical forcing induced by glacial disturbance. When the relation between the disturbance and the spatial heterogeneity of biological communities is studied, the relative scales of both the disturbance and the studied biotic patterns must be considered. Small-scale episodic disturbance events can increase biotic heterogeneity on a larger scale. For example, iceberg scouring of Arctic sediments can create a mosaic of patches of different successional stages following defaunations and, thereby, largely increase spatial heterogeneity on a larger scale (Gutt & Piepenburg 2003). The disturbance experienced by glacial bay benthic communities is chronic and operates on a bay-wide scale, i.e. several kilometers (Görlich et al. 1987), thus smoothing biological variability on a scale of hundreds of meters.

The spatial heterogeneity in the Outer site community was evident both in species composition and the numbers of dominant species populations. The site species pool and the sample species richness are very high at the Outer site. The outer basins of glacial fjords are inhabited by complex communities composed of animals from a wide range of size and functional types, presumably exploiting more resource niches and creating a complex system of biological interactions (Włodarska-Kowalczuk et al. 2005). For example, the Outer site samples contained large sipunculids *Golfin-*

gia margaritacea, which can influence the spatial variability of infaunal populations through sediment bioturbation (M. Kędra pers. comm.). Kendall & Widdicombe (1999) studied small-scale spatial patterns in the macrofauna of shallow, subtidal sediments in Plymouth Sound. They suggested that the occurrence and spatial variability of large bioturbating thalanassid shrimps were responsible for the patchiness observed in the spatial configurations of macrobenthic infaunal community at a scale of 500 m at one of the studied sites. Another site they studied was devoid of large bioturbators, and the infauna was homogenously distributed at scales from 50 cm to 500 m. The spatial structure of species distributions may be shaped by biological rather than physical factors as was shown by Hewitt et al. (1996), who found the same spatial patterns (in terms of intensity and patch size) of infaunal bivalve distributions at different sites irrespective of the contrasting hydrological regimes and sediment grain sizes.

A simple, monotonic relationship between sample similarity and distance is rarely observed in soft-bottom macrofauna studied on scales of tens or hundreds of meters (Somerfield & Gage 2000). Instead, patches of similar composition are formed (Morrisey et al. 1992). The patchiness of single-species distribution was detected at scales of ca. 10 m for estuarine soft-bottom bivalves (McArdle & Blackwell 1989) and 5 to 30 m for intertidal polychaetes and molluscs (Thrush et al. 1989). The spatial variation of selected groups of polychaetes dwelling in subtidal estuarine sediments was evident at scales ranging from 10 m to 3.5 km (Morrisey et al. 1992). How, and if, these small-scale, single-species spatial configurations translate into the coarser-scale multivariate spatial patterns of whole communities is not clear. Somerfield & Gage (2000) showed that strong patterns of aggregation of individual species do not necessarily induce similar patterns in multivariate patterns of the whole community. Multivariate pattern analyses average the patterns of variability of different taxa, which can differ considerably as was shown in, for example, major phyla for kelp holdfast-associated macrofauna (Anderson et al. 2005).

Spatial multivariate variation of undisturbed soft-bottom benthic macrofaunal communities seems to be evident on scales of hundreds of meters. Gray (2000) reported a 50% decrease of mean Bray-Curtis similarity of samples over 140 m and a 75% decrease over 450 m in the soft-bottom macrofauna of Norwegian oil fields. Kendall & Widdicombe (1999) observed a drop in similarity in sample pairs separated by 500 m (and consistent species composition at smaller scales) in the shallow-water, soft-bottom macrobenthic communities of Plymouth Sound. Patches with a radius of 200 m were evident in the undisturbed Outer locality in the present study in Hornsund. Patches 2.5 km in size and of consistent similarities were detected for large-bodied, soft-bottom epifauna studied at scales ranging from 600 m to 50 km (Stevens 2005). The soft-bottom macrobenthic heterogeneity seems to be less clear when larger scales (i.e. tens of kilometers) are considered. Ellingsen (2001) reported consistent composition of infauna across tens of kilometers on the Norwegian continental shelf and detected only a very weak negative correlation ($R = -0.4$) between Bray-Curtis similarity and sample distance and no relationship between the distance and the numbers of shared species across distances ranging from 10 to 130 km.

Spatial configuration of animals can be related to their spatial behavior mode (Reise 1979). The relation between mobility and patch size was apparent in the infaunal bivalves studied by Hewitt et al. (1996). We observed different patterns of mesoscale spatial variability in groups of species of different mobility: sedentary fauna was evenly distributed across the range of the present study and showed no sign of spatial aggregation, while clear patchiness was documented for motile and discretely motile organisms. These contrasts indicate the importance of post-settlement processes in setting spatial patterns in soft-bottom communities (see e.g. Olafsson et al. 1994). Motile species can react actively to, for example, the temporal and spatial variability of organic matter supply by burrowing through the sediments or passively migrating with the near-bottom water movements (e.g. Beukema & de Vlas 1989, Cummings et al. 1995). The distribution of sedentary fauna must be established at a settlement phase and can exhibit random configurations often associated with strong territoriality, as was shown with the tube-dwelling polychaetes by Reise (1979).

The spatial configuration of the fauna must be considered when sampling in order to describe the biotic variability within a given community or region. Spatial autocorrelation, i.e. the relationship between the position in space and the value being measured, can severely bias an accurate estimation of variance of replicates as well as alter the correct number of degrees of freedom in many statistical analyses (Legendre 1993). Our results support the opinion of Somerfield & Gage (2000) that replicate samples of soft-bottom benthos should be spatially dispersed to avoid autocorrelation pitfalls. The distance separating the samples collected from a ship in a subtidal basin at a single station can vary depending on depth and water movement, but the application of GPS to navigate should limit this variation to a range of a few meters. Somerfield & Gage (2000) recommended that replicate samples be taken at least 40 m apart. In undisturbed sediments of the Outer site, the samples collected at a single station were much more similar than samples separated by 200 m, and so treating them as replicates can bias subsequent statistical analyses. We strongly recommend spatial separation of replicate samples in routine soft-bottom macrobenthic studies.

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