Depth-related spatial patterns of sublittoral blue mussel beds and their associated macrofaunal diversity revealed by geostatistical analyses

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ABSTRACT: The blue mussel *Mytilus edulis* is a foundation species with ecosystem engineering functions in the brackish, non-tidal Baltic Sea. In this study from the western Gulf of Finland, the relationship between the spatial patchiness of blue mussels and the diversity of associated macrofauna was examined across small scales (centimeters to meters) for the first time in subtidal habitats. It was demonstrated using geostatistical tools that blue mussel abundance and the diversity of associated macrofauna varied and interacted at 2 depths. Classic analyses (ANOVAs, correlations and multivariate techniques) detected no relationships between the abundance of blue mussels and their associated macrofaunal diversity, or differences in the abundance of mussels or the diversity of associated macrofauna between depths. Using semivariograms, differences in spatial heterogeneity between depths emerged: i.e. patchiness at 5 m and random patterns at 8 m depth. Cross-semivariograms detected negative spatial co-variation between blue mussel abundance and diversity of macrofauna at 5 m, but positive and neutral spatial relationships at 8 m depth. Combining the approaches suggested that high dislodgment of mussels in shallow environments causes this pattern. Dislodgement effects may be compensated for by increased turnover of small mussels in patches within mussel beds, which would result in reduced habitat space for associated macrofauna. On the basis of our results, it is suggested that patchiness of a foundation species is an ecological response, or result of a disturbance, that reduces the diversity of the associated macrofaunal community.

KEY WORDS: Foundation species · Blue mussels · Baltic Sea · Biodiversity · Fractal dimension · Semivariogram · Cross-semivariogram · Spatial heterogeneity

INTRODUCTION

Theoretical and empirical studies predict that the number of species coexisting in a given area will increase with the amount of available habitat space and/or with structural complexity (Douglas & Lake 1994, Kostylev et al. 2005), and the provision of this space or complexity is a common function of a foun-dation species. Foundation species forming biogenic habitats such as kelps, sea grass meadows, coral reefs and bivalve beds, seem to vary in their function as ecological modulators of diversity (Jones et al. 1997, Stachowicz 2001, Connell 2003). In addition to species-specific differences among the foundation species, other mechanisms explaining this variation in function may be related to potential changes in the

arrangement of patches or groups of individuals (Jones et al. 1997, Cole 2010). The effects of habitat space or complexity on diversity have been studied on rocky shores and, among other results, it has been found that structural complexity directly leads to an increase in species richness, while surface area enhances the density of macrofauna (Kostylev et al. 2005). However, the effects of spatial patterns (e.g. patchiness) of foundation species on the diversity of associated fauna (or the relationship between patterns of foundation species and diversity across scales) have not been studied in marine ecosystems. Therefore a crucial gap in the knowledge of foundation species concerns the effect of their patchiness on their hosted community and diversity. Spatial patchiness is understood in this study as the tendency of individuals to position themselves close to each other (Rietkerk et al. 2002), creating a spatial dependence in their distribution which generates a greater variability at larger scales (i.e. more variability between samples further apart) and where heterogeneity can be estimated (Erlandsson et al. 2005). The formation of spatial patchiness often seems to be triggered by extrinsic forces (e.g. physical disturbance and predation), but can also be produced by intrinsic factors such as competition, facilitation and recruitment preferences (Rietkerk et al. 2002, Erlandsson & McQuaid 2004, Erlandsson et al. 2011, Commito et al. 2014). To study patchiness it is necessary to examine the spatial heterogeneity of the system (Kostylev et al. 2005). Spatial heterogeneity is the degree of dependence between the variability in abundance of a species and spatial lags, where a lag is defined as the space-interval between one point and another, here the range of different distances (either close or far apart) between the centers of 2 sampling quadrats (e.g. Dale 2000, Kostylev & Erlandsson 2001). Thus, lack of dependence between variability of a variable and the lags implies stochasticity in the distribution of a variable in space, and thus lack of spatial heterogeneity and absence of patchiness (Erlandsson et al. 2005).

In the Gulf of Finland, the blue mussel *Mytilus edulis* meets the edge of its range of distribution, which is determined by low salinity levels (5 to 6 psu) (Westerbom et al. 2002). Here, blue mussels exhibit 'dwarfism', caused by slow growth (typically around 5 mm yr^{-1}), evidenced by a small adult size class distribution (4 to 25 mm) in comparison to other sites in the world (Riisgård et al. 2014), including NW Europe (Wallace 1980, Loo & Rosenberg 1983, Dolmer 1998, Buschbaum et al. 2009). Historically, the relationship between abundance of blue mussels and the hosted macrofaunal community in terms of species

richness and biodiversity is expected to be positive. Nevertheless, in the Gulf of Finland and in some other regions in the world, this relationship has been found to be weak and results suggest that it varies across spatial scales due to changes in the quality of patches and mussel size structure (Buschbaum et al. 2009, Cole & McQuaid 2010, Koivisto et al. 2011).

Evidence demonstrates that small-sized blue mussels, solitary mussels or patches exhibiting more edge effects support a lower density and diversity of associated macroinvertebrates (Norling & Kautsky 2007, 2008, Cole 2010, Koivisto et al. 2011, Valdivia et al. 2014). Therefore, it is probable that the strong inter-patch variability in abundance and size structure in patches within the mussel bed is the first source of variability for invertebrate diversity in the Baltic Sea (Westerbom et al. 2002) as in other places around the world (Buschbaum et al. 2009, Cole & McQuaid 2010, Jungerstam et al. 2014, Valdivia et al. 2014). Changes in the abundance and mussel size structure among regions have been attributed to abiotic gradients such as wind-wave exposure and depth at specific locations (Westerbom et al. 2002, Koivisto & Westerbom 2012), and to primary productivity gradients at larger (100s of kilometers) scales (Cole & McQuaid 2010). In general, a clear relationship between mussel abundance and the diversity of associated macrofauna has not been established, since small-scale variability (at 10s of meters), such as among samples, tends to predominate in the Gulf of Finland (Koivisto et al. 2011). Therefore, this study focuses on the variation of blue mussels at a small scale, that is in terms of abundance and size structure from patch to patch (separated by centimeters or meters) and how the configuration of patches may be determining the total diversity (Cole 2010, Jungerstam et al. 2014).

In the Gulf of Finland, blue mussels extend their vertical distribution from ~1 to 30 m. In the shallow range of this bathymetric zone, at 1 to 4 m depth, they are found in low abundances due to interspecific competition and disturbance. In the deeper range, intraspecific competition is important, and they also struggle to find enough food as primary productivity becomes a limiting factor (Westerbom et al. 2002). At shallow depths (<5 m), mussel–diversity relationships may thus be driven by small-scale biotic interactions such as blue mussels competing for space with algae. Sometimes mussels are outcompeted by opportunistic algae or suppressed by the whiplash effect of the seaweed *Fucus vesiculosus*, resulting in a net reduction in the number of mussels and consequently reduced macrofauna diversity (Kiirikki 1996, Kiirikki & Ruuskanen 1996, Westerbom et al. 2002,

Kraufvelin et al. 2007, 2012, Koivisto & Westerbom 2010). Additionally, important regional mussel predators such as birds and fish, in the absence of important predators such as crabs and starfish, may also more easily harvest mussels at shallower depths and clearer waters than deeper down (Wallace 1980, Meissner & Bräger 1990, Öst & Kilpi 2000, Lappalainen et al. 2005). Among abiotic factors known to control mussel abundance and distribution within a region, the most relevant ones at shallow depths are ice abrasion and wave force (e.g. Nehls & Thiel 1993, Westerbom et al. 2002).

Here, the effects of the distribution of mussel patches on the diversity of the associated macrofaunal community within locations (centimeters to meters) were examined at 2 depths (5 and 8 m). A first step was to examine whether both density and biomass of mussels and the associated macrofaunal diversity differed between depths. Variability in the mussel/diversity relationship was investigated using a classic factorial analysis. The next step was to examine the spatial patchiness of the mussel bed and its associated macrofaunal diversity using geostatistical tools at different depths within islands, i.e. applying spatial pattern analyses at scales from centimeters to 10s of meters. Semivariograms and fractal dimension analysis were used in the study to detect spatial heterogeneity (see also Erlandsson et al. 2005, Díaz et al. 2011, 2012).

At shallow depths (4–5 m), it was hypothesized that larger mussels would dominate due to higher growth rates in response to higher food supply and improved water circulation. But, also it is possible that a dominance of small mussel size classes grouped in patches might be expected due to faster turnover caused by wave action and other disturbances, which may give rise to a more patchy distribution of mussels at shallower than at deeper depths (below 8 m). Both scenarios may have consequences for the associated macrofaunal diversity and were thus studied.

MATERIALS AND METHODS

Study sites and sampling of blue mussels and associated macrofauna

In order to compare abundances (density and biomass) and spatial patterns of blue mussels and the diversity of the associated macrofauna on rocky bottoms, mussel patches were sampled in September 2008 at 2 sites (ca 1.5 km apart), in the western Gulf of Finland, using 2 depths (5 and 8 m) at each site.

Visually, these sites exhibited similar coverage of mussels (>70% of the rocky substratum was covered by mussels); the depths of 5 and 8 m were chosen because mussel biomass is known to peak at these depths (Westerbom et al. 2002). Both sites were considered as independent from each other. It is worth noticing that at depths shallower than 4 to 5 m, the cover of mussels is reduced significantly and mussels are replaced by diverse types of macroalgae, whereas at depths deeper than 5 m, there seems to be a transition zone, moving from macroalgal domination to mussel domination. At 8 m, the mussel beds seem to contain more mussels and have fewer bare spaces within the bed, in contrast to 5 m depth, where the mussel bed more often exhibited gaps without mussels, probably caused by differential disturbances related to wave action (Kiirikki 1996, Westerbom et al. 2002). Due to safety and practical reasons, sampling depth was limited to 8 m.

The two sites, Örkobben (59° 47.653′ N, 23° 10.979′ E) and Vaktanlandet (59° 47.498′ N, 23° 11.756′ E), were both located in the outer archipelago, and they were characterized by moderate wave exposure (Baardseth index >4, see Westerbom & Jattu 2006). The Baardseth index describes the degree of wave exposure and it has been used in numerous other studies in the area (e.g. Kiirikki 1996, Ruuskanen et al. 1999, Westerbom et al. 2002, Westerbom & Jattu 2006). Also, the bathymetric slopes at both sites were similar, with 11.2 and 11.7° inclinations from 0 to 10 m at Örkobben and Vaktanlandet, respectively; additionally, salinity (5 to 7 psu) and oxygen concentration (>8 ml O_2 l^{-1}, i.e. oxygen saturated conditions) remain constant and stable in the area down to ~30 m depth. The concentration of chl a tends to decrease with depth, although it remains rather stable down to 10 m depth (~3 µg l^{-1}) (see e.g. Kraufvelin & Díaz 2015). Below 10 m depth, the food supply becomes a limiting factor for mussels (Westerbom et al. 2002). Finally, a low level of topographic complexity in the sampling scheme was achieved by choosing to sample platforms free from cracks and crevices. Transects, as well as random quadrats, were sampled at each depth and site (see 'Sampling for the explicit spatial pattern analyses').

Sampling for the classic factorial analyses (non-spatial analyses)

Thirteen randomly distributed samples were taken from each depth (5 and 8 m) and each site (N = 52 samples: 13 replicates × 2 depths × 2 sites). The sam-

ples were taken by 2 SCUBA divers using a metal frame of 0.15 × 0.15 m (the grain scale) which had a netbag attached to one of its ends; each bag had 6 compartments. The metal frame had a height of 5 cm, which allowed the rock surface contained within the area of the metal frame to be scraped with a sharpened metal scraper (specially designed to remove all biota). The scraped material was then easily introduced to the bag losing only a negligible proportion of organisms. The grain scale of the frame was used, since it has previously been demonstrated that the species-area curve flattens out above this scale (or patch size), i.e. diversity will not increase above this grain scale in blue mussel beds of the northern Baltic proper (Norling & Kautsky 2007, 2008).

Sorting process and analyses

All samples collected were placed in jars with 70 % ethanol for later analysis. To facilitate the counting of all individuals, the macrofauna was sorted by size through a series of sieves (mesh sizes 8, 4, 2, 1 and 0.5 mm), after which the macrofauna was identified to the lowest possible taxonomic level. The smallest fractions were analyzed with the aid of a dissecting microscope (Leica S6E). The abundance and richness of the macrofauna was used to calculate the Shannon-Wiener index of diversity (log base 10).

To test whether there was a relationship between blue mussels (density and biomass) and diversity of associated macrofauna, correlation analyses were performed on each combination of depths and sites. Blue mussel biomass (dry weight, shell free) was calculated from density and length values according to the formula presented in Westerbom et al. (2002) for each size class. The correlation analyses used were Pearson or Spearman tests depending on whether the data fulfilled the conditions for parametric tests or not. Differences in Shannon-Wiener diversity were tested for the factors Site and Depth using univariate analysis (2-way ANOVA). To test whether or not the species composition of the macrofauna assemblages inhabiting the blue mussel beds differed between sites and depths, a 2-way permutational multivariate ANOVA (PERMANOVA), with Site and Depth as factors, was performed on Bray-Curtis similarities (Anderson 2005). In all these analyses (univariate and multivariate), Site and Depth were treated as a random and as a fixed factor, respectively. In the multivariate analyses, data were transformed using fourth root-transformation to balance the influence between more dominant or rare species/taxa. Finally,

differences among sites and depths were gauged using canonical analysis of principal coordinates (CAP; Anderson et al. 2008), and the contribution of individual species/taxa to the observed differences between depths was listed using SIMPER analysis (Clarke 1993).

Size class structure of blue mussels was estimated for each combination of site and depth. The chosen size classes of blue mussels corresponded to the different sieve layers: >8, 8–4, 4–2, 2–1, and 1–0.5 mm. This was to test whether size-class structure varies between sites and depths and therefore influences the associated macrofauna diversity. To test whether blue mussels were homogeneous in density among size classes, contingency tables based on the Chi-square test were used. Finally, to test whether the density of each size class differed between different depths, goodness of fit Chi-square test was used. It is worth noting that mussels >10 mm were not numerically dominant in the sampling.

Sampling for the explicit spatial pattern analyses

Spatial patterns at each depth and site were assessed using 15 m long transects running parallel to the island shorelines on rocky substrata only. This transect extension was chosen as having enough length to capture spatial changes in mussel biomass at small scales (centimeters to meters). Transects were sampled using contiguous quadrats of 0.15 × 0.15 m (the grain scale). Each transect contained 60 quadrats. The minimum lag (i.e. the distance between the centers of 2 quadrats) used was 0.25 m and the maximum lag used was 7.5 m. The minimum lag was determined based on (1) a biological criterion: to avoid disturbing the mobile macrofauna of the contiguous quadrats; and (2) a statistical criterion: following Dungan et al. (2002) to calculate the lag using the formula (minimum lag = extent / number of samples), where 'extent' refers to the length of the transect. The samples were taken by 2 SCUBA divers (N = 240 samples: 60 samples × 4 transects). Thus, our analyses comprised 30 lags spanning from 0.25 to 7.5 m within a transect length of 15 m. The transects were placed randomly, following visual inspection of the surroundings and selection of a 15 m line where no large crevices, cracks or depressions were present which could affect spatial heterogeneity (see Díaz & McQuaid 2011). Then, a measuring tape was set on the rock and samples were collected in a bag attached to quadrats, as described earlier.

To investigate the existence and nature of spatial heterogeneity (or the presence of regularity in the spatial configuration of patches), semivariogram and fractal analyses were combined. Semivariograms are useful for spatial analysis or time series analysis. Both methods determine the variability of a variable depending on a range of lags, while fractal dimension is a measure of heterogeneity on the same range of lags, effectively distinguishing the periodicity peaks from which the variability of abundances increases and decreases (Kostylev & Erlandsson 2001, Erlandsson & McQuaid 2004). From a more general perspective, these analyses distinguish between 'scale sensitivity' and 'scale invariance' of variables in time or space series (Dal Bello et al. 2015). In this specific case, the periodic peaks represent patches on which mussels and the diversity are distributed in space (Erlandsson et al. 2005), i.e. changes in variability as a function of the lag (spatial dependence of the variability). Semivariance ($y_{(h)}$) was calculated for different lags across the shore using the formula:

$$Y_{(h)} = \frac{1}{2N_{(h)}} \sum_{i=1}^{N_{(h)}} (Z_{i+h} - Z_i)^2 \qquad (1)$$

where $N_{(h)}$ is the number of pairs of data points separated by the lag h, and Z_{i+h} and Z_i are the values of the examined variables at points/lags $i + h$ and i. Thirty lags were included in the analyses (see e.g. Erlandsson et al. 2005). The spatial heterogeneity, defined as the change in the value of variance across lags (detected by the presence of a significant linear relationship in the logarithmic semivariogram), was estimated using the fractal dimension D (e.g. Kostylev & Erlandsson 2001, Erlandsson et al. 2005), calculated as:

$$D = \frac{(4 - m)}{2} \qquad (2)$$

where m represents the absolute slope of the regression between the natural logarithm (ln) of the semivariance and the ln of the lag (e.g. Dale 2000). D is an index of self-similarity within the concept of fractal geometry (Erlandsson et al. 2005, Dal Bello et al. 2015) and here the self-similarity represents the resemblance of patches among themselves across spatial scales, indicated here by different lags (Díaz & McQuaid 2011). The value of D varies from 1 to 2, where values closer to 1 indicate 'gradient pattern' of the variability of a variable in relation to the lag. Values around 1.5 indicate a cut-off between a gradient pattern of the variability of the variable and the existence of large patches across lags, which tend to become smaller and less periodic as D approaches 1.97 (see Kostylev & Erlandsson 2001). Finally, the

range of values between ca. 1.97 and 2.00 indicates the presence of a homogeneous or random pattern (Erlandsson et al. 2005), i.e. a lack of periodicity across lags, and consequently a lack of patchiness/ spatial heterogeneity, indicating no correlation between variance and scale. The advantage of using semivariograms instead of spatial autocorrelation is the possibility for estimating heterogeneity and the detection of changes in the periodicity of variability across lags referring to different 'scaling regions'. These relationships between semivariance of a variable and the lag can consist of one or more subrelationships (scaling regions) with different slopes. A scaling region can be described as a particular type of patchiness at a range of lags which can be nested within another type of patchiness at a range of larger lags, creating an emergent hierarchical structure. Scaling regions were detected using the 3-step procedure described in Kostylev & Erlandsson (2001) and Erlandsson & McQuaid (2004): (1) residual analysis to determine break points between scaling regions, (2) regression analyses of the different slopes of suggested scaling regions, and (3) t-tests comparing different adjacent slopes to detect true scaling regions.

Co-variation between blue mussel biomass and diversity of associated macrofauna through cross-semivariogram analyses

The degree of spatial co-variation between the biomass of blue mussels and their associated macrofaunal diversity may exhibit positive spatial relationships at some lags, while at others the relationship may be neutral or negative. The relationships were analysed using cross-semivariogram analysis to examine the spatial co-variation of both variables at specific lags (Dale 2000). The cross-semivariance ($Y_{xz(h)}$) was calculated as:

$$Y_{xz(h)} = \frac{1}{2N_{(h)}} \sum_{i=1}^{N_{(h)}} (X_{i+h} - X_i)(Z_{i+h} - Z_i) \qquad (3)$$

where $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h; X_{i+h} and X_i, and Z_{i+h} and Z_i are the values of the variables blue mussel biomass and associated diversity, respectively, at points/lags $i + h$ and i.

A positive cross-semivariance value at a certain lag indicates a positive co-variation between variables at that scale (lag), whereas a negative cross-semivariance value indicates a negative co-variation. Cross-semivariance values around 0 indicate a neutral rela-

tionship between variables at that range of scales. The distributions of pairs of variables along each transect were randomized 1000 times and cross-semivariance values were calculated at each scale for each random permutation run in Matlab (see Quinn & Keough 2002). Each randomized value was then compared with the appropriate observed cross-semivariance value. Thus, the probability was calculated that each observed cross-semivariance value was high (positive relationship) or low (negative relationship) by chance alone, and an alpha level of 0.05 was applied on these calculations. The ecological implications of detecting a positive relationship between biomass of mussels and diversity of associated fauna in a cross-semivariogram is that, as predicted, an increase or decrease in variability of mussel biomass at certain lags will be accompanied by a similar increase or decrease in variability of diversity of associated macrofauna. In contrast, a negative relationship implies that an increase in variability of mussel biomass at certain lags will be followed by a decrease in variability of the diversity of macrofauna (and vice versa) at the same lags. A lack of relationships between diversity of associated macrofauna and mussels indicates that the 2 variables do not co-vary at the spatial lags considered.

RESULTS

Variability in blue mussel abundance (density and biomass) and macrofaunal diversity between sites and depths: classic factorial analyses

Contrary to expectation, no correlations or significant relationships were found between blue mussel abundance (density and biomass) and the diversity of associated macrofauna at any of the depth and site combinations studied ($p > 0.05$ for all Pearson or Spearman correlations). In the 2-way mixed effects ANOVA, there were significant differences (in mussel abundance, mussel biomass and the diversity of the associated macrofauna) between sites, but not between depths (Table 1A,B, Fig. 1A,B). In contrast, analyses using a 2-way mixed effect PERMANOVA on the species composition showed a significant difference for the interaction term Site × Depth (Table 1C). This significant interaction was expressed as more distinct differences in community composition between 5 and 8 m at Örkobben than at Vaktanlandet.

The differences in species composition are displayed using CAP plots (Fig. 1C,D), which show that depths within sites exhibit a separation in community

Table 1. (A) Univariate 2-way mixed effects ANOVA describing blue mussel density (data square root [$x + 1$] transformed) and biomass (data fourth root [Ln($x + 1$)] transformed). (B) Univariate 2-way mixed effects ANOVA describing the mussel-associated macrofaunal community using the Shannon index. (C) Multivariate analyses of species composition, using permutational multivariate ANOVA (PERMANOVA) (data fourth root transformed). Post-hoc test used for the interaction was 'multivariate pairwise comparisons'. These analyses included the same factors: 2 sites and 2 depths. *$p < 0.05$; ***$p < 0.001$; NS: non-significant

A	df	MS	F (p)
Density			
Site (random)	1	795.14	26.31 (0.001)***
Depth (fixed)	1	7.75	0.21 (0.73) NS
Site × Depth	1	37.64	1.25 (0.27) NS
Residuals	48	30.21	
Biomass			
Site (random)	1	1.25	27.83 (0.001)***
Depth (fixed)	1	0.13	2.78 (0.34) NS
Site × Depth	1	0.047	1.05 (0.31) NS
Residuals	48	0.045	
B	df	MS	F (p)
Site (random)	1	0.22	39.46 (0.001)***
Depth (fixed)	1	0.03	133.09 (0.055) NS
Site × Depth	1	0.0002	0.04 (0.83) NS
Residuals	48	0.005	

Significant differences:
Site: Örkobben > Vaktanlandet
Depth: 8 m > 5 m

C	df	MS	Pseudo-F (p)
Site (random)	1	575.9	2.7 (0.01)*
Depth (fixed)	1	2.334.4	0.5 (0.48) NS
Site × Depth	1	435.6	2 (0.047)*
Residuals	55	255.14	

Significant differences:
Site: Vaktanlandet ≠ Örkobben
Site × Depth: Örkobben & Vaktlandet: 8 m ≠ 5m

composition corroborating and complementing the PERMANOVA on composition. Both sites exhibit a similar degree of internal variability between depths (Fig. 1C,D). The taxa contributing most to differences in species composition between depths were revealed by SIMPER analyses. *Marenzelleria* spp., Oligochaeta, and Turbellaria contributed most to the average dissimilarity of 24% between depths. All these groups were more abundant at 8 m depth. Additionally, Oligochaeta, Turbellaria, Sabellidae and *Gammarus* spp. were the taxa contributing most to the average dissimilarity of 21% between sites.

The size class structure analyses of blue mussel beds revealed the predominance of small sizes below 8 mm, but individual mussels were still up to 20 mm.
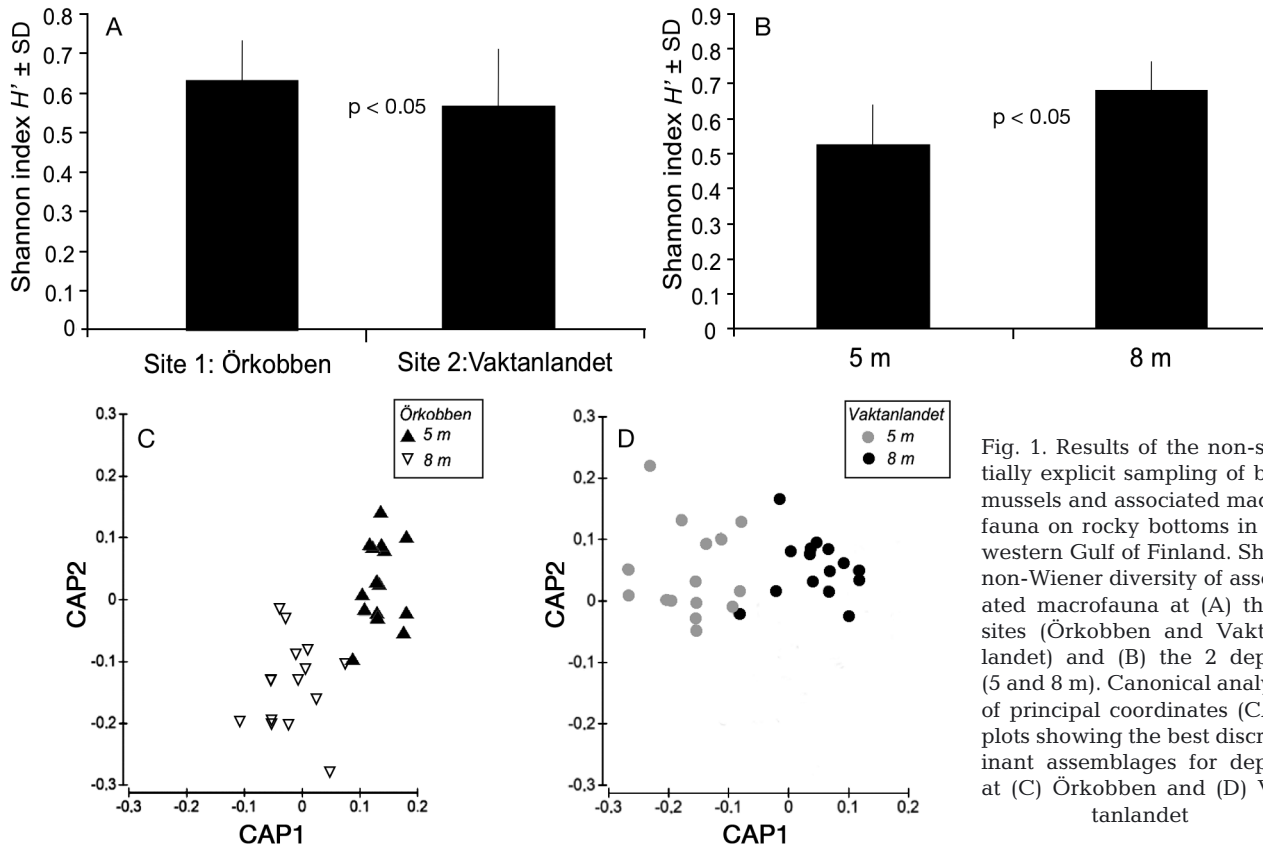
Fig. 1. Results of the non-spatially explicit sampling of blue mussels and associated macrofauna on rocky bottoms in the western Gulf of Finland. Shannon-Wiener diversity of associated macrofauna at (A) the 2 sites (Örkobben and Vaktanlandet) and (B) the 2 depths (5 and 8 m). Canonical analysis of principal coordinates (CAP) plots showing the best discriminant assemblages for depths at (C) Örkobben and (D) Vaktanlandet

At 5 m depth, the beds were dominated by the size classes 1–2 and 2–4 mm (Chi-square tests, p < 0.05). At 8 m depth, a well-mixed bed containing mussels of all size classes >1 mm was observed (Chi-square tests, p > 0.05; Fig. 2A,B). Nevertheless, a predominance of mussels <1 mm was observed at both sites and depths, representing mostly the recruits of the current sampling year (Fig. 2A,B).

Spatial patterns of blue mussel biomass and the associated macrofaunal diversity at different depths: semivariogram and fractal analyses

We detected the presence of patchiness in mussel beds at 5 m depth (significant regressions in semivariograms with slope deviating from 0: $D < 1.97$; Table 2), in contrast to mussel beds at 8 m depth. The biomass of blue mussels at 5 m depth showed spatial het-
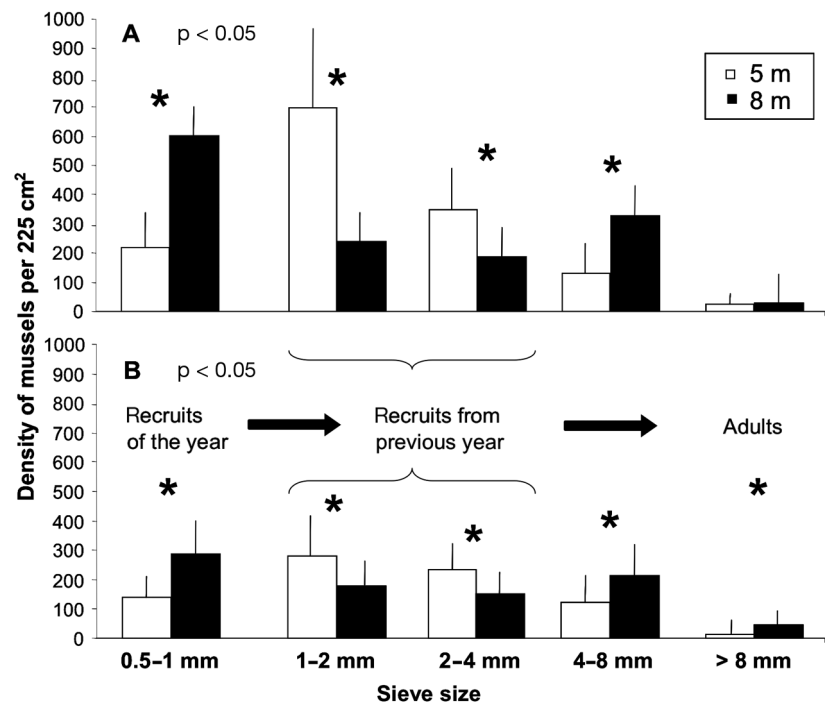

Fig. 2. Size class structure of blue mussel beds studied at (A) Örkobben and (B) Vaktanlandet at 5 and 8 m depth. There were significant differences (p < 0.05) among size classes for each site-depth combination (contingency table of Chi-square tests). Asterisks denote significant differences between depths in the corresponding size classes. Error bars are SD

Table 2. Detection of dependence between semivariance and lag in transects at each site. (A) Detection of spatial heterogeneity: regression components of the logarithmic semivariograms and fractal dimensions (D) for the different spatial scales of distribution of mussel biomasses and diversity of associated macrofauna at the different depths and sites. Significant spatial dependence or heterogeneity is marked in bold. Analyses significant at p < 0.05 in bold. (B) Multiple scaling regions for mussel bed at Örkobben (ÖR) and diversity of the associated macrofauna community at Vaktanlandet (VL)

Transect	Lag (m)	Regression components Slope	SE	R^2	t (df)	D	p	Spatial pattern
A								
Örkobben								
Mussels at 5 m	0.25–7.5	0.1	0.03	0.21	2.78 (27)	1.95	**0.01**	Patchy (2 scaling regions)
Diversity at 5 m	0.25–7.5	0.07	0.04	0.18	1.84 (27)	1.96	**0.05**	Patchy
Mussels at 8 m	0.25–7.5	−0.04	−0.05	0.02	−0.71 (27)	1.98	0.48	Random/ scale independence
Diversity at 8 m	0.25–7.5	0.01	0.04	<0.00	0.16 (27)	1.99	0.89	Random/ scale independence
Vaktanlandet								
Mussels at 5 m	0.25–7.5	0.12	0.03	0.40	4.5 (27)	1.94	**0.01**	Patchy
Diversity at 5m	0.25–7.5	0.22	0.02	0.77	9.72 (27)	1.89	**0.01**	Patchy (2 scaling regions)
Mussels at 8 m	0.25–7.5	−0.02	0.04	0.01	−0.60 (27)	1.99	0.55	Random/ scale independence
Diversity at 8 m	0.25–7.5	−0.05	0.03	0.10	−1.75 (27)	1.98	0.09	Random/ scale independence
B								
ÖR: mussels at 5 m	0.25–2.25	0.18	0.06	0.60	3.08 (7)	1.91	**0.02**	Patchy
	2.50–7.5	0.25	0.1	0.26	2.58 (19)	1.88	**0.02**	Patchy
VL: diversity at 5 m	0.25–4.75	0.25	0.03	0.81	8.65 (9)	1.87	**0.01**	Patchy
	5.00–7.5	0.72	0.24	0.50	3.10 (9)	1.64	**0.01**	Trend

erogeneity (spatial dependence between mussels and lags) indicating patchy distribution of mussels at both Örkobben (Table 2A, Fig. 3A) and Vaktanlandet (Table 2A, Fig. 4A). Similarly, the spatial pattern of diversity of associated macrofauna at 5 m depth exhibited significant spatial heterogeneity at both Örkobben (Table 2A, Fig. 3B) and at Vaktanlandet (Table 2A, Fig. 4B).

Additionally, 2 positive scaling regions, corresponding to 2 types of patchiness at different scales in the mussel distribution, were recognized at 5 m depth at Örkobben using semivariograms (Table 2B). The first scaling region ranged between lags 0.25 and 2.25 m, and the second between lags 2.5 and 7.5 m (Table 2B); the 2 scaling regions are represented by 2 significant slopes in the right-hand panel in Fig. 3A. In contrast, the diversity of associated macrofauna exhibited one scaling region ranging across all lags from 0.25 to 7.5 m (Table 2A), represented by a single significant regression line (Fig. 3B; right-hand panel). At Vaktanlandet at 5 m depth, the biomass of blue mussel distribution showed one scaling region ranging from 0.25 to 7.5 m (Table 2A, Fig. 4A; right-hand panel). Nevertheless, the diversity of associated macrofauna exhibited 2 positive scaling regions, denoting hierarchical patchiness, as was the case for mussels at Örkobben. The first scaling region was between the lags 0.25 and 4.75 m and the second between lags 5 and 7.5 m (Table 2B, Fig. 4B; right-hand panel).

The biomass of mussels and the diversity of associated macrofauna at 8 m depth did not exhibit spatial heterogeneity at either site, with scale invariance or random spatial patterns (slopes not deviating from 0 and therefore non-significant regressions in the semivariograms) with $D > 1.97$ (Table 2A, right-hand panels of Figs. 3C,D & 4C,D).

Spatial relationships between biomass of blue mussels and associated macrofaunal diversity at specific lags: cross-semivariogram analysis

Cross-semivariogram analyses quantify and represent changes of the relationship between variability of mussel biomass and of the diversity of associated macrofauna at each lag. The changes in the cross-semivariance values span from positive to negative among transects at different depths. For example, there was negative spatial co-variation at specific lags, between blue mussel biomass and the diversity of associated macrofauna at 5 m depth at both sites, especially at greater lags. In contrast, at 8 m depth, there was either positive or no co-variation between mussel biomass and the diversity of associated macrofauna (Fig. 5). More specifically, the cross-semivariograms detected the presence of negative co-variation between Örkobben blue mussels and the diversity of associated macrofauna at specific lags, ranging from 0.25 to 7.5 m, at 5 m
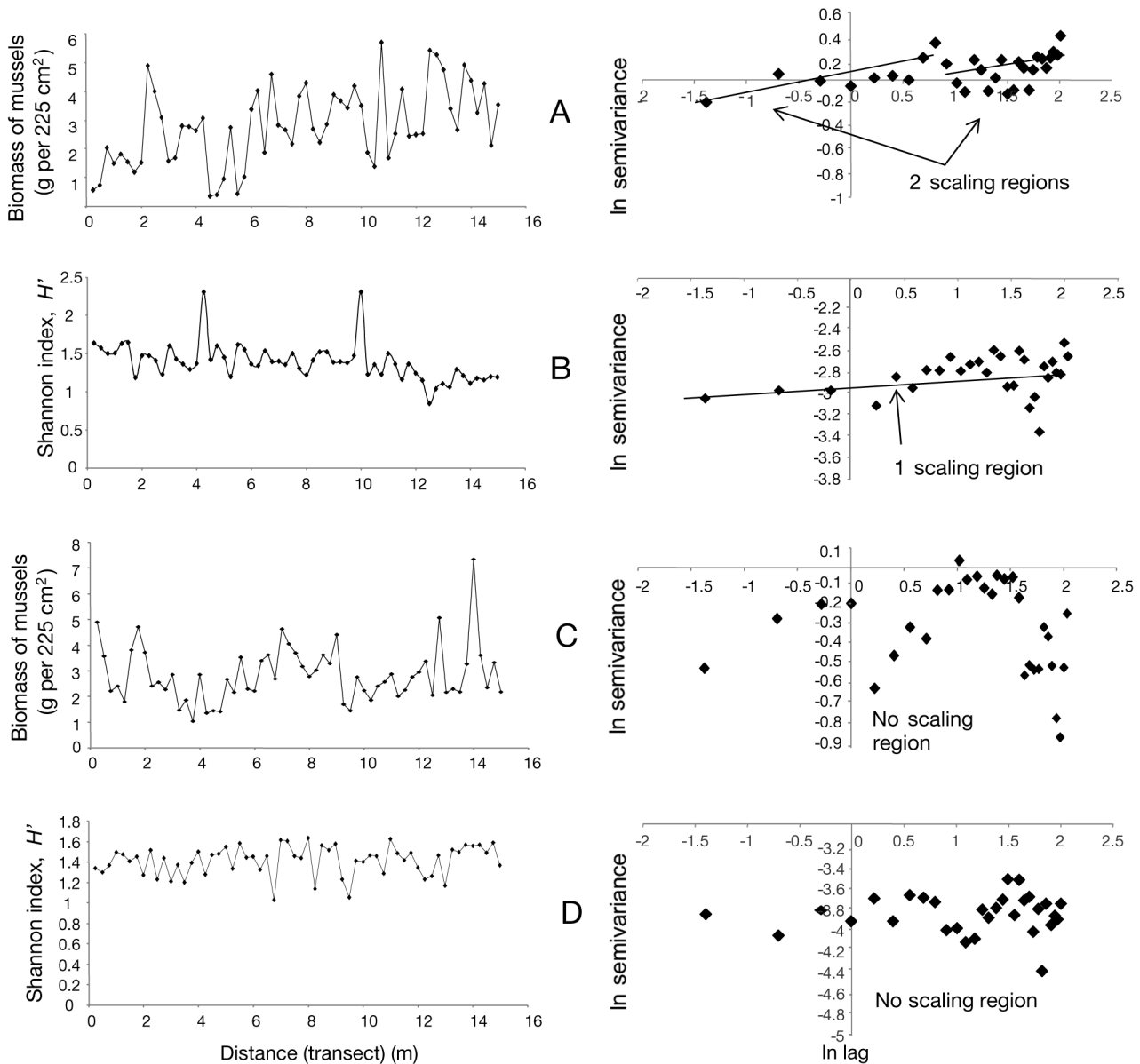
Fig. 3. Site 1: Örkobben (A,C) Distribution of mussel biomass at the different transects with corresponding semivariograms (right-hand panels); (A) and (C) correspond to a depth of 5 m and 8 m, respectively. Solid regression lines indicate significant scaling regions (patchiness) at p < 0.05. (B,D) Distribution of the diversity of the associated macrofauna community to the respective mussel beds, with the corresponding semivariograms on the right-hand side, where solid lines indicate the presence of scaling regions; (B) and (D) correspond to a depth of 5 m and 8 m, respectively. A scaling region is defined as the dependence between semivariance and lag, which denotes a specific type of patchiness. Lack of one or multiple scaling regions indicates spatial independence of the dependent variable

depth (Fig. 5A). It was possible to distinguish 2 sections where the lags were significant: 2 to 3.75 m and 5.75 to 7.5 m at 5 m depth at Örkobben. At Vaktanlandet, similar trends were detected: negative spatial co-variation at 5 m depth, which was significant at the larger lags 5 to 7.5 m (Fig. 5C). In fact, it is precisely at lags between 5 and 7.5 m that a negative spatial relationship between mussels and

the diversity of associated macrofauna was found at both sites.

In contrast, lack of spatial co-variation was detected at 8 m depth at Vaktanlandet (Fig. 5D). Yet, at Örkobben there was positive co-variation between mussels and their associated macrofauna diversity, significantly so at lags ranging from 0.25 to 6.5 m (Fig. 5B).
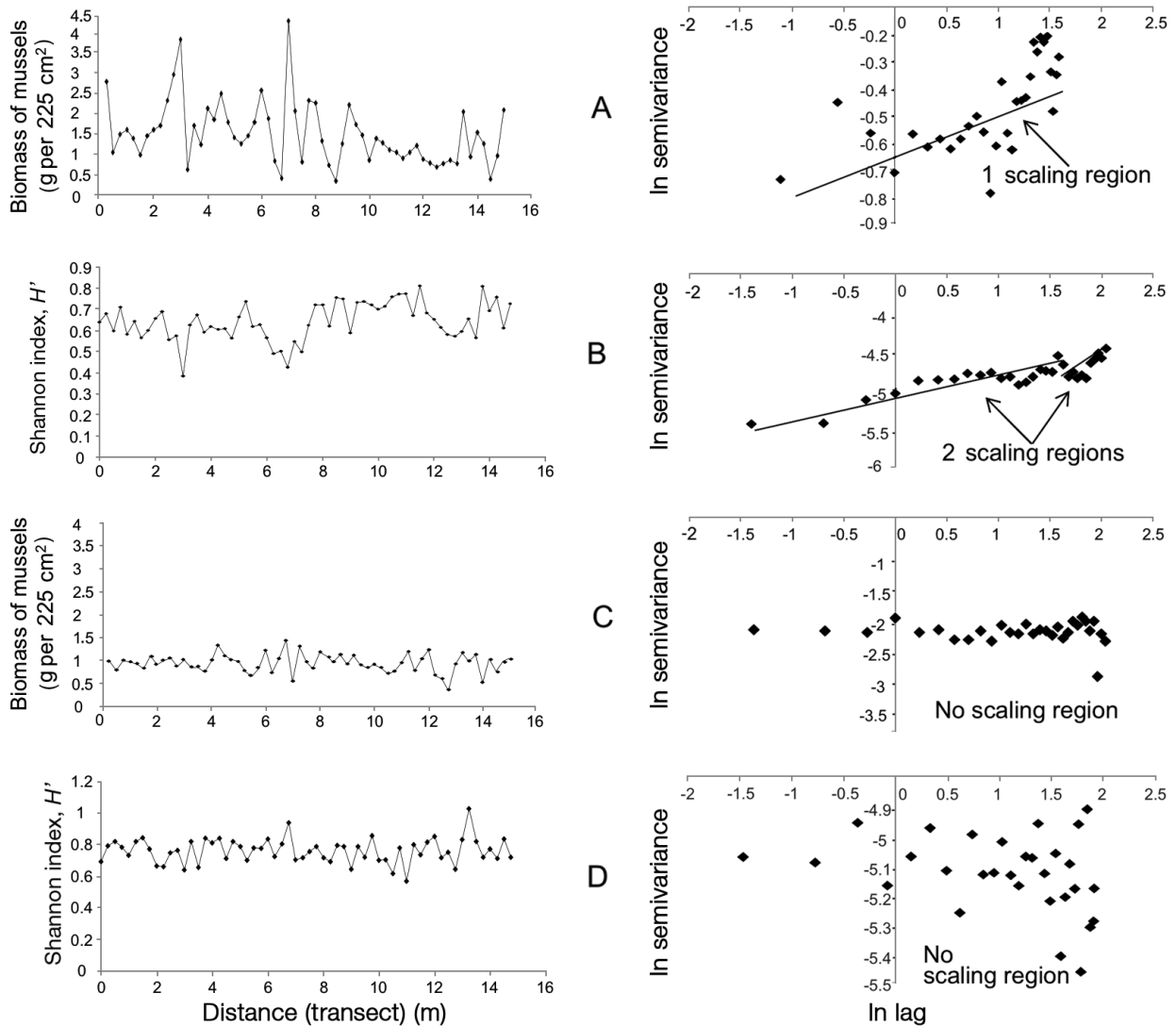
Fig. 4. Site 2: Vaktanlandet. See Fig. 3 legend for further details

DISCUSSION

In this study, it was found that a reduced blue mussel size structure together with an increase in their patchiness at shallow depths (5 m) could diminish their potential to effectively serve as a foundation species, since the higher spatial patchiness of blue mussels at 5 m depth generated negative co-variation between mussels and the diversity of associated fauna. In contrast, at 8 m depth the mussel distribution showed a random pattern with a positive or neutral co-variation between mussels and diversity, indicating that the mussel bed at greater depths was a true habitat for the associated species. A specific strength of this study is the description of the variability, heterogeneity and relationships of blue mussels and the diversity of associated macrofauna at a range of small spatial scales at which they usually interact. This was done for the first time in a marine habitat, to our knowledge, using geostatistical tools. Blue mussel patchiness was hierarchical, presenting small patches integrated within larger patches at 5 m depth, which has been found before for different mussel species on intertidal rocky shores around the world (Kostylev & Erlandsson 2001, Erlandsson & McQuaid 2004). In the present study, however, one new insight is that the associated macrofauna patchiness tends to resemble the distribution of mussels.

Progress in the field of landscape formation has led to identification of complex interactions among different drivers such as disturbances, competition, facilitation and recruitment influencing the possible generalizations about specific ecosystems (e.g. Sachak et al. 2008, Díaz & McQuaid 2011, 2014, Er-
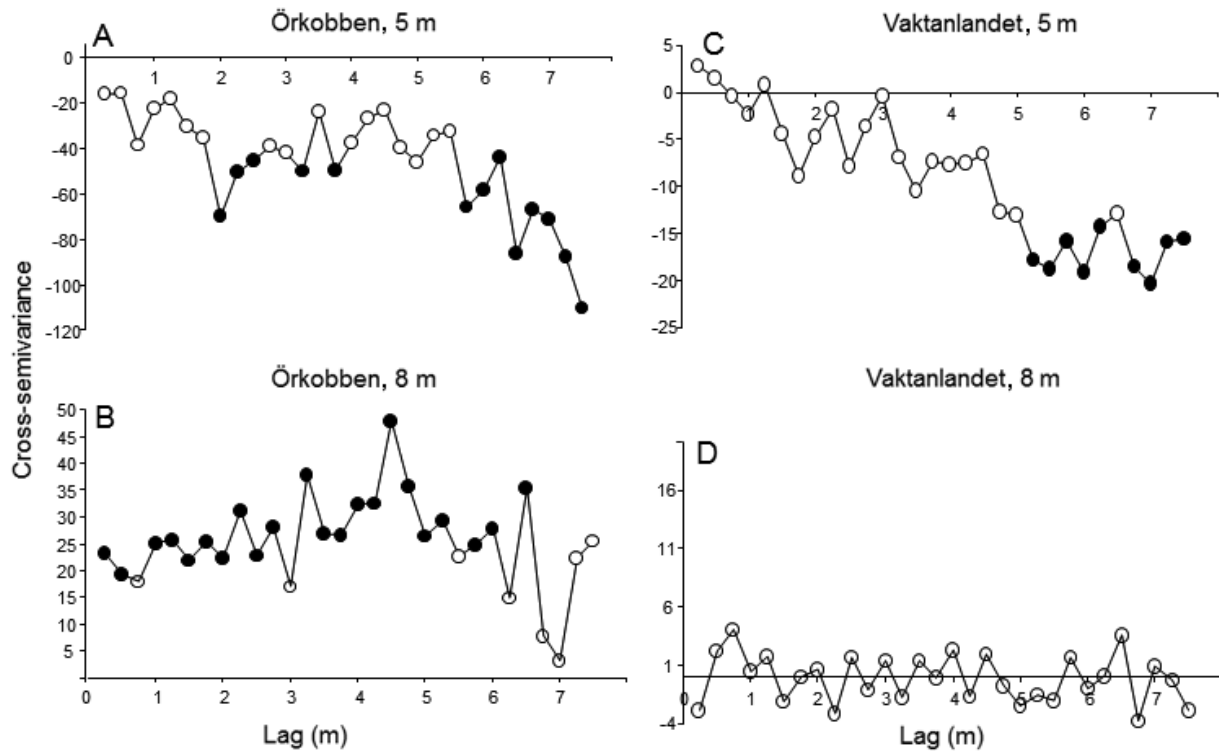
Fig. 5. Cross-semivariograms of the relationships between mussel biomass and the diversity of its associated macrofaunal community at different lags in each transect for each site-depth combination. (●) Significant relationship (p < 0.05), either positive or negative, between variables; (○) non-significant relationship between variables

landsson et al. 2011, Commito et al. 2014). Any change in the dominance of one of these forces would promote different types of spatial heterogeneity and a different hierarchical spatial structure (Kostylev & Erlandsson 2001, Lawrie & McQuaid 2001, Erlandsson & McQuaid 2004, Díaz & McQuaid 2011). For example at 8 m depth, a reduction in abiotic disturbances for mussels (Westerbom et al. 2002) and decreased competition with *Fucus vesiculosus* and other algal species has been documented for the Baltic Sea (Torn et al. 2006). These reductions resulted in the lack of spatial patchiness at both sites, and a positive or neutral co-variation between mussels and the diversity of their associated macrofauna. The changes in the spatial patchiness and the relationship between blue mussels and diversity seem to be related to differences between depths and thereby exposure to disturbance. Interestingly, despite the predominant conception of mussels being strong promoters of diversity (but see Branch & Steffani 2004, Buschbaum et al. 2009), in this study blue mussels were only found to promote diversity in one out of 4 cases (one site at 8 m depth). More importantly, this single case was related to lack of patchiness of blue mussels and a larger size structure of mussels.

The ANOVAs demonstrated differences in the diversity of macrofauna associated with blue mussel beds between sites, but not between depths. These analyses show that the diversity of associated macrofauna does not vary as a function of both density and biomass of blue mussels, which is in agreement with previous results from Koivisto & Westerbom (2010). Regarding this latter point, Koivisto & Westerbom (2010) suggested that this weak relationship is caused by the low overall species richness in the Gulf of Finland, which quickly saturates as mussel density/biomass increases monotonically (Norling & Kautsky 2007, 2008). According to Norling & Kautsky (2007, 2008) and Koivisto & Westerbom (2010, 2012), substrata devoid of mussels always have lower richness and abundance of macrofauna than substrata with mussels in the Baltic Sea.

Thus, the analyses of spatial patterns detected differences in patchiness and co-variation of species distributions between depths which were not detected using classic factorial analyses, and at the same time suggested the mechanisms driving the spatial relationship between blue mussels and their associated macrofauna. The role of blue mussels as a foundation species may therefore be related to depth

and modulated by spatial patchiness. These differences between depths seem to have their origins in different disturbance regimes which in turn seem to affect the patchiness of mussels described using fractal dimension. For example, at depths >8 m, less disturbances would induce a more mixed size structure in the mussel beds (Westerbom et al. 2002), which facilitates the provision of shelter for associated macrofauna. Blue mussels and their associated macrofauna both show random spatial patterns at 8 m depth, since the distribution of macrofauna depends on the spatial patterns of the mussel distribution (Table 2). This would imply, although this still needs to be tested, that blue mussels do not tend to form patches at greater depths, in contrast to shallower depth where there is high dislodgement risk. We therefore hypothesize that lack of spatial dependence/patchiness indicates benign conditions for mussel growth and survival. In contrast, at 5 m depth, wave action/ice scouring and inter-specific competition seem to provoke break-up of the mussel bed into smaller patches; this break-up could cause the removal of older and large mussel individuals, maintaining the domination of recruits and juveniles (small individuals) in the mussel bed. The distributions of mussels and diversity showed mainly spatial patchiness represented by D-values between 1.89 and 1.96 (Table 2). These values indicate high patchiness, and they seem to be common in the distribution of benthic marine species other than mussels (Erlandsson et al. 2005, Díaz et al. 2011, 2012). In this way, fractal dimension may inform about the stability and persistence in ecological systems and this would imply that undisturbed species would exhibit lack of patchiness (Sugihara & May 1990). Therefore, as a system is destabilized by disturbances, it becomes spatially fragmented or patchy and the D-values decrease (Commito & Rusignuolo 2000, Díaz et al. 2011). This idea has been partially tested and our results support the model presented by Sugihara & May (1990). In the context of this study, in highly disturbed environments (shallow depths), spatial patchiness is induced because mussel beds become disrupted by several forces, and therefore blue mussels may survive by aggregating themselves in patches (Côté & Jelnikar 1999, Erlandsson et al. 2005, 2011, Rius & McQuaid 2006, Zardi et al. 2006, 2008, Commito et al. 2014). This patchy spatial organization in *Mytilus edulis* has proved to increase population tolerance to disturbances or environmental stress (Rietkerk et al. 2002). This mussel behavior seems to occur at shallow depths (e.g. 5 m) and induce high dislodgment of biota; especially since blue mussels

stressed by low salinity have weak byssus anchoring strength (Kautsky 1982). In the northern Baltic Proper, densities of blue mussel recruits and juveniles in these clumps are usually high (sensu Westerbom et al. 2002; sizes varying between ~1 and 4 mm, Fig. 2). The predominance of small size classes is due to the faster annual turnover of recruits and mortality/dislodgment of adult mussels (Öst & Kilpi 2000, Westerbom & Jattu 2006). Future studies should use semivariograms to experimentally evaluate the spatial extent of disturbance affecting mortality/dislodgement of mussel size classes along depth gradients in the Gulf of Finland and elsewhere. This would assist in understanding the role of disturbance in creating spatial patchiness in mussel beds, and consequently the associated macrofaunal diversity.

Lack of co-variation of patches of macrofauna with respect to its 'blue mussel habitat' was observed at shallower depths using cross-semivariograms. For example, when variability of mussel biomass increased, the variability of diversity decreased and vice versa. This was also denoted by a negative co-variation, specifically at the larger scales (lags > 5 m; Fig. 5). Therefore, our results also suggest a cascading effect, starting with disturbances, which affect the size class structure and, simultaneously, the spatial configuration of patches within the mussel bed. These last 2 features will have consequences for the diversity of the associated macrofauna. The way in which patchiness of a single species may affect other species has been demonstrated in marine fouling communities and in terrestrial plant communities (Monzeglio & Stoll 2005, Hart & Marshall 2009). This study suggests that small-sized mussels reduce their function as foundation species through the induction of space exclusion towards their associated macrofauna in environments with high disturbance. Similar effects have been observed in other coasts in the world (Woodin 1976, Commito et al. 2008, Buschbaum et al. 2009).

The present study shows consistent results between depths, allowing the demonstration of the plastic role of spatial patterns of *M. edulis* for its associated macrofauna diversity (Commito et al. 2008). Similar plastic roles of foundation species have been observed in other systems such as terrestrial forests (Aide 1987), kelp forests (Connell 2003) and salt marshes (Bertness & Hacker 1994). However, the novelty with this study is that there is an unexplored aspect in the variation of patchiness for foundation species, affecting the net diversity of a community.

Even though we lacked transect replication at single depths within a site, making it difficult to draw

general conclusions about the small-scale spatial patterns for all other sites in the region, we have in this study gained knowledge that other studies of between-shore variability have left open to speculation. The study analyzed both spatial heterogeneity and co-variation between a foundation species and biodiversity at continuous within-shore scales of mussel beds at different depths, replicated at the site level, and obtained similar results at each depth between sites. Our results also suggest that a classic random sampling design is valid at 8 m depth in mussel beds in the region but will face problems at 5 m depth due to the spatial dependence found there.

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