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Contrasting spatial heterogeneity of sessile organisms within mussel (*Perna perna* L.) beds in relation to topographic variability

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Abstract

We examined the spatial heterogeneity in three sessile rocky shore organisms, the mussel *Perna perna*, the barnacle *Octomeris angulosa* (Sowerby) and the red alga *Gelidium pristoides* (Turn.) at a range of continuous local scales along horizontal transects within mid- and upper mussel beds of South African shores. We also examined the relationships between variability of organisms and topographic features (rock depressions, slope, aspect), and between mussel, barnacle and algal variability over the same scales. To estimate spatial heterogeneity, we analyzed scaling properties of semivariograms using a fractal approach. Relationships between different variables at the different scales were examined by cross-semivariograms. Spatial dependence of *P. perna* variability increased with spatial dependence of topographic variability, so that scaling regions of mussel and topographic distributions corresponded well. This relationship often improved with larger local scales (mussel cover increased with depressions, steeper slope and aspect towards waves), while at smaller spatial scales, variability in mussel cover was less well explained by variability in topography. The variability of the barnacle *O. angulosa* exhibited spatial dependence, even on topographically unstructured shores. In contrast, the distribution of the alga *G. pristoides* revealed high fractal dimensions, showing spatial independence on topographically unstructured shores. Algae also showed a very strong negative relationship with mussels at most local scales, and a negative relationship with barnacles in upper zones, especially at larger local scales. Barnacles may show clear spatial dependence because of hydrodynamics (at larger local scales) and the need to find a future mate in close proximity (at smaller local scales), while algae may show a strong negative relationship with mussels because of competition for space.

Keywords: Algae; Barnacles; Fractal dimension; Intertidal distribution; Mussels; Rocky shores; Spatial dependence

1. Introduction

While variability is a general term indicating changes in the value of a variable, heterogeneity refers to the structure in variability across different

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spatial scales, which may be categorized as patchy, uniform or random (Kolasa and Rollo, 1991; Ettema and Wardle, 2002). Spatial dependence is a concept dealing with the similarity between data points as a function of spatial separation (lag) between them (Legendre, 1993; Ettema and Wardle, 2002). Since spatial independence is a basic assumption in many statistical tests, and since spatial dependence can often be detected in ecological systems (Palmer, 1988; Wiens, 1989), the importance of the assessment of spatial heterogeneity at different scales becomes apparent. Thus, the design of a field experiment may be facilitated or complemented by first studying spatial heterogeneity of an organism.

High variability in abundances of organisms at spatial scales within and among shores has been found in many intertidal studies (e.g., Morrisey et al., 1992; Lindegarth et al., 1995; Harris et al., 1998; McKindsey and Bourget, 2000; Lawrie and McQuaid, 2001; Benedetti-Cecchi et al., 2003). Because these studies have examined variability across local (within shores: cm–m scales) meso (between shores: km scales) or regional (between regions: 10s–100s km scales) scales, the variability of organisms within shores has usually been estimated at only one or two small scales simultaneously. Thus, while the structure of the spatial variability has been studied across local to regional scales in these studies, this structure has not been analyzed within small scales. The intertidal studies that have quantified spatial structure in the variability of organisms at a range of within-shore scales have mainly been from soft-bottom habitats (e.g., Hall et al., 1994; Kostylev, 1996; Hewitt et al., 1997, 2002; Kostylev and Erlandsson, 2001), with only a few from rocky shores (Underwood and Chapman, 1996; Johnson et al., 1997; Guichard et al., 2000; Erlandsson and McQuaid, 2004). Relationships between spatial dependence in the distribution of an organism and of other organisms or of habitat features is commonly studied in plant, soil, freshwater and plankton ecology (Seuront and Lagadeuc, 1998; Dale, 2000; Schmid, 2000; Ettema and Wardle, 2002), but not on rocky shores, exceptions being Guichard et al. (2000) and Erlandsson and McQuaid (2004).

Nested heterogeneity, i.e., multiple scales of patchiness, with smaller patches or gradients integrated into larger ones, may occur because several physical and biological factors or processes that influence distribution patterns operate and interact at different characteristic spatial scales (Wiens, 1989; Sugihara and May, 1990). For example, hydrodynamics, substratum type and surface topography are important in the settlement and recruitment of marine invertebrates (Denny, 1987; Barry and Dayton, 1991; Booth and Brosnan, 1995; Abelson and Denny, 1997), especially for the aggregation of some barnacle species at smaller scales (LeTourneux and Bourget, 1988; Lemire and Bourget, 1996; Harvey and Bourget, 1997; Bourget and Harvey, 1998; Hills et al., 1999).

Mussel beds provide secondary space and microhabitats for a wide diversity of associated benthic species (Suchanek, 1985; Sebens, 1991; Lintas and Seed, 1994; Kostylev, 1996), generally because of their high architectural and horizontal complexity (Sebens, 1991; Kostylev et al., 1997; Snover and Commito, 1998; Commito and Rusignuolo, 2000). At within-shore scales, intertidal mussel beds can appear spatially homogeneous (80–100% cover), with distinct gaps often created by strong waves (Paine and Levin, 1981; Denny, 1987). On other shores, however, mussel abundance within beds may be very patchy. Some studies of intertidal mussel distribution over a large range of continuous local scales have found that there is often spatial dependence of this variability, with higher spatial heterogeneity at smaller local scales and several natural scaling regions of the spatial variability (Kostylev and Erlandsson, 2001; Erlandsson and McQuaid, 2004).

On rocky shores in southern Africa, the distribution of mussels varies markedly with the spatial scale considered, both at a regional scale between the west and the east coasts (Harris et al., 1998) and between shores within a region (Lawrie and McQuaid, 2001). Wave-exposed shores exhibit larger sizes, higher mortality and higher growth rates than sheltered shores (McQuaid and Lindsay, 2000; McQuaid et al., 2000). There is also high, unpredictable variability (especially in recruitment) at within-shore scales (Lawrie and McQuaid, 2001). This variability reveals strong spatial dependence in the density of adults at a range of within-shore scales (Erlandsson and McQuaid, 2004), while spatial dependence of recruitment variability increases with recruit size. Macroalgae and barnacles may compete with mussels for primary space, or use the surface of mussels as secondary space (McQuaid and Branch, 1985), and within beds of the mussel *Perna perna* on the south-east coast of South Africa (studied here), the commonest species are the barnacle *Octomeris angulosa* and the red alga *Gelidium pristoides*.

In the present study, we posed the following hypotheses for a range of local, within-shore scales in the mid- and upper mussel zones: (1) the high spatial variability in the within-shore distribution of *P. perna* cover shows spatial dependence, with different spatial heterogeneity between shore-levels and multiple scaling regions; (2) the barnacle *O. angulosa* and the alga *G. pristoides* also show nested patchiness (multiple scaling regions in their spatial variability), with the extent and heterogeneity of scaling regions differing between species; (3) there is different spatial heterogeneity in the distributions of these three sessile species in relation to topographic variability; (4) the relationships with the variability of topography (distributions of rock depressions, slope and aspect) over different local scales are species-specific; (5) there are differences in spatial covariance between pairs of organisms, i.e., the nature of the relationships between the variability of mussels and barnacles; mussels and algae; and algae and barnacles differ.

2. Materials and methods

Outside of bays, intertidal mussel beds on the south-east coast of South Africa are discrete, easily defined and often not longer than 25 m. Individual beds are usually separated by 100s of meters and vertically they extend from just above the subtidal fringe to the low shore. These mussel beds are monolayered, with the byssus threads of adults attached directly to the rock surface (McQuaid et al., 2000, personal observation) and can be clearly divided into mid-, low and upper zones within which mussel densities and sizes differ. These shores are all wave exposed, and wave action can be very strong, sometimes dislodging substantial mussel patches (personal observation).

Mussel beds were sampled on three sandstone shores (Waterloo Bay, Riet Point and Port Alfred) 15–20 km apart in the vicinity of Port Alfred (33°37′ 30S, 26°52′ 30E) on the south-east coast of South Africa. Sampling was done in mussel beds of 20 m or less, using 21-m belt transects to be sure that the whole bed was sampled. Transects were sampled using adjacent quadrats of 10×10 cm, which allowed a sample size of 60 quadrats per transect with a minimum lag (the distance between centers of quadrats) of 35 cm. With larger quadrats the minimum lag would have been larger and the sample size smaller. In April–June 2000, percent cover of *P. perna* was estimated in the mid-mussel zones at all three sites and the upper mussel zones at Riet Point and Port Alfred (upper zone of Waterloo Bay was sand inundated) along one transect per zone at each site. Cover was estimated visually using 100 small quadrats fixed within the larger quadrat. In March–April 2001, percent cover of the barnacle *O. angulosa*, the alga *G. pristoides* and *P. perna*, rock slope, aspect, and the mean depth of rock surface depressions (gullies and crevices >5 cm depth) were estimated along transects at Riet Point and Port Alfred. Slope and aspect were described thus: a totally horizontal surface had 0° slope, a totally vertical surface 90°, and slopes towards or away from the main wave direction were assigned positive and negative signs, respectively.

3. Data analysis

3.1. Distribution of biological and physical variables

To describe the spatial variability in the distribution of mussels, barnacles, algae and topographic features at different within-shore scales (30 different lags ranging between 0.35 m and 10.5 m), we used semivariogram analysis, which estimates the spatial dependence of the variability in a variable (Isaaks and Srivastava, 1989; Dale, 2000). The semivariance ($Y_{(\mathrm{h})}$) was estimated as:

$$Y_{(h)} = 1/\left(2N_{(h)}\right)_{i=1}^{N-h}\left(Z_{i+h} - Z_i\right)^2 \qquad (1)$$

where N is the total number of data points; $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h; Z_i and Z_{i+h} are the values of a variable (e.g., percent cover of an organism) at points i and i+h (Burrough, 1983; Palmer, 1988; Schmid, 2000). Fractal scaling analysis was used to estimate heterogeneity of spatial distributions over the range of scales. The fractal dimension (D) was calculated from the double logarithmic semivariogram (which is a plot of $Y_{(h)}$ vs. h) as:

$$D = (4 - m)/2 \quad (2)$$

where m is the absolute slope of the regression between semivariance and spatial scale (see e.g., Burrough, 1983; Schmid, 2000). Fractal dimension (D) is a non-integer measure of heterogeneity. Higher heterogeneity gives a flatter slope of the regression line in the semivariogram and a higher value of D. D varies between 1 and 2 where a value closer to 1 indicates persistent behaviour of increments between consecutive values of a test variable or a trend-like distribution (e.g., a gradient or large patches), while a value of D closer to 2 indicates anti-persistent behaviour of the increments or a more patchy distribution (Feder, 1988; Kostylev and Erlandsson, 2001). Simulations of distribution of intertidal organisms show that random distribution patterns have a semivariogram regression slope very close to 0 and D values between 1.97 and 2 (Fig. 1A). A structure of regular patches of low and high cover of organisms is shown in Fig. 1B, where the semivariogram reveals three scaling regions, i.e., smaller patches (3.5 m) within larger patches (7 m) within even larger patches (10.5 m), each scaling region having a D clearly deviating from 2. For simulations of other types of distribution patterns along a transect (e.g., small-scale trend and large-scale random pattern), see Palmer (1988).

Lags (h) up to half of the transect length were included in the regression analysis of the semivariogram. Semivariances do not represent variation between all data points at lags larger than half of the transect length (Palmer, 1988; Kostylev, 1996; Schmid, 2000; Kostylev and Erlandsson, 2001), because at each successive larger scale the number of comparisons decreases by one (from 59 pairs at lag 0.35 m to 30 pairs at lag 10.5 m). Using larger lags than this would result in overestimated spatial independence.

3.2. Patterns of relationships

The relationships between spatial heterogeneity (D) of mussel/barnacle/algal distribution and spatial heterogeneity (D) of distribution of depressions were

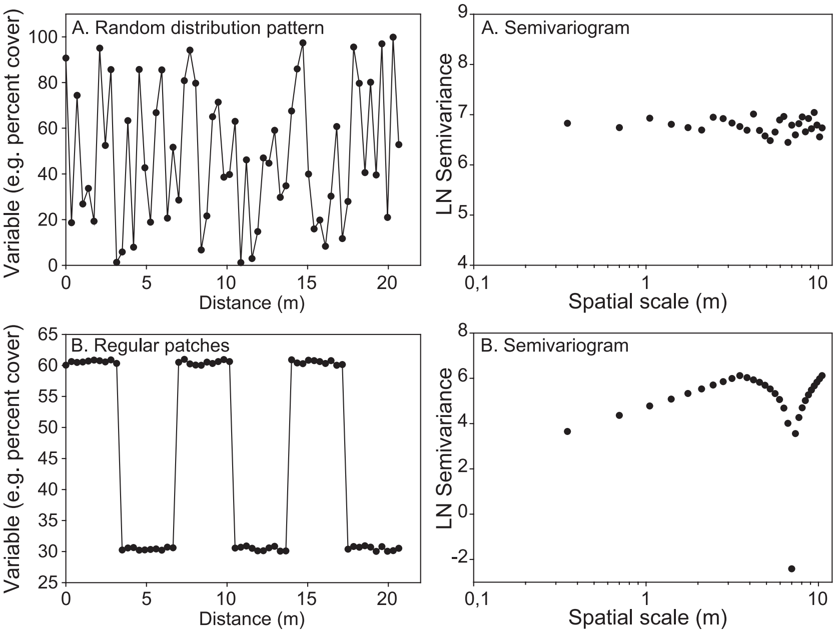

Fig. 1. Simulated horizontal transects of distribution of organisms and their corresponding semivariograms. (A) Random distribution pattern or complete spatial independence. (B) Structure of regular patches (each 3.5 m large) of high and low cover.

examined in linear scatter plots (each transect=one datum point). Distribution of rock slope showed too high a fractal dimension on most transects (mostly D>1.99) to be useful in these scatter plots.

To describe the relationship between the variability of two variables across different spatial scales (30 different lags ranging from 0.35 to 10.5 m), we used cross-semivariogram analysis, which is related to semivariogram analysis (Dale, 2000). The cross-semivariance ($Y_{(h)}$) was estimated as:

$$Y_{(h)} = 1/\left(2N_{(h)}\right)_{i=1}^{N-h}(X_{i+h} - X_i)(Z_{i+h} - Z_i) \qquad (3)$$

where N is the total number of data points; $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h; X_i and X_{i+h}, and Z_i and Z_{i+h} are the values of two different variables (e.g., percent barnacle cover and rock slope) at points i and $i+h$.

A positive cross-semivariance value at a certain lag indicates a positive relationship between variables and a negative value a negative relationship at that scale. Cross-semivariance values approaching 0 indicate no relationship between variables at that scale. Thus, cross-semivariograms can help to describe whether a relationship (negative or positive) between studied variables is stronger at certain scales. Negative or positive relationships may thus increase over certain scales showing spatial dependence.

To test whether cross-semivariance values were significantly different from 0, the distributions of pairs of variables along each transect were randomized 1000 times and cross-semivariance values calculated at each scale for each random permutation (see Quinn and Keough, 2002 for information on random permutation tests). Each randomized value was then compared with the appropriate observed cross-semivariance value. Thus, we calculated the probability of each observed cross-semivariance value being higher (positive relationship) or lower (negative relationship) than by chance alone, and applied an alpha level of 0.05. Since spatial dependence of relationships between variables makes statistical significance tests speculative (Dale, 2000), one should refer to significant negative or positive relationships with caution.

As a complement to the cross-semivariograms and as a guide to overall relationships, Pearson's correlation analysis of the relationships between percent cover of mussels, barnacles and algae was done for transects showing spatial independence of relationships.

3.3. Detection of multiple scaling regions

From a semivariogram, natural multiple scaling regions (within which variance changes monotonically with changes in scale) can be detected in a distribution. Fractal dimension can be estimated from a double-logarithmic semivariogram, and there is self-similarity within (D is the same) but different fractal dimensions between scaling regions. Spatial heterogeneity can be estimated within each scaling region. To detect significant scaling regions, a three-step procedure was followed (see also Kostylev and Erlandsson, 2001) for each double-logarithmic semivariogram and nonlogarithmic cross-semivariogram: (1) residual analysis, (2) regression analyses of the different slopes, (3) t-tests comparing different slopes.

(1) Analysis of patterns among residuals (i.e., estimated differences between observed data points and the fitted regression line) was done to distinguish partial regression lines with different slopes and to determine the scale where the break between them occurred. Starting with the whole range of scales, the maximum positive or negative value (opposite sign to the first point value) of residual data was considered to correspond to a transition between scaling regions (see Glejser, 1969; Kostylev and Erlandsson, 2001). The same analysis was repeated at the range of scales following a scaling break until all potential partial regressions had been distinguished. (2) Linear regression analysis was conducted for each region and a statistically significant slope suggested that partial regressions at the distinguished scales should be considered. (3) As a last step in the detection of real multiple scaling regions, slopes of significant partial regressions were tested against each other in t-tests in order to eliminate possible redundancy. If slopes of adjacent regressions were significantly different, then the scaling regions were considered valid. Since this procedure of partial regression analyses of a semivariogram may include multiple tests, significance was estimated using the Bonferroni correction.

There are other approaches for the determination of transition points for partial regressions (e.g., Nickerson et al., 1989; Yeager and Ultsch, 1989), but we believe that our approach involves sufficiently rigorous testing while safeguarding against redundancy and errors in interpretation (Kostylev and Erlandsson, 2001).

4. Results

4.1. Mussel distribution

The semivariogram regressions of mussel distributions had mainly positive slopes (Table 1), implying that variation increased with larger separation between samples. Variability in mussel cover was generally higher in mid-mussel than in upper mussel zones (Figs. 2 and 3). Riet Point mid- and upper transects showed spatial dependence of the variability in both 2000 and 2001 (Table 1; Fig. 2). Port Alfred mid-mussel zone did not show any spatial dependence in the variability of mussels in either 2000 or 2001 (Table 1; Fig. 3a–b), being more similar to a stochastic pattern. In Port Alfred upper zone, semivariance showed weak spatial dependence in both 2000 and 2001 (Table 1; Fig. 3c–d). Mussel distributions at Port Alfred all had very high fractal dimensions (see Table 1). Thus, generally the variability in the distributions of mussels along transects at Riet Point showed stronger spatial dependence than at Port Alfred.

All transects at Waterloo Bay and Riet Point showed multiscaling behaviour in the distribution of mussels, i.e., a pattern of multiple levels of heterogeneity or patchiness. Waterloo Bay mid-mussel zone exhibited two, Riet Point mid-zone three (in both 2000 and 2001), and Riet Point upper zone two (in 2001) significant scaling regions in the spatial variability of mussels (Table 1; Fig. 2). Mussel distribution within the first scaling region (on smaller scales) of all these transects was more patchy (higher D) than in the other scaling regions. In Riet Point mid-zone, the first scaling region was similar in extent (up to 3–4 m) and heterogeneity ($D \approx 1.9$) in

Table 1
Regression exponents of the double-logarithmic semivariograms, and fractal dimensions (D) for the different spatial scales of mussel (*P. perna*) distribution on the different transects and shores

Transect	Scale (m) (*df*)[a]	Slope	SE	R^2	p	D	Spatial pattern
RP mid 00	0.35–10.5	0.468	0.154	0.874	0.0000001	1.766	Depend.
RP mid 01	0.35–10.5	0.123	0.141	0.363	0.00043	1.938	Depend.
RP upper 00	0.35–10.5	0.151	0.202	0.295	0.0019	1.925	Depend.
RP upper 01	0.35–10.5	0.310	0.109	0.858	0.0000001	1.845	Depend.
PA mid 00	0.35–10.5	0.042	0.144	0.059	0.20	1.979	Independ.
PA mid 01	0.35–10.5	0.029	0.165	0.023	0.43	1.986	Independ.
PA upper 00	0.35–10.5	0.062	0.127	0.153	0.032	1.969	Depend.
PA upper 01	0.35–10.5	0.095	0.153	0.225	0.0081	1.952	Depend.
WB mid 00	0.35–10.5	0.046	0.228	0.029	0.37	1.977	Depend.[b]
Significant multiple scaling regions							
RP mid 00	0.35–3.15 (7)	0.218	0.092	0.768	0.0019	1.891	Patchy
	3.5–5.25 (4)	1.508	0.032	0.985	0.000088	1.246	Trend
	5.6–10.5 (13)	0.650	0.039	0.924	0.0000001	1.675	Patchy
RP mid 01	0.35–4.2 (10)	0.175	0.138	0.505	0.0096	1.912	Patchy
	4.55–8.05 (9)	−0.542	0.100	0.535	0.010	1.729	Patchy
	8.4–10.5 (5)	1.365	0.080	0.690	0.021	1.318	Trend
RP upper 01	0.35–5.95 (15)	0.234	0.068	0.888	0.0000001	1.883	Patchy
	6.3–10.5 (11)	0.972	0.055	0.903	0.000001	1.514	Trend
WB mid 00[b]	0.35–4.55 (11)	0.244	0.107	0.768	0.000086	1.878	Patchy
	4.9–10.5 (15)	−0.707	0.182	0.477	0.0022	1.646	Patchy

RP=Riet Point, PA=Port Alfred, WB=Waterloo Bay; 00=2000, 01=2001; Depend.=spatial dependence, Independ.=spatial independence.

[a] *df*=28 if not stated.

[b] Because of significant scaling regions, there is spatial dependence.

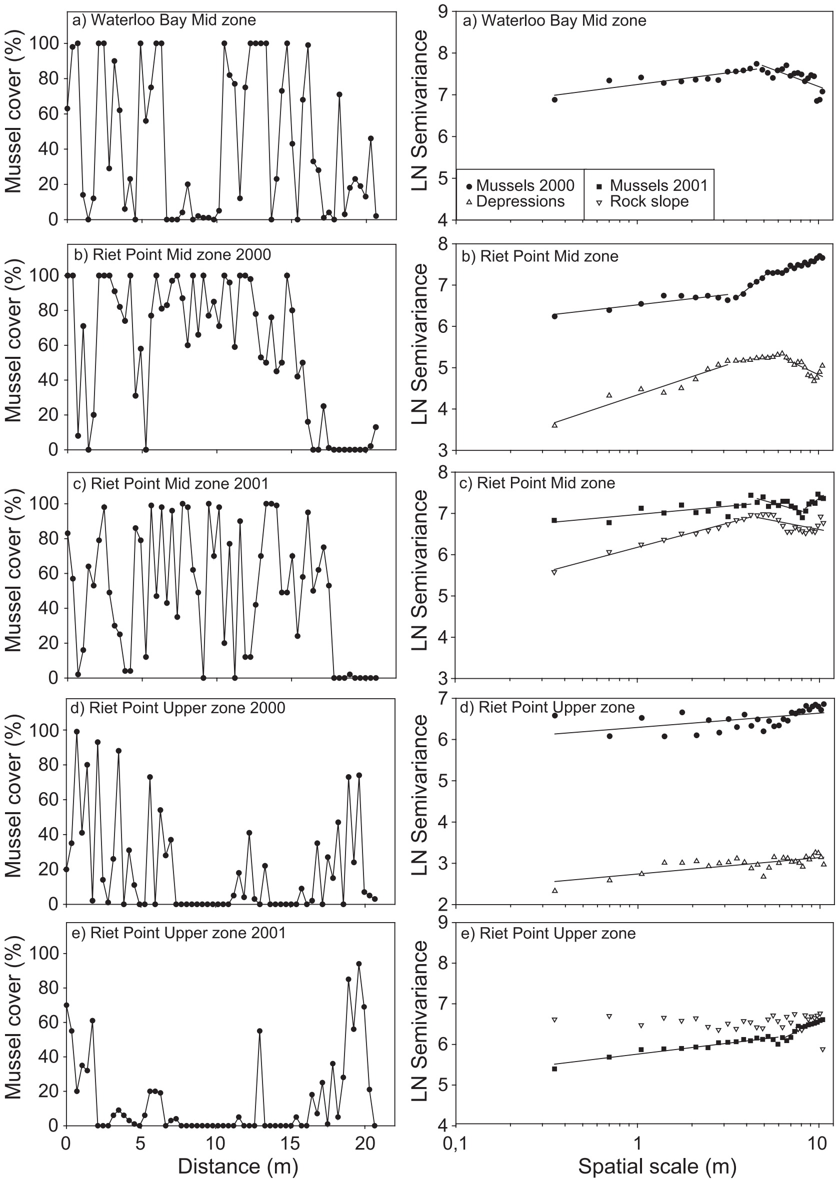

Fig. 2. Distribution of the mussel *P. perna* and semivariograms of mussel and topographic distributions at Waterloo Bay and Riet Point mid- and upper transects. Closed symbols in semivariograms represent variability of mussels in 2000 (a, b, d) and 2001 (c, e), while open symbols represent variability of depressions (b, d) and rock slope and aspect (c, e). Regression lines indicate significant scaling regions.

both 2000 and 2001, while this was not the case for the other scaling regions (Table 1; Fig. 2b–c). In the Riet Point upper mussel zone, there were similar scaling patterns for mussel distributions in both years (Fig. 2d–e), with two significant scaling regions in 2001 (Table 1). Variability of mussel distributions in Port Alfred mid- and upper mussel zones, on the other hand, did not show any multiple scaling regions (Table 1; Fig. 3).

4.2. Distribution of barnacles and algae

Distributions of the alga *G. pristoides* generally showed high spatial heterogeneity, with spatial depend-

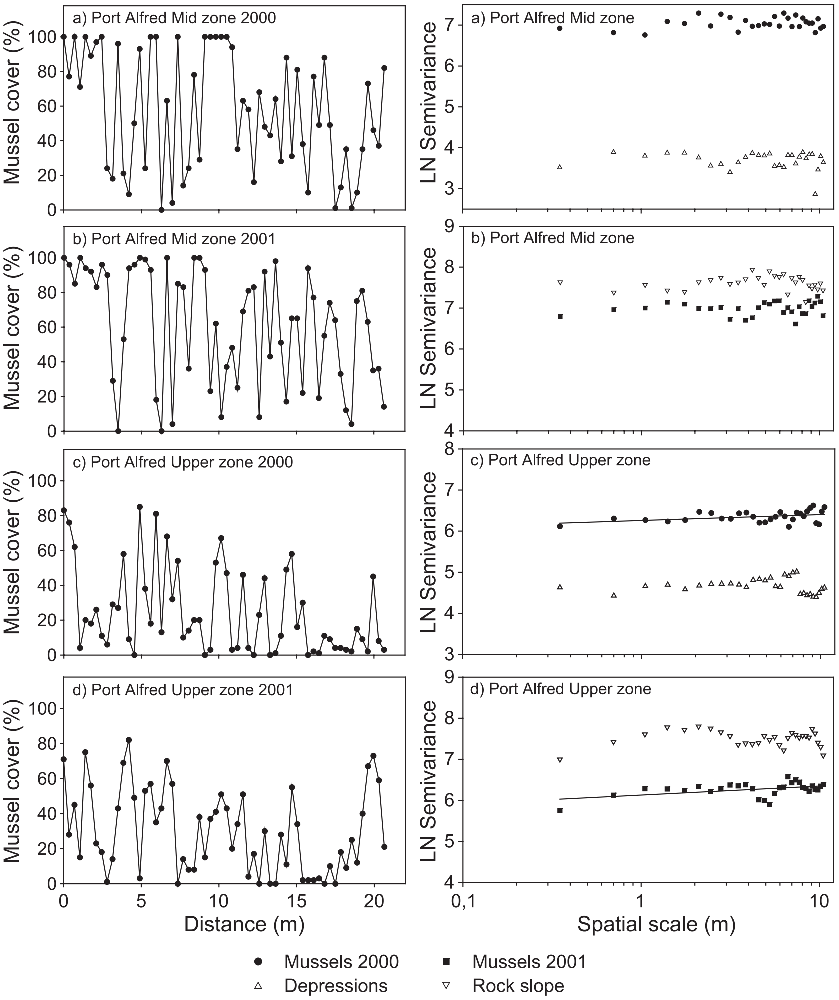

Fig. 3. Distribution of the mussel *P. perna* and semivariograms of mussel and topographic distributions at Port Alfred mid- and upper transects. Closed symbols in semivariograms represent variability of mussels in 2000 (a, c) and 2001 (b, d), while open symbols represent variability of depressions (a, c) and rock slope and aspect (b, d). Regression lines indicate significant scaling regions.

ence and lower *D* values at Riet Point transects compared to Port Alfred transects where complete spatial independence (random pattern) was found (Table 2; Fig. 4). No multiple scaling regions were detected for algal distributions.

The variability in the distribution of the barnacle *O. angulosa* showed mostly spatial dependence with a patchy structure, but lower fractal dimension than the distribution of algae (Table 2; Fig. 5). Fig. 5a visually suggests two or three scaling regions for barnacle variability in the Riet Point mid-mussel zone, although they were not significant because of a random pattern at the cm scales. Port Alfred mid-zone exhibited two apparent but nonsignificant scaling regions (heterogeneous small-scale distribution and a large-scale trend), and Port Alfred upper zone two significant scaling regions (small- and large-scale patchy structure) in barnacle distribution (Table 2; Fig. 5).

4.3. Distribution of depressions, slope and aspect

While Riet Point transects mainly exhibited spatial dependence in the variability of topographic distribution (rock depressions, slope and aspect), Port Alfred

Table 2
Regression exponents of the double-logarithmic semivariograms, and fractal dimensions (*D*) for the different spatial scales of distribution of algae (*G. pristoides*) and barnacles (*O. angulosa*) on the different transects and shores

Transect	Scale (m) (*df*)[a]	Slope	SE	R^2	*p*	D	Spatial pattern
Algae:							
RP mid	0.35–10.5	0.088	0.139	0.230	0.0073	1.956	Depend.
RP upper	0.35–10.5	0.145	0.123	0.509	0.00001	1.927	Depend.
PA mid	0.35–10.5	0.063	0.199	0.069	0.16	1.969	Independ.
PA upper	0.35–10.5	0.015	0.165	0.006	0.69	1.993	Independ.
Barnacles:							
RP mid	0.35–10.5	0.046	0.252	0.024	0.41	1.977	Independ.
RP upper	0.35–10.5	0.233	0.132	0.702	0.0000001	1.883	Depend.
PA mid	0.35–10.5	0.334	0.196	0.684	0.0000001	1.833	Depend.
PA upper	0.35–10.5	0.147	0.154	0.404	0.00016	1.926	Depend.
Significant multiple scaling regions							
Barnacles:							
PA upper	0.35–3.85 (9)	0.343	0.080	0.919	0.000003	1.829	Patchy
	4.2–10.5 (17)	−0.251	0.094	0.373	0.0054	1.874	Patchy
Suggestion of scaling regions							
Barnacles:							
PA mid[b]	0.35–5.6 (14)	0.174	0.172	0.406	0.0079	1.913	Patchy
	5.95–10.5 (12)	1.040	0.086	0.841	0.000004	1.480	Trend

RP=Riet Point, PA=Port Alfred; Depend.=spatial dependence, Independ.=spatial independence.

[a] *df*=28 if not stated.

[b] Not significant because data-point at lag 0.7 m in the semivariogram indicates that the first scaling break is at this scale and not at 5.6 m.

transects showed spatial independence (very high *D* values), that is stochastic patterns (Table 3; Figs. 2 and 3).

The variability in the distributions of topography in Riet Point mid-mussel zone exhibited three (depressions) and two (slope and aspect; tendency to a second scaling break at 6.65 m) significant scaling regions (Table 3; Fig. 2b–c). Port Alfred transects showed no multiple scaling regions in the distributions of topography (Table 3; Fig. 3).

4.4. Relationships between spatial variability of mussels and topography

As shown above, mussel variability exhibited spatial dependence and lower *D* values where topographic variability showed spatial dependence (Tables 1 and 3). The effect of spatial variability of topography on the variability of mussel distribution is clear from linear regression analysis, which shows a positive relationship between spatial heterogeneity (*D*) of mussel distribution and spatial heterogeneity (*D*) of distribution of depressions (df=6; r^2=0.51; p=0.048). Furthermore, the three scaling regions of mussel variability in Riet Point mid-zone corresponded well (similar extent) to the three (depressions) and two (slope and aspect) scaling regions in the variability of topography (Tables 1 and 3; Fig. 2b–c).

Cross-semivariograms suggest that up to about 2–3 m scale on Riet Point transects there was no relationship between mussel and topographic variability (Fig. 6a–b; cross-semivariance values close to 0), but there were significant negative relationships between spatial variability of mussels and depressions at many larger within-shore scales (Fig. 6a–b; Table 4). In contrast, there was an increasing positive relationship between mussel and rock slope variability with larger within-shore scales (Fig. 6a–b; Table 4).

On Port Alfred transects, cross-semivariograms suggest that here too there was generally a negative relationship between spatial variability of mussels and depressions and a positive relationship between mussel and rock slope variability, but these relationships showed spatial independence (Fig. 6c–d; Table 4).

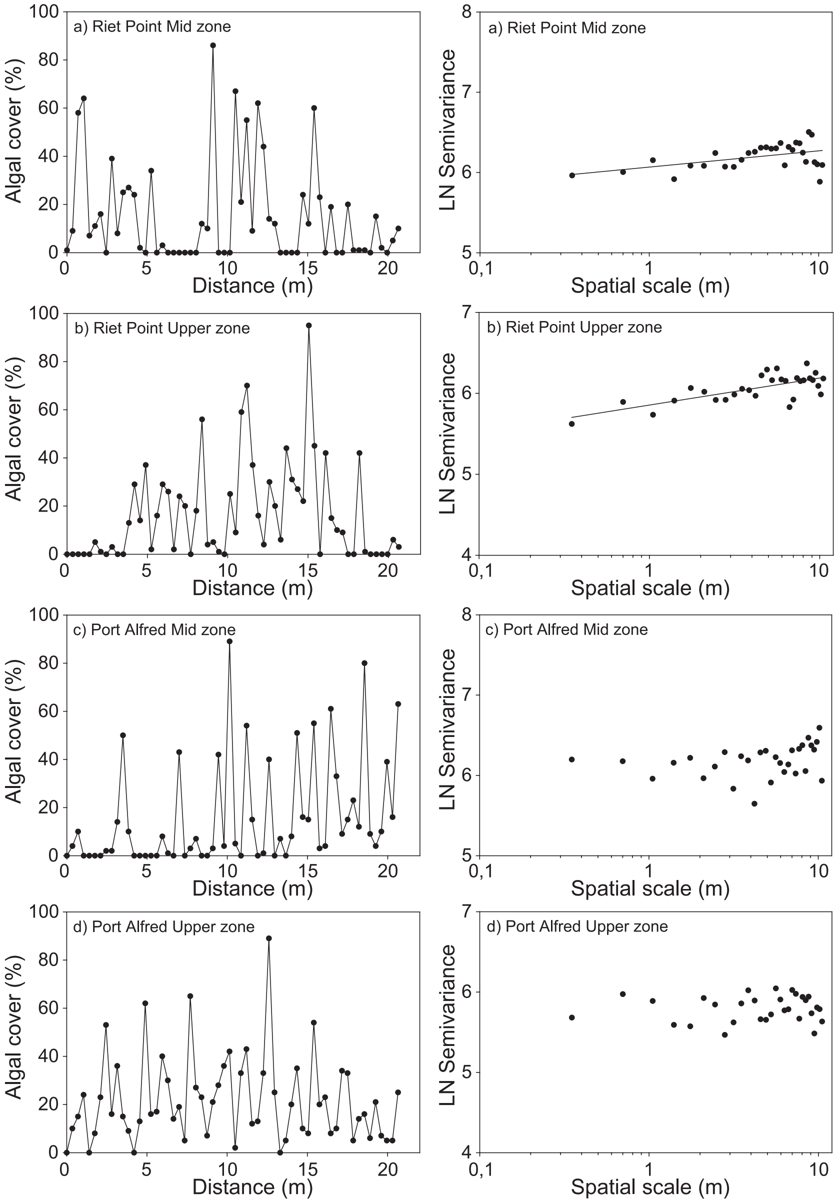

Fig. 4. Distribution of the alga *G. pristoides* at the different transects, with corresponding semivariograms. Regression lines indicate significant scaling regions.

4.5. Relationships between spatial variability of algae/barnacles and topography

As shown above, algal variability exhibited spatial dependence and lower *D* values on topographically structured transects, while barnacle variability exhibited spatial dependence on both topographically unstructured and structured transects (Tables 2, 3). Thus, scatter plots showed that spatial heterogeneity (*D*) of algal distribution tended to increase with higher spatial heterogeneity (*D*) of distribution of depressions (r^2=0.37), while *D* of barnacle distribution tended to decrease with *D* of distribution of depressions (r^2=0.40).

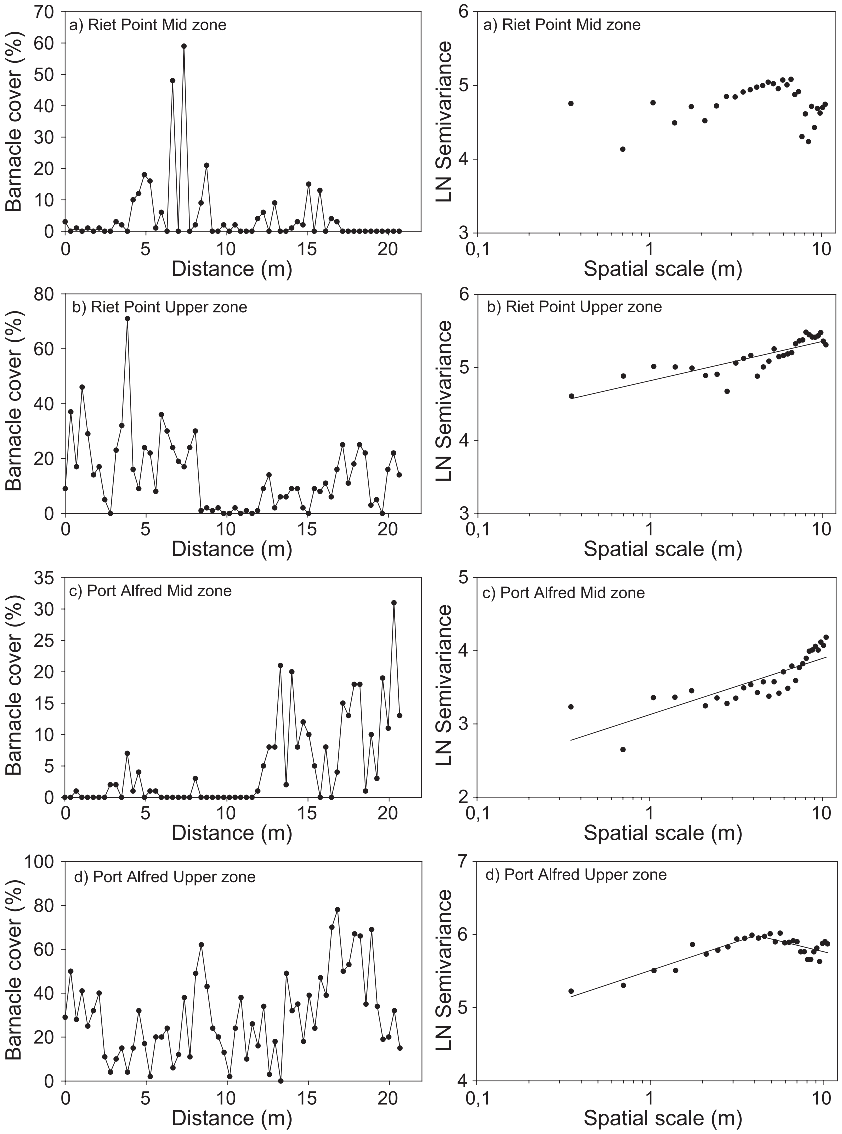

Fig. 5. Distribution of the barnacle *O. angulosa* at the different transects, with corresponding semivariograms. Regression lines indicate significant scaling regions.

Cross-semivariograms showed a positive relationship between spatial variability of algae and depressions at many scales (Table 4; Fig. 7a–d), although this was very weak in the Port Alfred upper zone. Riet Point transects showed spatial dependence and Port Alfred transects spatial independence in this relationship (Table 4; Fig. 7a–d). No clear or consistent relationship was found between algal and rock slope variability, although negative relationships were more common (Table 4; Fig. 7e–h).

Spatial variability of barnacles and depressions exhibited generally negative relationships at different scales (Table 4; Fig. 7a–d), mainly in the upper zones. Transects showed spatial dependence in this relationship, except Port Alfred mid-zone where the relationship was very weak (Table 4; Fig. 7a–d). Barnacle and rock slope variability mostly showed a

Table 3
Regression exponents of the double logarithmic semivariograms, and fractal dimensions (D) for the different spatial scales of topographic distribution (rock depressions, slope and aspect) on the different transects and shores

Transect and measurement	Scale (m) (df)[a]	Slope	SE	R^2	p	D	Spatial pattern
RP mid depressions	0.35–10.5	0.318	0.275	0.499	0.000013	1.841	Depend.
RP mid slope	0.35–10.5	0.243	0.217	0.484	0.00002	1.879	Depend.
RP upper depressions	0.35–10.5	0.172	0.133	0.557	0.000002	1.914	Depend.
RP upper slope	0.35–10.5	−0.018	0.181	0.007	0.65	1.991	Independ.
PA mid depressions	0.35–10.5	−0.033	0.214	0.017	0.49	1.984	Independ.
PA mid slope	0.35–10.5	0.012	0.178	0.003	0.76	1.994	Independ.
PA upper depressions	0.35–10.5	−0.003	0.178	0.0002	0.94	1.999	Independ.
PA upper slope	0.35–10.5	0.006	0.196	0.0006	0.90	1.997	Independ.
Significant multiple scaling regions							
RP mid depressions	0.35–3.15 (7)	0.638	0.146	0.918	0.000047	1.681	
	3.5–6.3 (7)	0.283	0.019	0.913	0.00006	1.859	
	6.65–10.5 (10)	−0.897	0.133	0.525	0.0077	1.552	
RP mid slope	0.35–4.2 (10)	0.512	0.049	0.986	0.0000001	1.744	
	4.55–10.5 (16)	−0.372	0.145	0.319	0.015	1.814	

RP=Riet Point, PA=Port Alfred; Depend.=spatial dependence, Independ.=spatial independence.

[a] df=28 if not stated.

weak positive relationship (Table 4; Fig. 7e–h; cross-semivariance values>0 but significant only in a few cases). Riet Point transects showed spatial dependence, while on Port Alfred transects there was spatial independence in this relationship (Table 4; Fig. 7e–h).

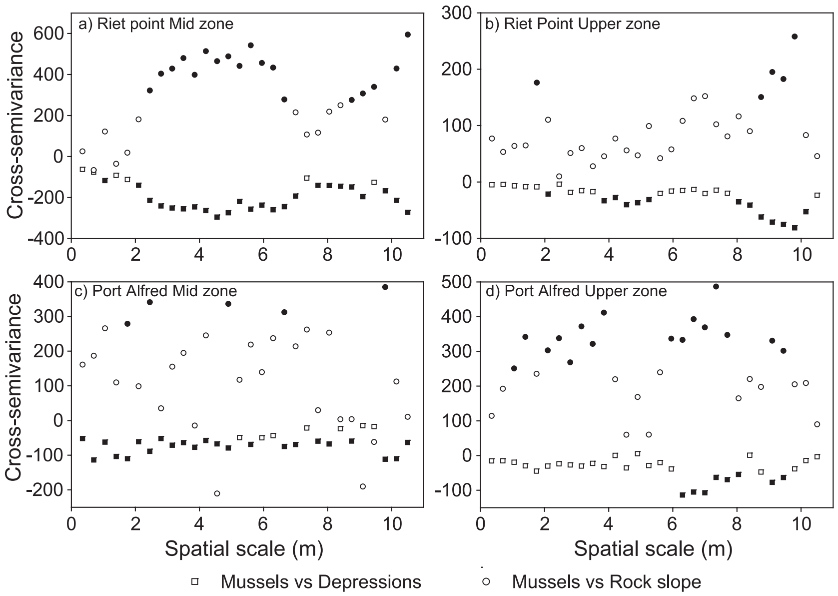

Fig. 6. Cross-semivariograms of the relationships between mussel and topographic variability (squares: mussels vs. depressions; circles: mussels vs. rock slope and aspect) at Riet Point and Port Alfred transects. Negative or positive relationships (indicated by the cross-semivariance values) significant at p<0.05, as estimated by random permutation tests (1000 permutations), are shown as closed symbols at each lag. Nonsignificant relationships are shown as open symbols.

Table 4
Summary of the general relationships between topographic variables (depressions and slope) and mussels/algae/barnacles examined by cross-semivariograms at the different scales (see Figs. 6 and 7, and Results)

Variables	RP				PA			
	Mid		Upper		Mid		Upper	
	Spatial pattern (SC)	General relationship	Spatial pattern (SC)	General relationship	Spatial pattern (SC)	General relationship	Spatial pattern (SC)	General relationship
Mussels vs. depr.	SD (3)	−	SD (1)	−	SI (1)	−	SI (1)	−
Mussels vs. slope	SD (3)	+	SD (1)	+	SI (1)	+	SI (1)	+
Algae vs. depression	SD (2)	+	SD (1)	+	SI (1)	+	SI (1)	+ (weak)
Algae vs. slope	SD (2)	− (weak)	SI (1)	−/0/+	SI (1)	+/0/−	SI (1)	− (weak)
Barn. vs. depression	SD (2)	−	SD (1)	−	SI (1)	− (weak)	SD (2)	−
Barn. vs. slope	SD (3)	+	SD (1)	+ (weak)	SI (1)	−/0/+	SI (1)	+

RP=Riet Point, PA=Port Alfred; depr.=depression, Barn.=Barnacles, SC=scaling regions, SD=spatial dependence, SI=spatial independence; +=positive relationship; −=negative relationship; 0=no relationship; +/0/−=variable relationship.

4.6. Relationships between spatial variability of mussels, algae and barnacles

The scatter plot of the relationship between *D* of algal distribution and *D* of mussel distribution showed a positive trend (r^2=0.65), suggesting that when there is spatial dependence of the variability of one of the organisms, this will be the case for the other as well. Relationships between *D* of barnacles and *D* of either mussels or algae showed no trends (r^2<0.01). It is not possible to do reliable statistical tests of these relationships.

The negative relationship between mussel and algal variability was very strong at most transects and scales (Fig. 8a–d; cross-semivariance values clearly<0), with the negative relationship in Riet Point mid-zone getting weaker and in Riet Point upper zone getting stronger at larger local scales (Fig. 8a–b; Table 5). Overall, there were strong negative relationships between mussel and algal cover, as seen in Pearson's correlation analyses on the spatially independent Port Alfred transects (mid-zone: df=58, r=−0.75, p=0.0000001; upper zone: df=58, r=−0.39, p=0.0023).

The cross-semivariograms of mussels and barnacles showed inconsistent and variable relationships (Fig. 8e–h; cross-semivariance values were both significantly positive or negative or not significant at all) at the different transects and scales. Most transects exhibited spatial dependence in the relationship between mussels and barnacles (Fig. 8e–h; Table 5).

There was generally a negative relationship between barnacle and algal variability, especially in upper zones (Fig. 8e–h; Table 5). This relationship showed spatial dependence on all transects (Fig. 8e–h; Table 5), with upper zones exhibiting an increasing negative relationship with larger local within-shore scales (Fig. 8f,h).

5. Discussion

5.1. Mussel distribution in relation to topography (hypotheses 1, 3, 4)

Mussel variability often showed spatial dependence, especially on topographically structured transects. The variability between samples was usually lower at smaller than at larger local scales (i.e., the semivariograms of *P. perna* distributions exhibited mainly positive slopes in the regressions), indicating that variation was larger with greater distances between samples, as is common for ecological data (Palmer, 1988).

Furthermore, mussel distribution often exhibited two or three natural scaling regions indicating nested patchiness (smaller patches within larger ones). In the transects showing multiscaling, mussel distribution showed highest heterogeneity (patchiness) in the first scaling region (i.e., at smaller scales). This also occurs in *Mytilus edulis* L. distributions on Swedish soft bottoms (Kostylev and Erlandsson, 2001). Patchiness at small scales may be caused by different processes from those operating at larger within-shore scales.

Spatial dependence of mussel variability was stronger on the topographically structured Riet Point transects than on the Port Alfred transects, which

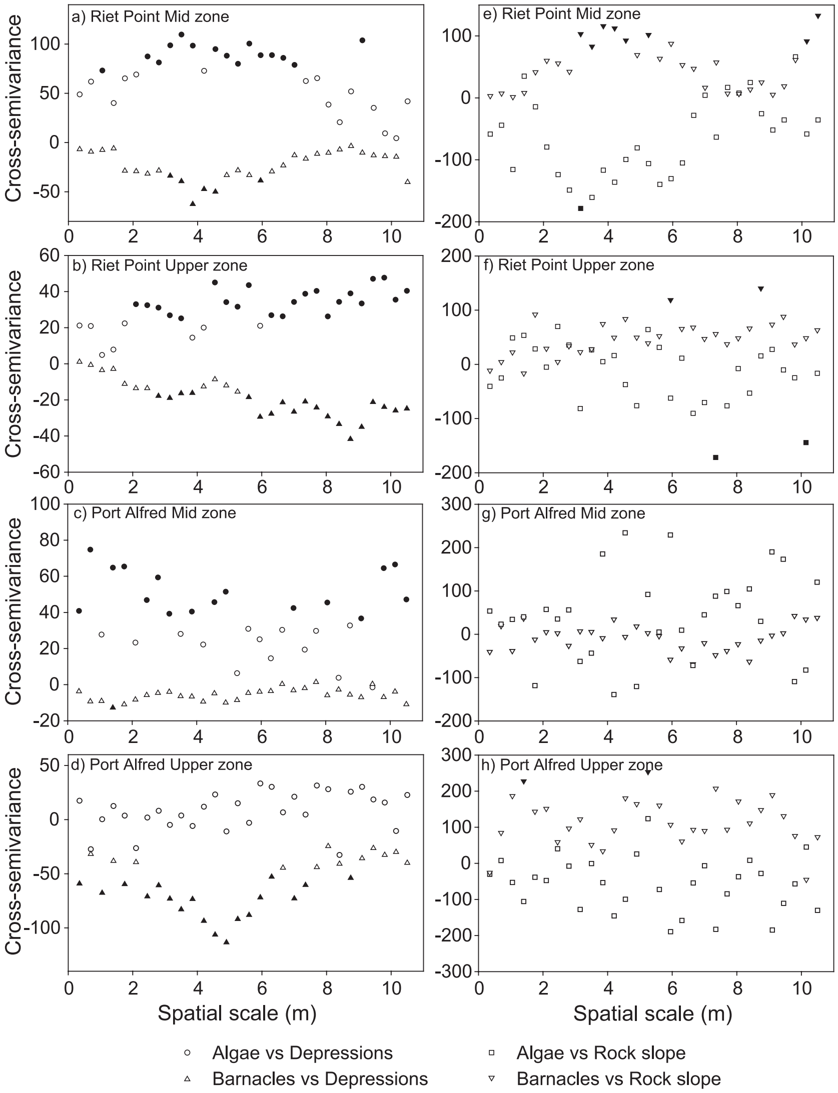

Fig. 7. Cross-semivariograms of the relationships between algal (*G. pristoides*) and topographic variability, and barnacle (*O. angulosa*) and topographic variability at the different transects. Negative or positive relationships significant at $p<0.05$ are shown as closed symbols at each lag. See Fig. 6 and M&M for more information about randomization tests.

showed stochastic patterns in topographic distribution (Figs. 2 and 3). Also, scaling regions of mussel and topographic variability in the Riet Point mid-mussel zone (where multiscaling was clearest) were similar in extent, showing a good correspondence (Fig. 2b–c). Cross-semivariograms confirmed a relationship between mussels and topography. Especially at larger local scales, steeper slope and aspect towards waves tended to be associated with higher mussel cover, while gullies and big crevices were negatively correlated with mussel cover at these scales. At smaller local scales, however, variability in mussel cover is less well explained by topography.

The correspondence between the spatial heterogeneity of mussels and topography may be explained directly by the distribution of topography, e.g., a fragmented distribution of gullies and crevices breaking up the rocky habitat, resulting in a discontinuous patchy mussel distribution (as in the Port Alfred transects). However, topographic distri-

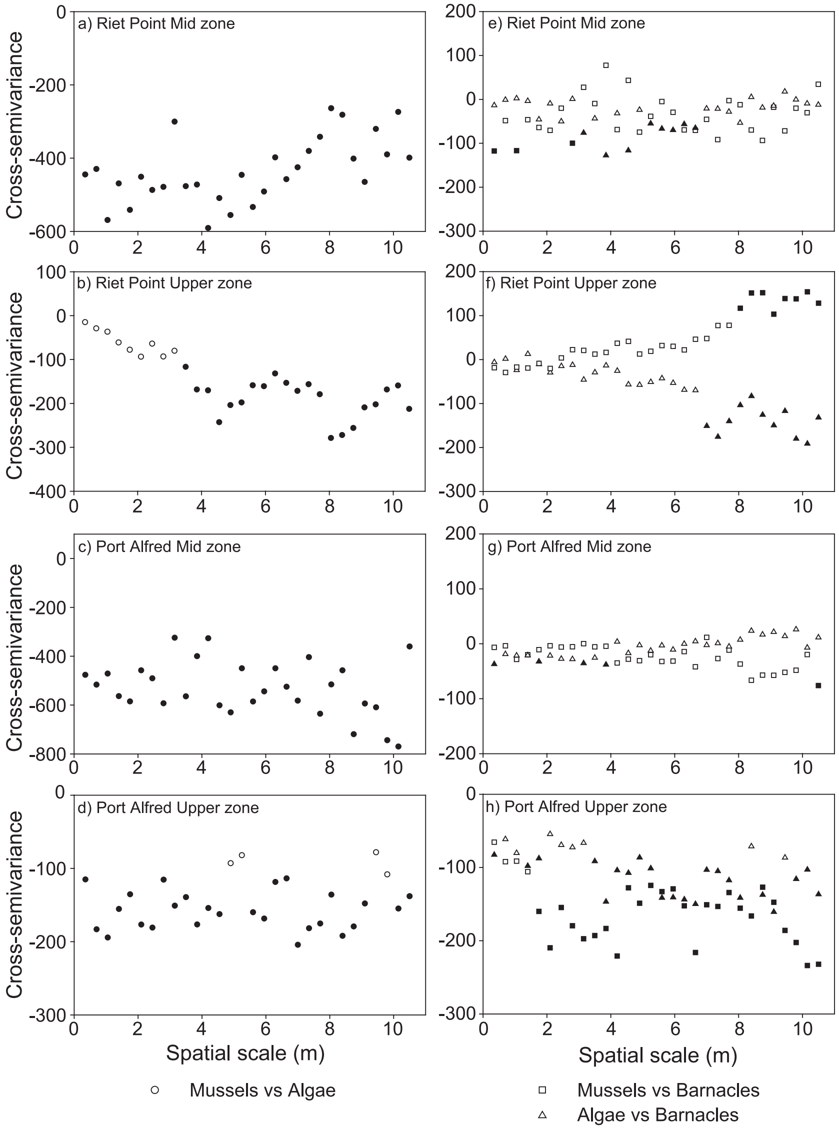

Fig. 8. Cross-semivariograms of the relationships between the variability of the mussel *P. perna*, the alga *G. pristoides* and the barnacle *O. angulosa* at the different transects. Negative or positive relationships significant at $p<0.05$ are shown as closed symbols at each lag. More information about randomization tests are shown in Fig. 6 and M&M.

bution may also affect mussel communities indirectly by interacting with other factors, such as hydrodynamics, shading, predation, intraspecific interactions and growth rate. Guichard et al. (2001) found that the effect of topographic heterogeneity on the abundance of *M. edulis* was mediated mainly by water flow. Archambault and Bourget (1996) found higher biomasses of *M. edulis* in crevices 10-cm deep than on smooth surfaces or deeper crevices, and explained this as a result of greater desiccation on smooth surfaces, and greater dislodgement by wave action or ice in gullies and bigger crevices.

Higher turbulence and water flow in microhabitats such as gullies, grooves and channels, or where there is greater variability in topography over small spatial scales (Carrington Bell and Denny, 1994) may explain low *P. perna* cover in gullies as enhanced turbulence

Table 5
Summary of the general relationships between mussel, algal and barnacle cover examined by cross-semivariograms at the different scales (see Fig. 8 and Results)

Variables	RP				PA			
	Mid		Upper		Mid		Upper	
	Spatial pattern (SC)	General relationship	Spatial pattern (SC)	General relationship	Spatial pattern (SC)	General relationship	Spatial pattern (SC)	General relationship
Mussels vs. algae	SD (1)	–	SD (1)	–	SI (1)	–	SI (1)	–
Mussels vs. Barn.	SI (1)	– (0/+)	SD (1)	+	SD (1)	–/0	SD (1)	–
Algae vs. Barn.	SD (2)	– (0)	SD (1)	–	SD (1)	–/0	SD (1)	–

RP=Riet Point, PA=Port Alfred; Barn.=Barnacles, SC=scaling regions, SD=spatial dependence, SI=spatial independence; +=positive relationship; −=negative relationship; 0=no relationship; +/0/−=variable relationship.

may affect settling larvae both positively and negatively (Abelson and Denny, 1997). Also, strong turbulence caused by breaking waves can generate lift forces strong enough to dislodge adult mussels and open gaps in mussel beds (Denny, 1987). Storm-generated waves can cause dramatic mortality of mussels, creating large areas of bare space within mussel patches (Paine and Levin, 1981; Denny, 1987) and this certainly occurs on South African rocky shores (Erlandsson, unpublished data). Because of the effects of flow on both settling larvae and adults, spatial independence (i.e., random distribution pattern) in topographic variability may result in water turbulence varying greatly over the rock surface, resulting in no spatial dependence in mussel variability.

Generally, the weaker relationships between mussel and topographic variability up to about the 3-m scale may explain the higher spatial heterogeneity of mussel distribution at the first scaling regions of the transects. Thus, the changes in mussel cover over small local scales will be less related to small-scale changes in topographic distribution, while changes in mussel cover at larger local scales will follow large-scale trends in the distribution of topography. It is likely that other processes, such as biological interactions, will influence the small-scale patchiness of mussels. For example, Okamura (1986) found an interaction among growth of *M. edulis*, patch size and crab predation.

5.2. Distribution of algae and barnacles in relation to topography (hypotheses 2–4)

The variability of percent cover of the alga *G. pristoides* exhibited spatial dependence and lower fractal dimension at Riet Point than at Port Alfred transects where it exhibited spatial independence and stochastic distribution patterns (Fig. 4). The same pattern was found for the distribution of biomass of *G. pristoides* (Erlandsson and McQuaid, 2004). This pattern corresponds to the spatial dependence of topographic variability on the different shores (Table 3). There was a positive relationship between algae and depressions (depth of gullies, etc.) at many scales (Fig. 7). Similarly, Guichard et al. (2000) found a negative relationship between elevation and algal biomass at scales larger than 8 m on a rocky shore in Canada, in a region where cm-scale crevices enhance algal biomass (Archambault and Bourget, 1996).

The variability of the barnacle *O. angulosa* showed clearer spatial dependence than the variability of the alga *G. pristoides* within both mid- and upper mussel zones. Barnacle variability basically showed spatial dependence on all transects sampled (Table 2; Fig. 5). Its distribution was still rather patchy, especially at small scales, while in the Port Alfred mid-zone there was more a trend-like structure at larger local scales (Table 2; Fig. 5). Since barnacle distribution showed spatial dependence even on the topographically unstructured Port Alfred shores, and a clear relationship was only found between barnacles and depressions in upper zones, the spatial structure of barnacle distribution should be explained by factors other than topography. At small scales (cm–m scales), one explanation could be that aggregation of barnacles is related to the need for larvae to settle close to potential mates on a favourable substratum (e.g., Bertness et al., 1992; Little and Kitching, 1996). Substratum topography affects barnacle settlement at very small scales, i.e., at scales of the size of individual barnacles or slightly larger (LeTourneux and Bourget, 1988; Raimondi, 1990; Hills et al., 1999). Small-scale patches of barnacles may explain the higher spatial heterogeneity at smaller local scales. At larger local scales (5–10 m), hydrodynamics may play an important role. Since *O. angulosa* is tolerant of high wave exposure, but not of high temperatures or desiccation (Boland, 1997), it may form larger spatial aggregations at more wave-exposed parts of its within-shore distribution, resulting in a trend-like spatial structure at larger local scales.

5.3. Relationships among variability of mussels, algae and barnacles (hypothesis 5)

In all beds sampled, there was a strong negative correlation between variability of *P. perna* and of *G. pristoides* cover at most local scales, especially in the mid-zone (Fig. 8). Strong negative relationships have also been found between adult *P. perna* density and *G. pristoides* biomass at many scales, especially at larger local scales (Erlandsson and McQuaid, 2004). These two species cover similar primary space, forming either large patches, or a mosaic of small patches. Competition for space between mussels and seaweeds is likely (McQuaid and Branch, 1985), and has been documented in studies of disturbance and succession and of low-shore boundaries between kelp- and mussel beds (Paine, 1984; Sousa, 1984; Suchanek, 1985). *P. perna* is not as competitively dominant as other mytilid mussels, showing slower recruitment rates and recovery from disturbance (Lasiak and Barnard, 1995; Erlandsson, in preparation). *P. perna* shows stronger relationships with topography than *G. pristoides*, so the spatial dependence of algal distribution on the topographically structured Riet Point shores may be more related to mussel distribution than to the topography itself. While there may be competition for space between adult mussels and algae, small individuals of *P. perna* (<5 mm) are often found in *G. pristoides* (Beckley, 1979; Erlandsson and McQuaid, 2004), although we do not know the fate of these individuals. *P. perna* is heavily exploited by people, and threatened by the invasive mussel *M. galloprovincialis* Lamarck (Calvo-Ugarteburu and McQuaid, 1998; Harris et al., 1998). It is likely that a decline in the abundance of *P. perna*, due to reduced recruitment in the absence of adult mussel clumps (Lasiak and Barnard, 1995; Erlandsson and McQuaid, 2004), will affect the interactions between *P. perna* and *G. pristoides*.

The barnacle *O. angulosa* does not cover space nearly as extensively as *P. perna* or *G. pristoides*, and it can inhabit space between and on mussels. Thus, the inconsistent relationship between mussels and barnacles on the shores sampled supports the observation that they do not necessarily compete for the same type of space. In Japan, the barnacle *Chthamalus challengeri* Hoek and the mussels *Septifer virgatus* Wiegmann and *Mytilus trossulus* Gould inhabit different surfaces (barnacles on horizontal and vertical surfaces, while mussels occur only in grooves), with habitat separation determined by recruitment and not interspecific competition (Chiba and Noda, 2000). However, there are no such distinctions between the surfaces used by mussels and barnacles in South Africa, where barnacles occur on many different substrata (personal observation). Since mussels also act as a secondary habitat for *O. angulosa*, competition for rock surface space with *P. perna* is decreased.

By contrast, there was generally a negative relationship between *O. angulosa* and *G. pristoides* in upper zones (especially in Port Alfred upper zone), with the negative correlation becoming stronger at larger local scales (Fig. 8). The greater negative relationship between algae and barnacles in upper zones may reflect higher barnacle cover in the upper mussel zone, especially at Port Alfred (unpublished data). Because of the lower mussel cover in upper mussel zones (McQuaid et al., 2000), barnacles may not be able to settle on mussels so often, and will have to compete more strongly with *G. pristoides* for primary space. The stronger negative relationship between barnacles and algae at larger local scales in the upper mussel zone means that there were opposite trends in the distributions of *O. angulosa* and *G. pristoides*.

In summary, we found that spatial dependence of *P. perna* variability increased with spatial dependence of topographic variability, and mussel distribution was more heterogeneous at smaller local scales. We also found that the variability of the barnacle *O. angulosa* generally exhibited spatial dependence, even on topographically unstructured shores, while the distribution of the alga *G. pristoides* was very heterogeneous or exhibited a random pattern, showing a very strong negative relationship with *P. perna* at most local within-shore scales.

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