Scales of mussel bed complexity: structure, associated biota and recruitment

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Abstract

Hierarchically scaled surveys were carried out on beds of the brown mussel *Perna perna* (Linnaeus) on the South coast of South Africa. The object was to assess spatial and temporal variations in the complexity of mussel beds and to investigate relationships between mussel bed complexity and mussel recruitment. Complexity was divided into three components: physical complexity; demographic complexity; associated biota. A series of variables within each component were recorded at two different scales (10 and 50 cm) within nested quadrats on three separate occasions. The nested ANOVA design explicitly incorporated spatial scale as levels of the ANOVA. These scales were: shores (areas 1 km in length separated by 25 km); transects (areas 20 m in length separated by 100s of meters); 50×50-cm quadrats separated by meters and 10×10-cm quadrats separated by cm) This approach was intended to generate hypotheses concerning direct associations between recruitment and complexity versus co-variation due external processes. Three main questions were addressed: (1) At what scale does each variable of complexity exhibit greatest significant variation? (2) At these scales is there similar ranking of variables of complexity and recruitment? (3) Within this/these scales, is there any significant relationship between the variables measured and mussel recruitment? On two occasions (Nov. 97 and Mar. 98) the majority of variables showed greatest significant variation at the transect-scale. On a third occasion (Oct. 97) most variables showed greatest significant variation at the quadrat-scale and the site-scale. On all occasions a markedly high percentage of the variation encountered also occurred at the smallest scale of the study, i.e., the residual scale of the ANOVA analyses. Some similarity in the ranking of variables occurred at the transect scale. Within the transect-scale, there was little indication of any relationship between variables of complexity and recruitment. Relationships were inconsistent either among transects or among sampling occasions. Overall, the results suggest that a high degree of variation in mussel bed complexity consistently occurs at very small scales. High components of variance generally also occur at one or more larger scales; however, these scales vary with season. Mussel recruitment does not appear to be directly affected by complexity of mussel beds. Instead it appears external factors may influence both complexity and recruitment independently. In addition recruitment may influence complexity rather than vice versa.

1. Introduction

The complexity of rocky shores has long been recognised (Stephenson and Stephenson, 1949; Stephenson and Stephenson, 1972; Field and Griffiths, 1991; Russel, 1991) but only recently has the explicit incorporation of spatial and temporal scale into studies been recognised as a key requirement to understanding the dynamics of ecological systems and managing them adequately (Frost et al., 1988; Levin, 1992; Underwood and Petratis, 1993; Schneider, 1994; Archambault and Bourget, 1996; Underwood and Chapman, 1998; Thrush et al., 1999). Mussel beds are one of the most prominent and well researched features of rocky shores and are frequently an informal human resource (Seed, 1976; Suchanek, 1985; Lasiak and Dye, 1989; Lasiak, 1991; Lasiak and Barnard, 1995). Mussel beds are intrinsically complex, in terms of their demography, physical structure, associated biota and interactions (Dayton, 1971; Paine and Levin, 1981; Suchanek, 1985; Whitman, 1985; Sebens, 1991; Suchanek, 1992; Lintas and Seed, 1994; Alvarado and Castilla, 1996; Kostylev, 1996). In addition, superimposed on this intrinsic complexity is the complexity of scale. Structural, demographic and biotic variations in mussel beds are apparent from biogeographic scales to scales of centimeters.

Mussel beds around the coast of southern Africa exemplify such spatial variation, with huge changes in structural complexity, dominant mussel species and associated fauna and flora as one moves around the coast (Stephenson and Stephenson, 1972; Van Erkom Schurink and Griffiths, 1990; Field and Griffiths, 1991; Branch and Branch, 1993; Harris et al., 1998). On the West coast, extensive, multi-layered mussel beds and mosaics are formed by *Choromytilus meridionalis* and the invasive *Mytilus galloprovincialis*. On the South and East coasts the warm water *Perna perna* forms mono-layered beds, mosaics and patches. In the last 5 years, *M. galloprovincialis* has begun to spread from the West on to the South coast, again as mono-layered beds (McQuaid and Phillips, 2000). This biogeographic transition in mussel and other rocky shore species assemblages along these coasts has been associated with variation in oceanographic and climatic conditions and nearshore productivity (Bustamante et al., 1995; Bustamante and Branch, 1996; Harris et al., 1998). At smaller scales great variation in mussel bed complexity is apparent (McQuaid and Branch, 1984; McQuaid et al., 1985; Lasiak and Dye, 1989; Lasiak and Barnard, 1995; McQuaid et al., 2000, pers. obs.). Smaller scale variation ranges from inter-shore to intra-shore scales and is associated with differences in human exploitation, rock substratum and wave exposure. However, in ecological studies variation at cm- and m-scales often becomes merely the residual, unexplained or random variation in analyses. Temporal variation in mussel beds and their associated species is also apparent with a continual turnover of individuals, combined with periods of high recruitment, or mass mortality, due to storms or sand inundation and fluctuations in interactions between species (Van Erkom Schurink and Griffiths, 1991; Harris et al., 1998; McQuaid and Lindsay, 2000).

In order to understand the dynamics of the relationships between the different aspects of complexity, we need to describe explicitly the dominant scales of variation in mussel beds, and to identify the processes underlying variation in complexity at each scale. Studies elsewhere in the world have suggested several possible interactions. Increased structural complexity in mussel beds (in terms of patch size and/or mussel size structure) has been associated with enhanced biotic diversity or species richness in mussel beds (Suchanek, 1985; Tsuchiya and Nishihira, 1986; Suchanek, 1992; Lintas and Seed, 1994; Kostylev, 1996). Potential limitation of settlement of planktonic larvae within mussel beds due to the filter feeding by adults and other mussel bed biota has also been suggested (Thorson, 1946; Bayne, 1964; Tsuchiya and Nishihira, 1986). Conversely, mussel beds may enhance the settlement and recruitment of certain species, including themselves, by providing a greater number of suitable settlement or recruitment sites (Suchanek, 1985; Alvarado and Castilla, 1996; Seed, 1996; Harris et al., 1998). Lastly, there may be a strong and direct influence of settlement and subsequent recruitment on the generation and maintenance of the structural and demographic complexity of adult mussel beds.

In a biogeographic study around the southern African coast, Harris et al. (1998) found a highly significant correlation between recruitment intensity and adult density of mussels, based on mean values from 10×10-cm quadrats. Highest recruitment occurred at locations where adults formed complex multi-layered beds. Whether complexity enhanced recruitment or vice versa or whether both complexity and recruitment were related to some other external factor was not determined. Furthermore, Lasiak and Barnard (1995) suggested that *Perna perna* may not undergo large scale secondary settlement (c.f. Bayne, 1964), and that recruitment of mussels may be heavily dependent on primary settlement into existing mussel beds. It seems likely that, in southern Africa, variations in nearshore and onshore productivity at a biogeographic scale are probably related to variation in both mussel bed complexity and mussel recruitment. At smaller scales, the intrinsic complexity of mussel beds may have significant effects on localised recruitment intensity.

In the present study, both the spatial scales of variation in complexity of *Perna perna* beds on the South coast and the relationship between recruitment and complexity were explored on three separate occasions. The intrinsic complexity of mussel beds was split into three components: physical structure; demographic structure (both for mussels); and associated biota. Variations in these components and their relationships with recruitment of mussels were investigated in a hierarchically and explicitly scaled manner. Three main questions have been addressed. (1) At what scale does each variable of complexity exhibit greatest significant variation? (2) At these scales is there similar ranking of variables of complexity and recruitment? (3) Within this/these scales, is there any significant relationship between these variables and recruitment?

The aim was to distinguish between direct associations between recruitment and variables of complexity from co-variation. Statistical analyses of association, both at the scale of greatest significant variation and within this scale allow some distinction to be made. At the scale of greatest significant variation, similar ranking of variables may result

from either co-variation or a direct association. If a correlation between these variables also occurs within scales of significant variation, a direct association could be inferred. A lack of correlation would point to co-variation or an effect of recruitment on complexity at the larger scale. Where variables do not show similar ranking at the scale of significant variation but do show correlation within that scale a direct association may also be inferred at the smaller scale. Obviously, where neither similar ranking nor correlation occur no relationship is suggested. Lastly, without further investigation coincidental relationships cannot be ruled out. This approach is thus used for hypothesis generation rather than as a method for testing causality.

2. Materials and methods

2.1. Design

Hierarchically scaled surveys based on a nested ANOVA design were carried out in October 1997, November 1997 and March 1998 on the South coast of South Africa. The timing coincided with expected periods of high settlement and/or subsequent recruitment for this coast, based on previous studies (Van Erkom Schurink and Griffiths, 1991; Lasiak and Barnard, 1995; Harris et al., 1998, unpublished data). The design (Fig. 1) incorporated two exposed rocky shore sites; Port Alfred (PA) (33°37′30S; 26°52′30E) and Dias Cross (DC) (33°43′00S; 26°37′45E), each 1 km in length and approximately 25 km apart. The Dias Cross site is a platform of aeolian dune rock, which is relatively soft and has little topographic relief at the m-scale, but is frequently pitted at the cm-scale. In comparison, the Port Alfred site consists of ridges of quartzitic sandstone, which is relatively hard and has much more complex and varied topography at scales of cm to 10s of meters. Both sites are typical of exposed rocky shore types in this region. Within each site there were one to three transects (X, Y, Z) each 20 m long, separated by 100s of meters, parallel to the shoreline and lying over the mid-zone of a mussel bed. Variation in relative exposure, height and m-scale topography occurred among transects. This variation was classified subjectively a priori. Along each transect there were between three and five large (50×50 cm) quadrats (numbered 1–5) positioned at one of 40 possible locations at random. Within each large quadrat there were three small (10×10 cm) quadrats (a, b, c) positioned at one of 25 possible locations at random on each occasion (Fig. 1). The same transects were used each time but different 50-cm quadrats were used in each survey because of the destructive sampling carried out at the smallest scale. Although ideally a balanced design of sampling would have been used, the short duration of spring low tides and degree of wave exposure of the sites limited the replication possible at any scale. Replication of transects and large quadrats thus varied between sampling occasions according to the available time, but maximised the information gained for these scales (Fig. 1). This lead to the design of sampling in October and November being unbalanced at the site level, with two transects within one site and one transect within the other.
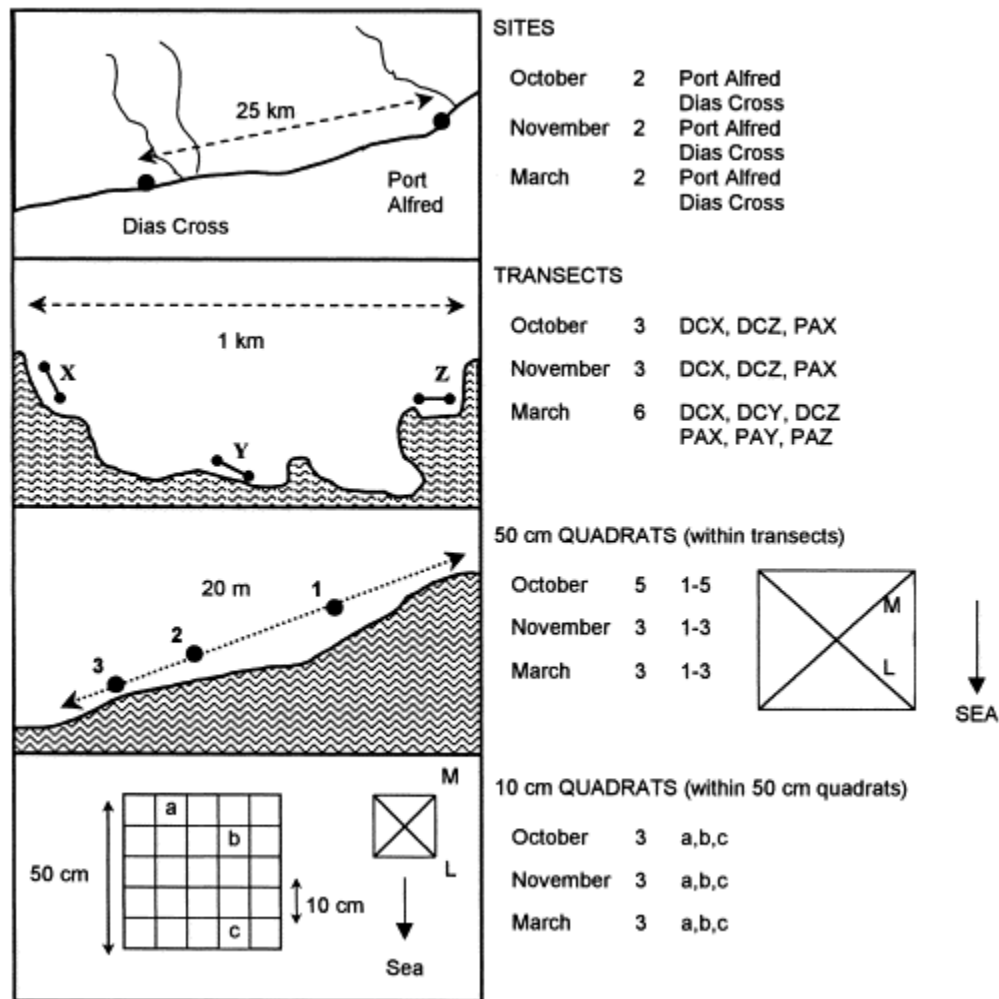
SITES

October	2	Port Alfred Dias Cross
November	2	Port Alfred Dias Cross
March	2	Port Alfred Dias Cross

TRANSECTS

October	3	DCX, DCZ, PAX
November	3	DCX, DCZ, PAX
March	6	DCX, DCY, DCZ PAX, PAY, PAZ

50 cm QUADRATS (within transects)

October	5	1-5
November	3	1-3
March	3	1-3

10 cm QUADRATS (within 50 cm quadrats)

October	3	a,b,c
November	3	a,b,c
March	3	a,b,c

Fig. 1. Schematic design of hierarchically scaled surveys carried out in October 1997, November 1997 and March 1998. Number of replicates (and names where appropriate) at each scale on each occasion are given and the positions of surface profiles L and M are shown with respect to direction towards the sea.

2.2. Sampling

For the three defined components of complexity (physical structure, demographic structure and associated biota), representative variables were chosen for measurement within each of the 10- and 50-cm quadrats (Table 1). Seventeen variables were recorded from the 10-cm quadrats (Table 1) which were sampled destructively after recording structural variables, such as bed height, form of cover and percentage cover in situ. Eight variables were recorded in situ within the 50-cm quadrats, including percentage cover of mussels within different size/age classes (Table 1). Two further variables mean recruits to mussel bed and mean recruits to algae, were calculated for this scale from data for 10-cm quadrats within each 50-cm quadrat. This allowed a more detailed analysis of the relationship between recruitment and complexity at the 50-cm scale. Two diagonal surface profiles (L and M) were recorded using customised contour gauges for each small and each large quadrat (Fig. 1), using 1 mm resolution for the small quadrats and 1-cm resolution

for the large quadrats. The profiles were scanned onto PC and the fractal dimension (*D*) for each profile calculated by the linear divider method (Kostylev, 1996; Hastings and Suighara, 1993) using image analysis software (Sigma Scan Image 1.20.09). This provided measures of the surface topographic complexity of the mussel bed. Resultant fractal dimensions for each quadrat were analysed separately rather than taking a mean value since variation within quadrats was considerable. It seemed possible that directional variation in topographic complexity might occur given the standardised orientation of the profiles measured with respect to the ocean, and thus prevailing wind and wave conditions. The contribution of mussel recruits and settlers to measurements of topography and percentage cover was very small. Their effects on these variables (apart from percentage cover of recruits within 50-cm quadrats) was considered negligible.

Table 1. Variables within three components of mussel bed complexity recorded within 10- and 50-cm quadrats

Component of complexity	Variables recorded within 10-cm quadrats	Variables recorded within 50-cm quadrats
Physical	Percentage cover of mussels	Fractal dimensions of diagonal
structural complexity	Mussel bed height	profiles (*L* and *M*)
	Fractal dimensions of diagonal profiles (*L* and *M*)	Form of cover:
	Mussel shell dry mass (volume)	(A) Continuous
		(B) Continuous with gaps
	Form of cover:	(C) Patches (>3 individuals)
	(A) Continuous	(D) Scattered individuals
	(B) Continuous with gaps	Patch size (if C or D)
	(C) Patches (>3 individuals)	Percentage cover of mussels
	(D) Scattered individuals	within size classes:
	Patch size (if C or D)	Recruits (≤10 mm)
		Sub-adults (>10≤30 mm)
		Adults (>30≤70 mm)
		Large adults (>70 mm)
Demographic	Mussel meat dry mass (biomass)	Mean abundance of recruits to
structural complexity	Adults (>30 mm)	mussels (calculated from 10-cm
	Sub-adults (>10≤30 mm)	quadrat data)
	Recruits on mussels (>1≤10 mm)	Mean abundance of recruits to
	Recruits on algae	algae (calculated from 10-cm
	Settlers on mussels (≤ 1 mm)	quadrat data)
	Settlers on algae	
Associated	Species richness in mussel bed	Species richness (from 10-cm
biota	Species richness in algae	quadrats and in situ record of
	Dry weight of algae attached to mussels	species with percent cover >10%)
	Dry weight of algae elsewhere	Percentage cover of foliose algae

Destructive samples were collected as two sub-samples: (i) mussel bed and attached biota and (ii) biota attached/located elsewhere within the quadrat. Frequently algae formed the dominant substratum in the latter sub-sample. Mussels>10 mm in length were cleaned of attached biota, and the byssus removed. The byssus was later checked for juvenile mussels. Individuals were sexed and meat and shells were dried separately to constant weight at 60°C. These two variables were used as indications of biomass and volume, respectively. The length of dried shells was measured using image analysis of video relayed images on a PC. All mussels of <10 mm were measured by hand, using vernier calipers or an eyepiece micrometer with a dissecting microscope. These small individuals were not included in the dry meat and dry shell mass estimations. Mussel abundance was calculated for each of four size classes): adults (>30 mm); sub-adults (>10–30 mm); recruits (>1–10 mm); settlers (<1 mm) (Hops, 1990; Lasiak and Barnard, 1995; Harris et al., 1998; McQuaid and Lindsay, 2000). Recruits as defined here were all late plantigrades, whereas settlers were early to late plantigrades (c.f. Lasiak and Barnard, 1995). Foliose algae from each sub-sample were identified and dried to constant weight after washing and thoroughly checking for small mussels. All other biota were identified to the lowest possible taxonomic resolution and presence/absence recorded. For the analysis, species richness of biota, mussel settler and recruit abundance within each sub-sample were recorded and coded as 'species on', 'settlers to' or 'recruits to' mussels or as 'species on', 'settlers to' or 'recruits to' algae/elsewhere (Table 1).

2.3. Analysis

To identify the scales at which greatest significant variation occurred, the continuous variables recorded for each small quadrat and each large quadrat were analysed using Hierarchical (nested) and one-way ANOVA. Although ANOVA is considered robust (Zar, 1996), transformed data ($\ln(x+1)$) were used, since analysis revealed non-normality and heterogeneity of variance in all cases. Components of variance were calculated for each variable at each scale including the scale of the replicate 10- or 50-cm quadrats from nested ANOVA analyses. Since the design of the study was unbalanced in October and November (with only one transect at the Port Alfred site), complete analyses of the data with time incorporated as a factor could not be carried out. To allow comparison of the data from the 10-cm quadrats between all three sampling occasions, two-level nested ANOVA (Eq. 1) were used to examine variation at the transect and 50-cm quadrat-scale, and one-way ANOVA were used to examine variation at the site-scale. In addition in March the balanced design allowed all scales to be analysed together using three-level nested ANOVA (Eq. 2). Scales of greatest significant variation for the data from 50-cm quadrats were investigated using one-way ANOVA at each scale for all sampling occasions as well as nested two-level ANOVA (Eq. 3) for March.

$$X_{jkl}=\mu+T_j+Q(T)_{k(j)}+\varepsilon_{jkl} \qquad (1)$$

$$X_{ijkl}=\mu+S_i+T(S)_{j(I)}+Q(T(S))_{k(j(I))}+\varepsilon_{ijkl} \qquad (2)$$

$$X_{ijk}=\mu+S_i+T(S)_{j(I)}+\varepsilon_{ijk} \qquad (3)$$

where X is the variable of complexity or recruitment being analysed, μ is the overall mean, S_i is the effect of the ith site, T_j or $T(S)_{j(I)}$ is the effect of the jth transect, $Q(T)_{k(j)}$ or $Q(T(S))_{k(j(I))}$ is the effect of the kth 50-cm quadrat and ε_{ijk} or ε_{ijkl} is the error term or residual. The residual is equivalent to the variation within and between 10-cm quadrats.

To test for the effects of greater replication at the 50-cm quadrat scale in October (five 50-cm quadrats were sampled rather than three), two-level nested ANOVA's using transects and three randomly chosen quadrats within each were employed (Eq. (1), above). In addition, one-way ANOVA's of standard deviations of each variable at the transect level among sampling occasions were calculated.

The categorical variable, 'form of cover' was used to provide a qualitative description of differences at the site and transect levels for each sampling occasion.

To examine relationships between recruitment and complexity within the identified scales of greatest significant variation, bivariate correlations (Spearman's rank), with a Bonferroni corrected level of α were calculated. Correlations were only carried out where the number of replicates (n) within a scale was greater than or equal to 5. Several other more powerful analytical techniques were used during the investigation of these data (e.g., partial correlations, stepwise linear regression, partial canonical correspondence analysis, and partial redundancy analysis). These tested both linear and unimodal relationships, and worked either within scales of significant variation, or else worked on pooled data but detrended the overlying larger scale variability in the initial phase of analysis. However, in all cases the results were remarkably similar to those from the much more straightforward bivariate correlations. Thus, only the results from these correlations are presented.

3. Results

3.1. Scales of variation

3.1.1. Ten-cm quadrat data

Variance components and nested ANOVA analyses (Fig. 2) indicated four clear trends. (1) Variance associated with the site scale was rarely high. (2) During October, most variables recorded exhibited greatest significant variation at the scale of 50-cm quadrats. (3) During November and March most variables exhibited greatest significant variation at the scale of transects. (4) On all occasions, most variables also exhibited a large component of variation at the scale of replication, the 10-cm quadrat scale. In several cases, particularly in March and for variables associated with settlement/recruitment, this small-scale variance was greater than, or equal to, the variance components calculated for larger scales.
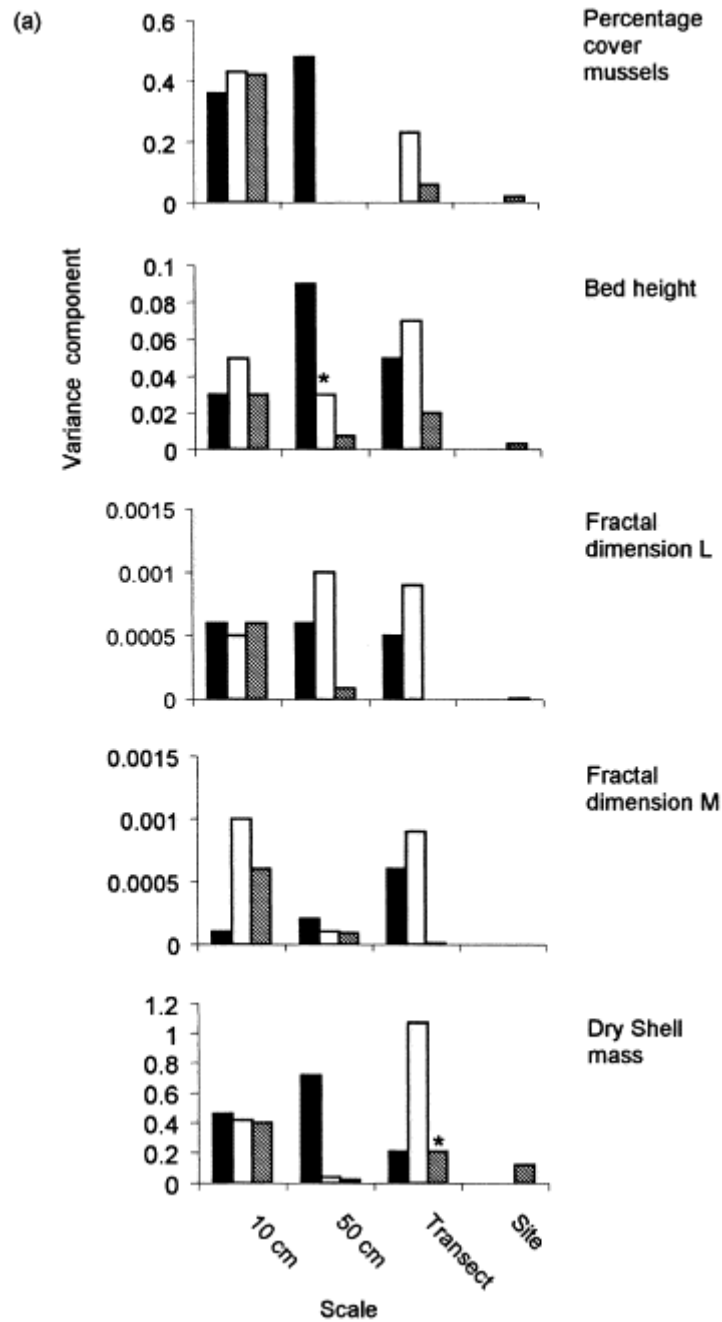
Fig. 2. Variance components for each variable of complexity, at each scale on each sampling occasion using the 10-cm quadrat data (October 97, filled bars; November 97, clear bars; March 98, hatched bars). Asterisks denote scales of significant variation (*P*<0.05) from two-level nested ANOVA analyses for October an November and three-level nested ANOVA analyses for March. Figures are divided into the three components of complexity: (a) structural variables; (b) demographic variables; and (c) variables of associated biota. Variance components for October and November at the site scale could not be calculated.
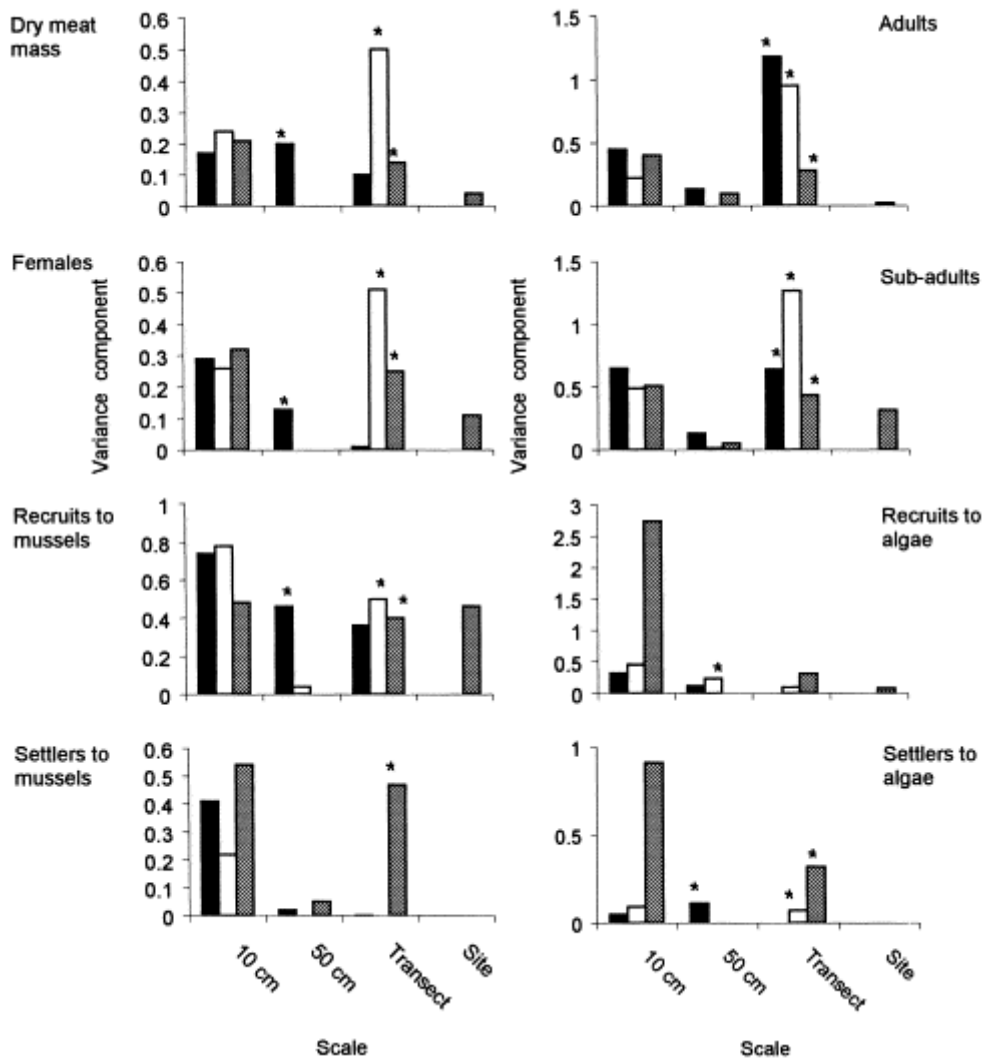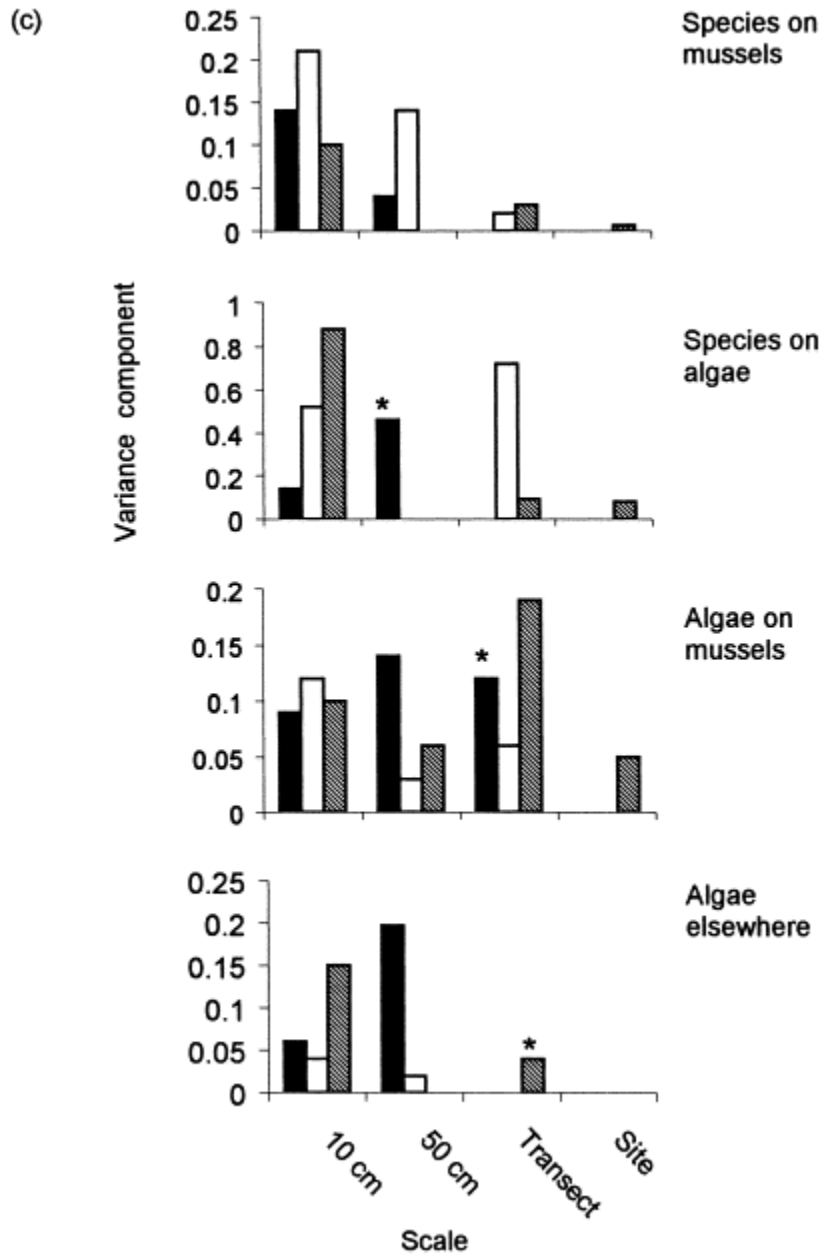
Fig. 2. (continued)

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The combination of one-way and two-level ANOVA analyses used to compare all sampling occasions frequently indicated significant variation ($P<0.05$) at both the site and transect scales for November and March. For March this was clarified by three-level nested ANOVA analyses, which determined that this variation was in fact due to variation at the transect scale. Although no such analysis was possible for November, it seems likely that again site scale variation indicated by one-way analyses was actually due to variation at the transect scale.

Two-level nested ANOVA using three randomly chosen quadrats for October indicated that the occurrence of significant variation at the quadrat level was not due to greater replication at this level in October. Again most variables showed greatest significant variation at the quadrat level. Furthermore, one-way ANOVA of standard deviations indicated that a similar amount of variation was encompassed within this level on each sampling occasion. No significant differences between sampling occasions were found for any variable ($P>0.05$).

More detailed examination of variance components, taking into account differences between possible range and units of measurement of the variables, within each component of complexity, reveals further patterns (Fig. 2). In general, demographic variables had higher values for variance components than either structural variables or variables of associated biota. The only variables that showed a notable component of variance at the site scale in March were recruits to mussels, and sub-adults. Recruits and settlers to algae showed particularly high relative variance in March at the 10-cm scale. Highest values of settlement and recruitment were recorded on this sampling occasion. The structural variables bed height and fractal dimensions L and M, had very low values of variance relative to their potential range, suggesting similar topographic relief of mussel beds within the areas sampled. The remaining two structural variables, percentage cover of mussels and shell mass (an indication of volume) had higher variance component values. Percentage cover showed persistently high variance components at the 10-cm scale, and at the 50-cm scale in October. Although shell mass variance was also consistent at around 0.4 at the 10-cm scale in October and November, greatest variance occurred at the 50-cm and transect scales, respectively. Variables of associated biota other than species on algae/elsewhere generally had low variance component values, suggesting similar numbers of species associated with mussels and similar algal cover within areas sampled.

Post-hoc comparisons at scales of greatest significant variation for each month revealed two general features (Table 2). Firstly, examination of the transect and site-scale variation in November suggested that for many variables, significant variation at both scales was due to higher values within transect PAX. Since only one transect represented the Port Alfred site for this month, the validity of site-scale differences cannot be confirmed. Given their absence in March, it seems unlikely. Secondly, at the transect-scale in March, significant differences for several variables showed similar ranking between transects. Often significantly higher values occurred at transect PAZ and to some extent PAY and DCY and/or significantly lower values at transect DCZ. Nevertheless, the trend was not universal and the other transects did not fit into a consistent ranking. During October transects rarely differed and there was no consistent ranking of quadrats. No further analysis was carried out for the October data collected at the 10-cm quadrat-scale.

Table 2. Post-hoc Tukey HSD multiple comparisons between transects using the data from 10-cm quadrats

		October 1997	November 1997	March 1998
Physical structure	Percentage cover	PAX DCX DCZ	PAX DCX DCZ	PAY PAZ PAX DCY DCX DCZ
	Bed height	PAX DCX DCZ	PAX DCX DCZ	PAZ PAX DCY PAY DCX DCZ
	Fractal L	PAX DCX DCZ	PAX DCX DCZ	PAZ PAY DCY DCZ DCX PAX
	Fractal M	PAX DCX DCZ	PAX DCX DCZ	DCY PAY PAZ DCX DCZ PAX
	Shell mass	PAX DCX DCZ	PAX DCX DCZ	PAY PAZ DCY PAX DCX DCZ
Demographic structure	Meat mass	PAX DCX DCZ	PAX DCX DCZ	PAZ PAY DCY PAX DCX DCZ
	Adults	FAX DCX DCZ	PAX DCX DCZ	DCY PAY PAZ DCX PAX DCZ
	Females	PAX DCZ DCX	PAX DCX DCZ	PAZ PAY DCY PAX DCZ DCX
	Sub-adults	PAX DCZ DCX	PAX DCZ DCX	PAZ PAY PAX DCY DCZ DCX
	Recruits on mussels	FAX DCZ DCX	PAX DCX DCZ	PAZ PAY PAX DCX DCY DCZ
	Recruits on algae / elsewhere	DCZ PAX DCX	PAX DCX DCZ	PAZ DCY PAX PAY DCX DCZ
	Settlers on mussels	DCZ DCX PAX	PAX DCX DCZ	PAZ DCX DCY PAY PAX DCZ
	Settlers on algae / elsewhere	DCZ DCX PAX	DCX DCZ PAX	PAZ DCX DCY PAX PAY DCZ
Associated biota	Species on mussels	PAX DCX DCZ	PAX DCX DCZ	DCY PAZ PAY PAX DCZ DCX
	Species on algae / elsewhere	DCX DCZ PAX	DCX DCZ PAX	DCZ DCX DCY PAY PAZ PAX
	Algae on mussels	DCX PAX DCZ	DCX PAX DCZ	DCY DCX PAX DCZ PAY PAZ
	Algae elsewhere	DCX PAX DCZ	DCX PAX DCZ	DCY PAZ DCX PAX DCZ PAY

3.1.2. Fifty-cm quadrats

Variance components and two-level nested ANOVA for March (Fig. 3) indicate that when there was significant variation it was at the transect scale. However, less than half of the variables showed significant variation at any scale. Again a relatively large component of variation also occurred at the smallest scale, in this case the 50-cm quadrat-scale. One-way ANOVA for each of the variables at each scale confirmed that most variables showed greatest significant

variation at the transect scale in March, whilst in October and November approximately equal numbers of variables showed significant variation at each scale (Table 3).
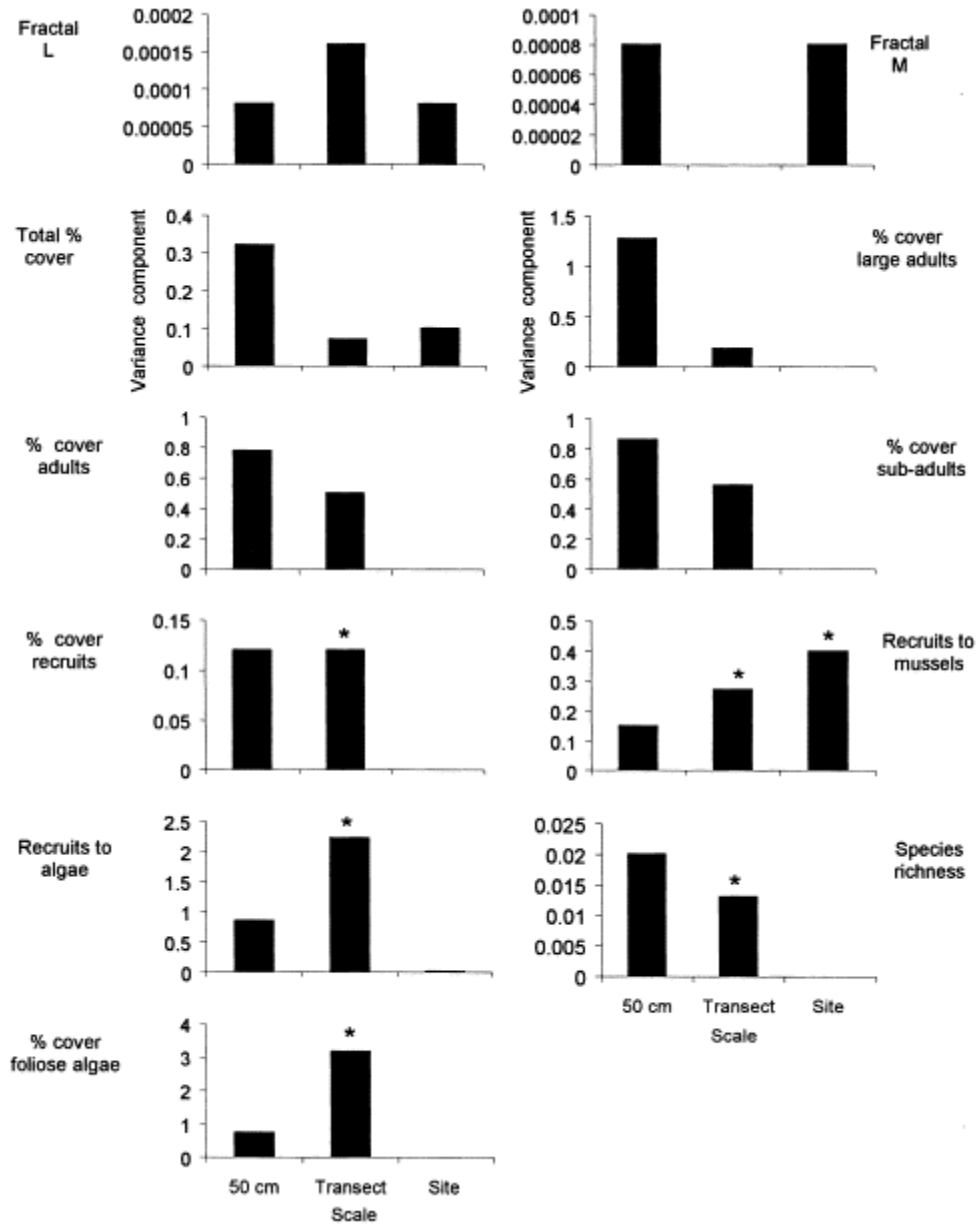

Fig. 3. Variance components for each variable of complexity, at each scale using the 50-cm quadrat data from March 98. Asterisks denote scales of significant variation (*P*<0.05) from two-level nested ANOVA analyses.

Table 3. F values and associated significance (P) for one-way ANOVA analyses carried out at the transect scale and at the site scale for variables of complexity recorded within 50-cm quadrats

	Scale					
	October 1997		November 1997		March 1998	
	Site	Transect	Site	Transect	Site	Transect
Fractal L	$F=0.24$ $P=$n.s.	$F=0.45$ $P=$n.s.	$F=0.02$ $P=$n.s.	$F=1.25$ $P=$n.s.	$F=1.05$ $P=$n.s.	$F=1.74$ $P=$n.s.
Fractal M	$F=0.89$ $P=$n.s.	$F=3$ $P=$n.s.	$F=0.2$ $P=$n.s.	$F=2.27$ $P=$n.s.	$F=0.08$ $P=$n.s.	$F=1.96$ $P=$n.s.
Total % cover	$F=7.88$ $P<0.025$	$F=3.91$ $P<0.05$	$F=6.74$ $P<0.05$	$F=3.43$ $P=$n.s.	$F=6.39$ $P<0.05$	$F=2.8$ $P=$n.s.
% Cover large adults	$F=4.77$ $P<0.05$	$F=2.52$ $P=$n.s.	$F=0.03$ $P=$n.s.	$F=1.14$ $P=$n.s.	$F=0.00$ $P=$n.s.	$F=1.14$ $P=$n.s.
% Cover adults	$F=0.06$ $P=$n.s.	$F=0.18$ $P=$n.s.	$F=15.99$ $P<0.01$	$F=7.38$ $P<0.05$	$F=0.89$ $P=$n.s.	$F=2.6$ $P=$n.s.
% Cover sub-adults	$F=6.54$ $P<0.05$	$F=3.3$ $P=$n.s.	$F=0.14$ $P=$n.s.	$F=0.06$ $P=$n.s.	$F=0.69$ $P=$n.s.	$F=2.55$ $P=$n.s.
% Cover recruits	$F=1.94$ $P=$n.s.	$F=0.94$ $P=$n.s.	$F=1.17$ $P=$n.s.	$F=0.5$ $P=$n.s.	$F=0.1$ $P=$n.s.	$F=3.38$ $P<0.05$
Recruits to mussels (mean)	$F=2.93$ $P=$n.s.	$F=3.44$ $P=$n.s.	$F=2.28$ $P=$n.s.	$F=6.16$ $P<0.05$	$F=22.97$ $P<0.001$	$F=15.74$ $P<0.001$
Recruits to algae/ elsewhere (mean)	$F=0.003$ $P=$n.s.	$F=0.15$ $P=$n.s.	$F=0.82$ $P=$n.s.	$F=0.87$ $P=$n.s.	$F=3.08$ $P=$n.s.	$F=8.92$ $P<0.001$
Species richness	$F=1.85$ $P=$n.s.	$F=1.83$ $P=$n.s.	$F=0.04$ $P=$n.s.	$F=1.48$ $P=$n.s.	$F=0.9$ $P=$n.s.	$F=3.41$ $P<0.05$
% Foliose algae	$F=4.21$	$F=285.97$	$F=2.33$	$F=4246.5$	$F=0.05$	$F=11.19$
Significant at scale	3	2	2	3	2	5
Insignificant at scale	8	9	9	8	9	6

Graphical examination of the 50-cm data for March (Fig. 3) and post-hoc tests for all occasions (Table 4) highlight interesting comparisons with the results from 10-cm quadrats. Taking units of measurement and possible range into account, variance components for demographic variables and those associated with foliose algae were generally considerably higher than variables of structural complexity or species richness (Fig. 3). Total percentage cover and percentage cover of sub-adults, adults and large adults and species richness showed similar patterns of variance, with highest levels at the 50-cm replicate scale. Percentage cover of recruits showed similar variance at both the 50-cm and transect scales but variance values were all low. Mean recruits to mussels and to algae (calculated from the 10-cm data) showed different patterns, with greatest variance at the site scale for the former, and greatest variance at the transect scale for the latter. These patterns are in fact similar to those found for the 10-cm quadrat analysis, as might be expected, but highlight the effect of removing the important 10-cm variation by taking mean values. Both recruits to algae and percentage cover of algae showed a similar pattern; greatest variance occurred at the transect scale.

Table 4. Post-hoc Tukey HSD multiple comparisons between transects using data from the 50-cm quadrats

		October 1997	November 1997	March 1998
Physical structure and demography	Fractal L	PAX DCX DCZ	DCX PAX DCZ	DCX PAZ PAY PAX DCY DCZ
	Fractal M	DCX PAX DCZ	DCX PAX DCZ	DCX DCY PAX PAZ PAY DCZ
	Total % cover	PAX DCZ DCX	PAX DCX DCZ	PAY PAZ DCY PAX DCZ DCX
	% cover large adults	PAX DCX DCZ	DCX PAX DCZ	DCX PAX DCY PAY PAZ DCZ
	% cover adults	DCZ PAX DCX	PAX DCX DCZ	PAY DCZ DCY PAZ PAX DCZ
	% cover sub-adults	PAX DCZ DCX	DCX DCZ PAX	PAZ DCY PAX DCZ PAY DCX
	% cover recruits	PAX DCZ DCX	DCX DCZ PAX	PAZ DCY PAX DCX DCZ PAY
	Recruits to mussels (mean)	PAX DCX DCZ	PAX DCX DCZ	PAZ PAY PAX DCX DCY DCZ
	Recruits to algae / elsewhere (mean)	DCZ PAX DCX	DCX DCZ PAX	PAZ DCY PAY PAX DCX DCZ
	Species richness	PAX DCZ DCX	DCX PAX DCZ	PAZ DCY PAY PAX DCZ DCX
Associated biota	% cover foliose algae	DCX PAX DCZ	DCX PAX DCZ	DCX DCY PAX PAZ PAY DCZ

At the site-scale for all sampling occasions, significant variation was due to higher values at Port Alfred compared to Dias Cross. At the transect-scale in October and November, transect PAX frequently ranked highest for variables related to mussels and transect DCX ranked highest for those associated with algae, although often no significant variation was found. In March, PAZ frequently showed highest values, often with DCY and PAY. However, DCX again had the highest rank value for foliose algae. On most occasions, DCZ had the lowest rank value.

The categorical variable, form of cover was examined graphically at both transect and site-scales using data from the 10- and 50-cm quadrats. Differences in forms of cover, both between sites in general, and between transects are apparent from data at each scale (Fig. 4). At the site-scale Port Alfred had a much greater proportion of continuous cover, with or without gaps, than Dias Cross, whereas Dias Cross was dominated by patches and scattered individuals at both scales. A similar pattern can be seen at the transect-scale, although variation both within transects between sampling occasions and between transects within sampling occasions is more apparent, especially for Port Alfred. Transect PAX, unlike the other two transects sampled on all three occasions, showed a relatively high degree of temporal variation. With reference to the general ranking found for the continuous variables, DCZ often ranked lowest

and was consistently dominated by patches and scattered individuals, whereas transects which tended to rank highest showed a greater variety of cover forms. In general, as might be expected, more variation in cover forms is apparent within transects from the 10-cm data.
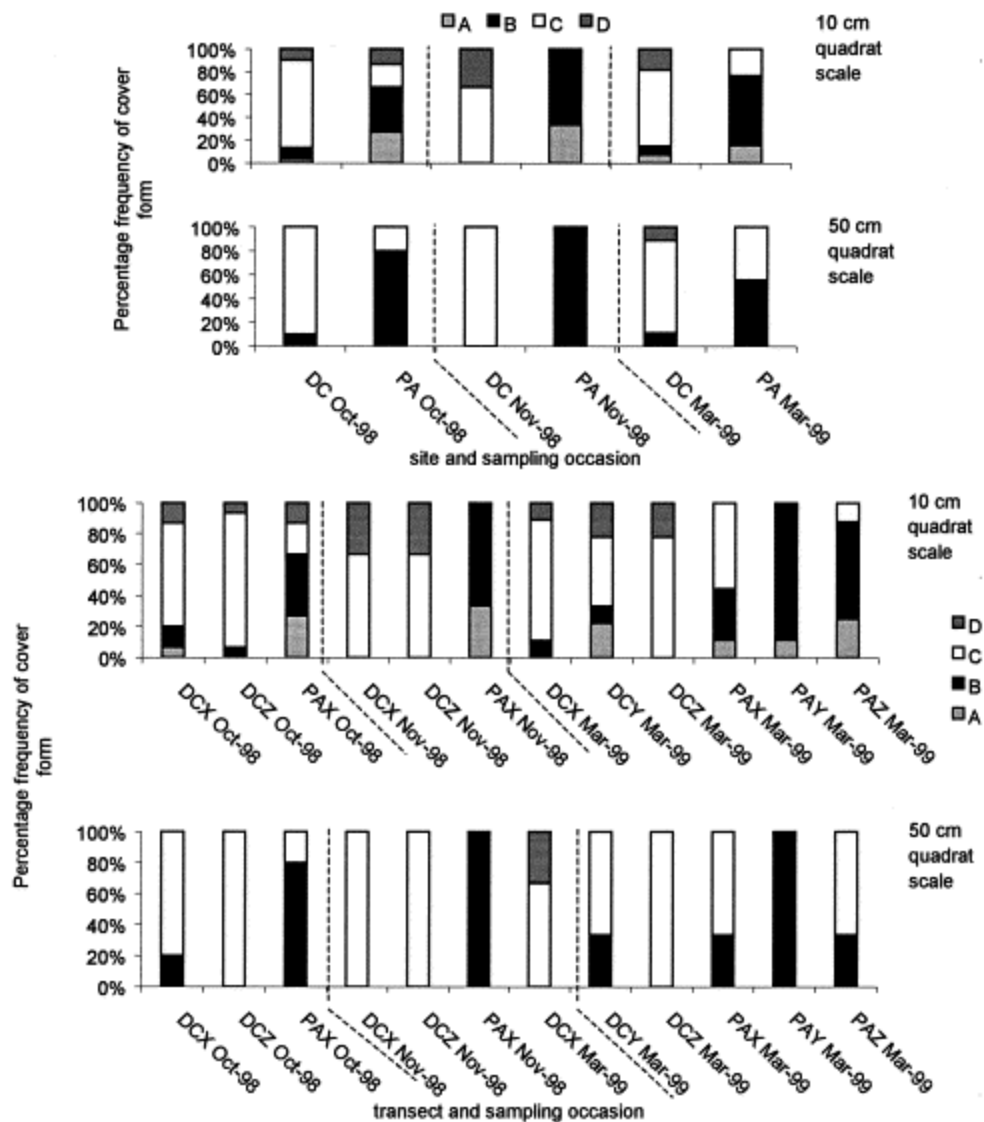
Fig. 4. Percentage frequency of each of the four cover forms for sites and transects on each sampling occasion from 10- and 50-cm quadrat data. Where cover forms are as follows: (A) continuous cover; (B) continuous cover with gaps; (C) patches of three or more individuals; and (D) scattered individuals.

3.2. Correlations between recruitment and complexity

Bivariate Spearman's rank correlations were used to examine the relationships between variables of recruitment and variables of complexity, within the scale of significant variation for each sampling occasion. For the 10-cm quadrat data, correlations were carried out at the transect-scale for November and March (Table 5). Since greatest significant

variation in October occurred at the quadrat-scale (n=3), correlations could not be calculated for this occasion using this analysis. Results shown as the frequency of significant positive or negative correlations between either recruits or settlers to mussels or recruits or settlers to algae and the variables of complexity indicate that, within the transect-scale, there was little correlation. Only 21 significant correlations occurred from a possible 558 (16 variables for recruitment and 15 variables for settlement and nine transects). Moreover, in the majority of cases there was no consistency in correlations. The only notable correlations were those between (a) recruits to algae with species richness in algae and (b) the dry mass of algae elsewhere. Examination of the raw data, however, indicates that several of these few correlations are due to a high number of zero values for both variables within particular transects. Furthermore, it seems likely that correlations with species richness are coincidental, both recruits and species richness being correlated with algal biomass.

Table 5. Frequency of Bonferroni corrected significant positive and/or negative bivariate correlations between variables of mussel recruitment/settlement and variables within the three components of mussel bed complexity within the transect scale for November and March using 10-cm data

	Variable	Recruits to mussels	Recruits to algae	Settlers to mussels	Settlers to algae
Physical structure	Percentage cover	+1			
	Bed height	+1			
	Fractal L				
	Fractal M				
	Shell mass	+1	−1		−1
Demographic structure	Meat mass	+1	−1		
	Adults				
	Females				
	Sub-adults				
	Settlers on mussels			Void	
	Settlers on algae		+2		Void
	Recruits on mussels	Void		Void	Void
	Recruits on algae		Void	Void	Void
Associated biota	Species on mussels		−1		
	Species on algae		+4		
	Algae on mussels	+1			
	Algae elsewhere		+4		+2

For the 50-cm quadrat data, correlations were carried out at the transect-scale for October only since replication at this scale during November and March was not sufficient to allow analysis. As with the 10-cm data, there was little evidence of correlations between the recruitment variables (percentage cover recruits, mean recruits to mussels and mean recruits to algae) and complexity. From the three transects, only two correlations out of a possible 81 (three

transects and nine variables per recruitment variable) were significant. These were between mean recruits to mussels and percent cover of large adults (r_s=1, d.f.=4, P<0.001) for transect DCX, and between percent cover of recruits and fractal dimension L (r_s=−1, d.f.=4, P<0.001) for DCZ. Although, both of these correlations are ecologically feasible, in each case there was no evidence of similar correlations at the other two transects. Examination of the raw data suggests that these relationships were influenced by outliers rather than reflecting a general trend.

For quadrats with either type C or type D form of cover, correlations between patch size and recruitment within those quadrats were assessed. For the 10-cm data from November and March and for the 50-cm data from October, this was carried out at the transect-scale. No significant correlations were found between recruitment to mussels and patch size from either data set.

In all, these results provide no evidence of a direct relationship between recruitment of *Perna perna* to mussel beds and the complexity of those mussel beds, whether in terms of physical structure, demographic structure or associated biota. Nevertheless, there is some evidence for an association between algal biomass and recruitment of mussels to algae. No consistent or strong association was found between any variable of complexity and any variable of recruitment to mussels using this or any of the other techniques mentioned in Section 2.

4. Discussion

Associations between habitat complexity and recruitment may reflect different types of interactions. Direct interactions may occur where either complexity limits recruitment, or recruitment limits complexity. Alternatively recruitment and complexity may be indirectly associated, being limited by the same external forcing processes or the association may be coincidental, being brought about by different forcing processes acting on each. The primary aim of the present study was to distinguish between possible direct effects of mussel bed complexity on mussel recruitment and these other types of associations. A descriptive approach was used, recording spatial and temporal variation in variables associated with complexity and recruitment over a hierarchy of scales. Three main questions were addressed. (1) At what scale(s) does each variable of complexity exhibit greatest significant variation? (2) At these scales is there similar ranking of variables of complexity and recruitment? (3) Within these scales, is there any significant relationship between these variables and recruitment?

The answers to these questions are very clear. From the results of ANOVA analyses and variance components values calculated from them, in October 1997 greatest significant variation in the majority variables of complexity occurred at the quadrat-scale, whereas in November and March 1998 greatest significant variation occurred at the transect-scale. In addition on all occasions for the majority of variables a large component of variation also occurred at the smallest scale of resolution for each analysis (i.e., 10 or 50 cm). Possible site-scale variation for November seems likely to be an anomaly associated with the separate analysis of the site-scale, due to the unbalanced design on this occasion.

Within the scales of greatest significant variation, correlations between these variables of complexity and recruitment to mussels were in most cases lacking, and where they did occur they were inconsistent. Thus, these analyses do not support the existence of a direct effect of mussel bed complexity on recruitment. Some indication of a relationship between recruitment to algae and algal biomass was found but even this was tenuous. Furthermore, since it is not yet clear whether mussels settling and recruiting to algae ever contribute to the adult mussel population (Lasiak and Barnard, 1995; Lindsay, 1998), such a relationship may be irrelevant to adult population dynamics.

Post-hoc multiple comparisons highlighted a degree of similarity in the ranking of transects. This suggests either indirect associations, variables of both complexity and recruitment being limited by some external forcing factor most apparent at an intra-shore-scale (i.e., in line with the transect-scale of this study), or alternatively a direct effect of settlement/recruitment on complexity at this larger scale.

4.1. Patterns of complexity: scales of variation and associations

The scales of greatest variation identified in this study are not inconsistent with the results of the other rocky shore studies either in South Africa or elsewhere (Menge and Menge; Lasiak and Barnard, 1995; Archambault and Bourget, 1996; Kostylev, 1996; Underwood and Chapman, 1996; Harris et al., 1998; Blanchard and Bourget, 1999). Although, Harris et al. (1998) suggested a correlation between recruitment and complexity, the resolution of their data is at a scale in line with the transect-scale of this study. If, for this study, correlations are carried out on data pooled from all transects rather than within each transect, a similar phenomenon results. This is an artifact caused by similarities in ranking of variables between transects.

Small-scale variation such as that occurring at the 10- and 50-cm quadrat scales is also evident in other studies; frequently as high residual variation or large standard deviations around a mean (for example: Menge, 1978a; Suchanek, 1979; Okamura, 1986; Petratis, 1990; Lasiak and Barnard, 1995; Tokeshi and Romero, 1995; Kostylev, 1996; Hunt and Scheibling, 1998). In most of these studies scale is dealt with implicitly, only a few studies have examined and documented small-scale variation explicitly (e.g., Hunt and Scheibling, 1995; Archambault and Bourget, 1996; Bendetti-Cechi et al., 1996; Underwood and Chapman, 1996; Blanchard and Bourget, 1999). Its occurrence is not wholly surprising, since ultimately all interactions take place between individual organisms. Such heterogeneity is thus likely to reflect individual scale biotic processes and interactions; e.g., predation, growth, competition, mortality, recruitment as well as the interaction of individuals with small-scale abiotic processes and features such as topography and hydro-dynamics. Such small-scale (cm) topographic effects are often apparent on the shore (McQuaid, pers. obs). The importance of small-scale heterogeneity within our study was reflected by the lack of significant variation for data collected at the 50-cm scale in comparison to that collected at the 10-cm scale. The greater variation described by the categorical variable 'form of cover' at the smaller scale provides additional evidence. Notably percentage cover

variables and species richness associated with mussels consistently showed much greater levels of variance at the smallest scales, perhaps reflecting the importance of small-scale processes or features to these variables.

Lasiak and Barnard (1995) examined settlement and recruitment to mussels and algae at two replicate sites only 50 m apart. The sites and their proximity to one another are again of a similar scale to the transect locations used in this study. Although the sites showed similar seasonal trends of settlement and recruitment, they differed significantly from each other during periods of high recruitment, indicating an interaction between scales of variation and time. A similar interaction was found here. In October significant variation of most variables occurred at the 50-cm quadrat-scale, whereas in November and March this occurred at the transect-scale. Analyses confirmed that this change in the scale of variation was not due to the change in replication at the 50-cm quadrat level between sampling periods, therefore it must be assumed to reflect real change in the scales of variation of complexity. The variance component values confirm this transition in scale dependence with sampling occasion. A further example of such a temporal shift in scale-dependence is apparent for some of the demographic variables. In November, meat dry mass, adults, females and sub-adults exhibited greatest variance at the transect scale. In March variance at the transect scale was much lower, and the relative contribution of 10-cm scale variation was thus increased. This was also apparent to some extent for structural variables. Thus, although greatest significant variation occurred at the transect scale in both November and March, the pattern of partitioning of variance on these two occasions differed markedly. Mechanisms for these temporal variations in spatial patterns cannot be inferred from our data. They may reflect seasonal demographic processes, such as recruitment, growth and/or mortality of dominant secondary substratum species such as mussels or algae. Such patterns would be comparable with the patch dynamics described for mussel bed communities elsewhere in the world (Paine and Levin, 1981; Sousa, 1984; Hunt and Scheibling, 1995; Petratis, 1995; Tokeshi and Romero, 1995).

In the present study the greatest levels of algal abundance, settlement and recruitment were all recorded during March. In November lowest settlement and recruitment values and intermediate levels of algal abundance occurred. Recruitment to algae exhibited a further temporal shift, with extremely high relative values of variance at the 10-cm scale in March, compared to the two previous sampling occasions. The coupled effect of higher levels of settlement and recruitment and higher levels of algal abundance in March compared to October and November may contribute to this, but cannot explain it fully. Interestingly, recruitment to mussels showed similar levels of variance both at the 10-cm scale and at one or more larger scales, whilst settlers to mussels had highest variation at the 10-cm scale on all occasions and larger scale variation was only noteworthy in March. This might reflect some density dependent effect on scales of variance with respect to settlement on mussels. Such patterns have been reported for barnacle settlement (Raimondi, 1990; Noda et al., 1998). The pattern of variance with scale for recruitment to mussels would conversely seem to be independent of density. This change in pattern and apparent uncoupling of settlement from recruitment could reflect post-settlement processes, such as mortality or relocation of individuals. Alternatively, since the range in size of individuals encompassed by recruits (1–10 mm) was much greater than that for settlers (<1 mm), the pattern may reflect the cumulative results of several settlement events.

4.2. External forcing processes and effects of recruitment on complexity

Significant scales of variation were consistent while variables showed similar ranking between areas. These facts, coupled with the lack of correlation found within these scales between components of complexity and recruitment, suggest that recruitment and complexity may be independently influenced by similar external forcing factors and/or that complexity is directly affected by recruitment. The present study does not allow these two types of interaction to be distinguished and it seems possible that both may take place.

An effect of settlement and recruitment on the complexity of mussel beds seems to be an obvious relationship. Such relationships are widely recognised under the title of supply-side ecology and have been documented for a variety of marine invertebrates with a pelagic juvenile phase (Connell, 1985; Gaines and Roughgarden, 1985, Lewin, 1986; Roughgarden et al., 1987; Delafontaine and Flemming, 1989; Underwood and Fairweather, 1989; Sutherland, 1990; Minchinton and Sheibling, 1991; Satchell and Farrell, 1993; Hunt and Hunt). The strength of the relationship will, however, depend on the role and strength of post-settlement and post-recruitment processes such as mortality, resettlement or migration due competition, predation, food supply or abiotic factors (e.g., exposure to radiation, turbidity) (Connell, 1985; Roughgarden et al., 1988; Underwood and Fairweather, 1989; Hurlbut, 1991; Menge, 1991; Woodin, 1991; Rodriguez et al., 1993; Olafsson et al., 1994; Gosselin and Qian, 1997).

Transects with the greatest levels of recruitment in this study seemed to have overall a greater range in types of mussel cover at resolutions of 10 and 50 cm. Factors that are likely to affect these features and the community dynamics of mussel beds, are topography and hydrodynamics. These factors may affect both complexity and recruitment variables directly, potentially leading to co-variation or may indirectly affect complexity because of their effect on settlement and recruitment (Roughgarden et al., 1987; Delafontaine and Flemming, 1989; Pineda, 1991; Gaines and Bertness, 1992; Shepherd et al., 1992; Hunt and Hunt). The a priori, subjective classification of the transects in terms of wave exposure, height and topographic complexity at the meter scale, suggests that those transects with greatest complexity and recruitment were more exposed and/or topographically complex than the others, so that the amount (frequency and extent) of 'wave splash' they received was greater. Seed and Suchanek (1992) presumed that the relationship between growth and period of tidal immersion for *Mytilus edulis* was affected by local variation in the degree of wave splash. In addition, several other authors have recorded differences in mussel beds and other rocky shore characteristics, associated with wave exposure and topography (McQuaid and Branch, 1984; Underwood and Denley, 1984; Gaylord et al., 1994; Alvarado and Castilla, 1996; Bustamante and Branch, 1996; Schoch and Dethier, 1996; McQuaid et al., 2000; McQuaid and Lindsay, 2000). However many of these studies examined effects at larger scales (e.g., between shores) and dealt with much greater ranges of variation in wave exposure and topography. Other studies have documented cm- and m-scale effects of topography on hydrodynamics and thus the biota and biological processes of both intertidal and subtidal environments (Bourget et al., 1994; McCormick, 1994; Breitburg et al., 1995; Harvey et al., 1995; Gregoire et al., 1996; Cusson and Bourget, 1997; Guichard and Bourget, 1998; Reusch, 1998). In this study both shores used have

previously been classified as exposed (McQuaid and Lindsay, 2000) in a South African context. Thus, it seems that more subtle, intermediate-scale (10s to 100s of meters) variation in the physical attributes of rocky shores may be important to the dynamics of the biological processes that structure them. Surge channels provide a clear example of such topography/hydrodynamic related variability at these scales (Denny et al., 1992; Dayton, pers. com.)

The overall picture presented by these results is one of heterogeneity at the smallest cm-scale, probably determined by inter-individual biotic and abiotic interactions. At one or more larger scales there is convergence to relative homogeneity, but patterns of homogeneity may differ between areas. These scales of convergence vary with season and are probably influenced by variations in topography and hydrodynamics and the effects of these features/processes on the population dynamics and interactions of mussels with other organisms.

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