



ELSEVIER

Journal of Experimental Marine Biology and Ecology,
216 (1997) 77–98

JOURNAL OF
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

Identifying relationships between adult and juvenile bivalves at different spatial scales

J.E. Hewitt^{a,*}, P. Legendre^b, B.H. McArdle^c, S.F. Thrush^a, C. Bellehumeur^b,
S.M. Lawrie^d

^aNational Institute of Water and Atmospheric Research, P.O. Box 11-115, Hamilton, New Zealand

^bDépartement de sciences biologiques, Université de Montréal, C.P. 6128, succ. Centre-ville, Montréal, Québec H3C 3J7, Canada

^cBiostatistics Unit, School of Biological Studies, University of Auckland, Private Bag 92019, Auckland, New Zealand

^dCulterty Field Station, University of Aberdeen, Newburgh, Scotland AB40AA, UK

Abstract

The variable results of field experiments on adult–juvenile interactions suggest that, under natural conditions, other processes may be more important. However, field surveys are less equivocal. A potential reason for this is that surveys, integrating information over larger scales than experiments, have a greater ability to match the scale of processes. In this survey, a transect design was utilised, with samples 1 m apart nested within samples 5 m apart, at three sites located 1 km apart on a homogeneous sandflat. Correlations between adult and juvenile bivalves were analysed for a variety of distances apart (0 to 80 m) and spatial extents (m to 1 km). Different intensities and directions of relationships were observed at different scales and at different sites. This study supports the hypothesis that processes of a larger scale than those commonly examined in small-scale field experiments may contribute to the variability of results of adult–juvenile interaction experiments. © 1997 Elsevier Science B.V.

Keywords: Adult–juvenile interactions; Bivalves; Scale; Soft-sediments; Surveys

1. Introduction

An emergent theme in ecology is that the processes influencing distributions of organisms may change with scale (e.g. Allen and Starr, 1982; Dayton and Tegner, 1984; Powell, 1989; Legendre, 1993; Ardisson and Bourget, 1992; Horne and Schneider,

*Corresponding author.

1994). Field experiments are often used to develop a mechanistic understanding of how ecological processes operate over a limited range of spatial and temporal scales. However, it is not at all clear how processes demonstrated experimentally on a limited scale may affect observations made on a larger scale, or even how experimental results from one scale may be compared with those from another.

In fact, the results of different field experiments investigating adult–juvenile soft-sediment bivalve interactions do not clearly reveal generalities (Olafsson et al., 1994), particularly when experiments which elevated adult densities well above natural levels are excluded. Olafsson et al. (1994) did report some degree of consistency in results by characterising the adult bivalves on the basis of feeding mode. For example, suspension feeders are less likely to inhibit juveniles than deposit feeders. However, even experiments on deposit feeders often fail to show consistent inhibition of larvae and juvenile abundance patterns (Hines et al., 1989; Thrush et al., 1992, 1996). Other factors, such as differences in habitat characteristics, may also be important in mediating the adult–juvenile interaction (Olafsson, 1989; Ahn et al., 1993; Thrush et al., 1996).

Results from small-scale field experiments (e.g. plot sizes of cm^2 – m^2) on the nature of adult–juvenile interactions of both deposit-feeding and suspension-feeding bivalves that have been carried out in conjunction with larger-scale surveys often have not supported the relationships identified by the survey (e.g. Andre and Rosenberg, 1991; Bachelet et al., 1992). There are a number of potential reasons for this dichotomy. For instance, surveys are usually conducted over a larger scale, and thus may incorporate more density and habitat variation, than field experiments. Also, the lack of effect demonstrated by many experiments has been attributed to the design and power of the experiment (Young, 1989). Surveys frequently have a larger number of samples than experiments, and thus a greater power to detect density dependence (Solow and Steele, 1990). However, Black and Peterson's (Black and Peterson, 1988) small-scale experiment found no inhibition by a large suspension feeding bivalve on juveniles, despite having high power. Still another potential reason for the dichotomy between survey and experimental results, is that the actual processes affecting the distribution of adults and juveniles are scale dependent.

Attempting to investigate distribution patterns and processes over a range of spatial scales can result in excessively large and expensive field programmes. In this paper we use a study design that allows characterisation of different scales of spatial heterogeneity (1 m to 1 km) with relatively few samples. Spatial patterns in abundance of size classes of the common bivalve species found in this study (*Macomona liliana* Iredale and *Austrovenus stutchburyi* (Gray)) are identified for use in the design of more extensive surveys and experiments (Legendre et al., 1997; Thrush et al., 1997b). Changes in the nature of adult–juvenile bivalve interactions with spatial scale are also investigated, as such changes could account for the observed variations in the outcome of experiments and the potential for discrepancies between experimental and survey results. Three complementary techniques are used: cross-correlograms (common in geostatistical analyses); principle component analysis; and tests for differences between correlation coefficients derived from different spatial extents. The survey design incorporated the possibility that the presence and size of spatial patterns, and the presence and scale of adult–juvenile interactions, may be dependent on the presence of hydrodynamic gradients within the study site.

2. Methods

2.1. Study species

Macomona ≤ 5 mm (longest shell axis) are restricted to the upper 2 cm of sediment and have routinely been found moving both with sediment bedload and in the water column (Cummings et al., 1993; Commito et al., 1995; Cummings et al., 1995; Hewitt et al., in press). Adult *Macomona* (here defined as > 10 mm longest shell axis) live deeper in the sediment (ca. 10 cm) and feed at the sediment surface by means of a long inhalent siphon. At some stage between ≤ 5 mm and > 10 mm, *Macomona* change their life style markedly. In contrast to *Macomona*, both the adult and juvenile life stages of *Austrovenus* live in the near-surface sediment and suspension feed with short inhalent siphons. Analysis of the spatial distributions of different size classes of this species (Hewitt et al., 1996; Legendre et al., 1997) reveals strong similarities between size classes, indicating that behaviour and patch size of different-sized individuals forms a continuum. *Austrovenus* ≤ 2.5 mm (longest axis) are frequently found moving with the bedload (Commito et al., 1995) and, less occasionally, in the water column (Pridmore et al., 1991; Cummings et al., 1995). Juveniles of this species were, therefore, separated into 2 size classes: ≤ 2.5 mm (small juveniles) and 2.5–10 mm (large juveniles).

2.2. Study sites

The study was conducted on an extensive intertidal sandflat near Wiroa Island ($37^{\circ} 01' S$, $174^{\circ} 49' E$) within Manukau Harbour (340 km^2), New Zealand. The 5 km^2 area of intertidal sandflat near Wiroa Island is exposed to the prevailing south-westerly wind with a fetch of 4 km (at mid tide) to 11 km (at high tide). A general description of the study area is presented in Thrush et al. (1997a). Recruitment of bivalves to the macrofauna occurs all year round, although it is especially pronounced in late January to early February (Thrush et al., 1996).

Three sites (Fig. 1(a)) of predominantly fine sand, spanning 1 km of the sandflat, were located at mid-tidal height. The three sites all represented one habitat type, with few visible differences observed. Site 1 was essentially flat; site 2 covered an area of long (25–30 m) sand waves with very low amplitude (10–20 cm), and site 3 included 10 *Zostera* spp. patches (mean radius ≈ 2 m), each of which raised the sediment surface up to 8 cm compared to non-vegetated areas.

2.3. Sampling design

At each site, samples were collected from two transects running perpendicular to each other to form a cross. The time between the tide first starting to cover (or expose) each cross and the cross being completely covered (or exposed) was less than 20 minutes at all sites. As we thought that hydrodynamic gradients may result in larger-scale patterns than would be the case if there was no gradient, we structured our sampling to be more detailed in the direction of the anticipated hydrodynamic gradient. Thus we used a long (150 m) and a short (110 m) transect to form each cross. The long transect ran parallel to the estimated direction of maximum wave exposure. At site 1 we were unable to

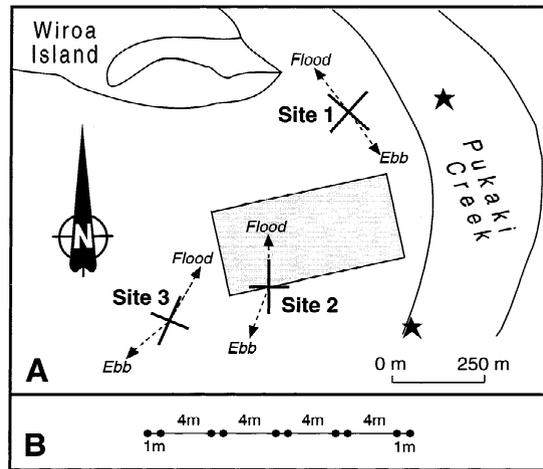


Fig. 1. (a) Position of the three sites and six transects on the Wiroa Island sandflat relative to channel markers (*) and a later (Legendre et al., 1997) study site. The flood and ebb directions are shown by dashed lines. (b) Sample positions were regular with a 1 m lag nested inside a 5 m lag along the 150 m transect.

determine this direction a priori so each transect was 150 m long. A hydrological model later showed that at each site, one transect ran roughly perpendicular to the direction of the flood and ebb tidal currents (Fig. 1(a)). Henceforth, this direction will be called the perpendicular direction, while the direction parallel to tidal flow and maximum wave exposure will be called the parallel direction.

In order to gain the maximum amount of information from the minimum number of samples, core samples (10 cm diameter, 13 cm deep) were collected at small (1 m) inter-sample distances (i.e. lags) nested within a larger (5 m) lags (Fig. 1(b)). Again the sampling was more detailed in the direction of the anticipated hydrodynamic gradient. Thus, samples on the 150 m transects were taken at 1 and 5 m lags over the whole transect. On the 110 m transects, however, samples were taken in 4 blocks with each block separated by 9 m. Ten samples, therefore, were collected from each block at distances of 1, 5, 6, 10, 11, 15, 16, 20, 21 and 25 m from the start of the block.

Samples were collected on 12 December 1993, sieved (500 μm mesh screen) and the residue fixed in 70% isopropanol with 0.1% rose bengal in seawater. In the laboratory, macrofauna were sorted, identified, counted, and preserved in 70% isopropanol. The longest shell axis of preserved specimens of bivalves was measured (with an ocular micrometer) and assigned to 1 of 5 size classes (i.e. $x \leq 2.5$ mm, $2.5 < x \leq 5$ mm, $5 < x \leq 10$ mm, $10 < x \leq 20$ mm, and > 20 mm). The remaining shell hash material from each sample was dried at 60°C for 48 h and weighed.

Samples of the surficial 2 cm of sediment were collected for grain size analysis (Folk, 1968), at 10 m intervals along each transect at sites 1 and 2 only. The geographic position of the transects relative to one another was determined by surveying with a Geodimeter 140, as was elevation at 1 m intervals along each transect at each site. The incoming tide prevented collection of elevation measurements on the 110 m transect at site 3.

2.4. Data analysis

2.4.1. Variations in abundances of bivalve species and size classes were studied at different scales

a) At the smallest scale, differences between pairs of samples 1 m apart were analysed. If there were no differences between pairs, the variation within pairs should follow a Poisson distribution (Crawley, 1993). Therefore, the null hypothesis that the variation in sample pairs was Poisson was tested by the chi-square from a general linearised model, (SAS/Insight, 1993). This method also allows us to determine whether departures from randomness are due to aggregation.

b) Spatial patterns on the scale of 1–150 m were examined for each individual transect. Moran's *I* spatial autocorrelograms were not used because most of the distance classes had too few points to allow significant results to be achieved. Instead, the presence of large-scale patterns at each transect (i.e. linear trends or large wave-like structures) was investigated by fitting a polynomial (4th order maximum, with only significant terms included) to the $\log_{10}(x + 1)$ transformed abundances. A smoother (LOWESS: SAS/Insight (1993)) that minimised the generalised cross-validation mean square error was also applied to the data. The small-scale patterns generated by the LOWESS smoother were not tested for statistical significance, as they are used only as an indication that such patterns may be present.

c) To identify generalized spatial patterns in the two transect directions (i.e. parallel or perpendicular to tidal flow and maximum wave exposure) on the 1–150 m scale, data from the three sites were combined. Moran's *I* spatial autocorrelograms ("The R Package": Legendre and Vaudor (1991)) were calculated for data that had been $\log(x + 1)$ transformed and standardised within transects in order to make the variability among transects comparable. Distances between samples were computed as if the three transects running in the same direction relative to tidal flow, were parallel to one another. This procedure allowed us to make only within-transect comparisons. Assuming second-order stationarity of the data (Legendre, 1993), the spatial autocorrelation coefficients were tested for significance ($p = 0.05$ level) against the null hypothesis of no autocorrelation at the given distance class. Multiple testing was accounted for by a "progressive Bonferroni" correction which assumes the process generating the autocorrelation to be stronger at small distances. That is, the first autocorrelation coefficient (distance 1 m) was tested against the 0.05 significance level; the second coefficient was tested against the Bonferroni-corrected level $\alpha' = \alpha/2 = 0.025$; and the k -th coefficient was tested against the Bonferroni-corrected level $\alpha' = \alpha/k$.

d) At the largest scale (1 km; the maximum distance between sites), differences in abundance between sites were analysed by general linearized modeling techniques using Poisson errors and a loglink function (McCullagh and Nelder, 1989; Crawley, 1993).

2.4.2. Adult–juvenile relationships were investigated using three techniques

Firstly, cross-correlograms were used to investigate whether interactions changed with differing distances between samples. That is, were adults and juveniles still correlated when adults from one core were compared with juveniles from a core 1 m away, 5 m away, etc. The second, more pictorial, technique to investigate interactions used principal component analysis. The closer variables are in the ordination space, the more

highly correlated they are. Thirdly, we tested the consistency of relationships found. Correlations between adults and juveniles were analysed at a variety of spatial extents (e.g. at each of the sites, then at each of the transects within a site) and the different correlations found within each extent compared. For example, were the correlations found at the various sites similar? Were those gained from the two transects at each site similar to each other? This technique also allows us to determine whether correlations found at smaller scales (e.g. samples 1 m apart) are really due to differences at larger scales (e.g. inter-site differences). These three methods are described in detail below.

(a) Non-ergodic cross-correlograms (Isaacks and Srivastava, 1989) were used to model statistically spatial covariation (Rossi et al., 1992) of data combined for the two directions (see Section 2.4.1(c)). The cross-correlogram methodology is given in Appendix A. Computations were done using the programs of Deutsch and Journel (1992), based on the Fortran library of geostatistical subroutines of these authors. Data were $\log(x + 1)$ transformed and standardised within transects (see Section 2.4.1(c)). The standard t test for correlation coefficients was used (Sokal and Rohlf, 1995), as all cross-correlation coefficients were smaller than 0.5 in absolute value. Significance of the Pearson coefficients was not corrected for autocorrelation in the data since little significant autocorrelation was found (Clifford et al., 1989; Dutilleul, 1993). The “progressive Bonferroni” correction described above was applied to account for multiple testing.

(b) Principal component analysis. Calculations were carried out from a matrix of both Pearson and Spearman correlation coefficients (Lebart et al., 1979) calculated for all size classes of both bivalve species on data from the two directions separately. Eigenvectors were standardised to the square root of their respective eigenvalues for the representation, in order to correctly represent the projections of the angles (correlations) among variables in the space of the first two principal components.

(c) Correlations were computed for three spatial extents: both the parallel and perpendicular directions; each site; and each individual transect, on $\log_{10}(x + 1)$ transformed data. Within each of these spatial extents, data were grouped into sets of 16 samples (i.e. samples ≤ 36 m apart), sets of 8 (samples ≤ 16 m apart), sets of 4 (samples ≤ 6 m apart); and pairs (samples 1 m apart). For the spatial extents of the two directions and each of the three sites, a further grouping of within-direction or within-site (i.e. samples ≤ 150 m) respectively was included. For each association, the covariance at each scale, from largest to smallest, was examined by pooling the within-group covariation and using this to calculate a new correlation coefficient, thus removing larger-scale differences. Although reference is made to whether correlation coefficients were significant at a 0.05 level unadjusted for the number of correlations run, we do not use this as a formal test statistic. Rather, it is a relative measure allowing us to explore the correlation structure, giving us an indication as to the result we would have got had that been the only analysis done. In order to determine whether the intensity (size of the correlation coefficient) or direction (sign of the correlation coefficient) of the relationships was consistent between directions, sites and individual transects, correlation coefficients were compared. A randomised permutation test was developed by B.H. McArdle (see Appendix B) that allowed us to compare correlation coefficients at all scales, within a particular spatial extent, simultaneously. Tests for

differences between correlation coefficients (Sokal and Rohlf, 1995) at each scale were conducted only if the overall test was significant. While it is arguable that differences in relationships would best be investigated by examining differences in the slopes of the interactions, we felt that the presence of major error in both x and y variables, together with the complexity of the analysis, made this impractical.

2.4.3. It is possible that significant correlations between numbers of adults and juveniles are due to some underlying physical factor affecting the distributions of both size classes

To investigate this, Pearson correlation coefficients were calculated for bivalve numbers with some environmental variables (i.e. grain-size, elevation, shell hash). Those environmental variables that showed significant correlations with bivalve numbers were then included in a stepwise regression analysis of number of juveniles with numbers of adults. As in Section 2.4.2b, analyses were carried out on a variety of spatial extents; both directions; each site; and each individual transect. Again, although reference is made to whether correlation coefficients are significant at a 0.05 level unadjusted for the number of correlations run, we do not use this as a formal test statistic.

3. Results

Austrovenus and *Macomona* exhibited mean densities of more than 1 individual per 10 cm diam. core at each site. For the purposes of this study, different size classes of each bivalve species were used (see methods). Unfortunately there were not enough *Macomona* in the 5–10 mm size class to warrant analysis. Similarly, very few adult (> 10 mm) *Austrovenus stutchburyi* were found; the majority (> 80%) of individuals were ≤ 2.5 mm (Fig. 2).

3.1. Spatial heterogeneity

(a) Abundances from samples 1 m apart were significantly overdispersed for both size

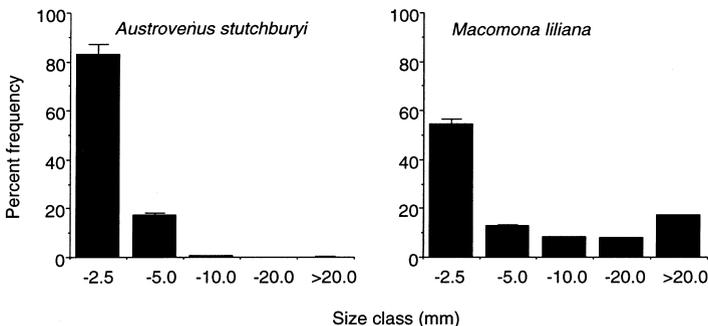


Fig. 2. Frequency (%) histograms of the size-class structure of *Macomona* and *Austrovenus*, calculated from the combined dataset of all 6 transects.

Table 1

Size of the spatial structure suggested by the distances from peak to trough of fitted polynomial curves (and LOWESS smoothed data)

	Perpendicular Direction			Parallel Direction		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
<i>Macomona</i> > 10 mm	60 m	40 m	60 m	gradient	–	–
<i>Macomona</i> ≤ 5 mm	75 m (15 m)	40–100 m (10–20 m)	60 m (15 m)	–	–	(10–20 m) gradient
<i>Austrovenus</i> 2.5–10 mm	(15–30 m)	–	–	–	–	
<i>Austrovenus</i> ≤ 2.5 mm	65 m (15 m)	30–50 m (15–20 m)	30 m	60 m	gradient (10–20 m)	75 m (15 m)

classes of both species ($df = 128$, $p = 0.0020$ for juvenile *Macomona*, and $p = 0.0001$ for all other size-classes/species combinations).

(b) Within individual transects, spatial patterns were exhibited at most sites (Table 1). Only small juvenile *Austrovenus* exhibited patterns in all transects (Figs. 3 and 4). Patchiness generally occurred at more than one scale. For example, the fitted polynomials generally revealed trends or large (i.e. 65–75 m) wavelike structures while the smoothed data generally showed recurring patterns on the scale of 10–20 m. The smallest-size patches exhibited by juvenile *Macomona* and small juvenile *Austrovenus* were generally similar (i.e. between 10 and 20 m). Juvenile *Macomona* exhibited patterns on all perpendicular transects but only at one site on a parallel direction transect. Patch structure and size for adult *Macomona* was also more similar between transects of similar direction than between transects at a particular site.

(c) The spatial autocorrelograms for the different directions (Figs. 3 and 4) confirm the general results found for the individual transects. Significant positive autocorrelation occurs in the first distance classes of most of the autocorrelograms on the perpendicular direction transects. For both adult *Macomona* and large juvenile *Austrovenus* this occurs at 5 m (also at 10 m for adult *Macomona*) with no autocorrelation detected at 1 m (Fig. 3). Juvenile *Macomona* and small juveniles of *Austrovenus* clearly display significant spatial autocorrelation at distances of 1 m and 5 m. However, only the small juvenile *Austrovenus* display significant positive autocorrelation in the parallel direction transects (Fig. 4). Thus, using a less detailed sampling strategy in the perpendicular direction at 2 of the sites did not apparently affect our ability to detect pattern. Many of the correlograms (Figs. 3 and 4, see Table 2 for summary) have overall shapes indicative of spatial structures at scales larger than 150 m (Legendre and Fortin, 1989); which is the maximum length of transects in the present study.

(d) Some differences in abundances between sites existed for the different size classes of the two bivalve species (see Fig. 5). Large juvenile *Austrovenus* were more abundant at site 3 than at either of the other 2 sites ($df = 2$, $p = 0.0001$). Small juvenile *Austrovenus* were also more abundant at site 3; however site 2 also had significantly larger numbers than site 1 ($df = 2$, $p = 0.0001$). Conversely, adult *Macomona* were significantly less abundant at site 3 than either site 1 or site 2 ($df = 2$, $p = 0.0001$).

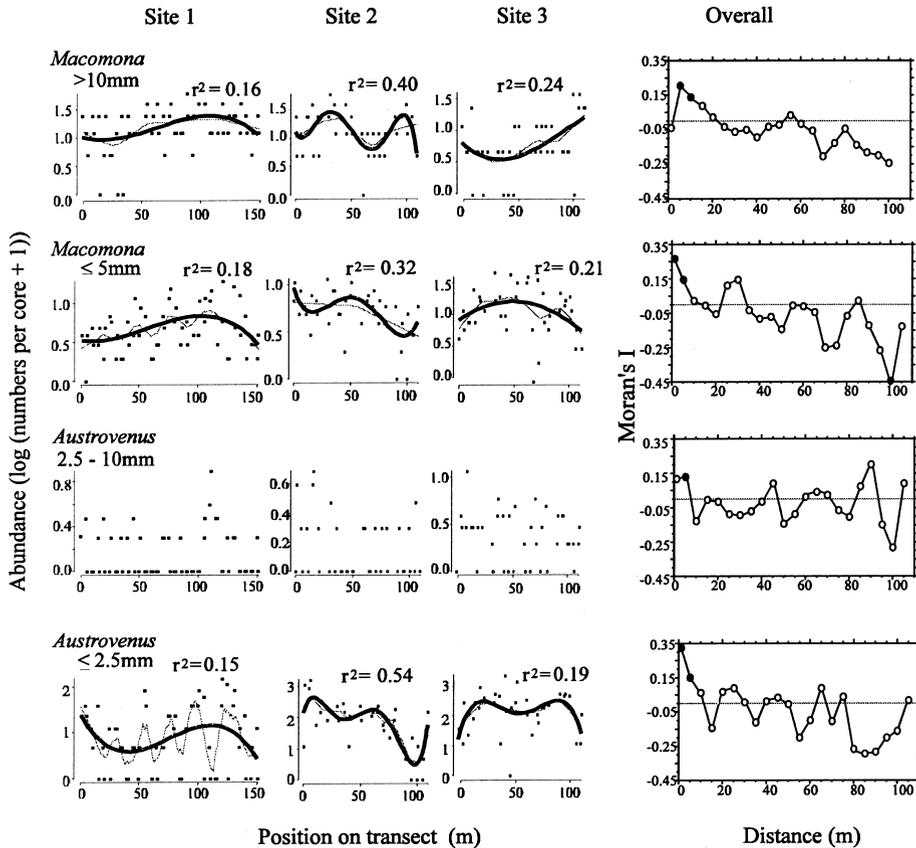


Fig. 3. Plots of variation in abundance of the two size classes of *Macomona* and *Austrovenus* along the perpendicular direction transects, together with the LOWESS smoothed curve (stipled line). When significant, the fitted polynomial trend surface (thick line) is also plotted and the r^2 value given. Also given are the Moran's I spatial autocorrelograms for each transect direction, with significant values indicated by black dots.

3.2. Adult–juvenile correlations

3.2.1. Results of cross correlogram analyses

(i) Adult–juvenile *Macomona*. A significant negative correlation at 0 m was found along the parallel direction (Table 3), and a correlation of the same sign, although not significant, for the other direction (Fig. 6).

(ii) Adult *Macomona*–large juvenile *Austrovenus*. Positive correlation at 5 m combined with a negative (non-significant) coefficient at 0 m was found for the perpendicular direction transects (Fig. 6).

(iii) Adult *Macomona*–small juvenile *Austrovenus*. A positive correlation at 5 m combined with a negative (non-significant) coefficient at 0 m was found for the parallel direction transects (Fig. 6). This was the only correlogram exhibiting a significant

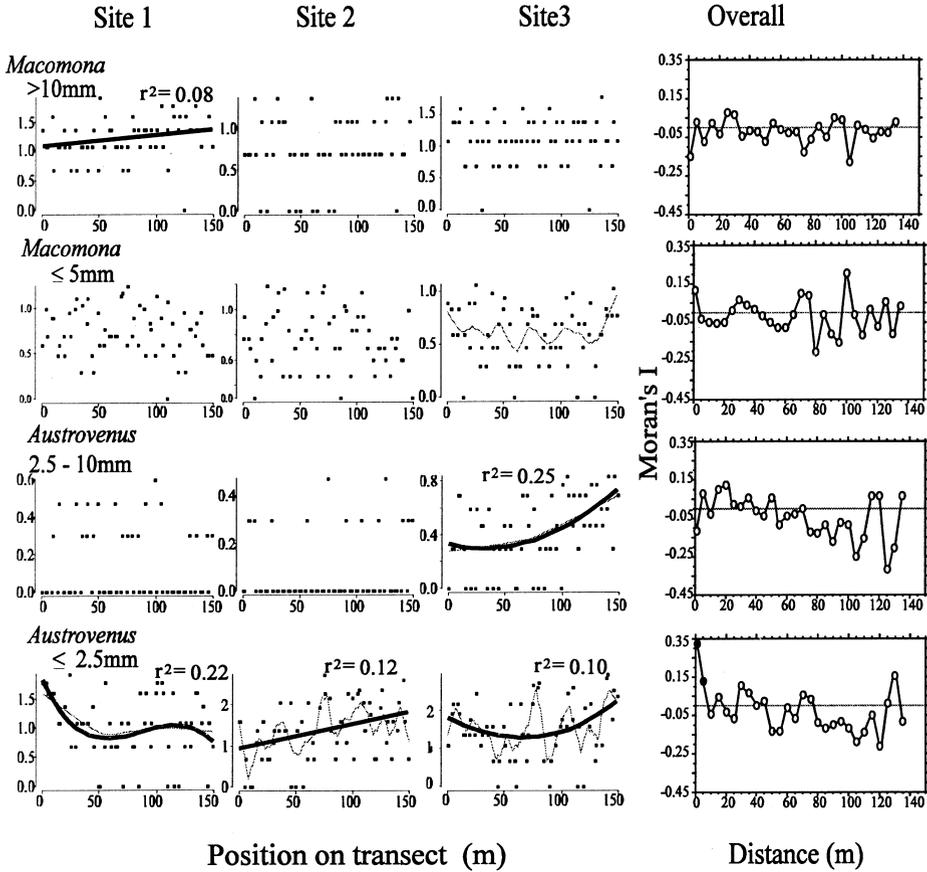


Fig. 4. Plots of variation in abundance of the two size classes of *Macomona* and *Austrovenus* along the parallel direction transects, together with the LOWESS smoothed curve (stipled line). When significant, the fitted polynomial trend surface (thick line) is also plotted and the r^2 value given. Also given are the Moran's I spatial autocorrelograms for each transect direction, with significant values indicated by black dots.

Table 2
Summary of the Moran's I spatial autocorrelogram analyses

	Perpendicular Direction	Parallel Direction
<i>Macomona</i> > 10 mm	5–10 m (gradient)	–
<i>Macomona</i> ≤ 5 mm	1–5 m (gradient)	small-scale heterogeneity
<i>Austrovenus</i> 2.5–10 mm	5 m	(gradient)
<i>Austrovenus</i> ≤ 2.5 mm	1–5 m (gradient?)	1–5 m

Comments on structures suggested by the overall shape of the correlogram rather than by significance test are given in brackets.

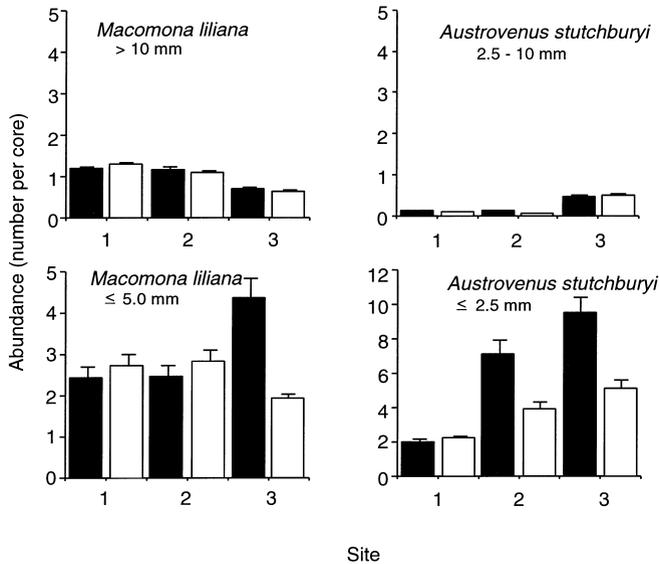


Fig. 5. Mean (+standard error) abundances of the two size classes of *Macomona* and *Austrovenus* for each transect at each site. Solid black bars represent perpendicular direction transects, while white bars represent parallel direction transects.

correlation at distance > 5 m which was not matched by significant correlation in the same direction at a distance of ≤ 5 m.

In summary, no consistent differences across species and size classes were found for the 2 different directions (Table 3). Generally, both intensity and direction of correlations changed with scale; the strongest relationship was not always apparent at 0 m. In fact, of all the relationships between abundance of adult *Macomona* and juvenile bivalves investigated here, only juvenile *Macomona* in the parallel direction exhibited a significant (negative) correlation at 0 m. It is worthwhile examining the overall shape of the cross correlograms (Fig. 6). In this case, the relationship becomes positive with increasing lags, reaching a positive correlation coefficient at the 20 m lag that is nearly as high as the significant negative coefficient found at 0 m. A similar overall shape was found for the perpendicular direction. Both size classes of juvenile *Austrovenus stutchburyi* exhibited either low negative or zero correlations with adult *Macomona* at the 0 m lag for both directions. As with the adult versus juvenile *Macomona*,

Table 3
Results of the cross correlogram analyses between adult *Macomona* and juvenile *Macomona* and *Austrovenus*

Interaction with	Perpendicular Direction	Parallel Direction
juvenile <i>Macomona</i>	–	negative at 0m
large juvenile <i>Austrovenus</i>	positive at 5 m	–
small juvenile <i>Austrovenus</i>	–	positive at 5 and 40 m, negative at 60 m

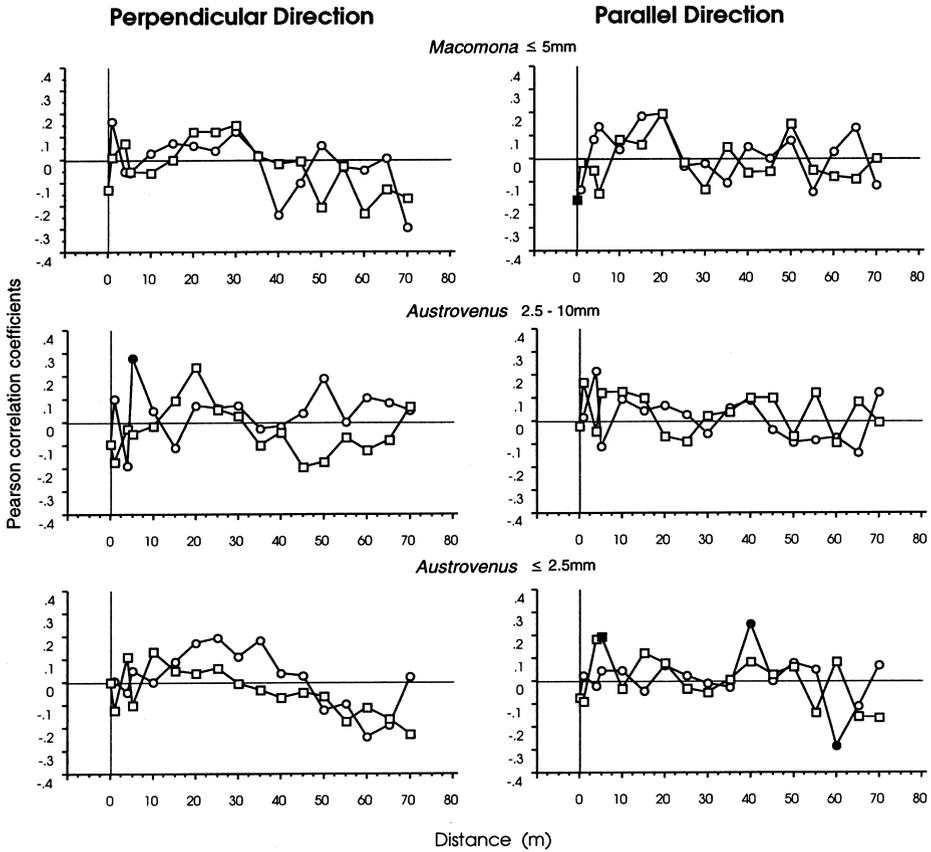


Fig. 6. Cross-correlograms between adult *Macomona* and juveniles of *Macomona* and *Austrovenus*. As cross-correlograms are not symmetrical, they were computed for both the + (circles) and - (squares) lag directions. Significant values are indicated by infilled symbols.

correlations became positive (sometimes significantly so) by 5 m, and either stayed positive thereafter or oscillated around zero.

3.2.2. Results of principal component analyses

Calculations performed on both the Pearson and the Spearman correlation matrix led to very similar graphs. As the percentage of variation represented in two dimensions is slightly larger for the Spearman correlations, only these results are presented here. Regardless of direction of the transect, three groups are apparent in the ordination space (Fig. 7): adult *Macomona*; intermediate sized *Macomona*; and the juveniles of both bivalve species. The short arrows indicate that the large juvenile *Austrovenus* size-class is badly represented in the space of the first two eigenvectors.

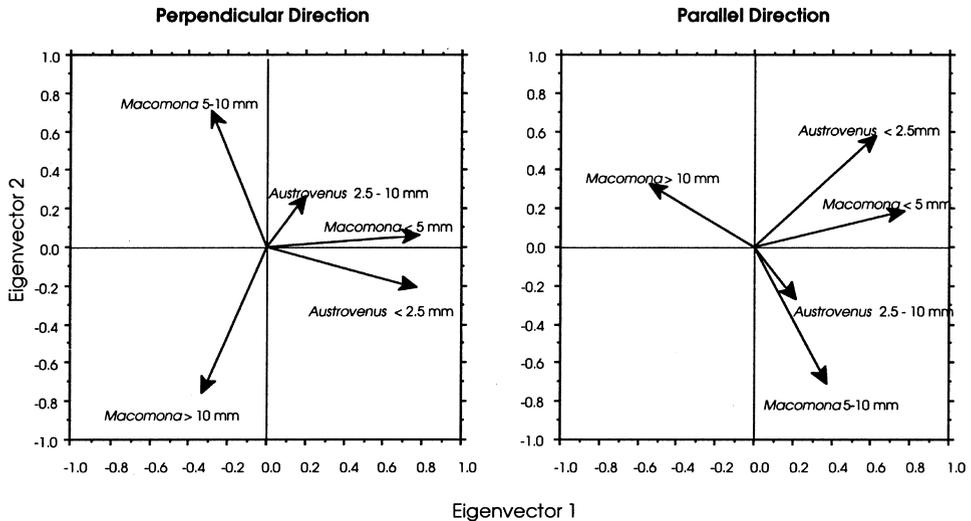


Fig. 7. Positions of variables in principal component ordination space. The first two eigenvalues explain 52.7% (29.0+23.7) of the variation.

3.2.3. Results of correlation analyses

(i) Adult–juvenile *Macomona*. No significant differences in correlation coefficients between directions or between sites (Table 4) were found, with all correlation coefficients being negative regardless of scale (Fig. 8(a) and (b)). However, significant differences in the correlation coefficients were found between individual transects (Table 4). This was mainly due to the size of the correlation coefficient (i.e. intensity), although there were indications of a difference in direction of the relationship at site 1 (Fig. 8(c)). At this site, a strong negative interaction was apparent in the parallel direction, and a non-significant positive relationship apparent for the other direction. This difference did not persist when smaller groups within the individuals transects were examined. In fact, no significant differences were found at the smaller scales, until pairs of samples 1 m apart were investigated. At this scale, correlation coefficients were negative for all transects except for the site 2 transect running in the parallel direction.

(ii) Adult *Macomona*–large juvenile *Austrovenus*. Only data from site 3 was analysed due to the low numbers of large juvenile *Austrovenus* found at the other sites. Correlation coefficients for the two directions were significantly different from each other (Table 4), with a nearly significant negative correlation in the perpendicular direction, and a non-significant positive interaction in the other direction (Fig. 8(d)). Although no significant differences between the directions were found for smaller scales, correlation coefficients were always negative for the perpendicular direction, and positive for the other direction.

(iii) Adult *Macomona*–small juvenile *Austrovenus*. No significant difference was found between transect directions (Table 4), when all the data was considered. Although no significant differences were found at any of the smaller scales, consistent negative

Table 4

The results of the tests for similarity between correlation coefficients of juveniles with adult *Macomona* at each scale are given as χ^2 value (or z value for the comparison of the 2 directions) with the associated probability level in brackets

	Extent of data group	Juvenile <i>Macomona</i>	Small juvenile <i>Austrovenus</i>	Large juvenile <i>Austrovenus</i>
directions	≤1 km	overall test not significant	overall test not significant	–
	≤150 m			
	≤36 m			
	≤16 m			
	≤6 m			
	1 m			
sites	≤1 km	overall test not significant	9.90 (0.007)	–
	≤150 m		9.90 (0.005)	
	≤36 m		5.41 (0.07)	
	≤16 m		9.59 (0.008)	
	≤6 m		12.05 (0.002)	
	1 m		6.04 (0.049)	
Transects	≤150 m	13.14 (0.022)	10.70 (0.06)	–2.13 (0.016)
	≤36 m	2.14 (0.54)	5.17 (0.16)	–
	≤16 m	5.23 (0.38)	9.71 (0.082)	–1.44 (0.075)
	≤6 m	5.84 (0.32)	0.79 (0.055)	–1.36 (0.087)
	1 m	8.12 (0.015)	5.44 (0.364)	–1.57 (0.058)

Results are only given if the overall permutation test was significant at the 0.05 level.

correlations were found at smaller scales for the parallel direction (Fig. 8(e)). Significant differences between the correlation coefficients for the different sites were found at most scales (Table 4): with site 1 showing positive correlations; site 2, negative correlations; and site 3, low negative correlations (Fig. 8(f)). Although no significant differences were found between correlation coefficients for the individual transects at any scale, all correlations for site 1 were positive and all those for site 2 were negative (Fig. 8(g)).

In summary, correlation coefficients were generally low (< 0.5 , Fig. 8). Relationships between adult *Macomona* and each size-class of juveniles, averaged over all 3 sites, were similar for the two transect directions. However, both adult–juvenile *Macomona* and adult *Macomona*–small juvenile *Austrovenus* relationships were variable in intensity and, more rarely, direction, depending on whether the spatial extent of the data was all 3 sites, each site separately, or individual transects. Generally, the direction of the relationship was consistent at all scales within each spatial extent used, with no particular scale showing stronger correlations than another.

3.3. Analysis of environmental variables

Out of all the environmental variables measured, only %sand content displayed no significant correlations with numbers of juveniles of either species at any scale. However, very little variation ($\sigma < 2\%$) was available in the sediment composition variables and the only correlations observed for %mud and %gravel were with numbers

Table 5

Results of stepwise regression analyses of numbers of juvenile *Macomona* and small juvenile *Austrovenus* with numbers of adult *Macomona*, with and without the effect of elevation (elev) and shell hash (hash)

Site	Direction	<i>n</i>	Juvenile adults only	<i>Macomona</i> adults plus other effects	Small juvenile adults only	<i>Austrovenus</i> adults plus other effects
1	Perpendicular	61			0.08 (0.069)	0.08 (0.069)
1	Parallel	60	0.15 (0.011)	0.15 (0.011)		
2	Perpendicular	40	0.10 (0.026)	0.16 (0.012) elev 0.15 (0.015) hash 0.07 (0.075)		0.12 (0.031) elev 0.40 (<0.001)
2	Parallel	60			0.07 (0.039)	0.07 (0.039)
1	both	121		0.03 (0.051) elev 0.04 (0.031)	0.04 (0.019)	0.04 (0.019)
2	both	100			0.03 (0.053)	0.04 (0.035) elev 0.09 (0.002)
1 and 2	Perpendicular	101		elev 0.07 (0.006)		
1 and 2	Parallel	121	0.03 (0.032)	0.07 (<0.001) elev 0.06 (0.003)	0.05 (0.009)	0.05 (0.009)
1 and 2	both	221		0.02 (0.040) elev 0.05 (0.001)	0.08 (<0.001)	0.08 (<0.001)

Analyses presented are for raw data as $\log(x+1)$ transformations generally resulted in less significant results. Partial r^2 (with p values) are given. Only sites 1 and 2 are used in this analysis as elevation was not measured for all of site 3.

is taken into account. Overall, densities of adult *Macomona* remain important, together with elevation, in explaining density variations in juveniles at both the km scale and the 150 m scale. Again all correlations are weak ($r < 0.50$).

4. Discussion

Preliminary surveys are often used to help design future experiments. If carried out in conjunction with experiments, they can also be useful in expanding experimental results into a broader context (Eberhardt and Thomas, 1991; Schneider et al., 1997). One of the major purposes behind this survey design was to collect data that would allow us to design another, more intensive survey at scales appropriate to the common species, in particular *Macomona*, inhabiting this sandflat (Legendre et al., 1997). Both the size distribution of species and their patch structure were analysed. The frequency histogram of the size classes of *Macomona* and *Austrovenus* suggested that to collect enough individuals sized > 5 mm to allow most types of analyses to be carried out, the sample unit would need to be much larger than the one in this study. Similarly, if we wished to investigate size classes with a smaller range (e.g. 0.5–1 mm, 1–1.5 mm) we would need bigger sample units. Analysis of spatial patterns for the smaller size classes of the two species within each transect found 10–20 m patches within 50–75 m patches at all three sites, with indications of even larger patterns. This suggests that gridcells of ≥ 20 m should decrease the variability found as a result of the small-scale patches. Also a grid

extent of >200 m should allow several of the larger-sized patches to be incorporated within the grid.

The inconsistent results of field experiments on adult–juvenile interactions may be due to the effects of such interactions on population dynamics being overwhelmed by a variety of physical and biological factors (Commito, 1982; Eckman, 1983; Butman, 1987). Physical factors such as substrate and habitat characteristics (Olafsson, 1989; Ahn et al., 1993; Thrush et al., 1996) and exposure to waves and tidal currents (Baggerman, 1953; Beukema, 1973; Grant, 1983; Moller, 1986) have been suggested as being important. Our study was conducted in one habitat, over an area of relatively homogeneous substrate characteristics. The design of this study incorporated the possibility of a gradient in hydrodynamics or elevation. Results obtained from the individual transects suggested that spatial patterns in the abundance of juvenile *Macomona* may be affected by such factors. Strong within-transect patterns were apparent only on the transects that ran perpendicular to the direction of maximum wave exposure and tidal flow. We might have expected the direction exhibiting a lack of spatial patterns to either show no significant relationships or to show strongest relationships at the larger scales. Instead it was this direction (i.e. that parallel to tidal flow and maximum wave exposure) that showed the clearest relationships at the smallest (0 m) scale. Significant differences between the two directions, in terms of relationships between adults and juveniles, were only found for large juvenile *Austrovenus* and were driven by one site only. Thus, effects due to hydrodynamic gradients did not generally overwhelm other effects at the scale of this study.

Biological factors that may affect the outcome of adult–juvenile interactions include the specifics of animal biology/behaviour (Weinberg, 1984; Hines et al., 1989; Olafsson, 1989; Posey, 1990; Ahn et al., 1993). We found that the intensity and direction of the adult–juvenile bivalve relationship was dependent on species and juvenile size. However, for particular size classes of a particular species, intensity and direction of interaction was variable over different spatial extents, suggesting other factors may be important (e.g. predation).

It is now well recognised that while careful experimental research is necessarily of limited spatial and temporal scale, many processes either change their importance with changes in scale or operate over larger than experimental spatial and temporal extents. This survey was structured to identify any variation in intensity and direction of adult–juvenile relationships with changes in scale. Our results suggest that while some small-scale (0–1 m) relationships occur, this is not the only scale, nor is it necessarily the scale showing strongest relationships. Larger-scale (>5 m) positive interactions are likely and, in some cases, this overlies smaller-scale inhibition or avoidance. Results of correlations between adult and juveniles were variable in intensity and, sometimes, direction depending on the spatial extent used. It is unlikely that the variability in results is dependent on the actual density range of the adults as the site most different from the others in this respect (i.e. site 3) does not give the most different results.

Findings of this study suggest that the exploration of the importance of adult–juvenile interactions remains fraught with difficulties. Field experiments need to encompass an appropriate scale not only for the mechanics of the interaction, but also for the potential effect on abundances. Interactions may also not be confined to one process or one scale. For example, Black and Peterson (1988) conducted their experiment at the scale at

which they considered interference competition for space to occur, but then concluded that this was the wrong scale for detecting preemptive competition. Furthermore, even systems comprised of small-scale homogeneous mosaics controlled by small-scale processes can produce patterns at larger scales that may sometimes appear unrelated to (and unpredictable from) the small scale dynamics (Gleick, 1988).

The stepwise regression analyses generally found that more variability could be explained by utilising environmental data. Like Legendre et al. (1997), we found elevation to be useful in explaining variations in the densities of juvenile bivalves. Our principal component analyses also suggested small juveniles of both species were highly correlated and probably under the control of the same dispersive processes. However, unlike Legendre et al. (1997), adding environmental variables did not remove the significance of adult–juvenile relationships. It is possible that this is a function of the differing scale of extent (1 km × 150 m vs. 250 × 500 m), lag (1 to 5 m vs. 5 to 40 m) and grain (10 cm diam. vs. 50 × 50 cm) of the two studies. We found that both extent and lag affected the correlations found in our study and Hewitt et al. (1996) found grain affected the significance of adult–juvenile correlations. We would also generally expect environmental variables to become more important with extents that take in larger gradients of these variables.

Our study supports the hypothesis that processes of a larger-scale than those commonly examined in field experiments may contribute to the variability of results from adult–juvenile interaction experiments. Different intensities and directions of relation were found at different scales and at different sites within one habitat type. While the relationships between adult *Macomona* and juveniles of both *Macomona* and *Austrovenus* found for the smallest lag (0 m) were negative, suggesting inhibition, positive associations were common at larger lags. However, while the results of field experiments may be variable and, at times, not support findings suggested by surveys, this does not mean that adult–juvenile interactions are unimportant. It becomes even more important to find methods of linking processes working at one scale with changes at other scales.

Acknowledgements

We thank Auckland Airport Security for access to the study site. This research was made possible by support from NIWA-NSOF and FRST-CO1517. Vonda Cummings, Tony Dolphin, Richard Ford and Michelle Wilkinson helped with the field work and preliminary sorting; and Graham McBride commented on a earlier draft of the manuscript.

Appendix A

Calculation of cross correlograms

Cross-correlograms can be used to model statistically the spatial covariation between

two variables (Rossi et al., 1992) to compare two series of data for various distance classes. The cross-covariance between two variables *A* and *B* is estimated as:

$$C_{AB}(\mathbf{h}) = \frac{1}{N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} \sum_{j=1}^{N(\mathbf{h})} [z_A(x_i - m_{A-\mathbf{h}})] \cdot [z_B(x_j - m_{B+\mathbf{h}})] \quad (1)$$

where $z_A(x_i)$ and $z_B(x_j)$ are the values of variables *A* and *B* at locations x_i and x_j , separated by the distance vector \mathbf{h} ; $N(\mathbf{h})$ is the total number of data pairs separated by \mathbf{h} and $m_{A-\mathbf{h}}$ and $m_{B+\mathbf{h}}$ are the means of variables *A* and *B* at each end of vector \mathbf{h} .

The cross-correlation is the cross-covariance standardized by the standard deviations:

$$r_{AB}(\mathbf{h}) = C_{AB}(\mathbf{h}) / (s_{A-\mathbf{h}} \cdot s_{B+\mathbf{h}}) \quad (2)$$

where $s_{A-\mathbf{h}}$ and $s_{B+\mathbf{h}}$ are the standard deviations of the variables *A* and *B* at each end of vector \mathbf{h} . Note that $r(\mathbf{h}=0)$ is the coefficient of linear correlation between the two variables. The plot of the cross-correlation *versus* distance \mathbf{h} is called a cross-correlogram.

Eq. (2) is called the non-ergodic cross-correlation (Isaacks and Srivastava, 1989). This statistical function accounts for any differences in mean and variance between the ends of distance vector \mathbf{h} and removes the effect of changing means and variances in the study area (Rossi et al., 1992). With transect data, it is the exact equivalent of the coefficient of cross-correlation used in time series analysis. The programs available for time series analysis require, however, the data to be equi-spaced (constant lag). This is not the case with our data; so we used a geostatistical cross-correlogram programme that correctly handles unevenly-spaced data.

The cross-correlation is not symmetrical. The value of this function is not the same if calculated in opposite directions: Consequently, cross-correlograms must be computed and compared for both the $+\mathbf{h}$ and $-\mathbf{h}$ directions to detect a lag effect, which is an offset between the locations of extreme values of the two variables. In time series analysis, the direction to consider is often dictated by the hypothesis of causality to be tested (e.g. predators eat prey, rarely the opposite). When analyzing spatial data, such guiding principles are usually not available, except when a time-oriented process is at cause (e.g. currents).

The significance of the cross-correlation coefficient can be assessed by the test for significance of the correlation between two samples drawn from normal populations, where:

$$t = r_{AB} \sqrt{\frac{(N(\mathbf{h}) - 2)}{1 - r_{AB}^2}} \quad (3)$$

The null hypothesis to be tested is that the correlation is zero.

Appendix B

Randomised permutation method for testing consistency of correlations

For clarity this explanation is based on testing whether correlations of paired samples are consistent between the three sites.

1. Residuals are calculated for both variables within each pair and standardised to unit variance. This is to ensure their exchangeability during the permutation process.
2. Correlations between residuals are then calculated for each site separately.
3. A χ^2 test statistic (Sokal and Rohlf, 1995) describing the difference between the correlations from the three sites is then calculated and stored
4. The pairs of residuals calculated in step 1 are then randomly permuted between the sites 2000 times and steps 2 and 3 are repeated, generating the null distribution of the test statistic
5. The observed χ^2 test statistic is then compared with the permuted null distribution. The p -value is the proportion of permutation values exceeding the observed χ^2 test statistic.

References

- Ahn, I.Y., Lopez, G., Malouf, R., 1993. Effects of the gem clam *Gemma gemma* on the early post-settlement emigration, growth and survival of the hard clam *Merceneria merceneria*. Mar. Ecol. Prog. Ser. 99, 61–70.
- Allen, T.F.H., Starr, T.B., 1982. Hierarchy Perspectives for Ecological Complexity. University of Chicago Press, Chicago, USA, 310 pp.
- Andre, C., Rosenberg, R., 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. Mar. Ecol. Prog. Ser. 71, 227–234.
- Ardissou, P.-L., Bourget, E., 1992. Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna. Mar. Ecol. Prog. Ser. 83, 15–34.
- Bachelet, G., Guillou, J., Labourg, P.J., 1992. Adult–larval and juvenile interactions in the suspension-feeding bivalve *Cerastoderma edule* (L.): field observations and experiments. In: Colombo, G., Ferrari, I., Ceccherelli, V.U., Rossi, R. (Eds.), Marine Eutrophication and Population Dynamics, 25th European Biological Symposium. Olsen and Olsen, Frededborg, pp. 175–182.
- Baggerman, B., 1953. Spatfall and transport of *Cardium edule* L. Arch. Neerl. Zoology 10, 315–342.
- Beukema, J.J., 1973. Migration and secondary spatfall of *Macoma balthica* (L.) in the western part of the Wadden Sea. Neth. J. Zool. 23, 356–357.
- Black, R., Peterson, C.H., 1988. Absence of preemption and interference competition for space between large suspension-feeding bivalves and smaller infaunal macroinvertebrates. J. Exp. Mar. Biol. 120, 183–193.
- Butman, C.A., 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr. Mar. Biol. Ann. Rev. 25, 113–165.
- Clifford, P., Richardson, S., Hemon, D., 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45, 123–134.
- Commuto, J.A., 1982. Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine. USA. Mar. Biol. 68, 77–81.
- Commuto, J.A., Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., 1995. Dispersal dynamics in a wind-driven benthic system. Limnol. Oceanogr. 40, 1513–1518.
- Crawley, M.J., 1993. GLIM for Ecologists. Blackwell Scientific Publications, Oxford, 379 pp.
- Cummings, V.J., Pridmore, R.D., Thrush, S.F., Hewitt, J.E., 1993. Emergence and floating behaviours of post-settlement juveniles of *Macomona liliana* (Bivalvia: Tellinacea). Mar. Behav. Physiol. 24, 25–32.
- Cummings, V.J., Pridmore, R.D., Thrush, S.F., Hewitt, J.E., 1995. Post-settlement movement by intertidal benthic macroinvertebrates: Do common New Zealand species drift in the water column? N.Z. J. Mar. Freshwat. Res. 29, 59–67.
- Dayton, P.K., Tegner, M.J., 1984. The importance of scale in community ecology: A kelp forest example with terrestrial analogs. In: Price, P.W., Slobodchikoff, C.N., Gaud, W.S. (Eds.), A New Ecology: Novel Approaches to Interactive Systems. Wiley and Sons, New York, pp. 457–483.

- Deutsch, C.V., Journel, A.G., 1992. GSLIB: Geostatistical Software Library. Oxford University Press, New York. 340 p.
- Dutilleul, P., 1993. Modifying the *t* test for assessing the correlation between two spatial processes. *Biometrics* 49, 305–314.
- Eberhardt, L.L., Thomas, J.M., 1991. Designing environmental field studies. *Ecol. Monogr.* 61, 53–73.
- Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* 28, 241–257.
- Folk, R.L., 1968. *Petrology of Sedimentary Rocks*. Hemphill, Austin, Texas, U.S.A., 159 pp.
- Gleick, J., 1988. *Chaos: Making a New Science*. Cardinal, London, 352 pp.
- Grant, J., 1983. The relative magnitude of biological and physical sediment reworking in an intertidal community. *J. Mar. Res.* 41, 673–689.
- Hewitt, J.E., Thrush, S.F., Cummings, V.J., Pridmore, R.D., 1996. Matching patterns with processes; predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. *Mar. Ecol. Prog. Ser.* 135, 57–67.
- Hewitt, J.E., Pridmore, R.D., Thrush, S.F., Cummings, V.J., in press. Short-term stability of spatial patterns in macrofauna of a dynamic estuarine system. *Limnol. Oceanogr.*
- Hines, A.H., Posey, M.H., Haddon, P.J., 1989. Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. *Veliger* 32, 109–119.
- Horne, J.K., Schneider, D.C., 1994. Lack of spatial coherence of predators with prey: A bioenergetic explanation for Atlantic cod feeding on capelin. *J. Fish Biol.* 45, 191–207.
- Isaacks, E., Srivastava, R.M., 1989. *An introduction to applied statistics*. Oxford University Press, New York. xix + 561 p.
- Lebart, L., Morineau, A., Fénelon, J.-P., 1979. *Traitement des données statistiques—Méthodes et programmes*. Dunod, Paris. xiii + 510 p.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673.
- Legendre, P., Fortin, M.J., 1989. Spatial pattern and ecological analysis. *Vegetatio* 80, 107–138.
- Legendre, P., Thrush, S.F., Cummings, V.J., Dayton, P.K., Grant, J., Hewitt, J.E., Hines, A.H., McArdle, B.H., Pridmore, R.D., Schneider, D.C., Turner, S.J., Whitlatch, R.B., Wilkinson, M.R., 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *J. Exp. Mar. Biol. Ecol.* 216 (1–2), 99–128.
- Legendre, P., Vaudor, A., 1991. *The R package: Multidimensional analysis, spatial analysis*. Département de sciences biologiques, Université de Montréal, Montréal, 142 pp.
- McCullagh, P., Nelder, J.A., 1989. *Generalised Linear Models*. Chapman and Hall, London, 2nd edn., 511 pp.
- Moller, P., 1986. Physical factors and biological interactions regulating infauna in shallow boreal areas. *Mar. Ecol. Prog. Ser.* 30, 33–47.
- Olafsson, E.B., 1989. Contrasting influences of suspension-feeding and deposit feeding populations of *Macoma balthica* on infaunal recruitment. *Mar. Ecol. Prog. Ser.* 55, 171–179.
- Olafsson, E.B., Peterson, C.H., Ambrose, W.G.J., 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Ann. Rev.* 32, 65–109.
- Posey, M.H., 1990. Functional approaches to soft-substrate communities: How useful are they? *Rev. Aqu. Sci.* 2, 343–356.
- Powell, T.M., 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. In: Roughgarden, J., May, R.M., Levin, S.A. (Eds.), *Perspectives in Ecological Theory*. Princeton University Press, Princeton, N.J., pp. 157–176.
- Pridmore, R.D., Thrush, S.F., Wilcock, R.J., Smith, T.J., Hewitt, J.E., Cummings, V.J., 1991. Effect of the organochlorine pesticide technical and deposit feeding bivalves. *Mar. Ecol. Prog. Ser.* 76, 261–271.
- Rossi, R.E., Mulla, D.J., Journel, A.G., Franz, E.H., 1992. Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecol. Monogr.* 62, 277–314.
- SAS/Insight, 1993. *Users' Guide, Version 6*. SAS Institute Inc., Cary, N.C., USA., 2nd edn., 490 pp.
- Schneider, D.C., Walters, R., Thrush, S.F., Dayton, P.K., 1997. Scale-up of ecological experiments: density variation in the mobile bivalve *Macomona liliana* Iredale. *J. Exp. Mar. Biol. Ecol.* 216 (1–2), 129–152.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. W.H. Freeman and company, San Francisco, 3rd edn., 859 pp.
- Solow, A., Steele, J.H., 1990. On sample size, statistical power, and the detection of density dependence. *J. Anim. Ecol.* 59, 1073–1076.

- Thrush, S.F., Hewitt, J.E., Pridmore, R.D., Cummings, V.J., 1996. Adult/juvenile interactions of infaunal bivalves: contrasting outcomes in different habitats. *Mar. Ecol. Prog. Ser.* 132, 83–92.
- Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., 1992. Adult infauna as facilitators of colonization on intertidal sandflats. *J. Exp. Mar. Biol. Ecol.* 159, 253–265.
- Thrush, S.F., Pridmore, R.D., Bell, R.G., Cummings, V.J., Dayton, P.K., Ford, R., Grant, J., Hewitt, J.E., Hines, A.H., Hume, T.M., Lawrie, S.M., Legendre, P., McArdle, B.H., Morrisey, D., Schneider, D.C., Turner, S.J., Walters, R., Whitlatch, R.B., Wilkinson, M.R., 1997a. The sandflat habitat: Scaling from experiments to conclusions. *J. Exp. Mar. Biol. Ecol.* 216 (1–2), 1–9.
- Thrush, S.F., Cummings, V.J., Dayton, P.K., Ford, R., Grant, J., Hewitt, J.E., Hines, A.H., Lawrie, S.M., Legendre, P., McArdle, B.H., Pridmore, R.D., Schneider, D.C., Turner, S.J., Whitlatch, R.B., Wilkinson, M.R., 1997b. Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult/juvenile interactions. *J. Exp. Mar. Biol. Ecol.* 216 (1–2), 153–169.
- Weinberg, J.R., 1984. Interactions between functional groups in soft-substrate do species differences matter? *J. Exp. Mar. Biol. Ecol.* 80, 11–28.
- Young, C.M., 1989. Larval depletion by ascidians has little effect on the settlement of epifauna. *Mar. Biol.* 102, 481–489.