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Measurement of density variability in the bivalve *Chione stutchburyi* using spatial autocorrelation

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ABSTRACT: The fine-scale density distribution of *Chione stutchburyi* Finlay, 1927 (Bivalvia: Veneridae) was studied in a soft shore estuarine lagoon. A pilot survey of density variability was made using a hierarchical sampling procedure. Densities were compared within and between 3 sampling locations, and within-site variability was shown to be important. Fine-scale spatial and temporal variability for a single systematically sampled site over a 30 mo survey period was examined using autocorrelation techniques. The advantages of systematic sampling and autocorrelation techniques for the detection and description of spatial and temporal patterns are discussed.

INTRODUCTION

Considerable attention is currently being given to the problems of scale in ecological studies (Taylor & Taylor 1979, Connell & Sousa 1983, Dayton & Tegner 1984, Sousa 1984, Steele 1985). It has long been known that the scale of sampling relative to the distributional pattern of the organisms to be sampled can influence both the precision and interpretation of the data (Greig-Smith 1983). However, ecologists have been slower to realise that similar considerations must be applied when designing experiments to investigate population dynamic processes. Prior to setting up the experiment it is important to have a clear idea of the scales, spatial and temporal, within which the processes of interest are expected to operate, so that the experiment can be performed over a suitable time period and area.

In the first part of this paper, a pilot study is reported which examined the scale of variation in population distribution of *Chione stutchburyi* within and between 3 randomly selected locations within Ohiwa Harbour, Bay of Plenty, New Zealand (177° 02 'E, 38° 00 'S). The second part of the paper examines small scale spatial and temporal distribution patterns derived from an analysis of repeated grid samples from a sampling area on the main channel using spatial autocorrelation techniques (Ripley 1981). Spatial autocorrelation (Sokal & Oden 1978a, b, Sokal 1979) is probably the simplest technique for the detection of pattern and estimation of the scale on which the influential processes operate. The aim was to identify the nature and scale of the local aggregation pattern detected by the pilot study, and to study the patterns in the local variation of population densities through time.

The New Zealand cockle *Chione stutchburyi* Finlay, 1927 is a dominant member of the benthic community in the soft shore sheltered habitat. It is an ecological equivalent of the northern hemisphere species *Cardium edule* and *Mercenaria mercenaria* (Grace 1973). Stephenson (1982) examined population dynamics in the Avon-Heathcote estuary (Christchurch New Zealand) under high levels of predation (notably the oystercatcher *Haematopus ostralegus*). Bird count data (Blackwell unpubl.) suggests that Ohiwa Harbour supports considerably lower oystercatcher densities and seems characterised by stable large-scale density patterns of *C. stutchburyi*. These distribution patterns, originally recorded by Paul (1964), remained relatively unchanged over the subsequent 20 yr (Paul 1966, Richmond 1977, Akroyd & Kilner 1980, Blackwell 1984). This paper forms part of an investigation into some of the factors that influence the observed distribution of *C. stutchburyi* in Ohiwa Harbour.

PILOT STUDY

Methods

Richmond (1977) recognised 2 major regions within Ohiwa Harbour: the sandy lagoonal region, subject to gross seasonal and tidal changes in sedimentology and

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topography, and the estuarine region of the more sheltered upper harbour reaches. Sampling areas were randomly selected within the lagoonal region (Harbour mouth location), midway along the major Eastern arm (Channel location), and at Hokianga Island (Hokianga location). These last 2 are estuarine sites.

Three transects, each ca 100 m long, and 100 m apart, were sampled within each area. Down each transect, replicate samples were collected at each high tide, mid tide and low tide sample site (1.2, 0.8 and 0.2 m above chart datum respectively, as determined by surveyor's level).

At each sample site, 4 samples (0.05 m^2) were randomised from within an area of 3 m^2. Each sample was collected by placing a steel quadrat frame on the sediment surface. All enclosed sediment to a depth of 10 cm was passed through a 2.00 mm mesh sieve and the density of *Chione stutchburyi* was recorded.

Results

To test whether the density data needed transforming and to gain insight into the dispersion of *Chione stutchburyi,* the log of the variance was regressed against the log of the mean of the replicate quadrats at each tidal height in each transect. The resulting straight line has a slope of 2.02 (SE 0.165). This suggests firstly that a log transformation would stabilise the variances and secondly that *C. stutchburyi* is heavily aggregated when sampled on this scale.

An ANOVA was then performed on the log $(x + 1)$ transformed data using the SAS package (SAS Institute Inc. 1985). Factors tested were location, transect and tidal height, with the transect factor nested within the location factor. Residual analyses were performed (Snedecor & Cochran 1980) to check the assumptions of heterogeneity of variance and normality.

A significant tidal height and transect interaction ($F = 1.96$, df = 12,81, $p < 0.05$) and significant height location interaction effects ($F = 9.1$, df = 4,12, $p < 0.001$) show that the pattern of variation is not simple. The sample means are plotted in Fig. 1. The lagoonal site (A) clearly has higher densities than the more estuarine sites (B and C). There is also a tendency for the mid tide areas to have the highest densities. The most obvious feature is that the sites differ in the pattern of variation down the beach and show quite large variation between transects. The existence of significant height × transect effects confirms the suggestion that factors operating within the locations are important in influencing *Chione stutchburyi* density. Indeed 65 % of the explained sums of squares is due to terms incorporating transect or tidal height effects

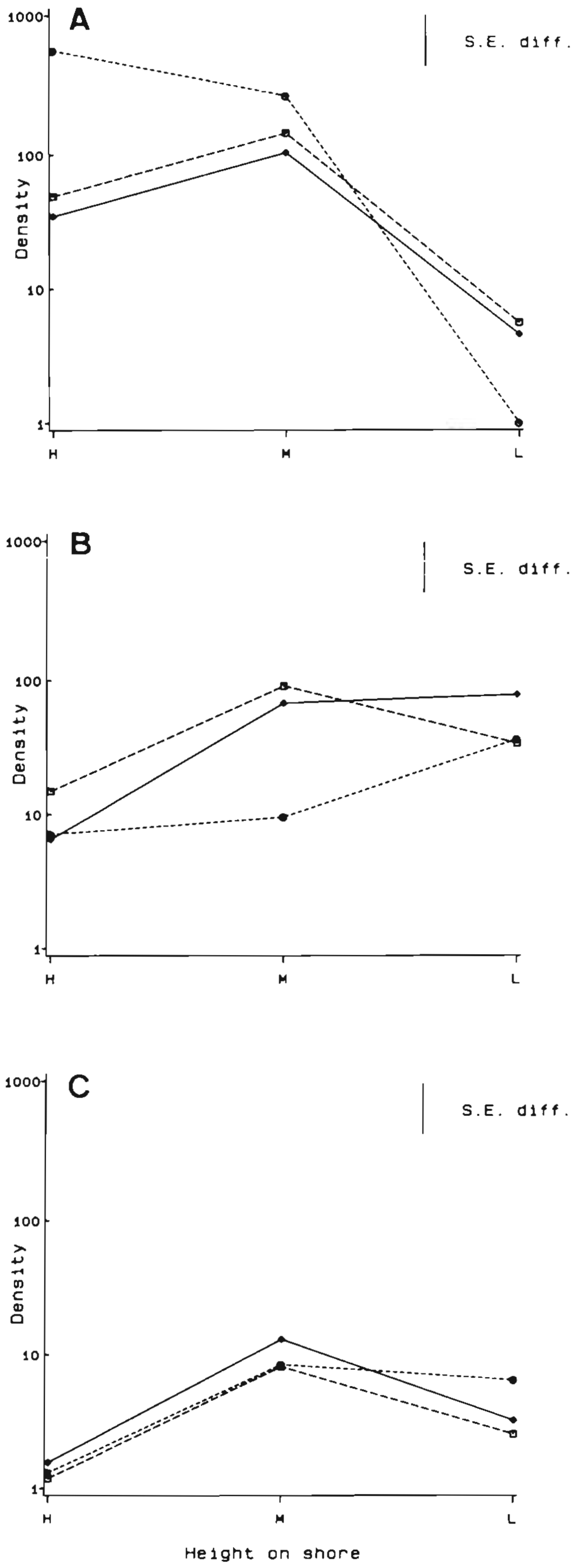

Fig. 1. *Chione stutchburyi.* Mean densities (no. m^{-2}) plotted against tidal height for 3 transects at (A) lagoon site, (B) Channel site and (C) Hokianga Island. The standard error of the difference between any 2 means is also given

The existence of effects at such different scales: between locations (km), between transects (tens of metres), and between tidal heights (tens of metres), raises the problem of which scale to study. It is a widely accepted principle that while large scales enhance pattern detection, studies at smaller scales often allow direct investigation of the proximal causes for changes in population densities – though sometimes at the cost of generality The study was therefore continued at a smaller sampling scale to identify the appropriate scale for the setting up of a series of experiments.

GRID STUDY

Methods

Five transects, each 5 m apart and 90 m long, were established from the high tide mangrove fringe to datum low tide, using a surveyor's level. A disused navigation marker at low tide provided a convenient reference point. By sampling at 5 m intervals down each transect an 18 × 5 grid was created. Within the region of each intersection, a random 0.025 m^2 sample was collected with replacement. Sediment to a depth of 10.0 cm was sieved through a 2.0 mm mesh plastic sieve, and the number of *Chione stutchburyi* recorded. All the macrofauna were then returned to the hole. The complete grid was sampled 12 times at ca 3 mo intervals.

Results

Mean density

The mean densities of *Chione stutchburyi* on each sampling occasion are reported in Table 1. When samples are from smoothly contoured spatial data (spatially autocorrelated), the true standard errors of a grid sample data will be smaller than would have been possible from random or stratified random sampling (Ripley 1981). It is however impossible to estimate the true sampling error, so we have to use biased standard errors (overestimates). The simplest method would be to treat the quadrats as a random sample. This gives an overestimate for autocorrelated data. A simple, more efficient, but still biased estimate can be calculated by dividing the observations into pairs of neighbouring points. These are then treated as strata and the standard error of the overall mean calculated as from a stratified sample with (r × c)/2 strata (Ripley 1981); where r is the number of rows, and c is the number of columns in the sampled grid. The advantage of the stratified estimator is apparent. The true standard errors will be generally smaller than these values.

Table 1 *Chione stutchburyi*. Mean, variance and 2 estimates of standard error for densities at the grid study site on 12 successive sampling occasions

Date	Mean (no. m^{-2})	Variance	Standard error	
			Random sample	Stratified sample
Sep 1978	17.0	382.5	2.06	1.59
Dec 1978	20.7	440.4	2.21	1.80
Mar 1979	18.4	383.8	2.07	1.32
Jun 1979	22.5	462.2	2.26	1.35
Sep 1979	24.5	623.9	2.63	1.56
Dec 1979	25.3	752.8	2.90	1.92
Mar 1980	23.9	539.2	2.45	1.87
Jun 1980	26.6	817.5	3.01	2.28
Sep 1980	32.0	1088.1	3.48	2.39
Dec 1980	30.7	869.7	3.11	2.27
Mar 1981	22.5	476.3	2.30	1.69
Jun 1981	22.5	473.1	2.29	1.56

Spatial patterns

Spatial autocorrelation calculates the degree of similarity of values at set distances apart. Thus we might for example calculate the degree of similarity of neighbouring grid points (5 m apart) in the north-south direction (parallel to the sea). In this case every data point would be paired to the value to the north. Then the ordinary correlation coefficient is calculated, i. e. the autocorrelation. There will of course be no pair for the northernmost grid points. The autocorrelation will be calculated from only (r − 1)c points. Perhaps less obviously, the coefficient would be identical if we paired each point to its neighbour to the south. It is also possible to calculate the autocorrelation for grid points 5 m to the east (or west) or for points to the north (or south) 10, 15, 20, 25 m apart etc. Indeed the autocorrelation can be calculated in any direction and for any distance that allows data to be paired, up to 85 m in the east-west direction (towards the sea) and 20 m north-south. Such a matrix of autocorrelations is an autocorrelogram. Sokal's original method (Sokal & Oden 1978a, b, Sokal 1979) was not followed as it considers distance only, and assumes that similarities are the same in every direction (isotropic). The nature of the intertidal habitat suggests that this assumption would be unjustifiable, therefore the full autocorrelogram (Ripley 1981) is used. This is sometimes used as the starting point for a 2 dimensional spectral analysis (e. g. Ford & Renshaw 1984). Since the autocorrelograms at the 12 time periods appeared very similar, a simple average is presented (Fig. 2). This does not mean that the contour maps for the time periods were identical – they were not: Fig. 3 shows the grid at the start (A) and the finish (B) of the study period. Clearly the system

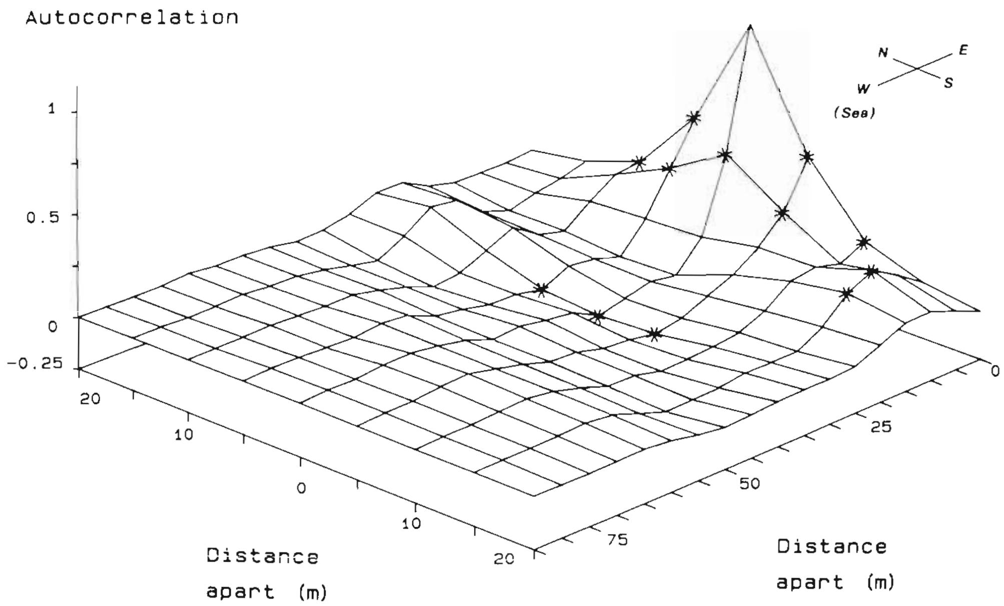

Fig. 2. *Chione stutchburyi.* Two-dimensional spatial autocorrelogram of density (average of 12 time periods). Autocorrelation coefficients that are significant at the 99.99 % level (using an approximate test) are marked by an asterisk

was not static; major changes of density occurred in the mid-tide region. However the degree to which neighbouring points were similar did not change. The factors causing change were operating at a characteristic scale that left the autocorrelogram relatively constant. An approximate significance test (Ford & Renshaw 1984) was performed. Since a large number of coefficients are involved (148), the 99.99 % level of significance was employed. Those coefficients that exceeded the critical value (0.118) are highlighted in Fig. 2. The peak is at distance zero and has a height of one. This is the correlation of every point with itself. The second highest point is at 5 m in the N-S direction (correlation coefficient $r = 0.442$). This suggests that on average, a sample taken at a point 5 m in the N-S direction (along the shore) from any starting point on the sample grid would have a roughly similar density. Continuing along the N-S axis we find that even at a 10 m distance there is still detectable similarity between points ($r = 0.122$). However, the densities at 2 points 15 m or more apart in the N-S direction are effectively independent ($r = 0.025$). In the E-W direction (towards the sea) the situation is different. While points 5 m apart are similar ($r = 0.405$), the densities are effectively independent at 10 m. That is, the degree of similarity of densities falls off more rapidly in the E-W direction than in the N-S. More interestingly, at 30 m distance in the E-W direction there is a significant negative correlation ($r = 0.141$). This suggests that if there is a high density area at one point, a 30 m walk in the E-W direction will lead into a low density area or vice versa. This is consistent with the contour maps (Figs. 3A, B) where there is a band of high density in the mid tide region so that moving 30 m will move from one zone to another. Most intriguingly of all, the autocorrelogram has picked up a significant autocorrelation in the NE-SW direction. This suggests that at a distance of about 20 m in this direction, significantly similar densities will be found. This directional trend is suggested in the contour maps, where a movement in this direction will pass from one major peak to the other.

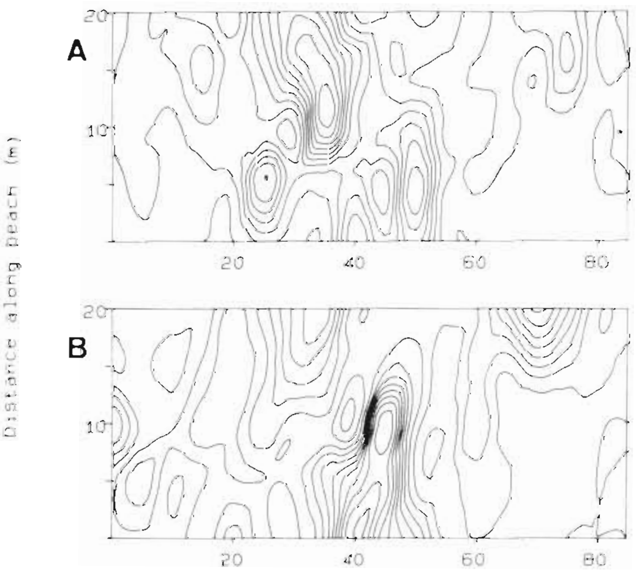

Fig. 3. *Chione stutchburyi.* Contour maps of density at (A) beginning (September 1978) and (B) end (June 1981) of study period. Interval between lines is 10 individuals. Peaks are in the mid-tide region

To summarise, the autocorrelogram shows that the scale of pattern is on the order of 5 to 15 m, that it is anisotropic (that it depends on direction) and that the major features visible on the contour maps are statistically significant.

It is worth pointing out that at no stage have the terms clump, patch or cluster been used. There are no sharply defined aggregations of *Chione stutchburyi*, there is a smoothly varying pattern that suggests an exposure to some environmental gradient (Sokal 1979), which varies anisotropically on a scale of 5 to 15 m.

Temporal pattern

Because the grids are replicated over 3 yr it is possible to look for temporal patterns. There are 2 lines of investigation. The first concerns densities of *Chione stutchburyi:* Is the spatial pattern constant over time? The second concerns the changes between sample periods: Are they seasonal, and is there detectable density-dependence?

The contour maps of densities at the beginning (September 1978) and end (June 1981) of the study suggest that major changes have taken place (Figs 3A, B). The temporal autocorrelogram for the data was calculated (Fig. 4). This is the correlation between successive observations 1, 2, 3 . . . 11 time periods apart, pooled over all grid points. This shows the short-term stability of the data; points 3 mo apart are heavily correlated ($r = 0.54$); but after 18 mo there is very little correlation left. The shape of the autocorrelogram is characteristic of smooth, gradual change. Sokal (1979), talking in spatial terms, refers to it as 'clinal'. At this site at least, the density of *Chione stutchburyi* at a point now is not a good predictor of its density in 3 yr time. Although the spatial pattern may change, as mentioned earlier the spatial autocorrelation structure of the data stayed remarkably constant. That is, the degree to which neighbouring points resemble each other remains constant, even though the overall pattern changes.

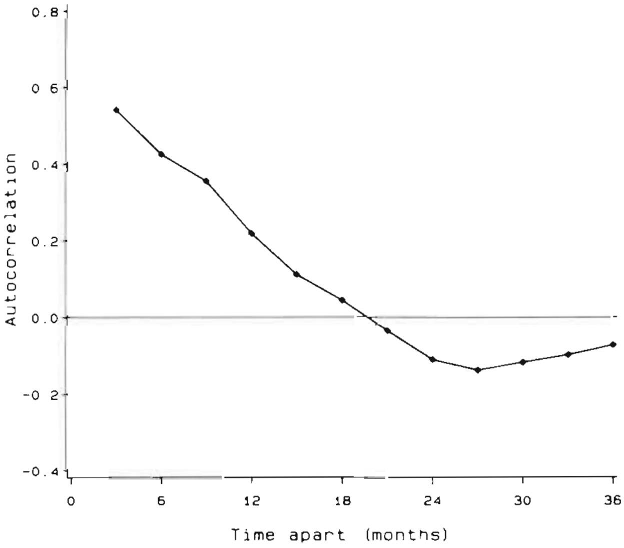

Fig. 4. *Chione stutchburyi*. Temporal autocorrelogram of densities (averaged over all grid points)

The contour maps show that the densities at the grid points changed considerably. It is possible to get some idea of the spatial scale of the factors that produced these changes by investigating the spatial autocorrelation of the changes in density. The spatial autocorrelogram is not presented since there was no statistically significant spatial autocorrelation in the changes in density (critical value of r, for 99.99 % level of significance = 0.411) though those for the 5 m points in the N-S ($r = 0.353$) and E-W ($r = 0.212$) directions are large enough to be plausible (critical value for 95 % = 0.206). This suggests that these changes over 3 yr have operated on a very local scale. The contour maps show that the major changes took place in the mid-tide region.

The changes in density were also investigated for temporal pattern. The differences in density between sequential 3 monthly sampling periods were calculated for each grid point. A temporal autocorrelation was then calculated, pooled over all grid points. A significant negative autocorrelation (–0.372) was found at 3 mo. In other words, on average, if a grid point showed a positive change over one 3 mo period, it could be expected to show a negative one over the subsequent time period. If it showed a negative one in one time period, a positive one would be expected in the next. This raises the possibility that *Chione stutchburyi* was showing local density dependence. In fact, the explanation is simpler. The changes in density over successive time periods, (N_t-N_{t-1}) and (N_{t+1}-N_t), both contain the term N_t. They are therefore correlated. It is simple to calculate the expected correlation that would exist for these data if there were no real relationship between successive changes. It is -0.42! Thus the observed correlation is probably an artifact and a salutary lesson on the dangers of derived variables and non-independence. The other elements of the autocorrelogram do not suffer from this artificial correlation, and show a number of positive and negative values which, though small, achieve statistical significance, suggesting some sort of periodicity. However no clear pattern emerges, so this is not presented. A periodogram (Ripley 1981) was calculated (Fig. 5). A significant ($p < 0.01$) peak is apparent at 3 cycles in 33 mo, i.e. approximately annual. The quarterly mean changes are shown in Table 2. There is clear evidence of a summer decline and an autumn-winter increase. This appears to be associated with a seasonal recruitment into the detectable size classes.

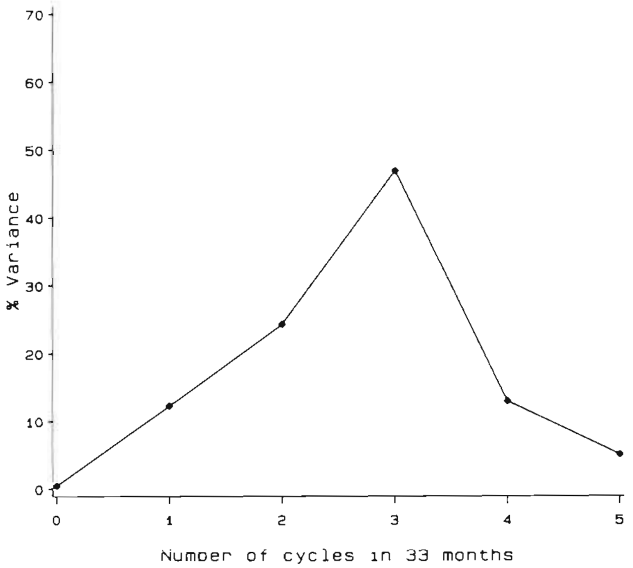

Fig. 5. *Chione stutchburyi*. Periodogram of changes in density, showing a clear peak at 3 cycles in 33 mo, i.e. annual

Table 2. *Chione stutchburyi*. Mean quarterly changes in density at the grid study site over 11 successive intersample periods

Starting dates	Mean (no. m^{-2})	Variance	Standard error	
			Random sample	Stratified sample
Sep 1978	3.74	442.5	2.21	1.43
Dec 1978	−2.32	162.3	1.34	0.84
Mar 1979	4.16	154.3	1.31	0.86
Jun 1979	2.00	187.5	1.44	0.89
Sep 1979	0.73	213.7	1.54	1.03
Dec 1979	−1.37	181.5	1.42	0.89
Mar 1980	2.65	288.8	1.79	1.29
Jun 1980	5.41	389.8	2.08	1.66
Sep 1980	−1.25	766.7	2.92	2.22
Dec 1980	−8.24	446.2	2.23	1.47

DISCUSSION

It is normal in introductory statistics courses and texts for biologists to stress the importance of random sampling and reject naive representative or systematic sampling. Unfortunately this has led to a tendency to reject systematic sampling, which in certain circumstances can be considerably more powerful and convenient than random sampling. When the aim of a study is to investigate the spatial and/or temporal pattern in a measured variable (e.g. counts), the use of random sampling is particularly limiting. In the present study both temporal and spatial patterns were expected. It was therefore important firstly to have a precise mean density of *Chione stutchburyi* at each time period to display differences over time; and secondly to be able to display and analyse the spatial pattern as simply as possible.

When sampling a variable with a spatial pattern, systematic sampling (e.g. grid sampling) will usually provide the smallest sampling error on the mean (Milne 1959, Ripley 1981). There is an exception: if there is periodicity in the pattern of the same wavelength as the distance between samples, then the mean could be very badly affected (Finney 1948, 1950, 1953). As a general rule however, such periodicities are usually obvious to the investigator (ploughed fields, sand dunes etc.), and seldom pose a threat. The chief criticism in the past has been that it was impossible to obtain an accurate estimate of the sampling error of the mean from an unreplicated systematic sample (Southwood 1978, Green 1979, Snedecor & Cochran 1980). However, as shown above there are ways of estimating this error, and though they are usually slightly conservative, they are quite adequate (Milne 1959, Ripley 1981). The estimates will nearly always be better than or equal to those for random sampling (Ripley 1981).

Another advantage of grid sampling is the ease with which spatial patterns can be detected and displayed. Contour maps can be easily prepared for data on a grid, and anisotropic spatial autocorrelograms are most easily prepared for such data, though see Oden & Sokal (1986) for a method for irregularly spaced data. Two-dimensional spectral analysis (Ripley 1981, Ford & Renshaw 1984) is only possible with regular data. We conclude therefore that systematic grid sampling is the appropriate sampling strategy for the investigation of spatial patterns in most situations.

In certain circumstances, as in our pilot study, the range of spatial scales to be sampled is so great that only a hierarchically organised regime is possible. By replicated random sampling at limited number of scales (e.g. sites, transects at each site, stations down the transect) the scale with the greatest variance can be identified using Analysis of Variance. However, this method lacks the resolving power of a correlogram, and is probably best suited to pilot studies.

A more formal use of Analysis of Variance for the detection of spatial pattern is the method of quadrat blocking pioneered by Greig-Smith (1983). This requires a block of contiguous quadrats, and is therefore impractical where the scale of the pattern is large compared with the size of the quadrat. Ripley (1981) shows that even where it can be used, calculating the autocorrelogram followed by a spectral analysis seems to be more efficient.

We suggest that calculation of the 2-dimensional correlogram will usually be the most efficient approach to the analysis of spatial data. We also feel that in most cases when periodicity is not expected, biologists would get a clearer picture of spatial pattern from the correlogram itself than from the corresponding spectral analysis.

Most studies on intertidal invertebrate population distribution patterns have indicated that along-shore variation in density distribution is minimal (Hedgepeth 1957, Newell 1979) but subtle variability in physical features and/or variability in recruitment success may create more heterogeneous distribution patterns. Edwards & Huebner (1977) have strongly cautioned against the extension of classical benthic population models (based upon hard sediment studies) to this more subtly complex habitat. It is clear from the pilot study data that a high degree of within-location density variation in population distribution occurs for *Chione stutchburyi* in Ohiwa Harbour. The grid data shows the existence of considerable spatial heterogeneity over comparatively short distances. From the spatial autocorrelogram we can suggest that this heterogeneity is consistent with factors operating on a scale of less than 30 × 20 m. The temporal correlogram for densities indicates that these factors operate on a 1 to 2 yr time scale. The periodogram of the quarterly changes in density further suggest a seasonal component. Interestingly, though the patterns of density as shown by the contour maps changed over time, their scale as described by the autocorrelograms remained constant.

In order to investigate experimentally the factors operating, these differing spatial and temporal scales have to be taken into account. Fine-scale variability in population distribution patterns may be of greater importance than realised by earlier workers. It seems that most theories on population distribution are based on broad-scale sampling studies and such an approach can describe only broad trends. To gain insight into the proximal factors determining population regulation and distribution, any such study should consider the fine-scale distribution patterns in survival, recruitment and growth. Use must be made of contour maps and any experiment should run for at least 1 yr, preferably 2 or more, to detect the changes which normally operate. A series of experiments examining these factors will be presented by Blackwell & Choat in a planned publication.

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