

IMPACTS ON SOFT-SEDIMENT MACROFAUNA: THE EFFECTS OF SPATIAL VARIATION ON TEMPORAL TRENDS¹

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Abstract. Long-term studies provide useful insight into the functioning of populations and communities. Gaining a long-term perspective may be important in providing background information upon which BACI (Before–After–Control–Impact)-type impact studies can be designed or in identifying many types of impact, particularly those of a large-scale and diffuse nature. Although marine soft-bottom communities commonly exhibit patchy distributions, in many long-term studies few replicates, from each site, are collected on each occasion. To illustrate potential problems encountered when spatial variation confounds temporal patterns, we use data collected from a monitoring program of the intertidal sandflat communities of Manukau Harbour, New Zealand. Randomization techniques were used to generate possible temporal sequences, based on a sample size similar to that used in many long-term studies. In the generated sequences the timing and size of annual density changes were often different from the observed sequence, and indications of trends in density were often missed. In order to provide accurate descriptions of temporal variability in the soft-bottom communities of estuaries and coastal embayments, low bias and highly precise density estimates from each sampling occasion are required.

Key words: *BACI-type studies; benthic monitoring programs; environmental impact analysis; large-scale impacts; macrofauna; Manukau Harbour, New Zealand; sandflats; spatial heterogeneity; time series.*

INTRODUCTION

Many aspects of environmental degradation can only be detected and accurately assessed when there are sufficient data to reveal long-term trends compared to short-term fluctuations. Without a long-term perspective natural fluctuations may be mistakenly attributed to human impacts. Impact studies should ideally be able to document density changes and demonstrate causality (Underwood and Peterson 1988), and treating a proposed impact as a large experiment (e.g., using BACI [Before–After–Control–Impact]-type designs) will be appropriate in some situations (Hilborn and Walters 1981, Underwood 1991). However, an experimental approach is often impractical when considering diffuse and complex impacts that operate over large spatial and temporal scales (e.g., urban runoff, habitat disturbance by fishing), especially where pre-impact assessment is not possible (Livingston 1987, Parker 1989, Tilman 1989). In these situations the use of time series data is particularly relevant to identify both trends and changes in cyclic data together with broad correlative relationships. Well-developed statistical tests exist for time series analysis (Chatfield 1980) and are frequently used to assess trends in pollution monitoring (e.g., see special issue of *Water Resources Bulletin*, Volume 21 (4) 1985) and to provide ecological insights (Jassby and

Powell 1990). To obtain the most from time series analyses, the data used should be as unbiased and precise as possible.

One factor that can markedly influence time series analyses in marine macrofaunal studies is spatial variation caused by aggregated distribution patterns. 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 the interpretation of the data (Greig-Smith 1983). However, even if sampling is conducted on an appropriate scale, poor estimates of abundance can result if insufficient samples have been collected to account for patchiness. To obtain accurate density estimates, some knowledge of the spatial arrangement of the organisms to be sampled must be acquired. Identifying spatial patterns in marine soft-sediment habitats is difficult, as the density of many species is not apparent from the sediment surface. Techniques are available however, that enable patterns to be described from sediment samples taken from known locations (e.g., Legendre and Fortin 1989, Legendre 1993). Where patterns have been quantitatively assessed in soft-sediment environments, homogeneous density patches ranging from 0.01 to 100 m radius have been described (Eckman 1979, McArdle and Blackwell 1989, Thrush et al. 1989, Thrush 1991, Trueblood 1991).

The potential for spatial variation to confound assessments is often an important consideration in short-

¹ Manuscript received 12 June 1992; revised 16 April 1993; accepted 7 May 1993.

TABLE 1. Sampling strategies used in long-term studies of soft-bottom macrofauna. Presented is a haphazard selection of material from peer-reviewed publications.

No. of sites	No. of replicates	Sample area (m ²)	Comment on sites	Time period	Reference
8	5	0.05	Located >1 km apart	Every 3 mo over 1 yr	Lincoln Smith 1991
14	3	0.1	Located >1 km apart	Twice over 10 yr	Josefson and Rosenberg 1988
12	4	0.05	Located >1 km apart	Every 3–6 mo over 4 yr	Jones 1990
2	5	0.0104	Different localities	Monthly over 10 yr	Barnett and Watson 1986
3	5 or 10 or 20	0.1	Different depths	20 times over 4 yr	Persson 1983
Varying (12–21)	3–4	Varying (0.1, 0.12, or 0.02)	Located >1 km apart and often different habitats	4 times a year for 13 yr, with some sites 10 times a year for 4 yr	Holland et al. 1987
4	5–10	0.01	Located >1 km apart and range in habitat from mud and silt to sand	Every 3 mo for 6 yr	Lie and Evans 1973
2	4	9.6×10^{-4}	Mud and sand habitats	Monthly for 3 yr	Coull and Fleegeer 1977
3	3	0.09	Located >1 km apart	Monthly for 11 yr	Flint 1985
2	3–4 2	5.7×10^{-4}	Mud and sand habitats	Monthly for 8 yr (1972–1980) Fortnightly (1980–1983)	Coull 1985
5	10	0.025 or 0.08	Located >1 km apart	Mainly every 2 mo for 5.5 yr	Hines et al. 1987
60–74	4–5	0.01	Located >1 km apart	Erratically for 5 yr	Govaere et al. 1980
3 or 6	12	4.6×10^{-3}	Located >1 km apart	Weekly for 3 yr Monthly for 12 yr	Livingston 1987
1	4 or 10	0.03 0.01		Every 2–3 mo for 10 yr	Ibanez and Dauvin 1988

term studies, where the precision of within-site sampling is emphasized (see Osenberg et al. 1994). In contrast, an examination of the methods used in a variety of long-term macrofaunal studies (Table 1) reveals that typically <5 samples are collected from within a site. Sites are usually situated kilometres apart and/or in different habitats, indicating that in most cases each site was considered to be representative of a relatively large area. In many of the studies, less emphasis has been placed on the number of within-site samples, possibly under the belief that increasing the number of sampling occasions increases the power and conservativeness of future statistical tests. Unfortunately, temporal autocorrelation, which is common in environmental data, can lead to frequently collected samples not being independent (e.g., see Edwards and Coull 1987). This raises the question of how best to apportion effort in accounting for spatial and temporal variability within a site. For many long-term macrofaunal studies effort may best be spent obtaining accurate density estimates at each time to prevent spatial variation from confounding the temporal sequence.

In this paper we use data collected from a monitoring program of intertidal sandflat communities to show how spatial variation can influence observed time series. We illustrate some of the problems likely to occur when analyzing and interpreting time series data based on sampling strategies that do not account for spatial

variation. No attempt has been made to interpret the ecological significance of the temporal sequences presented. In many of the examples given, such interpretations would be inappropriate until a much longer time series has been collected. Although all our examples are based on density estimates of macrofaunal populations, similar problems will occur with any other environmental variable that is patchily distributed.

METHODS

The monitoring program

Manukau Harbour is a large (340 km²) shallow inlet, adjacent to Auckland, on the west coast of the North Island of New Zealand. Intertidal sandflats constitute ≈40% of the area of the harbor and are commonly used for recreation and food gathering. The monitoring program was established in 1987 to provide managers with some stocktaking of the resource under stewardship and to create a framework against which more process-orientated studies could be conducted (e.g., Pridmore et al. 1991, Thrush et al. 1991).

Data on macrofaunal populations are collected every 2 mo from six sites, each 9000 m², situated on mid-tide sandflats, around the harbor. The six sites (AA, CB, CH, EB, KP, and PS) are situated >1 km from each other; their geographic location and a description of the macrobenthic community structure is given in

Pridmore et al. (1990). Each site is divided into 12 equal sectors. On the first sampling occasion (October 1987 at all sites except CB, which was first sampled on December 1987) 36 cores (13 cm diameter, 15 cm depth) were collected from each site (3 randomly located within each sector) to establish the optimum sampling intensity for future visits. On all subsequent occasions 12 cores have been collected from each site (1 randomly from each sector). The decision to collect 12 cores from each site was determined by a process of balancing effort against precision (Bros and Cowell 1987, Hewitt et al. 1993). As of June 1991 two sampling occasions have been missed (October and December 1988). After collection, samples are sieved (500- μ m mesh) and the residue fixed in a 5% formalin and 0.1% rose-bengal solution in seawater. In the laboratory macrofauna are sorted, identified to the lowest possible taxonomic level, counted, and preserved in 70% alcohol.

Data analyses

For the purposes of this paper each site is treated separately. The term "population" is thus used to refer to an individual species at an individual site. Analyses were only performed on populations that exhibited mean abundances ≥ 1 individual/core on most sampling occasions (i.e., > 16 of the 21).

Spatial patterns were investigated using the program SAAP (Wartenberg 1989) to construct correlograms and test for overall significance of both the correlogram and its individual points. Correlograms were constructed from values of Moran's I spatial autocorrelation coefficient calculated for each 5-m distance class, i.e., those samples lying within 0 to 5 m of each other, 5 to 10 m of each other, etc. Significant coefficients indicate that a spatial pattern exists, and allow estimates of the mean patch size to be made. To aid interpretation of the correlograms, three-dimensional plots of species abundance at a site were generated. Only some of the plots, which illustrate particular patterns, are presented, as this analysis is simply used to illustrate the types of patterns that can affect spatial variability.

In order to provide generalizations of how spatial variation can confound temporal sequences, we used the ratio of spatial to temporal variation to allocate individual populations to three categories (i.e., spatial variability less than, equal to, or greater than temporal variability). Allocation to the first or last category was based on spatial variability being less than half or greater than twice the temporal variability, respectively; populations not falling within these two categories were considered to exhibit spatial variation roughly equivalent to temporal variability. Two techniques were utilized to create the categories. First, we compared the magnitude of the range in abundance exhibited on each sampling occasion to the range in the mean abundances

over time. While this technique made no assumptions about the data, problems may have arisen if the range was not a good description of variation or if estimates of temporal variability were confounded by utilizing means from each sampling occasion. To assess the importance of these problems, the second technique we utilized involved estimating and comparing between-group variance (temporal variability) and within-group variance (spatial variability) using one-way ANOVAs for each population (log-transformed where appropriate). Approximately the same number of populations were found in each category using the two methods. A few populations close to the category boundaries switched depending on which technique was used.

To determine how our interpretation of temporal patterns may have been affected if fewer samples were collected on each occasion, we generated 100 unique time-series plots for each population based on a sample size of four, using randomization techniques without replacement from the samples available on each occasion. A sample size of four was chosen as 3–5 samples are commonly collected to quantify macrofaunal abundance in long-term studies (Table 1). We used these time-series plots to illustrate the changes in temporal patterns (e.g., timing and height of peaks) that can occur with decreased precision on each sampling occasion. This is done visually because it is not simply the increased level of variation with decreased sample size that is important but also the inability to identify features of the temporal sequence that can be attributed to biological/environmental events (e.g., recruitment periods). We also assessed the increased variation that can occur with decreased precision on each sampling occasion by testing for linear trends in the time series.

RESULTS

Spatial patterns of the macrobenthic populations were investigated at sites on the first sampling occasion only. For most of the populations studied (i.e., 45 of the 58 with mean densities > 1 individual/core), significant spatial correlograms were obtained. Fig. 1 illustrates the variety and complexity of spatial patterns that contribute to variations in density estimates within the 9000-m² sites.

At each site the number of individuals of a given species in a core commonly varied by an order of magnitude. Coefficients of variation on the first sampling occasion frequently exceeded 0.75 (Table 2). On subsequent sampling occasions, coefficients of variation for many (55%) of the populations varied little from those initially determined (e.g., Fig. 2, Table 3). Of the remaining populations, most (i.e., 85%) exhibited wide variations in the coefficient of variation because of low (< 1 individual/core) densities on one or more occasions. Approximately 86% of the populations studied have exhibited spatial variation which was equal to or greater than the observed temporal fluctuations in mean

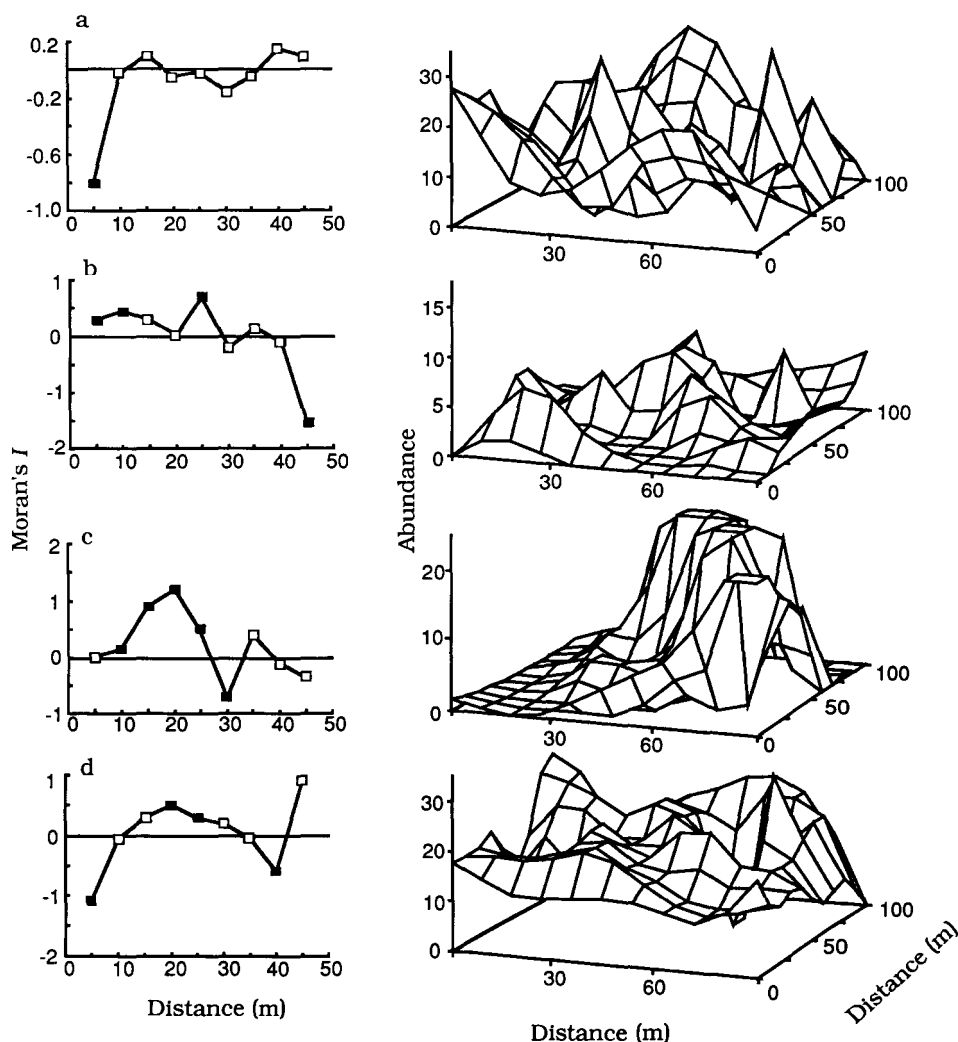


FIG. 1. Spatial autocorrelograms and corresponding three-dimensional plots (based on 36 samples from the first sampling occasion of the intertidal sandflat communities of Manukau Harbour, New Zealand) showing: (a) small-scale heterogeneity (*Heteromastus filiformis* at site EB); (b) homogeneous density patches of 5–10 m radius (*Goniada emerita* at CH); (c) large patches conferring a gradient (*Nucula hartvigiana* at PS); (d) gradient superimposed on small-scale heterogeneity within patches of 20–25 m radius (*Tellina liliana* at AA). Filled squares represent significant Moran's I .

density (Table 4). The ratios of temporal to spatial variation show no relationship with the coefficient of variation from the first sampling occasion (Fig. 3), indicating that the magnitude of spatial to temporal variation observed is not a product of the precision achieved by our sampling strategy.

Most populations exhibited density variations in time similar to or less than those in space. Populations that exhibited greater temporal than spatial variation usually showed distinct annual fluctuations in density (e.g., species with high levels of annual recruitment). Density variation in space was greater than that in time for only 33% of the populations. These populations did not form any distinct functional grouping based on mobility, size, or life history characteristics; however, bi-

valves were not represented. All populations exhibited very low levels of temporal variation, and the density distributions at any one time usually exhibited high maximum ranges relative to the 75th-percentile ranges, i.e., spatial patterns that include a small number of very high- or low-density patches.

Fig. 4 shows some of the time sequences generated for a population that to date has exhibited similar scales of spatial and temporal variation. Although data from only one population are used to illustrate our point, similar results were obtained for all other populations that exhibited similar scales of spatial and temporal variation. Routine monitoring with a sample size of 12 cores has established that the polychaete *Heteromastus filiformis* at site CB during the winter (June–

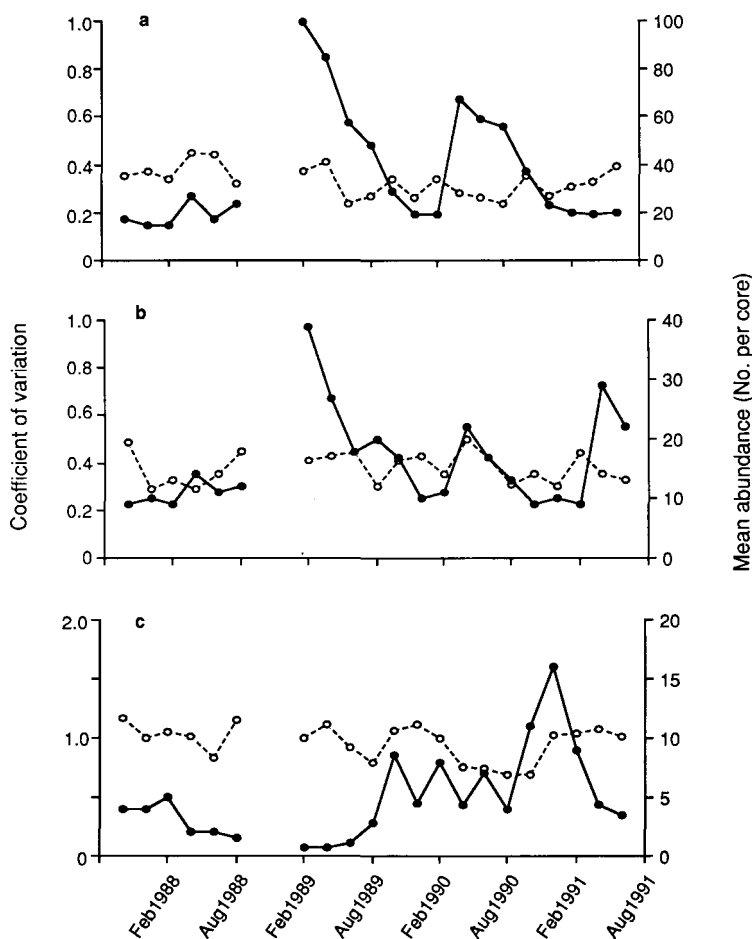


FIG. 2. Plots of mean abundance (—●—) and coefficient of variation (---○---) over time: (a) *Tellina liliana* at site AA; (b) *Tellina liliana* at PS; (c) *Nucula hartvigiana* at PS.

October) commonly attains a mean density (± 1 SE) of 17 ± 1.7 individuals/core (Fig. 4a). In 3 of the 4 yr sampled, the observed population has declined by at least 70% to <5 individuals/core in February/March (Fig. 4a: arrows). Of the 100 time sequences generated using a sample size of four, only 28 closely mimicked this pattern, with abundances in winter in the range of 17 ± 3.4 individuals/core and a decline of at least 50% in February/March (e.g., Fig. 4b). An additional 20 time sequences adequately described the three declines in population abundance but showed highly variable (i.e., $> \pm 20\%$) densities during the winter months (e.g., Fig. 4c). Fifty-two of the time sequences generated (e.g., Fig. 4d) showed little sign of the temporal patterns observed using a sample size of 12.

Fewer discrepancies in the generated time sequences were noted for the seven populations in which spatial variation was much smaller than the observed temporal fluctuations. For example, Fig. 5 shows some of the time sequences generated for the bivalve *Tellina liliana* at site AA. Routine monitoring with a sample

size of 12 cores indicated that little or no recruitment of *Tellina liliana* occurred during 1988 (Fig. 5a). Two periods of high recruitment were observed in February 1989 (or earlier) and April 1990, with the latter period being at least 30% lower than the preceding year. After each recruitment period the densities gradually declined to ≈ 25 individuals/core. Of the 100 time sequences generated, 44 closely mimicked the observed time sequence (e.g., see Fig. 5b): that is, no peak or

TABLE 2. Distribution of coefficients of variation calculated from the first sampling occasion for populations from individual sites.

Coefficient of variation	No. of populations
<0.5	4
0.5–0.75	11
0.75–1.0	11
1.0–1.25	10
1.25–1.5	4
>1.5	5

TABLE 3. Maximum change in coefficients of variation over time (as a percentage deviation from the coefficient of variation calculated on the first sampling occasion) for populations from individual sites.

% deviation of coefficient of variation	No of populations	Cumulative % of populations
<50	7	16
50–60	10	38
60–70	8	55
70–80	7	71
80–90	2	75
90–100	2	79
100–200	6	92
200–300	1	94
>300	3	100

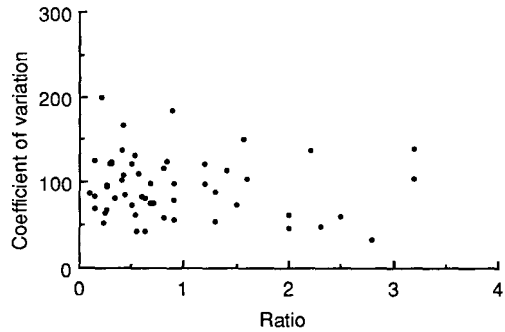


FIG. 3. Plot of coefficient of variation for the first sampling occasion vs. the ratio of temporal to spatial variability from one-way ANOVAs for individual populations.

gradual decline in abundance in 1988, maximal densities occurring in February 1989 and April 1990, followed on each occasion by a slow decline to 15–35 individuals/core and the 1990 maximal density being 20–40% less than that estimated the preceding year. The remaining 56 generated time sequences each depicted little or no recruitment in 1988 with periods of recruitment in 1989 and 1990, but either the timing (e.g., Fig. 5c) or magnitude (e.g., Fig. 5d) of recruitment was markedly different.

As expected, the time sequences generated for populations with relatively high spatial variation compared to temporal variation were the most divergent. Fig. 6, for example, shows some of the time sequences generated for the isopod *Exosphaeroma falcatum* at site PS. Routine monitoring with a sample size of 12 indicated that from February 1989 to October 1990 the mean density of this population was 40% lower than that observed at the beginning (October 1987–August 1989) and end (October 1990–June 1991) of

the time series (Fig. 6a). Few (<15%) of the generated time sequences however depicted a 30–50% decrease in mean density during this period (e.g., Fig. 6b). Most (70%) of the generated time series showed no decline in abundance at all, or if a pattern was apparent it bore little resemblance to that obtained with a sample size of 12 (e.g., Fig 6c). This increasing divergence of the generated from the observed time sequence with increasing spatial relative to temporal variability occurred irrespective of the size of the coefficient of variation of the observed population.

Spatial variation was also found to influence our ability to quantify step changes in abundance over time and to detect temporal trends. For example, routine monitoring with a sample size of 12 established that *Heteromastus filiformis* declined in abundance by 71% between August 1989 and February 1990 (Fig. 4a). Of the 100 time sequences generated, only 31 indicated a drop in abundance of 65–75% during this period; 17 indicated a change of <60%, whilst 21 indicated a

TABLE 4. Details of spatial and temporal variability of populations used to illustrate the effect of spatial variation on observed temporal sequencing (interquartiles are given in parentheses bounded by maximum and minimum values). Percentage of similar types of populations found in the study are also given together with the range of the ratios of temporal-to-spatial variability calculated from ANOVA.

Population	Site	Spatial pattern October 1987 (N = 36)	Spatial range October 1987 (N = 36)	Temporal range of means October 1987– June 1991	Type of population	% of pop- ula- tions	Range of ratios of temporal- to-spatial variability
<i>Tellina liliana</i>	AA	Small scale heterogeneity with patches of 20–25 m radius	8–(12–20)–36	15–(18–58)–100	Spatial variation less than temporal variation	14	2.0–3.2
<i>Heteromastus filiformis</i>	CB	No pattern at scale of sampling; Significant variance-to- mean ratio	3–(9–20)–45	2–(10–19)–21	Spatial variation equal to temporal variation	53	0.50–2.0
<i>Exosphaeroma</i> spp.	PS	Patches of 10 m radius	0–(2–8)–22	0–(1–5)–10	Spatial variation greater than temporal variation	33	0.10–0.50

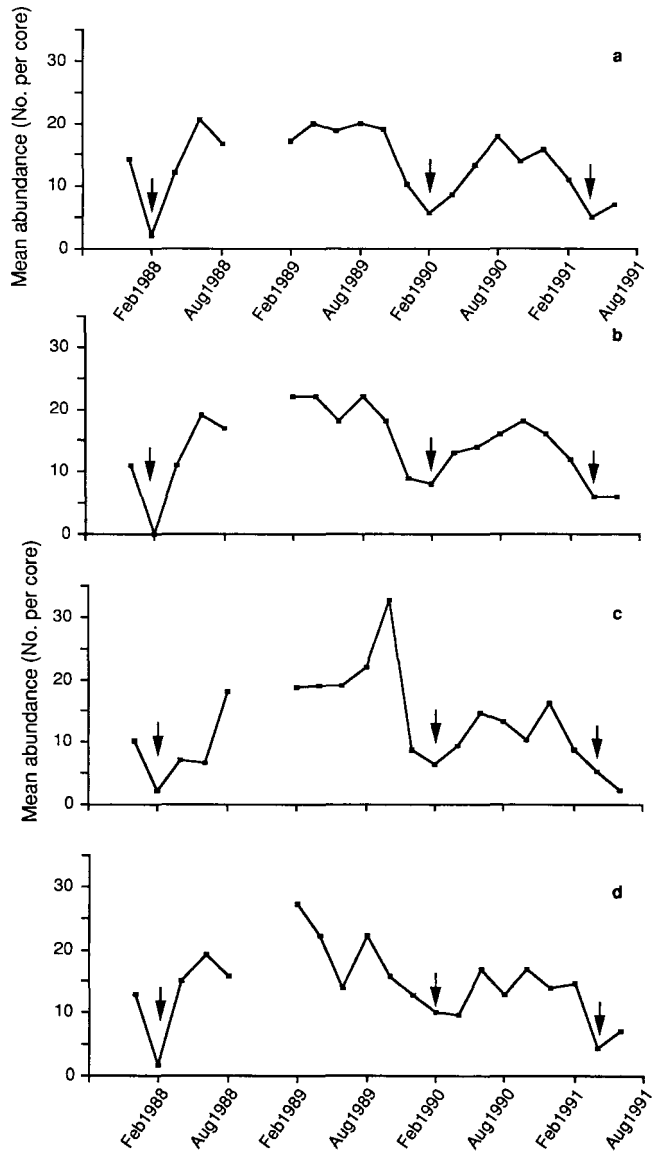


FIG. 4. Plots of the observed time series (a), and selected examples of randomly generated time series (b–d), of *Heteromastus filiformis* density at site CB. Arrows indicate events discussed in the text (see *Results*).

decrease of >80%. For populations, such as *Tellina liliiana* at site AA, that to date have exhibited low spatial relative to temporal variability, the quantification of step changes was much less affected by sample size. For example, routine monitoring has indicated that between February 1989 and February 1990 *T. liliiana* declined in abundance by 80% (Fig. 5a). Seventy-one of the 100 time sequences generated indicated a decrease in abundance of 75–85% during this period; only 6% indicated a change of <70% or >90%.

Although we do not recommend that analysis for cyclic patterns or trends be conducted with such a short time series, we illustrate how analysis of trend may be

affected by spatial variation. Few of the populations sampled have shown a general increase or decrease in abundance through the short time span of the monitoring program. Data for the isopod *Exosphaeroma falcatum* at site PS (Fig. 6a), however, can be used as an illustration. In the case of *E. falcatum* an apparent decline occurred between October 1987 and August 1990. Using autocorrelation tests (Chatfield 1980), no significant first-order temporal autocorrelation was found for this population. Using linear regression, a significant decline ($r = -0.71$, $n = 17$, $P = .0021$) can be detected using the routine monitoring data. In only 19 of the time sequences generated for this highly

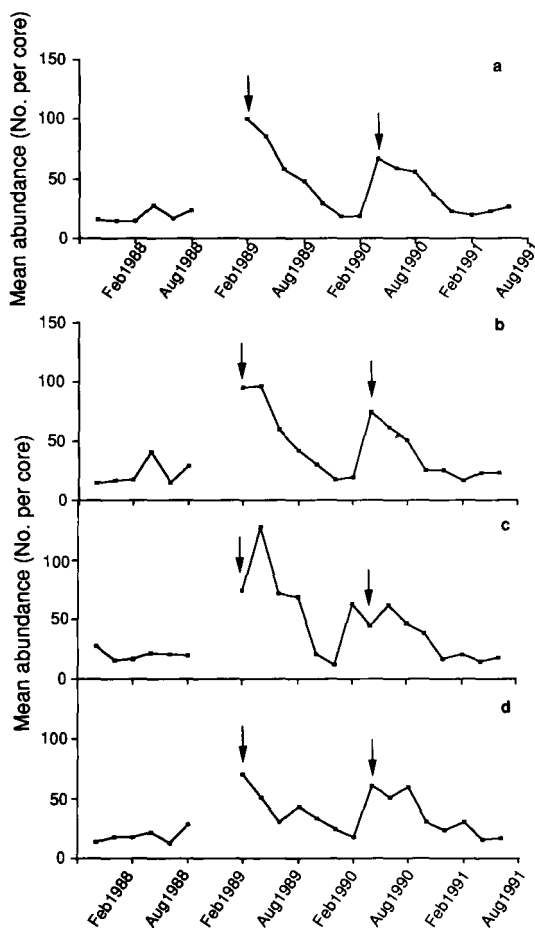


FIG. 5. Plots of the observed time series (a), and selected examples of randomly generated time series (b-d), of *Tellina liliana* density at site AA. Arrows indicate events discussed in the text (see Results).

patchily distributed population could a significant linear trend be detected during this period.

DISCUSSION

Macrofaunal populations within the 9000-m² intertidal sandflat sites mostly exhibited patchiness on various spatial scales. However, most populations that exhibited density variations in time similar to or greater than those in space usually showed distinct annual fluctuations in density. When we reduced sample size to a level similar to that frequently used in other long-term studies (Table 1) we were able to illustrate various anomalies. The timing and size of annual density changes often shifted, and trends in density were often missed. However, temporal patterns of populations exhibiting strong annual cycles frequently remained consistent even when the precision achieved on each sampling occasion was reduced by decreasing the sample

size. In contrast the largest anomalies were apparent for populations where spatial variation was much greater than temporal.

We have illustrated potential problems using data from within single large sites (9000 m²) and from a short time series. However, the problems mentioned above are unlikely to disappear in more complex sampling programs that encompass different scales of variation.

A crucial part of the design of a monitoring program, once the appropriate time scale has been determined, is choosing the sample size. This is usually done by examining the relationship between spatial variation and sampling intensity from data collected in a pilot survey. This approach contains two potential problems. First, it assumes that the true variance of a population will not change over time (e.g., with recruitment). The consistency in the coefficients of variation of many of the populations from the Manukau Harbour sites (Table 3) indicates that information gained during pilot sampling is likely to be relevant over time, even for populations that show large annual density fluctuations (Fig. 2). Second, commonly cited methods for the determination of sample size require specification of a level of difference that needs to be detected (e.g., Andrew and Mapstone 1987). But it may be difficult

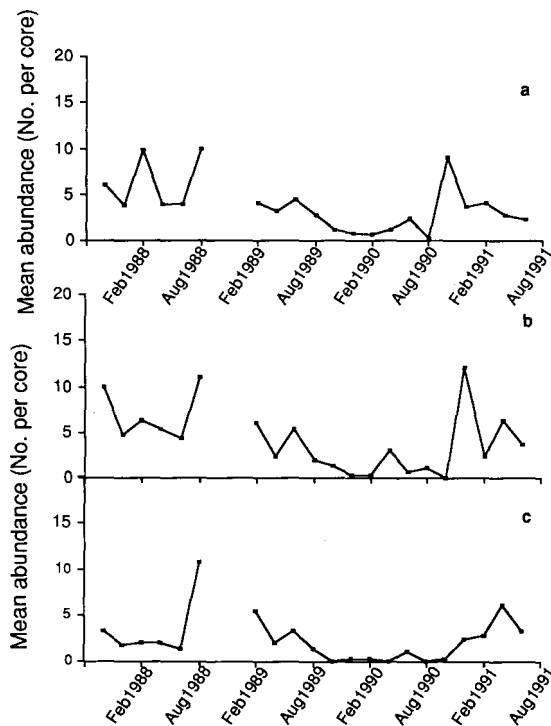


FIG. 6. Plots of the observed time series (a), and selected examples of randomly generated time series (b-c), of *Exosphaeroma falcatum* density at site PS. See Results for further explanation.

to decide whether 20%, 50%, or 100% changes in mean density will be ecologically significant. In making these kinds of decisions the relationship between spatial and temporal variance comes into play; a standard error of 20% might be sufficient if the population varies temporally by much more than this, or may be quite insufficient if the temporal variation is small. When designing a time series program the question then becomes, "what precision in density estimates at a site is required to prevent spatial variation from confounding the temporal sequence?", and the magnitude of the ratio of spatial to temporal variability becomes a dominant factor. Unfortunately, the magnitude of this ratio is unknown at the start of the time series, and many areas of the world will not have background information on temporal patterns of species available. Thus methods for determining sample size that allow recognition of when the increase in precision is low relative to the increase in sampling effort may be most appropriate. Once the time series program is under way, modifications can be made to the sampling strategy in light of the developing temporal sequence.

Unpredictability in density estimates over time suggests the importance of stochastic processes, at least at our level of observation (Frost et al. 1988, Rahel 1990). Where spatial variation contributes to apparent unpredictability this can influence environmental management decisions. For example, populations or communities may be considered too unpredictable for effective management or, for species with variable spatial and temporal dynamics apparently driven by stochastic processes, it may be difficult to identify localized extinctions and their relation to impact affects. Moreover, direct analysis of variability is itself useful in, for example, assessing the relative importance of processes operating on different scales. If abundance varies among sites but is consistent at each site over time, then a major influence on processes is associated with the sites. Conversely, if abundance shows strong variability among years at sites but a high degree of consistency in each year across sites, then a major influence of a large-scale factor (e.g., weather) is implicated (Kratz et al. 1987). Time series analysis is useful in evaluating the influence of impacts on population and community characteristics (e.g., persistence) because of the effect that observational scales in space and time have both on these characteristics and our ability to describe them (Connell and Sousa 1983, Dayton and Tegner 1984, Weins 1989).

Separating trends from greater-than-annual cycles will always be limited by the length of the time series (e.g., Loftis et al. 1991). However, confidence in the biological interpretation of events and the recognition of unusual events can yield potentially useful ecological insights (Carpenter 1988). Monitoring is inherently retrospective; therefore it is important to identify events that are likely to warrant remedial action before a crit-

ical and potentially irreversible level is reached. The ability that a time series gives of identifying patterns can be useful in this and in the design of associated experimental studies. For example, periods of bivalve recruitment identified in Manukau Harbour have been used to time studies on pesticide impacts (Pridmore et al. 1991). The ability to confidently identify repeatable density fluctuations is particularly important if the determination of temporal changes (e.g., level of recruitment) are deemed a sensitive measure of impact (Underwood 1991).

Ultimately it is important that the design of a time series or impact study defines specific and answerable questions, relevant to information users and environmental managers, so that appropriate data is collected within logistic and cost constraints. In the case of generating a time series, design is particularly important because of the long-term commitment and cost. If time series data are used, either to provide background information or for impact assessment, it is important that patterns and trends can be inferred confidently. It may be possible to reduce the overall cost of collecting time series data by pooling within-site samples and subsampling the aggregate. While this approach would not allow estimates of spatial variability to be generated, good estimates of mean density may be achieved with reduced effort. Whether this approach is appropriate will depend on the study objectives. It is likely to be relevant only when common species are to be studied and errors due to subsampling are small. While estimates of spatial variability may not be important in tests for temporal trend, the information may still be useful (e.g., demonstrating the consistency of coefficients of variation over time). Moreover, spatial variation should not be considered as noise, but as an important component of population dynamics. Information on the consistency or change in spatial patterns may provide useful ecological insights.

We have illustrated the problems that can arise in inferring patterns or testing for trends in time series when insufficient effort is expended in accounting for spatial variation. Our analysis indicates that the crucial feature is the relative magnitude of spatial and temporal variation. In Manukau Harbour this often varies for the same species at different sites or for different species at the same site. Thus it is not appropriate to generalize on the levels of variation that may be expected for particular species or groups of species. Sample sizes for each site must be chosen in such a way that low-biased and highly precise estimates are obtained on each sampling occasion. In general we do not recommend that any trade-off occur between the number of times a site is sampled and the number of within-site replicates collected. When sufficient data have been collected, analysis of the relative magnitude of spatial and temporal variation may indicate possible modifications to the sampling strategy.

ACKNOWLEDGMENTS

The monitoring program that provided data for this study was funded by the Auckland Regional Council—Auckland Regional Water Board. We thank Craig Osenberg, Russ Schmitt, Bob Whitlatch, and an anonymous reviewer for comments on early drafts of this manuscript.

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