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Small-scale patterns and processes in a soft-substratum, intertidal community[1]

by James E. Eckman[2]

ABSTRACT

Experimental manipulations and direct observations were combined to study small-scale dispersion patterns and their causes in an intertidal sand-flat community numerically dominated by sessile and sedentary tube dwellers. Individuals of several species exhibited gregariousness at scales as small as one centimeter. Experiments in which needles were placed in sediments to simulate animal tubes suggested that organisms are affected by patterns of flow which change over distances of several millimeters to a centimeter. At most sampling times, in a single transect of contiguous-core samples two or more species exhibited a common, larger-scale ($\cong 10$ cm) periodicity in abundances, which could not be attributed to direct biological interactions. An alternative mechanism affecting community dispersion patterns is hypothesized *a posteriori*: organisms may be affected by locally varying hydrodynamic environments produced by bed ripples. The resulting periodic dispersion pattern apparently persists after ripples have disappeared. These results suggest potential problems with commonly used sample sizes and manipulative techniques. Scales of environmental heterogeneity relevant to an individual may be too small to be resolved using traditional benthic sampling methods. Studies in which data are collected at arbitrary scales homogenize spatial patterns that reflect small-scale interactions, processes and responses, and could seriously affect between-sample variability, thereby leading to spurious conclusions regarding the pattern and control of community structure.

1. Introduction

Ecological studies of marine, soft-substratum benthic communities traditionally have been observational. Manipulative experimentation has only recently become more common, although it may be necessary for determining and documenting the mechanisms that structure a community (Schoener, 1974; Connell, 1975; Paine, 1977) and the scales at which these mechanisms operate.

In most observational and manipulative studies, data have been collected using devices that typically sample at linear scales exceeding a few centimeters (e.g., grabs,
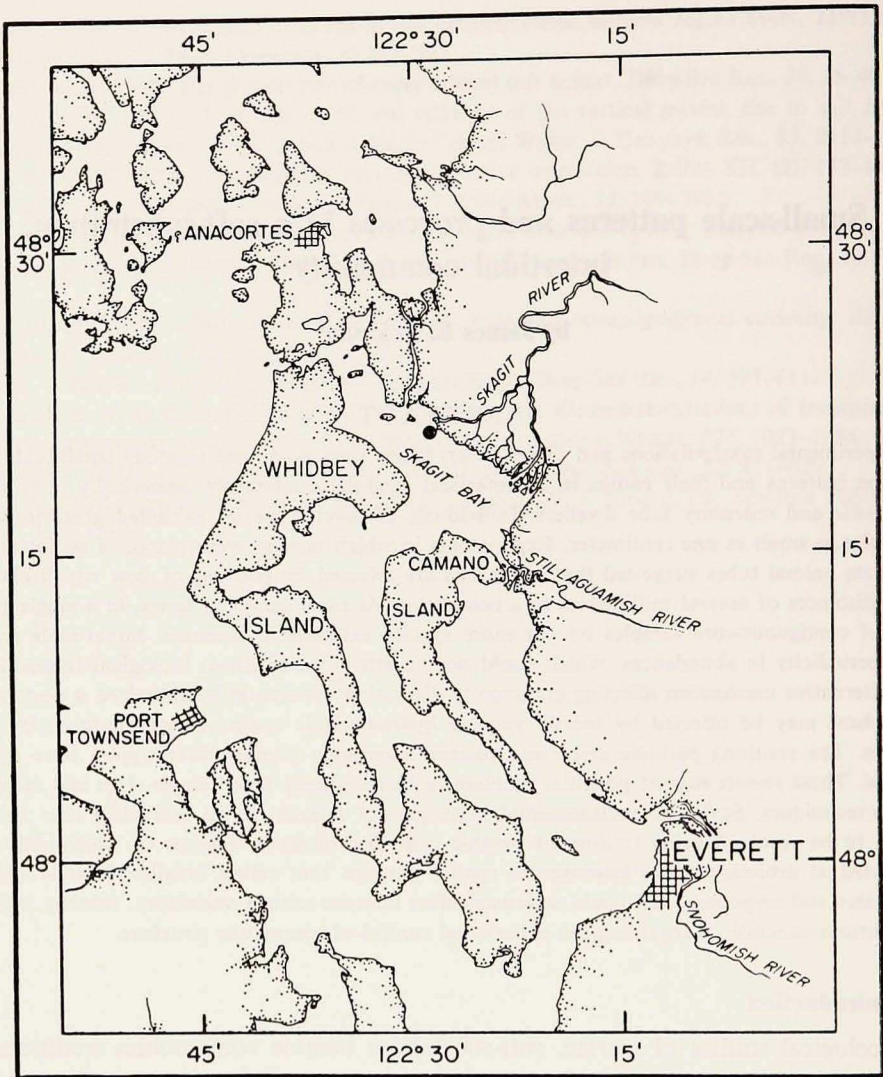
Figure 1. Map of northern Puget Sound showing the location of the study area (dot) in Skagit Bay.

box cores, most hand-operated cores). Such sampling devices generally collect many individuals of a given meiobenthic or small macrobenthic species per sample, resulting in a loss of potentially important spatial information. Since, in the extreme, the most information an investigator can obtain regarding a species' dispersion pattern is to know the exact location of every individual in space and time, a logical approach to sampling design would be to sample at a scale approaching the size of an individual (e.g., Jumars, 1975). Such an approach would maximize information on

species' dispersion patterns, given that enough samples are taken, and would provide a means for discerning mechanisms operating at small scales which affect community structure. For example, among sessile and discretely motile organisms (*sensu* Fauchald and Jumars, 1979) important biological processes such as competition and predation must operate at scales approaching the sizes of individuals.

Manipulative experiments were combined with direct observations to test for the existence and causes of nonrandom species' dispersion patterns at these relevant, small scales (i.e., millimeters to tens of centimeters) in an intertidal, sand-flat community in Skagit Bay, Washington (Fig. 1). Recruitment experiments were performed in order to study the sequences and mechanisms of development of such patterns during the critical (cf., Connell and Slatyer, 1977) early stages of succession. The community is numerically dominated by small, sessile and discretely motile tube dwellers (Table 1); consequently, any single inter-individual interaction (either intra- or interspecific) should affect the community locally (i.e., at distances less than 2 or 3 cm). Nonbiological processes which may be of local importance to the community include hydrodynamic processes operating at the benthic boundary. Specifically, organisms which feed and interact at the sediment-water interface might be affected by local patterns of flow. Flow patterns may be influenced, for example, by projections from the bed such as shell fragments, stones, or individual animal tubes (Lonsdale and Southard, 1974).

The study area (+2 m from Mean Lower Low Water [MLLW]) is composed of fine sand, usually with a thin mud veneer. The bed contains a dense mat of animal tubes (of order 10^5 m^{-2}), many of which protrude several millimeters above the bed. The beach has an extremely low slope (of order 10^{-3}). Tidal inflow begins as a

Table 1. Characteristics of species sampled in contiguous-core transects at Skagit tidal flat.

Species	Size Range (cm)	Basic Feeding Mode and Relative Motility
Eteone longa (phyllodocid polychaete)	0.1 -4.0	"pumping" carnivore; discretely motile
Pseudopolydora kempi japonica (spionid polychaete)	0.2 -6.0	tentaculate surface deposit feeder; discretely motile
Pygospio elegans (spionid polychaete)	0.1 -1.5	tentaculate surface deposit feeder; discretely motile
Hobsonia sp. (ampharetid polychaete)	0.1 -3.0	tentaculate surface deposit feeder; sessile
Manayunkia aestuarina (sabellid polychaete)	0.05-0.3	facultative tentaculate ciliary suspension feeder; facultative surface deposit feeder; discretely motile
Corophium salmonis (gammarid amphipod)	0.2 -1.2	antennal surface deposit feeder; discretely motile
Tanais sp. (tanaid)	0.2 -0.8	particle browser; discretely motile

"sheet" of water a few centimeters thick approaching at speeds of 10 to 30 cm sec^{-1} (personal observations). The direction of tidal outflow, inferred from asymmetric bed ripples, may vary by 90° over the course of several days. Whether comparable variability exists in the direction of tidal inflow is unknown. Bed ripples may be absent entirely. At times, however, ripples of approximately equal wavelength are omnipresent. Ripple wavelengths may vary between 4 and 10 cm over the course of several weeks.

2. Methods

A series of recruitment experiments were conducted between 20 April and 11 October 1977. In each, two 8 × 8-m areas were defined with a common border parallel to the predominant direction of tidal flow. Centered within each area, a 1 × 1-m sub-area was defined (with two sides normal to the predominant direction of tidal flow), within which all sampling was performed. The 7-m separation of sub-areas allowed sufficient room for sampling while minimizing possible community differences due to larger spatial separation. One sub-area was randomly designated a control and the other a treatment. To provide a defaunated "island" for recruitment, all oxic sediments were excavated from the treatment sub-area and replaced with anoxic sediments. This procedure effectively removed all members of the macroinfaunal species considered in this study (confirmed by sampling). The treatment sub-area was filled to the local sediment level to minimize any edge effects during subsequent exposure to tidal currents. Samples of sediments both removed from and implanted in the treatment sub-area were taken for grain-size analysis.

In order to test the possible effects of small, protruding bed structures on local recruitment, two experiments (initiated, respectively, on 11 August and 14 September 1977) were conducted. Stainless steel sewing needles (<1 mm diameter) were inserted vertically into the sediments in order to simulate the rigid, protruding tubes constructed by the two spionids and the ampharetid. Simulated tubes were placed in both treatment and control sites. The control sub-area, however, already contained a dense tube mat. For efficient use of statistical methods (described below) employed to detect effects of these simulated tubes on recruitment, needles were arranged in straight lines at regular intervals (every 6 cm) so that needles would occur with a distinct periodicity in sample transects. Consequently, the local abundances of any species affected by these simulated tubes would be expected to have shown an identical periodicity. Each needle was pushed into the sediment flush with the local sediment level. Subsequent settling and erosion of implanted sediments at the treatment site exposed the upper few millimeters of each needle after a few days (personal observations). To facilitate needle relocation for sampling a short (<2 cm) piece of monofilament fishing line (2 lb. test) was threaded through each needle.

The control sub-area was sampled at the start of each experiment and each time the treatment site was sampled—at intervals of four days to two weeks. Sampling

consisted of linear transects of 100 contiguous cores (6-mm diameter plastic drinking straws) taken to a depth of at least 10 cm. All transects were oriented normal to the predominant direction of tidal flow; only if transects were so oriented would the distance to the undisturbed community in the predominant direction of tidal flow be the same for every point on a transect across the treatment sub-area. Before extraction, sodium tetraborate-buffered formalin was injected, via squeeze bottle, into each core. Cores were then removed, capped and strung together in order.

In the laboratory, several core samples from both ends of the transect were sieved separately through a 61-μm mesh. This mesh was selected to retain all individuals of the macrofaunal species considered, including the most recently settled juveniles. By microscopic examination the largest mesh that would retain all individuals obtained from these cores was selected for processing the remaining cores in the transect. Mesh size varied among sampling dates from 61 μm to 350 μm—smaller mesh being necessary when juveniles of one or more species were present (Table 1).

For each species an ordered series of abundance per core was obtained by direct counts of transect core samples. To analyze these spatial data extensive use was made of parametric autocorrelative and cross-correlative techniques of time-series analysis (e.g., Chatfield, 1975). A direct analogue exists between a time series of measurements and a one-dimensional (linear) spatial series of measurements. The autocorrelation function may be used to test for the existence and scales of clustering and periodicities within the distribution of a single variable. The cross-correlation function may be used to test for the existence and scales of interdependences in the distributions of two distinct variables. An appendix is provided which briefly explains derivations and some potential uses of these two functions for the analysis of spatial data. Further recommendations for ecological applications are given by Platt and Denman (1975).

Autocorrelation coefficients were calculated for each species' abundances at all distances (lags) which are integer multiples of the core diameter (6 mm) and less than or equal to one-fourth the transect length (the accepted upper limit of analysis —Box and Jenkins, 1970). Raw counts were used for autocorrelation analysis. Logarithmic transformations of raw counts (to better meet assumptions of normality) had no appreciable effects on results: statistically significant values of autocorrelation coefficients occurred at the same lags (distances) using both raw and log-transformed data. Nonstationarity due to a linear trend in the data was corrected by subtracting predicted values of abundance in each core (obtained from least-squares linear regression) from observed values. Residuals were then subjected to autocorrelation analysis. Statistically significant ($P < 0.10$) linear trends in raw data rarely occurred.

Cross-correlation analysis was performed on each possible pair of species' abundances considered in autocorrelation analysis. Raw counts were treated prior to cross-correlation analysis using a first-difference, digital, high-pass filter of the form
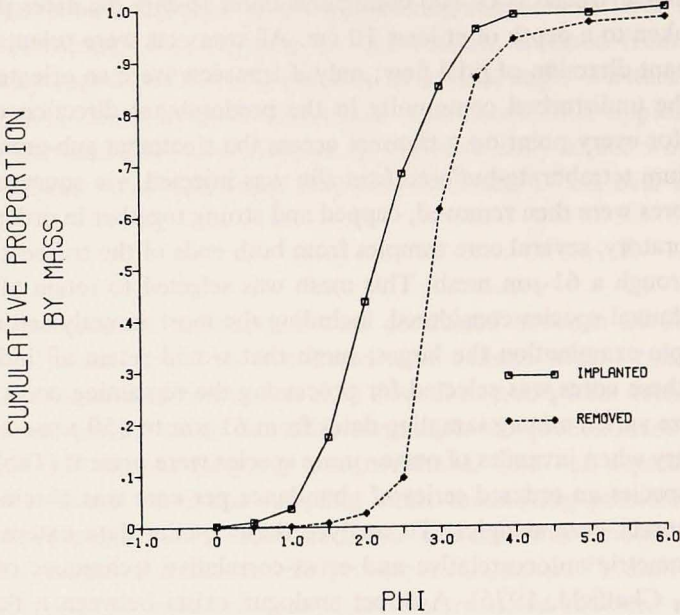
Figure 2. Cumulative proportion by mass versus phi ($\phi = -\log_2 D$, D = particle diameter in mm) for sediments removed from and implanted in a treatment sub-area on 11 August 1977.

$$y_i = x_i - x_{i-1}, \text{ where}$$

x_i = original abundance at location i

y_i = filtered abundance at location i.

High-pass filtering of raw counts was necessary because cross-correlation analysis is extremely sensitive to nonstationarity caused by the presence of low-frequency periodicities (Jenkins and Watts, 1968).

3. Results

a. Sediment analysis. Anoxic sediments implanted in treatment sites were coarser grained than the surface, oxic sediments removed (Fig. 2). A few days after defaunation, however, a fine-grained, surface flocculent layer characteristic of the natural bed appeared. This mud veneer persisted throughout the period of study.

b. Simulated animal tube experiments. In the two experiments designed to test effects of simulated tubes on recruitment, *Manayunkia aestuarina* once, and *Tanais* sp. (hereafter referred to as *Tanais*) twice, exhibited a periodicity in abundances in treatment sites equal to the periodicity of needle abundances. For example, fourteen days after anoxic sediments and needles were implanted in the treatment site, *Tanais'* transect abundances exhibited statistically significant positive autocorrelation at lags between 6.0 and 7.2 cm (peak at 6.6 cm), and showed statistically significant posi-
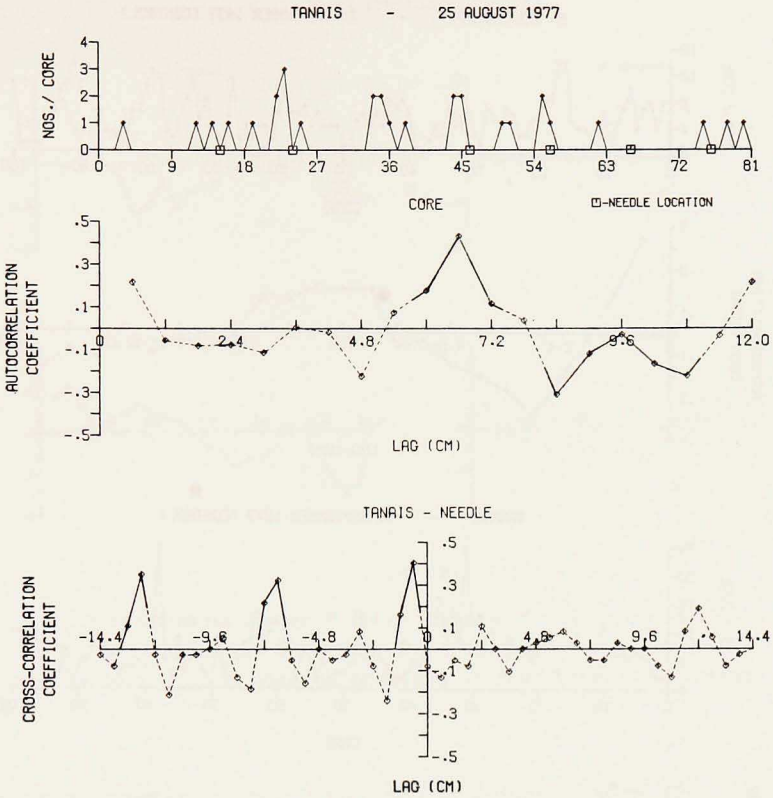
Figure 3. Raw abundances, autocorrelogram, and cross-correlogram with needle abundances for *Tanais* from treatment site samples fourteen days after defaunation and implantation of simulated tubes. Statistically significant (*P* <0.05) portions of autocorrelograms and cross-correlograms (denoted by solid lines) indicate that *Tanais* responded positively, and with a directional bias, to the simulated tubes.

tive cross-correlation with the needles' abundances at −0.6, −6.6, and −12.6 cm (Fig. 3), indicating a positive response to these simulated tubes. The cross-correlogram indicates an apparent directional response to the needles: no statistically significant cross-correlation occurred at any "positive" lags (distances). No such response to these simulated tubes was ever noted in transects taken in control sites where natural tubes were abundant.

c. Small-scale aggregation. In both treatment and control transects, several species commonly exhibited aggregation at scales from one to several centimeters. For example, Figure 4 shows abundances and associated autocorrelograms for *Tanais* and *M. aestuarina* in control-site transects sampled on 14 September and 25 September, respectively. The statistically significant (*P* <0.05) positive autocorrelations at all
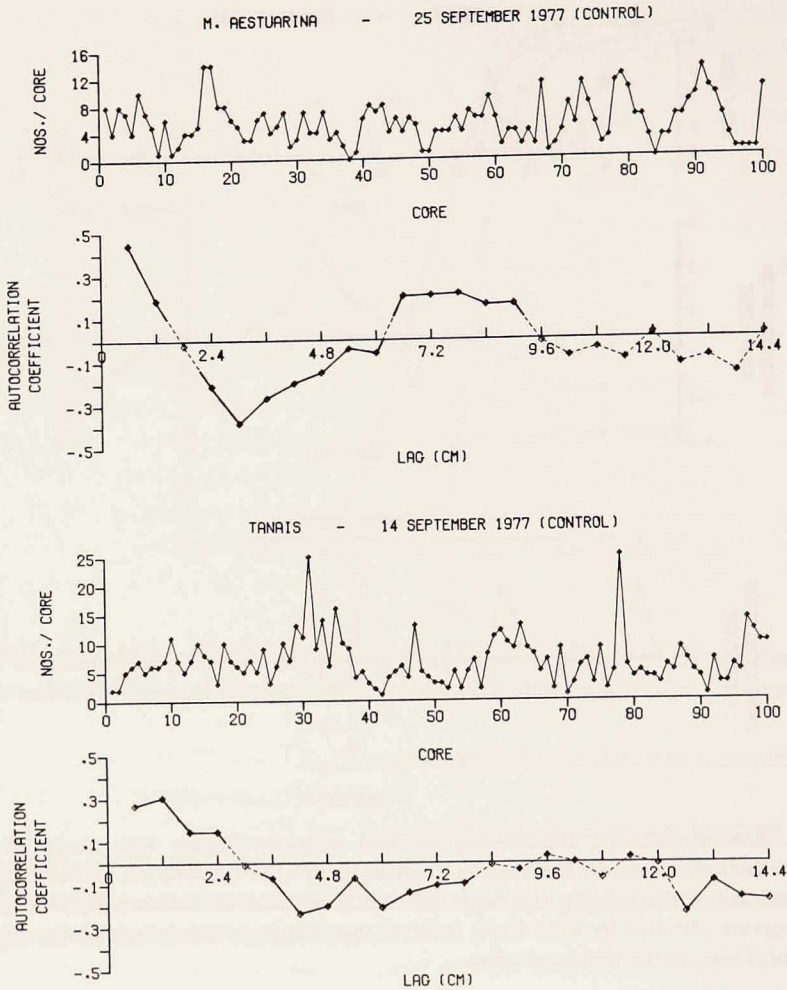
Figure 4. Raw abundances and autocorrelograms for *M. aestuarina* and *Tanais* from control site samples. Statistically significant (*P* <0.05) portions of autocorrelograms are denoted by solid lines. Both species exhibit gregariousness at scales less than 3 cm.

distances less than 3 cm and 2 cm, respectively, indicate gregariousness at these scales (see Appendix).

The frequency with which each species exhibited small-scale clustering in transects from both treatment and control sites was: *Tanais*, 4 times in 7 transects; *M. aestuarina*, 3 times in 8 transects; *Eteone longa,* twice in 4 transects; *Hobsonia* sp., once in 3 transects; *Pygospio elegans*, once in 4 transects; *Pseudopolydora kempi japonica*, once in 7 transects; *Corophium salmonis,* never in 6 transects. The variation among species in the number of transects analyzed is a result of the unreali-
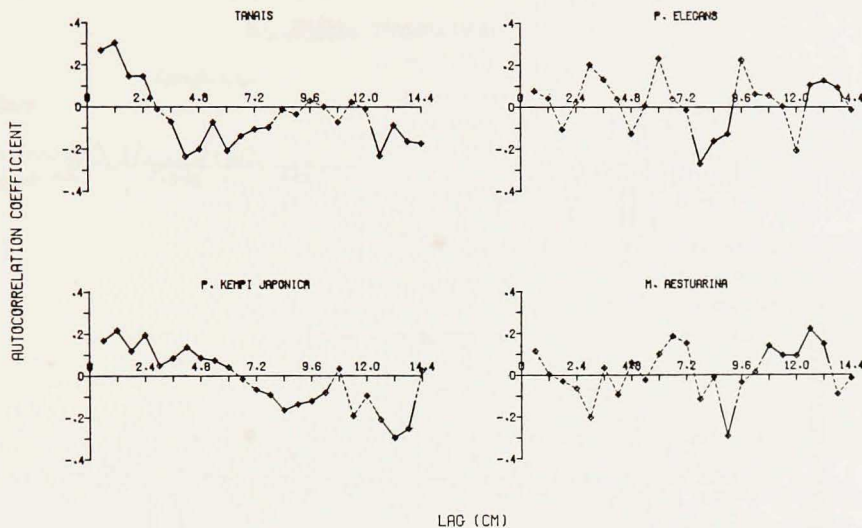
14 SEPTEMBER 1977 (CONTROL)

LAG (CM)

Figure 5. Autocorrelograms for *Tanais, P. kempi japonica, P. elegans,* and *M. aestuarina* from control site samples taken on 14 September 1977. Statistically significant (*P* <0.05) portions are denoted by solid lines. A common periodicity in abundances exists between 12.6 and 13.2 cm.

ability of autocorrelation analysis when the distribution of species' abundances per core has a high positive skew (i.e., mostly zero individuals per core).

d. Larger-scale periodicities and interdependences in species' abundances. Individuals and small clusters of all species often exhibited larger-scale (≅10 cm) periodicities in abundances. Within a transect, two or more species' abundances were often periodic at a common scale. For example, from a control-site transect sampled on 14 September, autocorrelograms for *M. aestuarina, P. elegans, P. kempi japonica,* and *Tanais* each indicate at least one statistically significant component (periodicity) not due to small-scale (≤3 cm) gregariousness (Fig. 5). The abundances of all four species exhibit statistically significant autocorrelation between 12.6 and 13.2 cm, indicative of a common periodicity in abundances at that scale. In five of seven transects taken in treatment sites, a common, larger-scale periodicity in abundances was exhibited by two or more species. In all control-site transects, three or more species exhibited a common, large-scale periodicity in abundances.

Most cross-correlograms contain no statistically significant values of the cross-correlation coefficient, considering all possible combinations of species pairs. However, nearly all the statistically significant cross-correlations that do occur are between species which exhibited common, larger-scale periodicities in abundances.
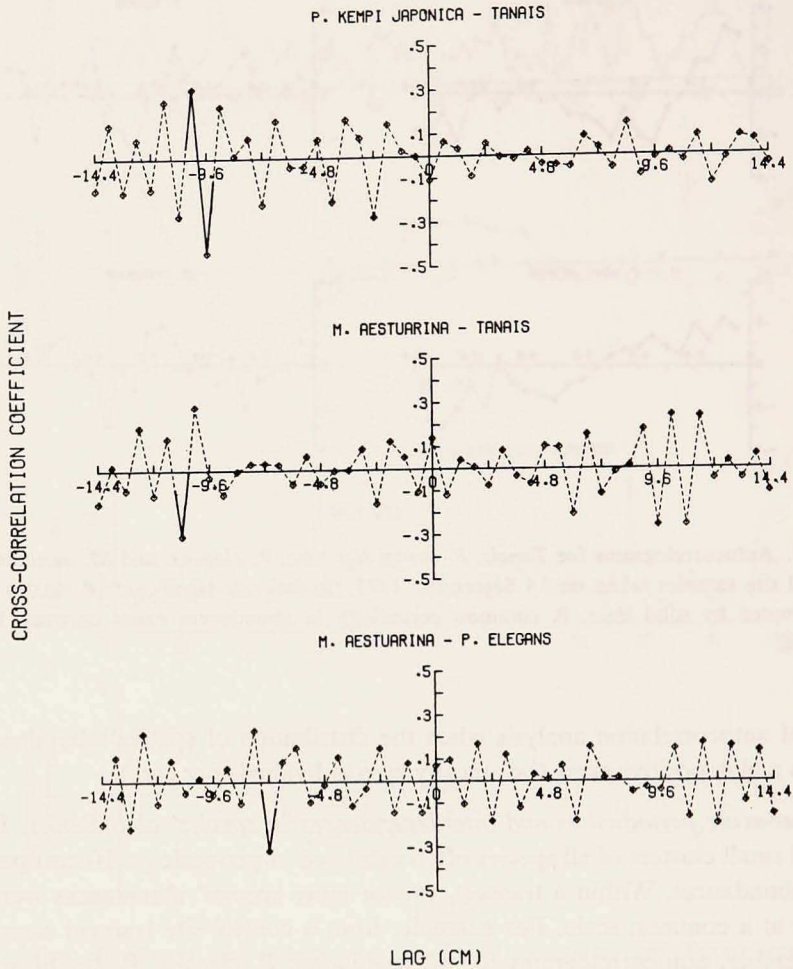
14 SEPTEMBER 1977 (CONTROL)

Figure 6. Cross-correlograms between pairs of species' abundances from control site samples taken on 14 September 1977 which exhibit statistical significance ($P < 0.05$, denoted by solid lines). The species pairs are all from those species which exhibited a common periodicity in abundance at 13 cm (Figure 5).

Furthermore, the statistically significant cross-correlations also occur at these larger scales. For example, Figure 6 shows all cross-correlograms containing statistically significant values from samples taken in the control site on 14 September. These species pairs are all formed from those species which exhibited a common periodicity in abundances at 13 cm (Fig. 5). All statistically significant cross-correlations occur at distances exceeding 7 cm (Fig. 6).

Table 2. Summary of statistically significant autocorrelative and cross-correlative patterns in contiguous-core transect abundances.

Intraspecific Dependences

Date	Small-scale Gregariousness	Larger-scale Periodicities in Abundance	Interspecific Dependences
14 September (control)	*P. kempi japonica, Tanais*	1) *C. salmonis, M. aestuarina,* and *P. kempi japonica* at 9 cm 2) *C. salmonis, M. aestuarina, P. kempi japonica, P. elegans,* and *Tanais* at 14 cm	1) *M. aestuarina* and *P. elegans* at 7 cm 2) *P. kempi japonica* and *Tanais* at 9-11 cm 3) *M. aestuarina* and *Tanais* at 9-11 cm
25 September (control)	*M. aestuarina, Tanais*	*C. salmonis, P. kempi japonica, P. elegans,* and *Tanais* at 15 cm	Many at lags exceeding 5 cm
25 September (treatment)	*M. aestuarina, Tanais*	No two species with periodicity at the same lag	1) *C. salmonis* and *P. kempi japonica* at 1-2 cm 2) *M. aestuarina* and *Tanais* at 0 cm 3) *C. salmonis* and *Tanais* at 2 cm
11 October (control)	*Tanais*	1) *C. salmonis, P. kempi japonica,* and *P. elegans* at 15 cm 2) *M. aestuarina, P. elegans,* and *Tanais* at 8 cm	Many at lags from 2 to 12 cm; most at lags exceeding 6 cm
11 October (treatment)	none	1) *C. salmonis, P. kempi japonica,* and *Tanais* at 8 cm 2) *C. salmonis, M. aestuarina,* and *Tanais* at 11 cm	*C. salmonis* and *M. aestuarina* at 3 cm and 6 cm

e. Temporal stability of dispersion patterns. Successional patterns at a single site may be studied by examining the results of one experiment conducted from 14 September to 11 October (summarized in Table 2).

The control site was sampled at initiation of the study and after 11 and 28 days. A common periodicity in species' abundances at 15 cm was consistent: three of five species exhibiting periodicity at this scale on 14 September still did so after 28 days. Significant cross-correlations between species pairs occurred almost exclusively at larger scales. *Tanais* consistently exhibited small-scale gregariousness.

After 11 days, dispersion patterns in the treatment site showed little similarity to patterns in the control area. Intraspecific periodicities in abundances were uncommon and of marginal statistical significance, and no two species exhibited periodicity at the same scale. All statistically significant cross-correlations occurred at scales

less than or equal to 2 cm. However, at this sampling *M. aestuarina* and *Tanais* exhibited small-scale gregariousness in both treatment and control sites.

After an additional 17 days, dispersion patterns in the treatment site were more similar to patterns observed in the control site. Larger-scale periodicities in abundances existed at the same lag for several species, and statistically significant cross-correlations also occurred at larger scales.

4. Discussion

The use of coarser-grained, anoxic sediments in treatment sites (Fig. 2) may have produced species-dependent effects on recruitment rates. The ability of some species to select for or against substrata on the basis of particle size is well documented for the marine benthos (e.g., Meadows, 1964; Gray, 1971). The surface deposit feeders (Table 1), which should preferentially select smaller-diameter particles (Taghon *et al.*, 1978) and may find anoxic sediments undesirable food resources, especially might avoid treatment sites. The appearance of all species in cores sampled within a week after treatment is consistent with the rapid reappearance and persistence of a fine-grained, surface flocculent layer. Meadows (1964) similarly demonstrated that, when provided with a mud overlayer, *Corophium volutator* built tubes in coarser-grained sediments it would normally avoid.

Small-scale gregariousness in benthic infaunal populations has often been suggested, but the scales of this gregariousness have not been well documented. Angel and Angel (1967) demonstrated clustering of three infaunal, subtidal species at the scale of their smallest sample size (12.5 cm) and reasoned that their core size may have been too large to detect the minimum size of patterns. Supportive results were reported by Gage and Coghill (1977), who used linear transects of 5-cm diameter contiguous cores to demonstrate aggregation at that scale or smaller for several infaunal species. The present study conclusively demonstrates that clustering at scales of one to several centimeters commonly occurs within populations of several small-macrofaunal species at the Skagit flats.

One of several postulated causes of aggregated populations in nature is the existence of a heterogeneous environment conferring varying probabilities of an organism's survival (Feller, 1943). The ability of settling larvae to discriminate habitats at scales less than one millimeter has been documented in hard-substratum environments (e.g., Wisely, 1960; Crisp, 1961; Wilson, 1968). Rhoads and Young (1971) demonstrated that species' dispersion patterns on soft bottoms may reflect small-scale spatial habitat diversity created by holothurian fecal mounds. One likely means of producing environmental heterogeneity in aquatic ecosystems is through various consequences of fluid flow. Fager (1964) suggested that concentration of an oweniid polychaete in distinct, shallow-subtidal patches was caused by rip current effects on settling larvae. In the present study the positive association of *Tanais* and *M. aestuarina* abundances with simulated animal tubes protruding from the bed suggests that

changes in patterns of flow at the benthic boundary create small-scale environmental heterogeneity which affects species' dispersion. The observed correlations may have been produced by an active response by individuals, by concentration of organisms in passive transport, or by differential mortality after juvenile and adult recruitment.

Increased animal abundances about these simulated tubes were restricted to a distance of approximately one centimeter (Fig. 3). This scale must be shown to be consistent with flow theory if dispersion patterns observed are to be attributed to hydrodynamic processes. For scaling arguments, flow about a rigid, protruding animal tube may be compared to theoretical and empirical studies of flow about a cylinder.

The dynamics of oscillatory flows are poorly understood. At the Skagit flats, tides would define the temporal scale of oscillation (of order 10^4 sec) in the absence of wind waves. Given their absence (calm summer days are common), flow over the tidal flats should behave as a simple, depth-limited boundary layer. The thickness of an oscillatory boundary layer is given by

$$\delta = \text{boundary layer thickness (cm)}$$

$$\delta = \frac{u_*}{\omega} \text{ , where } u_* = \text{shear velocity (cm sec}^{-1})$$

$$\omega = \text{tidal frequency } (\cong 1.4 \times 10^{-4} \text{ sec}^{-1}).$$

On a tidal flat, u_* should be of order 10^0 cm sec^{-1} (e.g., Wimbush, 1976), making δ of order 10^4 cm. As this scale is two orders of magnitude greater than the actual flow depth on the tidal flat, it is reasonable to postulate rapid local flow adjustment and local equilibrium (quasi-steady) conditions.

Protruding tube structures define the scale of local roughness when bed ripples are absent. Scaling arguments are applicable to periods of ripple absence: traditional models of near-wall flow characterize the boundary by only one length scale (z_0). The influence of multiple length scales has not been studied.

The thickness of the viscous sublayer (within which viscous flow conditions exist) may be defined by

$$\delta_v = \text{thickness of viscous sublayer (cm)}$$

$$\delta_v = \frac{11.6\,\nu}{u_*} \text{ , where}$$

$$\nu = \text{kinematic viscosity of seawater} \\ (\cong 1 \times 10^{-2} \text{ cm}^2 \text{ sec}^{-1}).$$

At Skagit Bay, u_* should vary from essentially zero during periods of slack tide to a maximum of 1 to 2 cm sec^{-1} during maximum ebb and flood. Consequently, the minimum thickness of the viscous sublayer should be of order 1 mm. We must deal, then, with a complex situation in which protruding tube structures spend part of a tidal cycle within the viscous sublayer and part in the external flow regime.

When a steady, viscous flow encounters a circular cylinder, a secondary circulation is produced around the cylinder and in its wake at values of the body Reynold's number (R_e) less than 100 (Batchelor, 1967, p. 351 and plates 1, 2; Coutanceau and Bouard, 1977). Given that

$$u = \text{local flow speed (cm sec}^{-1})$$

$$R_e = \frac{u\,d}{\nu} \text{ , where}$$

$$d = \text{cylinder diameter (cm)}$$

and that a tube has diameter 1 mm, secondary circulation will be formed at $u < 10$ cm sec^{-1}. Current velocities of 10 cm sec^{-1} a few millimeters above the bed are extremely unlikely. The resultant secondary circulation patterns are limited to distances less than five cylinder diameters downstream.

Addition of turbulence to the incident flow (Hunt, 1971; Castro and Robins, 1977) or the presence of a stationary boundary (i.e., the bed) nearby (Castro and Robins, 1977) would reduce the downstream extent of wake effects. Consequently, effects of individual tube structures on the flow should be limited to less than 5 mm. This scale is consistent with the extent of increased animal abundances about simulated tubes (Fig. 3).

M. aestuarina is a facultative ciliary suspension feeder (Table 1) which might benefit from secondary circulation patterns in the wake of a protruding bed structure. The tanaid is a particle browser and might not directly benefit from such flow patterns. One alternative explanation for the apparent attractiveness of a tube structure to tanaids is that protruding tubes might trap thin, filamentous epiphytes. Such epiphytes are present at the study area and serve as one food resource for the tanaid (personal observations).

Given the small sizes and low motilities of the species studied (Table 1), direct biological interactions should be restricted to distances less than 2 or 3 centimeters. The scales at which the common periodicities in species' abundances exist, as well as scales of interspecific dependences (indicated in cross-correlograms), are too large to be attributed to such interactions. An alternative mechanism to account for these larger-scale periodicities must be hypothesized *a posteriori*. Experimental studies (e.g., Raudkivi, 1976) demonstrate that flow patterns and velocities differ over various points on a rippled bed. One plausible hypothesis which explains these larger-scale dispersion patterns is that organisms may actively select or be passively transported to areas on a rippled bed experiencing different flow conditions. For example, suspension feeders might benefit from areas of locally increased turbulence, which occur as flow diverges at and in the lee of ripple crests. Deposit feeders may benefit from reduced boundary shear stresses occurring in ripple troughs. Additionally, lower boundary shear stresses may concentrate passively transported organisms in ripple troughs. Passive or active response to flow across a rippled bed would explain: (1) the common scale of periodicities in abundances observed among several species

in any one transect; (2) the majority of statistically significant cross-correlations occurring at larger (i.e., $\cong 10$ cm) scales; and, (3) the majority of statistically significant cross-correlations occurring among species that exhibited common, larger-scale periodicities in abundances. Because bed ripples are capable of migration, active site selection by individuals implies a capacity for horizontal movements of at least several centimeters. Aquarium observations confirm that all species studied are capable of tube or burrow reconstruction after manual displacement, and that *C. salmonis, E. longa, M. aestuarina,* and *Tanais,* at least, may actively select new tube or burrow sites.

Orientations of transects relative to the most recently produced ripples are unknown. Ripples were rarely noted in either treatment or control sites at times of sampling, and there is temporal variation in ripple orientation (see Introduction). However, wavelengths of ripples observed near the study area during the period of study suggest a minimum scale (of 4 cm) at or above which all common periodicities in species' abundances should occur—consistent with observed values.

Temporal stability of species' dispersion patterns is necessary over a minimum of several tidal cycles, if patterns noted were produced by bed forms not present at the time of sampling. By examining Table 2, one is tempted to conclude that patterns containing common, larger-scale periodicities in abundances may be stable for at least one month: three of five species exhibiting periodicity at 15 cm still did so 28 days later. However, at least three separate hypotheses explain this temporal consistency:

(1) The common periodicity in abundances established prior to initial sampling decayed. Rates of decay differed among the species exhibiting this periodicity. Consequently, progressively fewer species exhibited this periodicity as time passed (Fig. 7A).

(2) Pattern decay was rapid and proceeded at different rates among species. However, the common periodicity in abundances was regularly established at the same scale by a process(es) operating with a frequency greater than the sampling frequency (Fig. 7B).

(3) Some prior event(s) produced a long-term effect on species' dispersion patterns, resulting in the common periodicity in abundances among all five species. Inability to detect this periodicity in all species' abundances at all times is due to the low (statistical) power of the autocorrelation function.

In this same experiment, larger-scale periodicities did not appear in treatment site samples until after 11 days (Table 2). Prior to their appearance, interspecific dependences existed at scales less than or equal to 2 cm. This scale of interdependence is expected if direct biological interactions between individuals affect species' dispersion patterns. However, an alternative explanation is that the statistically significant cross-correlations observed represent mutual responses to small-scale hydrodynamic processes, such as flow patterns established in the wake of protruding ani-
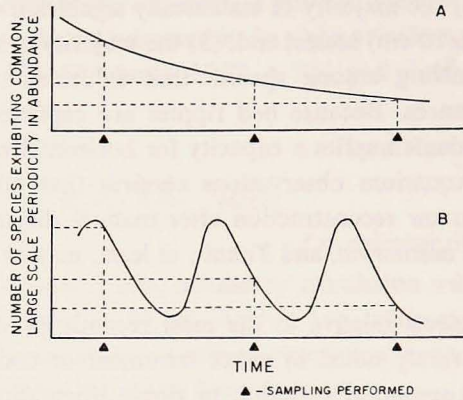
Figure 7. Two possible patterns which could explain the observed decrease, with time, in the number of species exhibiting a common, larger-scale periodicity in abundances.

mal tubes. After establishment of common, larger-scale periodicities in abundances, interspecific dependences existed only at larger scales (Table 2). Apparently, the mechanism(s) creating larger-scale periodicities in abundances have effects on the community great enough to render smaller-scale patterns and responses (i.e., at scales of one to several centimeters), other than aggregation within species, undetectable by autocorrelative and cross-correlative techniques.

5. Significance and conclusions

These results suggest that caution must be exercised in interpreting results of manipulative experiments which employ devices such as cages or settling containers. The presence of any such structures must alter local flow patterns. For example, increased sediment deposition within caged areas (McCall, 1977; Virnstein, 1977) and differential dispersal of marked sediments inside and outside caged areas (Virnstein, 1977) have been reported. Results of the present study suggest that the effects of flow disruption on smaller macrobenthos might be considerable. Similar effects are also likely among meiobenthos and settling larvae. For example, Hannan *et al.* (1977, unpublished ms.) found dramatic differences in larval settlement patterns among settling containers of different aspect ratios (height:width).

The results of this study have important implications regarding scales at which sampling should be performed in soft-substratum benthic studies in order to estimate abundances, describe patterns of spatial dispersion, and test for effects of biological and nonbiological processes on community structure. In an intertidal sand flat numerically dominated by tube-dwelling, sessile and discretely motile infauna, heterogeneity relevant to the individual has been documented at scales too small to be detected using more traditional methods of sampling. Pielou (1960) clearly demonstrated that conclusions about patterns of spatial dispersion reflect the scale

at which sampling is performed. Past failures of investigators to infer biological interactions from correlations may largely be due to inappropriate selection of sample size and spacing. Samples which are taken at arbitrary scales homogenize spatial patterns that reflect smaller-scale interactions, responses and processes, and could seriously affect between-sample variability, thereby leading to spurious conclusions regarding the pattern and control of community structure.

APPENDIX

The following is a brief, nonrigorous description of the autocorrelation and cross-correlation functions, and some of their potential uses in the analysis of spatial data collected in one dimension. For a more rigorous treatment, I recommend that readers consult some of the many references on the subject (e.g., Jenkins and Watts, 1968; Box and Jenkins, 1970; Chatfield, 1975), from which much of the following is derived.

Given N ordered pairs of observations (x_i, y_i), the ordinary parametric (product-moment) correlation coefficient, r, is defined as

$$r = \frac{\Sigma(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\{\Sigma(x_i - \bar{x})^2 \Sigma(y_i - \bar{y})^2\}}} .$$

This coefficient quantifies the degree of certainty with which one can predict the value y_i knowing the corresponding value x_i.

a. Autocorrelation. Given an ordered series of n equally spaced observations of X: $x_1, x_2, \ldots, x_n$ (an example of such a series might be the abundance of a species in successive cores of a transect), one can form $n-k$ ordered pairs $(x_1, x_{1+k}), (x_2, x_{2+k}), \ldots, (x_{n-k}, x_n)$ of the form (x_i, x_{i+k}). If one considers the two observations in each ordered pair to be observations of two variables, the autocorrelation coefficient at lag k, r_k, is given by

$$r_k = \frac{\sum_{i=1}^{n-k}(x_i - \bar{x})(x_{i+k} - \bar{x})}{\sqrt{\left\{\sum_{i=1}^{n-k}(x_i - \bar{x})^2 \sum_{i=1}^{n-k}(x_{i+k} - \bar{x})^2\right\}}} \cong \frac{\sum_{i=1}^{n-k}(x_i - \bar{x})(x_{i+k} - \bar{x})/(n-k)}{\sum_{i=1}^{n}(x_i - \bar{x})^2/n}$$

This coefficient quantifies the degree of certainty with which one can predict a value x_{i+k} knowing the value in the same ordered series k units away, x_i.

The autocorrelation coefficient may be calculated for lags $k = 1, 2, \ldots, n/4$. This information is commonly summarized in an autocorrelogram, a plot of values of the autocorrelation coefficient (ordinate) versus lag (abscissa). The autocorrelogram graphically provides information on the scales or lags at which dependences exist within the distribution of a variable.

A classical problem in ecological studies which may be addressed using autocorrelation analysis is the detection of an aggregation or patch of individuals. Consider a transect which en-
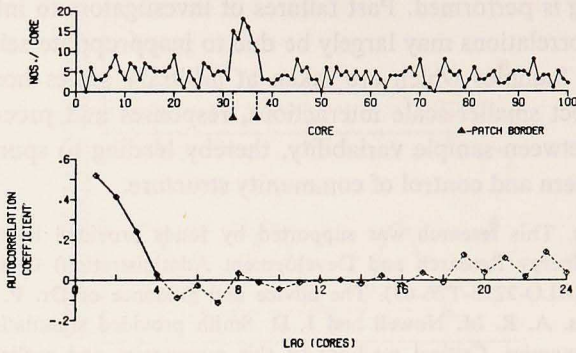
Figure 8. Hypothetical abundances of a species in transect core samples created by adding a constant to six consecutive values in a series of 100 random-normal integers to simulate encountering and passing through a "patch". All statistically significant portions of the autocorrelogram ($P < 0.05$, denoted by solid lines) are caused by the existence of the "patch".

counters and passes through a cluster of individuals. The abundance of individuals along the transect should exhibit a local increase as a cluster is encountered (Fig. 8). A series of 100 random-normal numbers (rounded to integer values, range: 0 to 9, inclusive) was generated to represent the abundance of individuals of a species in 100 equally spaced core samples. A constant (10) was added at six consecutive core locations to simulate encountering and passing through a cluster of individuals. By definition, random-normal numbers exhibit zero autocorrelation at any non-zero lag (or distance); however, statistically significant positive autocorrelation exists at lags 1 through 4 in the autocorrelogram (Fig. 8), indicating that adjacent values (lag = 1) and those separated by up to 4 units (lag = 4) tend to occur on the same side of the mean. The statistically significant autocorrelations observed are a direct result of a local increase in abundance caused by the existence of a single "patch" 6 units in length (statistical significance is discussed below).

Autocorrelation analysis also allows testing for the existence and scales of periodicities in variate values in the form of a one-dimensional ordered series. A series of 100 random-normal integers (range: 0 to 9, inclusive) was again generated to represent the abundance of individuals of a species in 100 equally spaced cores of a transect. A constant (10) was added to every tenth location to induce a periodicity or "spike" in abundance (Fig. 9A). The statistically significant positive autocorrelation at lags 10 and 20 in the autocorrelogram for sequence (A) (Fig. 9B) indicates a periodicity in the variate values at those scales. Periodic addition of a constant elevates the series mean slightly, causing the statistically significant negative autocorrelations at other lags.

b. Cross-correlation. Given n equally spaced observations of ordered series of two variables, X and Y, $x_1, x_2, \ldots, x_n$ and $y_1, y_2, \ldots, y_n$ one can form $n-k$ ordered pairs of observations $(x_1, y_{1+k}), (x_2, y_{2+k}), \ldots, (x_{n-k}, y_n)$ of the form (x_i, y_{i+k}). The cross-correlation coefficient between variables X and Y at lag k, $c_{xy}(k)$, is approximately given by

$$c_{xy}(k) = \frac{\sum\limits_{i=1}^{n-k} (x_i - \bar{x})(y_{i+k} - \bar{y})}{\sqrt{\left\{ \sum\limits_{i=1}^{n-k} (x_i - \bar{x})^2 \sum\limits_{i=1}^{n-k} (y_{i+k} - \bar{y})^2 \right\}}}$$
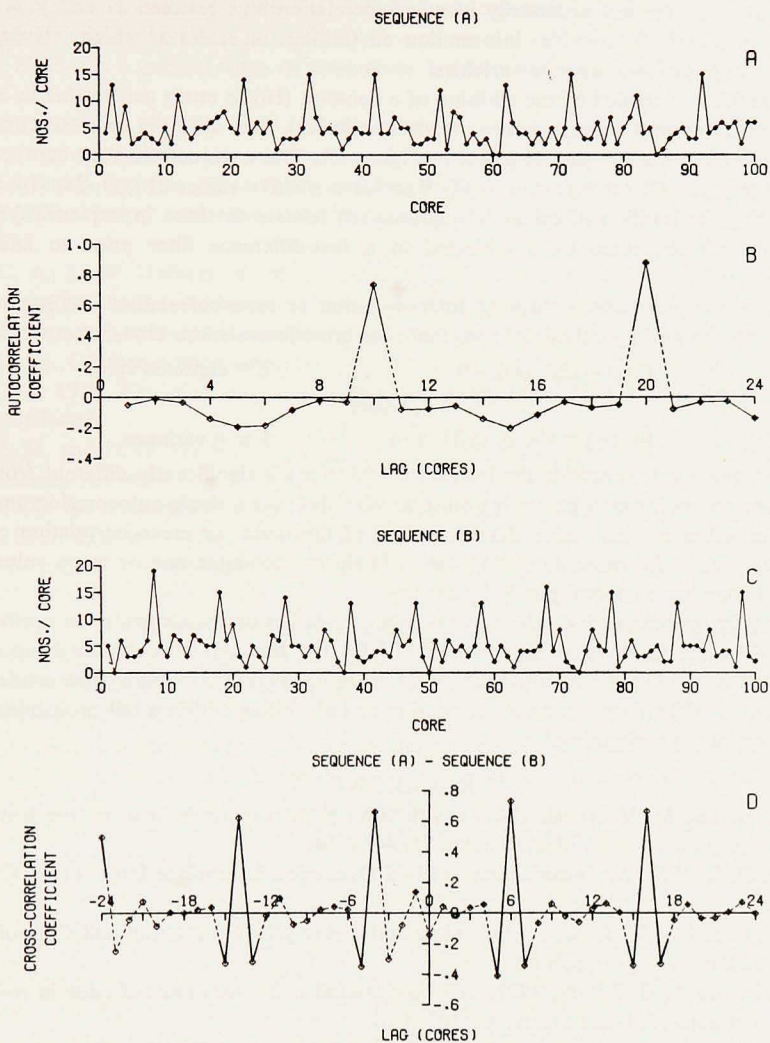
Figure 9. Hypothetical abundances (A and C) of two species in transect core samples created by adding a constant to every tenth value in separate series of 100 random-normal integers. Statistically significant values (P <0.05, denoted by solid lines) at lags of 10 and 20 cores in the autocorrelogram (B) for sequence A indicate the scale of the induced periodicity. Statistically significant values (P <0.05, denoted by solid lines) of the cross-correlogram (D) between the two sequences indicate the position of spikes in sequence B relative to those in sequence A.

This coefficient quantifies the degree of certainty with which one can predict the value y_{i+k} knowing the value of a separate variable k units away, x_i.

The cross-correlation coefficient may be calculated for lags $k = \pm 1, \pm 2, \ldots, \pm n/4$. Both positive and negative lags must be considered in cross-correlation analysis: relationships be-

tween x_i and y_{i+k} are not necessarily identical to relationships between x_i and y_{i-k}. A cross-correlogram graphically provides information on the lags or scales at which interdependences exist in the values of two separate variables.

Figure 9C was created by the addition of a constant (10) to every tenth value in a sequence of 100 random-normal integers (range: 0 to 9, inclusive), such that the spikes occur exactly 6 units ahead of (or 4 units behind) spikes in Figure 9A. The cross-correlogram between the two sequences (Figure 9D) exhibits statistically significant positive values at lags -24, -14, -4, 6, and 16, indicating the position of spikes in sequence (B) relative to those in sequence (A). Variate values for both sequences were subjected to a first-difference filter prior to analysis (see Methods).

c. Statistical significance. Values of autocorrelation or cross-correlation coefficients may be tested against the null hypothesis of zero (auto- or cross-)correlation. Under the null hypothesis

$$E(r_k) = E(c_{xy}(k)) = 0 \qquad\qquad E = \text{expected value}$$

, where

$$Var(r_k) = Var(c_{xy}(k)) = 1/n \qquad\qquad Var = \text{variance,}$$

so that individual values outside the interval $\pm 1.96/\sqrt{n}$ are significantly different from zero ($\alpha = 0.05$). Correction for multiple testing must be made because a single autocorrelogram or cross-correlogram often contains more than 20 values of the (auto- or cross-)correlation coefficient. Without correction for multiple testing one is likely to encounter one or more values outside the defined confidence interval purely by chance.

Additionally, m consecutive values of the autocorrelation or cross-correlation coefficient may occur on the same (positive or negative) side of $E(r_k) = E(c_{xy}(k)) = 0$. Although no one value may be statistically significant, the probability of m consecutive, mutually independent (under the null hypothesis) values having the same sign and all falling within a tail probability (P) may be significant at the desired level, α.

REFERENCES

Angel, H. H. and M. V. Angel. 1967. Distribution pattern analysis in a marine benthic community. Helgoländer wiss. Meeresunters, *15*, 445–454.

Batchelor, G. K. 1967. An Introduction to Fluid Dynamics. Cambridge Univ. Press, Cambridge, 615 pp.

Box, G. E. P. and G. M. Jenkins. 1970. Time Series Analysis—Forecasting and Control. Holden-Day, Inc., San Francisco, 535 pp.

Castro, I. P. and A. G. Robins. 1977. The flow around a surface-mounted cube in uniform and turbulent streams. J. Fluid Mech., *79*, 307–335.

Chatfield, C. 1975. The Analysis of Time Series: Theory and Practice. Chapman and Hall, London, 263 pp.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments, *in* M. L. Cody and J. M. Diamond, eds., Ecology and Evolution of Communities, Cambridge, Massachusetts, Belknap Press, 545 pp.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Natur., *111*, 1119–1144.

Coutanceau, M. and R. Bouard. 1977. Experimental determination of the main features of the viscous flow in the wake of a circular cylinder in uniform translation. Part 1. Steady flow. J. Fluid Mech., *79*, 231–256.

Crisp, D. J. 1961. Territorial behaviour in barnacle settlement. J. exp. Biol., *38*, 429–446.

Fager, E. W. 1964. Marine sediments: effects of a tube-building polychaete. Science, *143*, 356–359.

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev., *17,* 193–284.

Feller, W. 1943. On a general class of contagious distributions. Ann. Math. Statist., *14,* 389–400.

Gage, J. D. and G. C. Coghill. 1977. Studies on the dispersion patterns of Scottish Sea Loch benthos from contiguous core transects, *in* B. C. Coull, ed., Ecology of Marine Benthos. Columbia, South Carolina, Univ. South Carolina Press, 467 pp.

Gray, J. S. 1971. Factors controlling population localizations in polychaete worms. Vie Milieu, *2,* 707–722.

Hannan, C. A., L. W. Hulberg, K. M. Mawn and J. W. Nybakken. 1977. A study to develop standard procedures for life history analyses of benthic invertebrates for biological monitoring in marine and estuarine environments. Unpublished manuscript. Moss Landing Marine Laboratories, California State University Consortium, Moss Landing, California, 217 pp.

Hunt, J. C. R. 1971. The effect of single buildings and structures. Phil. Trans. Roy. Soc. Lond. A., *269,* 457–467.

Jenkins, G. M. and D. G. Watts. 1968. Spectral analysis and its applications. Holden-Day, Inc., San Francisco, 525 pp.

Jumars, P. A. 1975. Methods for measurement of community structure in deep-sea macrobenthos. Mar. Biol., *30,* 245–252.

Lonsdale, P. and J. B. Southard. 1974. Experimental erosion of North Pacific red clay. Mar. Geol., *17,* M51–M60.

McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res., *35,* 221–266.

Meadows, P. S. 1964. Substrate selection by *Corophium* species: the particle size of substrates. J. Anim. Ecol., *33,* 387–394.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory, *in* C. E. Goulden, ed., Changing Scenes in Natural Sciences, 1776-1976. Philadelphia, Academy of Natural Sciences, 362 pp.

Pielou, E. C. 1960. A single mechanism to account for regular, random and aggregated populations. J. Ecol., *48,* 575–584.

Platt, T. J. and K. L. Denman. 1975. Spectral analysis in ecology. Ann. Rev. Ecol. Syst., *6,* 189–210.

Raudkivi, A. J. 1976. Loose Boundary Hydraulics. Pergamon Press, London, 397 pp.

Rhoads, D. R. and D. K. Young. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). Mar. Biol., *11,* 255–261.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science, *185,* 27–39.

Taghon, G. L., R. F. L. Self and P. A. Jumars. 1978. Predicting particle selection by deposit feeders: a model and its implications. Limnol. Oceanogr., *23,* 752–759.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in the Chesapeake Bay. Ecology, *58,* 1199–1217.

Wilson, D. P. 1968. The settlement behaviour of the larvae of *Sabellaria alveolata* (L.). J. mar. biol. Ass. U.K., *48,* 387–435.

Wimbush, M. 1976. The physics of the benthic boundary layer, *in* I. N. McCave, ed., The Benthic Boundary Layer. Plenum Press, New York, 323 pp.

Wisely, B. 1960. Observations on the settling behaviour of larvae of the tubeworm *Spirorbis borealis* Daudin (Polychaeta). Aust. J. mar. Freshwat. Res., *11,* 55–72.