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Spatial autocorrelation with RUM (Remote Underwater Manipulator): vertical and horizontal structure of a bathyal benthic community*

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Abstract—The RUM/ORB unmanned submersible system (Marine Physical Laboratory, Scripps Institution of Oceanography) was used at 1220-m depth to collect precisely located samples separated by distances from 0.1 to 500 m in the San Diego Trough, Southern California continental borderland. Newly developed spatial autocorrelation procedures from the field of quantitative geography were used on this irregularly spaced network of samples to test the statistical significance of the calculated autocorrelations. Scales less than 200 m showed little spatial autocorrelation in total numbers of macrofaunal individuals per sample. Density of *Polyophthalmus* sp. (Polychaeta, Opheliidae), however, displayed a complex autocorrelative pattern; 'patches' of individuals of similar size were observed. *Ceratocephale pacifica* (Polychaeta, Nereidae), on the other hand, showed negative spatial autocorrelation at the smallest inter-sample distance, perhaps indicative of territoriality.

Vertical segregation among confamilial and congeneric species was observed in vertically sectioned subsamples. The majority (82%) of polychaetes, however, appear regularly to inhabit the uppermost centimeter of sediments, suggesting a refinement of current bioturbation models.

INTRODUCTION

SPATIAL patterns of variation are generally studied for one or both of two reasons: to determine the degree of sampling variability or error attributable to this variation, or to provide a basis for inferences about the processes responsible for the observed patterns. In the former context, the dispersion patterns of deep-sea benthic populations have been of particular interest to stratigraphers (e.g. PIPER and MARSHALL, 1969), geochemists (e.g. GUINASSO and SCHINK, 1975) and, more recently, to investigators of potential environment impacts (e.g. GERARD, 1976; HESSLER and JUMARS, 1977). In the latter context, spatial variations in deep-sea populations have been used to make inferences concerning the processes that structure benthic communities (e.g. GRASSLE, SANDERS, HESSLER, ROWE and MCLELLAN, 1975; JUMARS, 1975b; REX, 1976).

Information is scarce on all spatial scales in the deep sea. With the exception of megafaunal observations from submersibles, a decided gap exists in data between the scales of 1 and 100 m. From single lowerings of shipboard sampling devices, information has been obtained over centimeter or meter distances (e.g. JUMARS, 1976). Without the aid of bottom-relative navigation, the precision of sample location from a dangling wire in deep, open-ocean waters has been at best 0.1 km. To illustrate the seriousness of this gap, trying to understand the spatial structure of deep-sea benthic populations without more detailed knowledge on the intermediate scales from 1 through 100 m can be likened to attempting evaluation of the dynamics of a current system from hourly current meter readings taken over periods of a few days, but with the added constraint that

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the time between moorings be of the order of a year or more. Interesting phenomena could be poorly resolved or missed entirely in both cases.

Besides providing information on this intermediate horizontal scale, an additional aim of the present work is to assess the depth–frequency distribution of macrofaunal abundance in a bathyal community. The purpose of these observations is also two-fold. First, they allow a partial evaluation of the spatial adequacy of bioturbation models (e.g. GUINASSO and SCHINK, 1975). Second, they permit examination of vertical habitat segregation as a potential mechanism of resource partitioning.

Preliminary results are reported here. Although methodology and summarization of the three-dimensional dispersion patterns of total macrofauna are highlighted, selected species are treated as examples of the detailed interpretations possible on the spatial scales of this sampling. Such anlaysis is prerequisite to the rational design of experiments either to evaluate the processes controlling community structure or to measure bioturbation rates.

LOCALITY AND METHODS

Because of the extensive background data available for this region, the San Diego Trough was selected as the study area. Sampling was carried out during October and November of 1973 with the RUM/ORB system (Marine Physical Laboratory, Scripps Institution of Oceanography) as part of Expedition QUAGMIRE (THIEL and HESSLER, 1974). RUM (Remote Underwater Manipulator) is a tracked vehicle, suspended, remotely controlled, and powered from ORB (Oceanographic Research Buoy), a rectangular, floating research platform having a central well through which RUM can be lowered.

For Expedition QUAGMIRE, RUM was equipped with a holding rack containing five Ekman-type corers. Each of these corers was designed (largely by R. R. Hessler) to contain four nested 10×10-cm subcores [identical to those used in the 'vegematic' box core modification of JUMARS (1975a)] and to be triggered by a wrist rotation of RUM's single manipulator. Television cameras mounted on RUM allowed continuous monitoring of the coring process. Movie and still cameras provided additional documentation. Depending upon other experiments and upon mechanical and electrical difficulties, RUM was able to take from one to five Ekman cores per lowering.

During the expedition, ORB was maneuvered about a three-point mooring to position RUM with respect to a three-transponder array on the bottom. An approximately equilateral triangle with legs 450 m long was inscribed within the circle determined by the transponder locations, and, aside from a few cores taken for special purposes, samples were within that triangle (Fig. 1).

To ensure a wide range of inter-sample distances and equitable coverage for subsequent analyses, several steps were taken. By assigning each lowering to a different sector than the previous one—specifically to that other sector in which fewer successful samples had been taken—samples were approximately evenly distributed among the three sectors of the triangle (Fig. 1). The transponder interrogator on RUM was used to navigate ORB until RUM could be lowered onto a randomly selected point in the given sector. After the lowering of RUM onto the bottom, the vehicle was turned until a randomly selected heading was attained. The original plan was to have RUM take Ekman cores at five randomly selected points along 100-, 50-, 25-, or 10-m transects, one starting point for a transect of each length being allotted to each sector of the triangle. (New starting coordinates and a new compass heading were chosen at random for those transects that otherwise would have crossed the triangle's boundaries.)

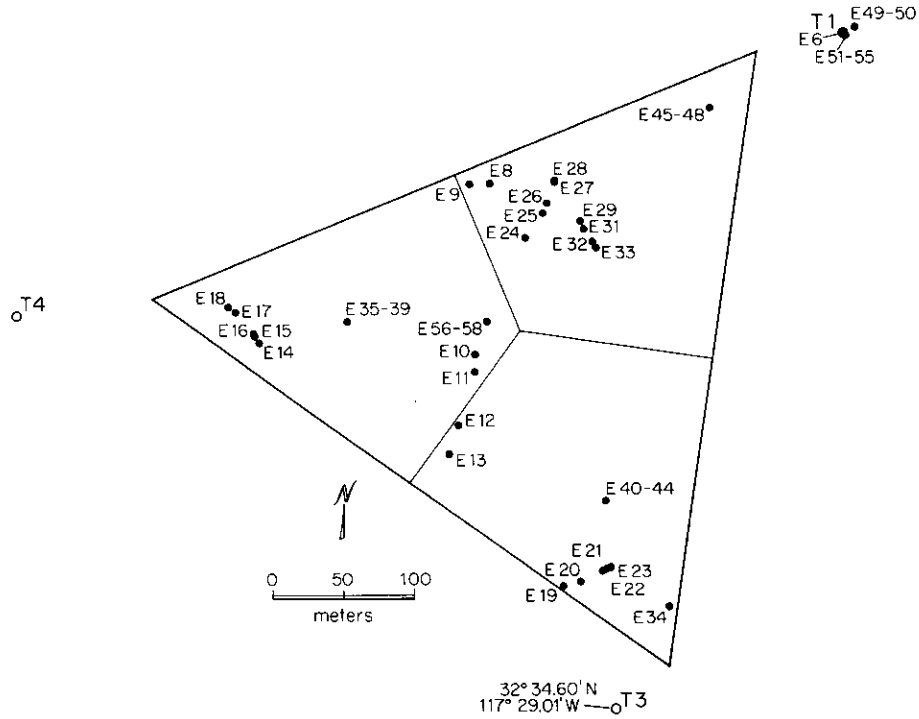

Fig. 1. Chart of study triangle and its three sectors. E: Ekman core; T: acoustic transponder.

On those occasions when electrical or mechanical problems precluded use of RUM's propulsion system, the vehicle was gently lowered onto the starting position within a given sector. Samples were then taken at random locations along the arc determined by the reach of RUM's manipulator, with the constraint that at least 20 cm be allowed between cores.

Except for details of the vertical subsampling, the subcores used for macrofaunal work were processed as described by JUMARS (1975a). One of the four subcores from each core was selected (at random) for a detailed analysis of macrofaunal vertical dispersion patterns in the sediments. During extrusion, the core was sliced into four or five layers as follows (the zero reference level being the sediment–water interface): 0 to 1 cm, 1 to 3 cm, 3 to 5 cm, 5 to 10 cm, and on some occasions, 10 to 20 cm. A second subcore from each core was sliced into a 0- to 1-cm layer, a 1- to 10-cm layer and, sometimes, a 10- to 20-cm layer. The other two subcores were used for various purposes, but a 0- to 10-cm layer was often taken from one of them for macrofaunal analysis. All the results reported here are based on those macrofaunal taxa (*sensu* HESSLER and JUMARS, 1974) retained on a 0.42-mm sieve after gentle sieving.

All macrofaunal individuals were separated from the sediments and identified to the lowest taxon my taxonomic ability and a dissecting microscope would easily permit. Identification to the species level continues on a highly selective basis.

Transponder ranges were used to map the locations of the observed subcore abundances within the study area (Fig. 1). Initial inferences about the spatial arrangement of organisms in this region were drawn from these results by using various indices of dispersion (PATIL and STITELER, 1974; JUMARS, 1975a). In addition, the weighted forms of Moran's

I and Geary's c indices of spatial autocorrelation (CLIFF and ORD, 1973) were applied with a weighting of distance^{-2} (JUMARS, THISTLE and JONES, 1977); these measures test the null hypothesis of no spatial autocorrelation (random permutation of the variate values among the sample locations) against the alternatives that sample similarity either decreases or increases as the square of the distance between samples. The relationships of all possible pairs of samples were examined in this analysis (maximal connection *sensu* JUMARS *et al.*, 1977).

Following CLIFF and ORD (1973),

$$I = \left(\frac{n}{W}\right) \sum_{\substack{i=1 \\ i \neq j}}^{n} \sum_{j=1}^{n} w_{ij} z_i z_j \Big/ \sum_{i=1}^{n} z_i^2,$$

and

$$c = \left(\frac{n-1}{2W}\right) \sum_{\substack{i=1 \\ i \neq j}}^{n} \sum_{j=1}^{n} w_{ij} (x_i - x_j)^2 \Big/ \sum_{i=1}^{n} z_i^2,$$

where n is the number of samples, x_i is the variate value in sample i, $z_i = x_i - \bar{x}$, $w_{ij} = f$ (distance between samples i and j), and

$$W = \sum_{\substack{i=1 \\ i \neq j}}^{n} \sum_{j=1}^{n} w_{ij}.$$

The expected values of I and c are, respectively, $-(n-1)^{-1}$ and 1. It can be seen that I is closely related to the autocorrelation function and that c corresponds with the structure function normally employed in oceanographic studies of spatial relationships (e.g. DANTZLER, 1976). I and c are of particular utility in establishing statistically significant spatial autocorrelation among irregularly spaced samples and are sensitive to different departures from randomness (JUMARS *et al.*, 1977). As can be seen from inspection of the formulas above, I is the more sensitive to extreme x_i values, while c is the more sensitive to the similarity or dissimilarity of x_i values, regardless of their departure from the mean, $\bar{x}$.

Given a sample value at a particular point, the finding of no spatial autocorrelation allows no prediction of the values expected if additional samples were to be taken at neighboring locations. If positive spatial autocorrelation is found $[I > -(n-1)^{-1}; c < 1]$ on the neighborhood scale, values similar to that of the sample would be expected at neighboring sites. If, alternatively, negative spatial autocorrelation $[I < -(n-1); c > 1]$ on the neighborhood scale is the case, then quite dissimilar values would be expected of additional samples from the neighboring area. Because the magnitudes and signs of spatial autocorrelation coefficients describing real biological patterns are generally dependent upon inter-sample distances, it is dangerous broadly to equate patchy or regular dispersion patterns with positive or negative spatial autocorrelation. 'Patchiness', the byword of ecological dispersion pattern studies, may in fact be too ambiguous to be useful descriptively; it is likely to be supplanted by the more precise terminologies of autocorrelation (CHATFIELD, 1975) and of studies in fractional dimensions (MANDELBROT, 1977).

Only when significant positive spatial autocorrelation was found was the SYMAP mapping algorithm (DOUGENIC and SHEEHAN, 1975) used to generate mapping interpolations for the variate in question. Under other circumstances, any resultant map must be

cautiously interpreted. Interpolating when no spatial autocorrelation is present is analogous to drawing a regression line when the regression coefficient is nonsignificant. A better (i.e. more conservative) guess in both the case of the map and the line is simply that the variate will at all unmeasured locations (in space or along the independent variable axis) equal its overall mean value. The SYMAP algorithm was chosen because it utilizes the tested assumption directly by using a weighting of distance^{-2} in interpolation.

As suggested independently by several authors (CLIFF, HAGGETT, ORD, BASSETT and DAVIES, 1975; HENLEY, 1977; JUMARS *et al.*, 1977; SOKAL and ODEN, in press a,b) more complex patterns of spatial autocorrelation (than the monotonic one entertained via the distance^{-2} weighting) were investigated through the use of correlograms of I and c versus inter-sample distance. Inter-sample distances were divided into intervals, and setting $w_{ij} = 1$ for values in an interval, and $w_{ij} = 0$ otherwise, produced the plotted values of I and c. The procedure is similar to that of HENLEY (1977) except that the mean inter-sample distance within the interval is plotted against I and c. The plot of I versus distance is nearly identical to the standard correlogram of time series analysis (e.g. CHATFIELD, 1975, Fig. 2.1), while the plot of c versus distance is essentially the so-called 'variogram' of structural analysis (HUIJBREGTS, 1975). Isotropy is implicit in these approaches; given a particular inter-sample distance, it is assumed that the same degree of (dis)similarity between sample values will on the average be observed regardless of the compass orientation of the line drawn between them.

Taylor's 'frozen field' assumption, i.e. that the pattern remained unchanged during sampling, was made in the analysis of all dispersion patterns. It appears to be reasonable for infauna during the 1-month sampling period—in particular because the samples closest to each other were taken at nearly the same time (on the same lowering).

RESULTS AND DISCUSSION

Horizontal spatial structure

One hundred twenty-five quantitative subcores were obtained for analysis of horizontal dispersion patterns (Table 1). The measured range in depth (with the 'up-looking' sonar mounted on RUM) over all sampling locations amounted to only 5 m (1218 to 1223 m), and no reliable depth contours could be determined. The mean and variance of the number of macrofaunal individuals per subcore (0.01 m^2) were 54.4 and 209.8, respectively, showing roughly double the mean density found in previous box core sampling only 12.1 km away and at about the same depth ($\cong$ 1230 m; JUMARS, 1976). Although it would be tempting to attribute this disparity in abundance to sampling technique, DICKINSON (1977) has clearly shown that dramatic differences in abundance and species composition can occur over 100-km distances within the same deep-sea basin—even without appreciable variation in depth. It is thus impossible to assign the divergence in abundance between the two San Diego Trough sampling programs uniquely to location, timing, or sampling method.

The variance-to-mean ratio for numbers of macrofaunal individuals per subcore clearly indicates that the numbers are not independently drawn from a single Poisson distribution ($s^2/\bar{x} = 3.86$, $P < 0.001$). While the strength of the conclusion must be tempered somewhat by the fact that the subcores are not entirely spatially independent, nonrandomness in standing crop is indicated nonetheless (COCHRAN, 1963, Theorem 8.4). Moran's I and Geary's c with weightings of distance^{-2} (excluding subcores from cores E1 to E5, for

Table 1. Station data for cores used in the analyses. Subcore designations include the core number and subcore letter. Number of macrofaunal individuals given for 0- to 10-cm layer only. (H): used in horizontal analysis; (B): used in both horizontal and vertical analyses; (H', B'): positions unavailable for calculating inter-core distances (excluded from between-core I *and* c *calculations).*

Subcore designation	1973 Date	Lowering	Macrofauna	Subcore designation	1973 Date	Lowering	Macrofauna
E1Y (B')	15 Oct	5	56	E31W (B)	29 Oct	15	56
E1Z (H')	"	"	51	E31X (H)	"	"	74
E2Y (H')	"	"	49	E31Z (H)	"	"	50
E2Z (B')	"	"	74	E32X (H)	"	"	73
E3X (H')	"	"	43	E32Y (B)	"	"	66
E3Y (B')	"	"	74	E33W (B)	"	"	53
E4X (H')	"	"	69	E33Y (H)	"	"	65
E4Z (B')	"	"	45	E34W (H)	30 Oct	17	50
E5X (B')	"	"	74	E34Y (B)	"	"	47
E5Y (H')	"	"	44	E35W (H)	1 Nov	18	65
E6W (H)	16 Oct	6	45	E35X (H)	"	"	44
E6X (H)	"	"	37	E35Z (B)	"	"	67
E8W (B)	19 Oct	8	41	E36X (H)	"	"	56
E8X (B)	"	"	53	E36Y (B)	"	"	64
E9W (B)	"	"	33	E36Z (H)	"	"	32
E10W (H)	"	"	66	E37W (B)	"	"	59
E10X (B)	20 Oct	9	81	E37X (H)	"	"	74
E11W (H)	"	"	43	E37Y (H)	"	"	61
E11X (B)	"	"	74	E38W (H)	"	"	54
E12W (B)	"	"	65	E38Y (B)	"	"	68
E12Z (H)	"	"	60	E38Z (H)	"	"	77
E13Y (H)	"	"	59	E39X (H)	"	"	48
E13Z (B)	"	"	32	E39Y (B)	"	"	77
E14W (H)	22 Oct	10	29	E40W (B)	2 Nov	19	50
E14X (B)	"	"	49	E40X (H)	"	"	72
E14Y (H)	"	"	47	E41W (B)	"	"	51
E15X (H)	"	"	45	E41X (H)	"	"	52
E15Y (H)	"	"	63	E41Z (H)	"	"	51
E15Z (B)	"	"	73	E42W (H)	"	"	45
E16W (B)	"	"	87	E42X (H)	"	"	59
E16Y (H)	"	"	46	E42Y (B)	"	"	96
E17W (B)	"	"	53	E42Z (H)	"	"	53
E17Y (H)	"	"	31	E43W (H)	"	"	32
E18X (B)	"	"	48	E43X (H)	"	"	29
E18Y (H)	"	"	55	E43Z (B)	"	"	38
E19W (B)	23 Oct	12	52	E44W (H)	"	"	41
E19X (H)	"	"	72	E44X (H)	"	"	55
E19Z (H)	"	"	31	E44Y (B)	"	"	70
E20W (H)	"	"	33	E44Z (H)	"	"	51
E20X (B)	"	"	57	E45X (B)	3 Nov	20	48
E20Z (H)	"	"	45	E45Z (H)	"	"	60
E21W (H)	"	"	38	E46X (H)	"	"	51
E21X (H)	"	"	45	E46Y (H)	"	"	53
E21Y (B)	"	"	60	E46Z (B)	"	"	76
E22X (H)	"	"	66	E47W (B)	"	"	57
E22Z (B)	"	"	68	E47X (H)	"	"	51
E23X (H)	"	"	48	E47Y (H)	"	"	43
E23Z (B)	"	"	57	E47Z (H)	"	"	54
E24X (H)	29 Oct	15	84	E48W (H)	"	"	33
E24Y (H)	"	"	15	E48X (H)	"	"	35
E24Z (B)	"	"	68	E48Y (B)	"	"	59
E25Y (B)	"	"	50	E48Z (H)	"	"	53
E25Z (H)	"	"	47	E56W (H)	9 Nov	24	63
E26Y (H)	"	"	71	E56X (H)	"	"	56
E26Z (B)	"	"	61	E56Y (H)	"	"	45
E27W (B)	"	"	52	E57W (H)	"	"	51
E27X (H)	"	"	59	E57X (H)	"	"	82
E27Y (H)	"	"	33	E57Z (H)	"	"	30
E28W (H)	"	"	54	E58W (H)	"	"	51
E28X (B)	"	"	74	E58X (H)	"	"	55
E29W (B)	"	16	62	E58Y (H)	"	"	35
E29Y (H)	"	"	34	E58Z (H)	"	"	37
E29Z (H)	"	"	67				

which no transponder ranges were obtained), however, show no significant spatial autocorrelation in per-subcore abundances ($P > 0.05$).

To explore a broader range of alternative autocorrelative patterns, correlograms were produced (Fig. 2). The results indicate some spatial autocorrelation at inter-sample distances of 200 to 350 m, with a tendency toward positive spatial autocorrelation at the larger of these distances. The more traditional mapping criterion (KELLEY and MCMANUS, 1969) of among-station (among-core) versus within-station (within-core, among-subcore) variance (Table 2) also shows that a substantial portion of the variance is found on the within-core scale. Thus, although the number of individuals is not randomly distributed

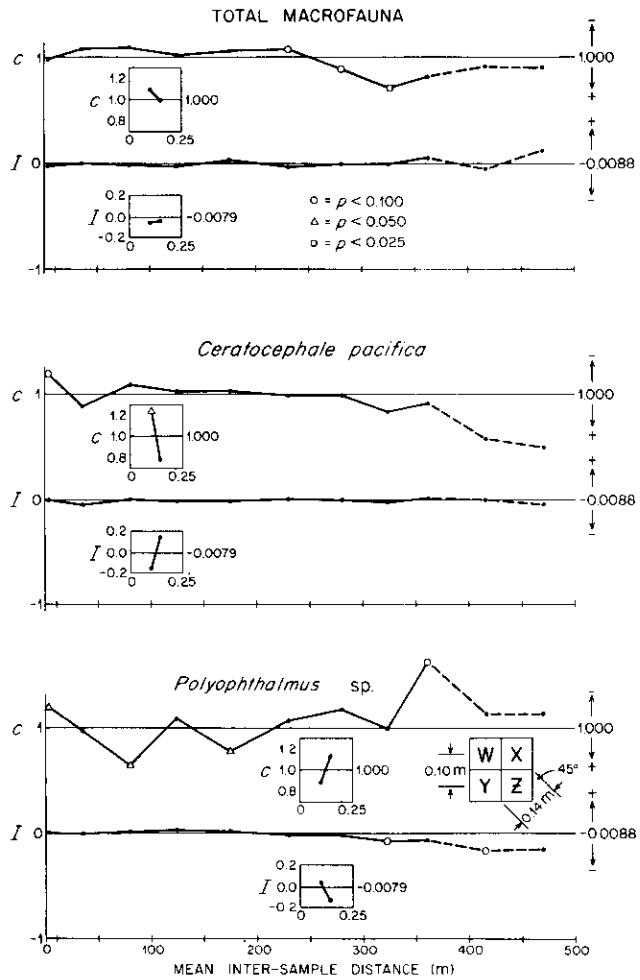

Fig. 2. Correlograms of I and c versus mean intersample distance. Intervals used in calculating I and c are shown by tick marks on the abscissa. Expected values are indicated by horizontal lines; deviations showing positive or negative autocorrelation are given in the right-hand margin. Dashed lines are based on few inter-sample distances; the magnitudes are unreliable. Insets show results on within-core scales and arrangement of subcores (W, X, Y, Z).

Table 2. Total macrofauna analysis of variance in abundance.

	df	SS	MS	
Among cores	48	8,870.08	184.79	$F_{48,76} = 0.819$
Within cores	76	17,141.92	225.55	$p > 0.10$
Total	124	26,012.00	209.77	

among subcores, the achieved density of samples does not readily permit contour mapping; a good estimate of the abundance at an unsampled locality within the triangle would simply be the mean density of 51.4 individuals 100 cm^{-2} (with some tendency to resemble samples 250 to 350 m away).

For those species thus far examined (Table 3) a lack of spatial autocorrelation (with

Table 3. Species examined for spatial autocorrelation using I *and* c *with a weighting of distance*$^{-2}$. *All except* Ilyarachna (*Isopoda*) *are polychaetes. Average abundances (numbers per subcore) are given.*

Species	$\bar{x}$	Species	$\bar{x}$
Ilyarachna profunda	0.16	*Fauveliopsis glabra*	0.45
Apistobranchus ornatus	0.16	*Glycera* cf. *capitata*	0.42
Braniella sp.	0.12	*Meiodorvillea apalpata*	0.16
Ceratocephale pacifica	1.35	*Ophelina* sp.	0.26
Cossura cf. *pygodactyla*	0.87	*Polyophthalmus* sp.	0.19
Cossura sp. A	0.31	*Sternaspis* cf. *fossor*	0.09
Exogone sp.	1.44		

the distance^{-2} weighting) appears to be the rule. There is, however, at least one dramatic exception. Even with due consideration for the degree of multiple testing involved and for the *a posteriori* nature of the examination, *Polyophthalmus* sp. (Polychaeta, Opheliidae) shows marked spatial autocorrelation. Extreme (high) values tend to occur in relatively close proximity, making the I coefficient larger than expected ($P < 0.00001$) and justifying interpolation of *Polyophthalmus* sp. density (Fig. 3).

Polyophthalmus sp. also demonstrates the difference between the analysis of variance (ANOVA) criterion (KELLEY and MCMANUS, 1969) and the spatial autocorrelation criterion for mapping. Assuming no *a priori* knowledge of the spatial pattern, spatial autocorrelation (with a weighting corresponding to the interpolation algorithm used in mapping) can be used to determine whether interpolation is justified. Within-station

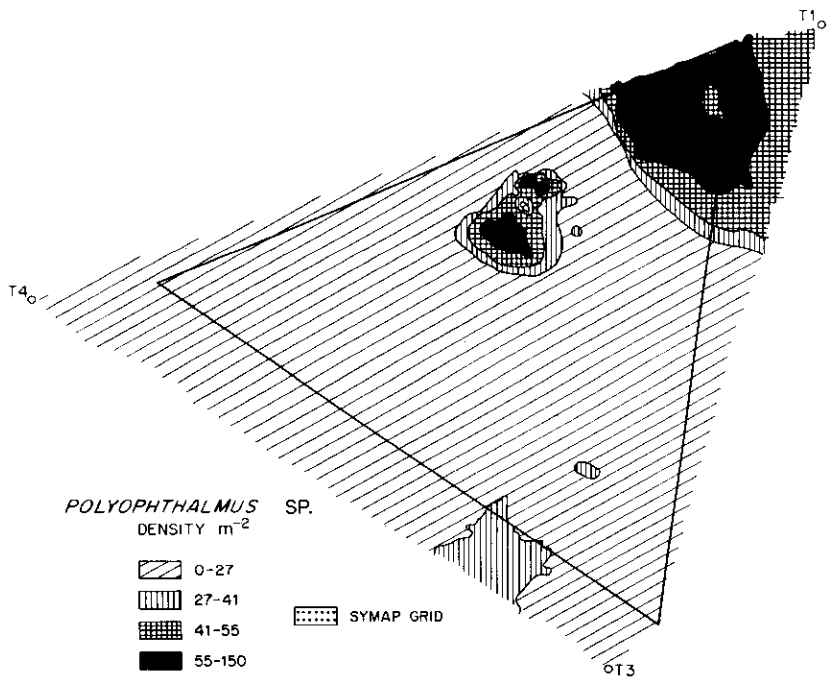

Fig. 3. Chart of estimated *Polyophthalmus* sp. density (see Fig. 1).

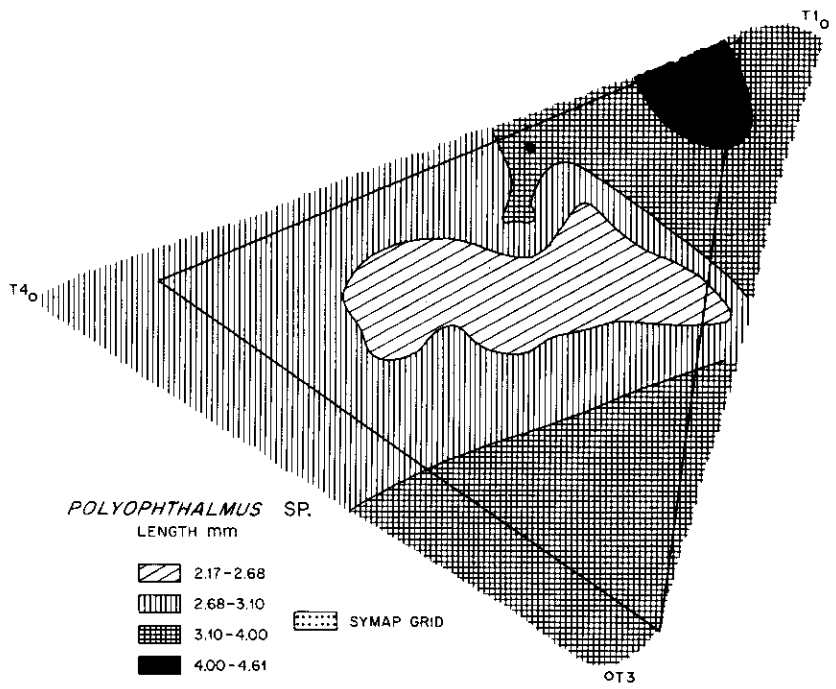

Fig. 4. Chart of estimated *Polyophthalmus* sp. individual size (see Figs. 1 and 3).

variance can then be used to specify a contour interval commensurate with sampling precision (KELLEY and MCMANUS, 1969). A high F ratio in the variances between stations (cores) versus within stations (among subcores within cores) is neither sufficient nor requisite to allow interpolation; nor is significant spatial autocorrelation a justification for a specific contour interval in mapping (cf. Table 4).

No confidence interval is implicit in the contours of Fig. 3. The SYMAP routine calculates interpolated values at each grid point (the grid spacing used to produce Fig. 3 being shown) and plots a given symbol for a specified range of densities. The contour lines of Fig. 3 simply enclose like symbols. Although no explicit degree of confidence in the contours is expressed, the finding of significant spatial autocorrelation implies that the mapped values are better estimates of local abundance of *Polyophthalmus* sp. than would be the overall mean abundance of 19.2 individuals m^{-2}. A better interpolation algorithm (than the one that uses distance^{-2}) might be derived from *Polyophthalmus* sp.'s correlograms (Fig. 2), but the achieved sampling density does not appear to warrant this sort of elaboration, and there are difficulties with the maximum likelihood approach (ORD, 1975).

In an attempt to find an explanation for the cause of the pattern in Fig. 3, sizes (length from tip of prostomium to posterior of last setiger, i.e. not including the anal tube, which is often lost or damaged) of the individuals were measured. Sizes of individuals also proved to be spatially autocorrelated (I larger than expected, $P < 0.005$, one-tailed), and a corresponding map was produced (Fig. 4). The two maps show good correspondence near the northeast vertex of the triangle, and Fig. 4 suggests the spatial coherence of cohorts, although locally differential growth and mortality cannot be discounted as

Table 4. Polyophthalmus *sp. analysis of variance in abundance.*

	df	*SS*	*MS*	
Among cores	48	10.975	0.2287	$F_{48,76} = 1.059$
Within cores	76	16.417	0.2160	$p > 0.10$
Total	124	27.392	0.2209	

alternative explanations. Because low-order trend surfaces did not provide a good fit to the data and coverage by samples was relatively sparse (SINGER and DREW, 1976), no formal map comparison (e.g. THRIVIKRAMAJI and MERRIAM, 1976) was attempted.

Among the possibilities classified by HUTCHINSON (1953), the causes of the observed pattern in *Polyophthalmus* sp. abundance thus remain unclear. Shallow-water species of similar morphologies are relatively active (CLARK and HERMANS, 1976). Other opheliids are known to be highly selective in choosing their larval settling locations (WILSON, 1952), and some species apparently migrate as juveniles and adults (AMOUROUX, 1974). Although their effects were not evident in bed forms, secondary circulation patterns in the benthic boundary layer may well have influenced larval settlement (HOLLISTER, SOUTHARD, FLOOD and LONSDALE, 1976). The pattern could thus have been vectorial or social (*sensu* HUTCHINSON, 1953). *Polyophthalmus pictus* has a remarkably short maturation period (GUERIN, 1971); the pattern might have been reproductively produced. The map (Fig. 3) and the correlogram (Fig. 2) are also suggestive of the 'travelling waves' (MURRAY, 1976) predicted of some coactive, predator–prey interactions. Although this *a posteriori* correlative approach cannot unequivocally establish cause and effect, it illustrates that scales from 0 to 350 m should not be ignored in entertaining possible causal processes and that size of the organism is likely to play a role, either directly or indirectly (e.g. as an indicator of age).

In contrast to the situation with *Polyophthalmus* sp. an *a priori* hypothesis was posed for *Ceratocephale pacifica* (Polychaeta, Nereidae). Although *C. pacifica* occurred at a lower density ($\bar{x} = 0.48$ individuals $0.01\,m^{-2}$) in the earlier San Diego Trough study (JUMARS, 1975b), it showed a trend toward a low variance-to-mean ratio among $0.25\,m^2$ cores (0.26, $P \cong 0.10$, one-tailed). A number of nereid species exhibit territoriality in the vicinity of their burrows (e.g. ROE, 1975). *Ceratocephale pacifica* also occupies burrows, and its gut contents consist almost exclusively of a wide range of both temporary and permanent meiofauna, Foraminifera (both agglutinated and calcareous) being by far the most frequent items (personal observations). Territoriality and the consequent spacing of individuals would not be surprising in this context.

What autocorrelative pattern would be expected if territoriality were indeed the case? Assuming that territories are exclusive, the average size of *C. pacifica*'s territories would be $< 73.96\,cm^2$ (the reciprocal of its mean density); a lower limit cannot be estimated precisely without knowing how many potential territories are unoccupied, but it probably exceeds the area swept by the length of the organism (roughly 0.2 to 2 cm). A simple representation of territoriality (Fig. 5) suggests that a first-order autoregressive model (CHATFIELD, 1975, p. 44) might be applicable. If the alignment of appropriately sized cores were perfect, as in the cross-hatched inset of Fig. 5, the coefficient (α) would equal -1.0. The imperfectly regular dispersion pattern of territories, their variation in size, and use of a corer of dimension not exactly equal to k would effectively make $\alpha > -1.0$ and cause the strength of the autocorrelation to drop rapidly with increasing inter-sample

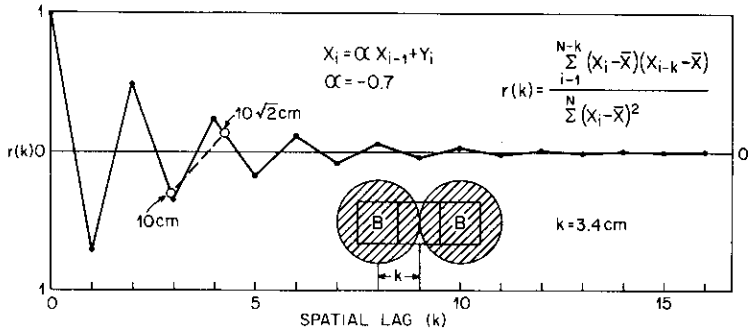

Fig. 5. Correlogram for a first-order autoregressive model with a negative coefficient (α). Y is a random variable with σ^2 = variance of x. Inset shows a hypothetical transect of three square cores across two circular territories (shaded) surrounding two burrow openings (B). Dashed line indicates conceivable segment of correlogram corresponding to intra-core distances for *Ceratocephale pacifica* (see Fig. 2). $r(k)$ is the autocorrelation coefficient often used in time series analysis (e.g. CHATFIELD, 1975). Note its close relationship to Moran's I.

distance or lag. Negative spatial autocorrelation is thus expected only on small, odd multiples of the average territory radius.

It is precisely the small scales on which significant spatial autocorrelation is observed (Fig. 2). The correlogram also shows that the variance-to-mean ratio (0.969, $P > 0.05$) for *C. pacifica* abundance among all 125 subscores may be grossly misleading. Because subcores having a side in common (centers 10 cm apart) are negatively autocorrelated in *C. pacifica* abundance, and subcores having a corner in common (centers $10\sqrt{2}$ cm apart) are positively autocorrelated, the total within-core variance in *C. pacifica* density is

Table 5. Ceratocephale pacifica *analysis of variance in abundance.*

	df	*SS*	*MS*	
Among cores	48	51.929	1.0818	
Within cores	76	110.583	1.4550	$F_{48,76} = 0.744$
Total	124	162.512	1.3106	$p > 0.10$

relatively high (Table 5). A regular dispersion pattern thus cannot be expected to produce a low variance-to-mean ratio under all sampling designs.

Again, no mapping of *C. pacifica* density over the study triangle is justified. The comparison of dispersion patterns in *Polyophthalmus* and *Ceratocephale*, however, suffices to show that it is naive to use single-valued indices to summarize complex dispersion patterns and that better (more nearly 'sufficient' in the statistical sense) descriptions lead to a narrowing of the possibilities for genesis of these patterns. Further observations and experiments should focus on the centimeter to decimeter scales for *C. pacifica* but should include larger scales for *Polyophthalmus* sp.

Vertical spatial structure

The results of a layer-by-layer examination of 45 subcores (Table 1) are summarized in Fig. 6. Only 20 of these cores had layers taken in the 10 to 20-cm depth range, so the

number observed there was multiplied by 2.25 in producing the figure. As expected of a region characterized by gradual sedimentation (GRIGGS, CAREY and KULM, 1969), macrofaunal individuals were concentrated near the sediment–water interface.

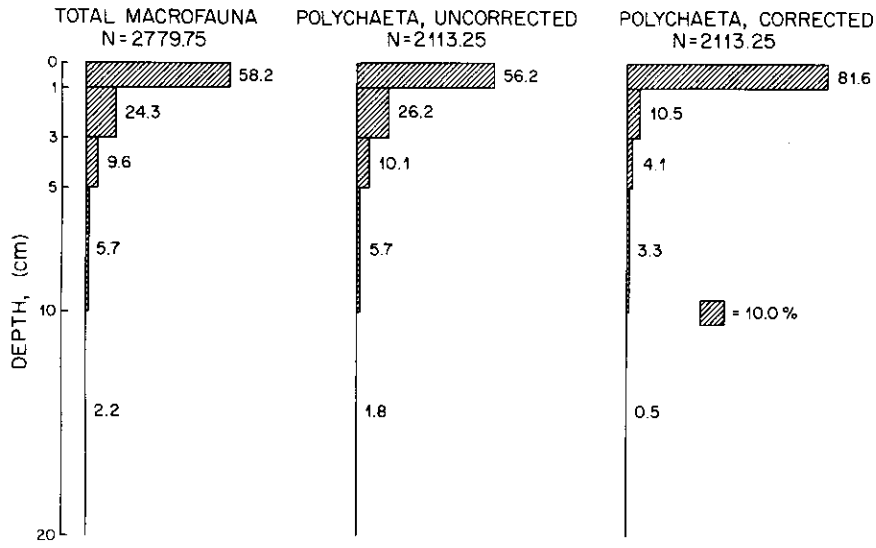

Fig. 6. Depth-frequency distribution of all macrofauna and of polychaetes alone. Correction applied as described in text; *N*: total number of individuals.

Because burrowing and withdrawal into tubes are natural responses to attempted predation and to coring (not to mention the trauma of changing temperature and pressure during retrieval), these results must be interpreted cautiously. No existing sampling device accurately retains organisms in the sediment layer which is their normal region of activity. In Polychaeta, for example, it may be possible to estimate the magnitude of the error by classifying species with regard to their feeding strata in the sediments. According to the scheme of JUMARS and FAUCHALD (1977), all the surface feeding polychaetes were reassigned to their presumed life position in the uppermost 1-cm layer of the subcores. Doing so substantially changes the vertical dispersion pattern (Fig. 6) and warns against ready acceptance of observed depth–frequency distributions.

There are, however, obvious and no doubt real differences in vertical dispersion patterns among taxa. A trivial example is found in the definitions of infauna and epifauna. Vertical segregation at lower taxonomic levels is also apparent (Fig. 7). The reduced prostomial appendages and narrowed prostomium in *Meiodorvillea apalpata* (JUMARS, 1974) apparently correspond with its burrowing habit. At an even finer taxonomic level, the vertical distribution of *Cossura* cf. *pygodactyla* abundance also differs significantly from that of its undescribed congener, *Cossura* sp. A [$P < 0.05$, two-tailed, by the conservative Kolmogorov–Smirnov two-sample test; KIM and JENNRICH, (1970)]. Because cossurids normally inhabit the subsurface layers, these results may be more reliable than those for polychaetes as a whole.

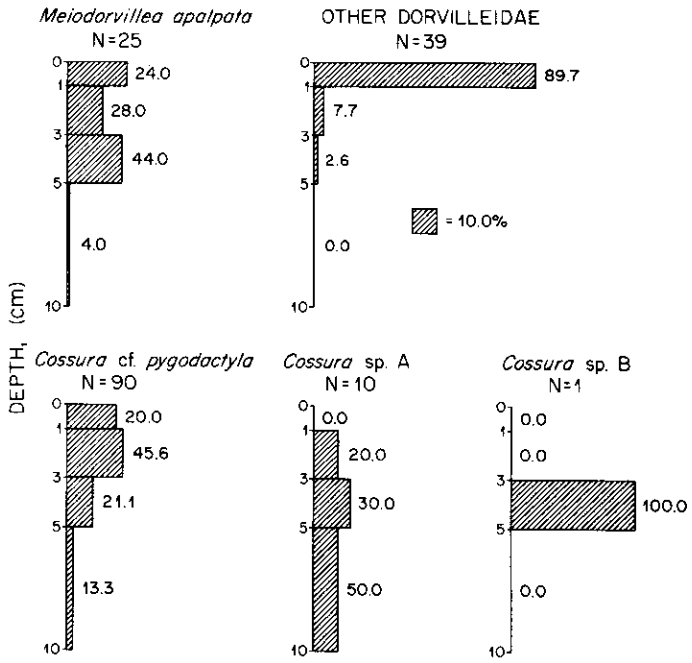

Fig. 7. Depth–frequency distributions of Dorvilleidae and Cossuridae (Polychaeta). *N*: total number of individuals.

Implications for species diversity maintenance

The potential role of vertical habitat segregation as a mechanism of resource partitioning is highlighted by the above examples. Vertical habitat segregation, however, is also observed among closely related shallow-water species (e.g. HOWARD and ELDERS, 1970). It thus is not clear without quantitative comparison whether vertical habitat segregation plays a major role in accounting for higher deep-sea species diversity. The limited number of species thus far examined (Table 3) does not yet permit such quantitative comparison.

Neither is the role of horizontal habitat segregation in resource partitioning clarified by the limited number of examples presented. As might be expected of an abundant, territorial species, *C. pacifica* has no congeners (or confamilial species) among the samples. *Ophelina* sp. (Opheliidae), the closest relative of *Polyophthalmus* sp. found at the study site, showed no apparent numerical response to the local variations in *Polyophthalmus* abundance. Both opheliid species were found only in the uppermost centimeter of sediment.

The present data do, nonetheless, add another dimension (the vertical) and another scale (0.1 to 500 m) to the discussion of patchiness versus deep-sea macrofaunal species diversity as summarized by JUMARS (1976). They show that meso-scale processes may be important in population regulation for some species (e.g. *Polyophthalmus* sp.) and thus may also be important for community evolution (WILSON, 1976). Failure to detect nonrandomness in most species' dispersion patterns—even with precise navigation and the present battery of statistics—supports (but by no means proves) the contention that most deep-sea species depart little from random dispersion patterns. The finger again points to the small scales (those experienced by individual organisms) in further investigation of processes maintaining deep-sea species diversity.

Determining the modes of resource partitioning among deep-sea species thus remains a major problem. Although both vertical and horizontal habitat partitioning have not been ruled out as potentially important mechanisms, the deep sea continues to provide an inadequately explained exception to FENCHEL, KOFOED and LAPPALAINEN's (1975) generalization that the number of coexisting detritus feeders is usually low.

Implications for bioturbation modeling

The implications for bioturbation modeling are clearer than those for diversity maintenance. *Polyophthalmus* sp.'s effects on the sediment, for example, cannot be expected to be spatially uniform or random on short time scales. Small cores 10 cm apart will tend to differ in the observed effects of *C. pacifica* burrowing—perhaps more than will cores 350 m apart (Fig. 2). If the local degree of bioturbation is proportional to total (numerical) macrofaunal standing crop, then perhaps the horizontal scale of observation is not so important in the 0- to 500-m range.

The vertical distribution of numbers of macrofauna (Fig. 6), when taken together with information on feeding mechanisms at all depths in the sea (JUMARS and FAUCHALD, 1977; JUMARS and HESSLER, 1976) suggests that a two-compartment model [zone of mixing versus zone of no mixing; reviewed in GUINASSO and SCHINK (1975)] could be markedly improved. Not only would a more realistic model include a gradually decreasing mixing coefficient with depth in the sediment, as has often been suggested, but this region of continuous change would be overlain by a thin layer (perhaps a few sediment grains thick) of dramatically more intense bioturbation. Half the polychaetes in most deep-sea areas, for example, feed and defecate on the sediment surface (JUMARS and HESSLER, 1976, Fig. 4), though most of them traditionally would be classified as infaunal.

The situation would be even more complex if either the subsurface or surface feeders were locally aggregated within a small region. Luckily, however, calculation of I and c for the surface and subsurface components taken individually (distance^{-2} weighting in the samples of Table 1) shows no tendency toward nonrandomness in the horizontal plane.

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Note added in proof

I have recently been made aware (by R. Beckwitt and D. Wartenberg, respectively) of two errors in the formulae printed on p. 122 of JUMARS *et al.* (1977). The computer program used in both that paper and the present one incorporates the following (corrected) forms:

$$b_2 = \frac{n \sum_{i=1}^{n} z_i^4}{\left(\sum_{i=1}^{n} z_i^2\right)^2}$$

$$c_z = 1 - \{y_z \sqrt{[\mathrm{var}(c)]} + (n-1)^{-1} \sqrt{(10\alpha)}\}.$$