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Patch structure of benthic populations on an intertidal sandflat

Benthos
Intertidal sandflats
Crowding
Western Atlantic
Spatial models

Benthos
Sables littoraux
Encombrement
Atlantique occidental
Modèles spatiaux

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ABSTRACT

Variation in density within patches of benthic animals cannot be detected by autocorrelative techniques such as spectral analysis. A general model was developed to distinguish mosaic patchiness, characterized by uniform crowding, from clusters, characterized by reduced crowding away from the center. Mosaics and clusters were identified in the pelecypod *Gemma gemma* along two intertidal transects. Clusters were identified in a sedentary polychaete *Clymenella torquata*, an errant polychaete *Nephtys caeca*, and an actively burrowing pelecypod *Tellina agilis*.

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RÉSUMÉ

La structure spatiale des animaux benthiques des sables de la zone de marées

Les techniques autocorrélatives, telles que l'analyse spectrale, ne permettent pas de distinguer la structure spatiale des agrégats d'animaux benthiques. Une méthode générale a été développée afin de distinguer les distributions en mosaïque, caractérisées par une densité uniforme à l'intérieur de chaque groupe, et les distributions en agrégat, caractérisées par une densité qui dépend de la distance au centre de l'agrégat. Les distributions en mosaïque et en agrégat ont été identifiées pour le pélécypode *Gemma gemma* le long de deux radiales benthiques; les distributions en agrégat l'ont été pour le polychète sédentaire *Clymenella torquata*, le polychète errant *Nephtys caeca*, et le pélécypode fouisseur *Tellina agilis*.

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INTRODUCTION

Benthic populations inhabiting marine sediments in shallow water exhibit significant spatial variability at scales ranging from a few centimeters (Levinton, 1972) to several kilometers (Cassie, Michael, 1968). At least 3 spatial patterns have been described: gradients, clusters, and mosaics. Intertidal gradients (change in density with change in elevation) were demonstrated by Stephen (1930) and were described statistically by Hughes and Thomas (1971). Gradients have been related to several biological and physical factors (Mills, 1969). Clustering can be defined as a monotonic decrease in density with increasing distance from a point location. Clustering has been attributed to mechanisms such as selective settlement of pelagic larvae (Thorson, 1966), release of juveniles from a point source (Buzas, 1968; Jackson, 1968), environmental heterogeneity (Connell, 1963) and hydrodynamic sorting (Gilbert, 1968; Eckman, 1979). Mosaics can be defined as regions of high density adjacent to regions of lower density. Mosaic distributions of animals in shifting substrates were first described by Fager (1964) and may result from either physical or biological disturbance; recent studies have been summarized by Thistle (1981).

Population processes in benthic environments depend on which of these spatial structures is present. If clusters are present, competitive interactions based on rate of contact with neighboring organisms will depend on distance from a cluster center. If mosaic boundaries are present, rate of contact will depend only on whether organisms are inside or outside a boundary. Predatory interactions based on rate of prey encounter will depend on foraging direction within a cluster, but will be independent of foraging direction within a mosaic patch.

Methods for distinguishing cluster and mosaic structures have not been developed for infaunal populations, where spatial structure cannot be assessed visually because organisms are hidden from view. Methods based on spectral analysis (Platt, Denman, 1975), spatial auto-correlation (Jumars *et al.*, 1977; Sokal, Oden, 1978), and variance-distance curves (Greig-Smith, 1964) all produce an estimate of an auto-covariance sequence that is at best a description of some aspects of spatial dependency within a population (Cox, Isham, 1980). Auto-covariances do not distinguish patches with uniform density (mosaic patchiness) from patches where density decreases away from the center (clusters). In order to distinguish cluster and mosaic structures along benthic transects I used an iterative method based on the following general model:

$$1/s\, ds/d|x| = k \tag{1}$$

where s is density of organisms (animals core^{-1}):

$|x|$ is the distance from a cluster center or mosaic border;

k is the rate of attenuation with distance from a cluster center or a mosaic border.

For clusters, $k>0$ and the shape of the patch is:

$$\ln s = \ln s_0 + k|x| \tag{2}$$

s_0 is animal density at the patch center;

k is the ratio of attraction to diffusivity (Okubo, 1980).

For mosaics $k=0$ and the shape of the patch is

$$s = d_1, \quad x>0 \tag{3a}$$

$$s = d_2, \quad x<0 \tag{3b}$$

d_1 and d_2 are average densities on either side of the border.

METHODS

Two transects were made along the eastern side of White Flat (42°00′N, 70°40′W) located in Plymouth Harbor, a coastal lagoon north of Cape Cod and 50 km south of Boston. Both transects were at right angles to the direction of flow off the flat during the falling tide. Transect A, 40 m long, was completed at low tide on 16 July 1976. Transect B, 20 m long, was completed at low tide 2 days later and 500 m to the south of transect A. Cores were collected at 2 m intervals along each transect by pushing a 10 cm diameter plastic tube to a depth of 10 cm into the substrate. Each core was broken free of the surrounding sediment and washed on a 1 mm sieve in the field. All organisms retained on the sieve were kept alive in plastic containers with fresh seawater. Animals were sorted by species within 10 hrs. of collection.

The model was evaluated by least squares regression (Sokal, Rohlf, 1981). Each point along a transect was first tested as a cluster center. In the cluster model, the logarithm of density was regressed against distance from the putative center of the cluster. Each position between sampling points was then tested as a border. In the border model, density was regressed against either zero or one, depending on which side of the putative border the core occurred. This regression is equivalent to performing a t-test; the relation between t and the explained variance, R^2 is:

$$R^{-2} = 1 + t^{-2} m$$

where m = degrees of freedom. Calculation of R^2 for the border model permits direct comparison with calculations of variance explained by the cluster model.

Patch size was evaluated by using a hill-climbing criterion. If a cluster were present and the choice of central point were correct, then explained variance will remain high as successively more distant point are added to the regression, until the edge of the patch is reached. Regression is sensitive to large outliers, so one large value outside the patch will substantially reduce the level of explained variance, R^2. If a border were present then R^2 will remain high as successively more distant points are added to the regression, until a large value is encountered outside the patch, or until a low value is encountered on the far side of the patch. The computational procedure was to take the 4 nearest points to a putative cluster center or putative border, compute R^2, and test for significance. The criterion for significance was:

$$(n-3)R^2(1-R^2)^{-1} = F < F_{.05\,(1,\, n-3)},$$

where n is the number of points in the regression. Three degrees of freedom were subtracted because the model has 3 parameters-location, maximum count, and rate of cluster attentuation in the case of the cluster model, or border location, density on one side, and density on the other side in the case of the border model. If the regression was significant then the next closest point was included and the regression was recomputed. If two points were equidistant from a putative border or cluster center, both points were added to the regression before computing R^2. The process was repeated until R^2 was not significant. Patch border was defined by the maximum significant R^2.

The minimum detectable patch size, using this procedure, is 2 L for a mosaic, and 5 L for a cluster, where L is the separation between cores along the transect. This procedure, when applied to randomly re-ordered data, resulted in one significant regression (at $p=0.05$) in 19 putative borders along a 20 sample transect. The procedure is based on the ratio of the explained to total variance (R^2), so its sensitivity will be high for closely spaced samples (L small), or where deviation from the general model is small.

RESULTS AND DISCUSSION

A total of 18,958 organisms belonging to 21 species was sieved from the 20 cores collected along transect A. Another 16,541 organisms, belonging to 28 species, were sieved from the 10 cores collected along transect B. Analysis was restricted to the 5 most abundant species within each transect (Tab. 1). The distribution of these species along the transects is shown in Figures 1 and 2. The count marked with a question mark was considered unreliable, and dropped from subsequent analysis.

Table 1

Mean number and variability of counts of 6 species collected at 2 m intervals along 2 intertidal transects. n = number of counts. Units (Y and s) are organisms per 10 cm diameter core.

	Mean (Y)	Variance (s^2)
Transect A (n = 20)		
Clymenella torquata	3.00	5.58
Nephtys caeca	3.35	5.92
Gemma gemma (n = 19)	942	26 218
Tellina agilis	5.45	11.10
Nassarius trivittatus	0.35	0.45
Transect B (n = 10)		
Clymenella torquata	6.00	15.78
Nephtys caeca	4.10	4.77
Gemma gemma	1 623	263 073
Tellina agilis	3.00	4.44
Acanthohaustorius millsi	1.30	1.12

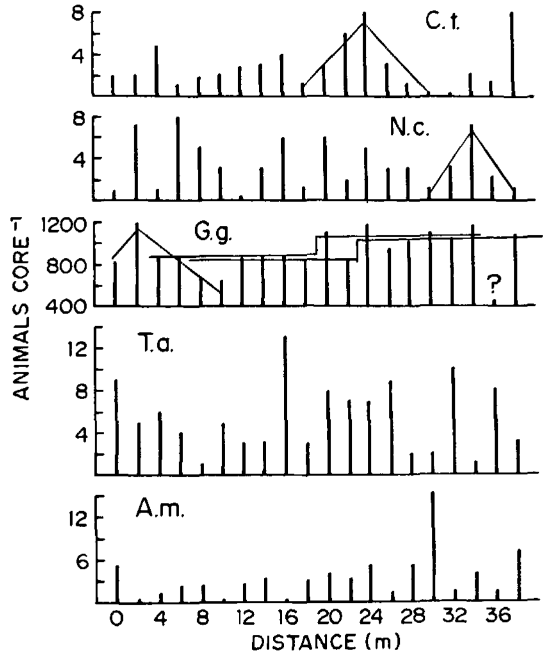

Figure 1

Invertebrate abundance along transect A on White Flat in Plymouth Harbor. Cores are 10 cm in diameter and 10 cm deep. C.t. = Clymenella torquata, *N.t.* = Nephtys caeca, *G.g.* = Gemma gemma, *T.a.* = Tellina agilis, *A.m.* = Acanthohaustorius millsi.

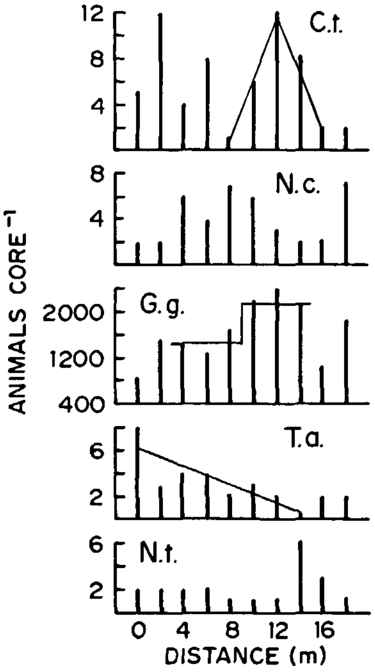

Figure 2

Invertebrate abundance along transect B on White Flat in Plymouth Harbor. N.t. = Nassarius trivittatus

Three significant borders were identified along the 2 transects (Tab. 2). All 3 occurred in the same species, the Amethyst gem clam *Gemma gemma*. Patch widths, based on the hilltop criterion, ranged from 6 to 16 m. Significant borders are shown in Figures 1 and 2. Five significant clusters were identified along the 2 transects (Tab. 2). Of the 5 clusters, 2 occurred in a sedentary polychaete (*Clymenella torquata*), one occurred in an errant polychaete (*Nephtys caeca*), one occurred in an actively burrowing clam (*Tellina agilis*), and one occurred in a less active clam (*Gemma gemma*).

Cluster size was small in the two polychaetes – attenuation rates were 48.1% m^{-1} in *N. caeca*, 35.8 and 57.2% m^{-1} in *C. torquata*. Cluster size were larger in the 2 pelecypods – attenuation rates were 6.6% m^{-1} in *G. gemma*, 10.8% m^{-1} in *T. agilis* (Tab. 2). Significant clusters are shown in Figures 1 and 2.

These results were based on repeated testing so it was of interest to compute the number of significant patches

Table 2

Significant patches identified by mosaic and cluster models, using an iterative fitting procedure and a hilltop termination rule (see text). Transects are located on White Flat, Plymouth Harbor, Massachusetts. df = degrees of freedom; R^2 *= explained variance; n = number of cores.*

Mosaic model	Border location	Maximum R^2	df 1, n−3	Patch width
Transect A				
Gemma gemma	23 m	0.59	1,13	16 m
	19 m	0.63	1,13	16 m
Transect B				
Gemma gemma	9 m	0.90	1,3	6 m

Cluster model	Center location	Maximum R^2	df 1, n−3	Attenuation $\%m^{-1}$
Transect A				
C. torquata	24 m	0.81	1,4	35.8
Nephtys caeca	34 m	0.97	1,2	48.1
Gemma gemma	2 m	0.82	1,3	6.6
Transect B				
C. torquata	12 m	0.86	1,2	57.2
Tellina agilis	0 m	0.74	1,5	10.8

expected by chance alone. The number of possible border locations was $(19\times 4)+18+(9\times 5)=139$. The number of possible cluster centers was $(4\times 20)+19+(5\times 10)=149$. The expected number of significant patches was 2.9 at $p=0.01$, 0.3 at $p=0.001$. The observed number of significant patches was 6 at $p=0.01$, 2 at $p=0.001$.

Numerical simulations were used to test whether the technique incorrectly identified clusters as mosaics, or *vice versa.* Two structured series of numbers and one series of random numbers (Tab. 3) were used in the simulations. A Fortran subroutine (GGPER) from the International Mathematics and Statistics Library (IMSL 1982) was used to obtain 100 random rearrangements of the random series in Table 1. These were added to each of the 2 structured series to obtain 100 simulated mosaics and 100 simulated clusters.

Table 3

Structured and random series of numbers used to simulate clusters and mosaics.

Location	Cluster	Mosaic	Random
1	0	0	4
2	0	0	6
3	0	0	8
4	1	0	7
5	6	0	0
6	36	10	8
7	6	10	4
8	1	10	9
9	0	10	5
10	0	10	8
Sum	50	50	59

Iterative analysis with the mosaic model resulted in 13 incorrect identifications of clusters in 2700 tests, 101 incorrect identifications of mosaic locations in 2400 tests (Tab. 4). Iterative analysis with the cluster model resulted in 23 incorrect identifications of mosaic boundaries in 3000 tests, no incorrect identifications of cluster locations in 2700 tests (Tab. 5). The rate of incorrect identification was 0 to 4% when the criterion for significance was set at 5%.

Table 4

Analysis of 100 *simulated mosaics and* 100 *simulated clusters, using mosaic model. Values are number of significant tests at* $p=0.05$.

Location	Width	Mosaic	Cluster
1-2	3	9	8
	4	5	0
	5	1	0
2-3	3	7	2
	4	0	0
	5	0	0
3-4	3	6	0
	4	1	0
	5	1	0
4-5	3	7	0
	4	0	0
	5	0	0
5-6	3	93	0
	4	0	0
	5	0	0
6-7	3	19	0
	4	17	0
	5	17	0
7-8	3	2	0
	4	0	0
	5	0	0
8-9	3	1	0
	4	0	0
	5	0	0
9-10	3	6	3
	4	2	0
	5	0	0

Table 5

Analysis of 100 *simulated mosaics and* 100 *simulated clusters, using cluster model. Values are number of significant tests at* $p=0.05$.

Location	Width	Mosaic	Cluster
1	4	0	0
	5	0	0
	6	0	0
2	4	3	0
	5	0	0
	6	0	0
3	4	0	0
	5	0	0
	6	0	0
4	4	0	0
	5	0	0
	6	0	0
5	4	0	0
	5	0	0
	6	0	0
6	4	0	68
	5	0	6
	6	0	1
7	4	2	0
	5	1	0
	6	1	0
8	4	11	0
	5	0	0
	6	0	0
9	4	3	0
	5	0	0
	6	0	0
10	4	2	0
	5	0	0
	6	0	0

Clustering was observed in several species. Cluster centers did not co-occur, which indicates that clustering results from species-specific processes. Selective settlement by larvae is a potentially important mechanism in populations of sedentary species such as *C. torquata.* Kineses and taxes are potentially important mechanisms in actively burrowing species. A more extensive study would be needed to determine the mechanisms responsible for clustering.

Mosaic patchiness was observed in only one species, *G. gemma.* Significant borders were not observed in co-occurring species. This suggests that mosaic-producing processes are less important than clustering processes in the generation of patchiness in these species at a scale of several meters. Mosaic-producing processes, such as gouging by horsheshoe crabs (*Limulus polyphemus*), may be more important at smaller spatial scales. More closely spaced cores of smaller diameter would be needed to investigate patch structure at the scale of centimeters rather than meters.

The method used to distinguish cluster and mosaic patchiness could be extended to measurements of rates (emigration, immigration, birth, death). Theoretical treatments of spatial variation in rates assume either a mosaic or a continuous distribution of rates in a plane (*e.g.* Pielou, 1965). An objective method of distinguishing mosaic and clustering processes can be used to choose an appropriate model.

Clustering has a number of important implications for benthic populations. The first is that crowding, and the potential for competitive interactions, is not uniform within patches. Competitive interactions based on rate of contact with nearest neighbors is likely to be higher toward the center of a cluster than toward the periphery. Competitive models based on uniform density within patches may not be appropriate for benthic organisms living on sandflats. For example, Lloyd's (1965) index of mean crowding, which is a measure of the number of potential contacts over the ambit of an individual, could be estimated from mean density and variance in density only if the ambit of the individual was greater than the observed patch size, which was on the order of 10 m in some species along the study transects. In cases of smaller ambit, the number of potential contacts will be far higher near the center of a cluster than near the periphery.

The second implication is that distance between infaunal organisms, and hence rate of discovery by predators, is not uniform within patches. The probability of contact between predator and prey will increase as predators move toward the center of a cluster and this is likely to result in higher predation rates near the center than near the edge of clusters. Foraging models based on uniform density within patches may not be applicable to predators on intertidal infauna.

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