

# Methods for Measurement of Community Structure in Deep-Sea Macrobenthos\*

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## Abstract

Methods are compiled and developed for the analysis of community structure in the deep-sea benthos. These methods are tailored to the conditions of high species diversity and low standing crop. A new modification of the 0.25-m<sup>2</sup> box corer is described. Fisher's index of dispersion is adapted by using each species as a replicate. When the resultant summary statistic is partitioned in the illustrated manner, it is possible to determine whether species indeed behave as homegeneous replicates of a single dispersion pattern, or, alternatively, whether habitat partitioning is indicated. Species are also used as replicates in a modification of Pielou's "joins" technique of determining whether high-density and low-density areas of given species are randomly mingled. An indirect analytical approach is developed which proposes that, if an environmental grain of relatively small dimensions has been important in structuring the community, species which have smaller ambits will be more diverse than species having larger ambits.

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## Introduction

Hessler and Sanders (1967) demonstrate that the benthic fauna of the deep sea is highly diverse. The high diversity values are, however, derived from trawls traversing roughly 1 nautical mile. Consequently, the possibility of having crossed a mosaic or gradient of conditions, each segment with its characteristic and correspondingly less diverse fauna, must be entertained. MacArthur (1969) and Diamond (1973), for example, display the importance of patchiness in determining how many species occur in a given area. With deep currents generally below 5 cm·sec<sup>-1</sup> and with sedimentation rates usually ranging from but 1 to 100 mm/1000 years, the establishment and persistence of small-scale environmental heterogeneity appears to be a likely possibility.

Furthermore, until animal dispersion patterns (*sensu* Pielou, 1969, p. 83)

are adequately known, a number of often-used techniques rest on untested assumptions. Among these procedures is Sanders' (1968) rarefaction estimator for determining the number of species expected in a subsample. Fager (1972) has shown the method to be biased when individuals are variably aggregated between species. Even with Hurlbert's (1971) statistically more consistent and efficient estimator,  $E(S_n)$ , randomness in species' dispersion patterns is implicit.

For the adequate analysis of animal dispersion patterns, the low density at which most deep-sea species exist (Sanders and Hessler, 1969) necessitates the use of powerful statistical techniques and of large or numerous samples. The following study treats a combination of field and analytical methods which appears to meet these criteria.

## Sampling Gear and Procedure

In order to investigate the patterns of species' dispersion on and in the bottom, the largest available quantitative sampler which would yield samples of uniform size was chosen. The basic device is the 0.25-m<sup>2</sup> United States

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Naval Electronics Laboratory spade (or box) corer (Hessler and Jumars, 1974). For more detailed analysis of dispersion patterns, the box of the corer was subdivided into 25 contiguous subcorers, each 10 cm x 10 cm outside dimensions. These subcorers were constructed of eighth-inch (3.175 mm) thickness, square [4 inches (10.16 cm) outside dimension], extruded aluminum tubing. They were milled to fit the 50 cm x 50 cm inside dimensions of the core box, sharpened so as to take a bite of 10 cm x 10 cm, and bolted to a frame which was in turn bolted to the core box. To prevent animals from moving between subcores after capture, each subcore was covered with a screen of 0.42-mm aperture, and the screening under the flap valves of the corer was removed to facilitate water flow and thereby minimize bow-wave effects (Wigley, 1967). The device was dubbed the "vegematic" modification because of its resemblance to a similarly named vegetable chopper.

Except for the removal of subcores, the sampling procedure is as described by Hessler and Jumars (1974). When the full core box comes on deck, each subcore is unbolted, and its covering screen rinsed clean into a 0.42-mm aperture sieve through which the subcore's overlying water is also decanted. A 10-cm thickness of the core is then extruded with a plunger of 4 inch x 4 inch (ca. 9.4 cm x 9.4 cm) wood gasketed at the top with a double layer of automobile inner tube. This 1-l cube of surface sediment is sliced into the sieve and washed free of smaller particles by gentle manipulation of the sieve in a washtub of seawater. Fixation, preservation, and sorting are accomplished as outlined by Hessler and Jumars (1974).

#### Sampling Design

While every scale from that containing all individuals in a community to that containing only one is of some biological interest, certain scales are of prime importance in the discussion of community diversity and its maintenance. Most obviously, the scale which contains all the species in the community is of immediate concern. At least ideally, this scale would contain all the species which, on an evolutionary time scale, have adapted to each other's presence. Disparity of species' geographic ranges causes difficulty with the concept, but the fact that species-area relations generally follow an

orderly pattern of decreasing rate of addition of species with increasing area both supports the validity of the concept and permits the treatment of community diversity, or an approximation thereof, on the basis of samples.

Because deep-sea community boundaries are impossible to draw *a priori*, individual cores are taken as close as possible to a single oceanographic station, which serves as the sampling site. The cores may not thereby represent a random sample with respect to community diversity, but the taking of the samples close to each other avoids, as much as is possible, a more serious source of error: close clustering minimizes the probability of crossing large-scale gradients and intercommunity boundaries of no direct interest in the question of within-community habitat partitioning.

Of nearly equal importance is what might be called an ambit (Lloyd, 1967) or "neighborhood" scale. This scale may be conceptualized as containing most of the individuals with which a given animal interacts from day to day. Clearly, considerations on this scale are the determinants of the intensity of biological interactions such as competition or predation. Again, boundaries for such a neighborhood are impossible to draw *a priori*, but the vegematic modification was designed in hopes of bracketing this scale for many members of the macrofauna.

#### Sampling Bias

Because trapped water may rush out at the bottom edges of the core box just before impact with the sediment, a bow wave would be expected to act with greatest severity on the peripheral 16 subcores of a vegematic core. One might, therefore, expect a reduction in the number of animals per subcore in these subcores. To examine this possibility, the null hypothesis is proposed - that the median abundance of animals for the inner 9 subcores equals that for the peripheral 16 - and is tested with a 1-tailed Mann-Whitney *U* procedure.

To approximate the magnitude of the apparent error, the central 9 subcores are used as an internal standard to estimate the efficiency of capture. "Efficiency of capture may be defined as the ratio of the number of animals in the volume of deposit collected by the grab, to the number present in the same volume *in situ*" (McIntyre, 1971, p. 144). Thus, apparent capture efficiency of the entire 0.25-m<sup>2</sup> corer

(expressed as per cent) equals 100 times the core total of individuals observed divided by the total for the inner 9 subcores alone multiplied by 25/9. Where an apparent error of the observed magnitude could bias further analyses, the peripheral 16 subcores are excluded from the calculations.

### Analytical Methods

No point estimator (single-valued diversity index) is adequate to describe species' diversity over the entire range of sample sizes of interest in the current study of the relationship between species' diversity and species' dispersion patterns. For this representational purpose, the suitability of Hurlbert's (1971) expected number of species,  $E(S_n)$ , is explored. His procedure allows the prediction of the expected number of species in a hypothetical subsample given that the distribution of individuals among species in the total sample is known. Implicit in this estimate is the assumption that the subsample is randomly drawn (without replacement) from the population represented by the total sample, i.e., that a multivariate hypergeometric distribution (Johnson and Kotz, 1969) is strictly applicable. If the dispersion patterns of individuals within species in the sampling area are non-random, the estimate based on the total sample may be severely biased upward or downward with respect to the number of species which would be encountered in a quantitative field sample containing a like number of individuals. Fager (1972) has shown the biasing effects of aggregation on estimates of subsample diversity based on Sanders' (1968) rarefaction method. Similar problems can be expected with the Hurlbert method.

To test the assumption that species are randomly dispersed within the total sample, a method based in part on Fisher's (1970) index of dispersion is developed herein (dispersion chi-square). First, the statistic  $\frac{s^2}{\bar{x}}$  is calculated for each species, as is often done to scan the data for obvious cases of strong aggregation of individuals within species (e.g. Gage and Geekie, 1973). Then, single-species indices of dispersion are summed as follows:

$$\chi^2_{S(n-1)} = \sum_{i=1}^S \left[ \frac{s_i^2}{\bar{x}_i} (n-1) \right],$$

where  $s$  equals the number of species,  $n$  the number of samples, and the term in brackets is Fisher's index of dispersion for the  $i$ th species. This total dispersion chi-square is partitioned into two components, designated "pooled" chi-square and "heterogeneity" chi-square by analogy with a more frequent usage (e.g. Sokal and Rohlf, 1969, pp 575-585). Extending Fisher's (1970, p. 58) arguments, if the number of individuals per sample fits a Poisson distribution for each species, all these chi-square values must approximate their respective degrees of freedom. The partitioning (demonstrated in Table 1) permits the detection of a particular kind of departure from random dispersion which does not bias the Hurlbert diversity estimate. Because the estimator incorporates the number of individuals in the hypothetical subsample as an independent variable, a departure from expectation in the pooled chi-square does not affect its accuracy. However, if the heterogeneity chi-square value deviates markedly upward from its degrees of freedom, Hurlbert's  $E(S_n)$  will be an overestimate, and, if the heterogeneity chi-square value is markedly lower than its degrees of freedom,  $E(S_n)$  will be an underestimate of actual numbers of species to be seen in a quantitative field sample of  $n$  individuals.

Dispersion chi-square analysis also indicates whether habitat partitioning (*sensu* Schoener, 1974) is likely on the spatial scales assayed. Unless the heterogeneity chi-square value exceeds its degrees of freedom, the data give no reason to suspect that habitat segregation occurs at all. If the proportion each species comprises of the total number of individuals per sample is essentially constant (within the stochastic limits expected of Poisson distributions), the heterogeneity chi-square value will not exceed the 95% confidence limits for chi-square with the appropriate degrees of freedom. Table 1, for example, gives no reason ( $P < 0.05$ ) to suspect that one species prefers the habitat of some samples more than do the other species.

This method of using all the species as replicates may, however, obscure stronger relationships (covariances) among subgroups of these species. In general, in the deep-sea benthos, individual species' densities are too low to make construction of a species-by-species covariance matrix from quantitative samples (e.g. Kershaw, 1961) worthwhile. Not only is the matrix usually filled with ones and zeros, but it is

Table 1. Two hypothetical extreme examples of deviations in dispersion chi-square statistics among 5 samples and 3 species. (I) Sample sums account for unexpectedly large portion of indices of dispersion (species' proportions unexpectedly constant); (II) sample sums account for unexpectedly small portion of indices of dispersion (total number of individuals per sample unexpectedly constant), column headings as in (I)

Species	Individuals in sample number					Index of dispersion	Degrees of freedom	Probability
	1	2	3	4	5			
(I)								
A	28	33	38	32	35	1.65	4	> 0.05
B	72	84	97	82	91	4.21	4	> 0.05
C	122	142	164	139	154	7.02	4	> 0.05
A+B+C	222	259	299	253	280	12.88	4	< 0.05
Total chi-square (sum of indices of dispersion of A,B,C)						12.88	12	> 0.05
Pooled chi-square (index of dispersion of sample sums)						12.88	4	< 0.05
Heterogeneity chi-square (total minus pooled)						0.00	8	< 0.001
(II)								
X	28	33	38	32	35	1.65	4	> 0.05
Y	72	84	97	82	91	4.21	4	> 0.05
Z	163	146	128	149	137	4.79	4	> 0.05
X+Y+Z	263	263	263	263	263	0.00	4	< 0.001
Total chi-square (sum of indices of dispersion of A,B,C)						10.65	12	> 0.05
Pooled chi-square (index of dispersion of sample sums)						0.00	4	< 0.001
Heterogeneity chi-square (total minus pooled)						10.65	8	> 0.05

also usually unmanageably large due to the extremely high species' diversity encountered. Because of the rarity problem and because many deep-sea genera are poorly known, the common approach of examining covariances in abundance among congeners (e.g. MacArthur, 1958; Fager and McGowan, 1963, Kohn, 1971) is usually impossible. For all these reasons, and in order to admit the possibility of detecting diffuse competition (*sensu* MacArthur, 1972, p. 29), species may be grouped by family.

The knowledge that an animal belongs to a given family indicates some degree of niche similarity with other members of the family. Three possibilities exist for any given pair of confamilial species. First, the factors which control their respective abundances may be

uncorrelated spatially. Second, if their niche similarity results in the same sort of place being optimal for both species, a positive covariance might be expected in numbers of individuals per species per sample. Third, if the niche similarity is so great that the species are potential competitors, some form of interspecific spacing (i.e., a negative covariance) might be expected. To approach the problem, the following null hypothesis is proposed (to be tested two-tailed against an *F* table according to the foregoing possibilities): the between-sample variance of the sum of individuals within a family equals the sum of the individual species' variances for the same samples.

When positions of contiguous samples are exactly known, as are the relative positions of the vegematic subcores, a

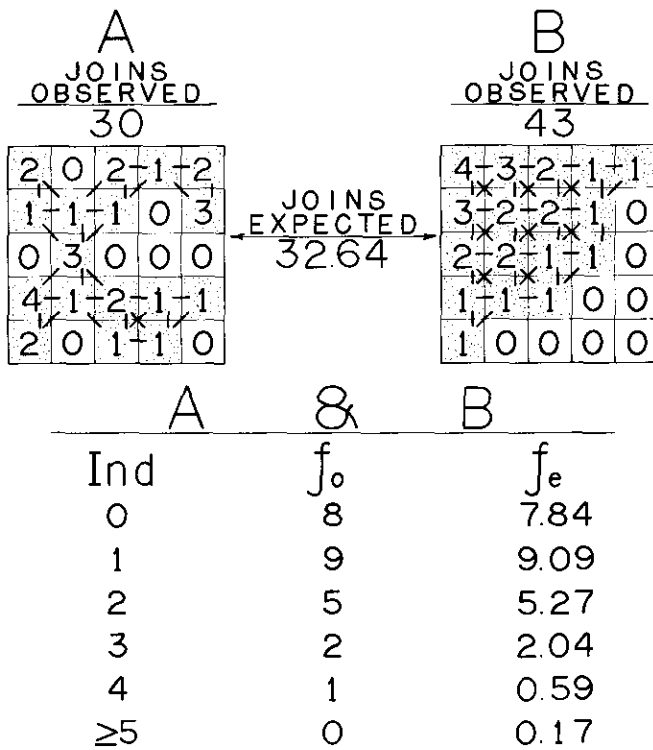


Fig. 1. Patterns of dispersion for individuals of one polychaete species among vegetative subcores. (A) Observed pattern of number of individuals per subcore in a *Tharyx* species (undescribed); (B) hypothetical pattern with same distribution of number of individuals per subcore. Note that while observed frequencies ( $f_o$ ) of number of individuals per subcore (Ind) are identical for (A) and (B), and correspond closely to Poisson expectation ( $f_e$ ), the high number of joins (short, thick lines connecting occupied subcores) indicates marked aggregation in (B).

very different sort of dispersion analysis is possible. Pielou (1969, pp 107-110) extends a method proposed by Krishna Iyer (1949) to test whether the cells of a two-phase mosaic are randomly mingled. Because of the generally low frequency of any particular species' occurrence in the subcores of any one core, the criterion used here to define phases of the mosaic is presence or absence. The number of adjacent (diagonally, vertically, or horizontally) pairs of one phase is tallied and compared to the number of such "joins" expected by chance. Fig. 1 illustrates that the number of joins is independent of the number of individuals per subcore and, hence, of the index of dispersion. The joins method can be thought of as a two-dimensional runs test in which the number of adjacent cells of one phase is tallied rather than the

number of adjacent pairs of differing phases. The latter number could also be used to test for randomness of mingling, but is not as sensitive for the 9-cell case in examining the hypothesis of intraspecific spacing.

Unfortunately, only the central 9 subcores usually prove to be sufficiently unbiased by bow-wave effects for an analysis of numbers of joins. For the 9-cell case, all the possible two-phase mosaics are relatively easy to list. Exact probabilities can thus be determined for all the possible numbers of pairs of adjacent cells of a given phase (Table 2). Again, due to the low densities at which most deep-sea species exist and due to the small number of apparently unbiased subcores per core, the number of joins between subcores in which a species occurs is recorded, and then the results for all species and all cores are grouped into one contingency table for a goodness-of-fit test against the expected values of Table 2 ( $G$  test, Sokal and Rohlf, 1969).

#### An Indirect Analytical Approach

Lack of departure from randomness in all the above analyses, however, does not necessarily imply that the sampled community is without structure. In particular, some theoretical considerations suggest that the predominant environmental grain (*sensu* Levins, 1968) may be of scales smaller than the smallest sample size ( $0.01 \text{ m}^2$ ) and that stochastic association of individuals and species may be of considerable structural importance. To explain adequately the latter point, a brief digression on the concept of "community structure" is necessary.

Community structure is often implied to be weak if species do not co-occur either more or less frequently than expected by chance (e.g. Pielou, 1972, p. 121). This interpretation obscures potentially overwhelming stochastic effects. Assume, for example, three species, A, B, and C. Suppose in addition that Species C is ten times as abundant as Species B and that all three are randomly and independently dispersed. No species are associated in the statistical sense, but individuals of Species C are an order of magnitude more likely than individuals of Species B to be close enough to individuals of Species A to affect them. To give fair weighting to such stochastic associations, community structure should be defined inclusively as the arrangement

Table 2. Number of joins expected by chance between adjacent cells of the denser phase in the 9-cell case. In each fraction, denominator is number of possible combinations of sparser and denser cells with the given number of denser cells, and numerator is number of these combinations with the indicated number of joins

Joins	No. of cells of denser phase						
	2	3	4	5	6	7	8
0	16/36	8/84	1/126				
1	20/36	28/84	8/126				
2		32/84	28/126	4/126			
3		16/84	24/126	12/126			
4			45/126	13/126	2/84		
5			16/126	28/126	4/84		
6			4/126	36/126	8/84		
7				16/126	12/84		
8				17/126	18/84	4/36	
9					12/84	0/36	
10					20/84	6/36	
11					8/84	4/36	
12						8/36	1/9
13						8/36	0/9
14						6/36	0/9
15							4/9
16							0/9
17							4/9

and interrelation of the component species.

In the deep sea or in any physically constant environment, the factor most likely to cause spatial heterogeneity on scales detectable by an individual is the activity of another individual. Animals can effect such heterogeneity, for example, by building tubes or burrows, by making tracks, by feeding on one size class of particles and excreting another, by locally depleting the sediment of one food resource, or by manufacturing a chemical concentration gradient. Unfortunately, most such structural effects are not apparent in the present vegetative sampling method because they are small, rare, difficult to identify, and susceptible to destruction resulting from washing and formalin fixation. One might, for example, envisage a chemical gradient exerting interspecific effects in the manner demonstrated by Chua and Brinkhurst (1973) for freshwater tubificid oligochaetes.

The most important characteristics of biogenic structures for the present argument are that they are roughly of the size and time scales of an organism. Most such structures change in size or intensity with the growth of an animal and may or may not persist for some time in altering form after the death of the producer. Predation, whether or

not it controls deep-sea populations directly (Dayton and Hessler, 1972), accelerates such changes. The result for any pair of interacting sedentary organisms is a temporally varying environment. Analogously, the environment for any pair of sedentary individuals at another location is probably different at any one time. Environmental inconstancy of precisely these temporal and spatial scales is likely to affect competitive advantage so markedly that competitive exclusion will often not occur (Hutchinson, 1953, 1961; Reddingius and den Boer, 1970; Richardson *et al.*, 1970). Although biologic and biogenic environmental variability has been largely ignored in discussions of genetic variability of deep-sea populations (Doyle, 1972; Gooch and Schopf, 1972), populations, either in terms of their individuals or in aggregate, must be adapted to an enormous array of potential neighbors.

Another facet of the present proposition is the stochastic pattern of change in environmental diversity with increasing area. Perhaps the best index of diversity of biogenic structures which remains in samples of the present type is the species' diversity of the animals themselves. While the magnitude of the diversity of such environmental features is not accurately estimated by species' diversity, only the pattern

of change of such diversity with sample size is of direct concern to the argument. Using the multivariate hypergeometric model, the expected number of species held in common between two samples of  $n$  individuals each (where  $N$  = the number of individuals in the population sampled and  $N_i$  = the number of individuals of the  $i$ th species in that population) is given by the following expression:

$$\sum_{i=1}^S \left[ 1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]^2,$$

which is ~~monotonically increasing~~ <sup>nondecreasing</sup> for all  $n$  values from zero to  $N$ . Hence, the larger are two samples, the more similar they will be in species' composition (in general).

For any two species, the implications of the relationship between sample size and similarity vary with the difference in ambit (*sensu* Lloyd, 1967) between the species. In species with very small ambits, the environment for any two individuals is likely to be very different in terms of proportions of species (and their associated structures) included within the ambit. For species with small ambits, the environment is coarse-grained (*sensu* MacArthur and Wilson, 1967, pp 95-96). Animals with larger ambits encounter species and associated structures in closer approximation to their actual proportions and, thus, experience a finer-grained environment. The foregoing is a direct consequence of the Law of Large Numbers (Rao, 1973, p. 112).

Thus, whether biologic disturbance is so intense that few populations ever reach levels at which competition is effective in population control (Dayton and Hessler, 1972), or whether these disturbances are so predictable that species have specialized on various microsuccessional stages (Grassle and Sanders, 1973), small-ambit species are potentially more diverse than large-ambit species. If the grain structure is dynamically stable, grain specialization is possible (Colwell, 1973). If it is unstable, contemporaneous disequilibrium (Richerson *et al.*, 1970) is likely. Because these mechanisms become correspondingly less probable in larger-ambit species, the hypothesis is formulated that, if an environmental grain approximating the size of an individual organism has played a role in the development of community structure, small-ambit species should be more diverse than large-ambit species.

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