

## Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance

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### ABSTRACT

Several models have been proposed to explain high macrofaunal diversity in the deep-sea benthos, but a mechanistic explanation of the maintenance of the enhanced diversity has not been demonstrated. This paper seeks evidence in meiofaunal harpacticoid copepod species' dispersion patterns of evidence of spatial scales at which diversity-maintaining processes act. Evidence of nonrandom dispersion is found at "100 meter," "meter" and "centimeter" scales of sample separation. Possible causes of these patterns are identified and the results are shown to be consistent with the "grain-matching" model of diversity maintenance.

The discovery that the deep-sea fauna is as diverse as that of tropical shallow-water soft bottoms (Hessler and Sanders, 1967) presented workers with an unexpected result because the deep-sea as an environment did not appear to have characteristics which readily explained the enhanced diversity observed. Since that time, several models have been proposed to explain how such high diversity is maintained. Sanders (1968, 1969) suggested that the great stability of the physical environment had permitted extreme resource specialization among potentially competing species to the extent that competition was alleviated and high diversity could be maintained. In contrast to this competition-based model, Dayton and Hessler (1972) argued that predation and disturbance keep potential competitors sufficiently low in abundance so that resources are rarely limiting. This predictable disturbance/predation minimizes competitive interactions, allowing the continued coexistence of many species which share the same resources. Grassle and Sanders (1973) extended the Sanders theory to include ideas on contemporaneous disequilibrium (Johnson, 1970; Richerson, Armstrong and Goldman, 1970). Their model views the deep sea as a spatial mosaic of out-of-phase successional states. Species are adapted by their dispersal and competitive abilities for a particular phase of the successional sequence. High diversity is maintained because individual species compete with only a small subset of the available species and because the patches are out of phase so that at any time many species are present locally in any group of

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such patches. Available data do not unambiguously favor any of the proposed models (Jumars, 1976; Thistle, 1977) so that the question of how diversity is maintained in the deep sea is still unresolved.

These models were proposed in the absence of data on species' spatial dispersions. Jumars (1976) reasoned that spatial scales at which species' dispersion patterns are discordant (that is, their abundance maxima tend to be separated in space) are scales at which processes maintaining diversity can be expected to operate. If such scales could be identified in species' dispersions, then such information might provide insight into the causes of that heterogeneity, that is, the mechanisms maintaining diversity. He examined the scales of dispersion in species of Annelida, Mollusca, Echinodermata, Crustacea and other taxa in two bathyal localities and found discordance on scales of 100 kilometers, kilometers and 10 centimeters. He reviewed literature reports to suggest potential sources of patchiness at these scales. His results demonstrated that mechanisms of diversity maintenance must operate on several scales for the taxa he considered, and that an adequate model of diversity maintenance must, therefore, be able to generate such scale-dependent heterogeneity in species' dispersions.

This paper applies Jumars' methods to harpacticoid copepods to further explore these issues. Harpacticoids are shown to be an example of a group with enhanced diversity in the deep sea; therefore, models proposed to explain high deep-sea diversity based on other taxa should apply to harpacticoids as well if they are to be general. The questions asked are the same: at what scales can one detect heterogeneity in species' dispersions indicative of the effect of a diversity maintaining process, and what potential sources of this heterogeneity can be identified? Further, Jumars (1975a) proposed a model of how diversity could be maintained based on matching the space and times scales of animal ambits and life spans with the length and time constants of environmental heterogeneity. Data are presented in support of this model of diversity maintenance in the deep sea.

## 1. Materials and methods

*Locality.* The operating depth limit of the remote underwater manipulator which was used as the sampling device limited possible sites to the bathyal. Given this restriction, a site was chosen in the San Diego Trough where the physical regime was relatively constant so as to typify deep-sea conditions. The San Diego Trough is the southernmost basin in the southern California Continental Borderland. It lies 24 km off San Diego, California and its long axis extends north-south for 80 km. Its 16 km breadth is bounded by steep escarpments (Fig. 1). It is a filled basin with excess sediment flowing into San Clemente Basin (Moore, 1969). The floor of San Diego Trough is essentially flat; its long axis has a 0.4% southward slope (Shepard and Einsele, 1962). San Diego Trough sediments are derived from pelagic sedimentation, slumping from the escarpments, and turbidity flows contributed via

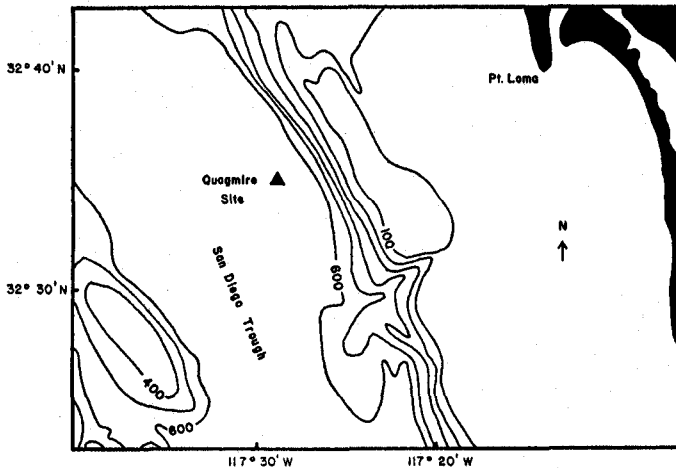


Figure 1. Chart of sampling area. The filled triangle marks the Quagmire site. Depth contours are in fathoms. Modified from Coast and Geodetic Survey Map N. 5101.

submarine canyons (Shepard and Einsele, 1962). Turbidites are confined predominantly to channels (Moore, 1969). Granulometric parameters are summarized in Table 1. In terms of the sediment texture experienced by the organisms, these values may be misleading because mineral grains are combined into larger units in nature. In particular, fecal pellets of sand size are conspicuous at the study site (Smith and Hessler, 1974; personal observation).

Hydrographically, the San Diego Trough lies under the highly productive California Current (Smith, 1974). Bottom currents are variable, but net flow is south to north. Unpublished current meter records taken at the study site over a one-month period (Hessler, personal communication) and diving observations made elsewhere in the San Diego Trough (Barham, Ayer and Boyce, 1967; LaFond, 1967) show no evidence of bottom currents of erosive magnitudes. The bottom water temperature and salinity are nearly constant (Table 1), ranging only 0.3°C and 0.02 part per mil respectively over a year (Rokop, 1974). Smith (1974) measured oxygen concentration values of 0.71 ml/l and a temperature of 3.5°C at the study site which agree well with the 0.7 ml/l reported by Emery (1960) and Rokop's values respectively.

The study site selected was at 1218.3-1223.8 m depth near the base of the Coronado Escarpment (32° 35.75' N, 117° 29.00' W) (Fig. 1) away from areas of known turbidite channels. The granulometric analyses showed no evidence of recent disturbance by turbidity flows. This fact combined with the constancy of temperature, salinity and dissolved oxygen values suggests that the study site can be characterized as physically stable.

**Sampling.** The samples analyzed in this study were taken as part of a larger program organized by Dr. Robert R. Hessler and designated Expedition Quagmire

Table 1. Physical environmental parameters at study site or at approximately the same depth in San Diego Trough. Sediment granulometric analyses were performed by Mr. J. A. Meador using the methods of Folk (1968) on the top 1 cm of eleven cores taken in the study site. The values reported are medians.

	Study Site	San Diego Trough
Median grain size (mm)	—	0.008 <sup>a,b</sup>
Graphic mean grain size (mm)	0.004	—
% sand	3.0	2.5 <sup>b</sup>
% silt	52.7	63.0 <sup>b</sup>
% clay	44.3	34.5 <sup>b</sup>
Porosity (%)	—	75-85 <sup>a</sup>
Sediment organic carbon (%)	—	1-3 <sup>c</sup>
Temperature (°C)	3.5 <sup>c</sup>	3.5 ± 0.3 <sup>c</sup>
Salinity (parts per mil)	—	34.53 ± 0.02 <sup>c</sup>
Oxygen concentration (ml/l)	0.71 <sup>c</sup>	0.7 <sup>b</sup>

<sup>a</sup> Barham *et al.*, 1967

<sup>b</sup> Emery, 1960

<sup>c</sup> Emery and Hulsemann, 1963

<sup>d</sup> Hamilton, 1963

<sup>e</sup> Rokop, 1975

<sup>f</sup> Smith, 1974

(Thiel and Hessler, 1974). This multi-investigator effort brought together experts on many aspects of deep-sea ecology in an integrated study of a single community. The primary tool involved was the Remote Underwater Manipulator, an unmanned, tractor-like vehicle connected to its surface support vessel by a cable with combined supportive and telemetric functions. RUM used its manipulator arm to take cores *in situ* while being monitored by closed-circuit television. As a result, the samples were taken with great care and with no visual evidence of disturbance. Specifically, the shock wave that precedes conventional ship-board samplers (McIntyre, 1971; Hessler and Jumars, 1974; Jumars, 1975a, b) was absent. In this sense, the present samples are among the least biased ever taken from the deep sea. Equally important, transponder navigation permitted relative positions to be known to within less than a meter. Such information had not been available for deep-sea samples and was critical to this study of small-scale spatial distributions.

The Quagmire Expedition study site was a roughly equilateral triangle 500 m on a side (Fig. 2). During the expedition, RUM took 58 benthic samples from it in a stratified random manner using a modified Ekman grab. The grab measured 20 × 20 cm and was partitioned internally by 10 × 10 cm inserts into four subcores. These 10 × 10 cm subcores are the units of this study. I selected pairs of subcores from each of six grabs and two single subcores to provide coverage of three spatial scales of *a priori* interest. Figure 2 shows the relative positions of the grabs; Table 2 gives the distances between them.

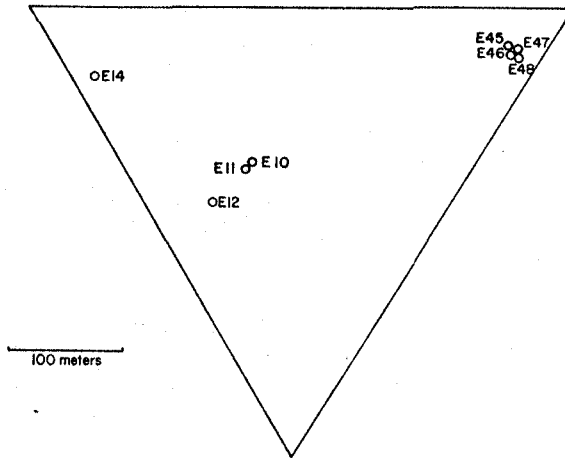


Figure 2. The Quagmire-site sampling triangle. The Ekman cores treated in this study are indicated by circles and labeled.

The top 1 cm layer and overlying water for each subcore were formalin fixed at sea. In the laboratory, each sample was washed on a 0.062 mm aperture sieve, transferred to ethanol, and then stained with rose bengal. Harpacticoid copepods present were sorted under a dissecting microscope. Adults were determined to species and counted.

*Analytical Methods.* The Shannon-Weaver diversity indices given were calculated using natural logarithms (Pielou, 1969).

Spatial autocorrelation is used in the assessment of variation of species' pattern with scale. Cliff and Ord (1973), Jumars, Thistle and Jones (1977) and Sokal and Oden (in press) provide mathematical development and give examples. The technique incorporates both the per-subcore abundances and the distances between subcores in a single statistic. The version of it I used tests the null hypothesis that the observed spatial arrangement is the realization of a random permutation of

Table 2. Distances between Ekman cores. Courtesy P. A. Jumars. Distances in meters.

	Sample						
	E11	E12	E14	E45	E46	E47	E48
E10	6.0	50.5	152.2	239.9	239.8	239.9	242.1
E11		44.6	152.3	244.5	244.5	244.5	246.7
E12			151.5	284.9	284.9	284.8	286.9
E14				356.6	356.9	357.6	359.9
E45					0.1	2.1	3.4
E46						2.0	3.4
E47							2.2

species' per-subcore abundances among the given subcore locations (Cliff and Ord, 1973). That is, neither too few nor too many large abundances occur in close proximity.

In the analyses below, Moran's "I" was the spatial autocorrelation statistic used and was evaluated without making assumptions about the underlying species' distributions (randomization assumption, see Cliff and Ord, 1973, p. 8). The method required the *a priori* specification of subcores which were considered to be likely to influence each other. In these analyses, all subcores were viewed as capable of affecting each other; therefore, a maximally connected weighting matrix was used (Jumars, Thistle and Jones, 1977). The relative distances between subcores were incorporated into the statistic by weighting the contribution to the index of each pairwise calculation of covariance between subcore abundances by the inverse of the distance separating the subcores. Standardized weights were used. This weighting tested the view that the strength of interactions should decrease linearly with distance.

*The Fauna.* Taxonomically, the harpacticoid copepod fauna of the Eastern Pacific is poorly known; and, with the exception of one study of the Peru-Chile Trench fauna (Becker, 1972), work has been confined to shallow water (Lang, 1965 and references therein). As a result, the Quagmire fauna has been treated as unknown. A working key based on characters used in the harpacticoid literature was developed *de novo* and is given in Thistle (1977, Appendix A). Subsequently, the fauna has been identified to family using Lang's (1948) key. Where possible, generic assignments have been made using, in particular, Lang (1965), preprints of Wells' (1976) keys, and the deep-sea taxonomic literature. These identifications appear in Thistle (1977, Appendix B).

Figure 3 summarizes the species' abundance relationships for the Quagmire-site harpacticoids, pooling over all subcores. One hundred and forty species were recognized from 3935 adult individuals. Two species were conspicuously abundant. These dominants constituted 13% of the fauna. If one replotted Figure 3 as a cumulative abundance graph, 11% of the species would contain 50% of the individuals. The median number of individuals per species is 11, and only 12 species were present as singletons. Table 3 gives a subcore-by-subcore description of the fauna. A table of species abundances at each station appears in Thistle (1977, Appendix C).

Little natural history information exists for the harpacticoid fauna of the Quagmire site or any deep-sea locality. However, one can make reasoned inferences about the habits of certain species on the basis of morphology. One group of five species appears to be adapted for burrowing. These species have a broad cephalosome with a tapering urosome. The second antennae appear to be burrowing appendages; they are short, stout limbs with heavy, modified setae. The periopods are

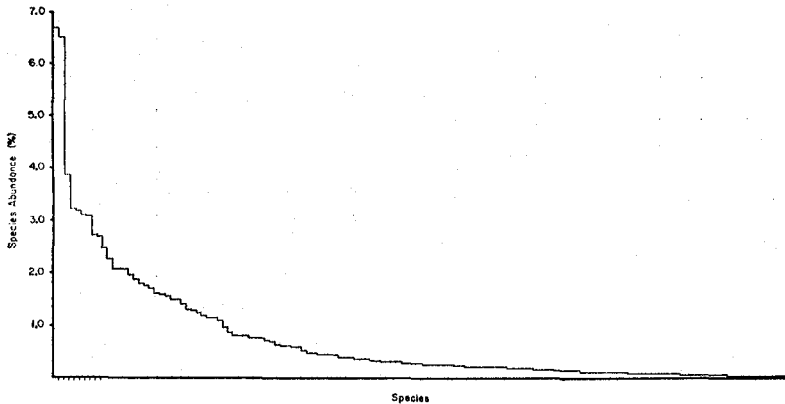


Figure 3. Rank-order of abundance histogram. The tick marks on the abscissa indicate the width of the bar for a species. The height of the bar for each species represents its per cent contribution to the harpacticoid fauna when all subcores are pooled.

reduced. A second, larger group seems adapted for life on the surface of the flocculent layer at the sediment-water interface. These species have elongate, often pinnulate setae which support their movement across the surface of this semifluid medium (Coull, 1972). Dorsally, these species bear large cuticular projections, seta-bearing projections and/or setae which anchor pieces of sediment and camouflage the animal. The remaining species provide few morphological hints as to their habits, but many are likely to be inhabitants of the flocculent layer.

Table 3. Summary of major descriptive features of the harpacticoid fauna by subcore.

Subcore	Total Harpacticoids	Number of Adults	Number of Species	Median Number of Adults per Species
E10X	474	239	70	2
E11X	514	241	63	2
E12W	591	289	77	2
E12Z	546	236	67	2
E14X	558	267	81	2
E14Y	711	295	78	2
E45X	507	244	59	3
E45Z	695	346	77	4
E46Y	607	288	69	2
E46Z	436	199	68	2
E47W	638	309	77	2
E47Z	738	364	84	2
E48Y	508	293	69	2
E48Z	643	325	75	3
Range	436-738	199-364	59-84	2-4

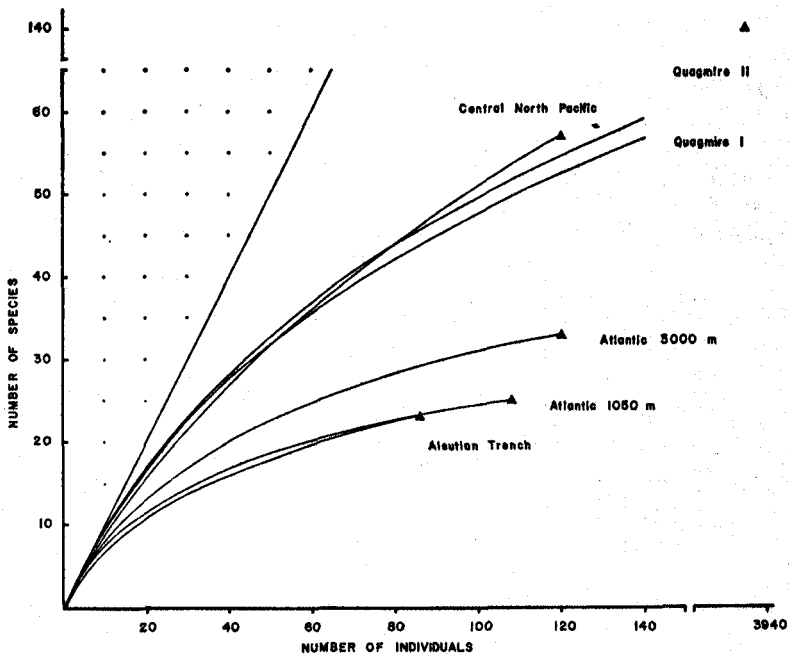


Figure 4. Number of species versus number of individuals reported for several deep-sea studies: "Quagmire I, II," the present study; "Central North Pacific," Hessler and Jumars (1974); "Atlantic 1050 m, 3000 m," Coull (1972); "Aleutian Trench," Jumars and Hessler (1976). The filled triangles indicate observed values. The curves predicting the expected number of species at smaller numbers of individuals were generated by Hurlbert's (1971) method of rarefaction. Notice the break in the axes. Stippling marks a region of impossible values.

The familial and generic composition of the Quagmire fauna fits a pattern which has characterized deep-sea harpacticoid studies to date. A few important shallow-water families extend into the bathyal zone and dominate the fauna with a small addition from primarily deep-sea groups (Noodt, 1971). Within this fauna, a list of characteristic genera has been found whenever a bathyal locality has been sampled (Por, 1965; Coull, 1972). This pattern in bathyal harpacticoids differs from that found in isopod crustaceans where families which evolved and have their primary radiation in the deep sea comprise the bathyal fauna (Hessler and Thistle, 1975).

## 2. Results

*Diversity.* Data on harpacticoid diversity are relatively rare; and because of variation in sampling, treatment of the fauna, and method of reporting diversity, the literature values are not readily comparable. Figure 4 summarizes the deep-sea reports except Drzycimski's (1969) bathyal data. These are Hurlbert (1971) rarefaction curves which permit, granted certain assumptions, the comparison of results



at a single sample size. The Hessler and Jumars (1974) data come from pooling animals from ten 0.25 m<sup>2</sup> box cores taken at 5500-5800 m depth in the Central North Pacific. The Jumars and Hessler (1976) curve comes from a single 0.25 m<sup>2</sup> box core from 7298 m in the Aleutian Trench. Both curves include adults and immatures retained on a 0.297 mm aperture sieve. To improve the comparison of the Quagmire data to these results, I calculated a curve (Quagmire I) based on three Quagmire samples selected at random (E12W, E12Z, E47W) which were treated as in the above studies. The curve labeled Quagmire II results from pooling adult harpacticoids from all 14 samples which were retained on the 0.062 mm sieve. At least in the San Diego Trough, Hessler and Jumars' methods seem to underestimate diversity slightly. Coull (1972) reports Sanders (1968) rarefaction curves for adults and immatures retained on a 0.062 mm sieve from shelf, slope, and abyssal plain stations between Cape Lookout and Bermuda. Dr. Coull has permitted me to use his original data to calculate Hurlbert rarefaction curves based on adults only, in order to make his results comparable to the Quagmire II curve. The curve labeled "Atlantic 3000 m" is his most diverse station; that labeled "Atlantic 1050 m" is the station nearest the Quagmire depth.

Coull's curves are dramatically lower than those of other bathyal and abyssal samples. This result may reflect a true difference between the regions considered, or it may be a result of methodological differences. In particular, Coull obtained his data from sled hauls while the remaining authors used wide-diameter cores. Hessler and Sanders (1967) discuss the tendency of sleds to selectively winnow small and delicate forms during recovery (see also Hessler and Jumars, 1974). This factor may have caused Coull's samples to underestimate the true diversity.

Other reports of harpacticoid diversity are summarized using the Shannon-Weaver diversity index " $H'$ " (Pielou, 1969). Drzycimski (1969) (as reported in Hartzband and Hummon, 1974) working subtidally in Norwegian waters reported the following mean diversities: coarse sand,  $\bar{H}' = 1.7$ ; muddy sand,  $\bar{H}' = 2.5$ ; and bathyal muds (to 680 m),  $\bar{H}' = 3.3$ . Marcotte and Coull (1974) in a study of a pollution gradient in the Bay of Piran, Yugoslavia measured a maximum  $H'$  of 2.502 in a relatively unpolluted, subtidal mud (station WD, 16 m depth). Among his Bermuda stations, Coull (1968) found a maximum  $H'$  of 3.1 at a low-energy, carbonate mud site (station CHD, 13 m depth). Hartzband and Hummon (1974) studied harpacticoid diversities at 19 subtidal stations in the United States Virgin Islands. The maximum  $\bar{H}'$  measured was 3.3 (station B3B, 3.1 m depth) in shifting sand. The Quagmire site  $H'$  of all subcores pooled is 4.2. Despite the lack of strict comparability among the reported values, it is clear that the Quagmire harpacticoid fauna is among the most highly diverse harpacticoid faunas yet reported.

*Species' Dispersions.* Given this high diversity, can patterns be detected in harpacticoid species' abundances which provide insight into how this diversity is main-

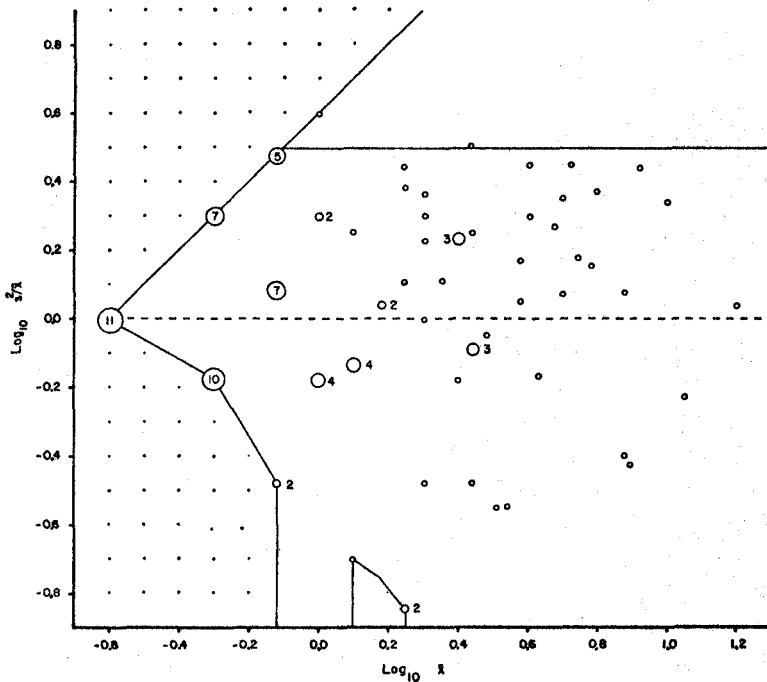


Figure 5. Variance-to-mean ratio versus the mean at the 100-meter scale. Each circle represents a species; circles with numbers associated with them indicate several species with the same value. The dashed horizontal line marks the expected value of a Poisson distribution. The solid horizontal line marks the upper 95% confidence limits of Poisson expectation; the  $\log_{10}$  of the lower 95% confidence limit ( $-1.143$ ) falls below the graph. Values in the stippled regions are arithmetically impossible.

tained? Fisher's (1970) index of dispersion was used to test individual species' abundance patterns for departure from the Poisson criterion of randomness. At the "100-meter" scale, subcores E10X, E11X, and a randomly selected subcore from E12 and E14 (E12Z, E14Y) were used to calculate the index. The median distance among these samples was 101.0 m. Figure 5 summarizes the results. Only four of 60 species which were sufficiently abundant to be detectably aggregated departed significantly toward aggregation. This number of aggregated species is slightly greater than one would expect by chance (binomial probability two-tailed equals 0.06). Two species departed significantly toward evenness, but because of the number of tests performed, the biological meaning of this apparent evenness is unclear.

These procedures were repeated on the "meter" scale using subcores E45Z, E46Y, E47Z, and E48Z (each subcore was selected randomly from the pair of subcores in each grab). The median distance among these samples is 2.2 m. Figure 6 summarizes the results. Eight of 69 species which were sufficiently abundant to be

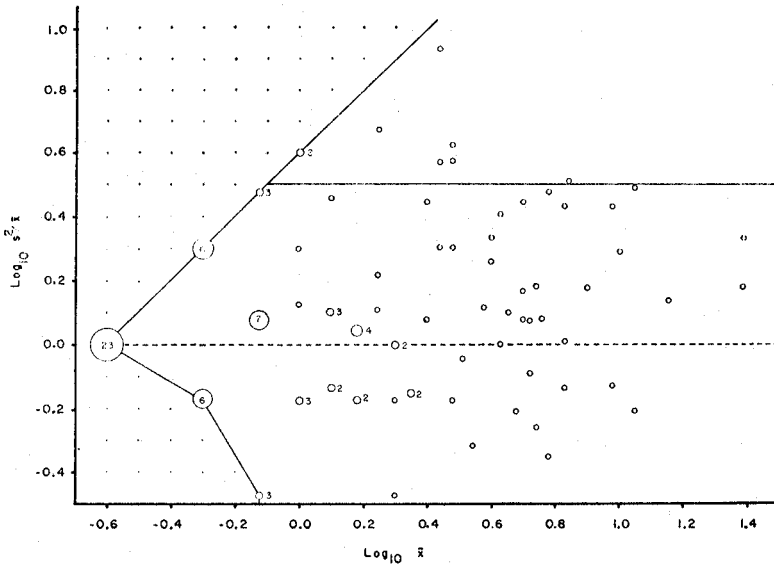


Figure 6. Variance-to-mean ratio versus the mean at the meter scale. See caption to Figure 5 for explanation of the symbols. The  $\log_{10}$  of the lower 95% confidence limit (-1.143) falls below the graph.

detectably aggregated were so. This number is significantly more than one would expect by chance (binomial probability two-tailed equals 0.0003). No species departed significantly from expectation toward evenness.

On the "centimeter" scale, these issues were investigated using a different statistic. Figure 7 plots for each species the average of the variance-to-mean ratio calculated between pairs of subcores from single grabs (E12W,Z; E14X,Y; E45X,Z; E46Y,Z; E47W,Z; E48Y,Z) except that pairs of subcores in which a species occurred only once were omitted because a single occurrence contains no information on the spatial pattern of the species (Jumars, 1975a). Here, 9 of 61 species of sufficient abundance to be detectably aggregated were aggregated. The probability of this result or a more extreme result occurring by chance is 0.0002. One species departed toward evenness; however, given the number of tests performed, there is no way to judge whether this apparent evenness has biological meaning.

These analyses of individual harpacticoid species revealed that few species departed from randomness at any of the three scales analyzed. There is little comparative data on harpacticoid species' dispersions in other environments to provide a context for this result because most workers have used total harpacticoids as the variate in studies of dispersion (e.g. Vitiello, 1968; Olsson and Eriksson, 1974). An exception is Heip (1975) who found aggregation in *Paronychocamptus nanus*, a brackish-water species. However, my results appear to parallel Jumars' (1975a)

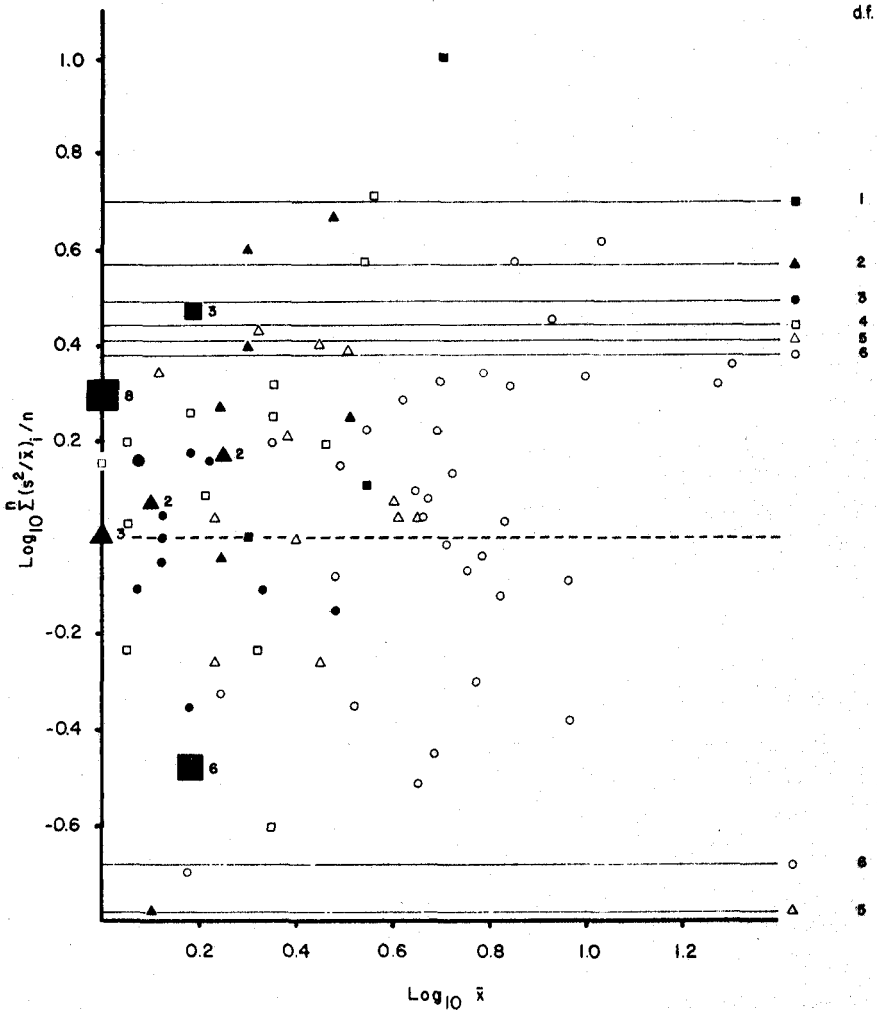


Figure 7. Average over cores of the variance-to-mean ratio calculated between paired subcores (the centimeter scale) versus the mean. Each symbol represents a species; symbols with numbers associated with them indicate more than one species with the same value. Depending on the number of cores in which a species occurred in both subcores, the confidence limits are based on chi square with 1, 2, 3, 4, 5, or 6 degrees of freedom. The species and confidence limits are labeled accordingly.

findings for polychaetes from San Diego Trough where within 0.25 m<sup>2</sup> box cores individual species' dispersions tended to be indistinguishable from randomness (see also Gage, 1977). If the San Diego Trough harpacticoids do tend to depart from randomness, then these departures must be small. Jumars (1975b) has proposed statistical methods to detect small departures from randomness. His dispersion chi

Table 4. 100-meter scale dispersion chi-square statistics.

## A. All species included.

	Value	Degrees of Freedom	Probability
Total chi square	1490.6776	896	< 0.0005
Pooled chi square	60.8723	7	< 0.0005
Heterogeneity chi square	1429.8051	889	< 0.0005

## B. Individually aggregated species omitted.

	Value	Degrees of Freedom	Probability
Total chi square	866.3576	721	< 0.005
Pooled chi square	29.3097	7	< 0.0005
Heterogeneity chi square	837.0479	714	< 0.005

square method extends Fisher's (1970) index of dispersion by using species as replicates. Mathematically, when indices of dispersion are calculated on random variates, the indices are additive and approximate chi square with appropriate degrees of freedom. If the sum exceeds the limits of stochastic variability as detected by the chi square test, then the assumption that the indices of dispersion were calculated on random variates may be rejected.

Using this method, one can treat species as replicates and accumulate small departures from randomness that could not be detected using indices of dispersion calculated on species individually. Jumars calls this sum the "total chi square." If it exceeds the limits of stochastic expectation, then the null hypothesis that for each species the numbers of individuals per sample fits a Poisson distribution (i.e. is a variate) may be rejected. He also partitions the total chi square into two components. The "pooled chi square" accounts for the variability caused by differences in the total abundance of all species from sample to sample. By difference, one obtains the "heterogeneity chi square" which is that portion of the variability resulting from discordance in species' abundances. If this value exceeds the 95% confidence limits of chi square, then one can reject the hypothesis that species' abundances are replicates of Poisson distributions with different means. That is, species' abundances do not vary proportionally among the subcores; some species are abundant where others are relatively rare.

Table 4A gives the results for dispersion chi square analysis at the 100-meter scale treating all species together. The significant total chi square indicates that on the average, species are aggregated. The significant pooled chi square indicates that total abundance (the total number of individuals of all species) is aggregated among subcores. The significant heterogeneity chi square implies that the non-randomness detected by the total chi square is not caused entirely by variance in

Table 5. Meter scale dispersion chi square statistics.

## A. All species included.

	Value	Degrees of Freedom	Probability
Total chi square	518.5301	351	< 0.0005
Pooled chi square	9.6712	3	< 0.025
Heterogeneity chi square	508.8588	348	< 0.0005

## B. Individually aggregated species omitted.

	Value	Degrees of Freedom	Probability
Total chi square	409.7642	327	< 0.005
Pooled chi square	6.7455	3	> 0.100
Heterogeneity chi square	403.0187	324	< 0.010

total abundance among samples, but results because species' abundances do not vary proportionally among the samples. That is, species are discordant in their abundance patterns on the average.

This result is perhaps not surprising. The index of dispersion showed that four species were significantly aggregated when treated singly. Their effect could swamp the dispersion chi square calculations. Table 4B gives the same statistics calculated with the individually aggregated species omitted. Although the probability levels associated with the total and heterogeneity chi squares are somewhat reduced, the conclusions remain the same. At the 100-meter scale, species' abundances are aggregated and their abundance maxima are discordant on the average.

Table 5 gives the results for the meter scale both with and without those species which were aggregated. The removal of the individually aggregated species causes the pooled chi square to fall below the 0.05 significance level (two-tailed test). However, the significant total and heterogeneity chi squares show that the species depart from Poisson expectation on the average and that this departure results from discordance in species' abundance patterns.

On the centimeter scale, the dispersion chi square calculation is more complicated. For each species in each pair of subcores from a grab, an index of dispersion is calculated. These indices are then summed (chi squares on Poisson variates are additive) while keeping track of degrees of freedom. This sum is then used for each species in the dispersion chi square analysis (Table 6). The results parallel those for the other scales; both with and without individually aggregated species, species are aggregated on the average and discordant in their abundance patterns.

Thus, using species as replicates one can detect significant patchiness in harpacticoid species' dispersions at three scales. My centimeter scale is analogous to Jumars' (1975a) within-core scale. At that scale, he found that polychaetes were randomly

Table 6. Centimeter scale dispersion chi square statistics.

## A. All species included.

	Value	Degrees of Freedom	Probability
Total chi square	744.7644	561	< 0.0005
Pooled chi square	46.7957	5	< 0.0005
Heterogeneity chi square	697.9687	556	< 0.0005

## B. Individually aggregated species omitted.

	Value	Degrees of Freedom	Probability
Total chi square	596.4296	509	< 0.005
Pooled chi square	23.9163	5	< 0.0005
Heterogeneity chi square	572.5133	504	< 0.025

to evenly dispersed and that there was evidence for intraspecific spacing. For harpacticoids, species are significantly aggregated on the average at this smallest scale. This result may simply reflect the difference in scale that the 100 cm<sup>2</sup> sampler used in both studies represents for an individual polychaete compared to the much smaller size of an individual harpacticoid. If a tendency for intraspecific spacing exists among harpacticoid individuals, then the scale of such spacing might well be smaller than that of polychaetes and not be detected by a sampler of this size. Alternatively, mobile harpacticoids may not have patterns of intraspecific spacing.

Is there evidence that the patchiness is more intense at a particular scale? The index of dispersion was used to contrast intensity of patchiness at the meter versus the 100-meter scales. At the 100-meter scale, intersample separation varied from 6.0 to 152.3 m; at the meter scale, intersample separation varied from 0.1 to 3.4 m. If scale had no effect, then the number of species whose 100-meter scale index of dispersion values exceeded their meter-scale index values should equal the number of species in which the reverse is true on the average. I calculated indices of dispersion on all species which were present in both data sets. There was no significant difference between the number of species which had larger index values at the 100-meter scale and the number which had larger index values at the meter scale (chi square 1 d.f. = 1.4578, nonsignificant, two-tailed test). The direction of departure was toward greater aggregation on the meter scale on the average.

This result indicates that for some species expanding the scale of sampling to the 100-meter scale introduces variability which exceeds that on the meter scale. For other species, the variability present at the meter scale dominates and no additional variability can be detected when the scale of sampling is expanded. That is, there is evidence of differences in species' responses to sources of heterogeneity.

Table 7. Spatial autocorrelation coefficients expressed as standard normal deviates for species which are significantly aggregated on the basis of the variance-to-mean ratio.

Species	Standard Normal Deviate (Z score) of Spatial Autocorrelation Coefficient
20	-0.8119
30	0.0829
33	0.6474
42	0.3518
44	-0.2246
53	1.1940
58	0.0472
60	0.1436
73	-0.2665
91	0.8644
92	-0.5122
96	0.0958
97	2.3326
121	-0.3157
144	0.1391

The question of scale of patchiness can be pursued further. At the meter scale, the index of dispersion detects 15 species which depart significantly toward aggregation when the index is calculated on the eight available subcores (E45X,Z; E46Y,Z; E47W,Z; E48Y,Z). What is the spatial arrangement of subcores with high and low abundances for each of these aggregated species? In particular, is there evidence that proximal subcores have similar abundances? Spatial autocorrelation as described above was used to ask this question. Table 7 gives standard normal deviates of the "I" spatial autocorrelation statistic for the 15 aggregated species. The statistic is constructed so that large positive values indicate that subcores with similar extreme abundances occur proximally; that is very large abundances (and as a consequence, very small abundances) occur near each other in space. Large negative values indicate regular spacing of extreme values. Indices of small absolute value are compatible with a random spatial arrangement of abundances.

Of the values in Table 7, one is significantly larger than random expectation and only one other value exceeds expectation by one standard deviation. Though the power of the "I" statistic is reduced when 10 or fewer replicates are analyzed and the calculation of accurate confidence limits requires Monte Carlo methods (Cliff and Ord, 1973), it seems unlikely that a more accurately determined confidence level would detect substantially more species departing significantly toward aggregation. Therefore, for most of these species there is no evidence that extreme abundances occur in proximal subcores even though the index was calculated on pairs of contiguous replicates. Patches appear to occur within subcores.



### 3. Discussion

To interpret observed scales of patchiness as scales at which mechanisms of diversity maintenance act requires the assumption that such mechanisms affect species' dispersions. Jumars (1976) provides arguments for the plausibility of this assumption. Briefly, in a food limited environment, potential competitors are unlikely to partition feeding time (Schoener, 1974) or food type (Hairston, 1973). Therefore, habitat partitioning is the most likely result of competition. If, in contrast, disturbance/predation limits populations and maintains high diversity, then a spatial mosaic of successional sequences is expected (Levin and Paine, 1974). In either extreme, patchiness is expected in species' dispersions, and species' abundance patterns can be expected to be discordant.

Following these arguments, the evidence of significant discordance in harpacticoid species' abundances indicates that at the "100-meter," "meter" and "centimeter" scales processes are operating which help to maintain diversity. Information as to the sources of this discordance in species' abundances on the appropriate scales is sketchy and largely anecdotal. San Diego Trough contains aggregations of the epibenthic holothurian *Scotoplanes* sp. which move over the sediment surface as they feed (Barham *et al.*, 1967; personal observation). The combination of their passage and feeding action may generate environmental heterogeneity on the 100-meter scale to which species may be responding. In addition, San Diego Trough contains organisms which build mud balls and tubes particularly, agglutinating Foraminifera and polychaetes (see Jumars, 1975a, Fig. 6). Their actions create a complex structuring of the sediment surface which animals may use as habitat patches and/or prey refuges. The most important constituent volumetrically (Thistle, 1977) is the cirratulid polychaete, *Tharyx luticastellus* Jumars (1975c). Jumars (1975a) documents the patchy distribution of this "mud ball cirratulid" on his between-core scale (setting aside his disclaimer based on considerations of multiple testing). Expedition Quagmire data indicate that this patchiness exists on the 100-meter scale as well.

Barham *et al.* (1967) report patchiness in the dispersion of the brittle star *Ophiomusium lymani*. They suggest that this species feeds as an opportunistic scavenger. LaFond (1967) reports that at densities he observed, the *O. lymani* population would require only 45 minutes for its movements to affect the entire surface of the sea floor locally. Both facts suggest that *O. lymani* could generate patchiness on scales grading into the meter scale. Visual observations and photographs obtained during Expedition Quagmire indicated that fish interact with the bottom. Fish lie on and burrow in the bottom as well as disturbing surface sediments with their head movements while feeding (personal observations; see also Barham *et al.*, 1967). Such disturbances could lead to organism-detectable environmental heterogeneity on the meter scale.

On the centimeter scale, local variations in the nature and frequency of the bio-

genic structures on the sediment surface appear to be likely sources of heterogeneity. The potential importance of this type of structuring is a special case of a more general view presented by Jumars (1975a) where the activities of macrofaunal organisms generally, not just those that build structures, is suggested as a likely source of organism-detectable heterogeneity. Jumars argues that in physically stable environments organisms themselves provide the dominate source of environmental variability. Further, the spatial and temporal scales of organism-generated heterogeneity are those most likely to minimize competitive exclusion. As a result, such "grain matching" of scale of environmental variability with the length and time scales of organisms may underlie the high diversities observed in the deep sea.

The harpacticoid data support this model, in part, in that for many species most of the detectable environmental heterogeneity present in the sample site occurs at the meter scale. In addition, there is some evidence that the scale of patchiness among individually aggregated species is less than that detectable by the contiguous sub-cores of the Quagmire sampling design. These data agree with Jumars' premise that much of the organism-detectable environment heterogeneity is generated by macrofaunal organisms, because patches generated by individual macrofaunal organisms are likely to be on the order of centimeters in dimension. However, as reported above, substantial patchiness occurs at larger scales in the harpacticoid data suggesting that other mechanisms are also participating in diversity maintenance.

#### 4. Conclusions

The harpacticoid copepods from San Diego Trough have been found to be patchily distributed on the average at 100-meter, meter, and centimeter scales of sample separation. Further, species tend to be discordant in their abundance patterns at these scales. This evidence that harpacticoid-detectable environmental heterogeneity occurs at the centimeter and meter scales agrees with Jumars' "grain-matching" model of deep-sea diversity maintenance because his model predicts that such patchiness should be a prominent feature of species' dispersions.

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