

Environmental Grain and Polychaete Species' Diversity in a Bathyal Benthic Community*

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Abstract

Patterns of polychaete species' dispersion in the San Diego Trough, Southern California Continental Borderland, North Pacific Ocean, at a depth of 1230 m are analyzed. Samples consist of 4 replicate 0.25-m² box cores, each partitioned into twenty-five 0.01-m² subcores, and of 1 unpartitioned core. The sampler is biased but, when this bias is taken into account, few species show strong aggregation either between or within cores. If all species are considered together as replicates, intraspecific aggregation is detected between cores, but uniform dispersion dominates within cores. Patchiness or habitat partitioning on the assayed scales can thus account for little of the extremely high species' diversity observed. Apparently due to an environmental structure having a "grain" smaller than 0.01-m², the diversity of species assumed to be sedentary is higher than the diversity of species assumed to be mobile. One evidence of such structure is a negative covariance between paraonid abundance and density of "mudballs" constructed by a cirratulid. Consideration of these results suggests that either grain specialization or simultaneous, biogenic disequilibrium or both act on spatial scales smaller than 0.01-m² to maintain high polychaete species' diversity in the San Diego Trough.

Introduction

The benthic fauna of the deep sea is highly diverse (Hessler and Sanders, 1967). However, the manner in which high species' diversity is maintained in an apparently constant environment is still debated (e.g., Dayton and Hessler, 1972; Grassle and Sanders, 1973). One issue which requires elucidation before the debate can be settled is whether the processes involved are predominantly local or global (*sensu* MacArthur, 1969). Is the total species' diversity observed in mile-long epibenthic sled and anchor-dredge trawls (Hessler and Sanders, 1967) principally within-habitat or between-habitat diversity?

Using methods outlined by Jumars (1975), this study examines the community structure of Polychaeta at one

bathyal locality. The methods are aimed specifically at detecting evidence of habitat partitioning (*sensu* Schoener, 1974) as a means of maintaining deep-sea species' diversity. Polychaetes were selected for this initial study for several reasons. They comprise roughly three-fourths of the individuals in the macrofauna of the study locality and show high species' diversity, both at the present site and at the localities where high deep-sea species' diversity was originally documented (Hartman, 1965; Hartman and Fauchald, 1971). Other macrofaunal taxa will be treated subsequently.

Locality, Samples, and Sampling Bias

The study site is in the northern sector of the Coronado Sea Fan, Southern California Continental Borderland, at a depth of 1230 m. Emery (1960), Shepard and Einsele (1962), and Moore (1969) document the geological stability of this area. Cores show no recent evidence of turbidity flows, and neither diving experiences (Barham et al., 1967;

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LaFond, 1967), unpublished free-vehicle current-meter records, nor bottom photographs reveal currents of erosive magnitudes, although a distinct tidal current is present. The fan forms a portion of the San Diego Trough, which is distinguished as the only filled basin in the borderland. Following channels which do not impinge on the sampling site, excess sediments flow into the adjacent San Clemente Basin (Moore, 1969). Physiography has been charted by the Deep-Towed Vehicle Group of the Marine Physical Laboratory, Scripps Institution of Oceanography; the study area is relatively featureless and has a slope of only 36 fathoms. mile^{-1} (ca. 36 m.km^{-1}).

Temperature and salinity of the bottom water have been measured by Rokop (unpublished) during each of the four seasons. His values agree with those obtained by Barham *et al.* (1967). Temperature at this station varies only from 3.0° to 4.0°C ; salinity is virtually constant at 34.5‰. At this depth in the San Diego Trough, oxygen concentration is about 0.68 ml.l^{-1} (Emery and Hülsemann, 1963). Mean diameter of sediment particles is $8 \mu\text{m}$ (Hamilton, 1963), moisture content about 60% (Hamilton, 1963), and organic carbon by weight 1 to 3% (Emery and Hülsemann, 1963).

All of these data indicate that the study area is a region of high physical stability. Epibenthic sled samples taken by Rokop (1974) for his study of reproductive periodicity of invertebrates reveal that this region supports the requisite high faunal diversity which is the object of the present study.

Five 0.25-m^2 samples were obtained for the present analysis (Table 1). One of these samples (H22) was collected with the unmodified 0.25-m^2 United States Naval Electronics Laboratory spade corer (Hessler and Jumars, 1974), while the other four were taken with the "vegematic" modification (Jumars, 1975), a set of internal partitions which subdivide the core *in situ* into a 5×5 array of contiguous 0.01-m^2 subcores. The unpartitioned core produced 390 polychaetes, while the vegematic cores produced the numbers of individuals shown in Fig. 1 when the uppermost 10 cm of sediment was passed through a 0.42 mm sieve.

Apparent capture efficiency, calculated by using the central 9 subcores as an internal standard (Jumars, 1975), is also given in Fig. 1. The null hypothesis that the median number of polychaetes per subcore for the inner

9 subcores equals that for the outer 16 subcores is rejected in Cores J15 and J22 (Mann-Whitney *U* test $P < 0.05$, one-tailed as per the arguments of Jumars, 1975). It seems likely that the contents of the peripheral 16 subcores of the 4 vegematic cores have been subjected to bow waves of variable severity. The outer 16 subcores are, therefore, excluded from those subsequent analyses in which errors of this magnitude and spatial pattern might seriously bias the results.

Results

Between-Core Scale of Pattern

A plot of $\frac{s^2}{\bar{x}}$ values for each species encountered in the 5 cores is shown in Fig. 2. Perhaps the most striking feature of the figure is the low number of species which show significant departure from an assumed Poisson distribution of number of individuals per core. Published shallow-water studies (cf. Gage and Geekie, 1973) generally reveal a much larger proportion of aggregated species.

A large portion of the apparent aggregation in Fig. 2 may be artifactual. Aside from an undescribed cirratulid species which houses itself in a mudball-like structure, one core accounts for each case of unexpectedly high variance. Three of the instances of apparent aggregation (unusually high numbers of *Braniella* sp. and *Paraonis gracilis oculata* Hartman, and unusually low numbers of *Melinnampharete* sp.) are due to Core H22, taken 2 years before the others. It is conceivable that the abundances of at least these three species have changed during the interim. Core J14 accounts for 4 other cases of apparent aggregation (in having unusually high numbers of *Spiophanes* cf. *bombyx* (Claparède), *Chaetozone* cf. *setosa* Malmgren, *Cossura* cf. *pygodactyla* Jones, and an apparently undescribed species of Fabricinae). For all but *Cossura* cf. *pygodactyla*, this observed aggregation could be attributed to the already mentioned core-edge sampling bias; J14 is unusually unbiased. The departures of the mudball cirratulid and of the cossurid in the direction of aggregation and of a nephtyid (*Aglaophamus paucilamellata* Fauchald) in the direction of uniformity are hardly unexpected in a scan of such a large number of species, even if all species are in actuality randomly dispersed.

To determine whether any overall trend in within-species dispersion

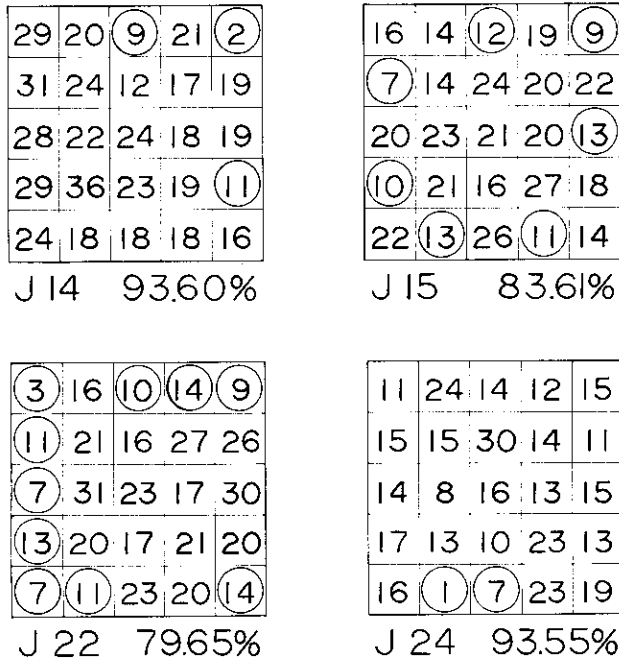


Fig. 1. Number of polychaete individuals per subcore from the 4 vegematic cores (J14, J15, J22, J24). Circles: suspect values; percentages: apparent efficiencies of capture

Table 1. Station data for 0.25 m² box core samples from San Diego Trough. H: Collected by R.R. Hessler without vegematic modification; J: collected by P.A. Jumars with vegematic modification

Sam- ple no.	Date	Depth (m)	Latitude (N)	Longitude (W)
H22	13.XII.1969	1224	32°28.2'	117°29.8'
J14	6.XII.1971	1224	32°28.2'	117°29.8'
J15	6.XII.1971	1229	32°28.1'	117°29.8'
J22	5. I. 1972	1223	32°28.9'	117°30.1'
J24	6. I. 1972	1248	32°27.3'	117°27.2'

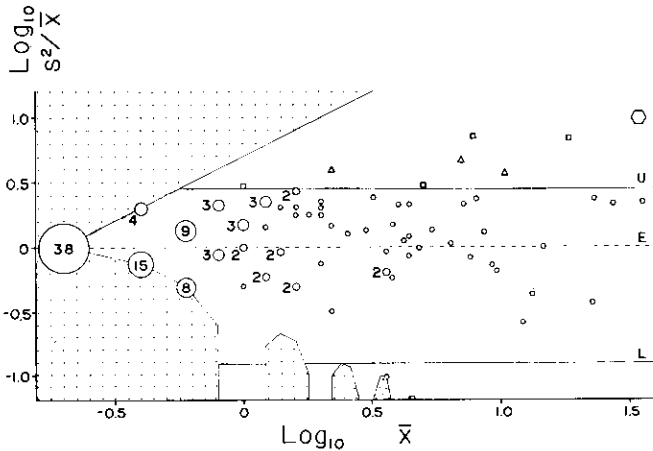


Fig. 2. Logarithm of variance-to-mean ratio versus logarithm of mean number of individuals per core for each of 146 polychaete species found in at least 1 of the 5 cores. Numbers: number of species (in excess of 1) showing indicated values; squares: aggregation due to Core H22; triangles: aggregation due to Core J14; hexagon: mudball cirratulid; stippling: statistically impossible region for the 5-sample case. Poisson expectation (E) and its upper (U) and lower (L) 95% confidence limits are given

Table 2. Between-core dispersion chi-square statistics based only on inner 9 subcores. (A) All 4 vegematic cores; (B) J24 excluded

Chi-square component	Value	Degrees of freedom	Probability
(A)			
Total chi-square	387.93	315	<0.01
due to species which occur only once	105.00	105	1.00
due to species which occur more than once	282.93	210	<0.002
Pooled chi-square	10.45	3	<0.05
Heterogeneity chi-square	377.48	312	≥0.01
(B)			
Total chi-square	243.75	196	<0.05
due to species which occur only once	70.00	70	1.00
due to species which occur more than once	173.75	126	<0.01
Pooled chi-square	0.23	2	>0.05
Heterogeneity chi-square	243.52	194	<0.05

pattern is apparent on the between-core scale, the dispersion chi-square method (Jumars, 1975) is employed. H22 is excluded, as are the outer 16 subcores of each of the vegemetic cores, to avoid artifactual aggregation of the sort suggested above. One hundred and five species are thereby included in the calculations, although 35 of these occur only once. Table 2A shows that, when all species are considered together as replicates in the chi-square analysis, a significant degree of aggregation is observed within species between cores. Since the heterogeneity chi-square value, as well as the pooled chi-square, is larger than expected, the aggregation is not due simply to more or fewer individuals of all species being found in some cores. Thus, estimates of subsample diversity derived from the population defined by the distribution of individuals among species for the summed cores by Hurlbert's (1971) method are likely to be biased (Jumars, 1975).

Before the Hurlbert method can be validly applied to trawl samples, it must be known whether its assumptions are met over the distances commonly traversed. If these assumptions are grossly violated (or if the devices are subject to other sampling biases as documented by Hessler and Jumars, 1974), it is difficult to interpret curves of expected number of species, $E(S_n)$, versus number of individuals, n . Because of navigational difficulties, Core J24 is beyond the distance from the intended station (coordinates of H22) that would likely be traversed, for example, by an epibenthic sled as used by Hessler and Sanders (1967). Table 2B shows that the heterogeneity chi-square value is essentially unaffected by the exclusion of this outlier. With only the inner 9 subcore totals for the 3 closely clustered vegemetic cores used in the analysis, however, very little of the total chi-square can be attributed to differences in total polychaete abundance among cores. Based on these considerations, the Hurlbert curve derived from an epibenthic sled haul in this region would, on the average, overestimate the number of species to be observed in a smaller, quantitative sample.

However, the Hurlbert procedure can also be tested empirically with the present data (Fig. 3). Although a slight tendency exists toward overestimation of the number of species (residual error: $\bar{x} = -2.94$, $s_x^2 = 2.42$), as predicted, the fit is reasonably good (residual error sum of squares = 91.61,

total sum of squares = 207.20), even when the peripheral subcores and the unpartitioned core are included. In the range of 390 to 507 individuals in this particular case, the Hurlbert method appears to be relatively insensitive to the degree of aggregation observed.

The small number of independent, relatively reliable samples in the present study makes examination of covariation in species pairs unproductive. A sampling design with a larger number of independent and precisely located samples (Thiel and Hessler, 1974), will address the questions of whether a mosaic or gradient is involved in the intraspecific patchiness documented above and of whether any covariance between potentially competitive species pairs is apparent (Jumars and Fauchald, unpublished).

Several additional remarks can be made when all the species are considered together in between-core comparisons. The median per-cent similarity index (Bray and Curtis, 1957) between cores (all peripheral subcores and the non-vegemetic core included) is 67.0% (range 62.0 to 74.9%), while the median Jaccard coefficient of similarity (Jaccard, 1912) in the same comparisons is 0.507 (range, 0.467 to 0.556). While there is little apparent correlation between the similarity in pairs of cores and the geographic distance between them or between this similarity and the difference in depth of water between core locations, the most similar pair of cores according to both measures is H22-J14. So far as could be determined with the satellite navigation system of the R.V. "Thomas Washington" and with its fathometer, these cores were taken at the identical spot. They were, however, taken 2 years apart.

Within-Core Scale of Pattern

As with the previous treatment, few values for individual species deviate from Poisson expectation. Rather than $\frac{s^2}{\bar{x}}$, Fig. 4 shows statistics obtained by summing the within-core values of this variance-to-mean ratio for a given species and then dividing by the number of cores in which the ratio is calculated for that species. Cores in which the species occurs only once among the central 9 subcores (the only ones considered reliable for this analysis) are, however, excluded from the calculations for the figure; they provide no information as to whether the species is aggregated, randomly dispersed, or uniformly dispersed within cores. Depending

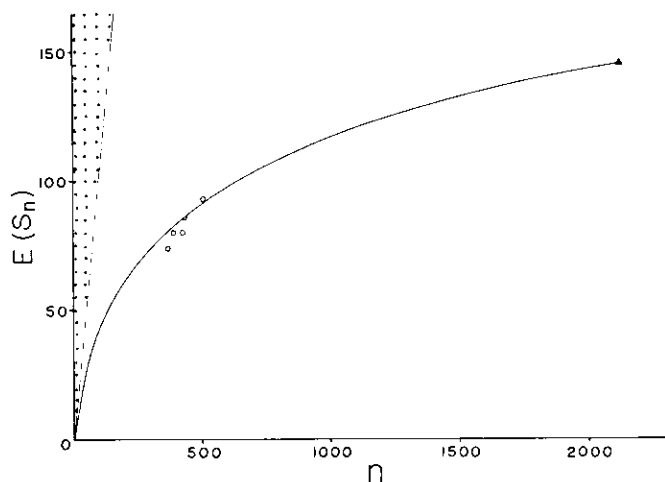


Fig. 3. Expected number of species, $E(S_n)$, versus number of individuals, n , calculated by Hurlbert (1971) method from distribution of individuals among species observed in the total of 5 cores. Circles: individual core totals observed; triangle: 5-core total. Stippled area bounded by thin, diagonal line, indicates region which cannot be occupied because number of species can never exceed number of individuals

on whether the calculation is based on 1, 2, 3, or 4 cores (in which these abundance criteria are met), the illustrated statistics should conform to a chi-square distribution with either 8, 16, 24 or 32 degrees of freedom. Of the 52 species figured, only 2 exceed the 95% confidence limits for chi-square with the appropriate degrees of freedom: an undescribed cirratulid (not that which constructs "mudballs"), and an apparently undescribed sabellid (also a fabricinid but not that which is aggregated on the between-core scale).

Fifty-three additional polychaete species never occur in an abundance of more than 1 individual per central 9 subcores, but do enter into the dispersion chi-square tabulation (Table 3). Two non-independent trends are apparent. Within the central 9 subcores, the number of individuals per species tends to be uniform and species tend to remain in constant proportions to each other (as shown, respectively, by the values of the total chi-square and the heterogeneity chi-square). Because there is some net positive covariance among species, these trends are not sufficient to insure that the total number of polychaetes per subcore will remain uniform (pooled chi-square is not correspondingly low).

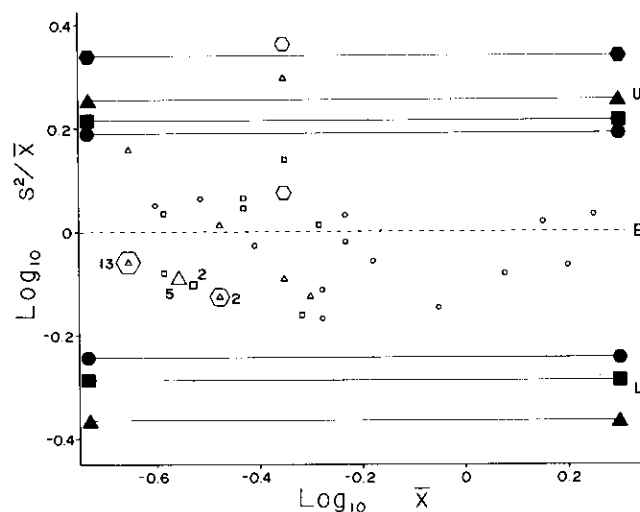


Fig. 4. Logarithm of variance-to-mean ratio versus logarithm of mean number of individuals per (inner 9) subcore by species as described in text. Symbols indicate number of cores from which data are drawn for that species: hexagon = 1, triangle = 2, square = 3, circle = 4. Open symbols: observed values; numbers adjacent to oversize symbols: numbers of species (in excess of 1) showing indicated values. Poisson expectation (E) and its upper (U , closed symbols) and lower (L , closed symbols) 95% confidence limits are given. *These limits are approximate due to the nested sample design.*

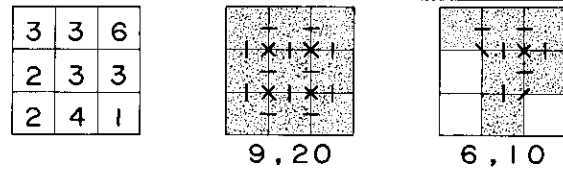
The direction of the deviation from randomness in the distribution of the number of individuals per subcore within species, as detected by the dispersion chi-square method, suggests some sort of spacing mechanism. This possibility is further explored with the joins method (see Jumars, 1975). The null hypothesis tested is that the number of adjacent pairs of subcores in which a species occurs or is relatively more abundant is no lower than expected by chance.

Because of the peripheral subcore bias problem, only the central 9 subcores can reliably be used in the analysis. In 105 of 120 cases in which a frequency of more than 1 occupied subcore out of 9 is encountered, presence or absence defines a two-phase mosaic that has only 2 to 6 subcores of the denser phase for the given core and species. In the 15 cases where the presence-or-absence criterion yields 7 to 9 cells of the denser phase, the phase-defining criterion is modified so that the minimum number of individuals per subcore which yields a mosaic having 2 to 6 denser cells is employed as the threshold value in defining phases of the mosaic (e.g. Fig. 5). If the presence or absence criterion is strictly followed, information is lost

Table 3. Within-core, between-subcore dispersion chi-square statistics based only on inner 9 subcores of the 4 vegematic cores

Chi-square component	Value	Degrees of freedom	Probability
Total chi-square	1541.93	1584	<0.60
due to cores in which a species occurs only once	592.00	592	1.00
due to cores in which a species occurs more often	949.93	992	<0.40
Pooled chi-square	54.78	32	<0.02
Heterogeneity chi-square	1487.14	1552	<0.40

MUDBALL CIRRATULID



EXOgone SP

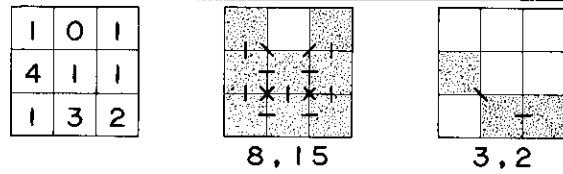


Fig. 5. Examples of exceptions to presence or absence criterion for joins method. Left: numbers of individuals per subcore for central 9 subcores; center: number of denser cells (stippled), number of joins (short, thick lines connecting subcores) with presence or absence criterion; right: number of denser cells, number of joins with modified criterion (see text)

Table 4. Expected versus observed number of joins for all cases in which a species occupies more than 1 subcore among central 9 of any vegematic core. J: number of joins; E: expected frequency; O: observed frequency

Ungrouped data:

J	No. of denser cells									
	2		3		4		5		6	
	E	O	E	O	E	O	E	O	E	O
0	24.000	33	2.476	3	0.127	0				
1	30.000	21	8.667	7	1.016	0				
2			9.905	12	3.556	5	0.476	3		
3			4.952	4	3.048	1	1.429	2		
4					5.714	8	1.548	2	0.214	0
5					2.032	1	3.333	3	0.429	2
6					0.508	1	4.286	1	0.857	2
7							1.905	2	1.286	1
8							2.024	2	1.929	0
9									1.286	3
10									2.143	0
11									0.857	1

Grouped data for significance test:

	No. of denser cells														
	2			3			4			5			6		
	J	E	O	J	E	O	J	E	O	J	E	O	J	E	O
0	24.000	33	≤1	11.143	10	≤3	7.746	6	≤5	6.786	10	≤6	1.500	4	
1	30.000	21	≥2	14.857	16	≥4	8.254	10	≥6	8.214	5	≥7	7.500	5	

from the cores in which all the inner 9 subcores are occupied by a given species, and the resultant contingency table has an undesirably large number of expected frequencies less than 5 (cf. Dixon and Massey, 1957, p. 222). Further grouping, as shown in Table 4, is required to maintain most of the expected frequencies above 5. Based on this contingency table, the null hypothesis is rejected (one-tailed G test, Sokal and Rohlf, 1969; $G = 13.60$, $P \approx 0.01$). Some form of intraspecific spacing is apparent. One somewhat surprising effect of this spacing, which is potentially troublesome for community ordination purposes, is that adjacent subcores are less similar than non-adjacent subcores in species composition (per-cent similarity index, Bray and Curtis, 1957).

These results lead quickly to the question of interspecific spacing. For numerous reasons (Jumars, 1975), species are grouped by family for an examination of covariances. The null hypothesis examined for each of the 16 families in which confamilial species co-occur among the central 9 subcores of at least one vegemetic core is that the between-subcore, within-core variance of the sum of individuals within a family equals the sum of the individual species' variances for the same subcores. Table 5 shows that, in general, this hypothesis cannot be discounted; i.e., the number of individuals per species per subcore appears to be independent of the local abundance of other species in the same family. The Paraonidae, however, display a large, positive covariance; in a subcore where one paraonid species is found, others are likely to occur. There is also a slight tendency toward positive covariance among species within families overall, with 9 of 15 showing a tendency toward confamilial cooccurrence.

Assuming that the significant F value for paraonids in Table 5 is not due to chance, a possible explanation can be proposed as to why some subcores are better than others for all paraonids. Photographs and relatively undisturbed samples reveal that the "mudball" cirratulid builds consolidated, roughly prolate spheroidal structures, each with its long axis perpendicular to the plane of the sediment surface. The major axis of such a spheroid (1 spheroid being occupied by 1 cirratulid) often reaches 4 to 5 cm in length, about half of which protrudes above the sediment surface, and the corresponding perpendicular diameter attains 2 to 3 cm. As the mudball is built, disused open-

ings seem to be sealed, resulting in the frilled appearance of the protruding portion (Fig. 6). Paraonids have no feeding appendages which could be used to reach around such obstructions. Available evidence, both observational (e.g. Day, 1967; references in Papentin, 1973) and morphological (unprotected branchiae on the anterior dorsal surface of the body), indicates that paraonids are shallow-burrowing deposit feeders. This line of reasoning leads to the null hypothesis that the number of cirratulid mudballs per subcore is independent of the number of paraonids per subcore, with the expectation that a negative correlation may be observed. Fig. 7A demonstrates that subcores containing large numbers of cirratulid mudballs do not contain large numbers

Family	Sum of variances Variance of sums	Sign of apparent covari- ance	Two- tailed proba- bility
Polynoidae	$F_{16,8} = 1.22$	-	>0.50
Phyllodocidae	$F_{16,8} = 0.500$	+	<0.40
Hesionidae	$F_{40,16} = 1.353$	-	>0.50
Syllidae	$F_{16,8} = 0.806$	+	>0.50
Lumbrineridae	$F_{88,32} = 0.964$	+	>0.50
Dorvilleidae	$F_{16,8} = 1.143$	-	>0.50
Paraonidae	$F_{224,32} = 0.602$	+	≈ 0.02
Spionidae	$F_{144,32} = 0.821$	+	<0.50
Cirratulidae	$F_{168,32} = 0.880$	+	>0.50
Cossuridae	$F_{16,8} = 1.960$	-	<0.40
Fauveliopsidae	$F_{32,16} = 0.776$	+	≈ 0.50
Capitellidae	$F_{128,32} = 0.948$	+	>0.50
Maldanidae	$F_{216,32} = 0.699$	+	<0.20
Ampharetidae	$F_{200,32} = 1.113$	-	>0.50
Terebellidae	$F_{88,32} = 1.067$	-	>0.50
Sabellidae	$F_{56,24} = 1.000 (=)$	(=)	>0.50

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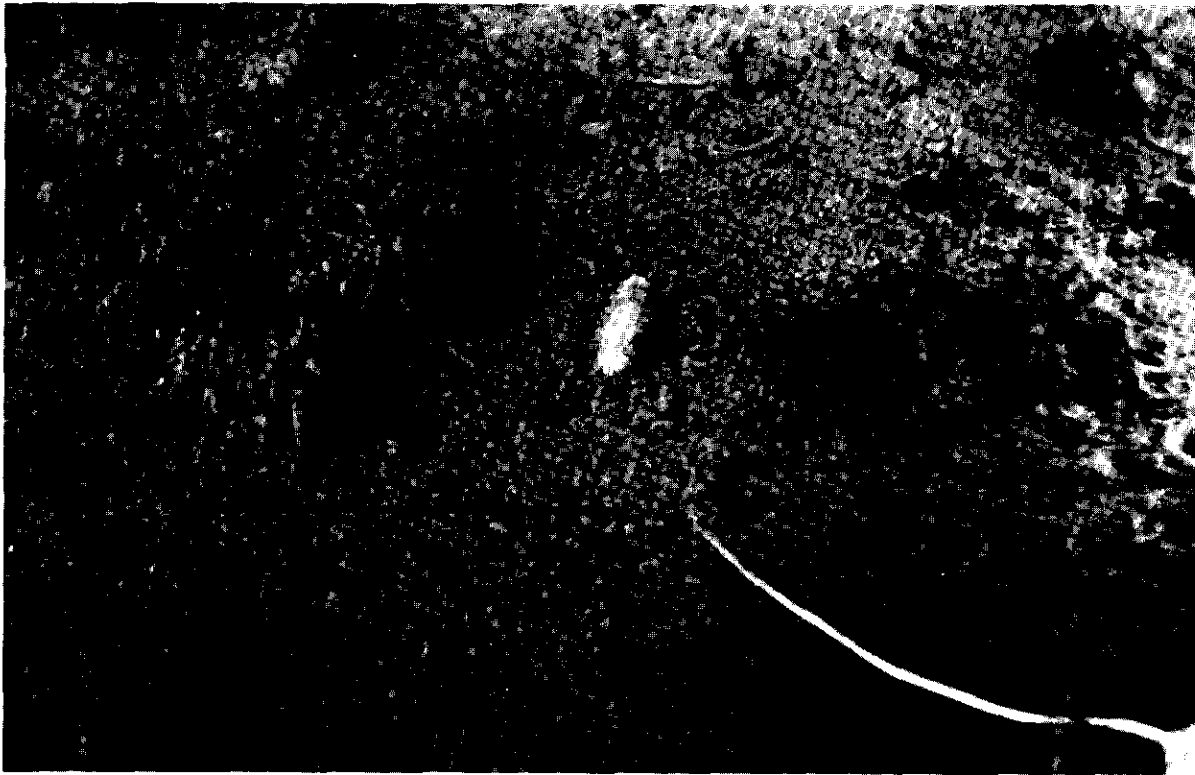


Fig. 6. Close-up view of bottom near study locality. In right foreground is an arm of *Ophiomusium lymani* and a coiled fecal casting, probably of *Scotoplanes* sp. The light-colored animal in center is a polynoid polychaete, a large-ambit species. To its immediate left is a trio of cirratulid mudballs, made by a small-ambit species. These mudballs cast shadows toward the polynoid and are frilled in appearance. Approximately 10 cm, the dimension of each side of a subcore, is indicated by scale line. (Photograph taken through port of D.S.R.V. "Deepquest", courtesy of R.R. Hessler)

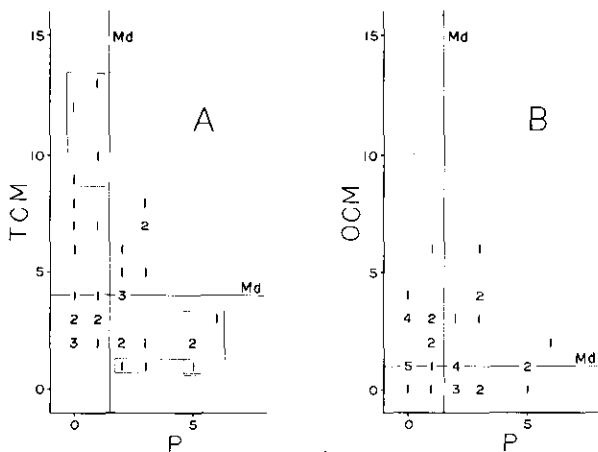


Fig. 7. Number of cirratulid mudballs versus number of paraonid individuals (P) per subcore of the 36 inner subcores. Numbers: frequencies of indicated coordinates; Md: median. (A) Total number of mudballs remaining after washing (TCM), enclosed values are of particular interest in the corner test; (B) only those mudballs still occupied by the cirratulid (OCM)

of paraonids and vice versa. The null hypothesis is rejected (one-tailed corner test, $P < 0.025$; Tate and Clelland, 1957, p. 67). Fig. 7B shows it is unlikely that the negative covariance is due to active, direct, competitive interaction between the living mudball cirratulid and paraonids. This is an example of organism-detectable environmental heterogeneity on both the within-core and the between-core scales.

In the light of all the above departures (biased subcores due to the presumed bow wave, within-species aggregation between cores, uniform abundances within species among the central 9 subcores, covariances among species' abundances, etc.) from its assumptions, it is again worthwhile to test the Hurlbert (1971) procedure empirically. Fig. 8 shows that, despite the observed violations of the assumption of random sampling from a multivariate hypergeometric distribution, the fit of $E(S_n)$ to the observed number of species per subcore is reasonably good. The fit is

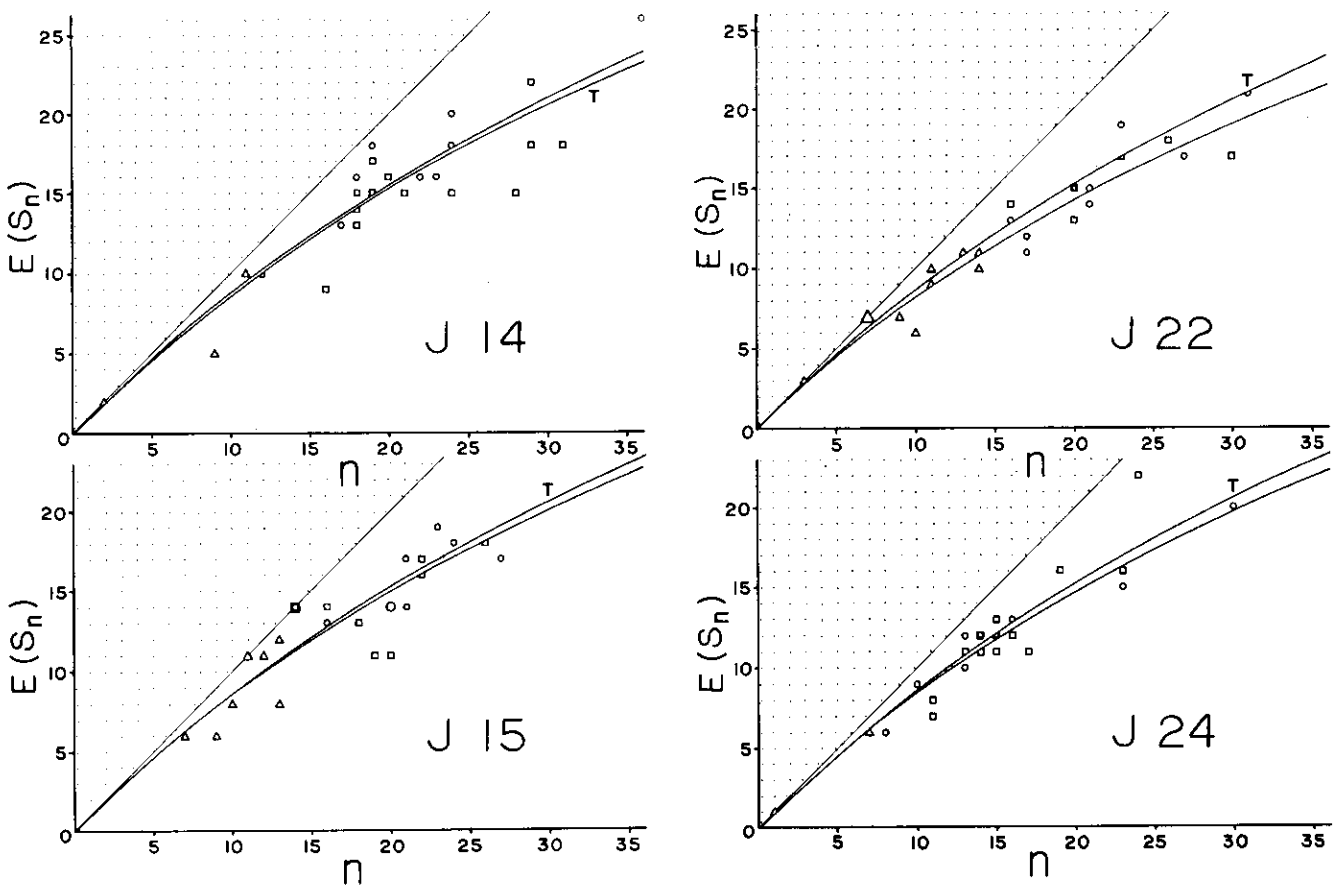


Fig. 8. Expected number of species, $E(S_n)$, versus number of individuals, n , calculated both from distributions of individuals among species in each core alone and from distribution of 2125 individuals among 146 species in the total of 5 cores (T). Symbols indicate numbers of individuals and species observed in each subcore. Circles: central 9 subcores; squares: outer subcores; triangles: apparently biased outer subcores; partially filled squares: circle and square coincide; oversize symbols: two subcores with same value; truncated symbols: fall close to curve on figured side

compared when $E(S_n)$ is predicted from individual core totals (residual error: $\bar{x} = -0.089$, $s_{\bar{x}}^2 = 0.029$) or from the total of all 5 cores (residual error: $\bar{x} = -0.35$, $s_{\bar{x}}^2 = 0.029$). The slightly greater apparent bias in the latter case is due to the between-core aggregation within species discussed earlier. However, the residual error sum-of-squares differs only slightly for the individual-core curves and the sum-of-cores curve (287.3 versus 296.5, respectively). In statistical terms, the Hurlbert method is relatively robust under the observed sources and degrees of departure from its assumptions. While a straight line might also account for a large portion of the total sum of squares (2055.6) in the observed range of 1 to 36 individuals, the same straight line could not adequately describe the relationship between number of individuals and number of species in the subsample sizes considered in Fig. 3.

Discussion and Conclusions

Level of Diversity Observed

The curve generated by the Hurlbert (1971) method for the San Diego Trough (SDT) polychaete community falls uniformly above any species-individuals relations thus far reported for the deep sea (Fig. 9). Because of differences in sampling gear (cf. Hessler and Jumars, 1974), the Gay Head-Bermuda transect relations figured are not easily comparable with the SDT or the central North Pacific (CNP) relations. The CNP values, though, were obtained with the identical corer (without the vegematic modification) used in the present study. The curves for the SDT and CNP are so similar that the difference might appear insignificant. However, a Monte-Carlo computer model reveals that, at an abundance level of

143 individuals (this level being chosen because of its interest in another investigation, Jumars and Hessler, unpublished), a number of species as low as or lower than that observed in the CNP could only be obtained by chance in the SDT community with a probability of less than 0.05. The program assumes a multinomial distribution defined by the proportions of individuals belonging to each species in the total SDT sample and draws the specified number of individuals repeatedly from it. A multinomial model is more conservative (less likely to show differences when there are none) in this comparison than would be the multivariate hypergeometric model used to generate the Hurlbert curves. If the latter model were used, the variance would be unrealistically reduced by the artificial constraint of sampling without replacement from a population much smaller than the community itself.

Although the curves do thus appear to differ significantly over part of the illustrated range of values, they do not permit definitive statements as to whether total community diversity is higher in one or the other area. In neither case has the number of species reached the plateau expected when nearly all the species have been sampled. While there is no proven method for estimating, from the data at hand, the total number of species in either community, Fig. 10 shows the result of grouping the species according to the logarithms of their respective abundances in the total sample. The natural logarithm base is used to avoid most ties of species between abundance classes. However, no matter what the base, a problem exists with those species which are encountered only once ($\log_n 1 = 0$). Half these species most probably belong in the -1 to 0 class, and half in the 0 to +1 class. The resultant number for the -1 to 0 class is a minimum estimate because only the most abundant species in that class are well represented, and an artifactual mode is produced in the 0 to +1 class. If a lognormal distribution of individuals among species holds (cf. Preston, 1962), and if the apparent mode is real, roughly 177 to 212 polychaete species are expected to occur in the SDT polychaete community. No such estimate can be made for the CNP; the real mode has not yet been reached. The exact number of species in the SDT community may not be known, but the number already encountered is great relative to the shallow-water, high-latitude situation (cf. Sanders, 1968).

Species Dispersion Patterns

While the dispersion chi-square statistics show that a part of this apparent diversity is due to patchiness on the between-core scale (beta diversity *sensu* Whittaker, 1965), this portion is small in comparison with shallow-water examples (e.g. Reys, 1971, Gage and Geckie, 1973), where aggregation on similar scales is much more pronounced. However, in most shallow-water studies (and in the present study as well) it is impossible to determine whether the statistical indication of aggregation is due to a biologically generated mosaic or simply to physically controlled gradients of abundance crossed during the sampling (Greig-Smith, 1960). Reports of high degrees of aggregation in shallow-water benthic environments may largely be due to the high probability of sampling across physically generated gradients where physical gradients are steep. At any rate, available evidence suggests that the high diversity observed in the SDT does not have its origins primarily in patchiness on the between-core scale, each patch having its own, much smaller diversity.

There is, furthermore, no evidence that patchiness on the within-core, between-subcore scale is important in producing this diversity. Quite to the contrary, individuals within species tend to be evenly dispersed among such sub-cores. While some sort of spacing mechanism is implied, the present data are compatible with a large number of hypotheses as to its mode of operation. Three hypotheses in particular appear plausible *a priori*: (1) conspecific individuals may actively avoid each other (e.g. Holme, 1950, *Tellina tenuis*); (2) recruitment to the population may be competitively limited unless some minimum distance is maintained from an already recruited individual (e.g. Connell, 1963, *Erichthonius braziliensis*); and/or (3) mortality due to predation or to other interspecific events may be relatively high in local aggregations of any one species (e.g. in the manner Connell, 1972, proposes selection has led to effective dispersal in rainforest trees). Without experimental manipulation or time-series observations, the contributions of these and other potential spacing mechanisms are impossible to determine.

Ambit Size and Community Structure

Unlike the case in some more familiar environments (e.g. MacArthur, 1969;

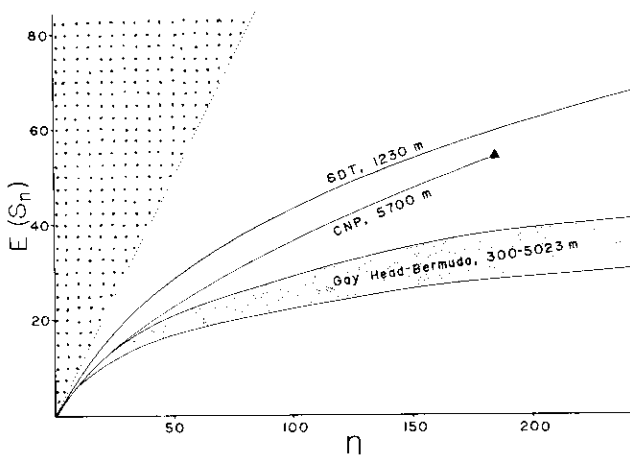


Fig. 9. Expected number of species, $E(S_n)$, versus number of individuals, n , for polychaetes of 3 deep-sea regions, calculated by Hurlbert (1971) method. SDT: calculated from the total of 5 cores in San Diego Trough; CNP: calculated from the total of 12 cores in central North Pacific Ocean (Hessler and Jumars, 1974). The Gay Head-Bermuda transect samples discussed by Hessler and Jumars (1974) fall in densely stippled region. Triangle: total observed; sparse stippling: region which cannot be occupied

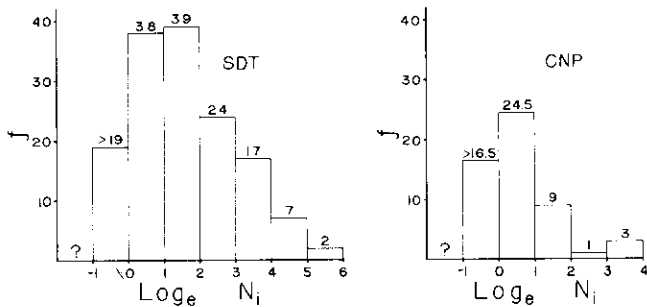


Fig. 10. Frequencies (f) of species falling in logarithmic abundance classes for 1.25-m² sampled in San Diego Trough (SDT) and from 3.00-m² sampled in central North Pacific (CNP; Hessler and Jumars, 1974; see text)

Diamond, 1973), it would appear from these cursory considerations that patchiness or spatial heterogeneity cannot account for the high species' diversity observed in the SDT. However, the possibility exists that the sampling design has missed spatial scales important in diversity maintenance. According to the arguments developed by Jumars (1975), if such scales are relatively small, one might expect that species with small ambits (*sensu* Lloyd, 1967)

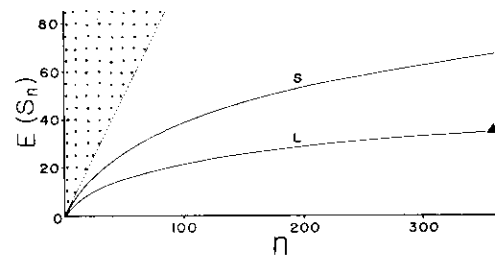


Fig. 11. Expected number of species, $E(S_n)$, versus number of individuals, n , for small-ambit (S) and large-ambit (L) species in San Diego Trough; calculated by Hurlbert (1971) method from distributions of individuals among species in the total of 5 cores. Triangle: total observed for large-ambit species; stippling: region which cannot be occupied

Table 6. Species richness of Polychaeta by family, based on the total of 5 cores. S_f : number of species in family; asterisk: borderline case which may belong in other category

Locomotory parapodia well developed	S_f	Locomotory parapodia poorly developed	S_f
Polynoidae	4	Orbiniidae	2
Sigalionidae	1	Paraonidae	16
Phyllodocidae	4	Apistobranchidae	1
Phyllodocida	1	Spionidae	12
undescribed			
Lacydoniidae	1	Chaetopteridae	1
Hesionidae	4	Cirratulidae	7
Pilargidae	1	Cosuridae	3
Syllidae	2	Flabelligeridae	2
Nereidae	1	Fauveliopsidae	2
Nephtyidae	1	Scalibregmidae	1
Sphaerodoridae*	2	Opheliidae	3
Glyceridae	1	Sternaspidae	1
Goniadidae	1	Capitellidae	10
Onuphidae	1	Maldanidae	16
Lumbrineridae*	6	Oweniidae	1
Dorvilleidae	4	Ampharetidae	17
		Terebellidae	8
		Trichobranchidae	1
		Sabellidae	7

would be more diverse than species with large ambits.

Although very little is known of ambit size in polychaetes, particularly in deep-sea polychaetes, a crude dichotomy can be constructed. At the family level, one can make a rough approximation of relative ambit size on the basis of parapodial development (Table 6). Fig. 6 dramatically illustrates the intended difference, but the polynoid seen is much larger than

the typical polychaetes collected. For the particular families encountered, the classification of ambit size happens to correspond with the nominal subclasses Errantia and Sedentaria. The null hypothesis tested is that the number of species per family is the same for both groups. It is tested one-tailed since it is suspected that the number will be greater in the sedentary category. The null hypothesis is rejected (Mann-Whitney U test, $P < 0.05$). Fig. 11 shows that this result is not due simply to the larger number of individuals in the sedentary category. Given any one number of individuals in each category, the smaller-ambit species are (on the average) more speciose and, according to the logic presented earlier (Jumars, 1975), grain specialization and contemporaneous disequilibrium are likely explanations. A likely size scale for such heterogeneity is of a size approaching that of individual polychaetes - the size of the cirratulid mudballs discussed above or smaller.

Implications for Diversity and Population Regulation

The present data are directly opposed to the contention about the deep-sea benthos by Dayton and Hessler (1972, p. 200) that "there is little chance for the kind of niche diversification that results from environmental heterogeneity." However, predation, which Dayton and Hessler suggest regulates most species' populations in the deep-sea benthos, is a likely driving force for contemporaneous disequilibrium. Grassle and Sanders (1973) also consider the possibility of contemporaneous disequilibrium, but discount the importance of predation on the basis of the small clutch size of deep-sea species. This argument is weakened by the fact that clutch size is affected by numerous other variables. In particular, in the deep sea, mortality due to physical stresses is likely to be low, and food is probably scarce (Sanders and Hessler, 1969). Price (1974) indicates that both these factors will lead to a small clutch size.

Dayton and Hessler (1972) also suggest that the finding of generalized food habits among deep-sea species would support their hypothesis that high deep-sea species' diversity is permitted by competitive undersaturation due to predation and other biologic disturbances. However, as Hairston (1973) outlines, competition is unlikely to result in food specialization

where food is scarce. If the environmental grain structure implied by the present results is dynamically stable (*sensu* Colwell, 1973), the most likely outcome of competition in the SDT is grain, or microhabitat specialization (by extension of Hairston's arguments). Because animals which occupy different grain types may utilize the same food resource (MacArthur, 1968), gut contents, without correlative information on grain structure, would give little information on the degree of competitive undersaturation in the community.

Whether it provides a stable background for grain specialization (*sensu* Colwell, 1973) or a shifting stage for contemporaneous disequilibrium (*sensu* Richerson *et al.*, 1970), the importance of environmental grain structure in regulating community diversity is argued by the high diversity of small-ambit species in the SDT. Verification of its role might be found on examining the genetic variability of large-ambit versus small-ambit species. If the environment is effectively coarse-grained for small-ambit species, they should show a relatively high incidence of genetic polymorphism (Selander and Kaufman, 1973).

If they are confirmed, the results of the present study lead to a general hypothesis concerning species' diversity in physically stable environments. The correlation of high species' diversity with high physical stability may be due to a "grain matching" of environmental variability with the size and life cycle of organisms. In stable environments, organisms themselves are likely to be the major source of environmental variability. The resulting spatial and temporal scales of such variability are precisely those which are predicted to produce the smallest probability of competitive exclusion (Hutchinson, 1953, 1961; Reddingius and den Boer, 1970; Richerson *et al.*, 1970).

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