Deep-Sea species diversity: does it have a characteristic scale?

by Peter A. Jumars[1]

ABSTRACT

Dispersion patterns and species diversities of deep-sea macrobenthos were examined for evidence that diversity-controlling processes operate predominantly on any one of several spatial scales. Identification of such scales, if any, would aid in the identification of the diversity-regulating processes themselves. The specific hypothesis that species diversity is independent of scale and location within the deep sea was tested with replicated, partitioned box cores taken at one station in the Santa Catalina Basin (1130 m) and one station in the San Diego Trough (1230 m) of the Southern California continental borderland. Attention was focused on within-community scales. Bathyal rather than abyssal sampling areas were selected to provide adequate animal densities for quantitative treatment.

The hypothesis was discredited for some taxa at all sampling scales: between the two localities, roughly 100 km apart; within localities, between 0.25-m^2 cores on the order of 1 km apart; and, within cores, between 0.01-m^2 subcores. Species diversity depended, to a different degree in the various taxa, on the sampling scale and pattern. Although a complete explanation of deep-sea species diversity must thus invoke processes operant at all the sampled scales, the observed degree of discordance in species' abundances did not suggest any particularly dominant scales or processes peculiar to the deep sea. Inferential evidence implied, however, that the characteristic scale of such processes in the deep sea may be smaller than 0.01 m^2, i.e., approaching the size of areas affected most heavily by single macrofaunal individuals, and that their effects were probably aliased in the present sampling program.

1. Introduction

The finding of high deep-sea species diversity (Hessler and Sanders, 1967) had not been predicted by theoretical ecologists. Experiments with artificial systems and field observations (e.g.: Crombie, 1947; Hutchinson, 1953) had suggested that spatially and temporally uniform environments with few distinguishable food resources could support few species, and the deep-sea benthos seemed to meet all these criteria. What mechanism, then, could allow such a large number of species, most of which appear to be deposit feeders, to coexist in the deep sea?

1. Department of Oceanography, WB-10, University of Washington, Seattle, Washington, 98195, U.S.A.

Slobodkin and Sanders (1969) proposed that specialization by individual species is the likely means for preventing competitive exclusion under such stable conditions. Dayton and Hessler (1972), on the other hand, suggested that, although food probably controls overall animal abundance, biological disturbance prevents potential competitors from reaching densities at which interspecific competition is likely, and hence no specialization is necessary to allow continued coexistence. As Grassle and Sanders (1973) have pointed out, these explanations are not necessarily mutually exclusive. Evidence presented to date has been insufficient to discredit either hypothesis (Jumars, 1975b).

A logical next step in attempting to identify the processes which maintain this high species diversity seemed to me to be the resolution of their spatial scales. In MacArthur's (1969) terms, are the processes that control community diversity local (relatively independent of location and scale within the community) or global (scale and location dependent)? In particular, the possibility existed that the species diversity found in the trawl and dredge samples upon which the original reports (Hessler and Sanders, 1967) were based had been inflated by the traversing of a mosaic of habitats, each with its own, much smaller, species diversity. In the deep sea, physical processes could not be expected to quickly eliminate local habitat differences due, for example, to the sinking of a log or to some local biological activity, be it disturbance or building of structures such as tubes and burrows.

To test the null hypothesis that deep-sea within-community diversity can be entirely locally explained (*sensu* MacArthur, 1969), I undertook a replicated, quantitative sampling program at two bathyal localities. Another way to phrase the same hypothesis is to propose that estimates of community diversity and of other community composition parameters are independent of location and sample size. The estimators used must of course be sample-size independent as well. If the null hypothesis could be rejected, the intent was to make a first approximation of the spatial scales and the possible causes of the heterogeneity in species' dispersion patterns.

In the interim between my initial sampling and this writing, rapid progress has been made in aspects of theoretical ecology that bear directly on deep-sea species diversity. The problems of identifying resources utilized by potential deep-sea competitors and of determining whether disturbance or resource limitation controls the sizes of most deep-sea populations remain, both theoretically and empirically. However, one weak inferential argument can be made. The relatively small body size of deep-sea benthic species (Rowe and Menzel, 1971) confers a turnover-time advantage in the disturbance-limited case but seems, at first inspection, maladaptive under food limitation. Larger body size on the average permits utilization of a wider range of food sizes and hence of more food overall. Schoener (1969, 1971), though, has used an optimal foraging model to demonstrate that if two food generalist species enter competition, they should both shrink in body size.

The observation of small body size also thus seems compatible with the proposition that the deep-sea species in question are potentially competing, food-limited food generalists.

If resources are limiting for the diverse suite of potential competitors, several predictions can now be made. Animals under these conditions have most frequently been observed to partition resources along three resource dimensions: habitat, food type, and time (Schoener, 1974a). Even though temporal cues in the form of tidal currents are present in most deep-sea communities, and some deep-sea species do display asynchronous reproductive cycles (Rokop, 1974), resource partitioning by segregation of feeding times is unlikely under conditions of scarcity (Schoener, 1974b). Furthermore, specialization on food types when food is limiting is generally maladaptive, and habitat or microhabitat segregation is much more likely (Hairston, 1973).

This conclusion has direct bearing on the anticipated results of the present study. If food limits populations, the analysis of heterogeneity in dispersion patterns should reveal the scales at which the likely habitat partitioning occurs. If, alternatively, disturbances are limiting, the analysis should reveal the scales of such disturbances. Spatially uniform or random disturbances of all individuals of all species could not be detected as discordance of species' dispersion patterns but would be of little interest because they do not provide a ready mechanism for preventing competitive exclusion (Schoener, 1974a; Van Valen, 1974). Under conditions of disturbance which aid in maintaining high species diversity, a mosaic of local successional sequences is expected (Levin and Paine, 1975). Thus, discordance in species' local abundances is expected under either resource or disturbance limitation.

How well have recent analyses of deep-sea dispersion patterns matched these predictions? Hessler and Jumars (1974) analyzed single-species' dispersion patterns at a central North Pacific locality in detail. Their results indicate that, if aggregations of animals exist in the sampling area, for most species they are either smaller than the 0.25-m^2 corer used, rare and unlikely to have been encountered in the 12 cores analyzed, or too weak to reveal significant departure from Poisson expectation with 12 replicates per species. Furthermore, concordance of abundances was observed among the more abundant taxa.

Jumars (1975b) has similarly documented that individual polychaete species in the bathyal San Diego Trough each showed little significant departure from random dispersion among 0.25-m^2 cores. However, this departure was significant ($P<0.01$) when all species were used as replicates. Thus the sampled individuals were not all likely to have been drawn from randomly dispersed populations. Indeed the analysis of heterogeneity for these replicates revealed that, as measured by local abundance, places (cores) which were more favorable for some species were not proportionally as favorable for all species ($P<0.01$). Within cores, between 0.01-m^2 subcores, few

polychaete species taken individually deviated markedly from random dispersion patterns, but, when all species were again considered as replicates, even or regular dispersion among conspecific individuals was found ($P \cong 0.01$). Evidence for physical exclusion of paraonids by the mudball-constructing cirratulid *Tharyx luticastellus* documented environmental heterogeneity of a spatial scale approaching the size of individual organisms. Greater diversity of the more sedentary species, as opposed to the more mobile species, also suggested that environmental heterogeneity on scales smaller than the smallest sampling unit (0.01 m^2) may be important in the maintenance of the extremely high polychaete species diversity observed.

At an alternate coring site in the Santa Catalina Basin (Jumars, MS), polychaete species diversity was found to be much lower than in the San Diego Trough, and most species showed little departure from random dispersion among all five 0.25-m^2 cores. Roughly a third of the species, however, were concordantly aggregated in the same one of the five cores, seemingly due either directly or indirectly to the presence of hexactinellid sponge remains. This multispecies aggregation did not appear to displace any of the "background" species; it was simply present in addition to them. Individual species and all species considered as replicates could be fitted to a random dispersion model within cores, among the 0.01-m^2 subcores.

Grassle et al. (1975) have analyzed dispersion patterns of bathyal mega-epifauna. Their observations are of particular interest in the present context of identifying potential sources and scales of local disturbances affecting the smaller, more diverse macrofauna. In particular, the feeding "herds" of *Phormosoma placenta* seem a likely source of both physical disturbance and resource depletion on scales of 40 to 50 m at any one time. Grassle et al. also noted that *Ophiomusium lymani* avoids local depressions of unknown origin. Either the initial producer of the depression, subsequently altered physical conditions in the depression, and/or the consequently patchy effects of *Ophiomusium* might aid in supporting species diversity of macrofauna as per the earlier theoretical arguments.

The foregoing results are difficult to synthesize and to integrate with the pertinent theoretical work in part because the knowledge of any one community has been so fragmentary. Most of the analyses of species diversity, for example, have been based almost entirely on one taxon, the Polychaeta. The present paper asks how valid generalizations based on one taxon are for other taxa in the same community or for the macrofaunal community as a whole. Again, the focus will not be placed on a description of the degree of patchiness of individual species but rather on an analysis of concordance in species' local abundances. Only if species are discordant (heterogeneous) in their abundance patterns—be their individual patterns regular, random, or patchy—does habitat partitioning or species- and location-selective disturbance appear likely. More generally, this discordance suggests that community diversity cannot be understood by studies performed at arbitrarily selected spatial scales and locations; the processes of concern might easily be aliased.

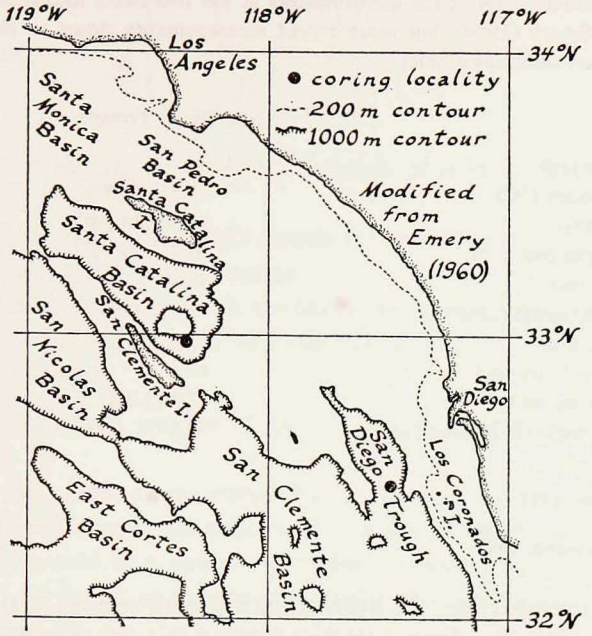

Figure 1. Sampling locations in the Southern California continental borderland.

2. Localities

Two bathyal localities, one in the San Diego Trough (SDT) and one in the Santa Catalina Basin (SCB), were chosen for the analysis of dispersion patterns (Fig. 1). The former locality had been the subject of extensive investigation by previous workers (e.g., Rokop, 1974), whose samples had revealed the high species diversity requisite for the present study. A second area was selected to examine the generality of the findings. Bathyal sampling sites were chosen for logistic reasons and because of the statistical difficulties in analyzing samples from deeper, sparser faunas (Jumars, 1975a). Both sites were located away from obvious sources of large-scale physical disturbances. In particular, the major paths of detrital sediment transport (Emery, 1960) were avoided.

In each of these basins of the Southern California continental borderland, the strategy was to remain as nearly as possible at one position on the chart, with the ship's drift and navigational error randomizing the precise sample locations. In the SDT, the cores designated H22, J14, J15, J22, and J24 fell within 1.19 mi (2.20 km) of the coordinates 32°28.1′N, 117°29.9′W; in the SCB, J9, J10, J11, J12, and J13 came within 0.40 mi (0.74 km) of 32°58.0′N, 118°22.3′W. Individual sample locations are given by Jumars (1975b, MS). Published values for some environmental parameters of the two areas are given in Table 1. Few marked differences

Table 1. Some characteristics of the environments at the two basin localities studied. Data are extracted from Emery (1960), but more recent measurements closer to the actual sampling sites are also given where available.

	San Diego Trough	Santa Catalina Basin
Approximate depth (m)	1230	1130
Temperature at bottom (°C)	3.5 (3.5[a])	4.02
Salinity at bottom (‰)	34.50 (34.50[a])	34.42
Dissolved O_2 at depth (ml l^{-1})	0.7 (0.71[b])	0.4
Effective sill depth (m)	none	1010
Median sediment diameter (μm)	5.6 (8[c])	4.0
Trask sorting coefficient	4.6	3.7
Calcium carbonate (% by wt.)	10.6	18.0
Organic carbon (% by wt.)	7.3 (1-3[d])	8.6
Median diameter, insoluble residue (μm)	8.2	8.9

[a] Rokop, 1974
[b] Smith and Hessler, 1974
[c] Hamilton, 1963
[d] Emery and Hülsemann, 1963

emerge from this comparison; the hydrography of both regions at this depth follows the eastern North Pacific pattern closely, and surface sediments are predominantly detrital silt-clays with a pelagic contribution of calcium carbonate. Although observed oxygen concentrations differ little between the two stations, at this low level the difference may be biologically important.

3. Methods

All samples were taken with the 0.25-m^2 United States Naval Electronics Laboratory spade or box corer (Hessler and Jumars, 1974). Coring procedures were described in detail by Hessler and Jumars (1974), and subsequent manipulations were treated by Jumars (1975a). Cores whose designations are prefixed with the letter "J" consisted of 25 contiguous 0.01-m^2 subcores partitioned *in situ* by the vegematic modification (Jumars, 1975a). The upper 10 cm of sediment were washed through a 0.42-mm aperture screen. Hence, only the macrofaunal taxa (*sensu* Hessler and Jumars, 1974) of these one-liter cubes of mud were reliably sampled. Core H22 was taken two years before all the others, without the vegematic modification, but was otherwise similarly treated. The few specimens of meiofaunal taxa (Harpacticoida, Nematoda, Ostracoda) captured were excluded from the analysis. These individuals appear to have been retained on the screen largely by virtue of unusually long appendages or due to particular death postures.

Hurlbert's (1971) expected number of species was used in assessing species diversity. The following form of the estimator and the following symbols were used throughout:

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right], \text{ for } n \leq N, \text{ where}$$

$E(S_n)$ = number of species expected in a sample of n individuals taken from the community;
N = total number of individuals in the sample at hand;
S = total number of species in that sample;
N_i = number of individuals of the ith species in that sample; and,
n = number of individuals in the hypothetical sample for which the number of species is estimated.

Both $E(S_n)$ and the actual number of species observed were displayed in plots of $E(S_n)$ versus n.

Smith and Grassle (MS) have proved that, if the sample at hand were a random sample from the multinomial distribution of individuals among species in the entire community, $E(S_n)$ would be a minimum variance unbiased estimator of the number of individuals to be found in a random sample of n individuals from that community. More generally for the present purposes, if the proportion of the fauna which each species comprised were independent of location and sample size but were free to vary stochastically, then $E(S_n)$ based on a contiguous collection of individuals (e.g., a core sample) or on a summed set of such samples would give an unbiased estimate of the number of species to be seen at any smaller (than N) sample size.

According to the arguments presented earlier, the assumption of independence of species' local abundances is of direct concern in deciding whether the mechanisms which maintain species diversity are local or global. Goodness of fit to $E(S_n)$ of the actual numbers of species observed in samples of size n (using the variance formulas derived by Smith and Grassle, MS) would provide one possible test of this assumption, but the more direct "dispersion chi-square" analysis (Jumars, 1975a) was applied instead. This method tests for any unexpectedly large concordance or discordance in species' local abundances relative to the expected stochastic variability if their local abundances are independent. In the tabled results of this analysis, the heterogeneity chi-square component would approximate its degrees of freedom if the assumption of independence were true.

When discordance in dispersion patterns was found (heterogeneity chi-square component exceeded its degrees of freedom, $P<0.05$), the discordant species involved were identified according to a simple clustering procedure. Species contributing the largest portion of the heterogeneity were removed one at a time until the largest possible primary group showing no significant heterogeneity ($P \geq 0.05$) remained. The procedure was repeated with the removed species, yielding one or

Table 2. Number of individuals and number of species by taxon and by locality contained in the total of all samples (five 0.25-m² cores per locality, where N = number of individuals, $\%N$ = percent of all individuals the taxon contains, S = number of species, $\%S$ = percent of all species the taxon contains). San Diego Trough Isopoda include three desmosomatid individuals which are unidentifiable and so are excluded from species diversity considerations.

	Locality							
	San Diego Trough				Santa Catalina Basin			
Taxon	*N*	*%N*	*S*	*%S*	*N*	*%N*	*S*	*%S*
ANNELIDA	2125	75.52	146	46.50	1800	76.60	58	35.80
Polychaeta	2125	75.52	146	46.50	1798	76.51	57	35.19
Hirudinea	—	—	—	—	2	0.09	1	0.62
CRUSTACEA	345	12.26	113	35.99	366	15.57	67	41.36
Cirripedia	1	0.04	1	0.32	—	—	—	—
Mysidacea	5	0.18	2	0.64	2	0.09	1	0.62
Cumacea	35	1.24	10	3.19	44	1.87	13	8.02
Tanaidacea	105	3.73	19	6.05	89	3.79	7	4.32
Isopoda	82	2.91	30	9.55	91	3.87	6	3.70
Amphipoda	117	4.16	51	16.24	138	5.87	38	23.46
Decapoda	—	—	—	—	2	0.09	2	1.23
MOLLUSCA	135	4.80	26	8.28	80	3.40	20	12.35
Gastropoda	28	1.00	6	1.91	9	0.38	8	4.94
Pelecypoda	86	3.06	16	5.10	34	1.45	8	4.94
Aplacophora	14	0.50	3	0.96	9	0.38	3	1.85
Scaphopoda*	7	0.25	1	0.32	28	1.19	1	0.62
ECHINODERMATA	88	3.13	9	2.87	61	2.60	4	2.47
Holothuroidea	15	0.53	4	1.27	2	0.09	1	0.62
Ophiuroidea	73	2.59	5	1.59	59	2.51	3	1.85
MISCELLANEOUS TAXA	121	4.30	20	6.37	43	1.83	13	8.02
Porifera	—	—	—	—	1	0.04	1	0.62
Coelenterata	2	0.07	2	0.64	2	0.09	1	0.62
Turbellaria*	—	—	—	—	2	0.09	1	0.62
Nemertinea*	44	1.56	8	2.55	15	0.64	4	2.47
Sipunculida	14	0.50	4	1.27	9	0.38	1	0.62
Priapulida	1	0.04	1	0.32	—	—	—	—
Ectoprocta**	38	1.35	2	0.64	3	0.13	2	1.23
Eneteropneusta	5	0.18	1	0.32	9	0.38	1	0.62
Pterobranchia	—	—	—	—	1	0.04	1	0.62
Pogonophora	8	0.28	1	0.32	—	—	—	—
Ascidiacea	9	0.32	1	0.32	1	0.04	1	0.62
TOTAL MACROFAUNA	2814		314		2350		162	

* The author is particularly uncertain of his taxonomy in these groups.
** Colonial forms are treated as single individuals.

Table 3. Median number of individuals per subcore for the 9 central and 16 peripheral subcores, and apparent sampling efficiency in each vegematic core. Apparent sampling efficiency (%) = 100 × core total observed ÷ (total for inner nine subcores × 11.111).

	Locality and Core								
	San Diego Trough				Santa Catalina Basin				
Taxon	J14	J15	J22	J24	J9	J10	J11	J12	J13
Annelida									
central	22.0	21.0	20.0	14.0	10.0	23.0	13.0	13.0	10.0
		*	*					*	
peripheral	19.0	15.0	13.5	14.5	14.0	20.5	15.5	9.5	13.5
efficiency (%)	93.60	83.61	79.65	93.55	114.12	93.03	119.56	81.98	106.92
Crustacea									
central	3.0	3.0	3.0	5.0	3.0	4.0	4.0	1.0	3.0
peripheral	2.0	2.0	3.0	2.5	2.0	3.0	2.0	1.0	1.0
efficiency (%)	108.00	79.45	93.00	72.95	74.25	87.30	94.38	74.25	82.13
Mollusca									
central	2.0	1.0	0.0	0.0	0.0	2.0	1.0	0.0	1.0
peripheral	1.0	1.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0
efficiency (%)	78.86	72.00	54.00	158.40	168.00	72.00	48.00	72.00	60.00
Echinodermata									
central	0.0	1.0	1.0	2.0	0.0	1.0	0.0	0.0	1.0
peripheral	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
efficiency (%)	135.00	75.60	61.20	50.82	108.00	49.26	90.00	63.00	67.50
Miscellaneous Taxa									
central	1.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
peripheral	1.0	1.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0
efficiency (%)	126.00	78.35	144.00	69.00	180.00	180.00	72.00	54.00	126.00
Total Macrofauna									
central	28.0	27.0	26.0	21.0	17.0	31.0	19.0	16.0	15.0
		*	*					*	
peripheral	24.5	20.0	18.0	19.0	17.5	27.0	20.0	10.5	15.5
efficiency (%)	95.57	82.06	81.00	86.64	110.15	88.96	109.13	79.89	97.78

* Central and peripheral medians differ, Mann-Whitney U test, $p < 0.05$.

more smaller secondary groups. This simple algorithm formed the fewest, largest groups possible under the criterion of no significant discordance in local abundance among species within groups.

Data to which the clustering procedure was applied were summarized by plotting the variance-to-mean ratio ($s^2/\bar{x}$) versus the mean ($\bar{x}$) for the per sample abundance of each species. According to arguments presented in Appendix I and in Jumars (MS), members of any of the resultant groups should fall along a straight line in such a plot, and this "expected" line was drawn for the primary group in each case. The slope of the line provides a density-independent measure of the degree of patchiness of group members. This line is *not* a standard least-squares fit to the data points. Such a fit is invalid for reasons detailed in Appendix I and Jumars (MS).

Finally, the resultant groups were examined for between-group differences that could account for the disparity in dispersion patterns and might thereby shed light upon the mechanisms maintaining species diversity.

4. Results

The total numbers of individuals and species obtained are summarized by locality and by taxon in Table 2. For each area, the numbers were derived from five 0.25-m^2 cores, and so should represent 1.25 m^2 of bottom. Results for the Polychaeta alone, however, implied that an edge effect, presumably due to the bow wave of the corer, had acted (most severely on the peripheral 16 subcores of the five-by-five array) to lower the estimates of polychaete density (Jumars, 1975b, MS).

Findings for the other taxa, given in Table 3, support this interpretation. Percentages in the table represent the apparent capture efficiency of the total corer calculated by using the central nine subcores as an internal standard. If there had been no peripheral bias, the calculated efficiencies should have fallen with equal frequency above and below 100%. Of the 45 percentages in Table 3, however, 32 fell below 100% ($P \cong 0.0024$). If a bow wave had been responsible for this bias, one might expect that different taxa (of presumably differing hydrodynamic properties and differing characteristic depths of burrowing in the sediment) would have been acted upon with varying severity and also that cores which had suffered a greater bow wave would reveal a stronger effect across all taxa. Setting up the null hypothesis that apparent capture efficiency is independent of both core and taxon (and using the miscellaneous category as a taxon), the Friedman rank-sum, two-way, nonparametric analysis of variance was applied (Hollander and Wolfe, 1973). The procedure revealed that some cores were probably more biased than others across all taxa ($P \cong 0.10$) and that taxa do differ in susceptibility to the presumed bow wave ($P \cong 0.05$), although the test does not determine which cores or which taxa were most seriously affected.

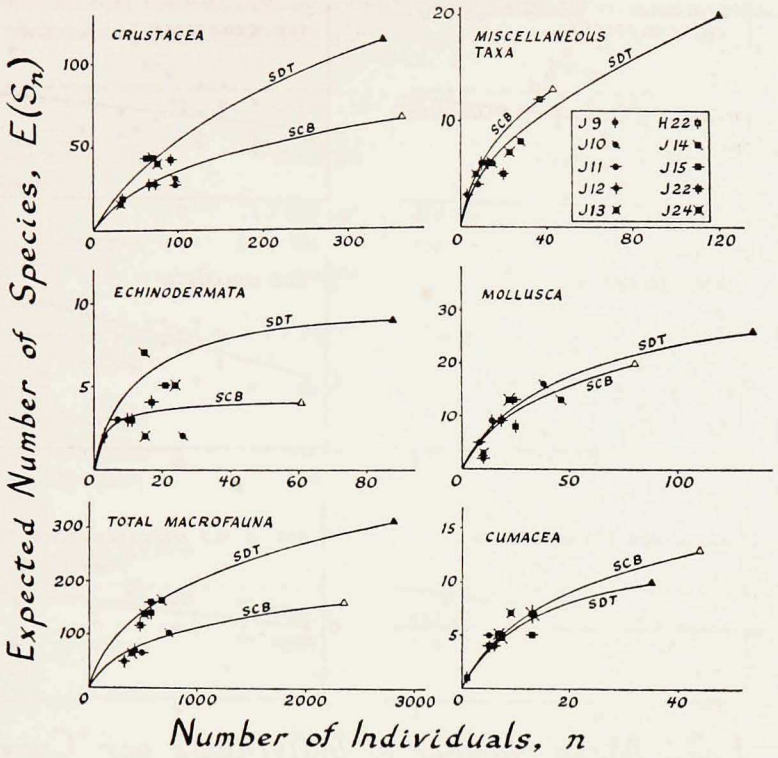

Figure 2. Expected number of species, $E(S_n)$, versus number of individuals, n, calculated by the Hurlbert (1971) method from the distributions of individuals among species of the indicated taxa and localities. All cores for each locality were pooled in the calculation. Squares: observed values in San Diego Trough (SDT) cores; circles: observed values in Santa Catalina Basin (SCB) cores; closed triangles: five-core totals for SDT; open triangles: five-core totals for SCB.

The pattern was pursued further with a distribution-free multiple comparison test based on the Friedman rank sums (Hollander and Wolfe, 1973, p. 151). At an experimentwise significance level of 0.05 (taking into account the degree of multiple testing performed), none of the cores or taxa differed significantly from each other in capture efficiency. Their orderings in terms of this apparent efficiency nonetheless affect subsequent interpretations and are summarized below. MT stands for the miscellaneous taxa, SDT cores are designated by underlining, and the least biased core or taxon appears at the left.

Least	Annelida		MT	Crustacea		Echinodermata		Mollusca		Most
Biased	J14	J9	J11	J13	J10	J15	J22	J24	J12	Biased

Because they determine the manner in which the remaining data can be legiti-

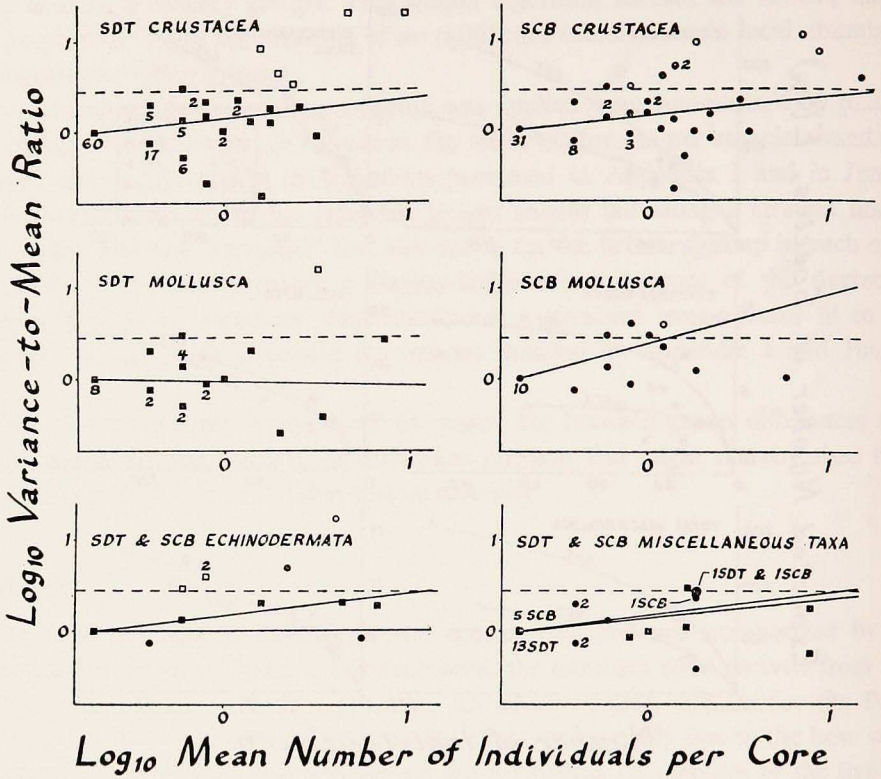

Figure 3. Logarithm of variance-to-mean ratio, $s^2/\bar{x}$, versus logarithm of mean number of individuals per core, $\bar{x}$, for species encountered in the San Diego Trough (SDT, squares) and in the Santa Catalina Basin (SCB, circles) by major taxon. Solid line: summary of dispersion patterns for members of the largest (primary) group homogeneous in dispersion pattern (see text and Appendix I) as per Table 5; closed figures: members of a primary group; open figures: members of a smaller (secondary) group; numbers: number of species (in excess of one) showing the indicated values; dashed line: upper 95% confidence limit for a Poisson distribution (lower limit falls below abscissa). This figure shows the low degree of patchiness and discordance among encountered species' abundances as well as summarizing those abundances.

mately presented, these results must be discussed prematurely. The differences in capture efficiencies among the major taxa are of greatest concern. These differences preclude a valid comparison of local discordance in abundance among the taxa, in particular because some cores were more biased than others. Therefore, all the following tabled analyses are limited to comparisons and groupings within the major taxa.

The above results might be suspect because *a priori* one might predict that a mollusc or echinoderm would be less likely to be displaced by a bow wave than

Table 4. Between-core dispersion chi-square analysis by taxon. *NS* = value approximates the number of degrees of freedom, $p > 0.05$.

	Taxon				
		Crustacea	Echinodermata		
SAN DIEGO TROUGH:	Annelida		Mollusca		Misc. Taxa
Total chi-square					
value	812.89	678.19	179.57	80.47	95.97
degrees of freedom	584	452	104	36	80
probability	<0.001	<0.001	<0.001	<0.001	NS
Pooled chi-square					
value	26.21	25.75	17.78	5.86	13.34
degrees of freedom	4	4	4	4	4
probability	<0.001	<0.001	<0.01	NS	<0.05
Heterogeneity chi-square					
value (among species)	768.68	652.44	161.79	74.61	82.63
degrees of freedom	580	448	100	32	76
probability	<0.001	<0.001	<0.001	<0.001	NS
SANTA CATALINA BASIN:					
Total chi-square					
value	643.45	455.49	125.53	97.29	68.67
degrees of freedom	232	268	80	16	52
probability	<0.001	<0.001	<0.01	<0.001	NS
Pooled chi-square					
value	141.64	38.26	29.00	25.80	8.98
degrees of freedom	4	4	4	4	4
probability	<0.001	<0.001	<0.001	<0.001	NS
Heterogeneity chi-square					
value (among species)	501.81	417.23	86.53	71.49	59.69
degrees of freedom	228	264	76	12	48
probability	<0.001	<0.001	NS	<0.001	NS

would a crustacean or annelid. A species-by-species examination, however, suggests that the ordering is related to the proportions of each taxon's members which live attached, burrowed, or in protective tubes. Most of the echinoderms encountered, for example, were small juveniles which had presumably inhabited the sediment surface. This hypothesis has been borne out in subsequent cores which were vertically subsampled (Jumars and Fauchald, unpublished; Thiel and Hessler, 1974).

Species diversities of the major taxa are presented in Fig. 2. The $E(S_n)$ values were calculated by using N_i values from the combined cores, making N and S for each calculation correspond to the taxon total in Table 2. Corresponding plots for the Polychaeta were presented by Jumars (1975b, MS).

Between-core dispersion patterns are summarized in Fig. 3 and Table 4. Species groups based on these data and formed as described above are briefly outlined in Table 5.

Table 5. Groups of species homogeneous in between-core dispersion patterns and the number of individuals per group per core. The most abundant species is used to name the group, but when they are equally abundant, both of the two most abundant species are indicated. G_p = primary group, G_s = secondary group, and S_g = number of species in the group.

SAN DIEGO TROUGH:

	S_g	Group Designation	Core H22	J14	J15	J22	J24
Annelida							
G_p	134	*Tharyx* sp. A	294	362	339	283	271
G_s	5	*Tharyx luticastellus*	39	56	67	128	71
G_s	5	*Spiophanes* cf. *bombyx*	34	77	21	13	24
G_s	2	*Paraonis gracilis oculata*	23	12	5	3	3
Crustacea							
G_p	108	*Ilyarachna profunda*	27	54	52	58	48
G_s	2	*Dulichia* sp. A	0	15	2	1	0
G_s	1	Cumacean sp. D	1	1	7	0	3
G_s	1	Dikonophoran sp. D	6	2	3	34	4
G_s	1	Phoxocephalid sp. B	2	0	0	0	22
Mollusca							
G_p	25	*Vesicomya* sp. A	25	30	24	18	22
G_s	1	?*Cocculina* sp. A	0	16	0	0	0
Echinodermata							
G_p	6	*Ophiacantha normani*	11	12	21	17	16
G_s	2	*Ophiocten pacificum* & *Ophiura kofoidi*	0	0	0	0	8
G_s	1	Holothurian sp. C	0	3	0	0	0
Miscellaneous Taxa							
G_p	20	Nemertean sp. A & Ectoproct sp. A	13	28	37	20	23

SANTA CATALINA BASIN:

			J9	J10	J11	J12	J13
Annelida							
G_p	46	*Chaetozone* cf. *setosa*	182	213	248	192	197
G_s	11	*Paraonis gracilis oculata*	96	263	63	49	59
G_s	1	*Tharyx* cf. *monilaris*	39	77	51	30	41
Crustacea							
G_p	62	*Ilyarachna profunda*	53	64	66	32	55
G_s	3	Dikonophoran sp. B	0	19	0	1	0
G_s	1	Dikonophoran sp. A	13	1	10	0	18
G_s	1	Dikonophoran sp. C	0	13	21	0	0
Mollusca							
G_p	19	*Cadulus californicus*	14	37	8	5	10
G_s	1	*Dacrydium* sp. A	0	1	0	5	0
Echinodermata							
G_p	3	*Ophiacantha normani*	3	7	10	6	15
G_s	1	*Amphiura* sp. A	0	19	0	1	0
Miscellaneous Taxa							
G_p	13	Enteropneust sp. A & Nemertean sp. A	10	15	8	3	7

Table 6. Within-core, between-subcore dispersion chi-square analysis by taxon. *NS* = value approximates the number of degrees of freedom, $p > 0.05$.

	Taxon				
	Annelida	Crustacea	Mollusca	Echinodermata	Misc. Taxa
SAN DIEGO TROUGH, based only on central nine subcores:					
Total chi-square					
value	1541.93	769.62	279.64	128.20	135.30
degrees of freedom	1584	752	208	120	144
probability	*NS*	*NS*	<.01	*NS*	*NS*
Pooled chi-square					
value	54.78	24.97	60.70	41.85	43.22
degrees of freedom	32	32	32	32	32
probability	<0.05	*NS*	<0.01	*NS*	*NS*
Heterogeneity chi-square					
value (among species)	1487.14	744.64	218.94	86.35	92.08
degrees of freedom	1552	720	176	88	112
probability	*NS*	*NS*	<0.05	*NS*	*NS*
SANTA CATALINA BASIN, based only on central nine subcores:					
Total chi-square					
value	789.87	756.19	179.25	116.48	86.00
degrees of freedom	752	672	168	72	88
probability	*NS*	<0.05	*NS*	<0.01	*NS*
Pooled chi-square					
value	55.18	59.97	44.81	89.53	32.00
degrees of freedom	40	40	40	40	40
probability	<0.05	<0.05	*NS*	<0.001	*NS*
Heterogeneity chi-square					
value (among species)	734.69	696.22	134.44	26.95	54.00
degrees of freedom	712	632	128	32	48
probability	*NS*	≅0.05	*NS*	*NS*	*NS*
SANTA CATALINA BASIN, based on the full 25 subcores of each core:					
Total chi-square					
value	3611.16	3831.56	903.06	416.01	557.00
degrees of freedom	3528	3120	840	288	576
probability	*NS*	<0.001	*NS*	<0.001	*NS*
Pooled chi-square					
value	153.10	242.90	150.75	249.27	103.67
degrees of freedom	120	120	120	120	120
probability	≅0.05	<0.001	≅0.05	<0.001	*NS*
Heterogeneity chi-square					
value (among species)	3458.06	3588.67	752.30	166.74	453.33
degrees of freedom	3408	3000	720	168	456
probability	*NS*	<0.001	*NS*	*NS*	*NS*

Table 7. Estimated number of individuals per m^2 at the two localities with ($\bar{x}_c$, Md_c) and without ($\bar{x}$, Md) corrections for apparent sampling inefficiency. $\bar{x}$ = based on mean number per core; $\bar{x}_c$ = based on mean number per the central 0.09 m^2 of each vegematic core; Md = based on median number per core; Md_c = based on median number per central 0.09 m^2 of each vegematic core. Note that for the San Diego Trough $\bar{x}$ and Md are based on only the four vegematic cores.

	San Diego Trough				Santa Catalina Basin			
Taxon	$\bar{x}$	$\bar{x}_c$	Md	Md_c	$\bar{x}$	$\bar{x}_c$	Md	Md_c
Annelida	1700	1989	1708	2106	1440	1418	1268	1211
Crustacea	276	353	288	361	293	349	292	356
Mollusca	108	139	96	133	64	87	40	67
Echinodermata	70	114	68	111	49	80	40	44
Miscellaneous Taxa	97	117	92	111	34	29	32	22
Total Macrofauna	2251	2711	2300	2811	1880	1962	1640	1644

Species were much more homogeneous in their dispersion patterns within cores. In fact, the only deviations which exceeded those expected by chance were in Mollusca of the SDT and in Crustacea of the SCB (Table 6, heterogeneity chi-square). Values for the total of 25 subcores in the SDT were excluded from Table 6 because they appeared to be seriously affected by the poor capture efficiencies observed in the peripheral versus the central nine subcores of J15, J22, and J24. For the SDT Mollusca, the exclusion of only one species, ?*Cocculina* sp. A, sufficed to make the remaining group homogeneous. While the exclusion of only two species (dikonophoran tanaid spp. A and C) sufficed to hold the Crustacea of the SCB above the 0.05 probability level for its heterogeneity chi-square value, eight species made substantial contributions to the heterogeneity (i.e., phoxocephalid spp. D and E, isaeid spp. A and B, eurycopid sp. A, and dikonophoran tanaid spp. A, B, and C). Their exclusion, in fact, would make the remaining group slightly more homogeneous than would be expected by chance. These eight species could not be combined into homogeneous secondary groups as could many of the excluded species in the between-core comparison; their aggregations did not consistently overlap.

Although not ideal for a study of patchiness *per se* of individual species' populations, the sampling design permits some conclusions about such patchiness. The species of concern and the necessary statistical qualifications are given in Appendix II.

Also somewhat aside from the goals of the present paper is the estimation of macrofaunal standing crops. In order to facilitate comparisons with other benthic studies, however, Table 7 is provided. Because the sum of medians need not equal the median of sums, those columns based on medians may not be completely additive. The generally high pooled chi-square values in Table 4 suggest that the most reliable figures to use would be those based on median abundance within the central 0.09 m^2 of each core.

5. Discussion and Conclusions

The null hypothesis that species' relative abundances are location and scale independent can be rejected on the basis of the observed heterogeneity chi-square values, especially on the between-core scale (Table 4). These relative abundances vary sufficiently over distances on the order of a few kilometers to permit detection of the variation with a very small number of samples. Community diversity, at least of these two communities, is therefore unlikely to be well understood by studies performed at one arbitrarily selected location or spatial scale within the community.

Do the observed dispersion patterns give any clues as to their probable generating mechanisms? Definitive data regarding food types selected, habitat types preferred, activity patterns displayed, and disturbance agents acting at some presampling time, are lacking. In a few cases, however, circumstantial evidence gives reasonable answers. All 16 individuals of *?Cocculina* sp. A in the SDT samples were found still attached to a single blade of eelgrass which had stretched across two subcores. This undescribed species of limpet (F. Rokop, Scripps Institution of Oceanography, personal communication) presumably requires eelgrass or a similar substrate for browsing. It may feed on the eelgrass or on the numerous fouling organisms (mostly Foraminifera) seen on this particular blade and found on vascular plant debris in other bathyal samples in the area. In examining several epibenthic sled and otter trawl samples, I have seen the species only on eelgrass (two occasions) and on a small piece of board (one occasion) dredged from bathyal depths off San Diego.

Other clues are not so straightforward. Jumars (MS) proposed that the amount of dead hexactinellid sponge material on the surface of core J10 might have been in some way responsible for the high concentration of the *Paraonis gracilis oculata* group in that core. Actually, a larger secondary group was formed in that study by the slightly different sorting strategy used. It was not clear, however, whether animals aggregating in this core recognized structural habitat differences or food resource differences, perhaps due to locally altered sedimentation patterns, or whether they obtained some measure of protection from disturbance from the sponge "cover." The concentration of all the SCB groups but two, including all the primary groups of Table 5, in either core J10, core J11 (which contained the second highest concentration of sponge fragments), or in both supports the contention that some correlate of sponge-fragment cover was responsible.

Perhaps a parallel effect is seen in core J14, where the eelgrass was found. Locally elevated allochthonous food supply might explain the concentration of the *Tharyx* sp. A, *Spiophanes* cf. *bombyx, Dulichia* sp. A, and *Vesicomya* sp. A groups. Besides *Dulichia* sp. A (a podocerid amphipod), for example, the group to which it belongs contains a corophiid amphipod—a tube-dwelling family not encountered in other cores.

A more ephemeral aggregation is suggested by the *Ophiocten-Ophiura* group and perhaps by phoxocephalid sp. B in core J24. *Ophiocten* (and perhaps *Ophiura*) has been observed to congregate at "windfalls" of particulate animal material, both in experiments (Thiel and Hessler, 1974) and in natural falls of *Pelagia* (Neil Marshall, Scripps Institution of Oceanography, unpublished color photographs) in the SDT.

Whatever its causes, the heterogeneity in dispersion patterns affects the accuracy of the estimator $E(S_n)$ when it is applied to summed core samples. One expects some stochastic variation about the number of species predicted by Hurlbert's (1971) equation, but the heterogeneity in dispersion patterns increments this variability in a biased fashion. In particular, when a group of one or a few species is strongly aggregated relative to the other species, the number of species in the core (or cores) in which it is concentrated is depressed relative to the expected value. For example, in core J14 all 16 individuals of ?*Cocculina* sp. A occurred. If only three of its individuals had been found there, as would have been expected if the species had conformed to the primary group's pattern, 33 individuals of 13 species would have been observed. These coordinates are much closer to the plot of $E(S_n)$ than are the actual coordinates (46, 13) for the Mollusca of J14. Analogous effects can be ascribed to other species, including tanaid sp. D in core J22, phoxocephalid sp. B in core J24, and *Amphiura* sp. A in core J10 (Table 5 and Fig. 2).

Heterogeneity in dispersion patterns, however, need not uniformly depress observed versus expected number of species. If a core contains an adequate representation of both the primary groups and the secondary groups (in particular the more speciose secondary groups) without extreme dominance by one or a few species, $E(S_n)$ may prove to be an underestimate (e.g., core J10 for total macrofauna).

Smith and Grassle (MS) have suggested that each field sample be treated as though drawn from a separate (multinomial) distribution of individuals among species. The point is well taken that this procedure would certainly eliminate the problem of between-core heterogeneity in dispersion patterns, but the accuracy of $E(S_n)$ would still hinge on smaller-scale heterogeneity in species' dispersion patterns. For example, it is unclear what area the ?*Cocculina*-containing core would accurately represent under Smith and Grassle's interpretation. Hurlbert's $E(S_n)$ implicitly assumes that each of the N individuals sampled had a probability of being drawn proportional only to its species' relative abundance in the area to be represented. Unless all species are independently dispersed, there is no reason to expect that a necessarily contiguous core, grab, or trawl sample of individuals from that region will behave statistically as would a truly random sample of individuals; a randomly located *core* does not necessarily provide a random sample of *individuals* for binomial or multinomial estimation. In lieu of the detailed information on dispersion patterns needed to improve estimates from core samples, however, the manifold

Table 8. $E(S_N) - E(S_{N-10})$, the increment of Hurlbert's (1971) expected number of species over the range from the total number of individuals actually observed to ten individuals fewer. This quantity is an estimate of the number of additional species which would be discovered if ten additional individuals of the indicated taxon were collected. Due to the monotonically decreasing slope of the relation between $E(S_n)$ and n (e.g., Fig. 2) it is most likely an overestimate.

Taxon	San Diego Trough	Santa Catalina Basin
Annelida	0.180	0.084
Crustacea	1.772	0.854
Cumacea	0.993	1.289
Mollusca	0.610	1.268
Echinodermata	0.117	0.025
Miscellaneous Taxa	1.075	1.372
Total Macrofauna	0.428	0.260

statistical advantages of $E(S_n)$ (Smith and Grassle, MS) make it preferable to other diversity estimators for the present purposes.

Keeping in mind the sources and magnitudes of the inaccuracies resulting from the use of $E(S_n)$ on the combined core samples, some patterns do emerge in a comparison of the SDT and SCB: (1) macrofaunal species diversity is higher in the SDT than in the SCB locality, and (2) not all taxa contribute equally or proportionately to the diversities or the difference in diversities. This latter point is underscored by an examination of Cumacea (Fig. 2), which appear to be more diverse in the SCB than in the SDT. Part of this apparent difference between taxa may be due to the fact that samples of one size and type do not sample all taxa equally well. An indication of the number of species yet to be discovered is given in Table 8 as the increment in $E(S_n)$ over the domain (N-10) to N. A relatively large value indicates that considerably more species probably remain to be discovered in that taxon (i.e., that a substantial portion of the species encountered are represented by small numbers of individuals). Nevertheless, the best guess that one can make on the basis of these samples is that the between-area comparisons of species diversity are taxon dependent, certainly in magnitude and perhaps in direction. This result underscores the need for caution in extrapolation from findings in one taxon (e.g., Rex, 1973) to the entire macrofauna.

Ascribing the differences in macrofaunal diversity between the two areas to any given cause is hazardous. Again, however, an analysis of patterns within and between taxa provides some tenable hypotheses. In particular, the major between-site differences lie in Annelida and Crustacea. At a finer level still, the principal between-site difference is due to lowered diversity of Isopoda, Tanaidacea, and Polychaeta at the SCB. Among the isopods, species of Desmosomatidae, which is by far the most speciose family in the SDT, are conspicuously absent from the SCB samples, where all the isopods are strong swimmers (i.e., Eurycopidae and Il-

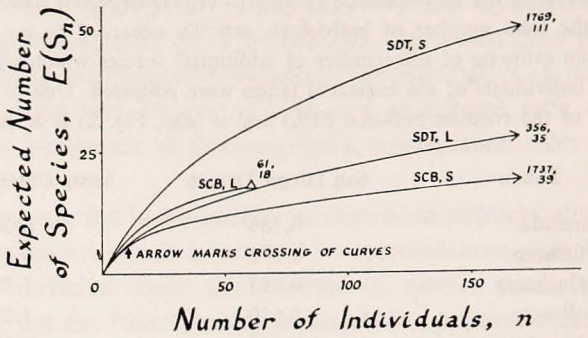

Figure 4. Expected number of species, $E(S_n)$, versus number of individuals, n, calculated by the Hurlbert (1971) method from the distributions of individuals among those species assumed to have large (L) areas of activity and among those species assumed to have small (S) areas of activity. Only the polychaetes of the San Diego Trough (SDT) and the Santa Catalina Basin (SCB) are treated. Numbers give the endpoints observed (e.g., the numbers adjacent to the open triangle indicate that 61 individuals of 18 species which presumably have large areas of activity were collected from the Santa Catalina Basin).

yarachnidae). Equating morphology with ambulatory and natatory ability (cf. Jumars, 1975a, b), the polychaetes can be divided into those species which presumably have a small area of activity (approximately corresponding to Sedentaria), and those which are probably more active over larger areas (approximately corresponding to Errantia). This area of activity is often termed the species' ambit (Lloyd, 1967), and Fig. 4 shows the between-site difference in polychaete species diversity to be due almost entirely to the "small-ambit" group. The change in tanaid species diversity between sites may reflect an analogous phenomenon in these largely tube-dwelling, and presumably small-ambit species.

The apparent general reduction in diversity of small-ambit species may be related to a dearth of small-scale environmental heterogeneity at the SCB locality. In particular, the mudball-constructing cirratulid species, *Tharyx luticastellus*, one of the two most abundant macrofaunal species at the SDT sampling site, is absent there, with a corresponding lack of obvious physical structures of this scale and abundance. Alternatively, small-ambit species may be disadvantaged by potential physical instability at the SCB site. It is near the edge of the basin, in which occasional seiching has been documented to a depth of over 1000 m (Emery, 1960), and evidence of turbidity flows has been found near the sampling locality (Jumars, MS).

The suggestion can also be made that the benthic community of the SCB is continually or aperiodically subjected to the stress of low oxygen tension (Table 1). In the polychaetes of the SCB, all but one of the burrowing species (a capitellid) which do not construct potentially ventilating tubes bear conspicuous gills. Lum-

brineridae, for example, are represented only by two species of *Ninoe*, a genus defined on the basis of its branchiae. One of the (probably non-burrowing) dorvilleid species present (of an undescribed genus) in fact bears elaborate gills, a morphological trait otherwise extremely rare in the family, but recently found in a congener from the immediate vicinity of White's Point sewer outfall off Los Angeles, where oxygen levels often fall below detectable levels (David Montagne, County Sanitation District of Los Angeles, personal communication).

Other possible causes of the between-site difference in species diversity cannot be excluded out of hand, but further discussion on the basis of only two localities seems unwarranted. Whatever the causes, diversity levels vary on the roughly 100-km between-locality scale as well as between and within cores at the same locality. Any complete explanation of deep-sea species diversity must therefore invoke mechanisms operating at all these scales. Do these and other observed spatial patterns, however, suggest what the mechanisms might be that permit the deep-sea, soft-bottom benthos to support a higher species diversity than its shallow-water counterparts? Are the observations compatible with the introductory predictions above?

Spatial environmental variation in general facilitates support of elevated species diversities, while temporal variation does not (May, 1974) unless it has a period approximating the generation times of potential competitors (Hutchinson, 1953). The effects of interacting spatial and temporal heterogeneity on species diversity depend on the scale parameters of this variation and on life histories of the species involved (Levin and Paine, 1975). For example, one must know how large habitat patches are and whether they persist long enough for one or more species to utilize them. Again, complete data for the application of Levin and Paine's (1975) model of diversity maintenance are lacking for any given deep-sea area, but some suggestive fragments have been resolved.

Dramatic changes in deep-sea community structure over 100-km distances (J. Dickinson, Oregon State University, personal communication; data herein) suggest that part of the diversity of concern (within-community diversity of the scales treated by Hessler and Sanders, 1967) may be supported by immigration. This effect is likely to be largest where habitat differences on this scale are marked, effectively yielding an "archipelago" of habitat islands (MacArthur and Wilson, 1967). The complex topography of the Southern California continental borderland in particular would generate such habitat islands. Some shallow-water environments also vary on this scale, however, and it is not obvious that this scale of environmental heterogeneity could account for the disparity in species diversity between shallow water and deep sea.

On a slightly smaller scale, deep-sea hills, with their topographically varying sedimentary regimes (Johnson, 1972) provide a structural heterogeneity which might be recognized directly by some species. Alternatively, this variation might

determine dispersion patterns indirectly through topographically varying rates of food supply or through thereby induced differences in the kinds or intensities of biological disturbances. Deep-sea animal dispersion patterns on this scale are poorly known largely because of technical difficulties in locating and holding a vessel over a particular segment of the topography. Nevertheless, if such variation were of unusual importance in deep-sea diversity considerations, Hessler and Jumars (1974) should have detected more patchiness in species' dispersion patterns. Furthermore, the continental slope region treated by Hessler and Sanders (1967) shows little topographic variation of this scale; it cannot be requisite to the diversity levels observed.

Approaching the between-core scale of the present study, as discussed earlier, Grassle et al. (1975) have documented the localized action of some potential sources of disturbance. The present study suggests that biogenic structures such as the encountered hexactinellid sponge remains also affect diversity on this scale. Again, the navigational problem of accurately locating samples relative to each other has made the spatial extent of such patches in the deep sea unknown with the exception of Grassle et. al.'s (1975) estimate of 40 to 50 m for *Phormosoma placenta* "herd" size. Information on the persistence of such patches (needed to apply Levin and Paine's, 1975, model) has been limited by an inability to age or relocate them. Incidental observations of man-made disturbances such as submersible or sampler tracks, however, suggest that minor physical features may persist on the order of years at bathyal depths (e.g., Deep-Towed Vehicle Group, Marine Physical Laboratory, Scripps Institution of Oceanography, unpublished photographs of epibenthic sled tracks in the SDT). Environmental variation of these spatial scales is common in shallow water, but is typically not so long lived due to physical disturbances (e.g., Draper, 1967) as well as to greater bioturbation rates with higher standing crops of biota. Whether the interaction of time and patches of this size supports high deep-sea species diversity hinges on still more parameters, such as generation times of the affected species, which are scantily known (Turekian et al., 1975).

Time scales and effects of features grading into 0.01-m^2 size and smaller are likewise poorly known. How long does a manganese nodule provide a substrate for attachment by Foraminifera and serpulid worms? How long does a blade of eelgrass or a piece of wood (Turner, 1973) remain recognizable at the sediment surface, and how do its effects on community composition vary during decomposition? How long does a vacated mudball of *Tharyx luticastellus* continue to provide a habitat used by other species (Jumars, 1975c)?

Until such questions and more about the parameters of Levin and Paine's (1975) model are answered, it is impossible to ascertain directly whether these and smaller-scale variations in the deep sea support its relatively high species diversity. The especially high diversity of small-ambit species found in the SDT (Jumars, 1975b

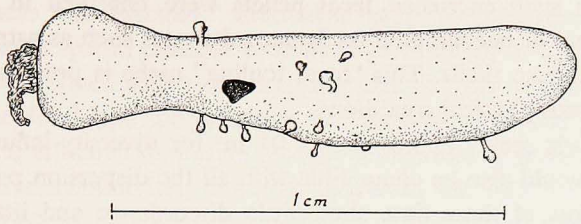

Figure 5. A presumed fecal pellet from the Santa Catalina Basin cores, showing fouling of the pellicle by numerous entoprocts and by a single agglutinating foraminiferan (triangular shape). It is an example of the kinds of biogenic, small-scale habitat structures which may be characteristic of the deep sea. Such seemingly fragile habitat structures could not be utilized under more rigorous environmental conditions.

and herein), however, suggests an exceedingly simple model which might account for stabilization of competitor populations. If food is limiting, an individual of a small-ambit species presumably depletes food within its area of activity or ambit. When this animal dies, it would seem reasonable that the area it had occupied would be slightly more suitable for occupancy by a species with slightly different resource requirements. In fact, Clifford and Sudbury (1973) have shown that, if each species' probability of re-inhabiting an opened area were slightly smaller than the species' proportional representation in the community, leading to an alternation of locations among species, species' relative proportions in the community would be stabilized. This mechanism implicitly requires a tendency toward territoriality, a situation suggested by the observation of spacing between individuals within species among Polychaeta in the SDT (Jumars, 1975b). The population stabilizing effect of such alternation should not be surprising. It is one possible spatial interpretation of the stable equilibrium solution of the Lotka-Volterra equations, found when intraspecific competition exceeds interspecific competition. This suggested model also corresponds roughly to Grassle and Sanders' (1973) concept of microsuccessional series except that (1) the only disturbance required is an individual mortality and that (2) the succession has no final stable state or climax locally. Predation without disturbance of the state of resource depletion in an ambit would be one driving force for the alternation of ambits among species.

Although shallow-water environments also vary on this scale, "houses built on sand" in shallow water cannot be expected to persist. For the suggested stabilizing feedback to act, an individual's effects must persist long enough to influence the succeeding generation (Southwood et al., 1974). That weaker "houses" will persist longer in the deep sea than in shallow water is graphically illustrated (Fig. 5) by some encrusting meiofauna from the SCB (not censused because they were retained only by attachment to a larger particle). These entoprocts and occasional Foraminifera use what appears to be the pellicle of a fecal pellet for attachment. Although

at least a dozen such encrusted fecal pellets were observed in the SCB cores, entoprocts were never encountered on firmer substrates such as astrorhizid foraminiferan tests or mollusc shells. This "fecal fouling" niche is presumably unavailable under more rigorous physical conditions.

A "characteristic scale" of less than 0.01 m^2 for diversity-influencing processes in the deep sea would also be compatible with all the dispersion pattern data available to date. Most of these data show little discordance and little patchiness in species' abundances per sample on the ($\geqq$0.01-m^2) scales sampled. In particular, the present study detected no spatial segregation, active or passive, among members of the primary groups, which contain the overwhelming majority of species. If these species do segregate by habitat, the patches of habitat they recognize are therefore likely to be smaller than 0.01 m^2 and are likely to accommodate only one individual of a given species; otherwise greater patchiness within species and greater discordance among species would have been expected in the per-subcore abundances. These arguments hold for disturbance events (Dayton and Hessler, 1972) as well. If such events were often larger than 0.01 m^2, they should have been reflected as discordance and patchiness on the appropriate scales.

The least attractive feature of the hypothesis that animals segregate among habitat patches approximating the size of the ambit or sphere of activity of a single individual is the difficulty in testing it. Unless ambit sizes are known (in which case negative covariance in abundance among potential competitors would be expected among replicate samples of this size), it is difficult to detect the level of discordance and "patchiness" expected under the hypothesis. It would be more difficult still to determine whether a vacated ambit or habitat patch of this size has a probability slightly smaller than the proportional global or community abundance of the previous tenant's species of being reoccupied by that species.

6. Summary

Dispersion patterns and species diversity of deep-sea macrobenthos were examined for evidence that diversity-controlling processes operate predominantly on any one of several spatial scales. Although effects of such processes were apparent at all scales examined (100 km to 10 cm), the degree of spatial segregation or discordance in species abundances did not suggest either that a strong environmental mosaic, to which most species respond, or that patchy disturbance (Levin and Paine, 1975) operates on these scales to explain high deep-sea species diversity. Indirect evidence suggested instead that the characteristic scale of diversity-controlling processes in deep-sea areas examined to date is smaller than 0.01 m^2, i.e., that the environmental grain (*sensu* Levins, 1968) recognized (actively in habitat selection or passively under disturbance) by most species approximates the size of an individual organism's sphere of activity. Until sampling and experimentation are

carried out on these "micro-scales," alternative mechanisms of resource partitioning that do not hinge on spatial patterns of habitat partitioning or of disturbance must continue to be entertained as possible explanations of high deep-sea species diversity. In particular, food-type specialization and temporal resource partitioning have not been ruled out, although they seem unlikely on theoretical grounds.

The present investigation has, however, narrowed the suite of tenable, general explanations of high deep-sea species diversity in two ways. First, a general explanation of this sort cannot invoke extensive within-community, between-habitat components of diversity on scales above 0.01 m^2. Second, any such thesis must explain, or at least allow, taxon-dependent differences in between-community comparisons of species diversity. Because the conclusions of the present study or any other investigation of deep-sea species diversity thus depend on the taxa considered (e.g., Fig. 2), caution is required in conclusions drawn about community diversity unless the taxa considered comprise a large fraction of the total macrofauna and equitably represent its life styles.

Acknowledgments. I wish to thank R. R. Hessler for the use of his seagoing gear and experience and for continuing encouragement and criticism. I am indebted to several scientific parties and the crew of the R. V. *Thomas Washington* for making this study possible. A. F. Carlucci, J. R. Curray, J. T. Enright, K. Fauchald, M. Goodman, J. F. Grassle, and R. R. Hessler have improved upon earlier versions, and R. R. Hessler, F. Rokop, G. D. Wilson, D. E. Thistle, and Hj. Thiel have given valuable taxonomic assistance. Voucher specimens of all taxa recognized in the present study are available from the author or from the Allan Hancock Foundation, University of Southern California. This work was supported by NSF Doctoral Dissertation Grant GA3242 as well as by NSF Grants GB14488 and GA31344X and a donation of computer time by the Shipboard Computer Group, Scripps Institution of Oceanography. The present paper is based on data gathered in a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree, Scripps Institution of Oceanography, University of California at San Diego.

APPENDIX I. Summarization of dispersion patterns by species' groups

Let the following set of numbers represent hypothetical per core abundances of three species which are perfectly homogeneous in dispersion patterns according to the dispersion chi-square criterion (Jumars, 1975a):

	Core								
Species	1	2	3	4	5	$\bar{x}$	s^2	$s^2/\bar{x}$	k
A	1	7	10	16	43	15.4	267.3	17.357	12.00
B	2	14	20	32	86	30.8	1069.2	34.714	6.00
C	9	63	90	144	387	138.6	21651.3	156.214	1.33
Total(g)	12	84	120	192	516	184.8	38491.2	208.286	1.00

Note that the per core abundance for each species may be obtained by dividing the total group's per core abundance by a constant k. Taking x as the per core abundance of any given species and g as the group's total abundance per core, then:

$$x = \frac{g}{k}, \text{ and } \quad \bar{x} = \frac{\bar{g}}{k}$$

Thus $$s^2_{A,B,C} = \frac{s^2_g}{k^2_{A,B,C}}. \text{ Substituting } \frac{\bar{g}}{\bar{x}} \text{ for } k \text{ yields}$$

$$s^2_{A,B,C} = \frac{s^2_g \bar{x}^2_{A,B,C}}{\bar{g}^2}, \text{ or, rearranging terms,}$$

$$\frac{s^2_{A,B,C}}{\bar{x}_{A,B,C}} = \left(\frac{s^2_g}{\bar{g}^2}\right) \bar{x}_{A,B,C} .$$

Because the term in parentheses is a constant for any one homogeneous group, the relation between the variance-to-mean ratio and the mean is linear for group members. This line provides a convenient summary statistic for describing the dispersion patterns of these members.

Estimating the relationship from real data with some degree of discordance (i.e., with stochastic variability) is not so simple, however. First, group members must be selected. The linear relation can not be expected to hold unless the group is selected to be homogeneous or unless the group could be made homogeneous by permuting the species' per core abundances. For example, a species showing abundances in cores 1-5, respectively, of 43, 10, 7, 16, 1, would not be a homogeneous group member with species A, B, and C above but would be collinear with them in a plot of $s^2/\bar{x}$ versus $\bar{x}$.

Second, when a relatively homogeneous group has either been formed (e.g., as in the methods section of this paper) or found, the summary line must be estimated. Standard least squares regression is not legitimate (Patil and Stiteler, 1974) because both $\bar{x}$ and thus $s^2/\bar{x}$ are measured with error. Furthermore, the distribution of $s^2/\bar{x}$ is not continuous (the x values being counts) and is sharply bounded for small values of $\bar{x}$ (e.g., Jumars, 1975b, fig. 2). In particular, any species whose mean number of individuals per core is the reciprocal of the number of cores must have a value of $s^2/\bar{x}$ exactly equal to one. Hence, all the summary lines of Figure 3 are forced through this point. In each case they are also drawn through the coordinates $\bar{g}$, $s^2_g/\bar{g}$. They should not be considered regression lines in the strict sense because of the sundry estimation problems noted above. If there were no continuity problem, however, the linear equation written above (slope = $s^2_g/\bar{g}^2$; intercept = 0) would provide the best summary for a homogeneous group, as per its derivation. Connecting of the two indicated points in the graphic procedure of Fig. 3 approaches this solution as the number of cores increases.

APPENDIX II. Single-species dispersion patterns

There are several problems inherent in the present sampling design insofar as discussion of patchiness in single-species dispersion patterns is concerned. First, the core locations were not truly random but were controlled to some degree by prevailing winds and currents. Second, only five cores per locality could be considered in the time available, and the mean number of individuals collected per species per core was generally quite small. Therefore, any test of the null hypothesis of Poisson dispersion pattern on the between-core scale is weak. In particular, the number of samples was too small to test fit directly to expected Poisson frequencies via, say, the G test of Sokal and Rohlf (1969). An estimate such as the proportion of species which are patchy on his spatial scale is thus likely to be an underestimate. Third, the observed pattern of sampling bias artifactually produced slight patchiness of single species (and thus a portion of the positive slope of the group lines in Fig. 3) but the densities of single species were generally too low to reliably estimate the magnitude of this effect.

Additional problems occur in between-subcore comparisons because of the systematic sampling design. If the numbers of individuals per subcore were spatially independent within

cores, the expected variance under the assumption of Poisson dispersion would be unchanged (Cochran, 1963, Theorem 8.4), but spatial dependence would place both the variance and its degrees of freedom in doubt. Pielou's (1969) "joins" method (modified from Krishna Iyer, 1949) was therefore employed to test for random intermingling of high and low numbers of individuals per subcore. This analysis corresponds to the "queen's case" in the more general treatment of spatial autocorrelation by join counts in Cliff and Ord (1973). More sensitive methods (described in the latter reference) were again not worthwhile due to the low densities at which most species were found. Contrasting with earlier findings for SDT Polychaeta (Jumars, 1975b), no significant spatial autocorrelation was apparent either for single species or for the SCB Polychaeta, SCB non-Polychaeta, or SDT non-Polychaeta when each species and each core was treated as a replicate (Jumars, 1975a).

Large departures (i.e., $P<0.01$) from the expected index of dispersion (Fisher, 1970) were thus considered valid criteria for rejection of the Poisson null hypothesis of $s^2 = \bar{x}$, both between and within cores. To reliably find all other departures at the $P<0.05$ level, Rao and Chakravarti's (1956) small sample tests and simple randomization (Mead, 1974) were used. Only one species departed significantly from Poisson expectation in the direction of a uniform dispersion (i.e., *Aglaophamus paucilamellata*, a nephtyid polychaete in the SDT). Those species which departed significantly ($P<0.05$) from this expectation by showing aggregation are listed below. The low power of the tests used and the degree of multiple testing involved should be considered in any interpretation based on these data. Species given a letter designation do *not* necessarily correspond between localities. Raw data for the between-core comparisons may be found in an appendix to Jumars (1974).

Between Cores	Within Cores
SAN DIEGO TROUGH	
Annelida	
Braniella sp. A	Cirratulid sp. B
Paraonis gracilis oculata	Fabriciinid sp. B
Spiophanes cf. *bombyx*	
Chaetozone cf. *setosa*	
Tharyx luticastellus ("mudball cirratulid")	
Cossura cf. *pygodactyla*	
Maldanid sp. J	
Maldanid sp. K	
Melinnampharete sp. A	
Fabriciinid sp. A	
Crustacea	
Cumacean sp. D	Phoxocephalid sp. B
Dikonophoran sp. D	
Corophiid sp. A	
Phoxocephalid sp. B	
Phoxocephalid sp. C	
Dulichia sp. C	
Mollusca	
?*Cocculina* sp. A	?*Cocculina* sp. A
Eulamellibranch sp. C	*Vesicomya* sp. A

	Echinodermata
Ophiocten pacificum	None
Ophiura kofoidi	
	Miscellaneous Taxa
Sipunculid sp. B	None

SANTA CATALINA BASIN

	Annelida
Harmothoe forcipata	None
Phyllodocid sp. A	
Exogone sp. A	
Paraonis gracilis oculata	
Tharyx sp. A	
Tharyx cf. *monilaris*	
Cirratulid sp. D	
Fauveliopsis glabra	
Maldane cf. *sarsi*	
Myriochele gracilis	
Anobothrus? sp. A	
Oriopsis sp. A	
	Crustacea
Cumacean sp. C	Dikonophoran sp. A
Dikonophoran sp. A	Dikonophoran sp. B
Dikonophoran sp. B	Dikonophoran sp. C
Dikonophoran sp. C	Eurycopid sp. A
Ilyarachna profunda	Isaeid sp. A*
Phoxocephalid sp. F	Isaeid sp. B*
Phoxocephalid sp. G	Phoxocephalid sp. D
Phoxocephalid sp. I	Phoxocephalid sp. J
Phoxocephalid sp. J	
	Mollusca
Dacrydium sp. A	*Dacrydium* sp. A
Pelecypod sp. A	
Pelecypod sp. D	
Aplacophoran sp. B	
	Echinodermata
Amphiura sp. A	*Amphiura* sp. A
Ophiocten pacificum	
Holothurian sp. C	
	Miscellaneous Taxa
Sipunculid sp. A	None

* reflects accepted usage in 1969.

REFERENCES

Cliff, A. D., and J. K. Ord. 1973. Spatial Autocorrelation. London, Pion Limited. 178 pp.

Clifford, P., and A. Sudbury. 1973. A model for spatial conflict. Biometrika, *60:* p. 581–588.

Cochran, W. G. 1963. Sampling Techniques, 2nd ed. New York. Wiley, 413 pp.

Crombie, A. C. 1947. Interspecific competition. J. Anim. Ecol., *16:* p. 44–73.

Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Res., *19:* p. 199–208.

Draper, L. 1967. Wave activity at the sea bed around northwestern Europe. Mar. Geol., *5:* p. 133–140.

Emery, K. O. 1960. The Sea off Southern California. New York. Wiley, 366 pp.

Emery, K. O., and J. Hülsemann. 1963. Submarine canyons of Southern California. I. Topography, water, and sediments. Allan Hancock Pacific Expeds., *27:* p. 1–80.

Fisher, R. A. 1970. Statistical Methods for Research Workers, 14th ed. Darien, Conn., Hafner, 362 pp.

Grassle, J. F., and H. L. Sanders. 1973. Life histories and the role of disturbance. Deep-Sea Res., *20:* p. 643–659.

Grassle, J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe, and T. McLellan. 1975. Pattern and zonation: A study of the bathyal megafauna using the research submersible *Alvin*. Deep-Sea Res., *22:* p. 457–481.

Hairston, N. G. 1973. Ecology, selection and systematics. Breviora, *414:* p. 1–21.

Hamilton, E. L. 1963. Sediment sound velocity measurements made *in situ* from the bathyscaph *Trieste*. J. Geophys. Res., *68:* p. 5991–5998.

Hessler, R. R., and P. A. Jumars. 1974. Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea Res., *21:* p. 185–209.

Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep sea. Deep-Sea Res., *14:* p. 65–78.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric Statistical Methods. New York. Wiley, 503 pp.

Hurlbert, S. N. 1971. The nonconcept of species diversity: A critique and alternative parameters. Ecology, *52:* p. 577–586.

Hutchinson, G. E. 1953. The concept of pattern in ecology. Proc. Acad. Nat. Sci. Phila., *105:* p. 1–12.

Johnson, D. A. 1972. Ocean floor erosion in the equatorial Pacific. Bull. Amer. Geol. Soc., *83:* p. 3121–3144.

Jumars, P. A. 1974. Dispersion patterns and species diversity of macrobenthos in two bathyal communities. Ph.D. dissertation, Univ. Calif., San Diego. 204 pp.

—— 1975a. Methods for measurement of community structure in deep-sea macrobenthos. Mar. Biol., *30:* p. 245–252.

—— 1975b. Environmental grain and polychaete species' diversity in a bathyal benthic community. Mar. Biol., *30:* p. 253–266.

—— 1975c. Target species for deep-sea studies in ecology, genetics, and physiology. Zool. J. Linn. Soc., *57:* p. 341–348.

MS. Patchy species diversity in a bathyal polychaete community.

Krishna Iyer, P. V. 1949. The first and second moments of some probability distributions arising from points on a lattice and their application. Biometrika, *36:* p. 135–141.

Levin, S. A., and R. T. Paine. 1975. The role of disturbance in models of community structure, *in* Ecosystem Analysis and Prediction. S. A. Levin, ed. Society for Industrial and Applied Mathematics, Philadelphia, Pa., pp. 56–63.

Levins, R. 1968. Evolution in Changing Environments. Princeton, N.J. Princeton Univ. Press, 120 pp.

Lloyd, M. 1967. Mean crowding. J. Anim. Ecol., *36:* p. 1–30.

MacArthur, R. H. 1969. Patterns of communities in the tropics. Biol. J. Linn. Soc., *1:* p. 19–30.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton, N.J. Princeton Univ. Press, 203 pp.

May, R. M. 1974. Ecosystem patterns in randomly fluctuating environments. Progr. Theor. Biol., *3:* p. 1–50.

Mead, R. 1974. A test for spatial pattern at several scales using data from a grid of contiguous quadrats. Biometrics, *30:* p. 295–307.

Patil, G. P., and W. M. Stiteler. 1974. Concepts of aggregation and their quantification: a critical review with some new results and applications. Res. Popul. Ecol., *15:* p. 238–254.

Pielou, E. C. 1969. An Introduction to Mathematical Ecology. New York. Wiley-Interscience, 286 pp.

Rao, C. R., and I. M. Chakravarti. 1956. Some small sample tests of significance for a Poisson distribution. Biometrics, *12:* p. 264–282.

Rex, M. A. 1973. Deep-sea species diversity: Decreased gastropod diversity as abyssal depths. Science, *181:* p. 1051–1053.

Rokop, F. J. 1974. Reproductive patterns in the deep-sea benthos. Science, *186:* p. 743–745.

Rowe, G. T., and D. W. Menzel. 1971. Quantitative benthic samples from the deep Gulf of Mexico with some comments on the measurement of deep-sea biomass. Bull. Mar. Sci., *21:* p. 556–566.

Schoener, T. W. 1969. Models of optimal size for solitary predators. Amer. Natur., *103:* p. 277–313.

—— 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst., *2:* p. 369–404.

—— 1974a. Resource partitioning in ecological communities. Science, *185:* p. 27–39.

—— 1974b. The compression hypothesis and temporal resource partitioning. Proc. Nat. Acad. Sci. U.S.A., *71:* p. 4169–4172.

Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol., *22:* p. 82–93.

Smith, K. L., and R. R. Hessler. 1974. Respiration of bentho-pelagic fishes: *In situ* measurements at 1230 meters. Science, *184:* p. 72–73.

Smith, W. K., and J. F. Grassle. MS. A diversity index and its sampling properties.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. San Francisco. Freeman, 776 pp.

Southwood, T. R. E., R. M. May, M. P. Hassell, and G. R. Conway. 1974. Ecological strategies and population parameters. Amer. Natur, *108:* p. 791–804.

Thiel, Hj., and R. R. Hessler. 1974. Ferngesteuertes Unterwasserfahrzeug erforscht Tiefseeboden. UMSCHAU in Wissenschaft und Technik, *74:* p. 451–453.

Turekian, K. K., J. K. Cochran, D. P. Kharkar, R. M. Cerrato, J. R. Vaisnys, H. L. Sanders, J. F. Grassle, and J. A. Allen. 1975. The slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. Proc. Nat. Acad. Sci. U.S.A., *72:* p. 2829–2832.

Turner, R. D. 1973. Wood-boring bivalves, opportunistic species in the deep sea. Science, *180:* p. 1377–1379.

Van Valen, L. 1974. Predation and species diversity. J. Theor. Biol., *44:* p. 19–21.

Received: *19 March, 1975;* revised: *6 January, 1976.*