

Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific¹

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Abstract

Five 0.25-m² box cores (four open cores and one vegemetic core subdivided in situ into 25 contiguous 10- × 10-cm subcores) reveal that populations of benthic agglutinated Foraminifera in the central North Pacific are extremely abundant and diverse. As many as 120 species and 10,310 total fragments occur in a single open core, and the Foraminifera outnumber all metazoan taxa combined by at least an order of magnitude. Significant patchiness occurs on both the between-core scale of kilometers and the within-core scale of centimeters. Few species occurred in all cores and those that did were not abundant. Hierarchical classification and multiple discriminant analysis on the resultant subcore groups in the vegemetic core suggest potential interactions between certain species of Foraminifera and such external variables as surface deposit feeders, subsurface deposit feeders, carnivores, filter feeders, biogenic surface structure, and manganese nodules. Multiple regressions of foraminiferan species against all the external variables substantiate the existence of patterns of association. Foraminifera are important components of the benthic fauna, acting, among other things, as predators and disturbance agents. It may well be that they have a more significant effect on the structure and dynamics of deep-sea benthic communities than have any of the metazoan macrofaunal taxa that are the usual objects of deep-sea studies.

Since the demonstration of high species diversity in deep-sea benthic communities, there has been considerable discussion regarding the control of this phenomenon. The two main alternate hypotheses have emphasized mechanisms centering on competition (Sanders 1969; Grassle and Sanders 1973) or predation (Dayton and Hessler 1972). More recent discussions have suggested intermediate explanations (Menge and Sutherland 1976; Rex 1976) and have placed the importance of rates of nutrient input into better perspective (Jumars and Fauchald 1977; Rex 1976).

The solution to this problem ultimately rests on our ability to resolve biotic interactions within the community. In shallow water this is a difficult task; in the

deep sea the operational difficulties make it a horrendous problem. However, we can at least approach a solution through analysis of spatial dispersion. If individuals or species interact, or if their environment is not homogeneously suitable to them, their dispersion should bear some imprint of it. These considerations have stimulated several recent studies of spatial dispersion in the deep sea (Hessler and Jumars 1974; Grassle et al. 1975; Jumars 1975*a,b*, 1976).

The nutrient-poor environment under central oceanic gyres offers special problems because the fauna is so sparse that patterns cannot be resolved with reliability. In spite of this sparsity, the community continues to show the high diversity that typifies the deep sea, making the elucidation of patterns there all the more interesting. There is, however, one taxon which is both taxonomically tractable and abundant even in these oligotrophic circumstances: the Foraminifera,

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a group normally ignored by deep-sea ecologists. Our study is based on this group.

The samples on which our work is based were taken at the Climax II locality, an oligotrophic abyssal station under the central North Pacific gyre, north of Hawaii (Hessler and Jumars 1974; Shulenberg and Hessler 1974). These samples make it possible to assess dispersion pattern on a range of spatial scales down to a distance of centimeters (Jumars 1975a) and to discern potential interactions among components of the fauna as well as between the fauna and the environment. Such relationships, when tested with future samples or actual experiments, should lead to a refinement of questions about deep-sea community structure and perhaps point the way to means of testing alternate hypotheses about the mechanisms important in determining that structure.

We thank F. B. Phleger, F. L. Parker, and R. G. Douglas for guidance in the taxonomy of Foraminifera, and D. E. Thistle for discussions as well as programing assistance. S. S. Bernstein also assisted with the programing.

Sampling methods

Samples were collected on two separate cruises to the Climax II study site (~28°N, 155°W), samples H-29 and H-32 in July 1970, and H-153, H-169, and H-170 in July 1973. All five were collected with a 0.25-m² USNEL (U.S. Naval Electronics Lab.) box corer, a device that gives relatively undisturbed samples of the bottom (Hessler and Jumars 1974). Station H-153 was subdivided in situ into 25 contiguous 10- × 10-cm subcores using the vegematic modification described by Jumars (1975a). The top 10 cm of H-29 and H-32 and the top 2 cm of H-169 and H-170 were used (a discussion of this source of bias and its effect on the analysis of these data is given below.) With H-153, the vegematic core, five of the subcores were sliced, for an analysis of vertical dispersions, into layers of 0-1, 1-2, 2-4, 4-7, and 7-10 cm. In 19 of the

subcores, only the top 2 cm were used. One subcore was used for purposes not relevant to this study and therefore the total is 24 subcores. All of the samples discussed here were washed through a 297- μ m screen.

The Foraminifera in all five cores were sorted to species. The Komokiacea (Tendal and Hessler 1977) are excluded from the analysis of horizontal spatial dispersion because their extreme fragility makes routine sorting unfeasible and renders quantification almost meaningless. Komokiaceans were completely sorted out of the five-layered subcores of H-153. These data are used to help document total foraminiferan diversity and to demonstrate the depth in the sediment to which they tend to be found. Although their horizontal dispersion was not analyzed, it is our impression that they would show the same sort of pattern revealed by the other Foraminifera.

We made no formal attempt to separate living from dead individuals, since the vast majority of the species have opaque walls which must be broken to determine whether the individual or fragment was alive. Because this destructive sort of analysis will make any further taxonomic work impossible, it has been put off for the present. It is apparent, however, from inspection of those that broke during processing, that most individuals and fragments, especially in H-153, H-169, and H-170, were alive at the time of collection. Gevirtz *et al.* (1971) found that "most" agglutinated Foraminifera on the continental shelf were alive at the time of collection. Inclusion of empty tests in the counts is a potential source of bias, but as will be seen, it has no substantial influence on many of our conclusions.

In the vegematic core from station H-153, we also collected and identified all living metazoans and classified them according to one of the following functional categories: filter feeder (ascidians, bryozoans, sponges, and polychaetes), surface deposit feeder (isopods, tanaisids, copepods, ostracods, and polychaetes), sub-surface deposit feeder (nematodes, scaphopods, and polychaetes), and carnivore

(polychaetes). All manganese nodules in the 24 subcores were counted and classified as small (≤ 5 mm), medium (6–10 mm), or large (> 1 cm in diameter). Twenty foraminiferan species were identified as structure species, that is, species whose tests, either tubular or spherical, were large enough to contribute substantially to physical heterogeneity at the sediment surface. All pieces of these species were measured in every subcore, and area and volume of biogenic structure calculated for each subcore. These data are used to test the hypothesis that differences in foraminiferan populations from subcore to subcore showed some relationship to the dispersion of metazoans and surface structure.

Analytical methods

Agglomerative hierarchical classification—This method is used to define groups of subcores from H-153 which show similar biotic characteristics. The species abundances are used to calculate the “ecological” distance (Whittaker 1967) between all possible pairs of subcores. The distance between two subcores, measured with the Bray-Curtis index, or the Czekanowski coefficient (Bray and Curtis 1957; Day et al. 1971; Clifford and Stephenson 1975), is inversely proportional to their biological similarity. Flexible clustering strategy (Lance and Williams 1967; Boesch 1973; Clifford and Stephenson 1975) was used to construct a dendrogram displaying the relationships between the subcores and groups of subcores.

The data were transformed to a weighted species-mean standardization (Smith 1976). The weights used in the mean calculations are proportional to the biotic, and presumably the environmental, uniqueness (Colwell and Futuyma 1971) of each sample. These weights are applied to overcome the distortion caused by unequal sampling of the different types of environment. A method based on the intersample ecological distances is used to calculate the weights.

The species can be likewise classified.

The interspecies distances, which should be inversely proportional to the species overlap, are generated by comparing the counts of the different species in each sample. As with the intersample distance calculations, these too can be distorted by uneven sampling of the environment; the sample “uniqueness” weights are again used to alleviate this problem. Colwell and Futuyma (1971) proposed a correctional procedure based on information theory, but Smith (1976) showed that the method used here (based on intersample Bray-Curtis distances and species-maximum standardized data) is preferable.

Before standardizations in both the subcore and species classifications, the raw data were square-rooted to remove overdominance of species with highly skewed abundance distributions.

Two-way coincidence table—A two-way table can display the defined subcore pattern in relation to the species pattern and is simply a data matrix in which the rows (species) and columns (subcores) are rearranged to correspond to their respective orders on the subcore and species dendrograms. Similar subcores and species will be together on the dendrograms. To increase readability and conserve space, the values are converted to symbols indicating relative abundance, on a scale of 0–1, using the species-maximum standardized data.

Multiple discriminant analysis—The correlations between the classification groupings and the environmental parameters are studied with multiple discriminant analysis (Cooley and Lohnes 1971; Hope 1969, as canonical analysis of discriminance). Green (1971, 1974) used multiple discriminant analysis in an ecological study, but, unlike Smith (1976) and us, did not use classification techniques to generate the groups used in the analysis. It should be emphasized that the term “environmental” as used here includes both physical and biotic aspects of the environment of the sampled organisms.

The subcores, which are points in a multidimensional space defined by the environmental variables, are projected

Table 1. Total abundance of foraminiferan fragments and individuals, and metazoan individuals in the five box cores used for this study. A—Fragments; B—species; C—individuals.

Station	Foraminifera			Metazoa	
	A	B	C	B	C
H-29	2,787	50	984	22	131
H-32	5,921	66	637	30	85
H-153	10,310	118	1,332	49	286
H-169	5,645	85	1,094	39	332
H-170	11,354	101	1,324	43	451

onto axes that minimize the within-group variation while maximizing the between-group variation. These axes are independent and are correlated with the variables potentially important in the group separation. The environmental variables correlated with the axes are determined with standardized coefficients (Green 1971) or with coefficients of separate determination (Hope 1969). The latter are used here.

The conditions necessary for statistically testing the significance of the separation of groups along the various axes (Green 1971) were not met in this study. Therefore, we determined visually from the plots how well the groups were separated and limited consideration to axes which showed good separation of at least some of the groups.

Multiple regression—Classification considers all species simultaneously in determining the subcore groups. If environmental parameters exist which cause variability in the counts of several species, this will be reflected in the classification results since the counts of such species will simultaneously affect the distance calculations.

In the event that individual species are all responding to different environmental factors, the abundance counts of each species are tested against the environmental variables with multiple regression. No variable selection procedure (such as stepwise regression) was used. The partial regression coefficients for each independent variable can be tested for significance to indicate which of the environmental parameters are correlated

with the tested species abundances. Since all the assumptions associated with the significance tests are probably not met, the tests should only be considered as a rough index.

As used here there are 441 separate significance tests (49 species times 9 environmental variables) in the multiple regression. A significance level of 0.05 would lead to 22 significant comparisons by chance alone. The results should be interpreted with this in mind.

The multiple discriminant analysis, on the other hand, does not suffer from the multiple testing problem. What is tested is the group separation along the various axes, and this involves only one test per axis of interest.

Results

Virtually all of the Foraminifera encountered were of the agglutinated type (suborder Textularina); that is, they construct their chamber walls of material from the surrounding sediment. Only six calcareous individuals (Miliolidae) were found, and they were not identified further. One of the most striking characteristics of the agglutinated foraminiferan fauna in this environment is its extraordinarily high density and diversity compared to all other taxa in the samples. In the five cores, counting both unit Foraminifera (those species that did not fragment) and fragments, there were 179 species and 36,017 total fragments (unit Foraminifera plus fragments). Of these, 76 species with 5,079 individuals could be readily identified as unit Foraminifera. The komoki from the five-layered subcores (500 cm²) of H-153 belonged to 56 species (2,004 individuals or fragments). The other Foraminifera from these subcores included 85 species among 5,980 individuals or fragments. In contrast to this there were only 935 individuals and about 165 species of Metazoa of all phyla in 10 previous Climax II box cores from this area (Hessler and Jumar 1974). In each of the five new box cores taken for this study, the abundance of Foraminifera was at least one order of

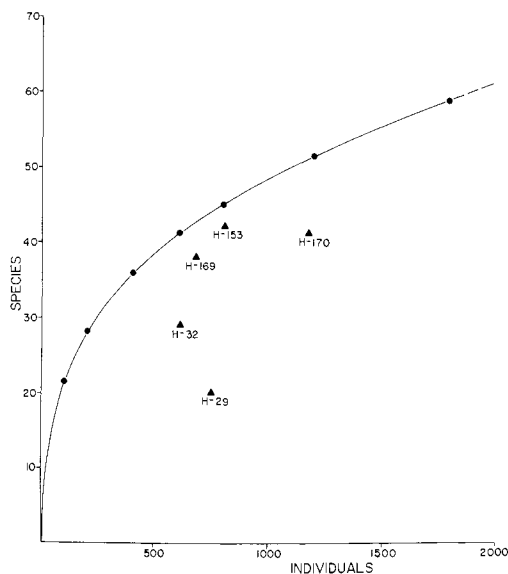


Fig. 1. Number of foraminiferan species vs. number of unit Foraminifera for five box core samples. Curve is produced by Hurlbert rarefaction method (see text). All five cores have fewer species than expected, indicating that species are patchily dispersed.

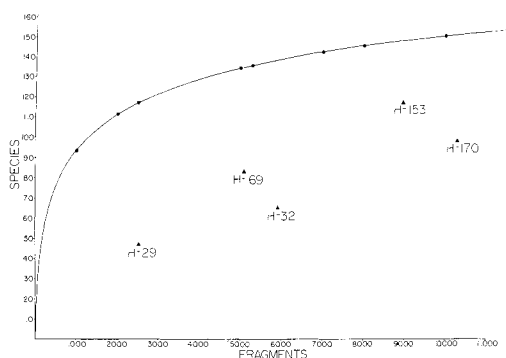


Fig. 2. Number of foraminiferan species vs. number of total fragments for five box core samples. All five samples are below Hurlbert rarefaction curve, indicating species are patchily dispersed.

magnitude higher than the total number of Metazoa (Table 1).

There were marked differences in foraminiferan numbers and diversity from core to core (Table 1), as well as in rank order of abundance and overall species composition (Table 2). Indeed, 105 species, representing 23.5% of the total fragments, occurred in only one or two cores, and the single most abundant species

was completely absent from three of the cores. In general, there were three groups of species: Those present in most or all of the cores at intermediate densities, those extremely abundant in only one or two cores, and those rare species that occurred in one or two cores at low densities.

To assess the degree of dominance of the most common, rather than the most abundant, species, we calculated P_c , the percent of the population in each core made up of those species that occurred in all cores, and S_c , the percent of numbers of species in each core that occurred in all cores (Lynts 1966). Both P_c and S_c are low (Table 3), indicating that widely dispersed species make up a small part of the population and that between-core

Table 2. The 10 most abundant species in each core. No species was among 10 most abundant for all five cores. Data are from total fragments counts.

H-29		H-32		H-153		H-169		H-170	
Species No.	Fragments (n)	Species No.	Fragments (n)	Species No.	Fragments (n)	Species No.	Fragments (n)	Species No.	Fragments (n)
155	650	283	1,465	156	1,495	155	2,343	181	3,703
131	342	344	592	225	795	225	487	156	1,273
101	252	104	463	184	790	250	355	225	673
234	201	367	346	252	521	176	345	180	485
134	178	343	316	180	507	326	235	363	441
104	147	369	275	307	474	283	213	252	375
130	132	306	187	146	441	141	126	177	341
226	115	285	141	155	381	252	124	131	317
136	99	288	141	234	362	285	112	137	228
137	88	341	135	177	288	137	110	387	213

Table 3. *Pc*, percent of the population in each core made up of those species that occurred in all cores; *Sc*, percent of numbers of species in each core that occurred in all cores. All values computed using total fragments counts.

Station	<i>Pc</i>	<i>Sc</i>	Subcore	<i>Pc</i>	<i>Sc</i>
H-29	29.35	23.21	1	23.23	9.68
H-32	55.35	19.12	2	10.28	6.00
H-153	32.97	10.74	3	10.62	8.82
H-169	30.56	13.83	4	19.57	7.69
H-170	27.14	12.87	5	18.66	8.57
Mean	35.07	15.95	6	14.14	8.57
			7	8.31	8.82
			8	11.98	6.38
			9	17.30	8.82
			10	20.76	7.89
			11	12.91	7.89
			12	20.84	10.71
			13	7.95	7.69
			14	18.25	13.64
			15	12.90	9.37
			16	10.56	9.37
			17	7.71	10.71
			19	7.92	10.34
			20	12.08	7.32
			21	15.00	13.64
			22	15.03	8.57
			23	17.64	9.68
			24	17.35	8.57
			25	17.98	14.28
			Mean	14.54	9.29

variability in abundance and diversity in large part is due to rarer, more patchily dispersed species.

The impression one gains is of extreme patchiness on the between-core scale of kilometers. To substantiate this observation, we drew two Hurlbert rarefaction curves (Hurlbert 1971) (Figs. 1 and 2), based on random selection of individuals from the total number of species and Foraminifera in the summed cores. These curves represent the ideal species:sample-size ratio that would be expected if all individuals of all species were dispersed independently among the cores.

Stations H-29 and H-32 were processed differently than stations H-153, H-169, and H-170 in that the top 10 cm were sampled rather than just the top 2 cm. Thus, comparisons between these two sets of cores would be biased by the accumulation in the lower 8 cm of H-29 and H-32 of tests of species that are resistant to dissolution.

211	44	613	77	358	48	327	82	359	55	
	31		50		34		39		35	
601	91	457	37	701	83	260	49	472	57	
	35		34		47		34		38	
519	58	216	54	692	85	263	35	814	67	
	38		28		39		22		32	
341	50	701	52	NO DATA			644	59	612	79
	32		28					29		41
180	28	339	66	221	37	323	59	178	30	
	22		35		31		35		21	

Fig. 3. Total number of fragments (upper left corner), individuals (upper right corner), and species (lower right corner) in each of 24 subcores from H-153. There is no significant difference between number of fragments in 16 outer cores and 8 inner cores (Mann-Whitney *U*-test).

An examination of the data from the layered subcores of H-153 reveals that this is indeed the case. However, 80% of the total fragments and 83% of the unit Foraminifera in the 2–10-cm layer belonged to only three species. Therefore, these species were thrown out of this analysis. The remaining few fragments and individuals, <15% of the total in all layers, were spread among several species. The residual bias resulting from their inclusion is unavoidable.

Other data from the five-layered cores in H-153 reinforce the impression that most of the living animals are concentrated in the top 2 cm. Of the 134 Metazoa, 123 were in the top 2 cm. In the Komokiacea, 97% of the fragments occur in the top 2 cm, and only one species, represented by one individual, was found only below that level.

Figure 1 shows the rarefaction curve for the expected number of species in samples of different sizes for the five box core samples, using the unit Foraminifera. All five samples fall below the expected line, which means that there are fewer species in each core than one

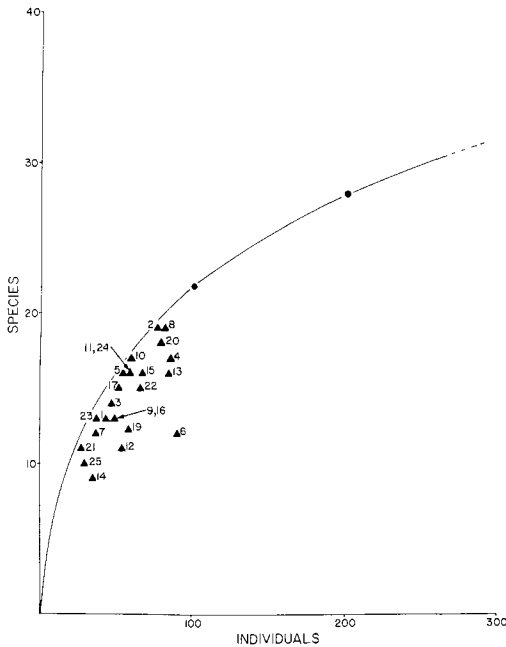


Fig. 4. Number of foraminiferan species vs. number of unit Foraminifera for 24 subcores of H-153. All subcores are below Hurlbert rarefaction curve, indicating species are patchily dispersed.

would expect from the number of individuals, that is, that the species are dispersed discordantly. If species dispersion patterns were independent, one would expect about as many samples to fall above the line as below, and the chance of all five falling below the line is small, about 0.03. Figure 2 gives the Hurlbert curve for the same five cores, this time with all the nonkomokiacean foraminiferan fragments included. Again, each sample has fewer species than expected.

It might be argued that the inclusion of fragment counts biases the analysis. This occurs only to the extent of exaggerating the pattern that is already clearly present on the basis of the unit Foraminifera analysis. Nor does it seem reasonable to discard all the information contained in the fragments, particularly if we assume that a given fragile species will fragment to the same degree in different samples.

The data from 24 subcores of H-153 were used to test for the occurrence of

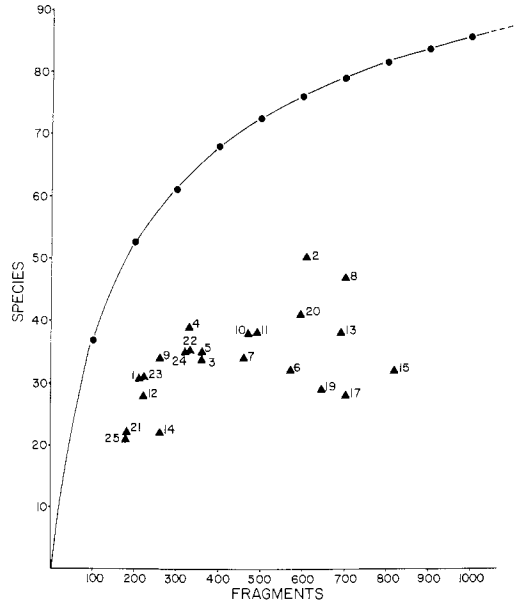


Fig. 5. Number of foraminiferan species vs. number of total fragments for 23 subcores of H-153. Again, all subcores are below Hurlbert rarefaction curve, indicating species are patchily dispersed.

patchiness on the within-core scale of centimeters. On this scale also there were differences in foraminiferan density and diversity from subcore to subcore (Fig. 3). On this smaller scale S_c and P_c were again small (Table 3). Figures 4 and 5 show the Hurlbert curves for the unit Foraminifera and the total fragments analyses for this core. In each case, all subcores shown fall below the expected line. The probability that this would happen by chance alone, if species were dispersed independently, is roughly 5.96×10^{-8} .

Since foraminiferan abundances are so high, even without the fragments, and since the Hurlbert analyses indicated significant patchiness at both the between- and within-core scales, the data are amenable to manipulation using techniques that reveal potential correlations between dispersions of Foraminifera and environmental features. For this analysis we used the unit foraminiferan data from vegetative core H-153, along with single occurrences of fragments, since this scale seemed the most likely to reveal poten-

Table 4. Continued.

Species groups	Site groups																						
	A							B					C					D				E	
	1	12	14	Subcores		22	13	15	Subcores			2	19	Subcores		5	7	10	Subcores			Subcores	
<i>Reophax</i> 108						2			1	1	4	2	1						1				
<i>Reophax</i> 117	4							2			4												
XI																							
<i>Thurammina</i> 215					4	2				2	2									2			
<i>Syringamina</i> 327					4																		
<i>Hormosina</i> 112						2				4													
XIII																							
<i>Saccamina</i> 196																				4			
<i>Thurammina</i> 213																				4			
<i>Thurammina</i> 236																				4			

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tial biological interactions between the foraminiferan species and metazoan and physical structural variables.

Hierarchical classification was used to cluster the sites (Q-mode) and the spe-

cies (R-mode). These two analyses were then combined in a two-way table that displays the distribution of the species groups in the various site groups (Table 4). Figure 6 shows the position of the five

Table 5. Partial regressions of individual species against external variables that were significant at 0.05 level. Signs signify positive and negative correlations. Total number of significant regressions, 45, is significant at 0.01 level. A—Filter feeders; B—surface deposit feeders; C—subsurface deposit feeders; D—carnivores; E—small nodules; F—medium nodules; G—large nodules; H—structure volume; I—structure area.

Species	A	B	C	D	E	F	G	H	I	r ²
<i>Reophax</i> 102								+		0.681
<i>Reophax</i> 104		+	+					+		0.821
<i>Reophax</i> 105			+	+						0.733
<i>Reophax</i> 107			+							0.684
<i>Reophax</i> 108			+	+						0.663
<i>Reophax</i> 110		+	+					+		0.784
<i>Reophax</i> 113						-		+		0.705
<i>Rhabdammina</i> 131							+		+	0.748
<i>Jaculella</i> 148							+			0.671
<i>Psammospaera</i> 190					+					0.609
<i>Psammospaera</i> 192				+	-					0.614
<i>Saccamina</i> 196					-	-		+		0.623
<i>Thurammina</i> 200				+						0.803
<i>Thurammina</i> 201			+							0.656
<i>Cystamina</i> 202								+		0.619
<i>Haplophragmium</i> 211								+		0.786
<i>Thurammina</i> 213					-	-		+		0.623
<i>Thurammina</i> 215	-									0.641
<i>Saccamina</i> 216				+						0.666
<i>Thurammina</i> 219			+							0.646
<i>Recurvoides</i> 225	+									0.714
<i>Ammobaculites</i> 227								+		0.884
<i>Glomospirella</i> 231	-									0.688
<i>Trochammina</i> 236						-	-	+		0.623
<i>Astrammina</i> 266			+				+			0.746
Unknown 301					+					0.589
<i>Astrorhiza</i> 325			-							0.667
<i>Astrorhiza</i> 411					+					0.589
Totals	3	2	9	5	7	5	3	10	1	

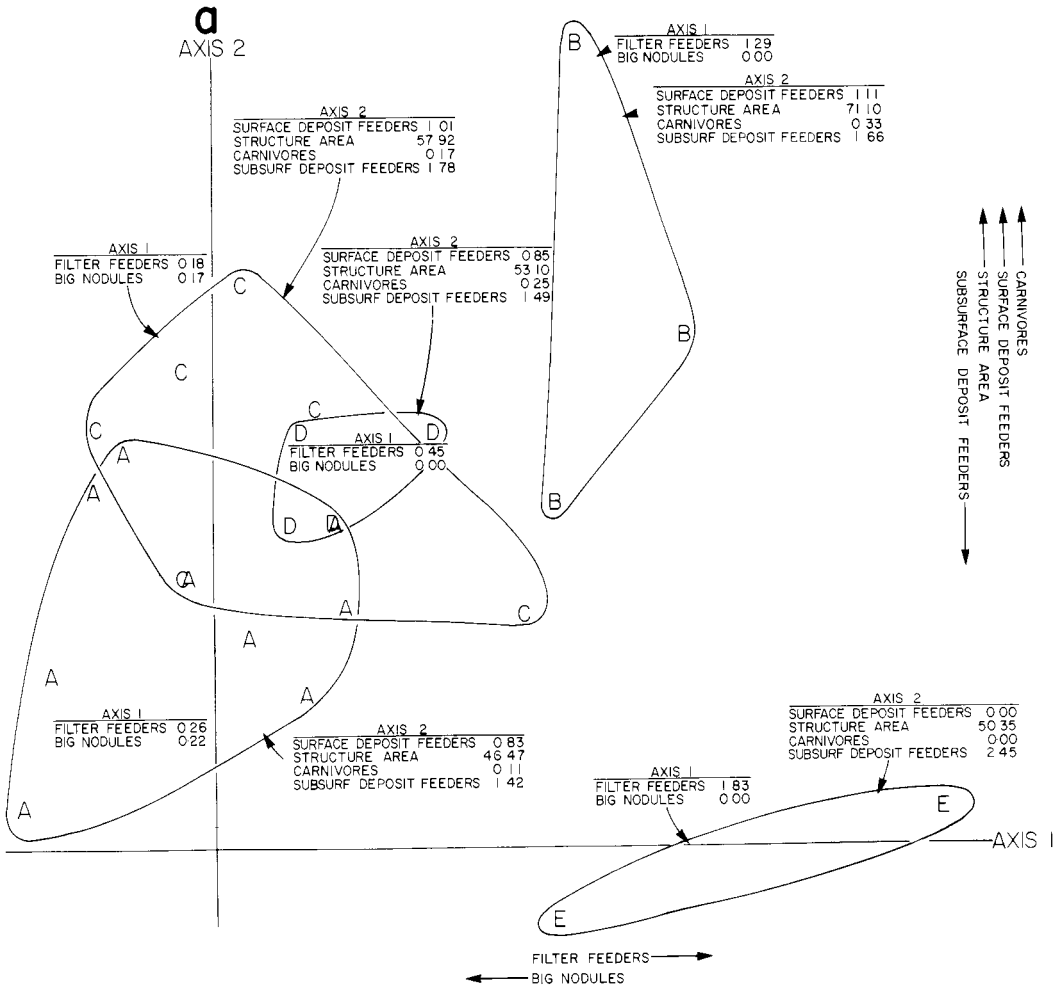
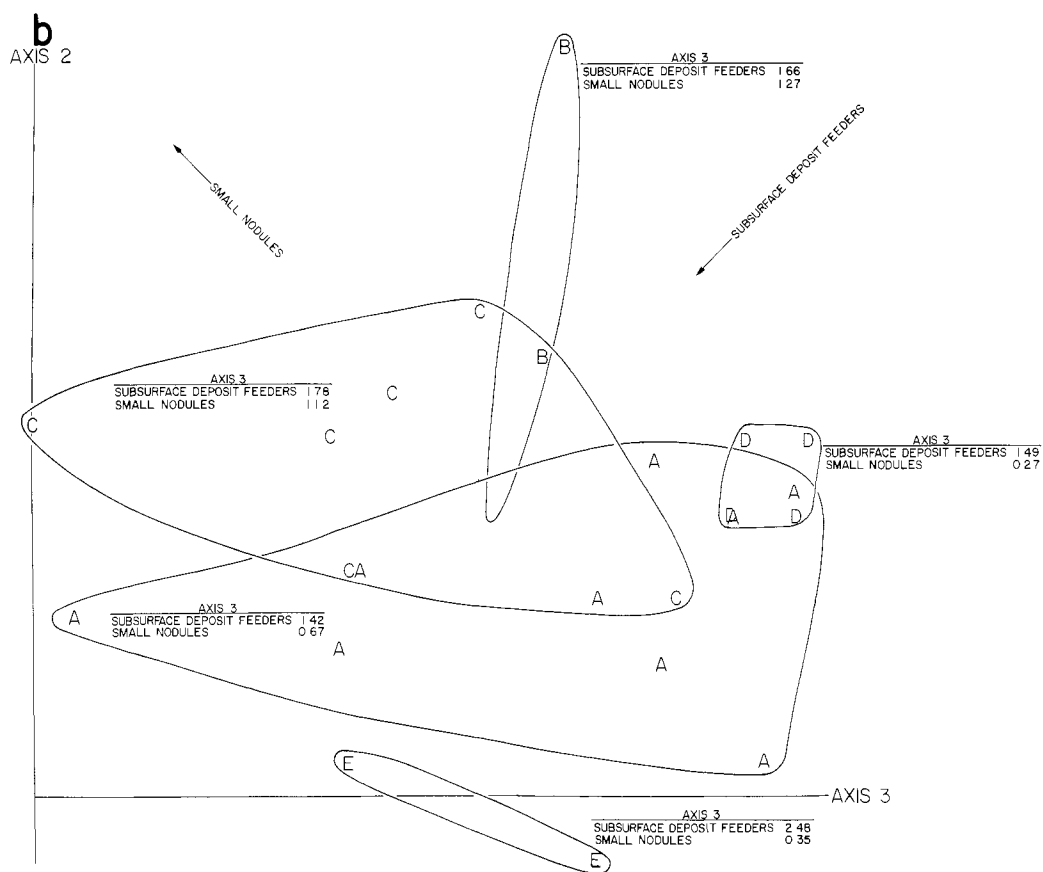


Fig. 6. a. Placement of site (subcore) groups in plane created by first two discriminant axes. External variables important in constructing axes are shown at edges of figure, and arrows indicate direction in

site groups in discriminant space. We see (Fig. 6a) that axis 1 separates site groups E and B from A, C, and D, while axis 2 separates site group E from the rest. Filter feeders and large manganese nodules contribute most heavily to axis 1, and the subcores which make up groups E and B have the highest mean value of filter feeders and the lowest mean value of large manganese nodules of all the groups. Groups E and B are at the extremes of axis 2 to which surface deposit feeders, area of surface structure, carnivores, and subsurface deposit feeders contribute most strongly. The subcores in

group B have the highest mean value of surface deposit feeders, area, and carnivores, and those in E the lowest. The subcores in group E have the highest mean value of subsurface deposit feeders and those in B the lowest. Axes 1 and 3 do not separate groups A, C, and D from each other (Fig. 6b), but axis 3, constructed chiefly by subsurface deposit feeders and small manganese nodules, provides good separation between groups D and C (Fig. 6b), as well as between group D and both E and B (Fig. 6b shows mean group values of subsurface deposit feeders and small manganese nodules). Nei-



which external variables increase along axes. For example, subcores found at right of figure have higher values of filter feeders and lower values of large manganese nodules (axis 1 variables) than subcores found at left of figure. Adjacent to each site group are mean values, in subcores that make up site groups, of axis 1 and axis 2 variables. b. Placement of site (subcore) groups in plane created by second and third discriminant axes. Axis 3 separates site groups C and D, whereas neither axis 1 nor axis 2 separated these groups.

ther the first three axes, nor any subsequent axes separated group A from either C or D.

Further evidence for pattern in the response of foraminiferan species to the external variables can be found in the results of multiple linear regressions of each unit foraminiferan species against every external variable (Table 5). Of the 441 partial regressions, 45 were significant at the 0.05 level. This is considerably more than the 22 expected by chance and is significant at the 0.01 level (confidence limits for proportions). The distribution of the significant regressions

among the nine variables is also significantly different from that expected ($\chi^2_8 = 16.4$, G-test; $0.05 < P < 0.025$; Sokal and Rohlf 1969). While it is, of course, impossible to determine which regressions are truly significant and which are spurious, the evidence nevertheless is suggestive, and, like the discriminant analysis above, can serve as the basis for concrete hypotheses.

Discussion

Heterogeneity in single- and multispecies populations of benthic Foraminifera

has been documented several times and on many different scales. Lynts (1966), working in an area about 1.8 km in diameter, found significant differences in standing crop among some samples on a scale of 30 m², and Olsson and Eriksson (1974) documented foraminiferan patchiness on a scale of centimeters in a shallow site off the Swedish coast. Similar results have been obtained by Boltovsky and Lena (1969) and Buzas (1968, 1970). This spatial heterogeneity has been explained most often by invoking the physiological response of individual foraminiferan species to spatial or temporal fluctuations of environmental variables such as salinity, temperature, dissolved oxygen, and sediment characteristics such as grain size. This predisposition to view physical variables as the causative agents of foraminiferan distributions frequently influences design of the sampling program, such as spacing samples along an estuary (Akpati 1975), a sound (Buzas 1969), or across the shelf (Gevirtz et al. 1971). Such an approach yields results only on larger scales. Gevirtz et al. (1971) found a major break in offshore faunal groups at the shelf-slope break where cold, low salinity shelf water meets warmer, higher salinity slope water and argued that the biofacies revealed by clustering were not real communities but were merely groups of species responding independently to environmental variables. Streeter (1973) found that present-day foraminiferan assemblages in the deeper parts of the North Atlantic are controlled more by the distribution of bottom water types than by bathymetry. In nearshore studies, temporal (Buzas 1969) and spatial (Akpati 1975) changes in foraminiferan abundance have been correlated significantly with the set of environmental variables measured, but not with any single variable.

At smaller scales, where environmental variables are presumed to be homogeneous (centimeters to meters), there has been little progress toward explaining patchiness, aside from Buzas' (1968)

hypothesis of clumps of asexually reproducing individuals and Olsson and Eriksson's (1974) comment that Foraminifera might increase the heterogeneity of the bottom. Furthermore, there has been no serious attempt to treat Foraminifera as an integral part of benthic communities.

The documentation of patchiness in our study is of special interest because we are dealing with an area where there can be little doubt about the homogeneity of most physical variables such as salinity, temperature, and dissolved oxygen. Consequently, disregarding the influence of manganese nodules, biological interactions provide the best hope of understanding the dispersion patterns of members of the benthic community. The little information available about the behavior and feeding habits of benthic Foraminifera suggests that these animals are likely to be active components of the community. Marszalek et al. (1969) and Lee et al. (1969) showed that some species that live within the sediment are actively mobile in this subsurface layer, and Frankel (1972, 1975) demonstrated that subsurface Foraminifera reproduce and develop pseudopodia used to capture food organisms. Richter (1961, 1964) published pictures of the considerable disturbance caused by *Elphidium excavatum* as it moved through the sediment. Buchanan and Hedley (1960) described the behavior of *Astrorhiza limicola*, an arenaceous species common in shallow British coastal waters, as well as in the Davis Strait off Greenland at a depth of 3,200 m. Individuals, which are up to 8 mm in diameter, move as much as 25 cm across the sediment surface in 24 h, leaving behind a furrow in the sediment to mark their passage. The animal periodically settles and develops a pseudopodial net which extends to a distance of 6–7 cm from the center of the individual and 2–3 mm into the sediment. Most interestingly, *A. limicola* is an active predator capable of capturing and killing copepods, amphipods including caprellids up to 2–3 cm long, nematodes, small echi-

noderns, and fully grown cumaceans. After 1–2 days, the prey are completely digested.

The benthic Foraminifera from the central North Pacific are as large as or larger than individuals of all categories of Metazoa collected in our samples. Two of the more common tubular forms averaged 2.11 and 2.92 mm long and 0.08 and 0.6 mm in diameter, with some fragments as long as 8 mm. The most common spherical species averaged 0.5 mm in diameter. It is quite likely that some of these species move through the top few millimeters of sediment, while others, the large, branching forms, construct networks of interlocking tubes that spread across the sediment surface. These Foraminifera extend pseudopodial nets many centimeters in all directions and the pseudopodia are very adhesive and pick up sediment particles (Buchanan and Hedley 1960). It seems likely that there is not a square centimeter of sediment surface which is not in some way affected by their activities. It may well be that the Foraminifera have a more significant effect on the structure and dynamics of deep-sea benthic communities than have any of the metazoan macrofaunal taxa that are the usual objects of deep-sea ecological studies.

With this in mind, we can now inspect the patterns revealed by the multivariate analyses and attempt to pinpoint individual foraminiferan species which might be responding most strongly to each other or to the external variables most important in constructing the discriminant axes or to both; e.g. axis 2 separates site groups B and E (Fig. 6a). The two-way table (Table 4) indicates that species groups VI and X, and *Lagenammia* 208 in species group VIII are relatively much more abundant in site group B than in E. It is therefore possible that these species, more than species dispersed more evenly, will show significant correlations with the important axis 2 variables (surface deposit feeders, area of surface structure, carnivores, and subsurface deposit feeders). Three of the four species in species

group IV are spherical, and eight of the nine species in groups VI and X belong to the genus *Reophax*, which has a distinctive, tapered morphology. Although virtually nothing is known about the relationships between morphology and behavior in Foraminifera, these hints are suggestive. It is possible that something about the behavior, microhabitat requirements, or life history of species in the genus *Reophax* causes their abundances to be positively correlated with those of surface deposit feeders, area of surface structure, and carnivores, and to be negatively correlated with those of subsurface deposit feeders. Likewise, spherical species such as those in species group IV might have behaviors that would cause them to be positively correlated with subsurface deposit feeders and negatively correlated with the other axis 2 variables.

Axis 2 also separates site groups E and C, and species groups I, V, and X contain species that occur much more abundantly in site group C than in E. Once again, we would expect these species to show a significant degree of correlation with the axis 2 variables. Two of the three species in species group I belong to the genus *Hormosina* and are spherical, while all three species in group X belong to the genus *Reophax*. Again, it is tempting to erect tentative hypotheses about possible relationships between morphology and dispersion. The same technique can be applied to the separation of other site groups on axes 1–3 to pinpoint species which appear to be responding. Site groups A and E are at the extremes of axis 1 (Fig. 6a) and species groups VI and VII occur in site group A to a much greater extent than in site group E. Five of the six species in group VI belong to the genus *Reophax*; all three species in group VII belong to a single spherically shaped genus. It must be remembered that the multivariate techniques we have used serve only to display pattern and to aid in the construction of hypotheses for future testing. There is a possibility that the patterns we have observed are due to ran-

dom variation, or that we cannot measure, even indirectly, what is causing faunal patterns. This is why additional cores are so important, since we would not expect the patterns to be duplicated if they are chance occurrences.

Neither the site groups nor the external variables were significantly spatially autocorrelated (Cliff and Ord 1973; Jumars et al. 1977); that is, there was no tendency for high values of any of the variables to occur in subcores that were adjacent. The discriminant analysis shows, however, that there were recognizable species groups associated with high or low values of certain external variables. This implies that patches, defined by associations of certain foraminiferan species and external variables, are smaller than the subcore size of 100 cm², and that the dispersion of these patches is random.

Correlations, however significant, only serve to substantiate the existence of pattern; they do nothing to explain it. Explanation and understanding can come only as the result of the formation and testing of alternative hypotheses about the actual physical and biological mechanisms acting to influence dispersion pattern. We feel that this is as true of this environment as any other, despite the obvious difficulties involved in observation and experiment. Woodin (1976) reviewed much of the recent work on soft bottom infaunal assemblages and discussed interactions among different assemblage types such as burrowing deposit feeders, suspension feeders, and tube builders. Her data were all collected in shallow water, but the inter- and inraassemblage interactions she described can serve as a guide to investigating biological interactions among members of the deep-sea benthic community. For example, large mobile Metazoa and Foraminifera such as *A. limicola*, which disturb the surface of the sediment, may inhibit the activity of those smaller, sedentary Foraminifera which depend for their food on the deployment of delicate pseudopodial nets. Conversely, the dense, interlocking structures of branching tubes which

some Foraminifera construct may impede the movement of mobile forms and actually exclude them from certain areas of the sediment surface. Adult-larval interactions of the kind Woodin (1976) described may also be occurring, especially if the pseudopodia of Foraminifera are as efficient at capturing small prey as Buchanan and Hedley (1960) suggested. Mangane nodules, which were important in constructing two of the first three discriminant axes, provide an element of surface structure absent in shallow-water soft-bottom habitats and add an extra dimension to small-scale heterogeneity in this environment.

Jumars (1976) suggested that mortalities of individual animals could open space suitable for another species and that these very small-scale disturbances could be the cause of microsuccessional events leading to a high diversity of small ambit species. This requires a very low level of the more classical kinds of physical disturbance, or the minute inhomogeneities in the bottom would be masked by larger scale events. Large, mobile Foraminifera could well be a source of physical disturbance in this environment and might be another cause of microsuccession, although on a slightly larger scale than Jumars (1976) postulated.

There is every reason to hope that yet more careful and numerous samples from this community will illuminate the ways in which its species disperse themselves with relation to each other and to physical variables. However, ultimately it will become necessary to know a great deal more about the natural history of deep-sea benthic animals before we can begin to understand the mechanisms maintaining diversity and spatial pattern in their environment.

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