

EVIDENCE FOR CONTROL OF ABYSSAL AGGLUTINATED FORAMINIFERAL COMMUNITY STRUCTURE BY SUBSTRATE DISTURBANCE: RESULTS FROM THE HEBBLE AREA

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ABSTRACT

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Deep-sea agglutinated foraminifera have been quantitatively examined from 28 core-top samples from seven box cores collected in June, 1983, at the HEBBLE (High Energy Benthic Boundary Layer Experiment) Site (40° 27' N, 62° 20' W, 4815-4825 m depth) and HEBBLE Shallow Site (40° 53' N, 63° 44' W, 4185 m depth) on the Nova Scotian continental rise.

Samples from the relatively tranquil HEBBLE Shallow Site can be distinguished from the HEBBLE Site on the basis of their microfauna. A Q-mode VARIMAX factor analysis of species-frequency data delineates three major faunal assemblages:

(1) A faunal assemblage from the HEBBLE Site dominated by *Ammobaculites* sp. cf. *A. americanus*. This assemblage exhibits lowest species diversity (suggesting a disturbed community) and strongly associated with box cores containing fine-grained, laminated sediments.

(2) An assemblage associated with box cores from the HEBBLE Meadow dominated by *Saccamina tubulata*, *Psammosphaera* sp., cf. *P. fusca*, a coarsely grained species of *Psammosphaera* and *Reophax* sp. 1.

(3) A fauna occurring at the HEBBLE Shallow Site, dominated by *Hormosinella distans*, with *Reophax bacillaris* and *Ammobaculites agglutinans* unique to the assemblage. This fauna displays a higher ratio of calcareous to agglutinated species, significantly higher species diversity, lower variability and a greater proportion of hormosinids and species utilizing finer grains than samples from the HEBBLE Site, which is interpreted as reflecting environmental stability.

Marked heterogeneity exists among agglutinated foraminiferal assemblages within box cores. At the HEBBLE Meadow, within-box-core faunal variability exceeds between-box-core variability, suggesting that environmental factors influencing the distribution of species are patchy on a scale of approximately 40 cm.

INTRODUCTION

Although it has long been recognised that agglutinated foraminiferal faunas are ubiquitous in the deep ocean, little is known of the environmental

conditions at the sediment/water interface influencing their community structure. Earlier investigations stressed the taxonomy and distribution of deep-sea agglutinated foraminifera, with few in-situ measurements of physical and chemical parameters (for a review of taxonomic references, see Kaminski, 1983). Recent studies of agglutinated foraminifera in which environmental parameters were measured deal mainly with the Peru—Chile Trench (Bandy and Rodolfo, 1964; Ingle et al., 1980; Resig, 1981), or the Gulf of Mexico (Phleger, 1960; Poag, 1981).

Studies of calcareous benthic foraminifera have revealed the correlation of certain taxa with sediment characteristics (Bandy and Rodolfo, 1964), water masses (Streeter, 1973; Schnitker, 1974, 1980; Lohmann, 1978; Corliss, 1979a, b; Ingle et al., 1980), or specific water-mass characteristics, such as the degree of calcium carbonate saturation (Bremer and Lohmann, 1982), and temperature (Resig, 1981). But until recently, agglutinated foraminifera have been largely overlooked by most workers due to their complex taxonomy or poor preservability of many forms in modern deep-sea sediments. The study of these organisms is, however, of interest since their tests may serve as indicators of high-energy environments.

Detailed multi-disciplinary studies carried out at the HEBBLE study area provide a comprehensive view of the environment in which an agglutinated fauna is found. The primary aim of this study is to examine the effect of bottom disturbance on deep-sea agglutinated foraminifera by: (1) comparing faunas of a disturbed area with that of a tranquil one (provided both areas possess similar water-mass characteristics), and delineating assemblages indicative of both environments; and (2) examining species diversity, abundance, dispersion and patterns in morphology and relating these to substrate parameters and theoretical environmental models.

STUDY AREA

Box cores examined in this study were collected at two localities on the continental rise off Nova Scotia, the HEBBLE Site at 4820 m and the HEBBLE Shallow Site at 4185 m. Portions of the continental rise below 4500 m are influenced by intermittently strong bottom currents with velocities among the highest recorded in the deep sea. A general increase in the degree of bedform development with depth is observed in the region, indicating increasing current speeds from nearly tranquil conditions near 4000 m to estimated speeds of around 40 cm s⁻¹ near 4900 m (Tucholke et al., this volume). Complementing this is an increase in the silt/clay ratio with depth from 4000 to 5000 m, accompanied by a zonation of benthic macrofauna (Driscoll and Tucholke, 1983). Surface deposit feeder traces are most common in areas of high clay content, and suspension feeders more abundant in the zone of high sand content below 4700 m. The strongest mean currents were found at the base of the continental rise (Richardson et al., 1981).

The HEBBLE Site is a 2 × 4 km area centered about 40°27'N, 62°20'W at approximately 4815–4830 m depth (Fig.1). This is the approximate

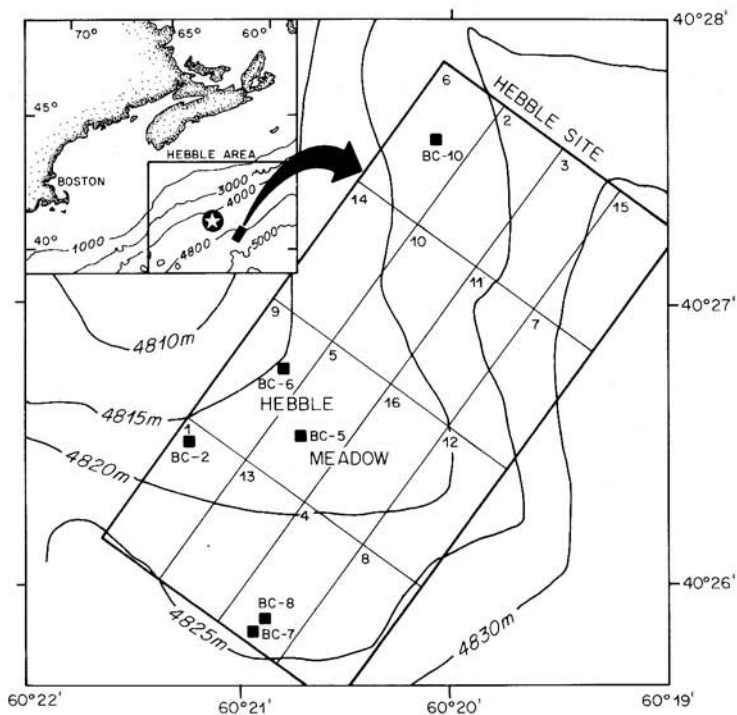


Fig. 1. Map showing location of HEBBLE Area and HEBBLE Site with sample locations. The star indicates the HEBBLE Shallow Site.

depth of the foraminiferal lysocline in this sector of the North Atlantic (Biscaye et al., 1976). The predominant water mass is North Atlantic Deep Water (NADW), with dilute Antarctic Bottom Water (AABW) in the Cold Filament of Weatherly and Kelley (1982).

Photographs of the sea floor at the HEBBLE Site have revealed a wealth of sedimentary features such as tool and scour marks, longitudinal triangular ripples, sediment tails behind biologically produced mounds, moats around pebbles, etc., which indicate high current speeds and transport and deposition of material. When the HEBBLE area was visited in July 1982 during Knorr Cruise 96, the sea floor was covered by a thin (2–5 cm) layer of freshly deposited sediments, indicating that the region had been subjected to a period of relatively low velocity currents. When the site was revisited in June 1983, the sea floor at the HEBBLE Meadow was covered with small, barchan-like ripples deposited on the downstream side of animal mounds and the bottom appeared murky in stereo-camera photos.

The stratigraphy of the area, based on examination of box cores, is remarkably uniform. The surface sediment is about 4 cm of soft brown clayey silt with 50–60% water content and 6% sand (1–25% range). This is underlain by about 30 cm of stiff, extensively burrowed foraminiferal mud. Beneath this layer, various lithologies occur, including turbidites, gravel, and

gray-brown clay (McCave, this volume). In some cores, a pebble lag layer is present. Open burrows with tube worms were found to a depth of 30 cm, indicating the whole unit is undergoing bioturbation. In June 1983, box cores from the HEBBLE Site contained a slightly firmer, burrowed brown mud at the surface. However, a box core collected at Area 6 (Fig.1), which is located in a shallow valley approximately 2 km north of the HEBBLE Meadow contained a soft, undisturbed, finely laminated surface layer of fine brown clay 3–4 cm thick underlain by a foraminiferal lag layer approximately 0.75 cm thick. This in turn was underlain by a more rigid, greenish foraminiferal clay.

While en route to the HEBBLE Site in June, 1983, one box core was taken at a location designated the HEBBLE Shallow Site, from a depth of 4185 m. This area is overlain by NADW, and is situated below the influence of the Western Boundary Undercurrent (WBUC), yet above reach of abyssal circulation which creates benthic storms at the HEBBLE Site (Weatherly and Kelley, this volume). Stereophotos reveal bottom topography typical of tranquil conditions.

METHODS

Sediment samples were collected with a 0.25 m² internally partitioned box corer with the "Sandia" modifications developed by R.R. Hessler, P.A. Jumars and J. Finger (see Thistle, 1983). Samples for benthic foraminifera were taken from the 0–1 cm surface layer of the four corner subcores of box cores 01, 02, 05, 06, 07, 08, and 10 collected in June 1983. The top layer from each subcore was extruded and sampled by scraping the core surface with a spatula to the appropriate depth. The sediment was then gently washed without dispersant through a 63 μm sieve and the >63 μm fraction was air-dried and dry-sieved through a 250 μm screen. Samples with abundant benthic foraminifera were split using a modified Otto microsplitter to yield an aliquot containing approximately 175–200 specimens of unit taxa (Bernstein et al., 1978). All agglutinated foraminifera were picked from the >250 μm fraction, mounted on a reference slide, identified and counted. In addition, a number of samples were picked at >63 μm to determine relative proportions of calcareous and agglutinated foraminifera.

No attempt was made to distinguish live from dead individuals since the majority of species have opaque walls containing organic compounds which also absorb the stain. This makes it necessary to crush each specimen to determine whether protoplasm was present at time of collection. However, Gevirtz et al. (1971) and Bernstein et al. (1978) concluded that most individuals were alive at time of collection. In this study, quantitative analyses were carried out only on the unit foraminifera. Discolored and fragmented unit species were also excluded, since these individuals were apparently dead at time of collection and would otherwise introduce a source of bias. At the HEBBLE Site, most agglutinated foraminifera are not preserved downcore, since the organic matter used in the construction of the test is apparently

metabolized by bacteria. The taxonomy used in this study is outlined by Kaminski (1983).

Q-mode factor analysis with VARIMAX rotation was used to delineate faunal assemblages using the PATS-1 statistical package of Lohmann (1980). To investigate between- and within-core variability of foraminiferal assemblages, a cluster analysis was performed on species-frequency data using the BMDP Statistical Package, and a second Q-mode VARIMAX factor analysis was performed on combined data from each box core.

Species diversity was measured by means of the Shannon-Weaver Diversity Index (Shannon and Weaver, 1949), which is defined as follows:

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

where S is the number of species and p_i is the proportion of individuals in the i th species. To test whether the diversities of two samples populations is significantly different, the t -test of Hutcheson (1970) was employed, which is defined as:

$$t = \frac{H'_1 - H'_2}{\sqrt{S^2_{H'_1} + S^2_{H'_2}}}$$

and S^2 (the variance of H') is approximated follows:

$$S^2_{H'} = \frac{\sum (f_i \ln f_i)^2 / f_i - (\sum f_i \ln f_i)^2 / n}{n^2}$$

where f_i is the number of individuals of a given species. This assumes random dispersal and gives a minimum estimate of variance. Mathematical formulas for other statistical parameters were taken from Sokal and Rohlf (1982).

RESULTS

Agglutinated benthic foraminiferal assemblages

A Q-mode VARIMAX factor analysis of the species-abundance data from KN 103 box cores delineated three faunal assemblages accounting for 91% of the initial variance (see Plate 1). The composition of the assemblages, which are derived from a three-factor solution of the frequency data, are shown in Table 1. Magnitudes of the factor scores indicate the relative importance of each species in a particular assemblage. Malmgren and Haq's (1983) two-thirds rule was used to establish the dominant species in each assemblage. Factor loadings indicate the importance of a given factor in explaining the faunal data for a particular sample. These are presented in Table 2.

Fauna 1

The first major faunal assemblage accounts for 36% of the variance of the faunal data and is dominated by *Ammobaculites* sp. cf. *A. americanus*

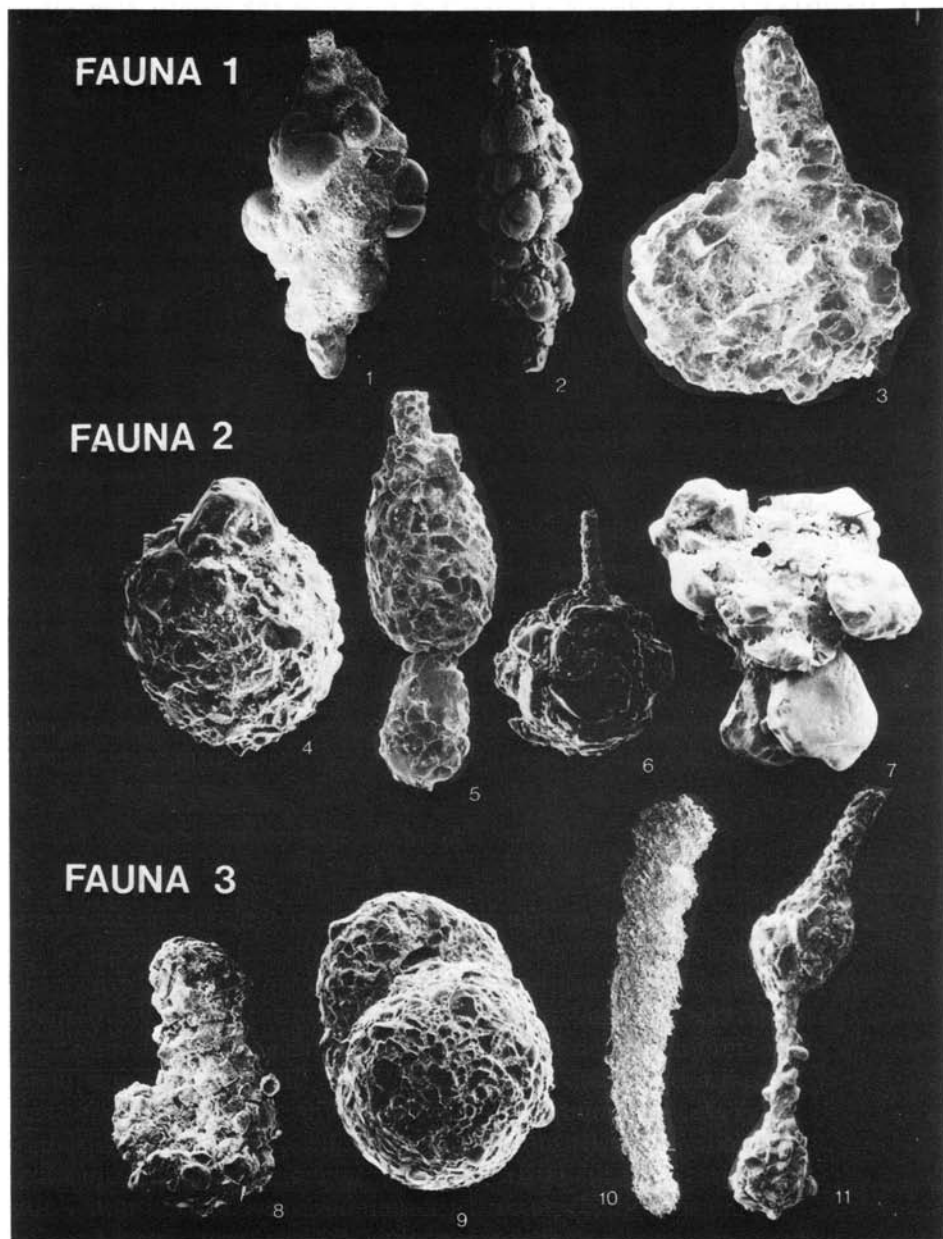
TABLE 1

Scaled Q-mode VARIMAX factor scores and coefficient of dispersion (CD) for each taxon found in this study. High scores indicate the most important taxa. High values of CD indicate a species is aggregated in distribution

Taxon	Factor			CD
	1	2	3	
<i>Psammosphaera</i> cf. <i>fusca</i> Schulze	-7.8	-46.8	-5.2	17.9
<i>Psammosphaera parva</i> Flint	0.4	-3.3	-0.3	
<i>Psammosphaera</i> sp.	-7.3	-45.9	10.0	17.3
<i>Saccammina sphaerica</i> G.O. Sars	-1.1	-8.1	-4.4	
<i>Saccammina tubulata</i> Rhumbler	20.6	-52.8	6.7	22.8
<i>Hormosinella distans</i> (Brady)	-11.3	3.5	-56.0	8.8
<i>Hormosina globulifera</i> Brady	-2.6	1.3	-7.6	
<i>Hormosina</i> sp.	-0.6	1.1	-5.2	
<i>Reophax bilocularis</i> Flint	13.1	-7.4	5.7	6.7
<i>Subreophax adunca</i> (Brady)	-0.7	2.0	-21.6	4.3
<i>Reophax bacillaris</i> Brady	-7.5	11.7	-29.5	
<i>Reophax dentaliniformis</i> Brady	7.2	3.8	-4.3	2.0
<i>Reophax dentaliniformis</i> Brady var. 1	7.6	3.1	-2.1	3.4
<i>Reophax dentaliniformis</i> Brady var. 2	35.6	11.9	10.7	11.6
<i>Reophax nodulosa</i> Brady	-1.5	1.8	-7.3	
<i>Reophax pilulifer</i> Brady	-2.2	2.5	-9.6	
<i>Reophax</i> sp. 1	-11.6	-42.6	14.7	12.1
<i>Cribrostomoides subglobosum</i> (G.O. Sars)	-2.7	-32.9	8.1	4.9
<i>Cribrostomoides scitulum</i> (Brady)	-2.8	-3.7	-4.8	7.5
<i>Cribrostomoides rotulatum</i> (Brady)	-2.5	-8.5	3.1	
<i>Recurvoides contortus</i> Earland	9.9	-13.2	-23.3	7.9
<i>Recurvoides turbinatus</i> (Brady)	4.7	-2.4	-4.1	5.2
<i>Cyclammina cancellata</i> Brady	-1.7	-10.9	-1.3	13.0
<i>Ammobaculites agglutinans</i> (d'Orbigny)	-2.4	-10.0	4.2	
<i>Ammobaculites</i> cf. <i>americanus</i> Cushman	83.9	-29.0	-0.5	17.0
<i>Ammomarginulina foliacea</i> (Brady)	4.2	-5.9	1.2	5.2
<i>Trochammina soldanii</i> Earland	-5.5	-8.5	8.1	5.1
<i>Trochammina globigeriniformis</i> (Parker and Jones)	-11.4	-17.4	20.6	12.9
<i>Trochammina pygmaea</i> Höglund	-8.3	-13.2	19.6	11.1
? <i>Conotrochammina bullata</i> (Höglund)	-4.0	2.7	-14.7	8.1
<i>Portatrochammina eltaninae</i> Echols	2.0	1.8	-1.2	
<i>Haplophragmoides</i> sp.	-1.0	-6.9	1.9	
<i>Cystamminella galeata</i> (Brady)	10.0	9.9	-18.1	3.9
<i>Cystamminella ringens</i> (Brady)	-2.3	-7.7	0.3	
<i>Eggerella bradyi</i> (Cushman)	-1.8	-1.9	-5.6	
<i>Karrerella apicularis</i> (Cushman)	1.9	-4.0	0.0	

Cushman, with subdominant *Saccammina tubulata* Rhumbler, and two species of *Reophax* which incorporate small planktonic foraminifera into their tests: *R. bilocularis* Flint, and *R. dentaliniformis* var. 2. This fauna exhibits low species diversity and high dominance, and is most strongly associated with box cores 10 and 7. Three distinct sediment layers were present in box core 10. The finely laminated, oxidized surface layer was

PLATE I



Fauna 1. *Reophax bilocularis* Flint $\times 45$, *Reophax dentaliniformis* var. 2 Brady $\times 90$, *Ammobaculites* sp. cf. *A. americanus* Cushman $\times 70$.

Fauna 2. *Psammosphaera* sp. cf. *P. fusca* Schultze $\times 80$, *Reophax* sp. 1 $\times 70$, *Saccamina tubulata* Rhumbler $\times 90$, *Psammosphaera* sp. $\times 150$.

Fauna 3. *Ammobaculites agglutinans* (d'Orbigny) $\times 45$, *Recurvoides contortus* Earland $\times 75$, *Reophax bacillaris* Brady $\times 45$, *Hormosinella distans* (Brady) $\times 70$.

TABLE 2

Q-mode VARIMAX factor loadings for factors 1–3 for Knorr 103 samples. High values indicate the greater importance of a particular factor in explaining the faunal data for any one sample. Community is a measure of the amount of faunal variance explained. *Pc* (the percent of the population in each sample of those species that occur in all subcores) and *Sc* (the percent of numbers of species in each core occurring in all subcores) are measures of the degree of dominance

Sample	Community	Factor			PC	Sc
		1	2	3		
BC 01-1	0.92	38.2	-33.7	-81.3		
01-2	0.87	16.7	-36.8	-84.3		
01-3	0.93	40.5	-23.7	-84.0		
01-4	0.91	30.4	-40.8	-80.8		
BC 02-1	0.92	42.3	-78.4	-36.0	55.2	19.2
02-2	0.92	46.4	-70.6	-45.4	46.8	16.6
02-3	0.91	44.3	-78.8	-31.1	50.0	20.0
02-4	0.97	71.5	-55.4	-39.4	60.4	16.1
BC 05-1	0.95	35.0	-79.7	-44.2	45.2	15.1
05-2	0.90	67.1	-40.2	-53.3	50.0	15.1
05-3	0.95	63.0	-59.9	-43.5	62.3	14.7
05-4	0.83	58.9	-56.0	-40.8	59.5	16.6
BC 06-1	0.90	51.3	-55.4	-57.2	62.1	17.8
06-2	0.79	57.5	-55.4	-38.7	52.8	20.8
06-3	0.93	48.3	-70.8	-44.3	49.3	17.2
06-4	0.94	42.9	-80.5	-32.5	44.5	16.1
BC 07-1	0.92	69.4	-52.0	-41.0	56.5	17.2
07-2	0.93	85.5	-37.2	-25.3	62.3	21.7
07-3	0.95	78.0	-35.6	-46.6	52.0	17.2
07-4	0.92	74.6	-49.3	-34.9	47.7	15.1
BC 08-1	0.85	50.8	-61.0	-47.0	51.9	17.8
08-2	0.92	60.9	-55.4	-49.5	50.7	16.6
08-3	0.95	62.1	-60.3	-45.1	51.6	16.1
08-4	0.88	71.2	-53.1	-45.1	49.4	18.5
BC 10-1	0.83	72.6	-46.9	-28.9	62.6	19.2
10-2	0.94	91.5	-22.9	-23.5	61.7	20.8
10-3	0.89	78.4	-44.8	-27.4	72.3	22.7
Variance accounted for:		36%	24%	31%		

3–4 cm thick, fine-grained, and contained high water content. This was separated from deeper, bioturbated stiff gray-green clay by a foraminiferal lag layer approximately 0.75 cm thick. Box core 7, which had the next highest factor loadings also displayed distinct, fine laminations in the surface layer.

Fauna 2

A second faunal assemblage, explaining 31% of the variance, has highest factor loadings on the remaining samples from the HEBBLE Site box cores 02, 05, 06, 08 from the HEBBLE Meadow, which is separated from Area 6

by a distance of approximately 2 km. The HEBBLE Meadow fauna is dominated by four species; *Saccamina tubulata* Rhumbler, *Psammosphaera* sp. cf. *P. fusca* Schultze, and a coarsely grained species of *Psammosphaera*, and *Reophax* sp. 1 being of lesser importance. Three species are unique to this assemblage: *Reophax nodulosa* Brady, *R. aff. dentaliniformis* Brady, and *Cystamminella galeata* (Brady).

Fauna 3

The third assemblage is found in samples from the HEBBLE Shallow Site and accounts for 24% of the faunal variance. At this site, agglutinated foraminifera are less abundant than calcareous forms, comprising on the average 32% of the total foraminiferal assemblage in the $>63 \mu\text{m}$ fraction. The agglutinated fauna is dominated by *Hormosinella distans* (Brady), with *Recurvoides contortus* Earland of lesser importance. *Reophax bacillaris* Brady and *Ammobaculites agglutinans* (d'Orbigny) are unique to the assemblage. Finely agglutinated species occur in greater proportions in this fauna than at the HEBBLE Site, and the assemblage is enriched in multi-chambered hormosinids at the expense of the evolutionarily less complex, single-chambered saccaminids. Tubular species, not treated quantitatively in this study, also occur in lesser proportions.

Species diversity

One drawback of the use of species diversity indices is that their values are affected by sample size. To overcome this problem, Sanders (1968) proposed a rarefaction method, later modified by Hurlburt (1971) which is especially useful when comparing samples of small sample size. This method was used by Thistle (1983) for the Harpaticoid fauna of the HEBBLE area, which is characterized by a greater number of species and fewer individuals than the agglutinated foraminiferal fauna.

In Sanders' plots of n (number of specimens) vs. S (number of species), S increases little in the 35–50 species range after about 500 specimens have been counted. By counting progressively larger samples, Liljelund (1977) showed that the Shannon-Weaver Index also does not change appreciably after enough specimens have been counted. In this study, all samples used in comparison of diversity between box cores contained greater than 500 specimens, so I consider the Shannon-Weaver Index with its associated significance tests a sufficiently robust measure of species diversity.

At the HEBBLE Site, diversity values of the unit foraminifera for pooled samples ranged from a low of 2.61 in BC-10 (faunal assemblage 1) to a high of 3.02 in a sample from the HEBBLE Meadow. Diversity at the HEBBLE Shallow Site is significantly higher ($P < 0.05$) than at the HEBBLE Site. Table 3 lists diversity and associated parameters for each pooled box core.

TABLE 3

Upper part: Number of species (S), number of specimens (n), Shannon-Weaver Index (H'), and standard deviations for pooled KN 103 box-core samples. BC 01 is from 4185 m depth, others are from 4820 ± 10 m.

Lower part: Multiple comparisons of diversity values. Entries are Student's t values. In all cases degrees of freedom can be assumed infinite. Significant values are >3.10

Sample	s	n	H'	Std. dev.			
BC 01 1-4	46	697	3.13	0.0368			
BC 02 1-4	39	737	2.96	0.0397			
BC 05 1-4	42	803	3.01	0.0382			
BC 06 1-4	37	654	3.02	0.0365			
BC 07 1-4	41	652	2.91	0.0449			
BC 08 1-4	38	724	3.04	0.0359			
BC 10 1-4	32	544	2.61	0.0499			
BC-01							
BC-02	3.22						
BC-05	2.38	0.87					
BC-06	2.29	1.03	0.15				
BC-07	3.05	0.79	1.06	1.77			
BC-08	1.86	1.47	0.59	0.45	2.18		
BC-10	8.53	5.58	6.40	6.64	4.58	7.05	
	BC-01	BC-02	BC-05	BC-06	BC-07	BC-08	BC-10

Spatial dispersion of species

Small-scale spatial heterogeneity in benthic foraminiferal populations has been documented both in shallow environments (Buzas, 1968; Boltovskoy and Lena, 1969) and in the deep sea (Bernstein et al., 1978; Bernstein and Meador, 1979). An important result of these studies as well as the biological sampling program at the HEBBLE Site is the realization that agglutinated foraminifera are non-random in distribution, and occur in small patches. In this study, several methods were employed to assess the degree of patchiness.

To determine the departure of species from randomness, the coefficient of dispersion (variance-to-mean ratio) was calculated for the more important species. To calculate this value, the species-frequency matrix was reconstructed, the x_{ij} entries being divided by the weight proportion of the sample picked for foraminifera to yield a hypothetical individual count per unit volume of sediment. Under the null hypothesis that individual species are distributed according to a Poisson distribution, the expected coefficient would yield a value of unity. Values greater than one indicate that species are clustered. Since the total abundance of species in each sample was estimated in most cases from a sample split, tests of significance were not performed on the departure of species from the Poisson and values of CD listed in Table 2 should be regarded as qualitative estimates of the degree of clustering.

To measure the degree of dominance of the most common species, P_c (the percent of the population in each sample of those species that occur in all subcores) and S_c (the percent of numbers of species in each core occurring in all subcores) were calculated for all samples from the HEBBLE Site (Table 2). Five species are common to all subcores. In order of decreasing abundance, these are: *A. sp. cf. A. americanus*, *S. tubulata*, *P. sp. cf. P. fusca*, *Reophax sp. 1*, and *C. galeata*. S_c is low, but P_c is relatively high, indicating strong dominance. Student's t -tests were also performed on diversity measurements from subcores. Although the test is less robust due to smaller sample sizes, the result of six significant differences from among 30 comparisons is greater than expected at a 95% confidence level.

Within-box-core variability was estimated by the use of an R -mode cluster analysis performed on the species-frequency matrix. The resulting dendrogram (Fig.2) illustrates two points: (1) in many instances, samples from different box cores are more similar than those from the same core; and (2) several samples vary markedly from the rest, and do not form clusters. This pattern suggests that even though individual 100 cm² subsamples were homogenized by the washing process, species are still patchy at the scale of sampling carried out in this study.

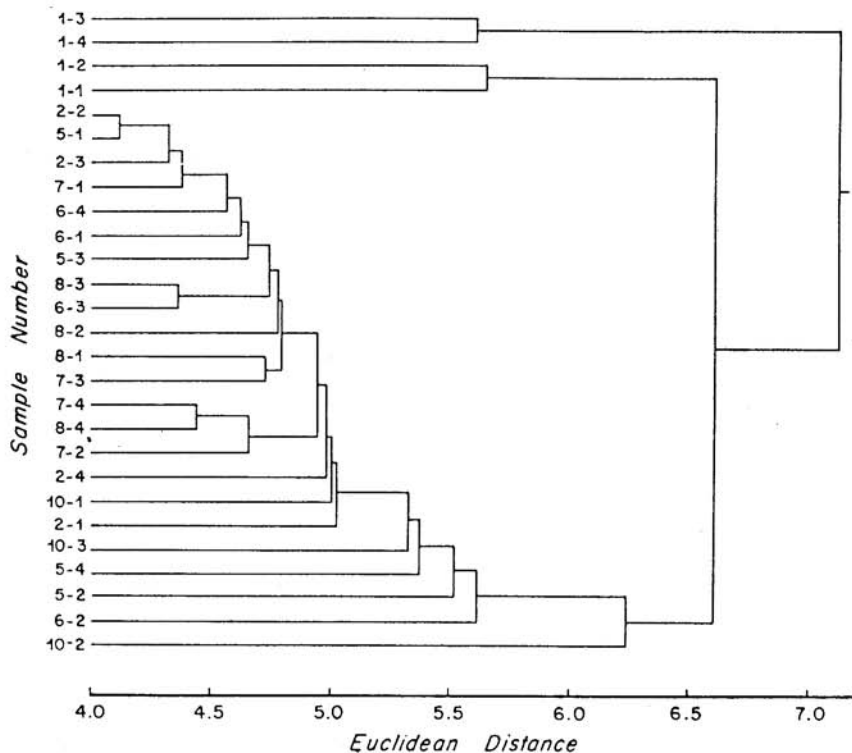


Fig.2. R -mode cluster analysis based on actual counts of 36 taxa in 27 samples. Numbers indicate box core and subsample numbers, respectively.

Another technique for assessing the variability of faunal assemblages is to calculate the variance of factor loadings of each fauna on the four subsamples from each box core. *F*-tests of the differences in variance between the HEBBLE Shallow fauna and the faunas at the HEBBLE Site were performed. When the magnitude of the variance of VARIMAX factors 1 (BC-01 assemblage) and 2 (HEBBLE Meadow assemblage) at the HEBBLE Site is compared with factor 3 loadings at the HEBBLE Shallow Site, the result is highly significant ($P < 0.01$). Figure 3 presents a plot of factor 1 versus factor 2. Error bars represent 67% confidence intervals of factor loadings on each subcore. A single-classification ANOVA of factor loadings indicate that 44% of the variation of fauna 1, and 53% of the variation in fauna 2 can be explained by within-box core variation.

For comparison, faunal counts from each subcore were combined to give a pooled sample for each box core, and a second factor analysis was performed. In this analysis, the relative importance of major elements of faunas 1 and 3 did not change appreciably, but fauna 2 is now dominated by only two

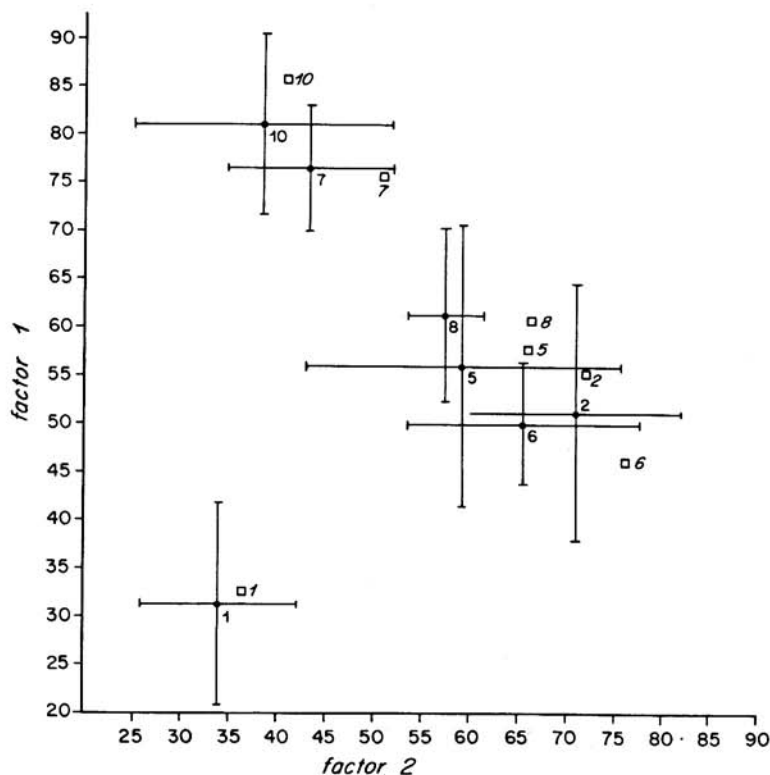


Fig.3. Plot of Q-mode VARIMAX factor loadings for fauna 1 vs. fauna 2. Error bars represent one standard deviation of subcore factor loadings. Numbered squares represent results of a second factor analysis in which subcore counts from a particular box core were first pooled.

species: *Psammospaera* sp. and *P. sp. cf. P. fusca*, *S. tubulata* was awarded fourth highest factor scores, after *R. contortus*. Factor loadings from this analysis are plotted as numbered squares in Fig.3.

DISCUSSION

Since the observation by Hessler and Sanders (1967) of high diversity among abyssal invertebrates, several hypotheses have been advanced to explain diversity patterns in the deep sea (for a review, see Lipps and Hickman, 1982; Rex, 1983). Among the first is Sanders' (1968) Stability-Time Hypothesis, which asserts that high deep-sea diversity is made possible by an environment physically stable over geologic time such that species originating in or immigrating into a community become "biologically accommodated" to one another. According to the theory, the predictability of the environment allows biological interactions to stabilize, resulting in elevated diversity through niche partitioning. Buzas and Gibson (1969) invoked this hypothesis to explain trends among benthic foraminifera, but observations performed by Gibson and Buzas (1973) were not consistent with their previous findings. In a test of the Stability-Time Hypothesis, Thistle (1983) compared harpacticoid faunas from the HEBBLE Area with those of the San Diego Trough and did not find significant diversity differences.

More recently, Huston (1979) proposed a general hypothesis of species diversity which assumes that most natural communities exist in a state of nonequilibrium. In this model, species diversity represents a dynamic balance between rates of competitive displacement and the frequency of population reduction through disturbance. At moderate levels of disturbance, diversity reaches a maximum; but when population reduction is more frequent the population cannot fully recover from the stress and diversity decreases. Low rates of disturbance leads to competitive displacement and exclusion as the population attains equilibrium. Such a pattern of diversity along a stress gradient has recently been reported from terrestrial communities (Moore, 1983).

Differences in the stability of the environments of the two sites on the Nova Scotian Continental Rise enables us to test whether the Huston's dynamic equilibrium model can adequately explain diversity patterns among agglutinated benthic foraminifera. The HEBBLE Shallow Site was selected because the area around 4200 m is unaffected by strong bottom currents and both sites are overlain by the same water mass (NADW), although there is periodic influence of dilute AABW at the deeper site. However, since the shallow site is situated 600 m above the HEBBLE Site, there is the question of introducing additional bias due to other depth-related factors influencing the distribution of species, such as the position of the foraminiferal lysocline and changes in sediment grain-size parameters. Because most species do not secrete CaCO_3 , agglutinated foraminifera are less affected by changes in the degree of calcium carbonate undersaturation of the bottom water than are calcareous foraminifera. This group is also apparently little affected by

changes in substrate parameters, such as the abundance of a particular type of material needed to construct their tests. For example, sediment samples from area 6 at the HEBBLE Site contained the lowest percentages of sand and silt fractions, yet the assemblage from that area contained the highest proportions of coarsely grained species. Therefore, the availability of silt-sized particles does not appear to be a limiting factor. At the HEBBLE Site, grain-size characteristics of the sediment show large spatial variability, and no correlation was found between faunal diversity and median grain size. Moreover I have observed that species utilizing calcareous particles in the construction of their tests are common even in the deepest reaches of the Hatteras Abyssal Plain where such particles are scarce. Agglutinated foraminifera are apparently efficient "scavengers". Therefore, this group lends itself well to the study of the effects of disturbance on the benthic fauna.

If we assume that benthic storms which periodically erode and redeposit the upper few centimeters of the sediment column are effective at reducing population levels of agglutinated foraminifera, we must then conclude that the finding of significantly lower diversity at the HEBBLE Site is consistent with Huston's Model. This finding is supported by macrofaunal data, which also display decreased diversity near the base of the lower continental rise (H. Sanders, pers. commun., 1984).

In terms of abundance, however, recent studies suggest that agglutinated foraminiferal faunas are adapted to and may actually prefer high-energy or otherwise stressed environments. Saidova (1976) reports high abundances of agglutinated foraminifera in areas of the Pacific underlying the Kuroshio Current, and Milam and Anderson (1981) found a *Psammosphaera*-dominated assemblage on the Adelie—George V Coast Continental Slope (883–2326 m depth) in an area of coarse sediments that reflect strong bottom-current activity. In the Atlantic, Gradstein et al. (1983) noted the similarity between agglutinated assemblages found in the HEBBLE Area and high-energy turbidite basins. Carter and Schafer (1983) investigated surface sediment in a region underlain by the WBUC of the Newfoundland Continental Slope and found that the axis of the current can be delineated by a band of coarser sediment containing greater numbers of "robust agglutinated foraminifera". The fauna at the HEBBLE Site is enriched in the abundance of agglutinated foraminifera by a factor of 4 when compared to the relatively tranquil, shallow site. This fauna dominated by *Psammosphaera*, contains a greater proportion of "robust" coarsely grained agglutinated foraminifera than at the shallower site. This assemblage resembles the "Type A" agglutinated fauna of Miller et al. (1982), which is comprised of robust, "simple" species. On the Hatteras Abyssal Plain, where bottom water is more sluggish, the same species are smaller in size, and the fauna contains a greater proportion of more complex species with more finely agglutinated tests.

The finding of a higher proportion of stratigraphically long-ranging, evolutionarily more primitive forms at the HEBBLE Site when compared to the shallow site has broad significance. Bretsky (1969) has shown that certain low diversity communities inhabiting unpredictable environments (e.g.

Lingula) display long-term biotic stability. Such environments support a community of relatively physically controlled opportunistic species which are better adapted to surviving environmental fluctuations, while the geologically rare major fluctuation can decimate a biologically accommodated community and cause extinctions. Electrophoretic studies indicate that species suited to unpredictable or trophically unstable environments display reduced genetic variability (Ayala et al., 1975; Ayala and Valentine, 1978). This together with the fact that opportunistic species possess increased dispersal capacity would tend to lower rates of speciation and extinction. *Psammosphera*, the dominant genus at the HEBBLE Meadow first evolved in the early Ordovician (Loeblich and Tappan, 1964) and its species are particularly long-ranged stratigraphically. *Reophax*, on the other hand, is first known from the Mississippian.

A common feature of plant and animal communities is the spatial heterogeneity, or patchiness of species distribution. In terms of an individual or population, a local patch is that unit of a habitat in which the great majority of its biotic and abiotic interactions with the environment take place (Osman and Whitlatch, 1978). Patch size depends on the size of the taxon in question, as well as its life strategy — e.g., vagile or sessile. The degree of patchiness in benthic foraminifera may be attributed to a combination of many factors. Buzas (1968) maintained that the clumped distribution of many species reflects the foraminifer's asexual mode of reproduction. Bernstein et al. (1978) and Bernstein and Meador (1979) invoked the "environmental grain" (Jumars, 1975), or "microhabitat specialization" hypothesis to explain patch structure in a biologically accommodated community. This hypothesis asserts that spatial heterogeneity is developed largely by small-scale biological interactions, sometimes on the scale of a single macrofaunal individual.

In a more physically controlled environment such as the HEBBLE Site, where environmental conditions are less predictable, in addition to lowered diversity, one might expect to find more spatial heterogeneity of species and species diversity than in a biologically accommodated community. Sanders' hypothesis predicts that "substrate utilization should be great and diverse" in a physically controlled community. Although the variance of diversity measurements of subcore samples is in fact higher at the HEBBLE Site than at the HEBBLE Shallow Site, an F -test gives a value short of being significant ($0.2 > P > 0.1$), so the null hypothesis that both sites have equal variability of diversity measurements cannot be rejected. Nevertheless, there appears to be a wider range of diversity measurements in the physically controlled environment. Similarly, a greater variability of loadings of VARIMAX factors 2 (HEBBLE Meadow fauna) and 3 (HEBBLE Shallow Site fauna) at the HEBBLE Site suggest that the benthic foraminifera are more heterogeneous in distribution than at the Shallow Site, however, observations based on a single box core should be viewed with caution. Values of P_c and S_c at the HEBBLE Site suggest that large proportion of between-core variability in abundance and diversity is due to rarer, more patchily dispersed species.

The effect of increased patchiness on within-habitat species diversity is unclear. Bretsky and Lorenz (1970), propose a model based on Paleozoic shallow marine invertebrate communities that asserts where spatial heterogeneity is great, high diversities should result regardless of environmental rigor. Results from the HEBBLE Area appear to be inconsistent with the model. Likewise, Grassle (1967) has shown that modern nearshore benthic communities do not display high diversity despite a considerable amount of spatial heterogeneity.

In general, populations of lowered diversity are typical of environments to which few species are adapted, although these may occur in large numbers. Slobodkin and Sanders (1969) classified low-diversity communities into three categories: (1) "new" environments, in which S is in the process of increasing; (2) "severe" environments; and (3) "unpredictable" environments, in which environmental parameters vary both temporally and spatially. Gibson (1966) attributed low diversity in foraminiferal populations in Mississippi Sound to the "variability" of the nearshore environment.

Figure 2 illustrates that at the HEBBLE Site, in addition to the 40 cm scale of within-core variability, a continuous trend exists in the faunal data from box cores 10-2. In factor analyses of both subcores and pooled box core data, factor 1 displays highest loadings on box core 10. This fauna exhibits significantly reduced diversity. Sediment parameters in this box core, such as distinct lamination, high water content and the presence of a foraminiferal lag layer all suggest recent and rapid deposition of the oxidized surface layer following a benthic storm (Hollister and McCave, in press). The fauna collected in June 1983 probably represented the early successional stages of recolonization by the foraminiferal fauna (a "new" environment), and the dominant species comprising it can therefore be interpreted as being more opportunistic. The same surface layer was probably deposited in the other box-core locations, however there the lamination has already begun to be disturbed by burrowing organisms. Thus the spectrum from fauna 1 to fauna 2 is likely to result from recolonization proceeding at different rates in this small area. This supports Grassle and Sanders' (1973) suggestion that faunal in the deep sea exist in a state of contemporaneous disequilibrium. Apparently, localized substrate disturbance may lead to diversity differences due in part to patches of species in different successional stages.

CONCLUSIONS

(1) Species diversity is higher at the more tranquil HEBBLE Shallow Site, which is consistent with Huston's diversity model. The agglutinated fauna contains a greater proportion of finely grained species and is characterized by *Hormosinella distans*, *Ammobaculites agglutinans* and *Reophax bacillaris* occur only at this site.

(2) The agglutinated fauna at the HEBBLE Site displays greater abundance and more spatial heterogeneity. Dominant forms at this site are *Psammosphaera* spp. and *Saccammina*. Species are apparently clumped in distribution

and dispersed in small patches in contemporaneous disequilibrium. This correlates with the degree of biological sediment mixing assessed visually on samples and X-radiographs. Opportunistic species are *Ammobaculites americanus*, *Reophax bilocularis*, and *R. aff. dentaliniformis* var. No relation was found between diversity and sediment grain-size parameters.

(3) Agglutinated faunas from the two sites differ in their morphologic complexity. The biologically accommodated community at the shallow site contains a greater proportion of multichambered hormosinids, whereas the physically controlled community possesses a greater percentage of more primitive tubular and single-chambered forms.

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