

Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response

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ABSTRACT: Cores were obtained with a multiple corer at a bathyal site (1320 to 1360 m depth) in the Porcupine Seabight during April and July 1982. In July (but not April) the sediment surface was overlain by a layer of phytodetritus, material rapidly sedimented from the euphotic zone following the spring bloom. The phytodetrital fraction of samples (0 to 1 cm layer of subcores; 3.46 cm² surface area) removed from the July cores harboured dense, low-diversity populations of benthic foraminifers which resembled the phytodetritus-dwelling assemblages already described from the much deeper (4550 m) BIOTRANS site in the northeast Atlantic. Our new observations consolidate the view that phytodetritus is a microhabitat for some deep-sea benthic foraminiferal species. The bathyal populations were dominated by *Alabaminella weddellensis* (75% of total) and also included *Epistominella exigua* and *Tinogullmia* sp. nov. These 3 species occurred also in the BIOTRANS phytodetrital assemblages. The April samples and the total July samples (phytodetritus plus sediment fractions) yielded diverse foraminiferal populations of similar density and species richness. However, there were some important taxonomic differences. In particular, the 8 species consistently present in the phytodetritus were significantly more abundant in the July samples, while the most common species in the April samples (*Ovaminina* sp. nov. A) was entirely absent during July. We argue that the influence of phytodetritus, rather than spatial variability (patchiness), was responsible for some of the differences in species abundances. Other species, however, maintain more stable population densities. Our results suggest that deep-sea benthic foraminifers, like those living in shallow water, probably display a variety of life-history strategies and population dynamics.

INTRODUCTION

The delivery of organic material to the food-limited deep-sea benthic ecosystem is a central topic in biological oceanography (Angel 1984, Fowler & Knauer 1986, Bruland et al. 1989). One potentially important pathway is provided by rapidly sedimented phytoplankton blooms (Takahashi 1986) which accumulate during the spring and early summer on the sea-floor as a layer of 'phytodetritus'. This material was first reported in sediment cores and bottom photographs taken at depths of 1000 to 4500 m in the Porcupine Seabight (an area centred around 51°30' N; 13°00' W) and on the adjacent abyssal plain (Billett et al. 1983, Lampitt 1985, Rice et al. 1986). Elsewhere in the northeast Atlantic it has been observed in the Rockall Trough (Barnett et al. 1982), the northern Bay of Biscay (Sibuet 1984, p. 105,

1987) and a more centrally oceanic site (47°00' to 47°30' N; 19 to 20° W) sampled intensively during the German BIOTRANS programme (Riemann 1989, Thiel et al. in press). Similar material has been recorded at bathyal and abyssal depths in the northwest Atlantic (Aller & Aller 1986, Grassle & Morse-Porteous 1987) and photographed at 4469 m in the eastern Pacific (Gardner et al. 1984). Phytodetritus is known to be ingested by deposit-feeding echinoderms (Billett et al. 1988) and other megabenthic animals (Thiel et al. in press). Evidence from the BIOTRANS site (4550 m depth) indicates that it is also degraded rapidly by deep-sea bacterial populations (Lochte & Turley 1988) and colonised and eaten by small benthic foraminifers (Gooday 1988a). The present paper explores further the impact of this seasonally deposited detrital material on deep-sea foraminiferal populations.

Gooday (1986) described abundant (> 1000 'living', i.e. rose Bengal stained, individuals per 10 cm²) and

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diverse (> 90 species) foraminiferal assemblages in small samples (3.46 cm² surface area) collected in April 1982 from bathyal depths (around 1340 m) in the Porcupine Seabight. These samples were taken with a multiple-corer while the spring bloom was occurring in the surface waters (Billett et al. 1983) but before the resulting phytodetrital material had arrived on the sea bed. A second set of cores was obtained in approximately the same position during July 1982 when the sediment surface was overlain by a layer of phytodetritus some 5 mm thick. In this paper we compare the foraminiferal populations, and their constituent species, from the April (pre-detritus deposition) and July (post-detritus deposition) samples. Two main questions are addressed. First, does the colonisation of phytodetritus by benthic foraminifers, which Gooday (1988a) described from BIOTRANS material, also occur at this much shallower site? Second, what effect, if any, does the presence of phytodetritus have on the overall abundance of benthic foraminiferal populations and species?

MATERIALS AND METHODS

The samples were collected in the Porcupine Seabight using a multiple-corer, which recovers simultaneously up to 12 cores with the sediment-water interface virtually undisturbed (Barnett et al. 1984). Cores obtained on 10 April 1982 at Stn 51502 ('Challenger' Cruise 6/82) and on 22 to 23 July 1982 at Stn 51615 ('Challenger' Cruise 10/82) form the basis for this study. The stations were located within the area 51° 35' to 51° 36' N, 12° 59' to 13° 01' W and the depth range 1320 to 1361 m (Table 1; Gooday 1986 Table 1). At each station, the corer was deployed 6 times. On each occasion, 4 cores (a to d) were selected at random and

subsampled using a 20 ml syringe (3.46 cm² cross-sectional area) modified by cutting off the end and sharpening the cut edge. The subcores were later cut into 1 cm thick horizontal slices down to a depth of 5 cm and each layer fixed and stored separately in 4% formaldehyde buffered with sodium borate. Only data from the 0 to 1 cm layer (including phytodetritus) of the subcores are considered in this paper.

In the laboratory the sediment was gently washed through a series of small (75 mm diameter) sieves (500, 150, 106, 63, 45 µm meshes) using filtered tap water, and then stained in rose Bengal for several hours. The sieve residues were sorted wet in a petri dish under a stereomicroscope for metazoans and foraminifers. Larger, hard-shelled foraminifers were mounted dry on micropalaeontological slides. Smaller species, including those with soft, flexible tests (Gooday 1986), were either stored in anhydrous glycerine in cavity slides, or mounted permanently in anhydrous glycerine on flat glass slides under supported cover slips (Gooday 1988b).

Phytodetritus was present on the surfaces of all cores collected during July. However, its importance as a foraminiferal habitat was realized only after 4 of the 9 subcores from this station had been already sorted. For the remaining 5 subcores (51615 nos. 1a, 1b, 5c, 5d, 6b), and an additional subcore (5b) which was examined for metazoans (Table 1), phytodetritus was picked out from the stained residues. This material forms coherent, gelatinous lumps ('aggregates') which were gently teased apart using fine entomological pins to extract the inhabitants. These were stored as described above.

Picking phytodetrital aggregates from sieve residues clearly was not an ideal procedure since the possibility of organisms being either incorporated into, or washed out of the phytodetritus during sample collection, stor-

Table 1. Location and fate of samples obtained at Stn 51615 (22 to 23 July 1982). Samples consisted of the 0-1 cm layer of subcores taken from cores collected with the multiple corer. They contained phytodetritus and sediment which were separated in sieve residues. Equivalent data for Stn 51502 (10 April 1982) are given by Gooday (1986, Table 1)

Deployment	Position		Depth (m)	Subcore	Sediment fraction sorted for		Phytodetrital fraction sorted for	
	°N	°W			foraminifers	metazoans	foraminifers	metazoans
1	51° 36.0'	12° 59.3'	1345	a	x	x	x	x
				b	x	x	x	x
4	51° 35.3'	12° 59.8'	1361	a		x		
				b	x	x		
				c	x	x		
				d	x	x		
5	51° 35.3'	13° 00.5'	1361	a		x		
				b		x	x	x
				c	x	x	x	x
				d	x	x	x	x
6	51° 35.1'	13° 00.6'	1356	a	x	x		
				b	x	x	x	x

age and sieving could not be eliminated. A few species which occurred only rarely and sporadically in the phytodetrital fractions (Table 3) may have become attached to aggregates accidentally. However, we believe this to be a minor source of error for the following reasons: (1) The phytodetritus formed coherent, gelatinous aggregates in which the foraminifers were often deeply embedded and from which they were rather difficult to extract. (2) If the association between foraminifers and phytodetritus were accidental, then specimens with rough, agglutinated test walls would tend to become entangled preferentially. In fact, such specimens were common only in the sediment fraction whereas the dominant phytodetrital inhabitants were rotaliins with generally smooth, glassy surfaces. (3) One species dominated the phytodetrital assemblages. There is no obvious reason why this species (*Alabaminella weddellensis*) should become associated accidentally with phytodetritus while other calcareous species, for example *Cassidulina teretis*, *Nonionella iridea* (which are abundant in the sediment at Stn 51615), did not. (4) The taxonomic composition of the phytodetrital assemblages showed a high degree of consistency (Table 3) which is unlikely to have arisen had these assemblages merely been artifacts of the sampling process. (5) *A. weddellensis*, and 2 other species, were present in phytodetritus from our samples and from the BIOTRANS site. Again, this coincidence is unlikely to have arisen by chance. (6) Finally, a sample of phytodetritus (and some admixed sediment), pipetted from the surface of a core obtained at Stn 51615, contained foraminifers dominated by species which also occurred in the phytodetrital aggregates extracted from our sieve residues (see below and Table 4). This indicates strongly that our detrital assemblages were not artifacts.

A transfer of foraminifers from the phytodetritus to the sediment is more likely, particularly during sample sieving. Unfortunately, the extent of this problem is impossible to assess and therefore we do not regard specimens extracted from the sediment residues (the 'sediment fraction') as constituting a distinct assemblage. While we report some data from the sediment fraction (Tables 5 to 7 and 9), our comparison of the foraminiferal assemblages in the April and July samples is based mainly on total populations.

Criteria for distinguishing live and dead foraminifers were discussed by Gooday (1986, 1988). For the present study, most of the specimens which stained red with rose Bengal were examined in glycerol (which renders the test more transparent) under a high-powered compound microscope to ensure that they contained material which resembled fresh protoplasm. However, it is impossible to be certain that specimens containing stained protoplasm were alive when cap-

tured. Stainable protoplasm can persist for weeks or months after a foraminifer dies (Boltovskoy & Lena 1970). Bernhard (1988) has compared the proportion of rose Bengal stained specimens in her Antarctic samples to the proportion of live specimens as determined by ATP assay. As many as half the specimens which stained with rose Bengal were dead. In our material we therefore regard rose Bengal stained tests as being merely 'stained'. When collected they were either alive or had died fairly recently and still contained fresh protoplasm.

For testing the significance of means we used a t-test assuming unequal variances. For testing between variances we used an F-test. Subcores are hereafter referred to as samples.

RESULTS

A considerable effort has been made to identify accurately the abundant species in our samples. Type material housed in the British Museum (Natural History) was examined where necessary. Species which are indicated as new in Tables 7 to 9 will be described elsewhere (Gooday unpubl.). Other important species are characterised and illustrated either by Gooday (1986, Figs. 10, 11, Table 5) or in Fig. 1 and Table 2 of the present paper. With one exception (*Alabaminella weddellensis* = *Epistominella levicula*) the names used in this paper are consistent with those used by Gooday (1986). The names and authorships of species mentioned in this paper are listed in the Appendix.

Our suprageneric classification follows Loeblich & Tappan (1988).

Phytodetrital populations

The phytodetrital fractions (each ca 0.5 to 1.0 ml in volume) from 6 July samples yielded 104 to 260 stained benthic foraminifers which represented 97.1% of all colonising organisms (Table 3). Most (87.0%) of the 979 specimens belonged to the suborder Rotaliina. Other higher taxa represented were the suborders Allogromiina (4.1%), Lagenina (2.6%), Textulariina, superfamilies Spiroplectamminacea (5%), Trochamminacea (1%), and Astrorhizacea, family Saccamminidae (0.3%). A total of 13 species was recognised, although only 8 of these occurred in 4 or more samples (Table 3). The remaining 5 were rare and possibly contaminants from the underlying sediment (see above). One species, *Alabaminella weddellensis*, was consistently dominant and accounted for 75% of all specimens. Most species which occurred in the phytodetritus were found also in the sediment fractions (Table

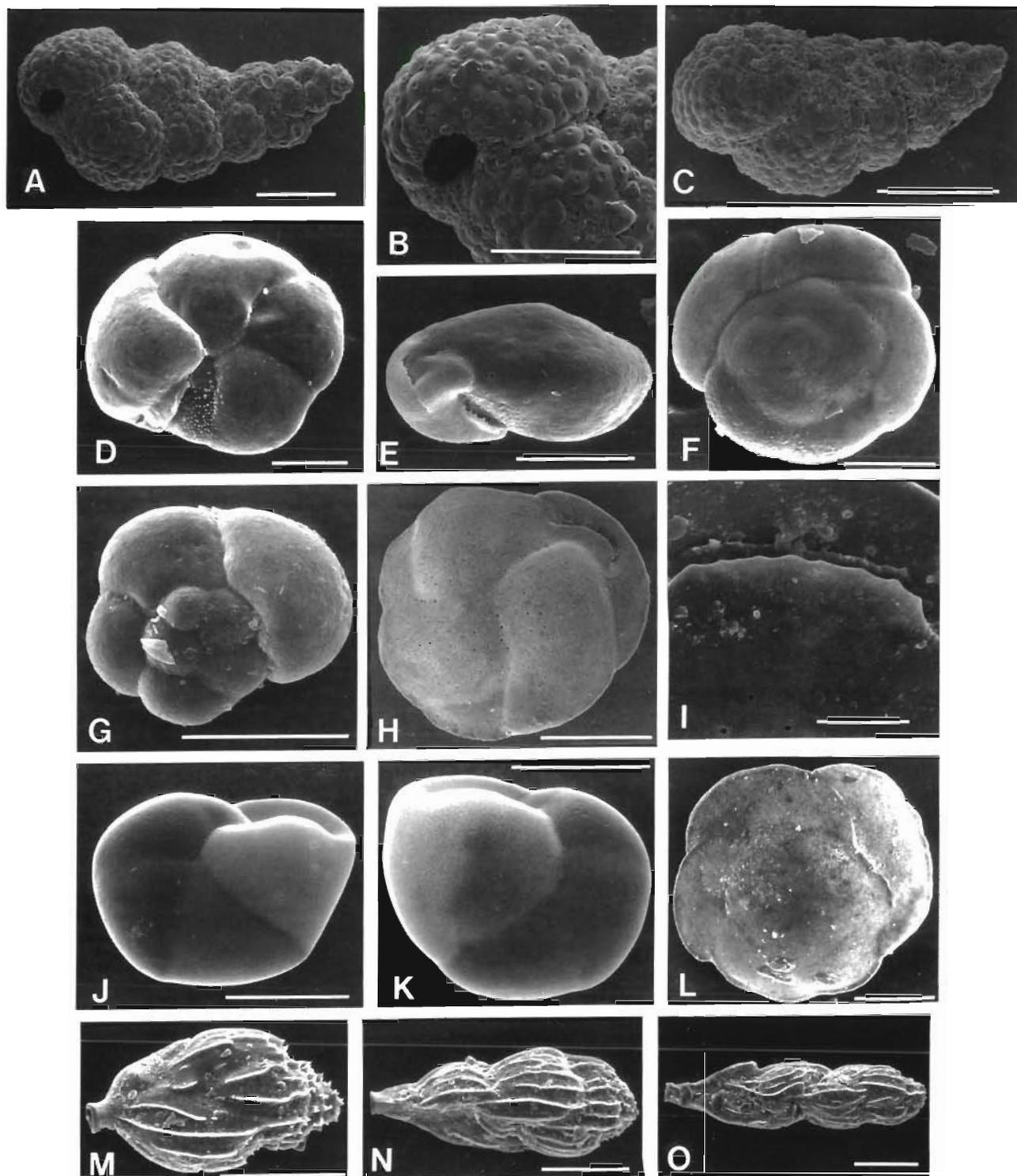


Fig. 1. SEM photographs of foraminiferal species common in the April and July samples. (A) to (C) *Morulaeplecta* sp. nov.; (D) to (F) *Alabaminella weddellensis* showing involute surface, side view, and evolute surface respectively; (G) ?*Alabaminella* sp., evolute side; (H), (I) *Cassidulina teretis* showing entire test and detail of aperture; (J), (K) *Epistionella exigua*; (L) *Gavinulinopsis lobatulus*; (M) to (O) *Trifarina pauperata*, showing the progressively larger and more elongate specimens. Scale bars = 50 μ m (A to G, I, K); 100 μ m (H, L to O); 20 μ m (I)

Table 2. Taxonomic comments on important species occurring at Stns 51502 (April) and 51615 (July)

Suborder and species	Original description and comments	Illustrations
Suborder Textulariina <i>Morulaepecta</i> sp. nov.	Tiny textulariniid (L = 60–160 µm long) with early chambers streptospirally coiled around proloculus and after chambers arranged biserially. Differs in several respects from <i>M. bulbosa</i> Höglund: test is more strongly flared, wall is composed largely of coccoliths rather than mineral grains, and aperture is oval areal opening near base of final chamber	Fig. 1A–C
Suborder Rotaliina <i>Alabaminella weddellensis</i> (Earland)	= <i>Eponides weddellensis</i> Earland (1936, p. 57, Pl. 1, Figs. 65–67). Gooday (1986) identified this species as <i>Epistominella levicula</i> Resig. Van der Zwaan (1980, Pl. 1, Fig. 1) illustrates typical pustulate specimen as <i>Eponides leviculus</i> . Present identification based on comparison with BIOTRANS specimens and type material (Royal Museum of Scotland); generic placement follows Loeblich & Tappan (1988, p. 548). See also Table 10	Figs. 1D–F, 3A–D
? <i>Alabaminella</i> sp.	Test 40–120 µm (\bar{x} = 79 ± 18 µm, n = 45) diameter with chambers increasing more rapidly in size than in <i>A. weddellensis</i> .	Fig. 1G
<i>Cassidulina teretis</i> Tappan	See Tappan (1951, p. 7, Pl. 1, Fig. 30). Our specimens identified according to criteria of Mackensen & Hald (1988). Diameter in our material = 50–230 µm (\bar{x} = 116 ± 42 µm, n = 302)	Fig. 1H, I
<i>Epistominella exigua</i> (Brady)	= <i>Pulvinulina exigua</i> Brady (1884, p. 696, Pl. 103, Figs. 13, 14) ^a See also Table 10	Fig. 1J, K
<i>Gavinulinopsis lobatulus</i> (Parr)	= <i>Discorbis lobatulus</i> Parr (1950, p. 354, Pl. 13, Figs. 23–25). Our specimens are identical to those illustrated by Weston (1985, Pl. 2, Fig. 2), which were also from the Porcupine Seabight	Fig. 1L
<i>Trifarina pauperata</i> (Heron-Allen & Earland)	= <i>Uvigerina angulosa</i> Williamson var. <i>pauperata</i> Heron-Allen & Earland (1932, p. 398, Pl. 12, Figs. 40–43) ^a Our specimens are closely similar to original material from 454–1036 m in the Falkland Islands area. This variety was given specific status by Parr (1950, p. 341)	Fig. 1M–O
Suborder Lagenina <i>Parafissurina fusuliformis</i> (Loeblich & Tappan)	Loeblich & Tappan (1953, Pl. 14, Figs. 18–19). A tiny, elongate species, usually < 100 µm long, generally occurs attached parasitically to tests of <i>A. weddellensis</i> . Our specimens closely resemble illustrations of Jones (1984, Pl. 6, Fig. 7–8) and Ward & Webb (1986, Pl. 3, Fig. 15)	

^a Original material examined in the British Museum (Natural History)

8). However, 2 species, ?*Alabaminella* sp. A and *Parafissurina fusuliformis* (the latter usually was attached epiparasitically to the test of *A. weddellensis*), were concentrated largely in the phytodetritus.

The foraminifers varied in size from 40 to 300 µm and therefore fell within the meiofaunal size range. The most abundant species, *Alabaminella weddellensis*, was 40 to 160 µm (mean 88.0 ± 21.7 µm, n = 750) in diameter, half the specimens were smaller than 90 µm and ca 80 % were smaller than 110 µm (Fig. 2).

An additional sample (1 to 2 ml volume) consisting of phytodetritus and some sediment (collected and made available by Dr R. S. Lampitt) was also examined. It had been removed from the surface of a core (Stn 51615 Deployment 1) using a Pasteur pipette. This sample yielded 157 stained benthic foraminifera of which 20 were found within lumps of sediment and 5 (all *Tinogullmia* sp. nov.) inside the moults of crustaceans (< 1 mm in length), probably harpacticoid copepods

(Gooday in press) (Table 4). The remaining 132 specimens occurred within aggregates of phytodetritus or lumps consisting of phytodetritus mixed with sediment. This sample contained more species (19) than phytodetritus extracted from the sieve residues. Also, *Alabaminella weddellensis* constituted < 50 % of the total numbers of specimens. These differences probably reflect the fact that the sample comprised an unsieved and unwashed mixture of phytodetritus and superficial sediment.

Total and sediment populations

The April samples yielded 253 to 491 (mean 385 ± 79) stained benthic foraminifera and the July samples yielded 356 to 1218 (mean 713 ± 218) specimens of which 161 to 958 (mean 474 ± 216) were found in the sediment fractions (Table 5). None of these mean val-

Table 3. Species extracted from the phytodetrital fractions of Stn 51615 (July) samples. Those occurring in 4 or more fractions are indicated by an asterisk. Except for those in the final column and bottom 2 lines, all values are percentages

Species	Fraction						Overall %	Mean number per sample \pm SD
	1a	1b	5b	5c	5d	6b		
Suborder Allogromiina								
* <i>Tinogullmia</i> sp. nov. A	5.43	3.85	8.13	0.53	5.00	0.96	3.88	6.2 \pm 4.3
Indet.	–	–	–	1.06	–	–	0.20	0.3 \pm 0.7
Suborder Textulariina								
Saccamminid sp.	–	–	–	–	1.67	0.96	0.31	0.5 \pm 0.8
* <i>P. aff. pygmaea</i>	2.17	–	–	1.06	1.67	1.92	1.02	1.7 \pm 1.4
* <i>Morulaepecta</i> sp. nov. A	6.52	3.85	3.25	6.91	4.12	4.81	5.01	8.2 \pm 3.6
Suborder Rotaliina								
* <i>A. weddellensis</i>	71.44	75.38	76.42	73.40	68.33	77.88	74.51	120.5 \pm 40.0
*? <i>Alabaminella</i> sp. A.	3.16	3.46	5.69	7.98	9.17	2.88	5.62	9.2 \pm 3.8
<i>Bolivina</i> sp. A	0.54	–	–	–	–	–	0.10	0.2 \pm 0.4
<i>C. teretis</i>	–	–	3.25	0.53	1.67	–	0.72	1.2 \pm 1.5
<i>C. pseudungerianus</i>	–	–	–	–	–	0.96	0.10	0.2 \pm 0.4
* <i>E. exigua</i>	5.43	2.69	0.81	2.66	3.33	1.92	2.96	4.8 \pm 3.0
* <i>G. lobatulus</i>	1.63	3.09	2.44	4.79	4.12	3.85	3.27	5.3 \pm 2.4
<i>G. subglobosa</i>	–	0.38	–	–	–	–	0.10	0.2 \pm 0.4
Indet.	1.63	0.38	–	–	–	–	0.41	0.7 \pm 1.1
Suborder Lageniina								
* <i>P. fusuliformis</i>	1.63	4.62	–	1.06	–	3.85	2.55	4.2 \pm 5.0
Total forams	184	260	123	188	120	104	979	163.2 \pm 53.9
Total Metazoans	–	16	2	3	2	1	24	4.0 \pm 5.4

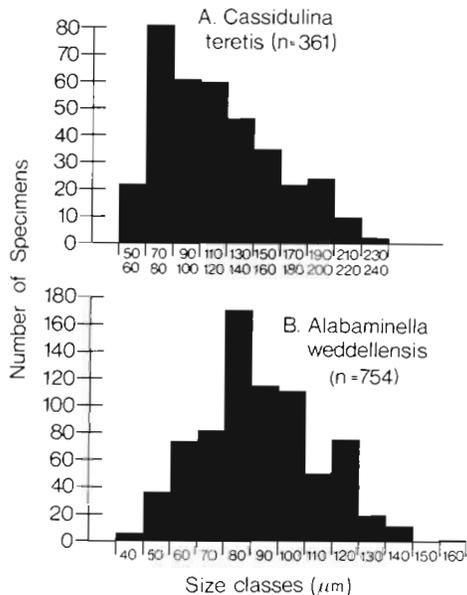


Fig. 2. Size distributions of *Cassidulina teretis* (specimens from sediment) and *Alabaminella weddellensis* (specimens from phytodetritus) in July samples

ues are significantly different ($p > 5\%$). However, the total July populations have a significantly greater variance ($p < 1\%$) than the April populations. Overall, foraminifers represent 59.0% (April), 56.7% (July sediment fraction) and 65.3% (July total population) of the

meiofauna. Although the same higher taxa were present in both sets of samples (Table 6), Rotaliina, the dominant taxon present in the phytodetritus, were more than twice as abundant in the total July populations ($> 50\%$) as in the April populations ($< 25\%$).

Both sets of samples contained about the same number of putative species, the overall range being between 58 and 94 per sample (Table 5). A total of 116 species were consistently recognised during this study. Table 7 shows the mean abundances of the top 30 species in the April samples compared with their abundances during July. Table 8 shows the equivalent data for the top 31 species in the July total populations. There are some notable differences between these populations. For example, the top 14 ranked species in the July populations were all significantly more abundant in July than in April (Table 8) while *Ovammmina* sp. nov., the top-ranked April species, was entirely absent during July (Table 7). The differences can be condensed into a list of 23 species divided into 3 groups.

Group A. Five species (including *Ovammmina* sp. nov.) were significantly more abundant in the April populations than in the July total populations and sediment fractions (Table 7).

Group B. Ten species which occurred only (or mainly) in the sediment fractions were significantly more abundant in both the total July populations and the July sediment fractions than in the April samples (Table 8).

Table 4. Abundance of species in sample pipetted from core surface (Stn 51615, Deployment 1). The number of specimens occurring in lumps of phytodetritus mixed with variable amounts of sediment, lumps of sediment without phytodetritus, and crustacean moults, are shown separately

	Phytodetritus/sediment	Sediment only	Crustacean moults
Suborder Allgromiina			
<i>Tinogullmia</i> sp. nov. A	8 (6.2%)	3 (15%)	5
Suborder Textulariina			
Saccamminid sp. F	2 (1.5%)	–	–
Saccamminid sp. G	1 (0.8%)	–	–
<i>A. glomeratum</i>	1 (0.8%)	–	–
<i>P. aff. pygmaea</i>	1 (0.8%)	2 (10%)	–
<i>Morulaepecta</i> sp. nov. A	23 (17.8%)	2 (10%)	–
Indet	–	1 (5%)	–
Suborder Rotaliina			
<i>A. weddellensis</i>	62 (48.4%)	–	–
? <i>Alabaminella</i> sp. A	9 (7.0%)	–	–
<i>Bolivina</i> sp. A	1 (0.8%)	–	–
<i>Bulimina</i> sp.	1 (0.8%)	1 (5%)	–
<i>C. teretis</i>	1 (0.8%)	3 (15%)	–
<i>E. exigua</i>	6 (4.6%)	–	–
<i>G. lobatulus</i>	6 (4.6%)	1 (5%)	–
<i>N. iridea</i>	–	4 (20%)	–
<i>T. pauperata</i>	–	3 (15%)	–
Suborder Miliolida			
Indet. species	1 (0.8%)	–	–
Suborder Lageniina			
<i>P. fusuliformis</i>	6 (4.6%)	–	–
Total numbers	129	20	5

Table 5. Abundance and diversity of foraminifers in samples from Stns 51502 (April) and 51615 (July)

Station/ Deployment	Subsample	Sediment fractions only			Sediment plus phytodetrital fractions ^a		
		Specimens	Species	% Total meiofauna	Specimens	Species	
51615/1	a	427	81	ND	611	83	
	b	958	85	68.2	1218	86	
	51615/4	b	172	59	51.0	ND	ND
		c	322	87	50.2	ND	ND
51615/5	d	548	93	61.4	ND	ND	
	c	509	79	47.4	698	80	
	d	562	91	65.3	682	91	
51615/6	a	515	85	58.6	ND	ND	
	b	250	76	37.0	356	78	
Mean ± SD		474 ± 216	82 ± 10		713 ± 281	84 ± 5	
51502/1	d	412	88	54.7			
51502/2	a	461	87	64.5			
	b	491	94	61.1			
	c	334	81	55.7			
	d	388	92	61.9			
51502/6	b	236	78	54.5			
	d	308	80	61.0			
51502/8	a	445	89	57.6			
Mean ± SD		385 ± 79	86 ± 6				

^a Stn 51615 only; phytodetritus did not occur at Stn 51502
 ND: no data

Table 6. Gross taxonomic composition of foraminiferal populations in samples from Stns 51502 (April) and 51615 (July). Except for the bottom 2 lines, figures are mean percentages \pm SD

	Stn 51502 Sediment	Sediment fraction	Stn 51615 Phytodetrital fraction	Sediment + phyto- detrital fractions (Total population)
Allogromiina	8.90 \pm 2.30	11.82 \pm 3.01	4.16 \pm 2.41	10.44 \pm 3.11
Globigerinacean inhabitants	8.00 \pm 3.40	3.74 \pm 3.30	–	1.95 \pm 0.50
Agglutinated tubes (Astrorhizacea)	2.72 \pm 0.73	3.50 \pm 2.12	–	3.22 \pm 1.90
Saccaminidae	30.44 \pm 8.51	21.27 \pm 2.45	0.44 \pm 0.65	14.01 \pm 4.70
Komokiacea	2.91 \pm 1.28	1.26 \pm 1.21	–	0.62 \pm 0.59
Multilocular agglutinated forms:				
(a) Hormosinacea	8.18 \pm 3.29	3.29 \pm 1.40	–	2.01 \pm 0.96
(b) Others	10.99 \pm 2.95	13.62 \pm 3.27	5.95 \pm 2.11	11.75 \pm 2.02
Calcareous forms:				
(a) Rotaliina	24.44 \pm 7.56	39.00 \pm 11.70	87.27 \pm 16.39	53.25 \pm 6.80
(b) Lagenina	0.59 \pm 0.34	0.71 \pm 0.34	2.00 \pm 1.67	1.10 \pm 0.23
(c) Miliolina	0.63 \pm 0.43	1.22 \pm 0.95	–	1.34 \pm 0.90
Others	2.21 \pm 1.15	0.66 \pm 0.65	–	0.31 \pm 0.25
No. of samples	7	9	6	5
Total no. of specimens	2663	4263	979	3565

Group C. Eight species which occurred in 4 or more phytodetrital fractions were also significantly more abundant in the total July populations (Table 8); all were ranked among the top 12 July species.

These 23 species are listed in Table 9 together with their abundances in individual samples. For certain species, Table 9 includes additional data from Stns 51502 (Samples 1d and 8b to d) and 51615 (Sample 5b) which were not used in compiling Tables 7 and 8. With 2 exceptions, the samples taken during April (Stn 51502) and July (Stn 51615) were collected in 2 rather distinct areas, about 1 n mile (1.85 km) apart. The exceptions are Samples 1a and 1b which were obtained in July at a position close to the April Sample 8a. The data in Table 9 are arranged so that species abundances in these samples can be easily compared (see below).

In addition to these more or less obvious differences in species abundances, the densities of individual species tended to be more variable following phytodetritus deposition. This is shown by the significantly greater variances of 3 abundant species in the total July populations (for *Nonionella iridea* and *Trifarina pauperata* $p = 0.1$ to 1.0% ; for *Cassidulina teretis* $p < 0.1\%$).

DISCUSSION

Phytodetritus populations

Our results from this bathyal site consolidate earlier observations (Gooday 1988a) that seasonally deposited phytodetrital aggregates are occupied by abundant,

low diversity populations of benthic foraminifers in the deep-sea. For the reasons discussed above, the Porcupine Seabight assemblages may have been modified by the way in which the samples were collected and processed. However, we are convinced that they are natural assemblages and not artifacts. The single unsieved sample examined (Table 4) suggests that the phytodetritus was, to some extent, mixed with superficial sediment on the core surface, probably through the activities of benthic animals. Hence, the phytodetritus should probably be regarded as part of the sedimentary environment rather than a distinct, suprabenthic microhabitat comparable to that provided, for example, by manganese nodules for encrusting foraminifera (Mullineaux 1987).

These phytodetrital populations could have arisen in several ways (Varon & Thistle 1988). First, the disproportionate abundance of certain species may develop incidentally from higher rates of dispersion into a habitat initially devoid of benthic organisms (apart from bacteria and flagellates; Lochte & Turley 1988). Second, these species may colonise the detritus in order to avoid competitors or predators. Third, they may be attracted because the detritus provides a good food source. Only the second and third explanations involve an active response by the foraminifers to the phytodetritus (Varon & Thistle 1988).

Without careful field and laboratory experiments, such as those conducted by Varon & Thistle (1988) on harpacticoid copepods from a shallow water marine locality, it is difficult to eliminate any of these possible explanations. Different rates of movement for deep-sea

Table 7 The 30 most abundant species in samples from Stn 51502 (April) and their corresponding abundances at Stn 51615 (July). Data for the July total populations are derived from Samples 1a, 1b, 5c, 5d, 6b; data for the July sediment fractions are derived from Samples 1a, 1b, 4b-d, 5c, 5d, 6a, 6b. \bar{x} = mean abundance per sample \pm standard deviation; % = overall % of total population. Mean April abundances which are significantly greater than mean July abundances are underlined ($p < 5\%$). See Appendix for full taxonomic names of species

Species	Stn 51502		Stn 51615			
	$\bar{x} \pm SD$	%	Total population $\bar{x} \pm SD$	%	Sediment fraction $\bar{x} \pm SD$	%
<i>Ovammia</i> sp. nov. A	<u>35.4 \pm 25.0</u>	9.27	0	0	0	0
<i>N. iridea</i>	28.9 \pm 10.0	7.55	64.8 \pm 34.5	9.11	50.9 \pm 32.3	10.76
<i>Lagenammia</i> sp. A	<u>13.6 \pm 4.0</u>	3.55	2.4 \pm 0.8	0.34	2.6 \pm 1.0	0.54
? <i>Nodellum</i> sp. nov. A	<u>10.4 \pm 10.0</u>	2.73	3.8 \pm 3.8	0.53	4.7 \pm 3.6	0.97
<i>P. aff. pygmaea</i>	8.9 \pm 2.1	2.32	20.2 \pm 5.2	2.84	15.6 \pm 7.2	3.29
<i>C. teretis</i>	8.6 \pm 7.6	2.24	73.4 \pm 79.7	10.32	58.4 \pm 65.2	12.36
<i>Crithionina</i> sp. A	<u>7.6 \pm 3.9</u>	1.98	1.0 \pm 1.1	0.14	1.3 \pm 1.3	0.28
<i>T. pauperata</i>	7.4 \pm 3.8	1.94	27.6 \pm 13.5	3.88	20.3 \pm 14.0	4.30
<i>S. biformis</i>	7.0 \pm 4.5	1.83	7.6 \pm 6.2	1.07	8.1 \pm 6.7	1.71
<i>R. micaeaeus</i>	<u>6.3 \pm 3.2</u>	1.65	2.2 \pm 1.3	0.31	1.8 \pm 0.7	0.38
<i>R. aff. subfusiformis</i>	6.1 \pm 4.7	1.61	2.2 \pm 1.2	0.31	1.7 \pm 1.7	0.35
<i>L. aff. catenulata</i>	5.3 \pm 7.7	1.38	1.2 \pm 1.9	0.17	1.1 \pm 1.6	0.23
<i>A. weddellensis</i>	5.3 \pm 3.7	1.38	145.62 \pm 51.4	20.47	17.7 \pm 12.4	3.74
? <i>Nodellum</i> sp. nov. B	5.1 \pm 1.5	1.35	1.4 \pm 1.4	0.20	2.0 \pm 1.9	0.42
<i>G. lobatulus</i>	5.0 \pm 2.9	1.31	22.8 \pm 9.5	3.21	13.3 \pm 9.8	2.82
<i>Crithionina</i> sp. B	5.0 \pm 3.0	1.31	0	0	0.7 \pm 1.7	0.12
Rotaliini sp. M	4.0 \pm 2.4	1.05	2.8 \pm 2.0	0.39	2.2 \pm 1.8	0.47
Allogromiini sp. C	3.7 \pm 2.3	0.97	7.8 \pm 4.7	1.10	9.3 \pm 6.7	1.97
<i>Lagenammia</i> sp. C	2.8 \pm 3.4	0.75	0.4 \pm 0.8	0.06	1.0 \pm 1.6	0.21
<i>Reophax</i> sp. A	2.8 \pm 2.9	0.75	0.2 \pm 0.4	0.03	0.3 \pm 1.5	0.05
Rotaliini sp. A	2.6 \pm 2.7	0.67	0	0	0.7 \pm 1.5	0.14
<i>C. argentea</i>	2.6 \pm 2.7	0.67	0.8 \pm 0.4	0.11	1.7 \pm 1.8	0.33
Saccamminid sp. A	<u>2.4 \pm 4.4</u>	0.64	0	0	0	0
Trochamminacean sp. A	2.3 \pm 2.0	0.60	2.0 \pm 1.8	0.28	3.1 \pm 2.1	0.66
<i>Reophax</i> sp. B	2.3 \pm 4.4	0.60	1.0 \pm 1.3	0.14	0.4 \pm 1.0	0.07
<i>Lagenammia</i> sp. B	2.3 \pm 1.9	0.60	1.0 \pm 1.5	0.14	1.1 \pm 1.9	0.23
<i>A. glomeratum</i>	2.1 \pm 2.3	0.56	8.8 \pm 6.2	1.24	8.7 \pm 9.2	1.83
<i>Reophax</i> sp. C	2.1 \pm 3.1	0.56	2.2 \pm 2.3	0.31	2.0 \pm 1.9	0.42
Saccamminid sp. D	2.1 \pm 2.9	0.56	2.4 \pm 2.1	0.34	2.2 \pm 2.3	0.47
<i>Lagenammia</i> sp. D	2.0 \pm 1.3	0.53	4.8 \pm 6.2	0.67	3.9 \pm 5.7	0.82
Samples		7		5		9
Total numbers		2663		3556		4263

foraminifers are likely in view of the 10-fold range of average velocities measured in different shallow water species by Kitazato (1988). Many of the specimens inhabiting phytodetritus are epibenthic, calcareous forms with smooth, rounded shells which probably can move rather rapidly (Kitazato 1988). In contrast, the sediment contains a variety of tubular astrorhizaceans, komokiaceans, and '*Globigerina* inhabitants' which, judging from their often complex morphologies, are likely to be more or less immobile and hence incapable of colonising the phytodetritus. Differential rates of colonisation by benthic foraminifers of azoic sediments in experimental trays have been reported by Kaminski et al. (1988).

To some extent, therefore, the composition of the phytodetrital assemblages may reflect the relative mobilities of species living in the sediment. However,

there is evidence from BIOTRANS samples that some foraminifers respond directly to phytodetritus. Microorganisms associated with the detritus are ingested by *Epistominella exigua*, *Alabaminella weddellensis* and *Tinogullmia* sp. nov. (Gooday 1988a, Gooday & Turley in press). Moreover, at both our bathyal site, and at the much deeper BIOTRANS site (Gooday & Turley in press), these 3 species are significantly more abundant in samples containing phytodetritus than they are in samples taken earlier in the year before detritus deposition. Such population fluctuations suggest that phytodetritus triggers a reproductive response in these species. This is consistent with the abundance of small specimens among our phytodetrital populations of *A. weddellensis* (Fig. 2). A similar reproductive response occurs in shallow water and littoral environments where some foraminiferal species undergo rapid popu-

Table 8. The 30 most abundant species in the total July populations (Stn 51615 Samples 1a, 1b, 5c, 5d, 6b), July sediment fractions (Stn 51615 Samples 1a, 1b, 4b-d, 5c, 5d, 6a, 6b) and April samples (Stn 51502). \bar{x} = mean abundance per sample \pm standard deviation; % = overall % of total population. Species occurring in 4 or more phytodetrital fractions are indicated by an asterisk. Mean July abundances which are significantly greater than mean July abundances are underlined ($p < 5\%$)

	Stn 51615				Stn 51502	
	Total population		Sediment fraction		$\bar{x} \pm SD$	%
	$\bar{x} \pm SD$	%	$\bar{x} \pm SD$	%		
* <i>A. weddellensis</i>	<u>145.6 \pm 51.4</u>	20.47	17.7 \pm 12.4	3.74	5.3 \pm 3.7	1.38
<i>C. teretis</i>	<u>73.4 \pm 79.7</u>	10.32	58.4 \pm 65.2	12.36	8.6 \pm 7.6	2.24
<i>N. iridea</i>	<u>64.8 \pm 34.5</u>	9.11	50.9 \pm 32.3	10.76	28.9 \pm 10.0	7.55
<i>T. pauperata</i>	<u>27.6 \pm 13.5</u>	3.88	20.3 \pm 14.0	4.30	7.4 \pm 3.8	1.94
* <i>E. exigua</i>	<u>27.2 \pm 19.0</u>	3.82	17.2 \pm 15.9	3.64	0.3 \pm 0.5	0.07
* <i>Tinogullmia</i> sp. nov. A	<u>25.8 \pm 13.5</u>	3.62	14.9 \pm 10.6	3.15	0.1 \pm 0.3	0.04
* <i>G. lobatulus</i>	<u>22.8 \pm 9.5</u>	3.21	13.3 \pm 9.8	2.82	5.0 \pm 2.9	1.31
* <i>Morulaepecta</i> sp. nov.	<u>22.4 \pm 11.1</u>	3.15	12.0 \pm 9.0	2.54	0.1 \pm 0.3	0.04
* <i>P. aff. pygmaea</i>	<u>20.2 \pm 5.2</u>	2.84	15.5 \pm 7.2	3.29	8.9 \pm 2.1	2.32
Allogromiun sp. B	<u>13.4 \pm 9.9</u>	1.88	9.2 \pm 8.8	1.95	0	0
<i>Adercotryma</i> sp. A	<u>12.6 \pm 25.2</u>	1.77	7.0 \pm 19.8	1.48	0	0
* <i>Alabaminella</i> sp. A	<u>10.4 \pm 4.6</u>	1.46	0.1 \pm 0.3	0.02	0	0
" <i>Psammospaera</i> " sp. nov. A	<u>9.2 \pm 7.7</u>	1.29	11.3 \pm 2.5	2.40	0.3 \pm 0.5	0.07
<i>Hyperammina</i> sp. A	<u>8.8 \pm 5.1</u>	1.24	5.5 \pm 5.3	1.17	0.1 \pm 0.3	0.04
<i>A. glomeratum</i>	<u>8.8 \pm 6.2</u>	1.24	8.7 \pm 9.2	1.83	2.1 \pm 2.3	0.56
Allogromiun sp. C	<u>7.8 \pm 4.7</u>	1.10	9.3 \pm 6.7	1.97	3.7 \pm 2.3	0.97
<i>S. biformis</i>	<u>7.6 \pm 6.2</u>	1.07	8.1 \pm 6.7	1.71	7.0 \pm 4.5	1.83
* <i>P. fusuliformis</i>	<u>6.0 \pm 5.1</u>	0.84	1.4 \pm 1.3	0.30	0	0
? <i>Pelosina</i> sp.	<u>6.0 \pm 4.2</u>	0.84	3.3 \pm 4.3	0.70	0	0
<i>S. schlumbergeri</i>	<u>5.6 \pm 4.5</u>	0.79	3.7 \pm 4.1	0.78	1.0 \pm 0.9	0.28
<i>Lagenammina</i> sp. D.	<u>4.8 \pm 6.2</u>	0.67	3.9 \pm 5.7	0.82	2.0 \pm 1.3	0.53
<i>C. pseudungerianus</i>	<u>4.8 \pm 1.7</u>	0.67	3.8 \pm 2.7	0.80	1.3 \pm 0.9	0.26
<i>Hyperammina</i> sp. B	<u>4.6 \pm 7.7</u>	0.65	2.7 \pm 6.2	0.14	0.3 \pm 0.4	0.07
<i>Brizalina</i> sp. A	<u>4.4 \pm 2.1</u>	0.62	3.0 \pm 2.3	0.28	1.0 \pm 1.1	0.28
? <i>Nodellum</i> sp. nov. A	<u>3.8 \pm 3.8</u>	0.53	4.7 \pm 3.6	0.99	5.1 \pm 1.4	1.35
<i>Tosaia</i> sp. A	<u>3.4 \pm 1.0</u>	0.48	2.2 \pm 2.3	0.34	0.6 \pm 0.7	0.19
<i>Rotaliniun</i> sp. Mf	<u>2.8 \pm 2.0</u>	0.39	2.2 \pm 1.8	0.47	4.0 \pm 2.4	1.05
<i>Brizalina</i> sp. B	<u>2.4 \pm 2.0</u>	0.34	1.4 \pm 1.6	0.30	0.3 \pm 0.5	0.07
<i>B. aculeata</i>	<u>2.4 \pm 0.5</u>	0.34	1.7 \pm 1.1	0.35	1.3 \pm 1.0	0.34
<i>Lagenammina</i> sp. A	<u>2.4 \pm 0.8</u>	0.34	2.6 \pm 1.0	0.54	13.6 \pm 4.0	3.55
Saccamminid sp. D	<u>2.4 \pm 2.1</u>	0.34	2.2 \pm 2.3	0.47	2.1 \pm 2.9	0.56
Samples		5		9		7
Total specimens		3556		4263		2663

lation increases following the sedimentation of phytoplankton blooms (Altenbach 1985, Erskian & Lipps 1987), and the development of intertidal diatom blooms (Lee et al. 1969).

Gooday (1988a) suggested that foraminiferal species which are disproportionately abundant in the phytodetritus are opportunists. Their life-history strategies may resemble those of the wood-boring xylophagid bivalves which settled as larvae on experimental wood panels located at 1800 m off the Bahamas and grew to maturity within 3 mo (Turner 1973). Opportunistic responses by deep-sea organisms to organic inputs will be discussed further by Gooday & Turley (unpubl.).

There are a number of morphological differences between abyssal and bathyal specimens of phytodetritus-dwelling species (Fig. 3). Bathyal specimens of *Alabaminella weddellensis* and *Epistominella exigua*

are smaller (mean diameters 88.0 \pm 21.7 μ m and 73.1 \pm 16.1 μ m, respectively) than those collected in the BIOTRANS area (mean diameters 101.6 \pm 21.7 μ m and 139.0 \pm 43.9 μ m, respectively). In *A. weddellensis* the final chamber may be somewhat inflated (Fig. 3C) and fine pustules (ca 1 μ m diameter) developed over parts of the surface (Fig. 1D), features not apparent in BIOTRANS specimens. In *E. exigua* the outer edge of the final chamber on the evolute side of the test is fairly straight and entirely obscures the aperture (Figs. 1J, K and 3E), whereas this edge bears a triangular projection and only partly obscures the aperture in BIOTRANS specimens (Fig. 3F). Differences between the bathyal and abyssal populations of *Tinogullmia* sp. nov. are discussed elsewhere (Gooday in press). These differences are not sufficient to separate the populations at the species level. The specimens which we

Table 9. Species abundances in samples from Stns 51502 (April) and 51615 (July). Group A includes species which are significantly more abundant during April; Group B includes species which are significantly more abundant during July but present only (or mainly) in the sediment fraction; Group C includes species significantly more abundant during July and consistently present in the phytodetrital fractions. Included are data from Stns 51502 Samples 1d, 8b–d and Stn 51615 Sample 5b which were sorted for selected species only. For Group C species, data are given only for samples where foraminifers were extracted from the phytodetrital fractions. –: no data

Species	Stn 51502										Stn 51615										
	1d	2a	2b	2c	2d	6b	6d	8a	8b	8c	8d	1a	1b	4b	4c	4d	5b	5c	5d	6a	6b
Group A																					
<i>Crithionina</i> sp. A	–	13	11	9	4	4	2	10	–	–	–	3	0	2	0	1	–	1	0	4	1
<i>Lagenammina</i> sp. A	–	21	14	11	15	10	8	6	–	–	–	3	1	3	2	3	2	3	2	3	3
<i>Ovaminna</i> sp. nov. A	–	69	68	15	52	24	4	16	3	11	2	0	0	0	0	0	–	0	0	0	0
<i>R. micaceus</i>	–	9	5	5	4	3	5	13	0	1	1	0	4	2	0	1	1	1	0	4	1
Saccamminid sp. A	–	1	0	0	3	0	0	13	–	–	–	0	0	0	0	0	–	0	0	0	0
Group B																					
<i>Adercotryma</i> sp. A	–	0	0	0	0	0	0	0	–	–	–	0	63	0	0	0	–	0	0	0	0
Allogromiini sp. B	–	0	0	0	0	0	0	0	–	–	–	2	25	5	1	7	–	23	3	15	2
<i>C. teretis</i>	11	5	8	8	9	1	2	26	16	1	0	57	226	10	26	102	41	22	47	27	9
<i>C. pseudungerianus</i>	5	3	0	1	1	2	1	1	2	1	0	6	5	0	1	1	3	4	7	8	3
<i>N. iridea</i>	43	16	34	27	33	11	40	39	23	5	8	46	115	17	16	63	5	49	92	39	21
<i>Hyperammina</i> sp. A	–	0	0	1	0	0	0	0	–	–	–	8	10	1	0	3	–	17	8	2	1
<i>Psammosphaera</i> sp. nov. A	–	0	0	1	0	0	0	1	–	–	–	10	1	6	19	10	12	9	23	21	3
? <i>Pelosina</i> sp.	–	0	0	0	0	0	0	0	–	–	–	3	9	0	0	12	–	0	0	0	6
<i>Tosaia</i> sp. A	–	1	1	0	0	1	2	0	–	–	–	5	3	0	2	1	–	4	3	0	2
<i>T. pauperata</i>	–	5	15	6	7	2	10	7	–	–	–	21	52	1	10	23	–	27	27	11	11
Group C																					
<i>Tinogullmia</i> sp. nov. A	–	0	0	0	1	0	0	0	0	0	1	29	45	–	–	–	25	12	34	–	10
<i>E. exigua</i>	–	0	0	1	0	0	0	1	0	1	0	28	63	–	–	–	11	15	21	–	9
<i>A. weddellensis</i>	–	3	7	7	3	2	13	2	–	–	–	146	238	–	–	–	100	152	108	–	89
<i>G. lobatulus</i>	–	3	7	4	11	3	2	5	–	–	–	18	39	–	–	–	12	24	23	–	10
<i>Morulaepecta</i> sp. nov. A	–	0	0	1	0	0	0	0	–	–	–	20	44	–	–	–	9	24	18	–	8
<i>P. aff. pygmaea</i>	–	6	13	9	10	9	8	7	–	–	–	21	27	–	–	–	9	21	21	–	11
? <i>Alabaminella</i> sp. A	–	0	0	0	0	0	0	0	–	–	–	6	15	–	–	–	7	15	12	–	6
<i>P. fusuliformis</i>	–	0	0	0	0	0	0	0	–	–	–	4	6	–	–	–	1	4	2	–	3

assign to *E. exigua* differ from *E. vitrea*, the shallow-water counterpart of *E. exigua*, in having 5 rather than 6 to 6½ chambers in the final whorl (Todd & Low 1967). The rather more inflated later chambers in *A. weddellensis*, and the smaller size of *E. exigua*, may indicate that the bathyal site is a stressful environment for these species, perhaps because it lies near the limit of their bathymetric ranges (Boltovskoy & Wright 1976, p. 91, Wang & Lutze 1986). Weston (1985) found that *E. exigua* only became the dominant species in the dead foraminiferal assemblage in the Porcupine Seabight below about 2400 m.

The occurrence, albeit occasionally, of the allogromiini *Tinogullmia* sp. nov. inside small crustacean (copepod) moults (Table 4) is of interest. These structures are small enough (<1 mm) to fall within the operational range (ambit) of individual foraminifers. They probably provide refuges stocked with large populations of bacteria on which *Tinogullmia* appears to feed (Gooday & Turley in press). Some allogromiini and saccamminid foraminifers, as well as nematodes, seek refuge inside empty *Globigerina* tests (Gooday

1984). Jumars (1976) illustrated a presumed faecal pellet (1.5 cm long) from the Santa Catalina Basin which provided a microhabitat for encrusting entoprocts and an agglutinated foraminifer. Moults, and other small organic remains, represent pockets of organic enrichment which contribute towards the small-scale (centimetre to submillimetre) fabric of the sedimentary environment and thereby probably help to maintain high levels of diversity among meiofaunal taxa such as the Foraminifera. Grassle & Morse-Porteous (1987) and Grassle (1989) have recently emphasized the decisive role played by somewhat larger (millimetre to metre sized) organic patches in the maintenance of high macrofaunal diversity in deep-sea sediments.

Total and sediment populations

Total foraminiferal population densities were higher in July, when phytodetritus was present, than in April (Table 4), but not significantly so. However, the total population densities were significantly more variable

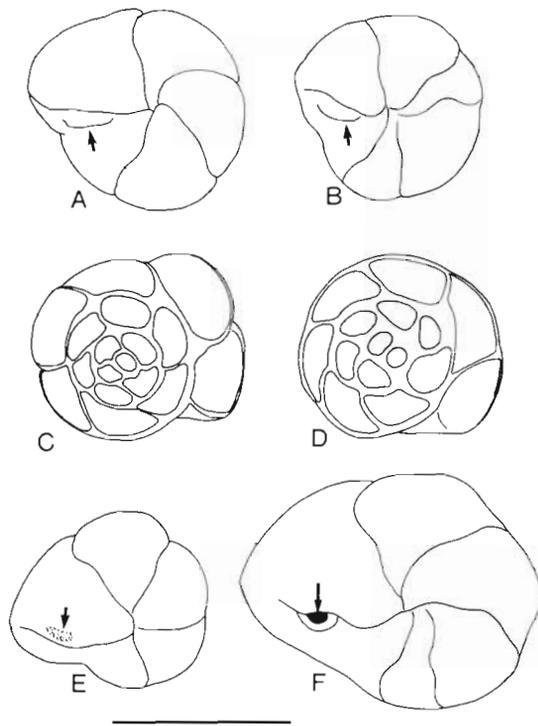


Fig. 3. (A), (B) *Alabaminella weddellensis*, involute side (apertural flap arrowed). (C), (D) *A. weddellensis*, evolute side. (E), (F) *Epistominella exigua*, involute side; aperture (arrowed) is completely obscured by edge of final chamber in (E) but only partly obscured in (F). (A), (C), (E) are from Stn 51615 (1340 m); (B), (D), (F) are from a BIOTRANS sample (4450 m). Scale bar = 100 μm

in the July samples. There were also some significant differences in the abundance and variance of species in the total populations (Tables 7 to 9). Patchy distributions of benthic foraminiferal populations are well documented in both shallow water (Buzas 1968, 1970, Lee et al. 1969, Matera & Lee 1972, Bernhard 1987, Hohenegger et al. 1989) and the deep-sea (Bernstein et al. 1978, Bernstein & Meador 1979, Kaminski 1985). Such spatial heterogeneity may have contributed to at least some of the differences observed between the April and July assemblages. For example, 3 species (*Adercotryma* sp. A, *Pelosina* sp. saccamminid sp. A) occurred in only a few samples (Table 9, Groups A, B) and seem to display obvious spatial patchiness. On the other hand, the significantly greater abundance in the July samples of 8 phytodetritus-dwelling species (Group C in Table 9) is more likely to be a seasonal phenomenon related to phytodetrital deposition. These species are all ranked among the top 12 in the July total population (Table 8). Note that they are consistently more numerous in Samples 1a and 1b (July) than in Sample 8a (Table 9), which was taken in the same area during April (see above). This indicates that spatial heterogeneity alone is unlikely to account for differ-

ences in their abundances. The increased abundance in the July samples of *Alabaminella weddellensis* (the dominant species of the phytodetrital fractions) is particularly striking (Tables 8 and 9).

Ovammmina sp. nov. A has a different pattern of abundance. It is the top ranked species in the April samples but is entirely absent from July samples (Table 7). This pattern, which is the inverse of that displayed by phytodetritus-dwelling (Group C) species, could have arisen by chance from spatial variability. Another possible explanation is that *Ovammmina* sp. is out-competed during summer by seasonally abundant species. Muller (1975) described saltmarsh foraminiferal communities in which *Allogromia laticollaris* Arnold, normally a rare species, became abundant when populations of the dominant species declined. Some of the less abundant species present in our samples, for example *Spiroplectammmina biformis*, seem to maintain fairly stable populations irrespective of whether phytodetritus is present or absent (Tables 7 and 8). Thus, deep-sea foraminifers may display a range of life-history strategies and population dynamics comparable to those of their shallow-water relatives (Erskian & Lipps 1987).

Cassidulina teretis is the top-ranked species in the July sediment fractions and is significantly ($p < 0.1\%$) more abundant in the total July populations than in the April samples (Tables 7 and 8). These July populations are dominated by small individuals (Fig. 2). Out of 361 specimens ranging in diameter from 45 to 245 μm , almost half were $< 106 \mu\text{m}$ and three-quarters $< 145 \mu\text{m}$. This size distribution suggests that, like some phytodetritus-dwelling species (see above), *C. teretis* may be actively reproducing during July. However, this species occurred only rarely in the phytodetritus (probably as a contaminant) and is almost certainly a sediment-dweller. Its apparent reproductive response may be linked to a relative abundance of food in the form of large bacterial populations. Bacterial densities are known to be higher in sediment beneath phytodetritus than in sediment collected before phytodetritus deposition (Thiel et al. in press). The distribution of *C. teretis* was also very patchy in July, a disproportionate number of specimens being present in a few samples (Table 9). This pattern suggests that *C. teretis* may reproduce most vigorously in localized areas where food (probably bacteria) is concentrated. Correlations between the small-scale distributions of benthic foraminifers and their probable food (cyanobacteria and diatoms) have been established in the intertidal North Adriatic (Hohenegger et al. 1989).

Sediment-dwelling species which are abundant in the July samples, for example *Cassidulina teretis*, '*Psammospaera*' sp. nov. and *Trifarina pauperata*, probably live on or within the soft, flocculent surface

sediment immediately beneath the detrital layer. One of these species, *T. pauperata*, is closely allied taxonomically and morphologically to the genus *Uvigerina*. Zahn et al. (1986, p. 38) suggested that 'the test morphology of *Uvigerina* species may indicate a near surface infaunal habitat - with a preference for the decaying 'soup' of organic matter on the sea-floor' (see also Altenbach & Sarnthein 1989). Deep-sea foraminiferal species therefore may display a fine-scale pattern of vertical zonation just below the sediment surface, in addition to the broader, centimetre-scale patterns described by Corliss (1985) and Gooday (1983, 1986).

CONCLUSIONS

(1) Seasonally deposited aggregates of phytodetritus provide a microhabitat for some benthic foraminiferal species at depths of around 1350 m in the northeast Atlantic. The most abundant inhabitant is *Alabaminella weddellensis*; others include *Epistominella exigua* and *Tinogullmia* sp. nov. The same species were found also in phytodetrital aggregates from the much deeper (4550 m) BIOTRANS site (Gooday 1988a).

(2) Certain species, including those which inhabit the phytodetritus, are significantly more abundant in the total (phytodetrital plus sediment) July populations than in the April populations. Others are either more abundant during April or display no significant fluctuations in abundance. These results suggest that some foraminiferal species respond opportunistically to phytodetritus while others react negatively or not at all.

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Appendix. Full names and authorships of species included in Tables 7 to 9

Adercotryma glomeratum (Brady 1878)
Alabaminella weddellensis (Earland 1936)
Bulimina aculeata d'Orbigny 1826
Cassidulina teretis Tappan 1951
Cibicides pseudungerianus (Cushman 1922)
Cystamina argentea Earland 1934
Epistominella exigua (Brady 1884)
Gavinulinopsis lobatulus (Parr 1950)
Leptohalysis aff. *catenulata* (Höglund 1947)
Nonionella iridea Heron-Allen & Earland 1932
Parafissurina fusuliformis (Loeblich & Tappan 1953)
Portatrochammina aff. *pygmaea* (Höglund 1947)
Reophax micaceus Earland 1934
Reophax aff. *subfusiformis* Earland 1933
Sigmoilina schlumbergeri Silvestri 1904
Spiroplectammina bififormis (Parker & Jones 1865)
Trifarina pauperata (Heron-Allen & Earland 1932)

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