BIOMASS OF FORAMINIFERA IN THE ST. ANNA TROUGH, RUSSIAN ARCTIC CONTINENTAL MARGIN

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SARSIA

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The abundance of large agglutinated tests in brown oxidized mud has suggested that high biomasses of foraminifera occur in troughs on the western Arctic Eurasian shelf. To verify this, we measured foraminiferal biomass (protoplasmic volume) at seven stations close to 80°N in the St. Anna Trough, a shelf depression open to the Arctic Basin. The abundance of arenaceous tests was high owing to good postmortem preservation within a thick (30 cm) surface oxidized layer of the sediment. Foraminiferal biomass was moderate (range = 0.06-1.7 g/m^2) compared with common shelf values and increased with increasing water depth. The foraminiferal contribution to the biomass of the benthic community was negligible on the slopes of the trough but below 500 m water depth, where the macrofauna is scarce, the foraminifera:macrofauna ratio reached 0.3. The bulk of the foraminiferal biomass consisted of specimens approximately 2 mm in diameter. The volume of cytoplasm in tests of the dominant foraminiferan *Reophax pilulifer* increased in response to the summer pulse of organic detritus.

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INTRODUCTION

Benthic foraminifera, a group of meiofauna (SNIDER & al. 1984), are thought to play an important role in nutrient cycling owing to their high biomass which occasionally exceeds that of the total macrofauna (LIPPS 1983; ALTENBACH & SARNTHEIN 1989; GOODAY & al. 1992). Nevertheless, only one previous study reports biomass values for this group of organisms in the Arctic (PAUL & MENZIES 1974) and we therefore present new data on foraminiferal biomass from a high Arctic area.

In the Kara Sea and northern Barents Sea the coarse fraction of surface sediment (> 0.5 mm) taken from shelf depressions below 100-150 m consists predominantly of agglutinated foraminiferal tests. The weight of these tests, up to 0.6 kg/m^2, exceeds macrofaunal biomass in the troughs by an order of magnitude (ZENKEVITCH 1963), resulting in speculation that very high biomasses of foraminifera might exist in these areas (MESYACEV 1929; ZENKEVITCH 1963; POGREBOV & al. 1995; KUZNETSOV 1996).

The aim of the present study was to investigate (1) whether the abundance of large tests in the region reflected a high foraminiferal biomass and (2) whether the biomass of foraminifera exceeded that of macrofauna. We compared the distributions of foraminifera and macrofauna across the St. Anna Trough, a deep depression in a region of the Barents-Kara shelf where high densities of large foraminiferal tests have been reported (ZENKEVITCH 1963; POGREBOV & al. 1995).

TERMINOLOGY

Body mass: wet weight of intratest protoplasm in one specimen.

Foraminiferal biomass: wet weight of intratest protoplasm of all specimens in a given area (g/m^2).

Macrofauna: metazoan organisms in the sieve fraction > 0.5 mm. We consider all foraminifera belong to the meiofauna thus following SNIDER & al. (1984, p. 1228) who 'regard meiofauna as those organisms which belong to taxa whose members are typically meiofaunal in size'.

St. Anna Trough: In 1912-1914, the Russian schooner *Svyataya Anna* drifted icebound in the Kara Sea before being wrecked north of Franz Josef Land. The trough is named after the vessel. We have adopted the English translation 'St. Anna'.

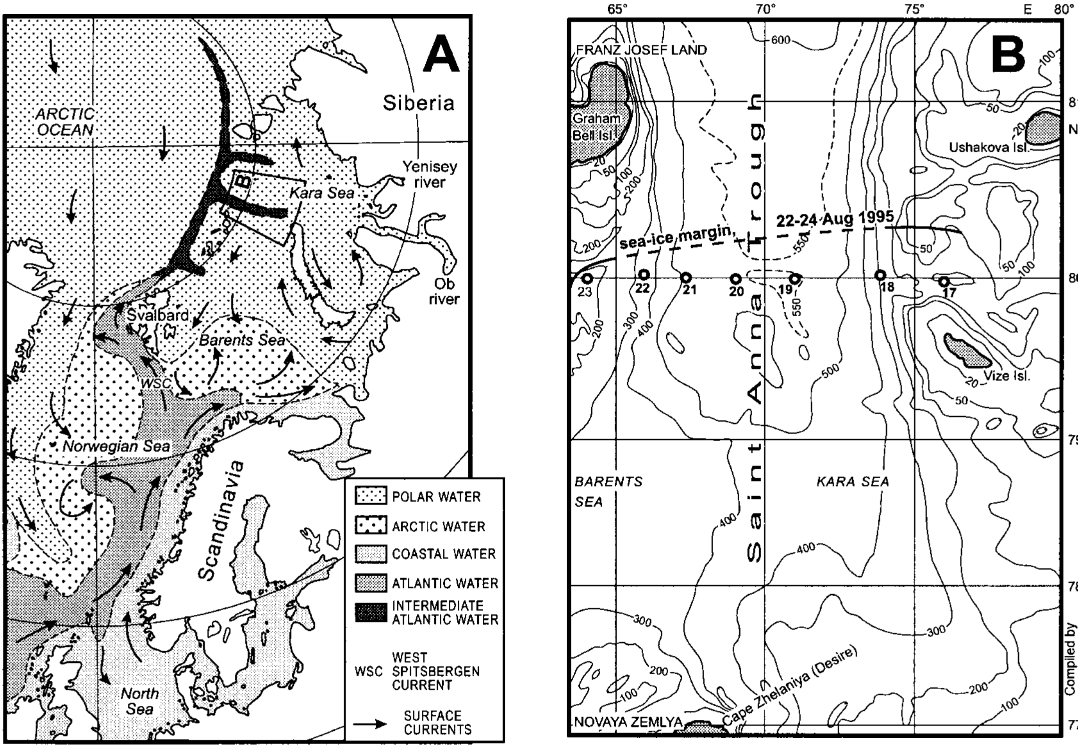

Fig. 1. Maps showing location of the sampling stations. A. Major surface water masses of the Barents-Kara and adjacent seas after Mosby (1968) and Hopkins (1991) and the main stream of intermediate Atlantic Water with the study area framed. B. Bathymetry of the St. Anna Trough and location of the sampling stations.

STUDY AREA

The Arctic continental margin of Eurasia is cut by a number of submarine valleys the largest of which is the St. Anna Trough. This trough is 550 km long, 170 km wide and 400 m deep in the flat central part off Novaya Zemlya and 600 m deep at its northern limit at the shelf break (Fig. 1).

Hydrography

The St. Anna Trough is ice covered most of the year. Gloersen & al. (1992) reported that during a ten year period (1978-87) only six summers were ice free and only then for one to two months. During the sampling period (August 1995) the sea-ice margin at the eastern flank of the trough was at 80°14'N while at the western flank it was at 80°02'N. The ice glow on the northern horizon indicated ice fields a few kilometers north of the route (Fig. 1B).

Warm Atlantic Water deepens north of Svalbard and reaches the St. Anna Trough as an intermediate water mass within 1.5 to 2 years (Timofeev 1962; Coachman & Aagaard 1974). All published hydrographic surveys of the St. Anna Trough show a western positioning of Atlantic Water (Hanzlick & Aagaard 1980; Milligan 1981; Hald & al. in press) which suggests Coriolis-forced advection from the north. By contrast, the transport of Atlantic Water to the St. Anna Trough across the Barents shelf has been recently suggested (e.g. Rudels & al. 1994; Schauer & al. 1995). This hypothesis has not been supported with empirical evidence.

During the sampling period a layer of Polar Water (Coachman & Barnes 1962) with a very low temperature (<–1.5 °C) and a decreased salinity (33.5-34.5 psu) occupied an interval of 20 to 60 m depth in the western part of the transect (Fig. 2, Korsun 1996). A warm body of surface water in the eastern part of the transect (Fig. 2) probably corresponded to the main northward extension of Continental runoff, emanating from the Ob and Yenisey estuaries (Hanzlick & Aagaard 1980; Milligan 1981). Atlantic Water (temperature > 0 °C) occurred below 75-100 m at the western flank of the trough. The core of Atlantic Water had a temperature above 2 °C and high salinity (34.85-35.0 psu). Arctic Bottom Water – relatively warm (ca. –0.6 °C), with a high salinity (34.8-34.9 psu) – occupied the lower part of the water column

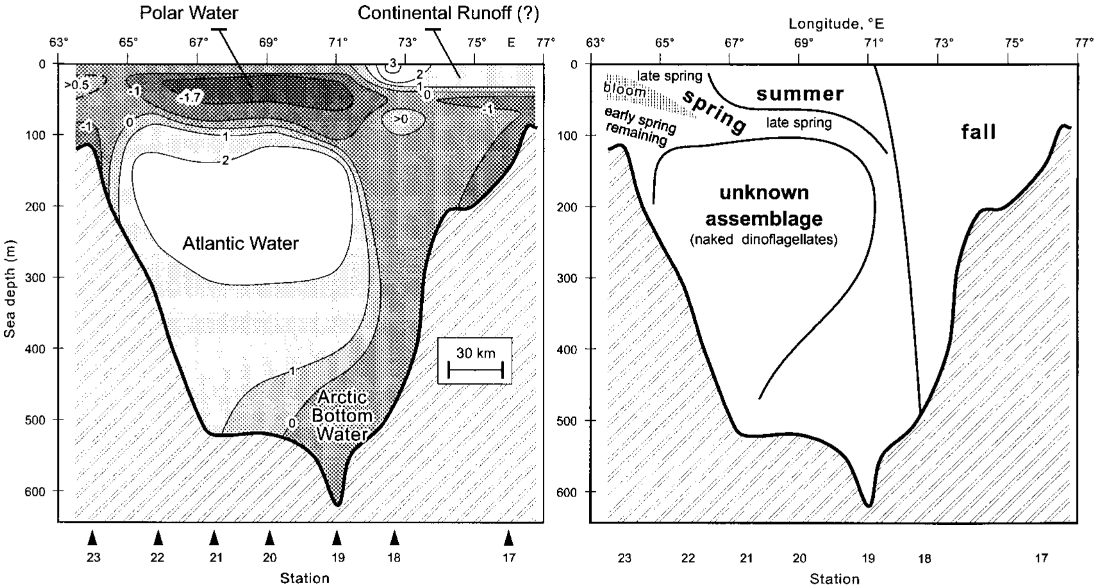

Fig. 2. Water characteristics in the St. Anna Trough at 80°N, 22-24 August 1995 (see Fig. 1 for location). A. Temperature (°C) distribution. B. Phytoplankton assemblages as stages of the seasonal succession (Larionov, unpublished data).

at the eastern slope (Fig. 2). Cold (ca –1.7 °C) bottom water, an inferred result of brine rejection (McClimans & Nilsen 1990), was not found in the trough.

Sediment

Fine grained sediments dominate the trough. An upper oxidized layer is brown reflecting a high concentration of MnO_2 (> 0.5%; Gorshkova 1957; Gurevich 1995). This 'brown mud' (Klenova 1960), which covers all shelf depressions in the Kara Sea and in the northern Barents Sea (Klenova 1960; Gurevich 1995), reaches its greatest thickness (20-30 cm) in the St. Anna Trough (Andrew & Kravitz 1974).

Organic carbon in the surface sediment, which is probably delivered by a northbound current from the Ob and Yenisey estuaries, reaches relatively high concentrations (> 1.6 %) along the eastern slope of the St. Anna Trough (Andrew & Kravitz, 1974). The lowest values (< 1 %) of organic carbon occur in the northwestern part of the trough where the Atlantic Water advection is maximal.

Biota

Vinogradov & al. (1995) characterized the Kara Sea area as oligotrophic based on analysis of phyto- and zooplankton. Macrofaunal biomass in the St. Anna Trough, like all areas of the Barents-Kara shelf covered with brown mud, is low (ca 10 g/m^2; Zenkevitch 1963).

The phytoplankton community aged eastward in the trough (Fig. 2B). At the western station, a pronounced bloom was dominated by the diatoms typical of late spring in the northeastern Barents Sea (Larionov 1995). The bloom deepened and weakened to the east, though still with densities numbering thousands of cells per litre. A summer mixo-heterotrophic assemblage occupied the Polar Water. In the eastern, warmest part of the transect, the phytoplankton community was degraded showing a late stage of the seasonal succession. The assemblage found in deeper parts of the western side of the trough consisted of small (12 to 20 µm) naked dinoflagellates with densities of 10^5 cells per litre. This assemblage, previously unknown from the Barents and Kara Seas, was presumably transported by incoming Atlantic Water. The relative abundance of organic detritus was highest in the central part of the trough, in and under Polar Water, and distributed throughout the water column.

METHODS

Samples were collected from 22 through 24 August 1995 along a transect of seven stations across the St. Anna Trough at 80°N lat. (Fig. 1B) during an expedition of the Murmansk Marine Biological Institute (Korsun 1996). Two stations (17, 18) characterize the eastern slope, three (19, 20, 21) the central flat area and two (22, 23) the western slope. The distance between the stations ranged from 25 to 50 km.

Sediment

Sediment was retrieved with an 'Ocean-50' grab, 0.25 m^2 (Boltovskoy & Wright 1976) at a penetration of 15-30 cm. Samples for the lithological analyses were taken from the upper 1 cm of the sediment. Boundaries between the grain size

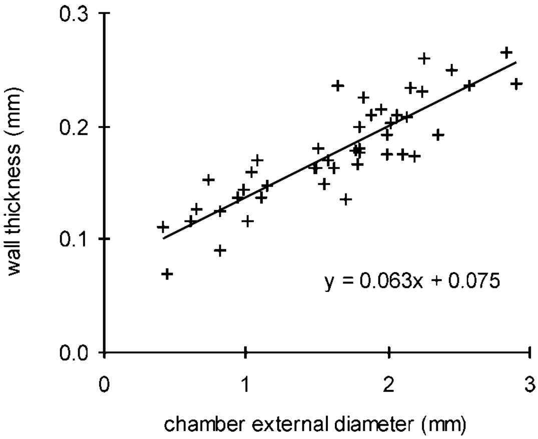

Fig. 3. Morphometry of *Reophax pilulifer*: wall thickness vs. chamber external diameter (n = 46). Each value of wall thickness is averaged from three measurements, chamber external diameter from two measurements.

fractions were 0.002, 0.063 and 2 mm. A Leco induction oven was used to quantify the content of total and organic carbon by measuring acid (HCl) treated and non-acid treated samples, respectively. The proportion of calcium carbonate was calculated as

$$\%CaCO_3 = 100\ 12^{-1}\ (\%TC - \%TOC)$$

where, TC = total carbon and TOC = organic carbon.

Macrofauna

Two or three full grab samples at each station were processed for the macrofaunal analysis. The sediment was washed through a 0.5 mm sieve and macrofauna were picked from the residue, identified and wet weighed to 0.01 g before being stored in 4 % formalin. Complete faunal lists are presented in Korsun (1996) or available on request.

Foraminifera

Size fraction. Large foraminifera (> 1.0 mm) comprise at least 90 % of foraminiferal biomass from the size fraction > 0.1 mm in muddy sediments in the Barents Sea (Korsun & al. 1994). Sediment samples (whole grab) were therefore washed on a 0.5 mm screen and we assumed that the underestimation of foraminiferal biomass due to omitting the fraction < 0.5 mm was negligible.

Handling and processing. Foraminifera and macrofauna were analyzed in the same samples. After removal of metazoans the > 0.5 mm residue of the grab samples was fixed in 4 % formalin and then transferred within one week to Rose Bengal stain (1 g/l) in 70 % ethanol. The stain and ethanol were removed before counting by washing on a 0.5 mm screen. Appropriate sample sizes were obtained with a wet micro-splitter. Foraminifera were identified and counted in water under a dissecting microscope with transmitted and incident light. With one exception (station 23) two samples were processed per station. Results from each pair of samples were combined and mean values were used in the analysis of data.

Biomass. The biomass of foraminifera was estimated after determination of protoplasmic volume (Saidova 1967). The shape of the intratest protoplasmic body in each specimen was approximated as a sphere or a cylinder, as appropriate, and was then measured with an ocular micrometer. Our values can be converted into the other commonly used biomass units from the relationships of Widbom (1984), Gerlach & al. (1985) and Gooday & al. (1995), where the ratio of

wet weight of soft body : ash free dry weight :
organic carbon : ATP content
= 10 : 2 : 1 : 0.0033.

Chambers of the dominant species, *Reophax pilulifer*, a large arenaceous foraminiferan, are almost ideal spheres. The test wall consists of a single layer of fine sand grains. Protoplasm is seen within the test through transparent grains of quartz; its presence is also distinguished by Rose Bengal staining of the apertural area. In dissected specimens, the diameter of the spherical protoplasmic body was averaged from two measurements. The robustness of the test makes dissection of every specimen unrealistic. In many individuals where the protoplasm appeared to fill up the whole inner volume, its diameter was taken as the external diameter minus the double wall thickness calculated by linear regression (Fig. 3).

The elongate protoplasmic bodies within the tubes *Rhabdammina abyssorum* and *Saccorhiza ramosa* were approximated to cylinders and their volumes were determined from measurements of the lengths and diameters. The spherical bodies of the unilocular arenaceous forms *Astrammina* sp. and *Reophax atlantica* were measured through the transparent test wall. The same procedure was applied for each protoplasm-containing chamber of *Reophax scorpiurus*.

Table 1. Station list and sediment characteristics.

Station no.	Position N	Position E	Sea depth m	Grain size, % clay	silt	sand	gravel	% $CaCO_3$	% C-org
23	79°59.7'	64°00'	95-110*	33.6	36.7	29.0	0.7	0.7	1.5
22	80°01.2'	65°54'	305-315	30.5	56.6	12.8	0.2	1.4	0.9
21	80°00.3'	67°30'	530-530	30.9	61.5	7.3	0.3	1.6	1.1
20	79°59.0'	69°06'	520-520	33.6	38.8	27.6	0.0	2.7	0.7
19	79°59.0'	71°02'	620-630	64.1	35.0	1.0	0	0	1.5
18	80°01.3'	73°34'	280-285	19.2	17.1	63.2	0.5	1.1	0.6
17	79°59.2'	76°01'	135-140	18.9	24.5	56.3	0.3	0.7	0.6

* Depth range due to ship drift

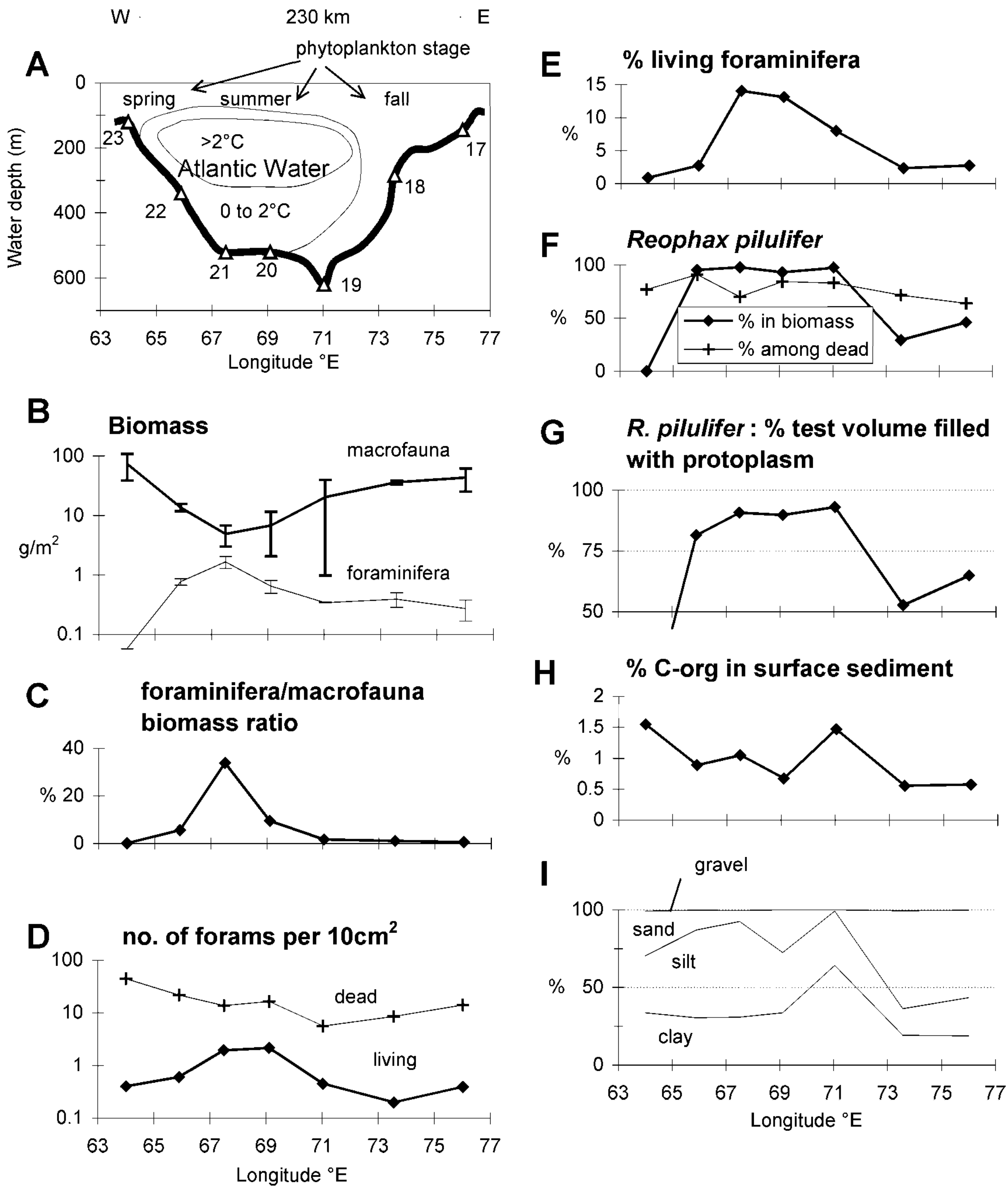

Fig. 4. Distribution of selected parameters across the St. Anna Trough, 80°N, in August 1995. A. Bottom profile, sampling site location, position of Atlantic Water and phytoplankton assemblages. B. Biomass of macrofauna and foraminifera (error bar = ± 1 standard deviation). C. Foraminifera:macrofauna biomass ratio. D. Foraminiferal density. E. % living foraminifera. F. *R. pilulifer* contribution to foraminiferal biomass and to dead foraminiferal density. G. Proportion of *R. pilulifer* intratest volume filled with protoplasm. H. % organic carbon. I. Grain size distribution.

Multilocular forms with complex inner cavities were of minor importance and so, in these cases, estimation of volume was based on only one measurement. Test width was measured in ovate miliolids. For planispiral spheroids (*Labrospira crassimargo, Cribrostomoides subglobosum, Elphidium bartletti*) we measured the diameter across the centre and the aperture of the test. The protoplasmic volume was assumed to be 0.1 × the cube of this measurement (KORSUN & al. 1994).

The specific weight of foraminiferal protoplasm is unknown. Estimates, based on a seawater density, vary from 1.02 to 1.027 g/cm³ (SAIDOVA 1967; WEFER & LUTZE 1976; SNIDER al. 1984). GERLACH & al. (1985) assumed a density of 1.13 g/cm³ calculated for nematodes. We adopted a specific weight of foraminiferal protoplasm of 1 g/cm³ and in our calculations, therefore, biovolume (ml/m²) is numerically equal to biomass (g/m²).

Standing crop. As the grab penetration depth was 15 to 30 cm, it is safe to assume that all living foraminifera, even deep infaunal, were sampled. Consequently, we expressed the density of living foraminifera as standing crop, i.e. the number of specimens per unit area, where our standard area was 10 cm² (MURRAY 1991).

RESULTS

Sediment

The surface sediment in the study area was a brown oxidized mud. At station 23 it was 2 cm thick and underlain by reduced grey sediment. At the other stations the thickness of the brown mud exceeded the penetration of the grab. The brown mud contained darker, stiff layers (crusts). The $CaCO_3$ concentration was < 2.7 % at all stations (Table 1). The organic carbon content showed two peaks of 1.5 % in the shallow area southeast of Franz Josef Land and under the eastern slope of the trough (Fig. 4H).

Macrofauna

Macrofaunal biomass was greater at the flanks (ca 50 g/m²) than in the central deep part of the trough (< 10 g/m²). Lowest values (minimum 5 g/m²) were recorded under the western slope (Fig. 4B).

Foraminifera

Tests of 19 species of foraminifera were present (Table 2). No living (stained) specimens of *Reophax nodulosus*? and *Hyperammina elongata* were found.

Dead foraminifera. *Reophax pilulifer* dominated (64 to 91 %) the dead assemblages at all the stations (Table 3A). *Reophax scorpiurus* and *Astrorhizoides polygona* also occurred throughout the transect but at lower frequency. *Cribrostomoides subglobosum* was present in the central deep. *Rhabdammina abyssorum, Hyperammina elongata, Saccorhiza ramosa, Astrammina* sp., *Reophax nodulosus*? and *Labrospira crassimargo* occurred only on the slopes of the trough. There was no asymmetry in the distribution of dead foraminifera across the trough.

Living foraminifera. The distribution of foraminiferal biomass was asymmetrical with a maximum of 1.7 g/m² in the deeper western part of the trough (Fig 4B). Biomass consisted mostly of *Reophax pilulifer* (Table 3B) which, in the central part of the trough, showed a very high (90 %) index of protoplasm filled intratest volume (Fig. 4G). The occurrence of living foraminifera increased to 14 % in the central deep (Fig. 4E).

Size spectrum. The size distribution of the foraminiferal standing crop was bimodal (Fig. 5). The first peak consisted of small foraminifera including *C. subglobosum, R. scorpiurus* and *L. crassimargo*. The second peak consisted mainly of *R. pilulifer*. Foraminifera with an external test diameter > 1 mm accounted for 37 % of the > 0.5 mm foraminiferal standing crop and 93 % of the > 0.5 mm foraminiferal biomass.

Reophax pilulifer morphology and taxonomy. *R. pilulifer* includes both unilocular and multilocular forms (Fig. 6A-B). Multilocular specimens had up to five chambers which increased progressively in size and only the last of which contained protoplasm.

Table 2. List of all foraminiferal taxa (size fraction > 0.5 mm) in the sediment samples from the St. Anna Trough.

1	Allogromiina gen. sp.	
2	*Astrorhizoides polygona*	(Heron-Allen & Earland, 1934)
	(= *Astrorhiza arctica*)	Stschedrina, 1964
3	*Rhabdammina abyssorum*	M. Sars, 1868
4	*Hyperammina elongata*	Brady, 1878
5	*Saccorhiza ramosa*	(Brady, 1879)
6	*Astrammina* sp.	
7	*Reophax pipulifer*	Brady, 1884
8	*Reophax nodulosus*?	Brady, 1884
9	*Reophax atlantica*	(Cushman, 1944)
10	*Reophax scorpiurus*	Montfort, 1808
11	*Labrospira crassimargo*	(Norman, 1892)
12	*Cribrostomoides subglobosum*	(G.O. Sars, 1872)
13	*Cornuspira foliacea*	(Philippi, 1844)
14	*Quinqueloculina seminula*	(Linné, 1758)
15	*Miliolinella subrotunda*	(Montagu, 1803)
16	*Planispiroides bucculentus*	(Brady, 1884)
	(= *Miliolinella subrotunda* var. *trigonia*)	(Weisner, 1931)
17	*Pyrgo williamsoni*	(Silvestri, 1923)
18	*Elphidium bartletti*	Cushman, 1933
19	*Nodosaria flintii*	Cushman, 1923

Although most specimens were free-living, attached specimens were also common (Fig. 6E). Attached individuals were encrusting (i.e., the test incorporated a large foreign object to which the soft body was directly in contact (POAG 1982)). The attached form of *R. pilulifer* seemed to occur whenever a dropstone was available for test building.

Reophax pilulifer agglutinated foraminiferal tests of just three arenaceous species: *R. pilulifer* itself, *C. subglobosum* and *L. crassimargo* (Fig. 6C and E-F). Some embedded specimens of the latter two species, *C. subglobosum* and *L. crassimargo*, were stained by Rose Bengal.

Macrofaunal studies in the Kara and Barents Seas following STSCHEDRINA (1949) have identified the species as *Hormosina globulifera* BRADY (e.g. ZENKEVITCH 1963; KUZNETSOV 1996). However, Schröder-Adams (written communication, 1996) identified the form from our material as *Reophax pilulifer* BRADY. KOLSTAD (1995) also recognized this species as *Reophax pilulifer* BRADY in surface sediment samples from the St. Anna Trough. TODD & LOW (1980), somehow, did not discern *Reophax pilulifer* in the St. Anna Trough and the only possible match for the unilocular form of *R. pilulifer* in their species list is *Saccammina sphaerica* M. SARS.

DISCUSSION

The abundance of large arenaceous tests in the brown mud

Several authors have predicted the primacy of foraminiferal biomass among the macrofauna of the Kara and Barents Seas owing to the reported abundance of large foraminiferal tests in the brown mud of the shelf

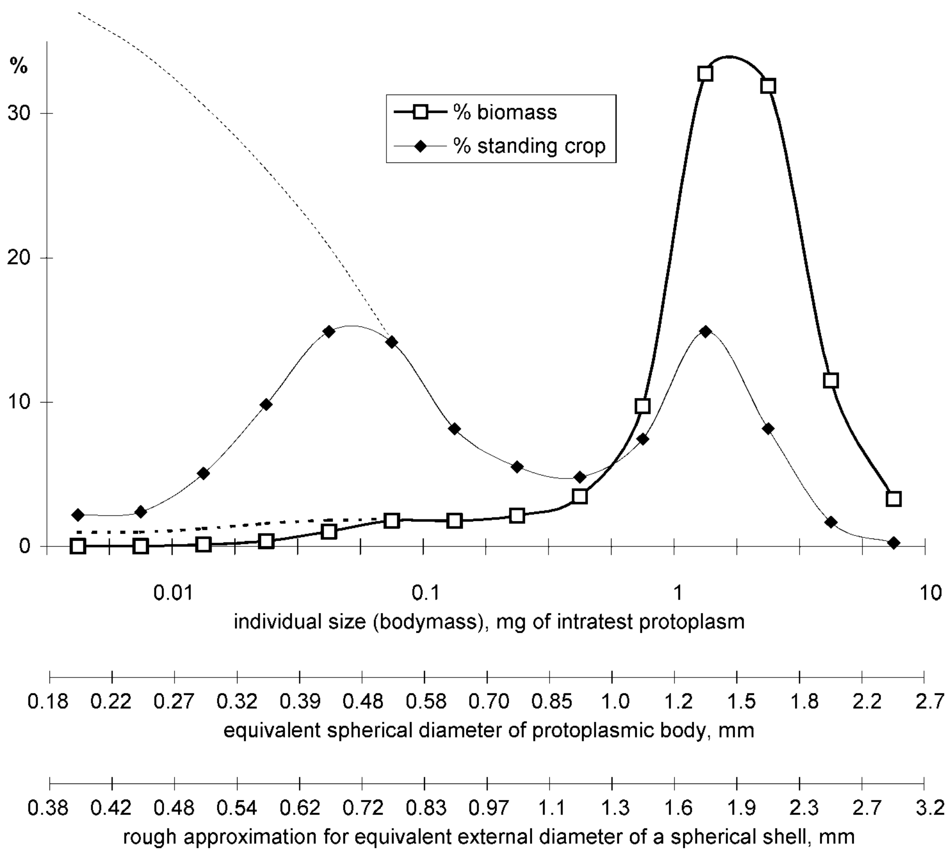

Fig. 5. Logarithmic size spectrum of foraminiferal biomass and standing crop in the St. Anna Trough. Specimens ($n = 416$) measured in the sieve fraction > 0.5 mm are separated into size classes with a logarithmic increment of $10^{0.25}$ mg (cf. GERLACH & al. 1985). The x-axes are plotted in alternative scales. The curves show the contribution of each size class to foraminiferal biomass and standing crop. No smoothing has been applied. Large specimens, ca 2 mm in external diameter, make up the bulk of foraminiferal biomass. The dashed curves show the probable contribution to the foraminiferal biomass and standing crop by specimens < 0.5 mm which were omitted from the sieved fraction.

depressions (Mesyacev 1929; Zenkevitch 1963; Pogrebov & al. 1995; Kuznetsov 1996). Our measurements show that the biomass of foraminifera in the St. Anna Trough is only moderate (0.06 to 1.7 g/m^2) compared with common shelf values, consistent with the notion of oligotrophy of this area.

The low occurrence (1 to 14 %) of living specimens indicates that the abundance of foraminiferal tests is a result of good postmortem preservation in the brown mud. Large foraminiferal tests are rare in areas lacking this mud. In the surface sediments of the southern-central Barents Sea, which are mostly green (Gurevich 1995), large arenaceous foraminifera (*Hyperammina subnodosa* Brady, *R. abyssorum* and *Pelosina variabilis* Brady) create biomasses of 1 to 10 g/m^2 (Korsun & al. 1994), which are in an order of magnitude higher than in the St. Anna Trough. The frequency of living specimens in these is high (ca 50 %) indicating rapid postmortem

Table 3. Foraminifera and macrofauna in the St. Anna Trough, size fraction > 0.5 mm. Each value is averaged from two or three subsamples.

Station	23	22	21	20	19	18	17
A. Dead foraminifera (% no.)							
Astrorhizoides polygona	6	1		<1	1	1	<1
Rhabdammina abyssorum	1	5				<1	<1
Hyperammina elongata	<1	<1				<1	<1
Saccorhiza ramosa	<1	<1				1	1
Astrammina sp.	<1					<1	<1
Reophax pilulifer	77	91	70	84	83	71	64
Reophax nodulosus?	<1	<1				1	<1
Reophax atlantica	<1						<1
Reophax scorpiurus	9	<1	2	2	1	7	19
Labrospira crassimargo	7	1			1	19	16
Cribrostomoides subglobosum		3	27	9	14		
Cornuspira foliacea	<1	<1	1	<1			<1
Quinqueloculina seminula		<1	<1	2	<1	<1	
Planispiroides bucculentus	<1	<1		1			
other five species	<1	<1		<1		<1	<1
no. of dead forams counted	112	109	114	206	100	129	146
B. Foraminiferal biomass, %							
Astrorhizoides polygona	60	<1			<1	37	
Rhabdammina abyssorum		<1				10	1
Saccorhiza ramosa		2				<1	21
Astrammina sp.	7				<1	1	1
Reophax pilulifer		95	98	93	97	29	68
Reophax scorpiurus	12	<1	<1	1	<1	7	1
Labrospira crassimargo					1	9	6
Cribrostomoides subglobosum		<1	1	3			
Cornuspira foliacea	10		<1				1
Quinqueloculina seminula		1	1	2	1		
other seven species	11	1		2		6	1
no. of forams measured	20	37	107	50	68	105	29
C. Biomass of foraminifera and major macrofaunal groups, g/m^2							
Foraminifera	**0.06**	**0.77**	**1.66**	**0.65**	**0.34**	**0.39**	**0.27**
±SD	N/A	±0.10	±0.38	±0.16	±0.00	±0.11	±0.10
Bivalvia	**5.04**	**0.86**	**0.99**	**0.03**	**2.63**	**3.02**	**0.92**
±SD	±7.01	±0.48	±1.11	±0.05	±1.37	±1.16	±0.45
Echinodermata	**15.00**	**0**	**0**	**0**	**10.45**	**9.20**	**13.60**
±SD	±9.33				±18.11	±3.96	±19.23
Polychaeta	**29.32**	**12.64**	**3.24**	**6.26**	**3.55**	**3.21**	**25.98**
±SD	±39.43	±1.47	±1.43	±4.02	±3.25	±0.55	±2.86
macrofauna total	**73.46**	**13.74**	**4.91**	**6.80**	**20.38**	**36.04**	**43.31**
±SD	±34.65	±1.90	±1.92	±4.74	±19.40	±2.49	±17.95
forams/macrofauna ratio, %	0.1	6	34	10	2	1	1

SD – standard deviation

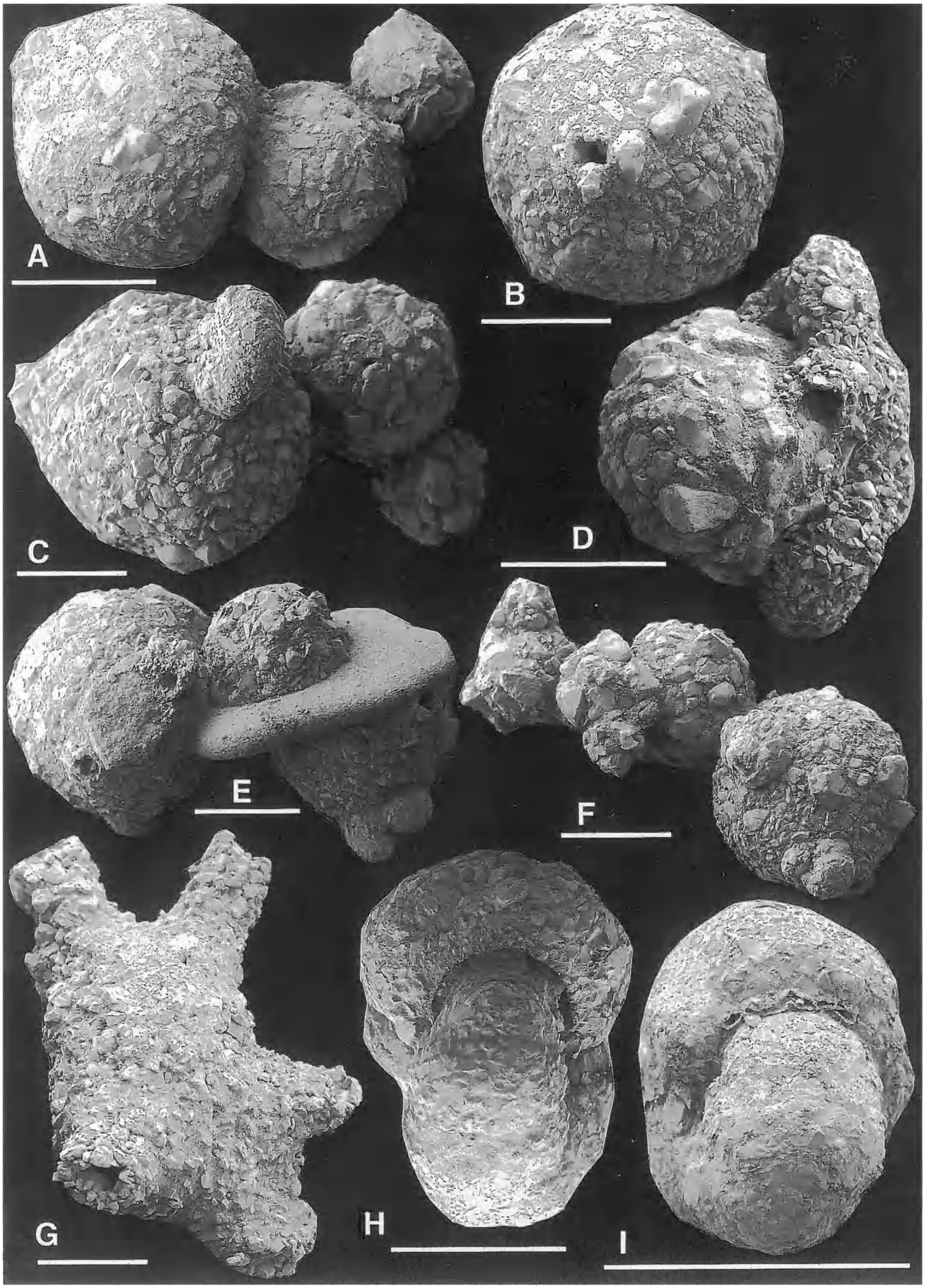

Fig. 6. Scanning electron micrographs of selected foraminiferal species from the St. Anna Trough. A. *Reophax pilulifer*, multilocular specimen. B. Unilocular *R. pilulifer*, apertural view. C. *R. pilulifer* embedding a *Labrospira crassimargo* test as a foreign particle. D. Fragment of *Saccorhiza ramosa* encrusting unilocular *R. pilulifer*. E. Three unilocular *R. pilulifer* encrusting a gravel. The front surface of the left specimen bears remnants of a forth, destroyed specimen. The right specimen embodies a *Cribrostomoides subglobosum* test. F. An agglomerate of four *R. pilulifer*. The two smaller specimens are bilocular, two larger ones unilocular. The right specimen embodies two *C. subglobosum* tests. G. *Astrorhizoides polygona*. H. *Labrospira crassimargo*. I. *Cribrostomoides subglobosum*. Scale bar 1 mm.

disintegration of arenaceous tests. We conclude that arenaceous tests are abundant in the brown mud because postmortem destruction is inhibited and that the abundance of dead tests causes an erroneous impression that large arenaceous foraminifera thrive in this environment.

Postmortem destruction of agglutinated tests results in the decrease in arenaceous foraminifera with increasing core depth (SCHRÖDER 1986). Many arenaceous taxa have iron in the organic cement (HEDLEY 1963). As long as such tests remain within the oxidized sediment, positive redox potential inhibits the reduction of Fe^{3+} to Fe^{2+} and prevents the bleaching and destruction of the agglutinated test (SIDNER & MCKEE 1976). A characteristic feature of the brown mud is its thickness. If, as in the other muddy areas of the Barents-Kara shelf, the upper oxidized layer is less than 2 cm thick (KLENOVA 1960), the brown (oxidized) mud can reach thicknesses of up to 30 cm (ANDREW & KRAVITZ 1974). Bioturbation in the Kara and Barents Seas is most intense in the upper 2-4 cm (HAMILTON & al. 1994; SMITH & al. 1995). When the oxidized layer is thin, bioturbation can move foraminiferal tests to the underlying reduced sediment resulting in the disintegration of arenaceous forms. Thus the occurrence of agglutinated tests with a ferruginous cement is likely to be higher in areas where the oxidized layer is thicker. ZENKEVITCH (1963) showed that there is a strong positive correlation between the total weight of foraminiferal tests (chiefly agglutinated) and the thickness of oxidized sediment (from < 1 to 18 cm) in the Kara Sea. This correlation indicates that the oxidized conditions of the brown mud are favorable for the postmortem preservation of agglutinated tests.

Dense accumulations of large arenaceous foraminifera typically occur along continental margins (GOODAY & al. 1997). When these abundant occurrences have been examined for live specimens they have appeared to consist largely of dead tests (GOODAY 1983; LINKE & LUTZE 1993). The studied assemblage from the St. Anna Trough also belongs to this type of cemetery-like accumulations.

Foraminifera and macrofauna

The foraminifera:macrofauna ratio in the St. Anna Trough increased with increasing water depth (Fig. 4C). The contribution of foraminiferal biomass was negligible on the slopes and accounted for approximately only 1 % of macrofaunal biomass. Deeper in the trough, however, foraminiferal biomass was comparable to that of the major macrofaunal groups, Polychaeta, Echinodermata, and Bivalvia, and reached 34 % of the total macrofaunal biomass (Table 3C). Thus, in the deeper parts of the St. Anna Trough, foraminifera were an important benthic group in terms of biomass. Considering that benthic foraminifera are able to maintain energy-turnover rates comparable to those of bacteria (LINKE 1992), we predict that in the deeper parts of the St. Anna Trough the role of foraminifera in the benthic community energy flux is likely to be at least as large as that of the total macrofauna.

Our data on macrofauna in the St. Anna Trough represent part of a trend, not a random pattern. The biomass of macrofauna decreased with increasing water depth from 75 to 5 g/m^2 (Table 3C; Fig. 4B) as reported previously for the brown mud of the Kara and Barents Seas (ZENKEVITCH 1963). A detailed survey of the macrofauna in the St. Anna Trough (POGREBOV & al. 1995) revealed a profound biomass minimum along the western slope. The minimum of our macrofaunal curve (Fig. 4B) probably represents the same feature and our transect of seven stations probably represents the trend of the distribution of macrofaunal biomass across the trough.

The distribution of foraminiferal biomass was inverse to that of macrofauna (Fig. 4B). Such an inverse relationship between meiofauna (foraminifera included) and macrofauna is common for marine biocoenoses and the meio:macrofauna ratio normally increases with water depth (e.g. GOLIKOV & AVERINCEV 1977; THIEL 1983; SHIRAYAMA 1984; GOODAY & al. 1992; GRAF 1992). It is generally thought that the meiofauna thrive wherever conditions for the macrofauna are unfavourable, probably reflecting predator pressure, the destructive effect of bioturbation or trophic competition (BUZAS 1978; CEDHAGEN 1993; GOLIKOV & AVERINCEV 1977).

Size spectrum

Most of the biomass consisted of a few large specimens (Fig. 5), reflecting the fact that the diameter-volume relation is allometric. The volume of a spherical object is a third power function of its diameter; a two-fold difference in diameter between two specimens will therefore correspond to an eight-fold (2^3) difference in volume and, hence, mass.

Two size groups (mean test diameter approximately 0.7 and 2.0 mm) were most frequent in the foraminiferal fauna (Fig. 5). The discontinuity between the two peaks occurred at a test diameter of approximately 1 mm which roughly corresponds in the size spectrum of marine benthos to the boundary between the meio- and macrofauna (FENCHEL 1969; GERLACH & al. 1985; WARWICK & JOINT 1987). Confirmation of this bimodal frequency distribution in other regions would provide a solid biological basis for the separation of foraminifera into meio- and macrofauna (e.g. GOODAY 1990).

Short-term foraminiferal response to the summer organic pulse

Short-term processes in benthic foraminiferal populations have been increasingly acknowledged as important in the utilization of organic pulses on the ocean floor

(Gooday & Turley 1990; Altenbach 1992; Graf 1992; Linke 1992; Pfannkuche 1993; Linke & al. 1995). The volume of foraminiferal cytoplasm declines during periods of starvation and increases within a few days, filling up the intratest cavities, when food becomes abundant (Linke 1992).

Describing an extremely abundant occurrence of the large tubular foraminiferan *Hyperammina crassatina* (Brady) on the East Greenland shelf, Linke & Lutze (1993) noted that the few live specimens (1-6 individuals per 10 cm^2) were associated with a high level of metabolic activity. Gooday & al. (1997) predicted that some of the large agglutinated species can undergo rapid growth when food becomes sufficient. Tubular agglutinated foraminifera form an ooze several centimetres thick in the southwestern Barents Sea (Kiær 1899; Mesyacev 1929; Vinogradov *in* Hedley 1964). In late October 1987 the biomass of large foraminifera (> 1 mm) in that area was 0.06 to 0.98 g/m^2 (five stations; Korsun & al. 1994). In early May samples, taken the same year in the same area, the biomass of large foraminifera reached 13 and 46 g/m^2 (two stations) probably following the spring diatom bloom.

The percentage of the intratest volume filled with cytoplasm in the dominant foraminiferan *R. pilulifer* changed substantially across the trough (Fig. 4G). High cytoplasm filling (ca 90 %) in specimens from the central part of the transect suggested good trophic conditions in this area.

In the Kara Sea the seasonal succession in the phytoplankton community is reduced to a single bloom which occurs at the beginning of the short ice-free period and which produces most of the annual phytoplanktic biomass (Savinov & Bobrov 1995). At the time when the samples in this study were collected, the bloom had crossed the trough from east to west (Fig. 2B). An increased concentration of suspended organic detritus observed in the central part of the transect (see the Study Area) was probably sinking residue of the bloom. We interpret the increased cytoplasm filling in *R. pilulifer* from the central deep (Fig. 4G) as a response to the pulse of fresh organic detritus.

CONCLUSIONS

The abundance of large foraminiferal tests in the brown mud does not reflect a high biomass but only good post-mortem preservation of arenaceous tests in the oxidized surface sediment. Foraminiferal biomass in the St. Anna Trough is moderate (0.06 to 1.7 g/m^2) compared with common shelf values and does not exceed the total macrofaunal biomass (5 to 75 g/m^2).

Foraminifera are an important benthic group in the deeper parts of the St. Anna Trough where macrofauna is scarce. In the deeper trough, foraminiferal biomass values are comparable to those of the major macrofaunal groups, including Polychaeta, Echinodermata and Bivalvia.

A total of 19 benthic foraminiferal species > 0.5 mm in size, including 17 living and 7 calcareous forms, occurred in the sediment. Arenaceous forms dominated in terms of both biomass and the density of dead tests. *Cribrostomoides subglobosum* was common in the central deep (> 500 m) whereas *Rhabdammina abyssorum, Hyperammina elongata, Saccorhiza ramosa, Astrammina* sp., *Reophax nodulosus*?, and *Labrospira crassimargo* occurred only on the slopes. Most of the foraminiferal biomass was *Reophax pilulifer*. This species also dominated dead assemblages throughout the transect.

Most of the foraminiferal biomass consisted of large specimens (ca 2 mm in external diameter).

The population of *Reophax pilulifer* seemed to respond to the summer pulse of organic matter, resulting in an increase in the cytoplasmic volume.

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