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ERRATA

page 4 : The locations of the sampling stations should be inserted on the geographic positions given on page 3.
page 7 : lines 15&16: 50 mm, 200 mm and 50 mm should be 50 µm, 200 µm and 50 µm.
line 44: 0.2 mm should be 0.2 µm.
page 8 : lines 1 & 2: 2 mm, 2 to 5 mm, 5 to 10 mm and 10 to 20 mm should be 2 µm, 2 to 5 µm, 5 to 10 µm and 10 to 20 µm.
lines 17, 33 & 34: 0.2 mm should be 0.2 µm.
page 9 : line 12: 200 mm should be 200 µm.
page 19: In the legend of Fig. 7 "and nauplii" should be inserted after "Copepoda".
page 25: Fig. 16 should be Fig. 13 (Fig. 16 is missing) .
page 25: Fig. 14 & Fig. 15 are given in this errata.
page 27: Fig.13: "microscoop" should be "microscope"
page 30: lines 11 & 12: 251 mmol, 129 mmol and 604 mmol should be 251 µmol, 129 µmol and 604 µmol.
lines 18 & 25: 960-1070 mmol and 3100-4100 mmol should be 960-1070 µmol and 3100-1070 µmol.
page 31: line 26: "surface-wat31er" should be "surface-water".

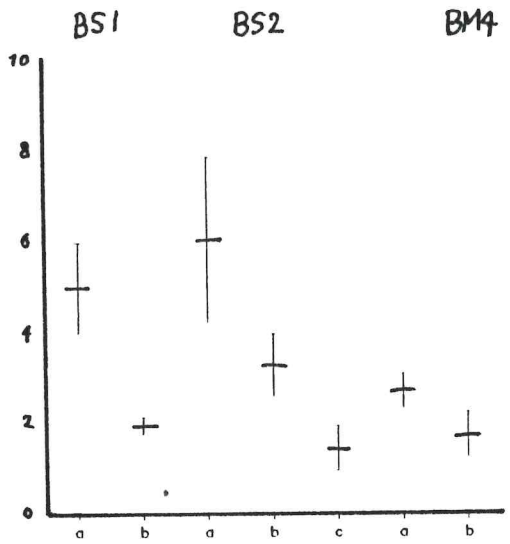

Fig. 14: Density of flagellates at BS1, BS2 and BM4 in number/cc x 1,000. a=0-3 mm, b=30-33 mm and c=60-63 mm.

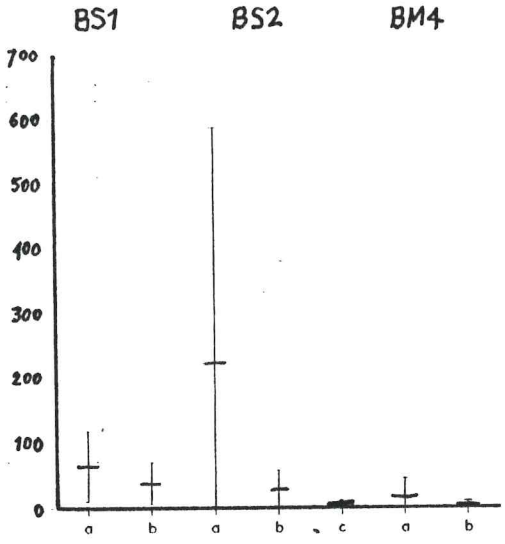

Fig. 15: Biomass of flagellates at BS1, BS2 and BM4 in mg C/cc. a=0-3 mm, b=30-33 mm and c=60-63 mm.

DENSITY, BIOMASS AND RESPIRATION OF DEEP-SEA MICRO-, MEIO-, AND MACROBENTHOS OF NORTH EAST ATLANTIC JGOFS SITES

a pilot study

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ABSTRACT

Within the JGOFS pilot programme a benthic survey of three stations in the N.E. Atlantic Ocean was made during September 1989. The stations were located at 39°, 37°, 33° N on 20° W and had depths between 4000 and 5000 metres. The density and biomass of macrofauna, meiofauna, flagellates and bacteria were investigated and the benthic community oxygen consumption was measured onboard at 1 atm. and 2.5°C. The vertical distribution of flagellates and bacteria was determined. Density and biomass of macro- and meiofauna correspond with earlier research in comparable environments. The estimated oxygen consumption also was within the range of earlier studies both from *in-situ* and from onboard measurements. A significant decline of bacterial abundance and biomass with depth in the sediment was observed. There is also a significant increase of bacterial abundance and biomass from north to south in the upper 3 mm surface sediment layer. The density of flagellates was very low and no statistical reliability could be found for abundance, biomass or horizontal and vertical distribution. Bacterial biomass outnumbered all other fauna groups with more than 90% of the total biomass.

INTRODUCTION

Benthic research in the JGOFS programme

The oceans cover two-third of the earth's surface. Despite their vast area, relatively little is known about the chemical and physical processes that occur within the oceans and the exchange of chemical compounds with the atmosphere. Knowledge of these processes is of great importance to obtain a better understanding of global environmental problems such as the greenhouse effect and the degradation of the ozone layer. For this reason an international research programme called JGOFS (Joint Global Ocean Flux Studies) for the decade 1989-1999 was established in 1987. JGOFS 's main goal should be:

"To determine and understand on a global scale the processes controlling the time varying fluxes of carbon and associated biogenic elements in the ocean, and to evaluate the related exchanges with the atmosphere, the sea floor and continental boundaries." (Anonymous, 1987)

So far, the Dutch contribution to JGOFS at this stage is restricted to a Pilot Programme for 1989 and 1990. Dutch scientists from different disciplines are engaged in an international coordinated study of the North Atlantic 20° West between Iceland and Madeira with the main stations on 60°, 47° and 33° North. A part of this project is focussed on studying the benthic fauna in connection with biological processes such as deposition of organic matter at the ocean bed, mineralisation, community respiration and bioturbation. Despite extreme conditions in the deep-sea environment (high pressure, low temperature, food scarcity), the consistency of the environment provides the existence of an extensive benthic community. Earlier studies concerning meio- and macrofauna of the North Atlantic deep-sea were carried out by Sanders *et al.* (1965), Thiel (1966,1971, 1972, 1983), Sanders & Hessler (1969), Rachor (1975), Rutgers van der Loeff & Lavaleye (1986), the German BIOTRANS programme (Pfannkuche & Thiel, 1988) and Lavaleye (1989). Metabolic processes in the deep-sea community respiration reflects the amount of organic carbon which is metabolised by benthic organisms (Lochte & Pfannkuche, 1988). Smith & Teal (1973), Smith (1978) and Lochte & Pfannkuche (1988) measured *in-situ* benthic community respiration from depths of 40 to 5200 m in the North West Atlantic. The benthic respiration has a strong correlation with water depth. Of lesser significance are correlations of benthic respiration with temperature, dissolved

oxygen content of the water, benthic animal biomass, surface primary productivity and sediment organic matter (Smith, 1978). The input of organic matter is the major factor for the existence and activity of the benthic system. How many organic carbon fixed at the surface which supposedly reaches the bottom, is dependent on the water depth (Smith, 1978). The benthic community respiration appears to be influenced by seasonal fluctuations (Smith, 1978; Smith & Baldwin, 1984; Lochte, 1988).

During the JGOFS II expedition in September 1989 onboard R.V. TYRO the composition, density and biomass of the meio- and macofauna at three stations in the North East Atlantic Ocean were studied (Fig. 1). Density and biomass of micro-organisms were also investigated. By means of onboard incubation of bottom samples the benthic community respiration was estimated. An attempt is made to link the benthic community respiration with the other measured components.

General description of the sampling area

The sampling stations were located in the Iberian and Canarian abyssal basins east of the Mid-Atlantic Ridge (Fig. 1). Table 1 presents the geographic positions, water depths and the sampling dates. The sediments of all these stations consist of cream coloured, high carbonate foraminiferal oozes with more clayey, darker ooze layers. The texture of the uppermost centimetres of the sediment is rather soft, but deeper down it becomes very sticky (Melkert, 1989). At all stations small ice-rafted stone grains were found. There is evidence for intense bioturbation of the clayey bottom layers. The temperature of the near bottom water was approximately 2°C (Veth, 1989).

TABLE 1: Positions, depths and sampling datas at JGOFS sites BS1, BS2 and BM4

station	BS1	BS2	BM4
co-ordinates	39°14.7'N 20°02.3'W	36°54.3'N 20°00.3'W	32°57.4'N 19°44.6'W
depth (m)	5038	4354	4135
date	23-09-89	24-09-89	26-09-89

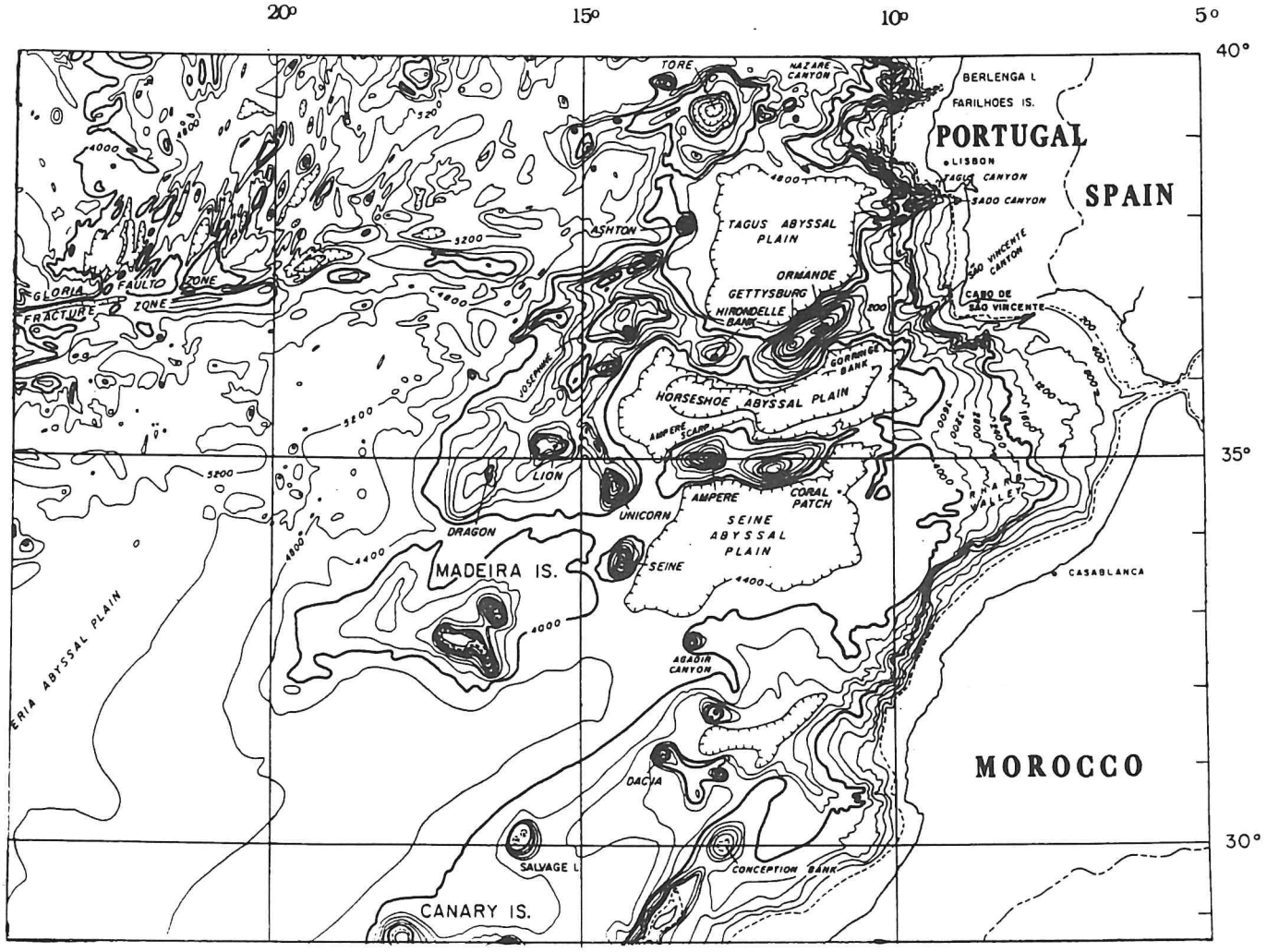


Fig. 1: Map of the North East Atlantic Ocean with the location of the statior

MATERIAL & METHODS

Boxcores

To obtain deep-sea bottom samples a large cylindrical boxcorer (NIOZ design) was used (Fig. 2). This apparatus recovered almost undisturbed samples with a surface area of approximately 0.20 m^2 and a height of 30 to 50 cm together with the near-bottom water. The boxcores were processed in the following way:

Benthic community respiration

Six Winkler-bottles were filled with bottom water, 3 to measure blanco respiration and 3 to determine the initial oxygen-concentration. Bottom water was removed from the boxcores to leave only a 10 cm layer above the sediment surface. Next, 4 sub-cores (78.5 cm^2 surface area) were taken including both the sediment and the remaining bottom water. At the upper side, they were closed under water by means of a conic coverplate with a rubber plug and an electric stirrer (Figs. 3, 4a, b). At the lower side a large rubber stopper was inserted. Then the cores were carefully extracted and placed for at least 24 hours in an incubator at *in-situ* temperature. The stirrer prevented an oxygen gradation inside the core, rotating slowly to avoid disturbance of the surface. After the period of incubation 2 Winkler bottles were taken from each core. Oxygen concentration was measured with Winkler-titration (Veth & Van der Werff, 1989). The colour break was first registered by a spectrophotometer. However, the high turbidity of the bottom water in combination with the high lime content, which caused an evasion of CO_2 after addition of sulphuric acid, made it impossible to register a colour break with this method. To solve this problem we changed to a visual registration of the colour break.

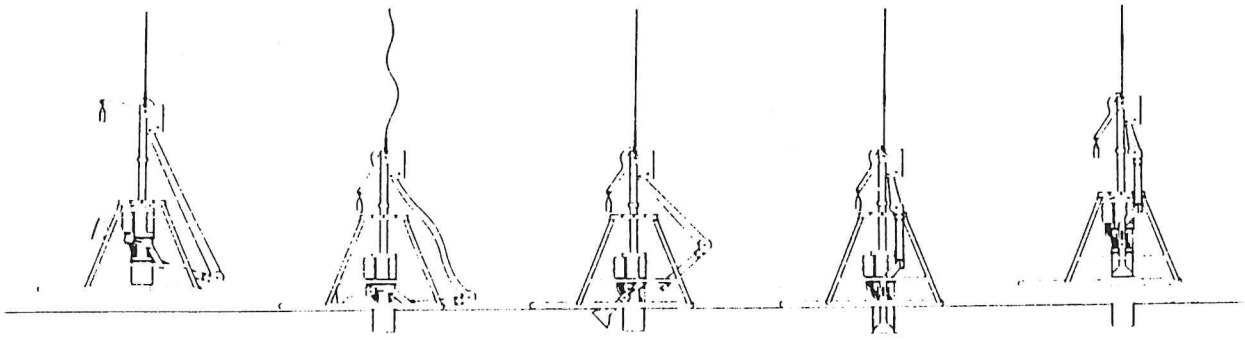


Fig. 2: Recovery of a bottom sample with a boxcorer

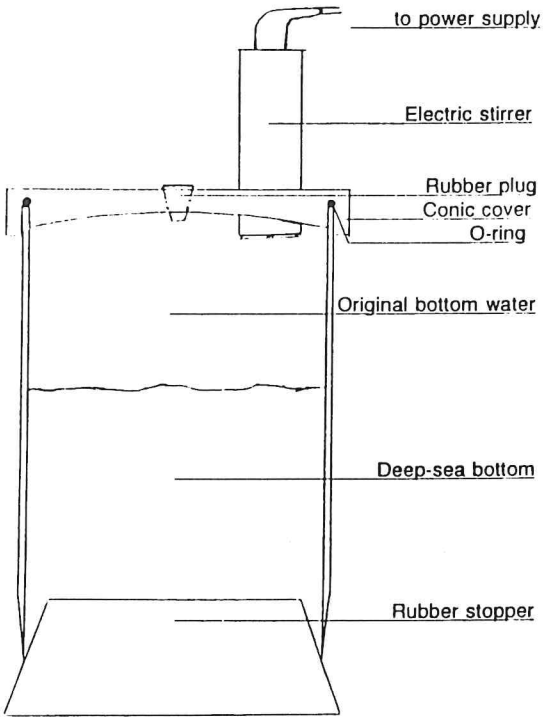
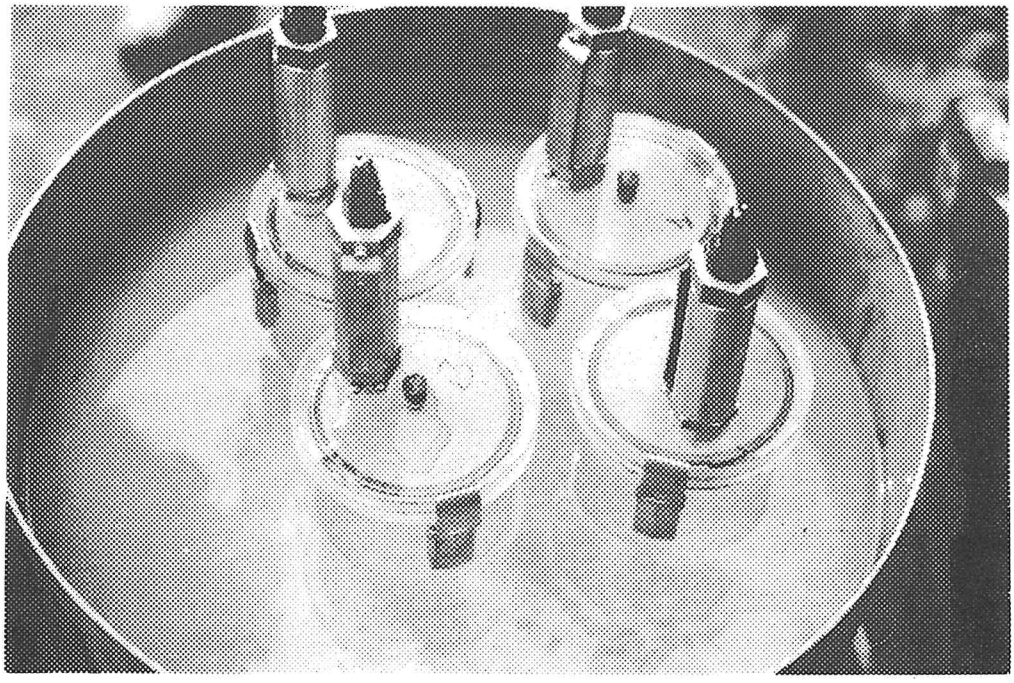


Fig. 3: oxygen incubation subcore



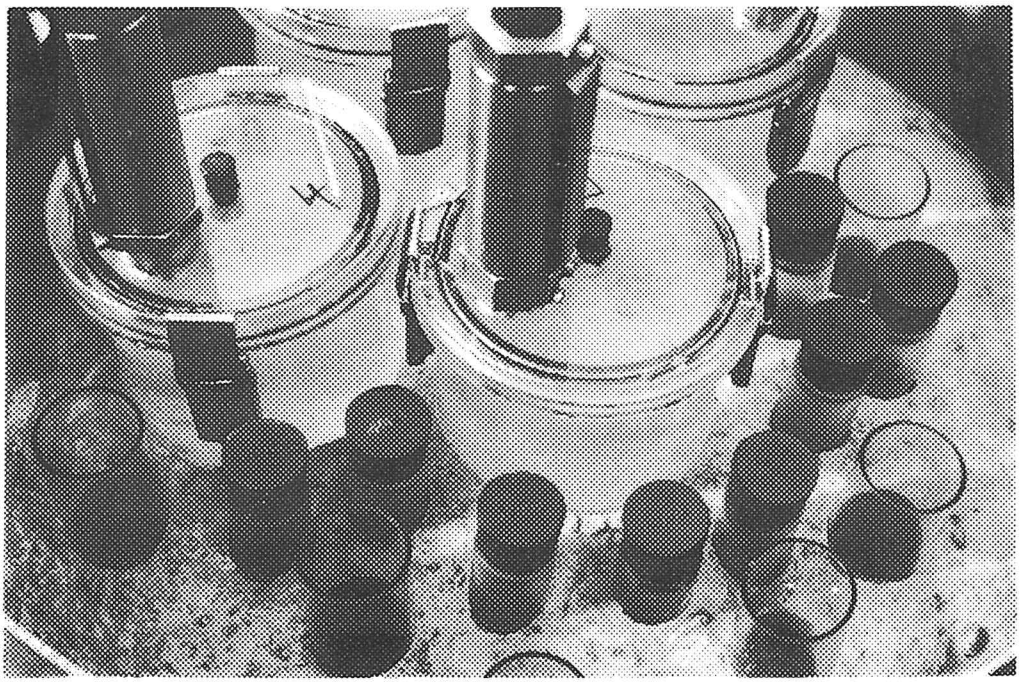


Fig. 4a: Boxcorer with O_2-incubation sub-cores

Fig. 4b: Boxcorer with all the sub-cores inserted

Photo's: Tom Tahe

Meiofauna

After the completion of the respiration measurements, additional sub-cores (5.31 cm^2 surface area) with a length of about 10 cm were taken from the oxygen sub-cores to study the meiofauna. From earlier research it appeared that the density of meiofauna below the top 10 centimetres of sediment is neglectable (Rutgers van der Loeff & Lavaleye, 1986). The meiofaunal cores were preserved in 6% buffered formalin. No investigation was made of the horizontal distribution of the meiofauna, because it is not known what influence oxygen incubation experiments have on migration of the animals.

In the laboratory the samples were stained with rose bengal which colours proteins red. Then the samples were split into four fractions using the elutriation method (Rutgers van der Loeff & Lavaleye, 1986). The first fraction was obtained by a tapwater current of 1 l/min.. A second fraction was obtained by a current of 2 l/min.. The fractions were sieved over a 50 mm screensize. The sediment residue was sieved over 200 mm and 50 mm sieves to obtain the third and fourth fraction.

The fractions were sorted under a stereomicroscope. The meiofauna was counted, picked out and mounted on a slide in a diluted glycerine-solution. The length and maximum diameter of all the Nematoda were determined by means of a Projectina stereomicroscope. The Nematoda biomass was calculated indirectly by the method of Andrassy (1956).

The volumes of Copepoda and nauplii were calculated by dividing the animals in spatial geometric shapes such as cones, cylinders etc. (Rutgers van der Loeff & Lavaleye, 1986). No attempt has been made to measure the biomass of the other less important meiofaunal taxa, since their contribution to the meiofaunal biomass is neglectable (Rutgers van der Loeff & Lavaleye, 1986).

Flagellates & bacteria

From each boxcore 10 replicate samples were cored with perspex tubes (5.31 cm^2 surface area) to a depth of about 10 cm. Consequently, the cores were sub-sampled and slices were cut off at sediment depths of 0 to 3 mm, 30 to 33 mm and 60 to 63 mm with a 3 mm thick mould. In the case of flagellate sampling of the 60 to 63 mm layer was omitted at station BS1 and BM4 because of a shortage of time.

For counting flagellates the sediment slices were fixated with glutaraldehyde (total volume 24 ml). One ml of proflavin was added to stain the protists (flagellates) (Haas, 1982). After gently shaking, the suspension was allowed to settle until the solution became just transparent (after about 30 minutes). Then 5 ml sample was taken from the centre of the column. After addition of another 0.5 ml of proflavin the sample was filtered at low vacuum over a 0.2 mm Nucleopore polycarbonate filter stained with Sudan black. The filters were stored frozen at -20°C in preparation for counting. The cells

were counted in the size classes < 2 mm, 2 to 5 mm, 5 to 10 mm and 10 to 20 mm using epifluorescence microscopy equipped with a HBO 50 Watt bulb and filterset BP 450/490, FT 510 and LP 520 and an eyepiece micrometer as a reference. In all cases 120 fields were observed (magnification x 1260). A more detailed description of this method is given in Bak & Nieuwland (1989).

In the case of bacteria the slices were put in 20 ml glass vials and fixated with 1.7 ml of old seawater containing 4% formaline. The samples were stored in a refrigerator until further processing. Each carefully shaken 1 ml sample was incubated for 15-20 min. with 0.5 ml pyrophosphate solution. The samples were then sonified for 3x10 sec with intervals of 10 sec at 6 micron on a Soniprep MSE. 0.5 ml was pipetted into a 3 ml medium and mixed carefully. Depending on the amount of bacteria present in the sample, 0.05 to 0.10 ml of this mixture was pipetted in a 2 ml medium and mixed. This solution was stained for 2 min. with 0.2 ml of acridine orange and filtered at low vacuum over a 0.2 mm Nucleopore polycarbonate filter stained with Irganan black. The filter was put on a microscope slice with cover to count about 200 bacteria in at least 20 microscopic fields using the same epifluorescence technique as mentioned before. For an estimation of the biomass the length and width of 100 individual bacteria were measured and arranged into corresponding size classes.

used solutions:

medium : old seawater with 2% formalehyde
0.1% acridine orange : 20 mg acridine orange in 20 ml H_2O with 2.5% NaCl and 2% formaldehyde
1.3% pyrophosphate : 65 ml H_2O+ 3.7 ml 37% formaldehyde + 1.62g NaCl + 0.8697 g $Na_4P_2O_7.10H_2O$
0.05% Irganan black : 100 mg Irganan black in 2% acetic acid
0.006% Sudan black : 0.006% in 50% ethanol
0.033% proflavin : 0.033% in H_2O
1% glutaraldehyde : 1% in filtered old seawater

All solutions were filtered 3 times over a 0.2 mm Nucleopore polycarbonate filter and finally, just before use, over a 0.2 mm FP 030/3 Red rim filter and with the exception of Irganan black, stored refrigerated. New acridine orange was made every week.

Macrofauna and large meiofauna

Consequent to the preparation of sub-cores for respiration, meiofauna and micro-organisms analyses (Fig. 4b), the rest of the bottomwater was removed and sieved through a 0.5 mm sieve to collect fauna. The upper 5 centimetre layer of sediment was then skimmed off as best as possible while the perspex sub-cores were still in place. Next, the sub-cores were removed. The upper 5 centimetre layer and the rest of the boxcore were sieved seperately onboard through a 1 mm sieve to collect macrofauna. For the study of the large meiofauna a 0.5 mm sieve was used in addition. To prevent contamination with plankton the seawater deckwash was covered with a 200 mm sieve. The collected fauna was stored in 6% buffered formalin.

The macrofauna and the large meiofauna were identified to the level of orders, classes or phyla. When it was not possible anymore to determine an animal (for example when an animal is broken), it was classified as "unidentified". The biomass was measured in a similar way to that described for the meiofaunal Copepoda and nauplii (Rutgers van der Loeff & Lavaleye, 1986).

Conversion factors

The following conversion factors were used to calculate biomasses for the different organism groups (WW=wet weight, DW=dry weight, C=carbon weight):

macrofauna and meiofauna (meiofaunal Nematoda excluded):

TABLE 2: Conversion factors for DW calculations of the different fauna taxa (Rowe, 1983). DW=volume x factor; C=DW x 0.4 (Witte & Zijlstra, 1984).

taxa	factor
Hydrozoa	0.245
Nematoda (macrofaunal)	0.131
Polychaeta	0.131
Oligochaeta	0.131
Sipunculida	0.137
Echiurida	0.137
Bivalvia	0.137
Copepoda	0.132
Ostracoda	0.132
Tanaidacea	0.103
Isopoda	0.132
Ophiurida	0.226
Echinoidea	0.200
Holothuroidea	0.216
Tunicata	0.250
Unidentified	0.100

meiofaunal Nematoda:

$WW=a^2b \times 0.665$
$WW=a^2b \times 0.436$ (Desmoscolecidae)
a=biggest diameter; b=length (Andrassy, 1956)
DW=WW x 0.25; C=DW x 0.4 (Witte & Zijlstra, 1984)

Flagellates and bacteria:

flagellates: 200×10^{-12} mg C/μm^3 (Fenchel, 1982; Børsheim & Bratbak, 1987)

bacteria : 2.2×10^{-10} mg C/μm^3 (Bratbak & Dundas, 1984).

Statistics:

Sokal & Rohlf (1981) was used for the statistical analysis.

RESULTS & DISCUSSION

Macrofauna

The density and biomass of the different metazoan macrofaunal groups are shown in Tables 3 and 4. Large Protozoa, mainly branching and agglutinating Foraminifera, have been excluded for practical reasons (see Foraminifera).

Density is highest in BM4 (144 ind./m^2) and lowest in BS2 (66 ind./m^2) (Table 3). The distribution of the biomass shows a similar pattern. The highest biomass is found in BM4 (502 mg DW/m^2) and the lowest in BS2 (16 mg DW/m^2) (Table 4). Although there seems to be a positive correlation between biomass and density, no statistical reliability could be found.

Considering the faunal composition of the stations, Polychaeta, Bivalvia and Tunicata dominate the biomass at BS1 with 32.3%, 27.4% and 31.0% respectively (Table 4). However, measuring the biomass for hard-shelled animals such as Bivalvia by estimating the animal-filled space in the shell is very difficult and may not be reliable. The share of Bivalvia to the density of BS1 is high at 50%. In BS2 Bivalvia are absent and in BM4 they are of minor importance (Tables 3 and 4). In BS2 half of the biomass is Sipunculida although they are not especially dominant in density (20%). The macrofaunal biomass of BM4 is totally dominated by one relatively big Holothuroidea which accounts for 97% of the biomass (Table 4).

However, these results are difficult to interpret. A single animal can cause big differences because densities are very low. For instance if the collected specimen of Holothuroidea is considered as a `lucky strike' and excluded from the biomass calculation the figures changes completely. The total macrofaunal biomass in BM4 is now 9.1 mg DW/m^2 (as opposed to 502 mg DW/m^2) and Polychaeta contribute 41% to this biomass (as opposed to 1%). The small-scale distribution of macrofauna is very patchy (Lavaleye, 1989) and it is therefore difficult to assess the density and biomass of macrofauna from one boxcore per station.

The amount of different macrofaunal groups is broadly the same for each of the three stations (8, 7 and 8 distinguished groups in BS1, BS2 and BM4, respectively). Unidentified animals were placed in one group and so the variance of BS2 and BM4 may be higher than is given here.

TABLE 3: Density of macrofauna (individuals) for the upper 5 cm (<5cm) and the rest of the sediment (>5cm) and the percentage composition of the different taxa at BS1, BS2 and BM4.

station	BS1			BS2			BM4		
taxa	<5cm	>5cm	%	<5cm	>5cm	%	<5cm	>5cm	%
Hydrozoa	1		7.14	1		10.0			
Nematoda							4	1	22.7
Polychaeta		1	7.14				1	1	9.09
Oligochaeta				1		10.0			
Sipunculida	1		7.14		2	20.0		1	4.55
Echiurida	1		7.14						
Bivalvia	5	2	50				1	1	9.09
Copepoda				1		10.0			
Ostracoda									
Tanaidacea								1	4.55
Isopoda					1	10.0	4		18.2
Ophiurida					1	10.0			
Echinoidea	1		7.14						
Holothuroidea	1		7.14				1		4.55
Tunicata	1		7.14						
Unidentified				2	1	30.0	5	1	27.3
Total/box	11	3		5	5		16	6	
Total/m^2	72	20		33	33		105	39	
Grand total/m^2	92			66			144		

TABLE 4: Biomass of macrofauna (mg DW/m^2) for the upper 5 cm (<5cm) and the rest of the sediment (>5cm) and the percentage composition of the different taxa at BS1, BS2 and BM4.

station	BS1			BS2			BM4		
taxa	<5cm	>5cm	%	<5cm	>5cm	%	<5cm	>5cm	%
Hydrozoa	0.022		0.15						
Nematoda				0.025		1.02	0.024	0.001	0.03
Polychaeta		4.61	32.1				0.53	0.45	1.27
Oligochaeta				0.076		3.12			
Sipunculida	0.079		0.55		1.25	51.2		0.36	0.47
Echiurida	0.50		3.47						
Bivalvia	2.39	1.55	27.4				0.01	0.04	0.07
Copepoda				0.21		8.72			
Ostracoda									
Tanaidacea								0.049	0.06
Isopoda					0.39	16.0	0.75		0.99
Ophiurida					0.029	1.18			
Echinoidea	0.41		2.86						
Holothuroidea	0.40		2.79				74.4		96.9
Tunicata	4.41		30.7						
Unidentified				0.16	0.30	18.7	0.076	0.069	0.19
Total/box	8.21	6.16		0.48	1.97		75.8	0.98	
Total/m^2	53.7	40.3		3.12	12.9		496	6.38	
Grand total/m^2	94.0			16.0			502		

A division is made between the upper 5 centimetres and the rest of the boxcore to study the vertical distribution of the macrofauna. Densities in the upper 5 centimetres are 78%, 50% and 72% of the total macrofauna density at BS1, BS2 and BM4, respectively. For biomass these figures are 57%, 20% and 59% of the total macrofaunal biomass, respectively. As expected, most of the density and biomass is located in the upper layer of the sediment. These results are comparable with those of Rutgers van der Loeff & Lavaleye (1989).

The biomass and density of the macrofauna differ a great deal between stations. However, the stations are relatively close together and the deep-sea is often considered as homogenous. The very low densities of the animals found may be a reason for this spread. Another explanation may be the small scale patchiness of fauna (Lavaleye, 1989). Differences between areas depends completely on the scale of sampling and can only be concluded if they are very great, otherwise they might be due to small scale patchiness.

It is difficult to compare the figures for macrofaunal density and biomass with other deep-sea macrofaunal studies because many other authors have used different methods to the method that was used in this study. However, Rutgers van der Loeff & Lavaleye (1986) used the same method and found a comparable mean density for macrofauna (124 ind./m^2) and biomass (79.9 mg DW/m^2). Lavaleye (1989) also gives a comparable mean density and biomass of 115 ind/m^2 and 161 mg DW/m^2, respectively, using a 1 mm sieve for samples from a comparable depth in the North East Atlantic Ocean.

Large meiofauna

The density of the large meiofauna (> 0.5 mm and < 1 mm) is shown in Table 5. Station BM4 accounts for the highest density (660 ind./m^2) and BS1 for the lowest (59 ind./m^2). Any relation between depth in the sediment and density is not clear.

Large meiofauna biomass is shown in Table 6. The distribution of biomass over the stations is similar to the density distribution over the stations. The highest biomass is found at BM4 (38.6 mg/m^2) and the lowest biomass at BS1 (1 mg/m^2).

According to the literature foraminifera are most abundant in the large meiofauna fraction (Gooday, 1986a, b; Pfannkuche & Thiel, 1988; Lavaleye, 1989). However, foraminifera were excluded for practical reasons (see Foraminifera). Considering this, these results show that Bivalvia form 56% of the density at BS1 (Table 5). For the biomass at BS1 this percentage is even higher (Table 6).

At BS2 unidentified animals account for 54% of the density. Copepoda, Nematoda and Bivalvia each contribute each 15% to the density at BS2. Unidentified animals account for almost 90% of the biomass at BS2.

At BM4 Nematoda, Polychaeta, Tanaidacea, Isopoda and unidentified animals have a density of more than 10% of the total large meiofauna density. The biomass at BM4 is defined by Isopoda (58%) and Polychaeta (28%).

A division is made between the upper 5 centimetres and the rest of the boxcore to study the vertical distribution of the large meiofauna. Densities in the upper 5 centimetres are 56%, 39% and 17% of the total large meiofauna density at BS1, BS2 and BM4, respectively. For biomass these figures are 75%, 2% and 11% of the total large meiofaunal biomass, respectively. In contrast with macrofauna, a concentration of large meiofaunal animals in the upper part of the sediment is not found. Rutgers van der Loeff & Lavaleye (1986) found that macrofauna biomass is mainly located 3-10 cm below the surface of the sediment and that the smaller the animals, the more they are located in the upper part of the sediment. In their study, the highest biomass of large meiofauna (between 2 and 5 centimetres) is a result intermediate between the optimum depth for meiofauna biomass (the upper centimetre) and the macrofauna biomass (below 3 centimetres).The vertical distribution of the large meiofauna compared with the macrofauna in this study does not show the same result. This is probable caused by the low density of animals together with only one core per station

At BS1 the biomass of large meiofauna is 1% of the macrofauna biomass, at BS2 and BM4 these figures are 45% and 8%, respectively. Pfannkuche & Thiel (1988) give an average figure of 25% for the macrofauna/large meiofauna biomass relation in the N. E. Atlantic. However, in their study Foraminifera are included.

TABLE 5: Density of large meiofauna (individuals) for the upper 5 cm (<5cm) and the rest of the sediment (>5cm) and the percentage composition of the different taxa at BS1, BS2 and BM4.

station	BS1			BS2			BM4		
taxa	<5cm	>5cm	%	<5cm	>5cm	%	<5cm	>5cm	%
Hydrozoa							1		0.99
Nematoda		1	11.1	2		15.4		36	35.6
Polychaeta	1		11.1				3	12	14.9
Oligochaeta									
Sipunculida									
Echiurida									
Bivalvia	4	1	55.6	2		15.4	1		0.99
Copepoda					2	15.4			
Ostracoda							1		0.99
Tanaidacea								12	11.9
Isopoda		1	11.1				1	12	12.9
Ophiurida									
Echinoidea									
Holothuroidea							2		1.98
Tunicata									
Unidentified		1	11.1	1	6	53.8	8	12	19.8
Total/box	5	4		5	8		17	84	
Total/m²	33	26		33	52		111	549	
Grand total/m²	59			85			660		

TABLE 6: Biomass of large meiofauna (mg DW/m²) for the upper 5 cm (<5cm) and the rest of the sediment (>5cm) and the percentage composition of the different taxa at BS1, BS2 and BM4.

station	BS1			BS2			BM4		
taxa	<5cm	>5cm	%	<5cm	>5cm	%	<5cm	>5cm	%
Hydrozoa							0.034		0.59
Nematoda		0.017	11.4	0.006		0.54	0.024	0.40	7.11
Polychaeta	0.012		7.94				0.29	1.22	25.5
Oligochaeta									
Sipunculida									
Echiurida									
Bivalvia	0.10	0.003	69.0	0.016		1.44	0.029		0.50
Copepoda					0.10	9.41			
Ostracoda							0.006		0.11
Tanaidacea								0.15	2.47
Isopoda		0.009	5.83				0.015	3.38	57.5
Ophiurida									
Echinoidea									
Holothuroidea							0.052		0.88
Tunicata									
Unidentified		0.009	5.80	0.002	0.97	88.6	0.22	0.092	5.31
Total/box	0.11	0.038		0.023	1.07		0.67	5.23	
Total/m²	0.74	0.25		0.15	7.00		4.38	34.2	
Grand total/m²	1.00			7.15			38.6		

Rutgers van der Loeff & Lavaleye (1986) found a comparably mean large meiofauna density (excluding the foraminifera) of 366 ind./m^2. For the biomass they found on average 14.6 mg/m^2. In this study these values are 268 ind./m^2 and 15.6 mg/m^2, respectively.

Meiofauna

The meiofauna smaller than 0.5 mm consist mainly of Nematoda, Foraminifera, nauplii and Copepoda. The major other taxonomical groups and the unidentified fauna are classified as various.

In agreement with most earlier meiofauna studies in the deep-sea Nematoda show the highest density (Fig. 5: 83-90% of the total meiofauna). The density of the Nematoda in the uppermost 10 centimetres ranges from 154,000 to 254,000 individuals per m^2 (Fig. 6). These figures are of the same magnitude as found in other studies from the same depth in the Atlantic but are rather low compared with the results of the DORA and NAZORG expeditions (Table 7).

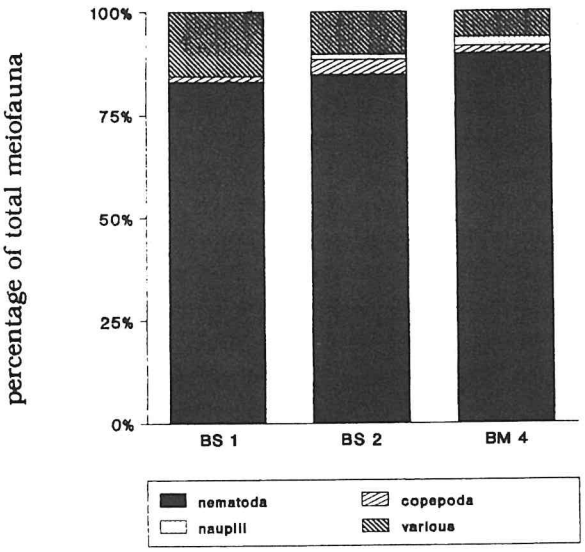


Fig. 5: Percentage of meiofaunal classes found at BS1, BS2 and BM4

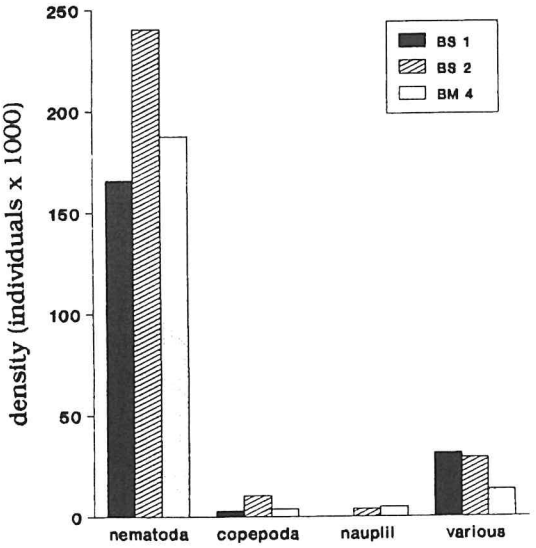


Fig. 6: Mean density of meiofaunal class individual x 1000 at BS1, BS2 and BM4.

TABLE 7: Nematoda density and biomass. Comparison of different studies in the North East Atlantic Ocean.

	depth (m)	area	density[1]	biomass[2]
Thiel, 1972	5272-5340	Iberian deep-sea	156 -278	150
Dinet, 1973	4100-5170	South Atlantic	294 -504	
Rachor, 1975	4878-5510	Iberian deep-sea	15.5- 76	5.9
Dinet & Vivier, 1977	4097-7425	Bay of Biskay	86 -383[3]	
DORA expedition, 1982	4000-4800	Iberian deep-sea	101 -989	16.4
DORA expedition, 1984	4000-4800	Iberian deep-sea	315 -720	11.1
Pfannkuche, 1985	4167-4850	Porcupine Seabight	272 -462	
NAZORG expedition, 1988	4000-4800	Iberian deep-sea		15.7
JGOFS II expedition, 1989	4135-5038	Canarian end Iberian deep-sea	154 -254	12.2

1 Density x 1000/m^2
2 Biomass in mg DW/m^2
3 Leaving out two probably biased samples with densities of 5 to 12 .10^3/m^2

The method of processing the samples affects the output. Many researchers use their own method of processing and it appears that this may cause considerable differences in numbers between comparable regions. To our opinion, the elutriation method concentrates the meiofauna better and works more gently than the normal sieving method used by Thiel (1972) and Rachor (1975). Rachor decanted the sediment samples before fixation. Fixation hardens the animals with the consequence that fewer animals are broken up and/or pressed through the sieve. The size limits of the meiofauna kept on by different authors is also of importance. Another difference is that most studies only deal with the upper centimetres of the sediment. If only the upper 6 centimetres are studied, which is common practise, densities of Nematoda, Copepoda and nauplii may be underestimated by 10%, 10% and 15%, respectively (Rutgers van der Loeff & Lavaleye, 1986). A uniform method is required to standardise comparisons between different studies.

The Nematoda biomass varies from 9.2 mg DW/m^2 to 16.7 mg DW/m^2 (Fig. 7). These figures are low compared with the DORA and NAZORG expeditions, but data still overlap (Table 7). Differences must be ascribed to the lower density of the JGOFS samples, although the average individual Nematoda biomass is higher (Table 8). Thiel (1972) calculated the Nematoda biomass assuming an average individual Nematoda biomass derived from much shallower water (290-2500 m). This likely accounts for his higher values (Thiel, 1983). Comparing stations BS1, BS2 and BM4 there is no correlation between biomass and density (Figs. 6, 7). The average individual Nematoda biomass of station BS1 is double those of stations BS2 and BM4 (Table 8). Using an average individual Nematoda biomass to calculate the total Nematoda biomass for different deep-sea areas may lead to considerable errors. This is consistent with the data of Rutgers van der Loeff & Lavaleye (1986).

The distribution of the Nematoda bodylength shows that at station BS1 the Nematoda are relatively large compared to the Nematoda at stations BS2 and BM4 (Figs. 8, 9, 10). So, even though the number of individuals is small the biomass may still be high. This is consistent with the previous mentioned difference in average individual Nematoda biomass. The distribution of the Nematoda bodylengths at stations BS2 and BM4 is similar, as are their average individual Nematoda biomasses. Nematoda density and biomass at BS2 and BM4 show similar patterns (Figs. 6, 7). It is notable that there is a decline of individual Nematoda length and biomass from north to south (Fig. 7). At the same time there is a decrease in the size of empty pelagic foraminifera shells which constitute the sediment. It is reasonable to assume that the constitution of the sediment can affect the fauna. The larger interstitial spaces in the sediment of BS1 could be an explanation for the larger Nematoda.

The density of Copepoda and nauplii varies from 1900 to 19000 individuals per m^2. Copepoda and nauplii constitute 1.4% to 5% of the total meiofauna density (Fig. 5) which is comparable to other studies in the North East Atlantic (Table 9). The biomass of Copepoda and nauplii varies from 0.32 to 6.11 mg DW/m^2. Average values for BS1, BS2 and BM4 are 0.71 mg DW/m^2, 2.65 mg DW/m^2 and 3.37 mg DW/m^2 respectively. Compared with Nematoda these figures are rather variable, caused by the low density and high diversity in body size of Copepoda and nauplii (Rutgers van der Loeff & Lavaleye,1986). The biomass of Copepoda and nauplii in this study lies between the values of Thiel (1972)/Rachor (1975) and Rutgers van der Loeff & Lavaleye (1986) (Table 9).

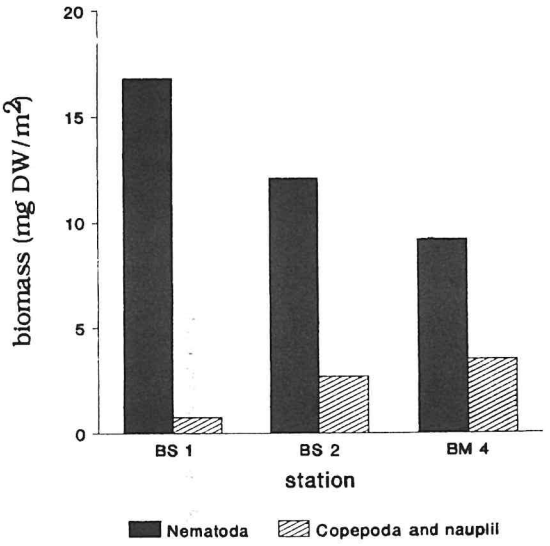


Fig. 7: Biomass of nematoda and Copepoda in mg DW/m2 at BS1, BS2 and BM4.

TABLE 8: Mean individual nematoda biomass at BS1, BS2 and BM4.

	MINB (ugDW)	SD
BS1	0.0974	0.0375
BS2	0.0483	0.0020
BM4	0.0496	0.0146

MINB = mean individual biomass of Nematod
SD = standard deviation

TABLE 9: Copepoda density and biomass. Comparison of different studies in the North East Atlantic Ocean.

	depth (m)	area	density[1]	biomass[2]
Thiel, 1972	5272-5340	Iberian deep-sea	4.7	1.9
Dinet, 1973	4100-5170	South Atlantic	14.7	
Rachor, 1975	4878-5510	Iberian deep-sea	11.6	1.5
Dinet & Vivier, 1977	4097-7425	Bay of Biskay	20.5	
DORA expedition, 1982	4000-4800	Iberian deep-sea	18.4	10.0
DORA expedition, 1984	4000-4800	Iberian deep-sea	11.1	8.6
Pfannkuche, 1985	4167-4850	Porcupine Seabight	45	
JGOFS II expedition, 1989	4135-5038	Canarian end Iberian deep-sea	8.5	2.32

1 Density x 1000/m^2
2 Biomass in mg DW/m^2

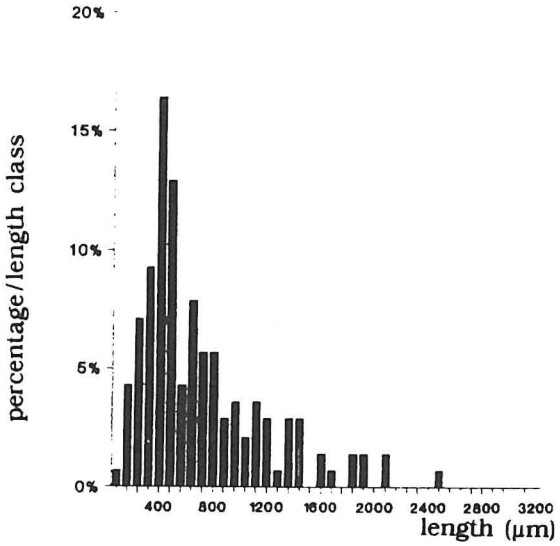


Fig. 8:Nematoda body length distribution at BS1 in length class to the percentage of the total number of Nematoda at BS1

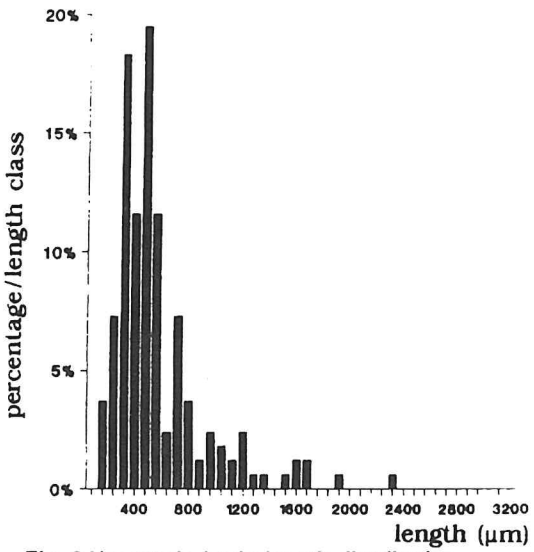


Fig. 9:Nematoda body length distribution at BS2 in length class to the percentage of the total number of Nematoda at BS2

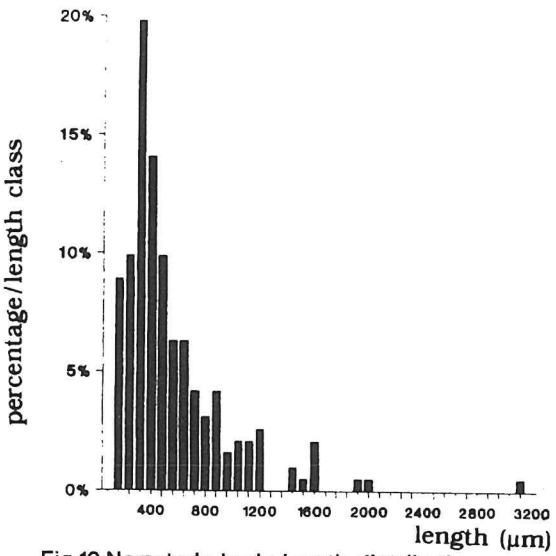


Fig.10:Nematoda body length distribution at BM4 in length class to the percentage of the total number of Nematoda at BM4

Foraminifera

Benthic foraminifera can be divided into hard-shelled and soft-shelled forms, the latter with or without agglutinated particles. Recent research has shown that benthic foraminifera have a much higher density in the deep-sea than was previously thought (Schafer & Cole, 1982; Gooday, 1986a, b; Pfannkuche & Thiel, 1988). The high numbers of Gooday (1986a, b) are believed to occur because he analysed the seldom investigated 45-62 µm fraction, the multiple corer was used (which is able to take almost undisturbed samples) and he `picked' the foraminifera in the sediment residue (Gooday, 1986b). Lavaleye (1989) also found high numbers of foraminifera when paying special attention to the sediment residue which contained predominantly empty pelagic foraminifera shells. In this study the meiofaunal foraminifera density equals the Nematoda density and sometimes it is higher. Macrofaunal foraminifera outnumber all metazoan macrofaunal groups (Lavaleye, 1989).

The benthic foraminifera densities of the JGOFS-samples were hard to determine because of the `treelike' agglutinating forams, which disaggregate during collection and subsequent processing. Another problem is whether the life-tubes contain living animals or are dead forms with an organic layer in the tube which causes the red colour by rosebengal. A similar problem arises with the hard-shelled foraminifera. They have to be opened to discover whether they are `alive' or occupied by other benthic organisms. This was performed in only some cases and thus excludes a reliable biomass determination.

Solving these practical problems would take up to much time in this graduation subject. Nevertheless, it is evident that the density and biomass of foraminifera in the macro- and meiofauna should not be underestimated and that they contribute substantially to the benthic community respiration.

Bacteria

The results of the bacteria countings are presented in figures 11 and 12. There is in each station a significant decrease in abundance or biomass with depth in the sediment. The same results were found by Meyer-Reil (1984), Deming & Colwell (1985) and Alongi (1986). In the upper 3 mm of the sediment there is a significant increase in amount of bacteria between BS1, BS2 and BM4 (all tested with Kruskal-Wallis, $p<0.05$). There is in every case a correlation between biomass and density as tested with the product-moment computation. This is probably caused by a homogeneous size distribution of bacteria in contrast to the lack of correlation of density and biomass in macro- and meiofauna classes.

There is no correlation between biomass/abundance of bacteria and water depth. Comparing these results with earlier research, it appears that this correlation with water depth in the upper 3 mm of the sediment is hard to find. Nieuwland (unpublished data) did not find a correlation with depth on the Mauretania expedition in 1988 (10-1000 m). The same result was found on the Antarctica expedition (250-2000 m) in January and February 1989. In contrast, Alongi (1986) did find that bacterial number decreased significantly with water depth.

Average annual bacteria abundance in the Dutch Wadden Sea is of the same order as the amount of bacteria found in the upper 3 mm at BM4 and BS2 and only 2 times the amount at BS1. In contrast, the biomass at BS1, BS2 and BM4 is the same as, or up to 2 times higher than the average biomass of the Wadden Sea (Van Duyl & Kop, 1990) using the same conversion factors. Depending on the season, abundance in the Wadden Sea can be 2 to 3 times higher than at BS1, BS2 and BM4 (Van Duyl & Kop, 1990; Nieuwland, unpublished data). Lochte (1988) found that bacterial number in sediment changes significantly between 4.10^9 and 45.10^9 cells/ml., depending on the season. Data of Lochte (1988) of september 1985 compared with the data in this study of september 1989 show that abundance of Lochte is 4 to 10 times higher. This difference may occur because Lochte took her samples at 47°N, while the JGOFS II samples were taken between 33°N and 39°N. The north is considered to be richer. Surprisingly, data of Lochte (1988) also outnumber data of Van Duyl & Kop (1990) of the Dutch Wadden Sea, although the same method was used.

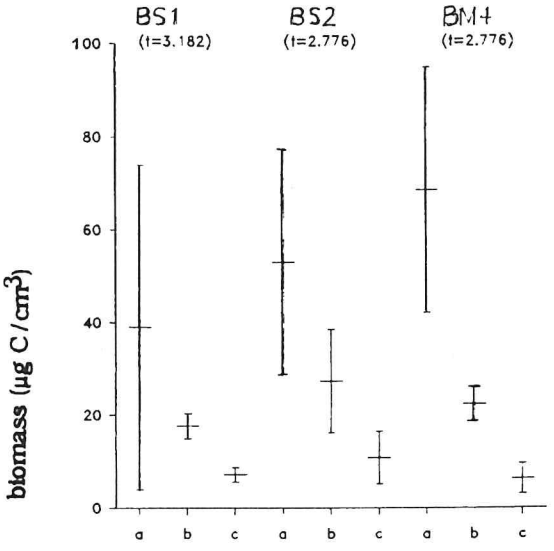


Fig. 11: Biomass of bacteria at BS1, BS2 and BM4 in ug C/cc.
a=0-3 mm, b=30-33 mm and c=60-63 mm.

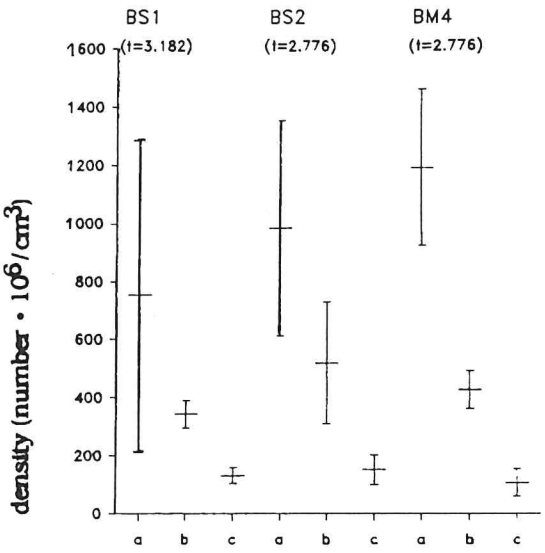


Fig. 12: Density of bacteria at BS1, BS2 and BM4 in number/cc x 1,000,000
a=0-3 mm, b=30-33 mm and c=60-63 mm

Error bars for figs. 11 and 12 are SE x t (t=3.182 for n=4 and t=2.776 for n=5).

TABLE 10: Comparison of the biomass (mg C/m²) of the discriminated organism groups in the Wadden Sea and North East Atlantic JGOFS sites

	macro fauna	meio fauna	protists	bacteria
Wadden Sea	10[1]	0.45[1]	0.091–0.025[2]	10-15[3]
deep-sea JGOFS sites	0.081	0.012	0.0024	2

1=Witte & Zijlstra (1984)
2=Bak & Nieuwland (1989)
3=Van Duyl & Kop (1990)

Assuming an exponential decrease in bacteria density with depth in the sediment, integration shows that biomass values range from 1.39 gC/m^2 to 2.02 gC/m^2. In the Wadden Sea the values are 5 to 8 times higher (Bak & Nieuwland, 1989), probably caused by a greater substrate availability. Comparing the abundance of bacteria in the Wadden Sea and deep-sea with other fauna in the Wadden Sea and deep-sea it appears that the other fauna decreases far more dramatically with depth than bacteria (Table 10). Regarding total fauna, bacteria account for 90.0% to 99.0% of the biomass (foraminifera not included) (Table 11). Hence in deep-sea sediments bacteria are of major importance in the benthic community.

Meyer-Reil (1984) found that salinity, ammonia, nitrate, dissolved monosaccharides, organic matter and chlorophyll-a may be regarded as key parameters influencing bacteria biomass and activity in the sediment. Bacteria numbers are positively correlated with organic matter content, which is dependent to water depth. This may cause the significant difference in abundance of the upper 3 mm between the stations. Salinity, ammonia and nitrate are quite homogeneously dispersed (Bakker *et al.*, 1989). Moriarty (1989) found that especially deeper in the sediment, were animals are absent, bacterial productivity and biomass is controlled by the availability of organic matter. Unfortunately no data on organic matter were available for this study. The fact that bacterial biomass is relatively high while organic matter content is considered to be low, is an argument for the presence of bacteria in inactive forms. Lochte (1988) and Lochte & Turley (1988) found that sedimented phytodetritus causes a higher growth of micro-organisms. The input of phytodetritus depends on the season indicating that a quantitative comparison within and between sites can only be made for studies carried out in the same season.

Another explanation for the increase in number of bacteria in the upper 3 mm at BS1 to BM4 can be found in a finer grain size at BS2 and BM4. Meyer-Reil (1984) found that bacterial number is negatively correlated with grain size, which is obviously caused by the greater surface area available in fine than coarse grained sediment. The foraminifera shells found at BS1 were larger than at BS2 and BM4 where the foraminifera were the smallest. The decline in abundance and biomass with depth in the sediment could also be due to decline in organic matter. Compared with other benthic ecosystems, very little organic matter reaches the deeper parts of the deep-sea sediment (Gilbert & Deming, 1985; Alongi, 1986). Deming & Colwell (1985) found a decrease in total bacteria with depth in the sediment core as did utilisation of glutamic acid. This is in contrast to the Wadden Sea, where the sediment is heavily bioturbated. Here, no changes in abundance and biomass from 0-63 mm sub-bottom can be found. This is probably caused by organic matter reaching these depths.

Flagellates

Figure 16 shows some protists found in the JGOFS samples.

The results of flagellate countings are shown in figures 14 and 15. Abundance and biomass do not show the same significant decline with depth in the sediment as bacteria. A significant change between the stations per sediment depth could not be found (tested with Kruskal-Wallis, $p>0.05$). No correlation could be found between biomass and density as tested with the product-moment computation. This indicates that there is a great spread in flagellate sizes within and between the stations. Since flagellates graze on bacteria (Galvao *et al.*, 1989) the correlation between these two was tested but could not be defined.

Especially the low density of flagellates in the microscope slices and the sometimes low quality of these slices make it very difficult to say anything significant about biomass, dispersion and correlations. Next time, a minimum amount of flagellates per slice has to be examined and special attention has to be paid to obtain good quality microscope slices.

Figures to compare with are those of Bak and Nieuwland (1989) from the Dutch Wadden Sea. Using the same method they find 50 to 300.10^3 protists/cm^3 in the upper 3 mm sub-bottom. This is much higher than the 3 to 6.10^3 flagellates/cm^3 in the upper 3 mm sub-bottom at the JGOFS-sites. Biomasses in the Wadden Sea range between 1.2 and $8.5.10^{-6}$ g C/cm^3, whereas the biomasses at BS1, BS2 and BM4 are 65, 39 and 20.10^{-9} g C/cm^3 respectively. The mean individual flagellate biomass at these stations are lower than that of the Wadden Sea, according to the observation that flagellates at the JGOFS-sites are smaller than in the Wadden Sea.

Using other methods, deep-sea protozoan research has been done by Burnett (1972, 1976, 1981), Snider *et al.* (1984), Alongi (1986) and Turley *et al.* (1988). The figure Burnett finds for density of deep-sea sediment is 208.10^3 cells/cm^3. Compared with the 3 to 6.10^3 cells/cm^3 at the JGOFS-sites this figure is rather high. But most of the cells encountered by Burnett (1981) in the deep-sea were yeast-like cells, organisms not included in this enumeration. Figures of Alongi (1986) for flagellates vary between 10.10^3 and $1.8.10^6$ individuals/m^2. Assuming exponential decrease in density with depth in the sediment, the density at the JGOFS-sites/m^2 range from 94.10^6 to 234.10^6 individuals/m^2. These values are much higher than that of Alongi (1986). The use of a complete different method of flagellate recovery and an area (Coral Sea Plateau, between the Queensland and Townville troughs on the continental slope of northeastern Australia in the Coral Sea) which is not comparable to the North East Atlantic Ocean, hinder a comparison with this study. The $1.5.10^3$ cells/cm^3 Turley *et al.* (1988) found, which was obtained by a method comparable to that used in this study, matches the figures of this study, but their biomass of 5.10^{-9} g C/cm^3 is much lower, probably caused by the use of a different conversion factor for biomass.

In addition to flagellates some foraminifera-like organisms and a considerable amount of cyst-like cells were found in the JGOFS-samples. The foraminifera-like organisms are comparable with those found by Snider *et al.* (1984) at 5800 m. As far as is known, the cyst-like cells have not been described previously and may be subject of further studies.

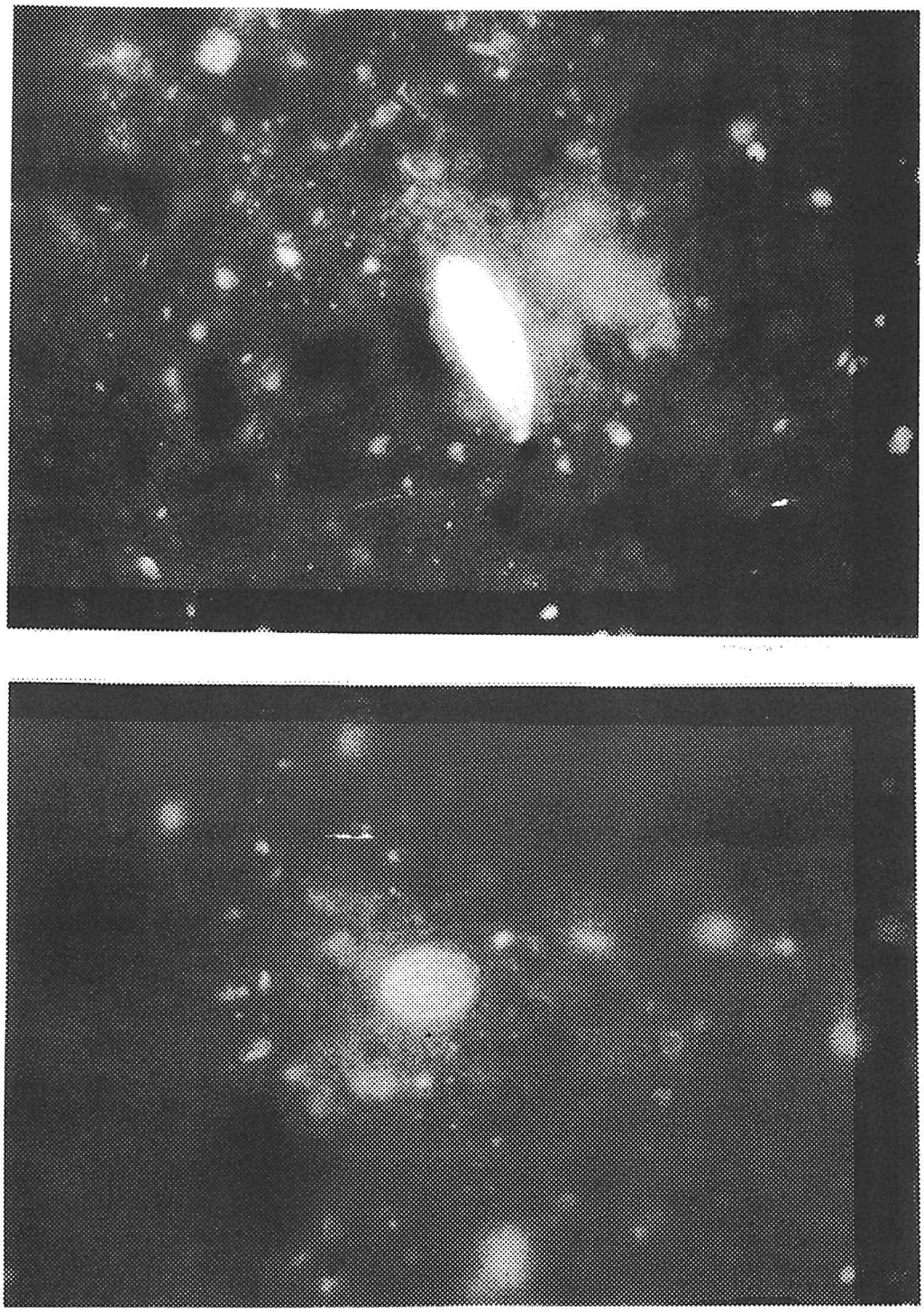


Fig. 13: Flagellates as seen through an epifluorescense microscoop

Photo's: Tom Tahey

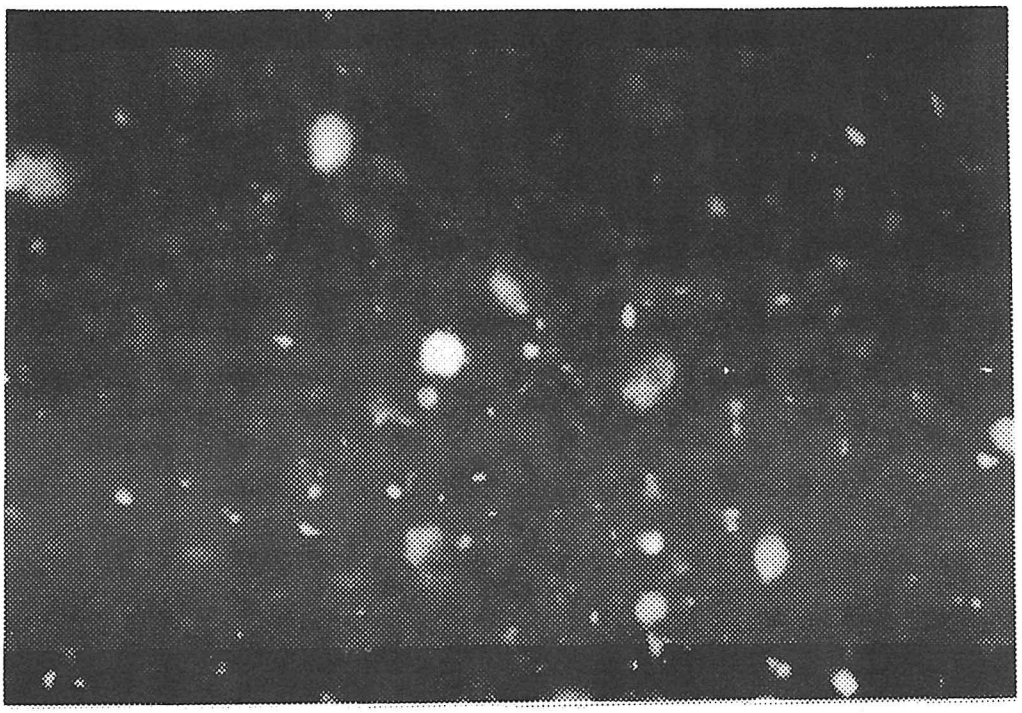


Fig. 13: Flagellates as seen through an epifluorescense microscope

Photo's: Tom Tahey

Comparison of biomasses

Table 11 shows the total biomass divided into the distinquished groups. It appears that bacteria is the most important group in the biomass at the deep-sea JGOFS sites. They constitute more than 90 % of the total biomass at each station. Until now bacteria were often neglected because methods of processing and counting are rather complicated. Bacteria may contribute substantially to the benthic community respiration (see Benthic community respiration). Further, it is clear that the macrofauna biomass is more important than the total meiofauna biomass (except at BS2). As a mean it is 5 times more important. If it was possible to input figures for foraminifera this would only slightly change the total biomass. In the case of macro- and meiofauna the foraminifera remain important

TABLE 11: Total biomass (mgC/m^2) and percentage for all the organism groups at BS1, BS2 and BM4

station	BS 1		BS 2		BM 4	
fauna group	M	%	M	%	M	%
macrofauna	37	2.6	6.4	0.31	201	9.08
large meiofauna	0.40	0.03	2.86	0.14	15.4	0.70
meiofauna	7.00	0.49	5.94	0.29	5.18	0.10
protists	2.22	0.15	4.59	0.23	0.38	0.02
bacteria	1392	96.8	2022	99.0	1992	90.0
total biomass	1438		2042		2214	

Benthic community respiration

The community respiration of the deep-sea bottom is that part of the oxygen which is respired by benthic organisms. For the sake of completeness it should be mentioned that the benthic respiration is distinguished from the chemical oxygen demand caused by the oxidation of reduced organic and inorganic compounds in the sediment. Earlier measurements show the chemical oxygen demand is not an important factor in deep-sea oxygen consumption (Smith, 1978).

The respiration rates of the bottom are given in Table 12. At station BS1 the mean oxygen consumption is 251 mmol $O_2/m^2/day$, at BS2, 129 mmol $O_2/m^2/day$ and at BM4, 604 mmol $O_2/m^2/day$. The high standard deviation at station BS1 is due to difficulties with the Winkler-titration method (see Material & Methods).

TABLE 12: Oxygen concumption at the stations BS1, BS2 and BM4

	BS1	BS2	BM4
µmol $O_2/m^2/day$ +/- 2.776 x SE	251 +/- 362	129 +/- 142	604 +/- 185

On average, the respiration rates are high compared to previous studies at the same depth (Fig. 17; Smith & Teal, 1973; Smith, 1978; Smith & Hinga, 1983). Lochte & Pfannkuche (1988) found a higher oxygen consumption (960-1070 mmol $O_2/m^2/day$), using a bottom lander designed for *in-situ* oxygen respiration measurements. However, they used stainless steel jars to carry out their measurements. Cramer (1989) showed that this can cause an artefact showing that the figures of Lochte & Pfannkuche (1988) may be too high. Consequently their figures will be closer to those of this study. Helder (in press) calculated even higher respiration rates (3100-4100 mmol $O_2/m^2/day$) from the flux of *in-situ* oxygen profiles on the same JGOFS cruise. A higher respiration rate could be explained by the fact that Pfannkuche & Thiel, 1988 found that a bottom lander during measurement does not disturb the fluff-layer on top of the sediment as a boxcore does during recovering. This fluff-layer is considered to be most important for biological and chemical processes in deep-sea sediments. However, the figures of Lochte & Pfannkuche (1988) compared with the figures of Helder (in press) and the figures of this study, do not prove the importance of the fluff-layer.

No correlation is found between total biomass and respiration. However, if we exclude bacteria, there seems to be a correlation between biomass and oxygen consumption, mainly caused by macrofauna. In contrast with Smith (1978) there is no correlation between depth of water and respiration. This is probably due to the small number of samples in this study. Besides, the measuring of properties non-*in-situ* undermines the reliability of these results. It is reasonable to assume that the enormous pressure change that occurs during recovering of a boxcore causes a big mortality among the deep-sea organisms and this may lead to an underestimation of the respiration values. It is also reasonable to assume that the mortality causes enhanced mineralisation of the dead animals which consequently will effect the oxygen consumption. Besides, stress caused by the pressure change may cause a higher respiration in the surviving organisms. But despite this, the figures do not differ dramatically from earlier *in-situ* measurements (Fig. 17; Lochte & Pfannkuche, 1988).

If the assumption is made that bacteria would be able to survive the pressure change then it is not surprising that respiration values are similar, since bacteria are more than 90% of the biomass. However, it is not exactly known how these bacteria react to pressure changes. From earlier research it was known that deep-sea bacteria which are not decompressed show a lower metabolic rate than the same bacteria which are incubated at bottom temperature but at atmospheric pressure (Janaasch & Wirsen, 1977) or show the same production under deep-sea conditions and surface-wat31er incubation conditions (Lochte & Turley, 1988). In contrast, Deming & Colwell (1985) found a higher metabolic rate at *in-situ* pressure. Lochte (1988) shows that bacterial production is highest when incubated at their *in-situ* circumstances. Furthermore it is not known whether the bacteria counted in this study were either active, in cyst forms, in rest stadia, or starving. However, if oxygen consumption is actually the measured quantity this will be due to the bacterial biomass as opposed to other processes that can produce the same effect.

With the help of a newly designed bottom lander it will be possible to measure *in-situ* community respiration. This device will be used in June 1990 during JGOFS IV benthic leg in the Atlantic Ocean. In addition an onboard incubation method will be used to compare the results and also compare them with the findings of this study. During the June 1990 cruise special attention will be paid to bacteria.

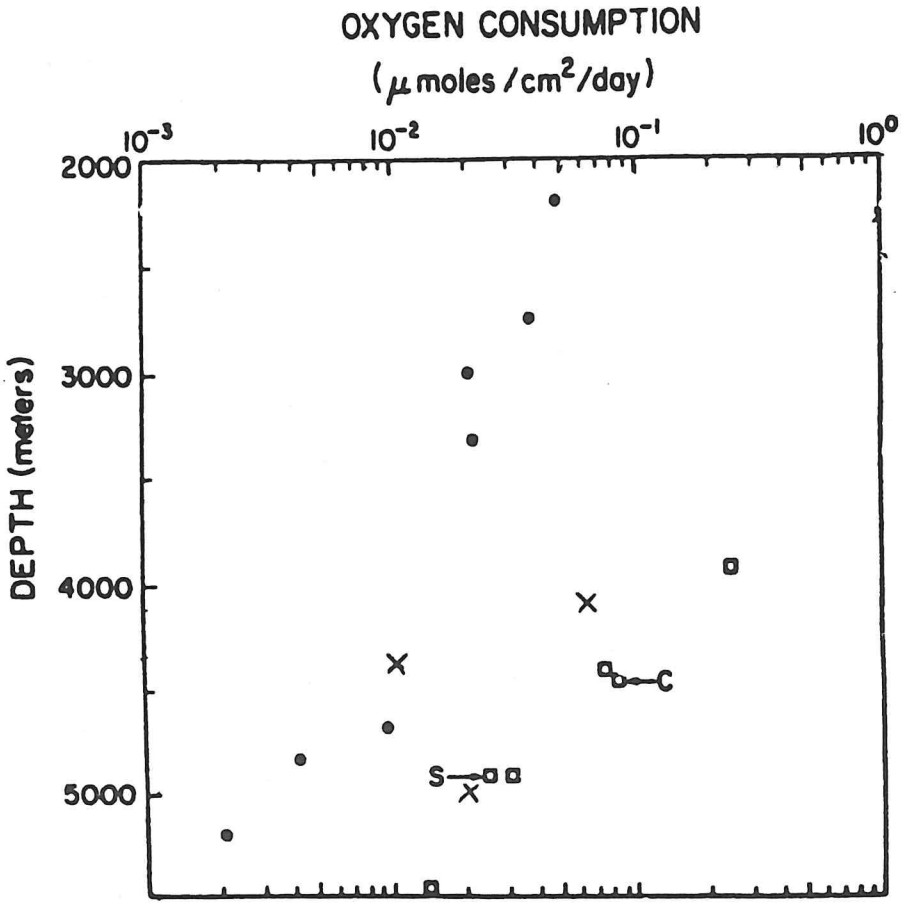


Fig. 17: Oxygen consumption versus water depth for deep stations in the north Atlantic (•) and northeastern Pacific (□). Exept for the sites C and S determinations, all the oxygen concumption rates were measured *in-situ* (Smith & Hinga, 1983) and represent averages of as many 28 replicate determinations. X: oxygen consumption at North East Atlantic JGOFS-sites. Oxygen consumption was measured by an onboard incubation method.

CONCLUSIONS

1 The observed densities and biomasses of both macrofauna and meiofauna are similar to other deep-sea studies in the North East Atlantic Ocean.

2 Differences may be explained by various phenomena such as small scale patchiness of animals, seasonality, differences in methods, statistical errors caused by low densities and natural variability in time and space.

3 Flagellate densities and biomasses are difficult to interpret because earlier studies are scarce and methods differ.

4 Bacteria constitute more than 90% of the total biomass. Bacterial biomass declines with depth in the sediment.

5 The reliability of onboard measurement of the benthic community respiration is debatable, but does not show clear differences with earlier *in-situ* measurements. To enable comparison of the results of *in-situ* and onboard respiration measurements, they must be carried out at the same time and place.

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