

Advances in MARINE BIOLOGY

Edited by

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Meiobenthos of the Deep Northeast Atlantic

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1. INTRODUCTION

Although the first ecological investigations on the meiobenthic communities of the deep northeast Atlantic were carried out 20 years ago (Thiel, 1972b), it is only recently (1990) that co-operative research has been initiated by the European Community under the EC MAST I (Marine Science and Technology I 1990–1992) programme: “Natural variability and the prediction of change in marine benthic ecosystems”. The general objectives of this EC programme, which continues in a MAST II project (1993–1996), are (i) to describe the natural structure and variability of offshore benthic populations in the northeast Atlantic, (ii) to relate the structure and variability to processes in the physical, chemical and biological environment, (iii) to describe the trophic network in the benthic boundary layer and to estimate the organic carbon flux through the deep-sea benthic ecosystem, and (iv) to attempt to predict the changes that are likely to be associated with natural and anthropogenic disturbance. An important component of benthic ecosystems, particularly in the deep sea (Thiel, 1975, 1983), is the meiobenthos, generally considered to include organisms in the size range 31–500 μm . The combined efforts of five laboratories in four of the countries participating in the MAST project have highlighted the gaps that exist in our knowledge of the meiobenthos of the northeast Atlantic and have prompted this review. Our main purpose is to summarize literature data and new results from an area lying between 15°N and 53°N and extending from the continental margin of western Europe and northwest Africa to the Mid-Atlantic Ridge (Figure 1).

Since the first quantitative investigation by Wigley and McIntyre (1964), data on deep-sea meiobenthos have been gathered from all oceans and attempts made to relate the broad geographical patterns observed to various environmental factors. On a planetary scale, one of the major environmental gradients is created by the slope of the ocean floor, a gradient which has important effects on benthic communities. As in the case of macrobenthos (Lampitt *et al.*, 1986), the data available on meiobenthic densities in deep-sea environments also show trends which can be related to the amount and nature of organic matter reaching the seafloor (Thiel, 1983; Shirayama, 1983; Pfannkuche, 1985; Pfannkuche and Thiel, 1987). The distribution patterns of deep-sea organisms are

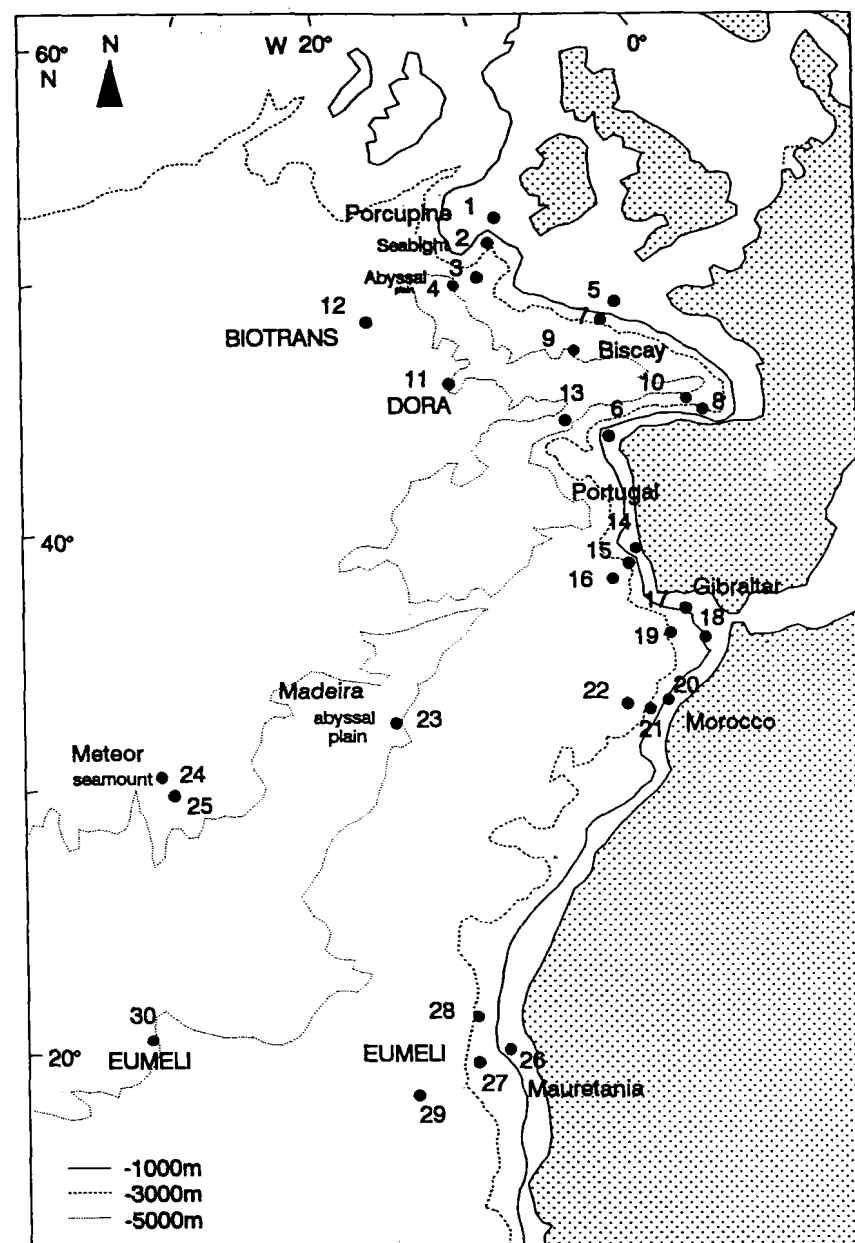


Figure 1 The northeast Atlantic showing the positions of the 30 sampling areas.

influenced by other variables such as sediment type, bottom currents and bottom water masses. Local topographic and hydrodynamic features, such as canyons, seamounts and deep boundary currents, are also important. In addition, the ever-improving resolution of the physical structure of the deep sea, and technical advances in sampling gear and surface navigation, have permitted biologists to address small-scale variability, on scales ranging from centimetres to kilometres.

In this review we consider first the nature and scope of meiofaunal research in the northeast Atlantic and then discuss the environmental parameters which are believed to influence meiofaunal organisms. Next, we discuss the various types and scales of pattern observed among meiofaunal populations within our study area, progressing from the large-scale bathymetric and latitudinal trends and then to small-scale horizontal patterns within particular areas. Faunal densities and faunal composition are considered separately and compared with data from other regions. Finally, we discuss the distribution of meiofauna within sediment profiles and the temporal variability of populations. Our approach differs, therefore, from that adopted in Tietjen's (1992) recent review of deep-sea meiofauna which focused mainly on abundance and biomass data from different oceans and on the relationship between the biomass of the meiofauna and that of other faunal components.

2. MEIOBENTHOS IN THE NORTHEAST ATLANTIC

2.1. Physiographic Setting

The area under investigation consists of a series of deep basins separated by ridges. Basin depth tends to increase from north to south, with depths in excess of 5000 m occurring in basins to the west and northwest of the Cape Verde Islands.

A number of physiographic zones can be recognized within this region: continental shelf, continental slope, continental rise, abyssal apron and abyssal plain (Emery and Uchupi, 1984; see also Rona, 1980; Udintsev *et al.*, 1989–1990). Secondary features include the zone of abyssal hills which separates the continental rise from the Mid-Atlantic Ridge and a number of major seamounts and volcanic islands. Notable aspects include the abyssal aprons (sediment masses deposited by geostrophic bottom currents) of the northwest African margin and around and to the west of the Rockall Trough (Hill, 1987) and the series of abyssal plains (from north to south the Porcupine, Biscay, Iberian, Tagus, Horseshoe, Seine, Madeira, Cape Verde, Gambia) which lie seaward of the continental rise.

The area consists of different biogeochemical provinces of plankton productivity, such as upwelling (NW-Africa), trade wind regime, subtropical gyre, etc., which are of great consequence to the supply of food to the seabed and ultimately for the sediment type where pelagic sedimentation prevails.

2.2. Historical Background

The study of some meiobenthic taxa, particularly foraminifera, living in this region has a long history (e.g. Parker & Jones, 1856; Brady, 1884). However, sampling for meiobenthos was incidental until the 1960s and 1970s when the first quantitative meiobenthic samples were collected from the German research vessel *Meteor*; numerical abundance data from these samples were published by Thiel (1972a, b, 1975, 1978, 1983) and Rachor (1975). Another quantitative investigation which included the meiobenthos was the BIOGAS programme, carried out during the 1970s in the Bay of Biscay (Dinet and Vivier, 1977; see also Dinet *et al.*, 1985). More recent papers devoted partly or exclusively to the meiobenthos are those of Pfannkuche *et al.* (1990), Pfannkuche (1992, 1993b) in the BIOTRANS area and Rutgers van der Loeff and Lavaleye (1986) at the DORA site.

Other studies have focused on particular aspects of the meiobenthos. Some authors have considered just the nematodes (Riemann, 1974; Dinet and Vivier, 1979, 1981). Desbruyères *et al.* (1985) evaluated meiobenthic taxa as part of a recolonization experiment in the Bay of Biscay. Another approach has been to look for correlations between meiobenthic densities and environmental parameters such as bathymetric depth and the amount of organic matter in the sediment (Thiel, 1979b, 1983; Dinet and Khrpounoff, 1980; Sibuet *et al.*, 1989; Vanreusel *et al.*, 1992). Although taxonomic studies of deep-sea meiobenthos are fairly rare in our area, some new taxa have been described among the harpacticoids (Bodin, 1968; Dinet 1977), nematodes (Decraemer, 1983), ostracods (Kornicker, 1989, van Harten, 1990) and tardigrades (Renaud-Mornant, 1989). Some of these investigations have dealt exclusively with the metazoans while others have included foraminifera within the scope of the meiobenthos. Several papers by Gooday (1986a, b, 1988), Gooday and Lamshead (1989), Lamshead and Gooday (1990) have described the foraminiferal meiobenthos in the northeast Atlantic. Gooday and Turley (1990) presented some additional data and Gooday (1990) established a new, ecologically important allogromiid species. The numerous geologically orientated studies of modern deep-sea foraminifera in the northwest Atlantic (Murray, 1991) deal only with the hard-shelled taxa and are not considered further.

2.3. Sampling Areas

Nine of the papers cited above provide data on the density and composition of metazoan and foraminiferal meiobenthos in the area under consideration and are further treated in a general data analysis (Thiel, 1972a, 1975; Diné and Vivier, 1977; Pfannkuche *et al.*, 1983, 1990; Pfannkuche, 1985, 1992; Rutgers van der Loeff and Lavaleye, 1986; Vanreusel *et al.*, 1992). Information on foraminifera published by Gooday (1986a, b, 1988) and Gooday and Lamshead (1989) is not considered in the general approach because no total meiobenthic data are given in these articles. However, this information is discussed in the sections on foraminifera. For reasons explained below, we exclude the data of Rachor (1975) from this survey. Additional unpublished results are available from the Porcupine Seabight (Gooday, IOSDL benthic biology programme), Porcupine and Madeira Abyssal Plains (Gooday and Ferrero, IOSDL DEEPSEAS and EC MAST Programmes), Bay of Biscay (Vincx and Vanreusel, EC MAST programme), BIOTRANS site (Soltwedel and Gooday, BIOTRANS Programme) and from off north-west Africa (Diné, EUMELI and EC MAST programmes).

In order to recognize general trends among the meiobenthos, we have grouped all the stations sampled during these published and unpublished studies into 30 *areas* (identified by number in Table 1) on the basis of geographical and bathymetric proximity. In what follows, density data and other relevant abiotic information on *areas* will always be an average value of the sampling stations situated within one of the 30 *areas* as defined in Table 1. References to *area* numbers in the following text refer always to one of the *area* numbers shown in Figure 1. Bathymetric proximity is arbitrarily defined with limits of following depth zones: < 1000 m, 1000–3000 m, 3000–4500 m and > 4500 m. Inevitably, most of these *areas* are broader in their areal and bathymetric extent than the stations described in the original publications. *Area* locations and numbers are summarized in Figure 1. The original data from all sampling stations are summarized in Table 2.

2.4. Collection and Processing

Methods for the collection and processing of meiobenthic samples are discussed by Thiel (1983), Fleeger *et al.* (1988) and Pfannkuche and Thiel (1988). The data reviewed in the present chapter were obtained from samples collected with various kinds of coring devices (Table 1). A Reineck box corer was used in some of the early studies (Thiel, 1972b, 1975; Diné and Vivier, 1977) but most investigators have used either an

USNEL box corer or multiple corer (Hessler and Jumars, 1974; Barnett *et al.*, 1984). Blomqvist (1991) has identified four factors which bias the sampling of soft bottom sediments, namely, the loss of superficial sediment, the distribution, resuspension and loss of enclosed sediments, core shortening, and repenetration. He urges extreme caution when evaluating results based on grab samples but considers box corers to be fairly reliable if used with a supporting stand and mechanism which secures the lids during retrieval through the water column. Blomqvist (1991) concludes that the Barnett Watson (SMBA) multiple corer (Barnett *et al.*, 1984) "seems to be the best device for general sampling of open-sea, soft bottom sediments at present". It is equipped with a battery of up to 12 coring tubes and the penetration of these into the sediment is slowed by a hydraulic damping system. The multiple corer collects samples in which the sediment–water interface is virtually undisturbed; it is the only remotely operated coring device capable of reliably recovering phytodetritus. Sampling bias, within the data-set considered here, is investigated in detail in Bett *et al.* (1994).

Box core and multiple core samples have been subsampled in a variety of ways. Early German studies used a "meiostecher" with a cross-sectional area of 25 cm² or 10 cm² (Thiel, 1983). Diné and Vivier (1977) and Rutgers van der Loeff and Lavaleye (1986) used transparent tubes with a cross-sectional area of 10 and 25 cm² respectively. More recently, smaller subcores have been taken from both box and multiple corers using modified 20 or 50-ml syringes (3.46 and 5.31 cm² across sectional area respectively). Some complete multiple corer samples have been sorted for metazoan and foraminiferal meiobenthos. Gooday and Lamshead (1989) and Lamshead and Gooday (1990) examined only the upper 1 cm of sediment for foraminifera analysis. However, most authors have followed the lead of Thiel (1966) by examining 1-cm thick sediment slices down to a depth of 4–7 cm. Samples have generally been fixed and preserved using 4% formaldehyde, buffered with borax.

Similar methods have been used to extract meiobenthos from the fixed samples (cf. Pfannkuche and Thiel, 1988). The sediment is passed through a sequence of sieves, the smallest mesh size used varying from 50 to 31 µm. The sieve residues are stained with Rose Bengal with added phenol and hand sorted under a binocular microscope. Rutgers van der Loeff and Lavaleye (1986) used elutriation to concentrate the meiobenthic organisms before sieving on a 50- or 31-µm mesh sieve. Rachor (1975) shook and decanted his samples at least eight times before preservation and sorting, a procedure which must account for the low densities of meiobenthos in his samples (Thiel, 1983). Because of these methodological difficulties, the data of Rachor (1975) are not included in our survey. In order to distinguish dead foraminiferal tests from those

Table 1 Source data on meiofauna of the northeast Atlantic (nr, area number, cf. Figure 1; st, number of sampling stations per area; sa, total number of samples per area).

nr	Author	Area of study	Depth (m)	st	sa	Corer
1	Goody, unpubl. Pfannkuche, 1985	Porcupine Seabight	398	1	1	Multi
2	Goody, unpubl. Pfannkuche, 1985	Porcupine Seabight	500-960	3	3	Multi
3	Goody, unpubl. Pfannkuche, 1985	Porcupine Seabight	1340	2	2	Multi
4	Goody, unpubl. Pfannkuche, 1985	Porcupine Seabight	1492-2785	4	4	Multi
5	Goody, unpubl. Pfannkuche, 1985	Porcupine Seabight	4090-4495	2	2	Multi
6	Lambshead and Ferrero, unpubl. ^a	Porcupine Seabight	3567-4167	2	2	Multi
7	Pfannkuche, 1985	Porcupine Abyssal plain	4850	1	6	Multi
8	Vanreusel <i>et al.</i> , 1992	Porcupine Abyssal plain	4500-4850	2	2	Multi
9	Vanreusel <i>et al.</i> , 1992	Bay of Biscay N	70-170	3	6	Box
10	Dinet and Vivier, 1977	Bay of Biscay S	190-325	2	4	Box
11	Dinet and Vivier, 1977	Bay of Biscay N	2035-3370	20	20	Reineck
12	Dinet and Vivier, 1977	Bay of Biscay S	1912-2480	7	7	Reineck
13	Dinet and Vivier, 1977	Bay of Biscay N	4097-4725	12	12	Reineck
14	Dinet and Vivier, 1977	Bay of Biscay S	4315-4460	3	3	Reineck
15	Rutgers van der Loeff and Lavaleye, 1986	DORA	3958-4800	15	15	Box
16	Pfannkuche <i>et al.</i> , 1990 ^b	BIOTRANS	3900-4300	2	7	Multi
17	Sothwedel, unpubl.	BIOTRANS	4560	1	3	Multi
18	Goody, unpubl.	BIOTRANS	4560	-	1	Multi
19	Pfannkuche <i>et al.</i> , 1990 ^b	BIOTRANS	4550	1	18	Multi
20	Thiel, 1975 ^a	Iberic sea	5272-5340	11	11	Box
21	Thiel, 1975 ^b	Portugal	250-1250	2	2	Box
22	Thiel, 1975 ^b	Portugal	1250-2250	2	2	Box
23	Thiel, 1975 ^b	Portugal	3250-5250	2	2	Box
24	Thiel, 1975 ^b	Gibraltar	250-1250	2	2	Box
25	Pfannkuche <i>et al.</i> , 1983 ^b	NW Africa	131-818	5	5	Box
26	Pfannkuche <i>et al.</i> , 1983 ^b	Morocco	1163-3093	5	5	Box
27	Thiel, 1975 ^b	Morocco	250-1250	2	2	Box
28	Thiel, 1975 ^b	Morocco	1250-2250	2	2	Box
29	Thiel, 1975 ^b	Morocco	4250-4750	1	1	Box
30	Goody, unpubl.	Madeira Abyssal plain	4856-5120	2	2	Multi
31	Lambshead and Ferrero, unpubl. ^a	Madeira Abyssal plain	4856	-	7	Multi
32	Thiel, 1975 ^b	Great Meteor seamount	250-750	1	1	Box
33	Thiel, 1975 ^b	Great Meteor seamount	1250-1750	1	1	Box
34	Thiel, 1975 ^b	Mauretania	190-1250	3	3	Box
35	Thiel, 1975 ^b	Mauretania	1750-3250	2	2	Box
36	Dinet, unpubl.	Eumeli	1543-2041	6	12	Box
37	Dinet, unpubl.	Eumeli	3107-3137	9	18	Box
38	Dinet, unpubl.	Eumeli	4568-4652	8	16	Box

^aOnly nematode densities available.

^bOnly total metazoan meiofauna densities available.

Table 2 Meiofaunal densities for samples collected in the northeast Atlantic (ar.nr, area number; Nem, Nematoda; Cop, harpacticoid copepods + nauplii; Turb, Turbellaria; Pol, Polychaeta; Oli, Oligochaeta; Ostr, Ostracoda; Hydr, Hydrozoa; Gas, Gastrotricha; Tar, Tardigrada; Kin, Kinorhyncha; Amp, Amphipoda; Hal, Halacaroida; Lor, Loricifera; Iso, Isopoda; Biv, Bivalvia; Tan, Tanaidacea; Fora, Foraminifera; Meio, total meiofauna; Metaz, metazoan meiofauna).

Author	Area	ar.nr	Depth (m)	Sample	Nem	Cop	Turb	Pol	Oli	Ostr	Hydr
Dinet, unpubl.	Eumeli	28	1970	KGS44 a	476.5	9.4		18.8		0.0	
		28		b	256.1	30.1		28.2		1.9	
		28	1543	KGS38 a	849.3	97.9		1.9		1.9	
		28		b	764.6	58.4		24.5		0.0	
		28	1590	KGS41 a	1235.4	71.6		45.2		9.4	
		28		b	1033.9	75.3		13.2		1.9	
		28	2041	KGS43 a	1182.7	47.1		18.8		1.9	
		28		b	1367.2	94.2		32.0		1.9	
		28	1970	KGS45 a	862.5	16.9		13.2		3.8	
		28		b	779.7	30.1		5.6		0.0	
		28	1618	KGS39 a	1389.8	37.7		33.9		0.0	
		28		b	1133.7	26.4		15.1		1.9	
		29	3120	KGS10 a	333.3	16.9		7.5		1.9	
		29		b	337.1	30.1		11.3		1.9	
		29	3137	KGS13 a	256.1	30.1		20.7		0.0	
		29		b	421.8	16.9		5.6		0.0	
		29	3136	KGS14 a	474.6	43.3		15.1		0.0	
		29		b	655.4	32.0		11.3		0.0	
		29	3124	KGS11 a	455.7	33.9		3.8		0.0	
		29		b	559.3	16.9		13.2		0.0	
		29	3107	KGS12 a	551.8	13.2		33.9		5.6	
		29		b	448.2	11.3		13.2		5.6	
		29	3118	KGS18 a	572.5	13.2		11.3		0.0	
		29		b	540.5	11.3		9.4		0.0	
		29	3130	KGS15 a	745.8	33.9		13.2		0.0	
		29		b	476.5	33.9		3.8		1.9	
		29	3128	KGS16 a	1122.4	20.7		18.8		0.0	
		29		b	587.6	24.5		15.1		1.9	
		29	3118	KGS21 a	201.5	9.4		3.8		0.0	
		29		b	113.0	24.5		3.8		0.0	
		30	4629	KGS02 a	167.6	0.0		3.8		0.0	
		30		b	154.4	5.6		1.9		0.0	
		30	4582	KGS03 a	120.5	1.9		1.9		0.0	
		30		b	99.8	11.3		0.0		0.0	
		30	4590	KGS09 a	131.8	0.0		7.5		0.0	
		30		b	286.3	5.6		1.9		0.0	
		30	4582	KGS04 a	96.0	13.2		3.8		0.0	
		30		b	152.5	1.9		3.8		0.0	
		30	4568	KGS05 a	49.0	5.6		3.8		0.0	
		30		b	81.0	7.5		3.8		0.0	
		30	4580	KGS07 a	96.0	5.6		0.0		0.0	
		30		b	105.5	7.5		0.0		0.0	
		30	4652	KGS08 a	64.0	1.9		0.0		0.0	
		30		b	113.0	3.8		0.0		1.9	
		30	4569	KGS06 a	60.3	16.9		0.0		0.0	
		30		b	111.1	7.5		0.0		0.0	
Ferrero, unpubl.	Porcupine Abyssal Plain	4	4850	16(5)	331.0						
		4		41(1)	220.9						
		4		5(11)	374.0						
		4		24(7)	285.7						
Gooday, unpubl.	Porcupine Seabight	1	398	51620	695.5	84.0	0.0	0.0	0.0	11.6	0.0
		2	1340	51502	1211.0	118.0	0.0	11.8	0.0	15.0	0.0
		2	1340	51615	1026.0	162.0	0.0	7.5	0.0	4.6	0.0
		3	4090	51504	215.6	38.0	0.0	3.6	0.0	0.7	0.0
Gooday, unpubl.	Madeira Abyssal Plain	3	4495	51606	372.8	29.0	0.0	2.9	0.0	3.0	0.0
		23	5120	354	40.5	1.3	0.0	0.0	0.0	0.0	0.0
		23	4856	12174(88)	179.6	19.0	0.0	2.4	0.0	0.4	0.0
		23	4856	12174(93)	79.5						
Ferrero, unpubl.	Soltwedel, unpubl.	23	4856-4950	12174(94)	106.9						
		23		12174(88)	59.9						
		23		12174(24)	69.0						
		23		12174(26)	55.0						
Vanreusel and Vincx, unpubl.	Bay of Biscay	5	70	1a	809.0	166.0	49.0	35.0	9.0	7.0	7.0
		5		1b	658.0	72.0	48.0	25.0	5.0	2.0	4.0
		5	170	3a	193.0	66.0	73.0	20.0	0.0	14.0	3.0
		5		3b	172.0	34.0	188.0	13.0	1.0	0.0	1.0
Vanreusel et al., 1992		5	148	S11a	255.0	145.0	10.0	27.0	0.0	20.0	3.0
		5		S11b	171.0	64.0	24.0	29.0	0.0	8.0	2.0
		6	123	6a	1031.0	45.0	10.0	18.0	0.0	0.0	0.0
		6		6b	773.0	46.0	32.0	21.0	0.0	3.0	0.0
		6	300	8a	419.0	30.0	4.0	10.0	0.0	0.0	0.0
		6		8b	479.0	15.0	0.0	9.0	0.0	0.0	0.0

Gas	Tar	Kin	Amp	Hal	Lor	Iso	Biv	Tan	Others	Fora	Meio	Metaz	Nem (%)	Cop (%)
	0.0	0.0					0.0	0.0	0.0			504.7	94.4	1.9
	0.0	1.9					0.0	3.8	3.8			325.8	78.6	9.2
	0.0	3.8					3.8	0.0	5.6			964.2	88.1	10.2
	0.0	3.8					0.0	0.0	7.5			858.8	89.0	6.8
	0.0	7.5					0.0	0.0	0.0			1369.1	90.2	5.2
	0.0	1.9					0.0	1.9	0.0			1128.1	91.7	6.7
	0.0	3.8					0.0	0.0	0.0			1254.2	94.3	3.8
	0.0	5.6					0.0	0.0	1.9			1502.8	91.0	6.3
	0.0	5.6					0.0	0.0	1.9			904.0	95.4	1.9
	0.0	1.9					0.0	0.0	0.0			817.3	95.4	3.7
	0.0	3.8					0.0	0.0	1.9			1467.0	94.7	2.6
	0.0	0.0					0.0	0.0	0.0			1177.0	96.3	2.2
	0.0	0.0					0.0	0.0	1.9			361.6	92.2	4.7
	0.0	0.0					1.9	0.0	0.0			382.3	88.2	7.9
	1.9	0.0					1.9	0.0	0.0			310.7	82.4	9.7
	0.0	0.0					0.0	0.0	0.0			444.4	94.9	3.8
	0.0	1.9					0.0	0.0	0.0			534.8	88.7	8.1
	0.0	0.0					1.9	0.0	0.0			700.6	93.5	4.6
	0.0	0.0					0.0	0.0	0.0			493.4	92.4	6.9
	0.0	0.0					0.0	0.0	1.9			591.3	94.6	2.9
	0.0	0.0					1.9	0.0	0.0			606.4	91.0	2.2
	0.0	1.9					0.0	0.0	1.9			482.1	93.0	2.3
	0.0	0.0					0.0	0.0	0.0			597.0	95.9	2.2
	0.0	0.0					0.0	0.0	1.9			563.1	96.0	2.0
	0.0	0.0					0.0	0.0	0.0			792.8	94.1	4.3
	1.9	0.0					0.0	3.8	0.0			521.7	91.3	6.5
	0.0	0.0					0.0	0.0	0.0			1162.0	96.6	1.8
	0.0	0.0					0.0	0.0	0.0			629.0	93.4	3.9
	0.0	0.0					0.0	0.0	0.0			214.7	93.9	4.4
	0.0	0.0					0.0	0.0	0.0			141.2	80.0	17.3
	1.9	0.0					0.0	0.0	0.0			173.3	96.7	0.0
	0.0	1.9					0.0	0.0	0.0			163.8	94.3	3.4
	0.0	0.0					0.0	0.0	0.0			124.3	97.0	1.5
	0.0	0.0					0.0	0.0	0.0			111.1	89.8	10.2
	0.0	0.0					0.0	0.0	0.0			139.4	94.6	0.0
	0.0	1.9					0.0	0.0	0.0			295.7	96.8	1.9
	0.0	0.0					0.0	1.9	0.0			114.9	83.6	11.5
	0.0	1.9					0.0	0.0	0.0			160.1	95.3	1.2
	0.0	0.0					0.0	0.0	0.0			58.4	83.9	9.7
	0.0	0.0					0.0	0.0	0.0			92.3	87.8	8.2
	0.0	0.0					0.0	0.0	0.0			101.7	94.4	5.6
	0.0	0.0					0.0	0.0	0.0			113.0	93.3	6.7
	0.0	0.0					0.0	0.0	0.0			65.9	97.1	2.9
	0.0	0.0					0.0	0.0	0.0			118.6	95.2	3.2
	0.0	0.0					0.0	0.0	0.0			77.2	78.0	22.0
	0.0	0.0					0.0	0.0	0.0			118.6	93.7	6.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1098.3	1890.3	792.1	87.9	10.6
0.0	4.9	4.9	0.0	0.0	0.0	0.0	3.8	0.0	9.0	1835.2	3213.6	1378.4	87.9	8.6
0.0	9.2	3.8	0.0	0.0	0.0	0.0	1.7	0.0	9.2	2060.7	3284.8	1224.1	83.8	13.2
0.0	0.1	0.7	0.0	0.0	0.0	0.0	0.1	0.0	0.0		258.9	258.9	83.3	14.7
0.0	0.0	3.0	0.0	0.0	0.0	0.0	3.0	0.0	3.0	956.3	1373.0	416.7	89.5	7.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		76.2	41.8	96.9	3.1
0.0	0.0	0.8	0.0	0.0	0.0	0.4	0.0	0.0	0.0	234.0	436.6	202.6	88.6	9.4
24.0	14.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			1120.0	72.2	14.8
5.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			823.0	80.0	8.7
5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			374.0	51.6	17.6
0.0	1.0	0.0	7.0	1.0	0.0	0.0	0.0	0.0	0.0			418.0	41.1	8.1
8.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			470.0	54.3	30.9
1.0	2.0	1.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0			304.0	56.3	21.1
0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			1112.0	92.7	4.0
0.0	1.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			880.0	87.8	5.2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			463.0	90.5	6.5
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			503.0	95.2	3.0

Author	Area	ar.nr	Depth (m)	Sample	Nem	Cop	Turb	Pol	Oli	Ostr	Hydr		
Dinet and Vivier, 1977	Bay of Biscay	7	2110	12-1	394.0	70.0	0.0	7.0	0.0	1.0	0.0		
		7	2200	16-1	912.0	49.0	0.0	4.0	0.0	2.0	0.0		
		7	2035	17-1	396.0	35.0	0.0	2.0	0.0	2.0	0.0		
		7	2150	37-1	766.0	122.0	0.0	6.0	0.0	1.0	0.0		
		7	2235	38-1	278.0	27.0	0.0	11.0	0.0	0.0	0.0		
		7	2125	39-1	280.0	6.0	0.0	9.0	0.0	0.0	0.0		
		7	2136	40-1	228.0	25.0	0.0	1.0	0.0	0.0	0.0		
		7	2091	41-1	228.0	28.0	0.0	9.0	0.0	4.0	0.0		
		7	2111	42-1	317.0	54.0	0.0	3.0	0.0	1.0	0.0		
		7	2080	44-1	506.0	147.0	0.0	9.0	0.0	2.0	0.0		
		7	2288	02-2	507.0	32.0	0.0	5.0	0.0	1.0	0.0		
		7	3039	03-2	250.0	28.0	0.0	3.0	0.0	1.0	0.0		
		7	2726	11-2	428.0	40.0	0.0	7.0	0.0	0.0	0.0		
		7	2690	18-2	323.0	59.0	0.0	4.0	0.0	0.0	0.0		
		7	3370	19-2	291.0	42.0	0.0	7.0	0.0	3.0	0.0		
		7	2835	34-2	140.0	0.0	0.0	1.0	0.0	0.0	0.0		
		7	2864	45-2	246.0	26.0	0.0	7.0	0.0	0.0	0.0		
		7	2920	47-2	306.0	59.0	0.0	7.0	0.0	0.0	0.0		
		7	2765	58-2	296.0	17.0	0.0	4.0	0.0	0.0	0.0		
		7	2853	59-2	742.0	102.0	0.0	5.0	0.0	1.0	0.0		
		8	1920	24-6	306.0	63.0	0.0	3.0	0.0	1.0	0.0		
		8	2480	26-6	527.0	29.0	0.0	7.0	0.0	7.0	0.0		
		8	1913	27-6	451.0	28.0	0.0	3.0	0.0	0.0	0.0		
		8	1960	53-6	403.0	37.0	0.0	2.0	0.0	0.0	0.0		
		8	1960	54-6	435.0	37.0	0.0	7.0	0.0	0.0	0.0		
		8	1957	70-6	748.0	33.0	0.0	16.0	0.0	1.0	0.0		
		8	1920	71-6	543.0	45.0	0.0	8.0	0.0	0.0	0.0		
		9	4150	20-3	356.0	28.0	0.0	6.0	0.0	2.0	0.0		
		9	4097	31-3	155.0	7.0	0.0	3.0	0.0	0.0	0.0		
		9	4130	32-3	309.0	7.0	0.0	3.0	0.0	6.0	0.0		
		9	4096	35-3	261.0	20.0	0.0	2.0	0.0	1.0	0.0		
		9	4300	48-3	149.0	13.0	0.0	0.0	0.0	0.0	0.0		
		9	4220	16-3	287.0	19.0	0.0	5.0	0.0	0.0	0.0		
		9	4225	61-3	383.0	48.0	0.0	5.0	0.0	0.0	0.0		
		9	4202	62-3	330.0	36.0	0.0	0.0	0.0	1.0	0.0		
		9	4590	22-4	192.0	19.0	0.0	1.0	0.0	0.0	0.0		
		9	4550	51-4	12.0	3.0	0.0	1.0	0.0	0.0	0.0		
		9	4725	56-4	215.0	13.0	0.0	0.0	0.0	0.0	0.0		
		9	4700	66-4	280.0	12.0	0.0	0.0	0.0	0.0	0.0		
		10	4415	09-5	152.0	15.0	0.0	2.0	0.0	1.0	0.0		
		10	4315	23-5	86.0	16.0	0.0	1.0	0.0	1.0	0.0		
		10	4460	69-5	5.0	1.0	0.0	1.0	0.0	0.0	0.0		
		Pfannkuche, 1985	Porcupine Seabight	1	500	51507	2382.0	98.0	0.0	3.0	0.0	18.0	0.0
				1	510	51112	1676.0	121.0	0.0	26.0	0.0	9.0	0.0
1	960			51103	1429.0	81.0	0.0	25.0	0.0	5.0	0.0		
2	1492			51104	820.0	75.0	0.0	11.0	0.0	7.0	0.0		
2	2000			51105	702.0	101.0	0.0	6.0	0.0	4.0	0.0		
2	2510			51106	658.0	66.0	0.0	6.0	0.0	2.0	0.0		
2	2785			51110	717.0	151.0	0.0	5.0	0.0	8.0	0.0		
3	3567			51108	595.0	54.0	0.0	4.0	0.0	1.0	0.0		
3	4167			51109	462.0	48.0	0.0	1.0	0.0	4.0	0.0		
4	4500			51505	300.0	52.0	0.0	1.0	0.0	2.0	0.0		
4	4850			51506	272.0	35.0	0.0	1.0	0.0	1.0	0.0		
Pfannkuche et al., 1983	Morocco			18	131-133								
		18	191-207										
		18	381-407										
		18	598-607										
		18	800-818										
		19	1163										
		19	2014-2064										
		19	1463-1478										
		19	2435										
		19	2999-3093										
		Pfannkuche et al. 1990	Biotrans peak	12									
				12	3900								
12													
12													
Slope	12												
	12		4300										
	12												
	12												
	12												
	12												
	12												
	12												
Plain	12	4550											
	12												
	12												
	12												
	12												
	12												
	12												
	12												

Gas	Tar	Kin	Amp	Hal	Lor	Iso	Biv	Tan	Others	Fora	Meio	Metaz	Nem (%)	Cop (%)
0.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0			478.0	82.4	14.6
0.0	2.0	2.0	0.0	1.0	0.0	0.0	0.0	2.0	4.0			978.0	93.3	5.0
0.0	2.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0			440.0	90.0	8.0
0.0	4.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0			907.0	84.5	13.5
0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			320.0	86.9	8.4
0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	8.0			304.0	92.1	2.0
0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			257.0	88.7	9.7
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			270.0	84.4	10.4
0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0			380.0	83.4	14.2
0.0	2.0	3.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0			671.0	75.4	21.9
0.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0	0.0	1.0			549.0	92.3	5.8
0.0	2.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	2.0			288.0	86.8	9.7
0.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0	1.0	3.0			536.0	79.9	7.5
0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0			387.0	83.5	15.2
0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0			346.0	84.1	12.1
0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			142.0	98.6	0.0
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0			281.0	87.5	9.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			374.0	81.8	15.8
0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			315.0	94.0	5.4
0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0			853.0	87.0	12.0
0.0	1.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	3.0			379.0	80.7	16.6
0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	7.0			579.0	91.0	5.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			482.0	93.6	5.8
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			445.0	90.6	8.3
0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0			483.0	90.1	7.7
0.0	1.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0			808.0	92.6	4.1
0.0	4.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0			603.0	90.0	7.5
0.0	0.0	1.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0			395.0	90.1	7.1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			165.0	93.9	4.2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			320.0	96.6	2.2
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0			287.0	90.9	7.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			62.0	240.3	21.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			311.0	92.3	6.1
0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			437.0	87.6	11.0
0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0			369.0	89.4	9.8
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			213.0	90.1	8.9
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0			16.0	75.0	18.8
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0			230.0	93.5	5.7
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			297.0	94.3	4.0
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			171.0	88.9	8.8
0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0			105.0	81.9	15.2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			7.0	71.4	14.3
20.0	0.0	8.0	0.0	2.0	0.0	0.0	62.0	0.0	1.0			2604.0	91.5	3.8
81.0	0.0	6.0	0.0	3.0	0.0	0.0	12.0	0.0	29.0			1963.0	85.4	6.2
33.0	3.0	4.0	0.0	3.0	0.0	0.0	8.0	0.0	2.0			1593.0	89.7	5.1
8.0	3.0	2.0	0.0	7.0	0.0	0.0	4.0	0.0	5.0			943.0	87.0	8.0
7.0	0.0	4.0	0.0	1.0	0.0	0.0	1.0	0.0	2.0			828.0	84.8	12.2
5.0	1.0	1.0	0.0	1.0	0.0	0.0	1.0	0.0	3.0			744.0	88.4	8.9
12.0	0.0	5.0	0.0	8.0	0.0	0.0	0.0	0.0	1.0			900.0	79.7	16.8
7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0			663.0	89.7	8.1
4.0	0.0	2.0	0.0	5.0	0.0	0.0	1.0	0.0	1.0			528.0	87.5	9.1
4.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0			362.0	82.9	14.4
4.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0			315.0	86.3	11.1
												2656.0		
												1778.0		
												2480.0		
												1465.0		
												1175.0		
												631.0		
												570.0		
												620.0		
												550.0		
												557.0		
												364.0		
												376.0		
												352.0		
												308.0		
												386.0		
												302.0		
												302.0		
												316.0		
												475.0		
												434.0		
												270.0		
												306.0		
												397.0		
												281.0		
												307.0		
												375.0		
												315.0		
												409.0		
												429.0		
												315.0		
												434.0		
												348.0		
												450.0		
												457.0		
												326.0		

Author	Area	ar.nr	Depth (m)	Sample	Nem	Cop	Turb	Pol	Oli	Ostr	Hydr
Soltwedel, unpubl.	Biotrans	12	4560	113	124.8	20.0	0.0	0.0	0.0	0.0	0.0
		12		114	229.0	40.0	0.0	5.8	0.0	2.0	0.0
		12		115	120.4	15.0	0.0	2.9	0.0	0.0	0.0
Gooday, unpubl.		12		179(2)	760.1	53.0	0.0	0.0	0.0	0.0	0.0
Rutgers and Lavaleye, 1986	DORA	11	4787	21	315.0	10.5	0.0	1.2	0.0	0.6	0.0
		11	4325	5	386.0	16.7	0.0	1.2	0.0	2.0	0.0
		11	4333	23	534.0	14.7	0.0	3.2	0.0	2.0	0.0
		11	4310	22	403.0	3.9	0.0	0.8	0.0	1.2	0.0
		11	3958	24	560.0	19.3	0.0	1.4	0.0	0.8	0.0
		11	4725	25	622.0	16.1	0.0	1.8	0.0	0.6	0.0
		11	4540	26	720.0	12.0	0.0	2.0	0.0	0.6	0.0
		11	4800	1	322.0	5.7	0.0	0.0	0.0	0.4	0.0
		11	4200	2	101.0	9.7	0.0	0.4	0.0	0.8	0.0
		11	4300	4	246.0	11.7	0.0	0.0	0.0	0.8	0.0
		11	4570	6	300.0	15.4	0.0	0.0	0.0	0.4	0.0
		11	4725	8	373.0	13.0	0.0	0.0	0.0	0.4	0.0
		11	4725	11	401.0	12.6	0.0	0.8	0.0	0.8	0.0
		11	4700	13	595.0	32.1	0.0	1.2	0.0	0.4	0.0
		11	4000	15	985.0	48.7	0.0	5.7	0.0	2.4	0.0
Thiel, 1972	Iberic sea	13	5325	12-89-1	156.0	3.0	0.0	0.4	0.0	0.0	0.0
		13	5325	12-89-2	246.0	6.0	0.0	0.4	0.0	1.2	0.0
		13	5335	18-91-1	192.0	5.6	0.0	0.4	0.0	1.2	0.0
		13	5340	21-92-1	172.0	3.6	0.0	0.0	0.0	0.8	0.0
		13	5340	21-92-2	80.0	2.0	0.0	0.0	0.0	1.6	0.0
		13	5305	29-93-1	242.0	1.6	0.0	0.4	0.0	0.0	0.0
		13	5305	29-93-2	200.0	4.4	0.0	0.4	0.0	0.4	0.0
		13	5320	31-94-1	256.0	5.6	0.0	0.0	0.0	2.0	0.0
		13	5320	31-94-2	176.0	2.4	0.0	0.8	0.0	1.2	0.0
		13	5272	35-95-1	302.0	10.4	0.0	1.2	0.0	2.2	0.0
Thiel 1975	Mauretania	13	5272	35-95-2	257.0	4.8	0.0	1.2	0.0	2.2	0.0
		26	190-250								
		26	250-750								
		24									
		20									
		17									
		14									
		26	750-1250								
		20									
		17									
		14									
		25	1250-1750								
		21									
		15									
		27	1750-2250								
		21									
		15									
		27	2750-3250								
		16	3750-4250								
		22	4250-4750								
		16	4750-5250								

which were living when collected, Gooday (1986a, b, 1988) and Gooday and Lambshead (1989) mounted stained specimens in glycerol and examined them under a compound microscope to ensure that the stained material was foraminiferal protoplasm. Only specimens with a convincing protoplasmic mass were regarded as living.

A controversial issue in benthic research is the standardization of size groups. During the Sixth Deep-Sea Biology Symposium in Copenhagen (1991), a workshop was organized by Hjalmar Thiel on the "Standardization of methods for benthos studies and biochemical measurements in sediments" (Thiel, 1993). For meiobenthos, this workshop recommended a lower limit of 31 μ m and an upper limit of 1 mm for all benthic work in the deep sea. In fact, these mesh-size based categories have little ecological and even less taxonomic justification in the deep sea because a

Gas	Tar	Kin	Amp	Hal	Lor	Iso	Biv	Tan	Others	Fora	Meio	Metaz	Nem (%)	Cop (%)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	196.0	343.4	147.4	84.7	13.6
0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	319.0	598.8	279.8	81.8	14.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	464.3	602.6	138.3	87.1	10.8
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	864.2	1677.3	813.1	93.5	6.5
0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	4.8	12.6	374.2	361.6	87.1	2.9
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.7	37.8	462.1	424.3	91.0	3.9
0.0	0.6	1.0	0.0	0.0	0.0	0.0	0.0	0.0	4.6	22.8	667.3	644.5	82.9	2.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	2.2	4.6	453.6	449.0	89.8	0.9
0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	5.4	6.8	630.3	623.5	89.8	3.1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	8.8	4.6	705.3	700.7	88.8	2.3
0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.2	8.4	11.2	831.4	820.2	87.8	1.5
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	22.8	352.9	330.1	97.5	1.7
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.2	262.5	124.5	81.1	7.8
0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.0	13.8	341.4	327.6	91.6	4.7
0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.4	8.1	19.1	415.7	396.6	94.0	3.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	7.3	429.1	421.8	95.1	3.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	7.3	669.5	662.2	89.9	4.8
0.0	0.4	1.2	0.0	0.0	0.0	0.0	0.8	0.0	6.1	34.1	1120.9	1086.8	90.6	4.5
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0			162.0	96.3	1.9
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			257.0	95.7	2.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			200.0	96.0	2.8
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			176.0	97.7	2.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			176.0	97.7	2.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0			84.0	95.2	2.4
0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0			245.0	98.8	0.7
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			210.0	95.2	2.1
0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0			264.0	97.0	2.1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			180.0	97.8	1.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			317.0	95.3	3.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			366.0	70.2	1.3
												156.0		
												417.0		
												246.0		
												629.0		
												370.0		
												1387.0		
												1082.0		
												331.0		
												298.0		
												1250.0		
												48.0		
												306.0		
												521.0		
												315.0		
												140.0		
												474.0		
												1099.0		
												192.0		
												130.0		
												123.0		

trend towards miniaturization has occurred among the benthos above the size of nanobenthos (Thiel, 1975). This trend has not affected the larger macrofauna and megafauna in which, for some taxa, a reverse trend towards gigantism has occurred.

Therefore, as suggested by Hessler and Jumars (1974), the use of the term "meiobenthic taxa" is more appropriate in the context of deep-sea habitats. These taxa consist of metazoan animals traditionally regarded as "meiobenthos", and larger protozoans, almost exclusively foraminifera. Nearly all meiobenthic phyla have been found in deep-sea sediments. The numerical dominance of a few taxa, notably foraminifera, nematodes and copepods, however, is more pronounced in comparison with shallower areas.

3. ENVIRONMENTAL VARIABLES

3.1. Sediment Type

Bottom sediments in the northeast Atlantic originate from terrestrial or volcanic sources, from turbidity currents and related catastrophic phenomena, from bottom currents and from pelagic sedimentation. In general, coarse sediments (sands and gravels) of terrestrial or biogenic origin are restricted to the continental shelf and upper slope and become progressively finer (silty muds and muds) with increasing bathymetric depth and distance from land (Emery and Uchupi, 1984; Auffret, 1985; Lampitt *et al.*, 1986). However, in some areas, for example off the western approaches to the English Channel (Mart *et al.*, 1979; Auffret, 1985; Weston, 1985), the continental slope is dissected by active submarine canyons which channel coarse sediments onto the continental slope and rise. Coal, clinker (derived from steamships) and ice-rafted debris are also widespread in the northeast Atlantic (Kidd and Huggett, 1981) and provide a substratum for sessile organisms.

Over much of the northeast Atlantic the superficial sediments consist of pelagic calcareous oozes with a calcium carbonate content exceeding 30 or 50% and a mean particle size of <0.01 mm (Apostolescu *et al.*, 1978; Emery and Uchupi, 1984; Auffret, 1985; Lampitt *et al.*, 1986; Udintsev *et al.*, 1989–1990). Clay particles (<0.01 mm) generally make up 50% or more of the sediment (Udintsev *et al.*, 1989–1990). The carbonate compensation depth (CCD) in the northeast Atlantic exceeds 5000 m (Berger, 1975; Biscaye *et al.*, 1976) and hence areas of very fine grained red clay (from which the carbonate has been removed by dissolution) are restricted to the deepest basins, located west and northwest of the Cape Verde Islands.

Many continental slopes in the northeast Atlantic are characterized by widespread slope failure leading to turbidity currents, debris flows and sediment slides which have deposited sediments across huge areas of the adjacent rise and abyssal plain (Emery and Uchupi, 1984; Stein, 1991). Sediment slides and debris flows have been most fully described off the northwest African coast where some cover a great area (Embley, 1976; Jacobi, 1976; Kidd *et al.*, 1986; Masson *et al.*, 1994). Turbidity currents originating from slope failure may travel considerable distances across the ocean floor, depositing progressively finer sediments as they do so. Distal turbidites are typically fine grained and carbonate rich and have a higher total organic carbon content (1–3%) than sediments of pelagic origin (Wilson and Wallace, 1990; Stein, 1991). Such deposits are known to blanket the Madeira Abyssal Plain where the Quaternary succession consists of thick turbidite units separated by thin pelagic layers (Weaver

and Kuijpers, 1983; Weaver *et al.*, 1986). They clearly influence the abyssal biota since areas of the Madeira Abyssal Plain underlain by turbiditic and pelagic sediments have quite different assemblages of animal traces (Huggett, 1986).

Turbidity currents must have devastated benthic life over large tracts of ocean floor and controlled the nature of recolonizing communities. However, such events have been rare along the northwest African margin with only one major turbidite being deposited, on average, every 30 000 years during the last 730 000 years (Masson *et al.*, 1994). Hence, all but the most recent turbidites are blanketed by pelagic sediments. Bottom current deposits (contourites) are well developed on the abyssal aprons, for example around the Rockall Plateau (Hill, 1987).

Detailed information on sediment grain size composition of the *areas* (Figure 1) reviewed in this chapter are only available for *area* 6 (Vanreusel *et al.*, 1992), *areas* 7–10 (Dinet and Vivier, 1977) and *area* 13 (Thiel, 1972a). Some *areas* less than 1000 m deep have coarser sediments, while most of the other *areas* are characterized by fine silty clays.

3.2. Oxygen

Unlike those in shallow water, deep-sea sediments are usually well oxygenated. Oxygen profiles for abyssal plain sediments in the northeast Atlantic are given by Sorensen and Wilson (1984), Wilson *et al.* (1985, 1986), Wallace *et al.* (1988), Rutgers van der Loeff and Lavaleye (1986) and Rutgers van der Loeff (1991) (*area* 11; Figure 2). Oxygen invariably penetrates to a depth of at least several decimetres and usually much deeper. At Discovery Station 10554 on the Madeira Abyssal Plain (*area* 23), oxygen levels were reduced to zero at a depth of less than 30 cm (Wilson *et al.*, 1985, 1986). This was attributed by Wilson *et al.* (1985) to the oxidation of organic matter in a turbidite layer. A relatively shallow depth (25–30 cm) of oxygen penetration was also observed by Rutgers van der Loeff (1991) (*area* 11) in a core from the Porcupine Abyssal Plain. However, even at such localities, meiobenthos living in the upper 5 cm of sediment in the northeast Atlantic should not normally experience a lack or shortage of oxygen.

3.3. Food Supply

Food availability often exerts a decisive influence on faunal densities. Except around hydrothermal vents, the food that sustains benthic communities originates mainly from surface water primary production

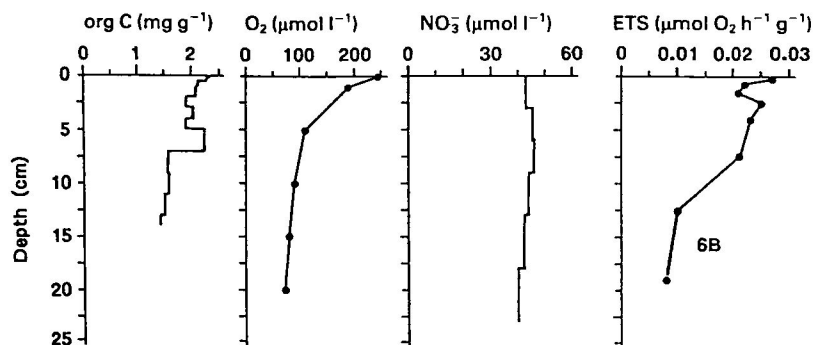


Figure 2 Vertical profiles in the sediment of organic carbon, O₂, NO₃⁻ and ETS activity at the DORA site (area 11; sample 6B) (after Rutgers van der Loeff and Lavaleye, 1986).

with some input from terrestrial sources. The most recent map of surface production in the Atlantic Ocean (the "Dahlem Map"; Berger, 1989; Figure 3) shows decreasing values from the northern margin of our region to about 35°N. Further south surface productivity increases in association with the coastal upwelling off northwest Africa. Export production (net particulate flux of carbon across the thermocline) shows a similar pattern (Berger *et al.*, 1988).

Only scattered data are available regarding the distribution of organic matter in northeast Atlantic sediments. Emery and Uchupi (1984) present a generalized map, based on literature sources, showing the organic carbon content of dried sediment for the whole of the Atlantic. In the northeastern part, values tend to decrease with increasing bathymetric depth. Seaward of the continental margin the organic carbon content generally lies between 0.25 and 0.50% with a southwest to northeast trending zone of higher values (0.5–1.0%) between about 25–35°N and 20–40°W. According to Sibuet (1984), the organic carbon content of sediments from deep basins in the Atlantic Ocean varies from 0.17 to 0.85%. Auffret (1985) gives values ranging from 0.2 to 0.7% at depths between 2000 and 4800 m in the Bay of Biscay. CHN analyses of Porcupine Seabight sediments after acid digestion yield organic carbon values of 0.5% dry weight with no distinct trend with depth (Rice *et al.*, 1991). Higher values (0.5–4.0%) have been recorded in late Pliocene and Pleistocene sediments from ODP (Ocean Drilling Project) site 658, situated under the upwelling area off Cap Blanc (Stein, 1991). As noted above, higher values are also associated with turbiditic sediments.

A more meaningful indication of food availability is provided by

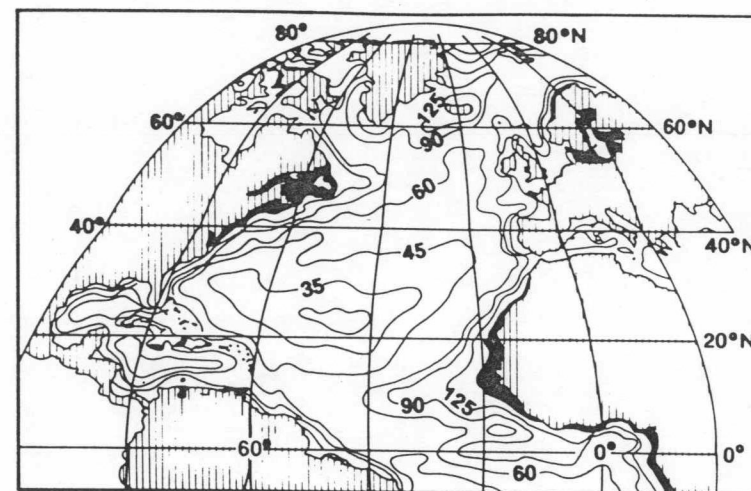


Figure 3 Surface primary production (g C m⁻² year⁻¹) map of the North Atlantic (after Berger, 1989). Black areas near the coast indicate values >150 g C m⁻² year⁻¹.

chloroplasic pigment equivalents (CPE) which reflect the amount of organic matter originating from primary production. Detailed information of CPE values from particular areas off northwest Africa and Europe are given by Thiel (1978, 1983), Pfannkuche *et al.* (1983) (area 18), Pfannkuche (1985) (areas 1–4). Off northwest Africa, particularly high CPE values in the sediments are associated with intense upwelling; although the patterns are complicated by local currents which influence the deposition of organic matter (Thiel, 1978, 1982; Pfannkuche *et al.*, 1983).

Most chloroplasic pigments probably originate from phytodetritus which represents an important mechanism for rapidly delivering organic matter originating from surface production to the ocean floor (Gooday and Turley, 1990). Large amounts of this material have been observed on the ocean floor in the Porcupine Seabight (areas 1–3), on the Porcupine Abyssal Plain (area 4) (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986, 1991), the BIOTRANS area (area 12) (Thiel *et al.*, 1989–1990), the Rockall Trough and the Bay of Biscay (Gooday and Turley, 1990). In these northern areas, phytodetritus deposition seems to be associated with deep (>500 m) winter mixing (Robinson *et al.*, 1979), in addition to relatively high surface productivity. However, recent evidence indicates that phytodetritus is also deposited further south in areas where the mixed layer is <150 m in depth. Christiansen and Thiel (1992) observed

abundant flocculent material in depressions and around mounds on the Madeira Abyssal Plain (34°N) and small amounts were present in multiple corer samples taken at the IOSDL southern site (31°N). Phytodetritus has also been photographed on the seafloor even further south, at 19°S (McCave, 1991). Pfannkuche (1993b) provided data on seasonal variation in CPE.

3.4. Deep Bottom Water Masses

In the North Atlantic, and other oceanic regions, some modern foraminiferal species assemblages show good local correlations with the water masses which bathe the ocean floor (Streeter, 1973; Schnitker, 1980; Weston and Murray, 1984). A similar correlation has not been established for meiobenthic taxa other than foraminifera, but this may reflect a general lack of species level distributional data for the metazoan meiobenthos. The only other examples of a correlation between water mass and animal distributions in the deep sea are provided by Patterson *et al.* (1982) for five North Atlantic species of the ophiuroid genus *Ophiocten* and by Tyler and Zibrowius (1992) for suspension feeding echinoderms southwest of Iceland. In the latter case the associations clearly are linked to the current activity rather than to water masses as such.

In the eastern North Atlantic, the deep waters consist mainly of North Atlantic Deep Water (NADW), a composite water mass with an upper, low salinity (<34.94‰) layer, a middle layer of Norwegian Overflow Water (salinity 34.96–35.03‰), and a lower layer which consists of Norwegian Overflow Water diluted by mixing with Denmark Strait Overflow Water (Worthington, 1976; Weston and Murray, 1984; Gage and Tyler, 1991). The upper NADW layer, which unlike the lower layer originates from the Labrador Sea, is often considered as a separate entity, the North East Atlantic Deep Water (NEADW). At depths less than about 2000 m, the dominant water mass in the northeast Atlantic is Mediterranean Water which flows through the Straits of Gibraltar, around the European continental margin, through the Rockall Trough and into the Norwegian Sea, becoming progressively diluted as it proceeds northwards. Mediterranean Water is characterized by its high density and salinity and by its variable physical properties (Weston, 1985).

Below about 4500 m, the deep basins off the African coast are occupied by a distinct water mass which originates from the Antarctic. This Antarctic Bottom Water (AABW) is restricted to areas south of about 36°N, where its passage is blocked by ridges associated with the Azores

Fracture Zone. AABW is characterized by low temperatures and salinities and by relatively high dissolved oxygen and nutrient concentrations.

3.5. Near-bottom Currents

In the northwest Atlantic, unusually high current speeds (20–25 cm s⁻¹) occur during periodic “benthic storms” which originate when eddy kinetic energy derived from near-surface eddies impinges on the ocean floor (Richardson *et al.*, 1981; Hollister and McCave, 1984; Gross *et al.*, 1988). These events erode and redistribute bottom sediments and strongly influence the character of meiobenthic communities (e.g. Thistle *et al.*, 1985). Recently there has been some evidence for benthic storms in the northeast Atlantic; currents capable of eroding and depositing sediments are associated with the sediment drifts which are extensively developed to the west of the Rockall Trough and elsewhere (Emery and Uchupi, 1984). At BIOTRANS (area 12), the deep mean flow is 3–5 cm s⁻¹ but benthic storms occur with durations between 3 and 27 days with maximum velocities of 27 cm s⁻¹ (Klein and Mittelstaedt, 1992). Maximum current velocities here may approach 40 cm s⁻¹ (Dickson and Kidd, 1987) and must have an impact on the benthic fauna similar to that described by Thistle *et al.* (1985). Away from such areas, the near-bottom currents are fairly gentle and probably have little impact on the meiobenthos beyond the transportation of nutrients and larvae. A residual boundary current flows northward along the continental margin of northwestern Europe and has superimposed on it diurnal or semidiurnal tidal currents (Dickson *et al.*, 1986). Rice *et al.* (1991) summarize information on currents flowing near the floor of the Porcupine Seabight. At a depth of 4025 m, near the mouth of the Seabight, current speeds varied semidiurnally and reached a maximum on the western side of the Porcupine Bank (Norris and McDonald, 1986). Measurements made during the BIOGAS programme indicate current speeds of generally less than 10 cm s⁻¹ at abyssal depths (Vangriesheim, 1985). Current speeds in more central oceanic regions are presumably lower than along the continental margins.

4. HORIZONTAL SPATIAL PATTERNS

When comparing quantitative meiobenthos data at an ocean-wide scale, one must take account of the variability in population density on different

scales: from small-scale (within one corer) and medium-scale (between corers from nearby locations) to large-scale (ocean-wide scale; e.g. Thiel, 1983). In this section both bathymetric and latitudinal trends in meiobenthic density, and composition at different taxonomic levels, will be discussed. The lack of standardization in sampling (Bett *et al.*, 1994) and in processing techniques (e.g. different mesh sizes) complicates the comparison of data from different meiobenthic investigations. Data evaluation is therefore a challenge and observations of differences in faunal densities and changes in faunal composition have to be made with some caution.

4.1. Bathymetric Trends

4.1.1. Faunal Densities

There is a general tendency (see reviews Thiel, 1983 and Tietjen, 1992) for metazoan meiobenthic densities to decrease with increasing bathymetric depth within limited geographical areas (i.e. under constant climatological and ecophysiological life conditions). This tendency does not hold for the total northeast Atlantic ocean, as illustrated in Figure 4, in which the mean densities per *area* are plotted as a function of mean water depth. In general the lowest densities are recorded at abyssal depths where mean densities for each *area* are never higher than 600 individuals (ind)/10 cm², and the highest densities are found in the shallowest *areas* (<1000 m: mean per *area* up to 2000 ind/10 cm²), but occasionally densities of less than 500 ind/10 cm² are recorded on the upper slope and in the shelf break area.

Densities do not always decrease in relation to depth within smaller geographical regions (Figure 5) which may show different and sometimes conflicting patterns of density gradients: for example off Mauretania, off Morocco, off Gibraltar, in the Bay of Biscay, and on the Iberian, Madeiran and Porcupine abyssal plains.

In the southern part of the northeast Atlantic, off the coast of Mauretania, densities were relatively high at the deepest sites (*areas* 27, 28 and 29: means 500–1000 ind/10 cm²), higher than on the upper slope and in the shelf break area (*area* 26: 500 ind/10 cm²) (Thiel, 1975; Dinét, unpublished). The lack of any depth-associated gradient in this area, and the relatively high densities on the lower part of the slope, are due to increased primary production resulting from intense upwelling activity in the water column, and providing high food input to these deeper *areas*. Low densities on the upper slope can be explained by hydrodynamic processes, which cause erosion and prevent organic matter from reaching

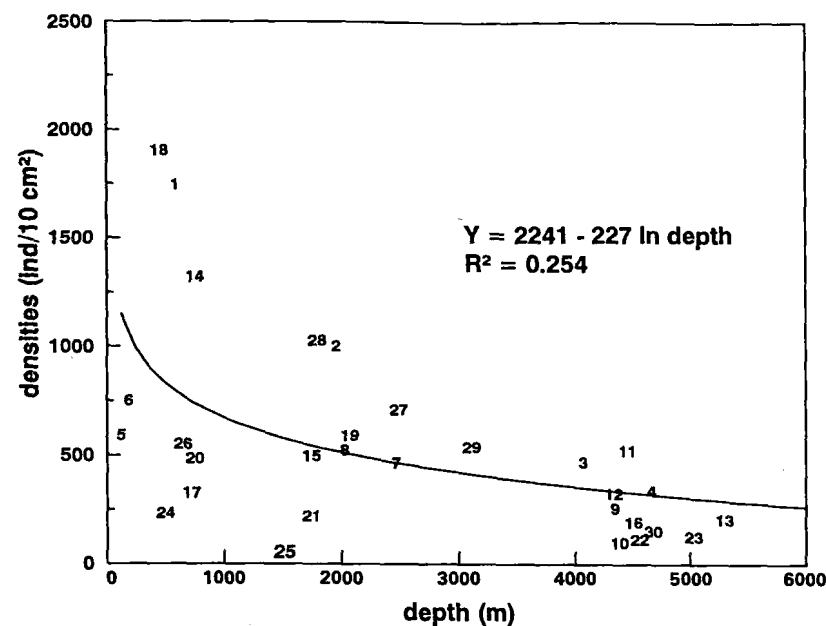


Figure 4 The relationship between mean metazoan density and mean water depth of each *area* (30 *areas* as defined in Table 1) in the northeast Atlantic.

the seafloor (Thiel, 1983). At the oligotrophic abyssal site (*area* 30) situated on the same latitude, and intensively studied by the EUMELI project (Dinét, unpublished), much lower densities are found in comparison to the slope (200 ind/10 cm²).

Along the NW African coast, off Morocco, densities are in general low. Some higher values were recorded for the upper slope (*area* 20: 500 ind/10 cm²), but deeper down the meiobenthos is very poorly represented (*areas* 21 and 22: <250 ind/10 cm²). From 1000 m depth, the densities are similar to those of *area* 23 on the Madeira Abyssal Plain, which has been intensively investigated by IOSDL (Gooday, unpublished).

Two relatively shallow (<1750 m) sites located on the Great Meteor seamount, near the western border of the Madeira Abyssal Plain, also have low meiobenthic densities (*areas* 24 and 25: <250 ind/10 cm²). Beside their central oceanic location, a higher predation pressure and current activity are possible causes of the low abundances (Thiel, 1983).

Off Gibraltar, Thiel (1975) found much lower densities on the upper slope (*area* 17: 300 ind/10 cm²) than Pfannkuche *et al.* (1983) on a nearby transect off the African coast (*areas* 18 and 19: 600–2000 ind/10 cm²). In the latter study, meiobenthic abundances showed a significant correlation with CPE concentrations, which decreased with water depth. Thiel (1983)

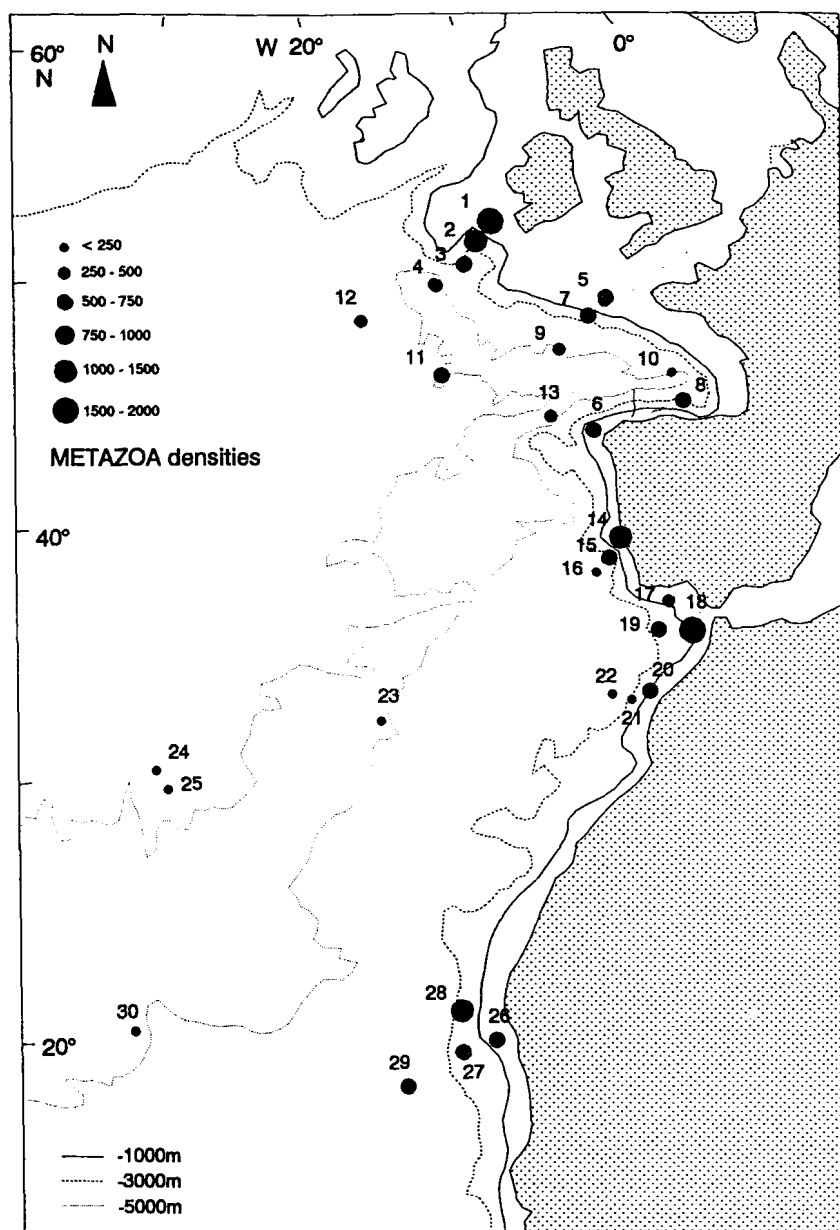


Figure 5 Map of the northeast Atlantic showing the mean metazoan density for each area (as defined in Table 1) (ind/10 cm²).

explained the lower densities found during the *Meteor 21* cruise by the outflow of warm Mediterranean water, which accelerates along the Atlantic slope due to its higher density, preventing the sedimentation of detritus.

On a transect near the Portuguese coast (Thiel, 1975), meiobenthic densities decrease from 1400 to 100 ind/10 cm² in relation to bathymetric depth (areas 14, 15 and 16).

In the Bay of Biscay, densities decrease more-or-less with depth, although the upper slope and the shelf break sites are characterized by relatively low numbers (areas 5, 6, 7 and 8: 450–750 ind/10 cm²) (Vanreusel *et al.*, 1992 and unpublished; Diné and Vivier, 1977; Thiel, 1975). Vanreusel *et al.* (1992) explained these low numbers in terms of the low chlorophyll-a content and/or the coarseness of the sediments. In adjacent abyssal regions (areas 9 and 10), Diné and Vivier (1977) observed a larger variability, which they associated with sedimentological heterogeneity and hydrodynamical disturbance. In these areas, the sediments seem to be unusually coarse and unstable, due to the presence of submarine canyons which elevate current activity (Diné and Vivier, 1977).

Finally, an obvious decrease in the meiobenthic densities, related to diminishing CPE content with depth, is found in the Porcupine Seabight (from 2000 to 450 ind/10 cm²) (Pfannkuche, 1985).

Tietjen (1992) described the distribution of metazoan meiofauna of the global Atlantic Ocean by the following logarithmic function of depth: $Y = 6238 - 710.5 \ln \text{depth}$ ($R = -0.89$). As shown in Figure 4 this relationship is not found for data of the northeast Atlantic. This function is only approached (Figure 6; $Y = 5837 - 666 \ln \text{depth}$, $R^2 = 0.896$) when mainly shallow areas which were characterized by much lower densities than expected (as discussed above) because of hydrodynamical processes (areas 17, 20, 21, 26), their off-shore location (areas 24, 25) or sedimentological characteristics (areas 5, 6) are omitted. Tietjen (1992) also considered only four sites shallower than 1000 m in describing this strong functional relationship.

Nematode densities range from 5 ind/10 cm² in the Gulf of Biscay (Diné and Vivier, 1977) to 2382 ind/10 cm² in the Porcupine Seabight (Pfannkuche, 1985). Nematodes represent 80–99% of the total metazoan abundances and are therefore mainly responsible for the depth-related tendencies found for the metazoans (see Figures 4, 6). This is illustrated by Figure 7 which shows a weak negative relationship between nematode densities and water depth. However, excluding the two most shallow areas 5 and 6 at the shelf break of the Bay of Biscay strengthens the relationship ($R^2 = 0.870$, $Y = 5400 - 613 \ln \text{depth}$). The exclusion of these two areas can be justified by their exceptional coarse sediment and their shallow location at the shelf break.