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The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (NE Atlantic)

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Abstract

We provide an overview of the role of biological processes in the Benthic boundary layer (BBL) and in sediments on the cycling of particulate organic material in the Goban Spur area (Northeast Atlantic). The benthic fauna, sediment and BBL characteristics were studied along a transect ranging from 208 to 4460 m water depth in different seasons over 3 years.

Near-bottom flow velocities are high at the upper part of the slope (1000–1500 m), and high numbers of filter-feeding taxa are found there such that organic carbon normally passing this area during high flow conditions is probably trapped, accumulated, and/or remineralised by the fauna.

Overall metabolism in shelf and upper slope sediments is dominated by the macrofauna. More than half of the organic matter flux is respired by macrofauna, with a lower contribution of metazoan meiofauna (4%) and anoxic and suboxic bacterial mineralisation (21%); the remainder (23%) being channelled through nanobiota and oxic bacteria. By its feeding activity and movement, the macrofauna intensely reworks the sediments on the shelf and upper slope. Mixing intensity of bulk sediment and of organic matter are of comparable magnitude.

The benthos of the lower slope and abyssal depth is dominated by the microbiota, both in terms of total biomass (>90%) and carbon respiration (about 80%). The macrofauna (16%), meiofauna (4%) and megafauna (0.5%) only marginally contribute to total carbon respiration at depths below 1400 m. Because large animals have a lower share in total metabolism, mixing of organic matter within the sediments is reduced by a factor of 5, whereas mixing of bulk sediment is one to two orders of magnitude lower than on

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the shelf. The food quality of organic matter in the sediments in the shallowest part of the Goban Spur transect is significantly higher than in sediments in the deeper parts. The residence time of mineralisable carbon is about 120 d on the shelf and compares well with the residence time of the biota. In the deepest station, the mean residence time of mineralisable carbon is more than 3000 d, an order of magnitude higher than that of biotic biomass. © 2001 Published by Elsevier Science Ltd.

1. Introduction

Sediments are an important component in global biogeochemical cycles, and benthic fauna play a major role in determining their geochemical behaviour. Suspension-feeding fauna actively remove particles from the water column and deposit it as faeces either within or on top of the sediment, a process called biodeposition (Graf and Rosenberg, 1997). Feeding pits, faecal pellet mounds, and tube-structures of the benthos locally can change the current regime and cause resuspension and passive biodeposition of particles (Carey, 1983; Jumars and Nowell, 1984; Miller et al., 1984). Bioturbation due to moving animals or due to bulk feeding by deposit feeders substantially modifies the physical and geochemical properties of sediments (Boudreau, 1994; Gage and Tyler, 1991; Soetaert et al., 1996a, b).

The organic fraction of the particle input to the sediment is a potential energy source for benthic organisms. It is remineralised, and carbon dioxide and nutrients are produced and flow back into the pelagic system (Wassmann, 1990). Part of the organic matter is not remineralised and is buried in the sediment preventing return of its degradation products to the pelagic system. Therefore, the mineralisation of organic matter through respiratory processes is an important aspect of the global ocean carbon cycle.

Benthic mineralisation processes can be modelled by means of early diagenetic models, which describe the sediment depth profiles of organic carbon, oxygen and nutrients (e.g., Berner, 1980; van Weering et al., 2001). These models allow to quantify the relative importance of the various competing pathways (oxic mineralisation, denitrification, sulphate reduction, etc.) in total mineralisation, the direction and magnitude of sediment-water exchanges of solutes, the intensity of mixing, and even the food quality (Soetaert et al., 1998). The activity of animals is largely parameterised in these models. The impact of animal movement and feeding is represented by a bioturbation coefficient (Boudreau, 1986), and respiration is modelled as a first-order decay of organic matter. Obviously, these are simplifications which only schematically represent the complexity of benthic biological processes.

An alternative approach to assess benthic respiration is by looking at the actors, the benthic animals and bacteria. Respiration by the various benthic groups can be estimated based on weight-specific allometric relationships (Mahaut et al., 1995). Although estimating animal biomass may be tedious and time-consuming, it is necessary for an adequate partitioning of total system respiration in the different biotic categories, which may be instructive as to the recycling capacity and residence time of organic matter in the sediments.

In the OMEX project, the general aim was to study the physical, chemical and biological processes at ocean margins—the shelf break and the continental slope—that determine the transport of material from the shelf to the deep sea. The aim of the subproject Benthic Biology

within OMEX was to evaluate the role of biological processes in the benthic boundary layer and in the sediments in the cycling of particulate organic material. Both the geochemical approach and the more biologically oriented study of ocean margin sediments were adopted, therefore, offering a unique opportunity to understand the functioning of these important components of the global ocean.

In this synthesis paper we focus on the role of benthic animals in sedimentary metabolism and benthic-pelagic coupling. We briefly summarise information on the benthic community already described in several papers from the project (Duineveld et al., 1997; Flach and Heip, 1996a, b; Flach et al., 1998, 1999; Flach and Thomsen, 1998; Soetaert et al., 1996c, 1997; Thomsen and Flach, 1997; Vanaverbeke et al., 1997). The flow of organic matter through all the different biotic compartments is assessed by re-evaluating the available data.

This paper, therefore, describes the ultimate fate of organic matter that originates in the euphotic zone (Joint et al., 2001), sinks through the water column (Antia et al., 1999; Herman et al., 2001), and is deposited on the sediments of the Goban Spur area. In contrast to the paper of van Weering et al. (2001), where emphasis is on biogeochemical and geological aspects of the sediment, our paper centres mainly around the biological properties.

2. Material and methods

2.1. Study site

The OMEX-transect (Fig. 1, Table 1) is situated at the Goban Spur area in the NE Atlantic, reaching from the continental shelf of the Celtic Sea (Station A, 208 m), along the continental slope, down to the Porcupine Abyssal Plain (Station E, 4460 m). Bottom-water temperature decreased from ~11°C at the shallowest stations (~200 m) to ~2.5°C at the deepest stations (~4 km). The bottom water was well oxygenated (200–300 µmol l^{-1}); lowest oxygen concentrations were observed at around 1000-m depth (van Weering, 1994).

Samples were taken in October 1993, May/June 1994, and August 1995 (Table 1).

Median grain-size decreased from ~95 µm at 208 m to ~8 µm below 2000 m, and the percentage of CaCO$_3$ increased with increasing water depth from ~20% at 208 m to ~70% at ~4000 m (Flach and Heip, 1996a). Sediments were homogeneous to a depth of 15 cm at all stations (Flach and Heip, 1996a), and no changes in sediment composition between the 3 years were observed (Flach and Heip, 1996b). The organic content of the sediment was low and varied between about 0.1% and 0.7% C in the upper 1 cm (Lohse et al., 1998).

2.2. Benthic boundary layer (BBL) characteristics

Water samples at 5, 10, 20 and 40 cm height above sea floor were taken with the BIOPROBE bottom-water sampler (Thomsen et al., 1994) during five cruises to Goban Spur in October 1993, January, May and September 1994, and August 1995. Flow velocity in the BBL was measured with a thermistor flow meter at 30-cm height above bottom (ADM Instruments) and by analysis of pictures obtained by the particle cameras. A normal launch involved lowering the instrument system to the sea floor using a single conductor cable (10-mm diameter, 200 g m^{-1} in water)
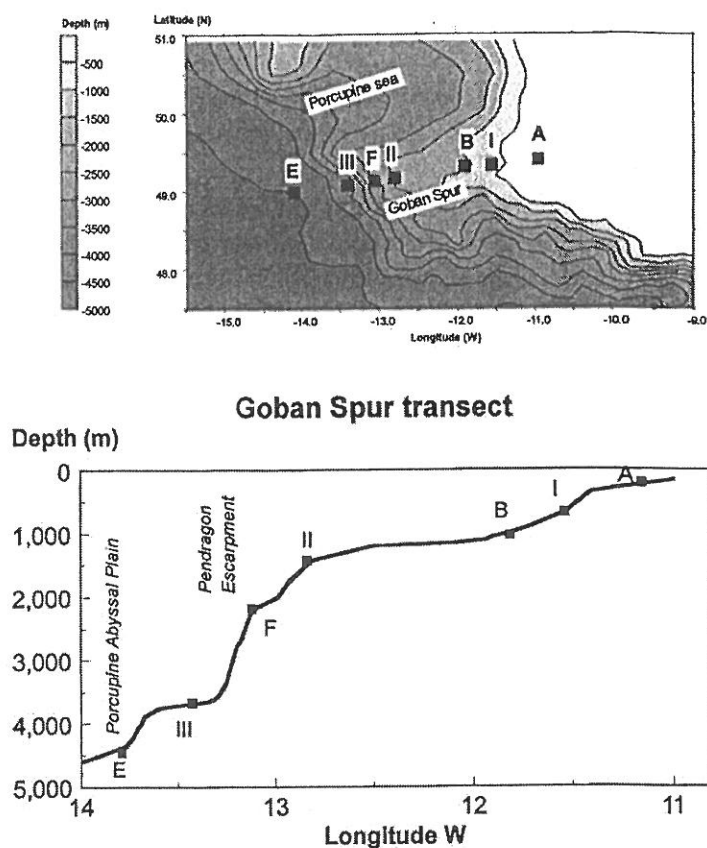
Fig. 1. Location of the OMEX transect and sampling stations.

monitoring flow velocity, light transmission in the BBL, compass direction (position), and battery capacity of BIOPROBE.

Particulate organic carbon (POC) of water was measured with a Heraeus CHN-Analyser after removal of calcium carbonate. Chloroplastic pigment equivalents (CPE) were analysed spectro-fluorometrically with a Turner-Designs Fluorometer and calculated using the equations of Lorenzen (1967). Total particulate matter (TPM) was determined using the method of Bodungen et al. (1991).

2.3. Benthic density and biomass

Density values of the different faunal groups were compared for May 1994 when data were available for all of them except the megafauna (all stations), which was sampled only in August 1995. Biomass values were averaged over all samples that were obtained (see Table 1). In view of the different numbers of samples, no attempt was made to attribute errors to these values.

The biomass of the smallest benthic organisms (bacteria, protozoans, and a small fraction of the meiofauna) was assessed by analysis of phospholipid concentration (indicative of cell-wall

Table 1
Sampling stations and data used[a]

Station	°N	°W	Depth (m)	Date	Mega	Macro	Meio	Bact	Db (^{210}Pb)	Diagenetic model
A	4929	1108	208–231	10/93			B, R	B	+	+
				05/94		D, B, R	D	B	+	
				08/95	D, B, R	B, R		B		
I	4925	1132	670–693	10/93		B, R	B, R		+	+
				05/94		D, B, R	D	B	+	+
				08/95	D, B, R	B, R		B		
B	4922	1148	1021–1034	10/93		B, R	B, R	B	+	+
				05/94		D, B, R	D	B	+	+
				08/95	D, B, R	B, R		B		
II	4911	1249	1425–1457	10/93		B, R	B,R	B	+	
				05/94		D, B, R	D	B	+	
				08/95	D, B, R	B, R		B		
F	4909	1305	2182–2254	10/93		B, R	B,R		+	
				05/94		D, B, R	D	B	+	
				08/95	D, B, R	B, R		B		
III	4905	1326	3648–3673	10/93					+	
				05/94		D, B, R	D	B		+
				08/95	D, B, R	B, R		B		+
E	4902	1342	4460–4470	10/93					+	
				05/94		D, B, R	D	B		
				08/95	D, B, R	B, R	B, R	B		

[a] D, density; B, biomass; R, respiration.

material) from five replicate samples per station for each sampling date (Soltwedel, 1997). Phospholipid concentrations were converted to biomass using the conversion $100 \, \mu mol$ $P \, cm^{-3} = 0.1 \, g \, C \, m^{-2}$ for each cm depth layer (Soltwedel, 1997; after Findlay and Dobbs, 1993, who assumed $100 \, \mu mol \, P \, g \, C^{-1}$ for prokaryotes).

Sediment samples for faunal analysis were taken with the circular boxcorer of the Netherlands Institute of Sea Research (NIOZ). Because of logistic reasons different numbers of boxes of different sizes were taken at different stations. Boxcores with a diameter of 30 cm (mainly used at the shallow stations) and 50 cm, both equipped with a top valve to prevent leakage, were used. For the study of living benthic foraminiferal communities, a boxcore subsample was collected at each sampling station in May 1994, by carefully inserting a PVC tube of 9-cm inner diameter into the box core until at least 10 cm depth as described by Flach et al. (1998). One subsample for the meiofauna was taken using $10 \, cm^2$ plastic cores out of two boxcores per station in October 1993 (Vanaverbeke et al., 1997), May 1994, and for the deepest station in August 1995 (Flach et al., 1999). Station III was not sampled, and the data shown in Figs. 4 and 5 are interpolations from the values of Stations F and E. Density was estimated as described in Vanaverbeke et al. (1997) following Heip et al. (1985), and nematode biomass was calculated from Andrassy's formula (Andrassy, 1956), assuming a carbon-to-wetweight ratio of 0.125 (Vanaverbeke et al., 1997).

For macrofaunal analysis, the boxcore samples were sliced and sieved on a 0.5-mm sieve (Flach and Heip, 1996a). This sieve size is larger than the one normally used by deep sea biologists, but

was chosen to decrease overlap with the meiofauna fraction and because of a very considerable time gain in the analysis. Flach (unpublished) compared samples washed through 0.5 and 0.3 mm sieves and found a consistent difference along the transect of about 40% in density estimates but no significant difference in biomass and respiration estimates. The macrofaunal taxa were divided in carnivores/scavengers, filter-feeders (feeding from the water column), interface-feeders (which can switch from filter-feeding to deposit-feeding; Taghon and Greene, 1992), surface and subsurface deposit-feeders. Feeding-types were determined on the smallest taxonomic level possible (see Flach et al., 1998). Biomass values were converted into organic C-content per major taxon using the conversion factors given by Rowe (1983). The megafauna was sampled quantitatively in August 1995 with a 3.5-m Agassiz trawl (see Duineveld et al., 1997). The mesh width of the net was 1 cm. When possible the animals were identified down to species. As a lower arbitrary size limit for megafauna, we used the definition of Rutgers van der Loeff and Lavaleye (1986), i.e. an animal must have a diameter of at least 1 cm or weigh at least 50 mg (blotted wet weight). The animals were divided according to feeding guilds into deposit-feeders, filter-feeders and carnivores. Demersal fish, living close to the sea floor (within 1 m), were included in the megabenthos.

2.4. Benthic respiration

Sediment community oxygen consumption (SCOC) was measured in situ and in decompressed cores on board (see Duineveld et al., 1997). For the shipboard measurements two intact boxcore samples of 30-cm diameter were used. After sealing the incubation cores with a lid holding a stirrer and O_2 probes (Yellow Spring Instr.), they were transferred to a thermostatically controlled incubator set at bottom temperature. The O_2 decrease in the overlying water was continuously recorded. The initial linear decrease of O_2 was used for calculating SCOC. In situ measurements of SCOC were made with a free-falling benthic lander, the BOLAS, as described by Tahey et al. (1996).

The respiration of the various faunal groups was estimated based on mean individual dry weight using a power law (Mahaut et al., 1995):

$$R = aW^b$$

where R is the respiration rate of an individual (d^{-1}), W the biomass in mg C. The individual rates were summed up over all individuals in the sample and extrapolated to a 1 m^2 surface area.

For the macro- and megafauna, respiration rates, valid at temperatures of 2–4°C, were estimated as:

$$R = 0.0074\ W^{-0.24}$$

Corrections for temperature were made using Krogh's "normal curve" (Winberg, 1971). Annual respiration of the macrofauna was calculated out of the three different seasons.

Nematode respiration, valid at 20°C, was estimated as:

$$R = 0.0164\ W^{-0.1456}$$

(de Bovée and Labat, 1993; Soetaert et al., 1997). Conversion to the in situ temperatures was done assuming a Q_{10} value of 2 (Soetaert et al., 1997).

The respiration of the small biota (bacteria and protozoans) was estimated as the difference between total SCOC rates and respiration rate of the metazoan organisms.

2.5. Food quality

The total amount of mineralisable organic matter ("food") in the sediment can be estimated based on the diagenetic modelling results of Herman et al. (2001), using the method outlined in Soetaert et al. (1998). We ignored the totally refractory compounds as they are not consumed by organisms, although they constitute the largest component of carbon below, say, 5-cm depth. In short, the degradability of organic matter settling on the sediment surface was assessed by modelling oxygen, nitrate, ammonium and organic carbon versus sediment depth profiles. The mean degradability of mineralisable organic matter in the sediment was then calculated by integrating its concentration over the entire sediment depth.

3. Results

3.1. Densities

In May 1994, living Foraminifera decreased from $\sim 10 \, cm^{-2}$ ($1 \times 10^5 \, m^{-2}$) at the shelf to less than $2 \, cm^{-2}$ ($2 \times 10^4 \, m^{-2}$) at the base of the slope (Fig. 2; Table 2). A secondary peak in density was observed at the mid-slope station II at 1465 m, due to high numbers of *Astrorhizidae* (Flach et al., 1998). Meiofaunal densities were more or less similar along the whole depth range, ranging from 423 per $10 \, cm^2$ ($4 \times 10^5 \, m^{-2}$) at station A to 649 per $10 \, cm^2$ ($6 \times 10^5 \, m^{-2}$) at St. II. Meiofauna mainly consisted of *Nematoda* (88–95%) (Vanaverbeke et al., 1997). Macrofaunal densities strongly decreased with increasing water depths, from about $8000 \, m^{-2}$ at the shelf to about $500 \, m^{-2}$ at the two deepest stations. Polychaetes were the most abundant taxon at all stations, although their relative share decreased with increasing water depth from $\sim 75\%$ at the shelf to $\sim 40–50\%$ at mid-slope depths and increased again at the deepest stations to $\sim 60\%$

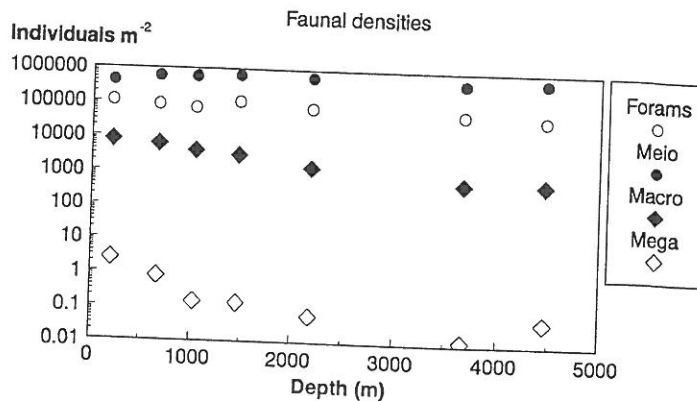

Fig. 2. Densities of the various benthic taxa in May 1994 (except for the megafauna, which was sampled in August 1995).

Table 2
Densities per m^2 of different faunal groups in 1994 (Megafauna in August 1995)

Station	Depth	Forams	Meio	Macro	Mega
A	208	107800	423000	7980	2.478
I	670	87000	589000	6169	0.782
B	1034	71400	578000	3952	0.143
II	1465	110400	649000	3062	0.133
F	2182	76400	603000	1413	0.059
III	3670	53800	446000	518	0.013
E	4460	42600	529000	542	0.049

(Flach and Heip, 1996a). Megafaunal densities (in August 1995) also decreased with increasing water depths, from ∼2500 per 1000 m^2 (2.5 m^{-2}) at the shelf to ∼50 per 1000 m^2 (0.05 m^{-2}) at the lower part of the slope. On the shelf *Ophiuroidea* dominated the megafauna, whereas at the deeper stations *Holothuroidea* were more abundant (Duineveld et al., 1997).

The different rates of decrease in abundance of the different faunal groups with increasing water depths resulted in different community structures at different depths. Megafauna decreased faster than macrofauna, whereas macrofauna and foraminiferans decreased faster than metazoan meiofauna. With increasing water depths benthic communities thus become more dominated by smaller taxa.

3.2. BBL characteristics and feeding characteristics of the macrofauna

In Fig. 3 the variation of total density of filter- and interface-feeders with station depth is compared with several independent variables measured in the water of the benthic boundary layer (concentrations at 5 cm above the bottom of total particulate matter, TPM, particulate organic carbon (POC), chloroplastic pigment equivalent (CPE) and flow velocity at 30 cm above the bottom; see material and methods). Most variables are negatively correlated with station depth; the correlation is better after log-transformation than for the arithmetic values. The correlation coefficients of POC ($p = 0.08$) and CPE concentrations ($p = 0.16$) with water depth are not significant. Due to this general depth-dependence of all variables, the correlation between environmental variables and density of filter- (+interface−) feeders was investigated using partial correlation coefficients, correcting for depth as a common variable (Sokal and Rohlf, 1995). Only CPE concentration showed a marginally significant partial correlation with density of filter- and interface-feeders ($r_{12,3} = 0.86$, $n = 6$, $p = 0.06$). The probability level of the other partial correlation coefficients was > 0.5.

3.3. Biomass

The biomass of the different benthic groups is given in Table 3. The average value and the relative share in the total biomass are shown in Fig. 4. The microbiota (bacteria and protists) dominated everywhere; they contributed more than 75% to the total biomass in the three shallowest stations (<1050 m; stations A, I, B), about 90% or more in the deeper stations. The
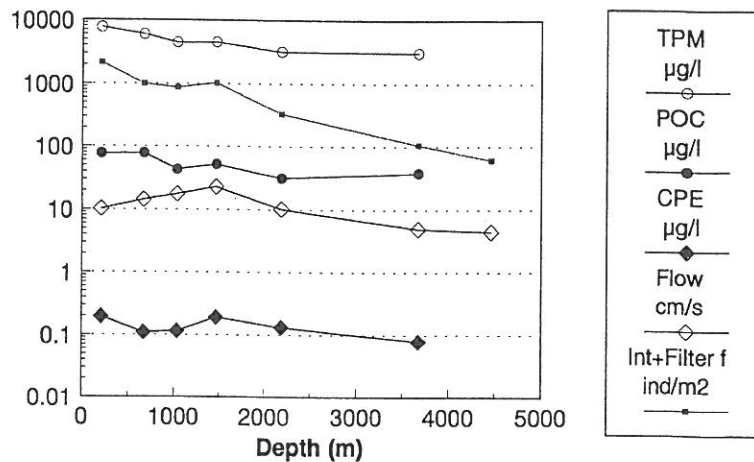
Fig. 3. Total particulate matter (TPM, $\mu g l^{-1}$), particulate organic carbon (POC, $\mu g l^{-1}$), chloroplastic pigment equivalents (CPE, $\mu g l^{-1}$), flow velocity (cm s^{-1}) and density of filter- and interface feeders (ind m^{-2}) versus water depth.

Table 3
Mean concentration at 5 cm above the bottom in the BBL of total particulate matter (TPM), Particulate organic carbon (POC) and Chlorophyll pigment equivalents (CPE). Mean flow velocity 30 cm above the bottom (Flow). Density of filterfeeders and interface feeders (individuals m^{-2})

Station	Depth (m)	TPM (mg l^{-1})	POC ($\mu g l^{-1}$)	CPE ($\mu g l^{-1}$)	Flow (cm s^{-1})	Filter feeders (ind m^{-2})	Interface feeders (ind m^{-2})
A	208	7.7	77	0.196	10.2	826	1334
I	670	6	77.5	0.109	14.25	534	459
B	1034	4.45	43	0.115	17.5	532	343
II	1425	4.5	51.5	0.191	22.75	532	500
F	2182	3.2	31.5	0.132	10.15	201	129
III	3670	3.1	38	0.079	5	35	71
E	4460				4.5	61	0

macrofauna was the second most important group. About 10% of total biomass was due to small macrofauna on the stations below 100 m (stations A, I, B). Some exceptionally large animals (1 *Pennatulacea* and 1 *Sipunculida* at station B in May 1994; 2 *Echinoidea* at station A in August 1995, 1 *Holothuroidea* at station E in May 1994) contributed 10% to total biomass at these stations (called "large macrofauna" in some tables and figures). As these animals are not quantitatively estimated by the sampling procedure, they were considered separately. Both the meio- and megafauna were unimportant in terms of biomass (about 1% on average; Fig. 4).

In general the biomass of all benthic groups was lower in the deep stations than on the shelf (Fig. 4), but only nematode biomass exhibited a monotonous decline with depth (Vanaverbeke et al., 1997). The highest microbial biomass was observed at station II (1420 m). Macrofaunal biomass was rather constant at the shelf and upper slope (<1050 m; stations A, I, B) and was
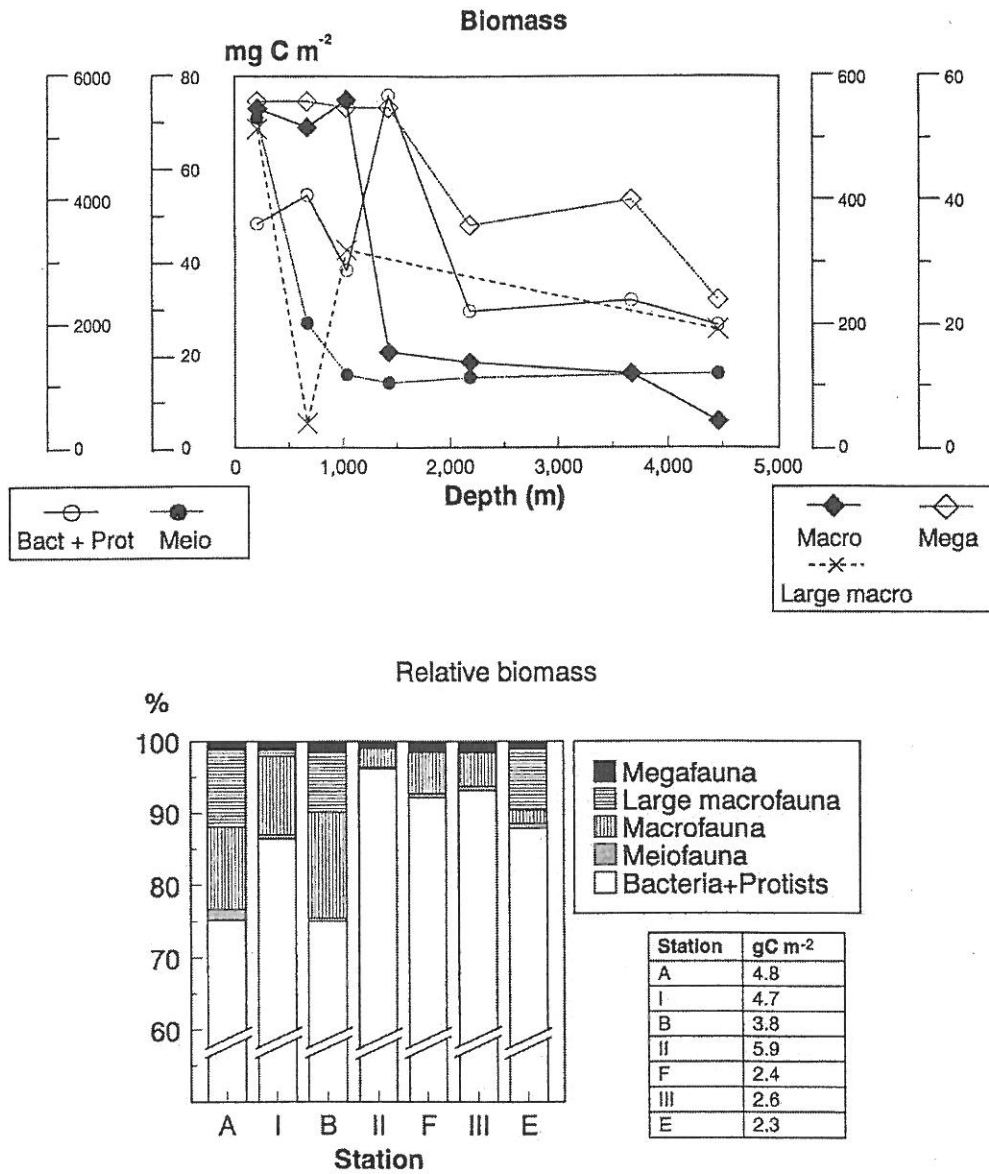
Fig. 4. (a) Biomass of the various taxa, (averaged over all sampling dates, see Table 1); (b) relative share of the various taxa.

significantly depressed below that depth. Similarly, megafaunal biomass was about double at the shelf and upper slope stations (<1500 m; stations A, I, B, II). However, when calculated in wet weight a peak in megafauna biomass was observed at mid-slope station II (Duineveld et al., 1997), due to a high abundance of large sponges (*Porifera*).

Using the results of the diagenetic model (Herman et al., 2001; Soetaert et al., 1998), the total amount of mineralisable carbon (food) in the sediment was estimated to be about 4, 10, 27 and 39 $gC\,m^{-2}$ at stations A, I, B, and III, respectively (Table 4).

Table 4
Biomass (mg $C\,m^{-2}$) of biota on the Goban Spur, amount of mineralisable carbon C min (mg $C\,m^{-2}$) and % of C min consisting of biota

Station	Depth	Micro	Meio	Macro small	Macro large	Mega	Total biota	Cmin	%Cmin in biota
A	208	3623	71	549	516	56	4815	4439	100
I	670	4083	27	518	40	56	4724	9548	49
B	1034	2877	16	562	320	55	3830	27358	14
II	1425	5699	14	155	0	55	5923		
F	2182	2220	15	138	0	36	2409		
III	3670	2388	15	121	0	40	2564	38654	7
E	4460	1989	16	43	192	24	2264		

3.4. Carbon mineralisation

Total carbon mineralisation rates, calculated from SCOC, measurements decreased with increasing water depth, from about 13 g $C\,m^{-2}\,a^{-1}$ at the shelf to about 2.5 g $C\,m^{-2}\,a^{-1}$ in the abyss (Duineveld et al., 1997; Soetaert et al., 1997) (Table 4). Carbon mineralisation due to respiration of the benthic metazoans also decreased with increasing water depth, from ~8 g $C\,m^{-2}\,a^{-1}$ at the shelf station to 0.7 g $C\,m^{-2}\,a^{-1}$ at the deepest station. Animal respiration decreased monotonously with water depth for all metazoan groups (Fig. 5). Bacterial and protozoan respiration was high at station II (1420-m depth), in accordance with higher biomass there.

The respiration rates per unit biomass varied between 2.3–3.5% d^{-1}, 0.9–2.8% d^{-1} and 0.1–0.2% d^{-1} for nematodes, macrofauna and megafauna, respectively, reflecting the size dependence (Table 5). Turnover rates calculated for bacteria and protozoa were significantly lower, ranging from 0.2 to 0.4% d^{-1}. Because of the small size of the microbiota, much higher turnover rates were expected (about two orders of magnitude higher), indicating that a significant proportion of microbial biomass was probably dormant in the sediment. Turnover times of the total mineralisable carbon in the sediment decreased from 0.82% d^{-1} to 0.03% d^{-1} (Table 5).

Some 50–60% of the carbon mineralisation on the shelf and upper slope was due to metazoans, whereas at greater water depth, only ~20% of the carbon mineralisation was due to multicellular organisms (Table 5, Fig. 5). Metazoan respiration was dominated by the macrofauna at all depths (Fig. 5).

4. Discussion

4.1. Benthic community structure

The size of benthic biota covers several orders of magnitude, from micrometres (bacteria) to decimetres (megafauna). Because metabolism is weight dependent (Mahaut et al., 1995), smaller organisms have relatively higher metabolic requirements, which may affect the degree to which food is recycled in the benthic food chain. Sediment mixing is more impacted by the movement of
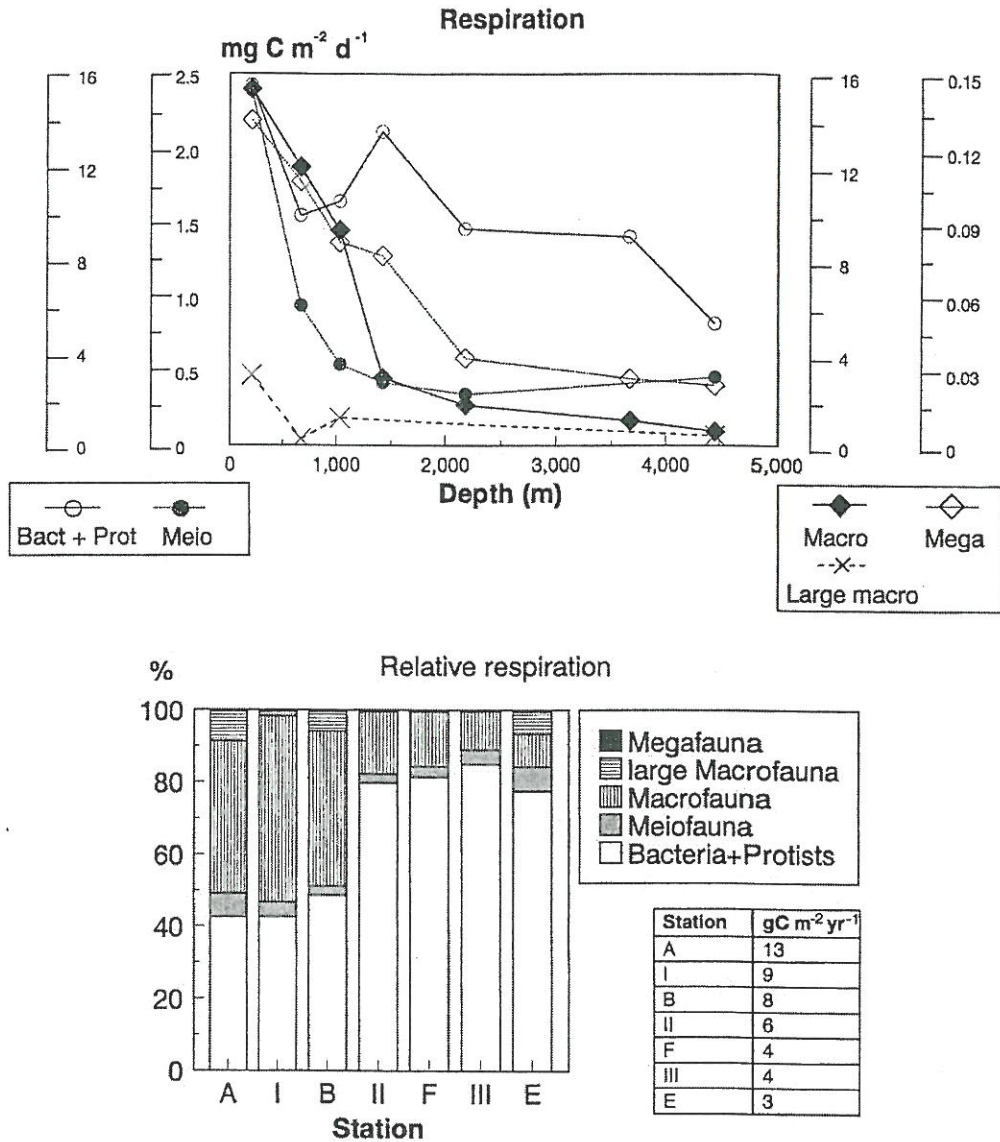
Fig. 5. (a) Respiration of the various benthic taxa, (averaged over all sampling dates, see Table 1); (b) relative share of the various taxa.

big rather than small animals (Wheatcroft et al., 1990), and larger animals may in addition alter the geochemistry of the sediment by ventilation (Aller, 1984) and biodeposition. Hence, the size distribution of benthic organisms may strongly determine the recycling of organic matter in the sediments. Nevertheless, for logistic reasons it is very difficult to obtain estimates of the importance of benthic groups covering the entire size spectrum, and there are consequently few data covering the ocean margin (Rowe et al., 1991; Eldridge and Jackson, 1993; Piepenburg et al., 1995; Mahaut et al., 1995).

Table 5
Daily respiration (mg C m^{-2} d^{-1}) of different biota and sediments

Station	Depth	Micro	Meio	Macro small	Macro large	Mega	SCOC	%Micro biota	%Meta- zoans
A	208	15.5	2.4	15.3	3.1	0.1	36.4	42.6	57.4
I	670	9.9	0.9	12.0	0.3	0.1	23.2	42.7	57.3
B	1034	10.5	0.5	9.3	1.2	0.1	21.6	48.6	51.4
II	1425	13.5	0.4	2.9	0.0	0.1	16.9	79.9	20.1
F	2182	9.4	0.3	1.8	0.0	0.0	11.5	81.7	18.3
III	3670	8.6	0.4	1.1	0.0	0.0	10.1	85.1	14.9
E	4460	5.3	0.5	0.6	0.4	0.0	6.8	77.9	22.1

In this study, we combined quantitative estimates of the micro-, meio-, macro-, and megafauna at several stations along a depth transect in the Goban Spur area. The approaches adopted for measuring biomass of each benthic group were different and this may in part bias our results. For instance, there may be some overlap between bacterial and protozoan biomass estimates (based on a biochemical assay) and nematode biomass estimates (based on length-weight conversions after sorting) (Soltwedel, 1997). However, nematode biomass is only a tiny fraction of the microfaunal biomass, and therefore, there is no need to correct for this potential overlap. Microfaunal biomass was measured by phospholipid concentrations, a method that is well documented in deep-sea research (Soltwedel, 1997), but independent confirmation through direct cell counting or other methods was not available. Moreover, microbiota biomass values are given for the first 5 cm of the sediment only and no attempt was made to correct for deeper occurring biomass. Macrofaunal sampling strategy was adequate to survey the small animals, at the expense of equally good quantitative data of the larger macrofauna. Occasionally, an exceptionally large animal was present in the macrofaunal samples, and this was considered separately in the subsequent presentation of results.

One of the striking results of this study is the dichotomy between the shelf-upper slope stations dominated by metazoan and especially macrofaunal metabolism and the deep slope stations dominated by microbial metabolism, even though the microbial biomass is high everywhere. Respiration estimates of the various metazoan groups were based on an allometric regression with body weight, whereas the microfaunal contribution was assessed by difference between total sediment mineralisation rates (based on SCOC measurements) and metazoan respiration. Because of that, the budget is closed by an unknown term (microbial respiration), and therefore, it is impossible to assess the accuracy of our estimates. A possible artefact could relate to the assumed temperature dependence of respiration rates. If the depression of metazoan respiration at low temperature would be overestimated, this would give too much weight to bacterial respiration at depth. However, the dichotomy between upper and lower slopes in the respiration estimates does not reflect temperature differences, which decreases more gently from the shelf station (11°C) to the deep station (2°C). Also, the similarity in the pattern of microbial respiration and biomass, e.g., the conspicuously large value at 1420-m water depth, is encouraging and lends validity to the estimates obtained (Figs. 3 and 5).

Furthermore, the meiobenthos and megabenthos data were obtained from one sampling occasion, whereas data for the macro- and microbenthos biomass were pooled from three

campaigns, possibly aliasing seasonality with observed trends. Notwithstanding these caveats, our results seem robust and they are probably the best attempt to date to unravel the carbon pathways in sediments at the Goban Spur area.

4.2. Impact of the biota on benthic-pelagic fluxes

Whereas the sinking of organic matter through the water column may be mainly a physical process, once the organic matter enters the benthic boundary layer, its fate is to a large extent controlled by the benthic animals. Mesocosm experiments showed that during summer, even under supercritical flow conditions with erosion, the macrofauna was able to reduce phytodetritus and POC from the BBL with a 50–60% higher rate than sediments of similar bottom roughness without macrofauna (Thomsen and Flach, 1997). Such conditions prevailed on the upper part of the slope, where relatively high current velocities were measured in the bottom water, with an average of $9\,\mathrm{cm\,s^{-1}}$ in spring/summer and $37\,\mathrm{cm\,s^{-1}}$ in autumn/winter (Thomsen and van Weering, 1997, where also long-term observations on hydrodynamical conditions are reported) and where sediment accumulation rates were very low (van Weering et al., 1998). The feeding guilds at this depth were dominated by suspension feeders in the macrofauna, megafauna and even in the foraminiferans (Flach et al., 1998; Table 6), and these animals feed on particles that would otherwise remain in the water column. Sediment community oxygen consumption rates in this area of the Goban Spur were in the usual range for this water depth despite the high current velocities (Duineveld et al., 1997; Middelburg et al., 1997), demonstrating the importance of biodeposition. Organic carbon that would normally pass this area is trapped by the fauna and deposited in the sediment. In the other areas of the Goban Spur, the physical conditions were less adverse to settling and suspension feeders were not as prominent (Table 6).

Nevertheless, none of the environmental variables measured in the water 5 cm above the bottom showed the same range of variability as the density of filter- and interface-feeders (Fig. 3). The latter varied over more than an order of magnitude across the depth gradient, whereas the environmental variables varied by a factor 2–3 at most. Most probably the POC, CPE and (*a fortiori*) the TPM measured in the benthic boundary layer reflect what remains after the feeding activity of the filter-and interface-feeders, rather than what arrives in the benthic boundary layer. If the material arriving is a mixture of highly degradable organic material that is easily taken up and digested, and a refractory fraction that has a long residence time in the BBL, then the bulk of

Table 6
Estimated turnover time (% per day) of carbon in biota and total mineralisable carbon in the sediment

Station	Depth	Micro	Meio	Macro small	Macro large	Mega	Biota total	Cmin
A	208	0.43	3.36	2.80	0.59	0.23	0.76	0.82
I	670	0.24	3.51	2.32	0.72	0.19	0.49	0.24
B	1034	0.37	3.47	1.65	0.37	0.15	0.56	0.08
II	1425	0.24	3.06	1.89		0.14	0.29	
F	2182	0.42	2.30	1.28		0.10	0.48	
III	3670	0.38	2.62	0.91		0.07	0.40	0.03
E	4460	0.27	2.91	1.47	0.22	0.10	0.30	

the material present will belong to the refractory fraction, even if the latter is only a small fraction of the arriving flux. This is comparable to the difference between organic flux and organic content of the sediment (see below). The nearly significant ($p = 0.06$) partial correlation (corrected for station depth) between CPE and density may reflect the generally shorter residence time of the chloroplastic pigments in the BBL; the degradable fraction in the pigment pool may be relatively more important than in the POC pool.

Even at the more quiescent stations along the Goban Spur transect, animals may increase the net flux of organic matter to the sediment. Soetaert et al. (1996c) were able to demonstrate that large animals, by injecting particles directly at depth into the sediment, significantly impacted activity versus depth profiles of the radionuclide ^{210}Pb in the Goban Spur area. This biodeposition phenomenon was shown to be most prominent on the shelf and upper slope (up till a depth of 1425 m), in accordance with the prominence of larger animals there. Similarly, it was argued that the presence of subsurface maxima in the nitrogen versus depth profiles in the two shallowest stations of the Goban Spur could reflect the importance of relocating organic matter from the surface directly into deeper layers of the sediment (Soetaert et al., 1997).

Apart from biodeposition effects, movement and feeding activity of benthic animals may affect the distribution of particles within the sediment and the substances that are required for animal growth may be handled preferentially. This may lead to a discrepancy between the so-called bulk mixing coefficients reflecting mixing of more long-lived sediment compounds, such as those based on ^{210}Pb, or those derived from tracers preferentially absorbed to fresh particles such as ^{234}Th (Smith et al., 1993; Middelburg et al., 1997). The difference between bulk sediment mixing rates and mixing intensity of food-related particles in the sediments of the Goban Spur may be evaluated by comparing ^{210}Pb-derived bioturbation coefficients (Soetaert et al., 1996c) with organic matter mixing rates, obtained by diagenetic modelling (Soetaert et al., 1998; Herman et al., 2001). Results (Fig. 6) show a three-order-of-magnitude difference between sediment mixing intensity based on ^{210}Pb along the transect, whereas organic carbon mixing intensity varies with a factor of 5 at most. Both values of the mixing coefficient are of comparable magnitude at the shelf station, but diverge substantially at greater depth.
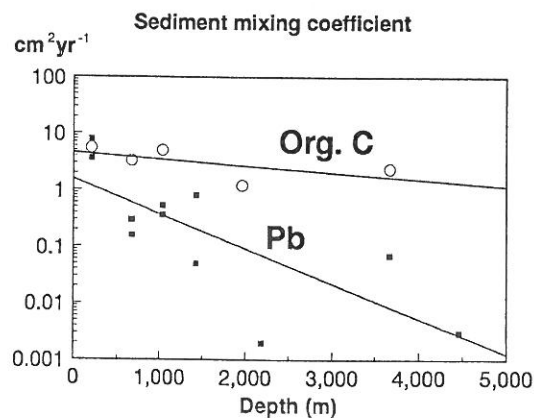

Fig. 6. Bulk sediment mixing coefficient, based on ^{210}Pb (Soetaert et al., 1996c) and mixing intensity of organic carbon versus water depth.

4.3. Carbon flows through the benthic communities

Benthic animals feed from organic matter derived, either directly or indirectly, from the euphotic zone. After ingestion, part of the food is used for respiration, part of it is egested as faeces or is excreted, the remainder (if any) is then diverted into somatic or reproductive growth. Simplified, the latter terms can be considered as repackaging of organic matter in a different form (faeces, dissolved organic matter or new animal biomass), which may be food for other organisms. As such, organic matter may cycle several times through the benthic food chain. In contrast, respiration transforms organic carbon into carbon dioxide, which is (largely) unavailable for further consumption. When there is no annual build-up or export of organic matter, the yearly integrated total system respiration, expressed in carbon units, must thus equal the flux of organic matter *minus* the burial flux.

Not all oxygen consumption is due to direct oxidation of organic matter. Some 20–30% of SCOC is due to nitrifying bacteria, which oxidise the ammonium liberated by the mineralisation process. The remaining part is associated with carbon respiration (about 1 M of oxygen per mole of carbon), either directly through oxic respiration, or indirectly through reoxidation of reduced by-products of the anoxic mineralisation process (e.g., Soetaert et al., 1996a). Therefore, SCOC rates may be easily converted into total mineralisation or carbon respiration rates.

The contribution of the various benthic groups to total carbon respiration was distinctly different between the shelf and upper slope compared to the lower slope and abyssal plain (Fig. 5 below), and this has been simplified in Fig. 7. In the shallower part of the transect, metazoan animals accounted for more than 50% of the carbon respiration, whereas in the deeper regions, their share was reduced to about 20% or less. The remaining part may be ascribed to the microbiota and can be further subdivided. Part of the total system mineralisation may be due to the consumption of oxidants other than oxygen, such as nitrate, nitrite, manganese and iron oxides, sulphate, etc. (Heip et al., 1995), which is predominantly mediated by bacteria. The contribution of these suboxic and anoxic processes to total carbon mineralisation in the Goban Spur was assessed by diagenetic modelling by Lohse et al. (1998), Soetaert et al. (1998) and Herman et al. (2001). Some 20–25% of all carbon respiration can be attributed to these suboxic and anoxic processes at the shelf and upper slope of the Goban Spur (<1100 m, stations A, I, B), whereas at greater depths, less than 10% of total mineralisation is mediated by anoxic/suboxic bacteria (Fig. 7).

Only a limited number of studies have partitioned shelf and deep-sea respiration rates among different faunal groups (Table 7). For a 2100-m deep station in the nearby Bay of Biscay (NE Atlantic), Mahaut et al. (1995) estimated respiration of meio-, macro- and megabenthos based on weight-specific relationships and combined this with microbial respiration rates provided by Rowe and Deming (1985). The latter were considered to be minimal estimates by the authors and moreover, did not include respiration due to protozoans. Therefore, the respiration rates of microbiota and total community respiration are probably too low, and the values for this station should be considered approximate at best. Piepenburg et al. (1995) used shipboard SCOC measures in conjunction with weight-specific estimates for meio-, macro- and megafauna to arrive at a respiration budget for the shelf-upper slope of arctic stations (NW Barents Sea). Microbiota respiration was assessed as the difference between SCOC and meio- and macrofaunal respiration. By means of inverse modelling, Eldridge and Jackson (1993) estimated
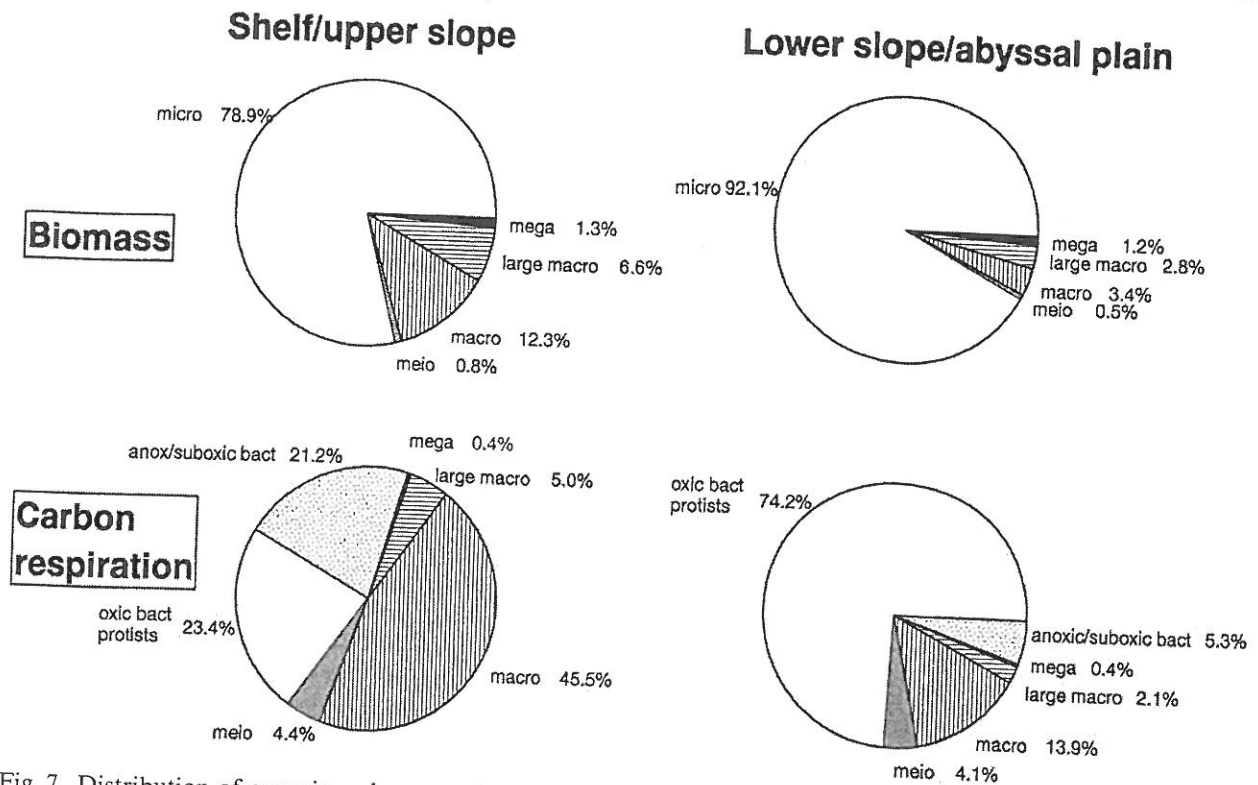
Fig. 7. Distribution of organic carbon over the various faunal groups (above) and partitioning of benthic respiration (below) for shelf/upper slope (left) and lower slope stations (right).

Table 7
Contribution of different biota to total respiration[a]

Area	Reference	Depth (m)	Temperature (°C)	Micro (%)	Meio (%)	Macro small (%)	Macro large (%)	Mega (%)	SCOC mgC m^{-2} d^{-1}
Arctic Ocean	Piepenburg et al. (1995)	200–1010	1–2	47	8	26	15 (3)	4(3)	31.5(1)
OMEX upper slope	This study	200–1030	11–9	44	4	46	5	0.4	27.0
OMEX lower slope	This study	1460–4460	7–2	79	4	13	2	0.4	11.4
Bay of Biscay	Mahaut et al. (1995)	2100	2	30	39	26		5	4.0
California Patton escarpment	Eldridge and Jackson (1993) (4)	3700		65	22	13			13.6

[a] S(ediment)COC is called B(enthic)COC in this paper, because respiration by large macrofauna and megafauna is not measured by classical whole sediment oxygen uptake measurements.
   Oxygen consumption converted to carbon respiration assuming that 30% of SCOC was due to oxidation of ammonium.
   Endobiotic megafauna, equal to large macrofauna; epifauna and fish, equal to our megafauna 32% aerobic bacteria, 7% anaerobic, 20% microfauna, 7% burial rate.

biotic contribution to total respiration in a 3700-m deep station on the Patton Escarpment (California Basin).

The estimates for the OMEX shelf and upper slope stations agree very well with the estimates for the arctic stations situated in the same depth range (Piepenburg et al., 1995). Less than half of total respiration is due to microbiota, less than 10% by meiofauna, the remainder by the larger size groups. Similarly, the OMEX lower slope and abyssal stations compare favourably with the deep station on the Patton Escarpment (Eldridge and Jackson, 1993). In both areas, more than 60% of the organic matter is respired by microbiota, while the remainder is due to metazoans. However, the contribution of meiofauna is significantly larger on the Patton Escarpment compared to the OMEX area.

Thus the predominance of metazoan respiration on the shelf and upper slope, compared to prevalence of microbiota on the lower slope-abyssal plain, appears to be a phenomenon common to otherwise distinct areas of the ocean. However, the number of comparable studies is meagre and more research in this area is needed to substantiate this result.

4.4. Characterising the organic matter in sediments of the Goban Spur

There is a large discrepancy between the composition of organic matter arriving at the sediment surface and the organic matter in the sediment. This is because the more labile fraction of the input flux will be decomposed rapidly, whereas the more refractory compounds accumulate in the sediment. From the point of view of a biologist, the former fraction of organic matter is the most interesting, because it constitutes food for organisms. Geologists on the other hand are more interested in the refractory compounds, because of their predominance in the sedimentary record and because this fraction is involved in the burial flux and constitutes the long-term carbon sink.

For the Goban Spur area, it was argued that the organic matter is deposited on the sediment in a very fresh state (Soetaert et al., 1998; Herman et al., 2001), its reactivity decreasing about 5-fold from the shelf to the abyss. This may reflect to a certain extent the quality of food as experienced by filter feeders that capture their food from the water column. However, except for the upper part of the slope, the majority of benthic animals were deposit feeders (Flach et al., 1998) and their food is diluted with inert sediment grains. The concentrations of mineralisable organic carbon increase from 4.5 g C m^{-2} at the shelf to 38.5 g C m^{-2} at the abyssal station (Table 3). On the shelf there is thus about as much mineralisable carbon as organisms, whereas there is about 10 times more food than biotic biomass at the abyss. As the total flux of organic matter decreases with depth, the higher concentrations of organic matter at greater depth imply a strongly reduced quality of organic matter in these sediments; indeed, roughly estimated, the mean residence time of organic matter at the shelf is in the order of 100 d, whereas in the abyss it is in the range of 10 yr (Table 5).

Rowe et al. (1991) compared biotic biomass and total organic carbon (upper 15 cm) with sediment community oxygen consumption rates to evaluate the turnover time of biota and organic matter. They concluded that the turnover of biota occurred in a time span of months, whereas the residence time of the sedimentary carbon was in the order of years to centuries. One of the drawbacks of using total organic carbon concentrations is the dependence of the obtained turnover time on the depth of the sediment considered and on the sedimentary environment. Depth into the sediments relates to age by the sedimentation rate, hence, in rapidly settling

sediments, the time window of 15 cm of sediment will be much smaller compared to sediments where deposition is slow. Moreover, with decreasing grain size, the sorption surface increases, causing higher background carbon concentrations in fine-grained, deep sediments, compared to coarser shallow sediments. The estimates of organic carbon used in our study do not suffer from this drawback. Our values of "mineralisable" organic carbon estimate the amount of sedimentary organic matter contributing to the biogeochemical profiles of oxygen, nitrate, ammonium and TOC in the sediment. In contrast to total organic carbon, the "mineralisable" organic matter has disappeared at a certain depth into the sediment, hence estimates are independent of the sediment depth considered (as long as it is deep enough). This facilitates comparison among sites with different sedimentation characteristics. Nevertheless, the results we obtain agree qualitatively with results from Rowe et al. (1991). Benthic biomass on the Goban Spur area had a residence time ranging from about 130 d at the shelf station to more than 300 d at station II at ~ 1400 m (the latter mainly due to the low turnover time of microbiota). Turnover time of mineralisable carbon ranged from 0.8% d^{-1} at the shelf station to 0.03% d^{-1} at the deepest station, and hence the organic matter became more refractory with increasing water depth. The residence time of organic matter was comparable to biotic residence time at the shelf (about 120 d compared to 130 d), whereas mineralisable carbon resided significantly longer than the average organism (3300 d compared to 250 d) at the deepest station.

Acknowledgements

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