OCEANOLOGICA ACTA - VOL. 17 - N°6

Boundary layer characteristics of the continental margin of the western Barents Sea

Benthic boundary layer
Continental margin
Barents Sea
Particulate matter
Bacteria

Néphéloïde benthique
Marge continentale
Mer de Barents
Matière particulaire
Bactéries

Laurenz THOMSEN and Gerhard GRAF

GEOMAR, Wischhofstr. 1-3, D 24148 Kiel, F.R.G.

Received 22/09/93, in revised form 23/06/94, accepted 28/06/94.

ABSTRACT

Characteristics of suspended particulate matter in the benthic boundary layer of the continental margin of the western Barents Sea were studied during three cruises in July 1990, Winter and Summer 1991 by collecting water samples 10, 15, 25, 40 and 500 cm above the sea-floor. At all stations gradients of oxygen and particulate matter within the benthic boundary layer were evident. Oxygen varied between 266 and 376 µmol l^{-1} and did not correlate with height above the sea-floor. Total particulate matter concentrations ranged from 0.75 to 11.3 mg l^{-1}. Particulate organic carbon concentrations ranged from 16 to 107 µg l^{-1} and chlorophyll equivalent concentrations ranged from 0.0 to 0.18 µg l^{-1}. Bacterial biomass measured at 5 stations varied between 0.05 and 2.07 µg bacterial organic carbon l^{-1} with highest values at 25 and 40 cm height above sea-floor. From 10 to 40 cm above the sea-floor the distribution of individual bacterial volume shifts to higher size classes. 10 to 40 cm above the bed 35 to 65 % of the bacteria were particle-associated, while more than 85 % of the bacteria were free-living 500 cm above the sea-floor.

Data from the Barents Sea site indicate that, within the suspended matter in the near-bottom water layers, particle stratification due to hydrodynamic sorting occurred. Generally, particulate organic carbon increased from the sea bed into the water column with decreasing values between 40 and 500 cm above the sea-floor. Chlorophyll equivalents decrease above the sea bed into the water column. Chlorophyll equivalent / particulate organic carbon ratio in the near-bottom water did not exeed 0.5 %.

RÉSUMÉ

Caractéristiques du néphéloïde benthique sur la marge continentale dans l'ouest de la mer Barents.

Les caractéristiques du néphéloïde benthique sur la marge continentale de la partie ouest de la mer Barents firent l'objet de trois échantillonnages successifs en juillet 1990, en hiver et en été 1991. Les échantillons d'eau récoltés à 10, 15, 25, 40 et 500 cm du substrat benthique permettent de mettre en évidence les gradients d'oxygène dissous et de matériel particulaire dans le néphéloïde benthique.

Les concentrations d'oxygène dissous varient entre 266 et 376 µmol l^{-1} et ne présentent aucune corrélation avec l'élévation au-dessus du sédiment. Les concentrations en matériel particulaire total se situent entre 0,75 et 11,3 mg l^{-1}. Le carbone organique particulaire atteint des concentrations variant entre 16 et 107 µg l^{-1} et les concentrations en équivalent-chlorophylle varient de 0,0 à

0,18 µg l^{-1}. La biomasse bactérienne mesurée à cinq stations varie entre 0,05 et 2,07 µg de carbone organique bactérien par litre et est maximale à 25 et 40 cm au-dessus du substrat benthique. De 10 à 40 cm au-dessus du sédiment, la distribution du volume des bactéries prélevées se décale vers des tailles plus grandes; 35 à 65 % des bactéries retrouvées entre 10 et 40 cm au-dessus du sédiment sont associées à des particules, alors que plus de 85% des bactéries sont libres à 500 cm au-dessus du sédiment.

Les données récoltées dans la mer de Barents indiquent qu'une stratification des particules en suspension survient dans le néphéloïde benthique suite à une action hydrodynamique. De façon générale, les concentrations en carbone organique particulaire augmentent à partir du fond puis diminuent de 40 à 500 cm du fond. Les concentrations en équivalent-chlorophylle décroissent en s'éloignant du fond. Le rapport équivalent-chlorophylle/carbone organique particulaire ne dépasse pas 0,5% dans l'eau voisine du fond.

Oceanologica Acta, 1994. **17**, 6, 597-607.

INTRODUCTION

Particulate matter reaching the sea floor primarily originates in the ocean's surface layers. As the particles sink, their concentration and composition are altered by aggregation, disaggregation, zooplankton grazing, decomposition, and dissolution. Understanding these processes is complicated by horizontal advection and by the existence of nepheloid layers caused by resuspension of already-deposited particles from the bottom.

Once deposited in deep-sea environments, sedimented detritus decays rapidly (Lampitt, 1985; Thiel *et al.*, 1989; Rice *et al.*, 1986). For Norwegian Continental Margin environments, benthic-pelagic coupling is tight and the benthic community responds rapidly to a pulse of natural organic matter (Graf, 1989; Altenbach, 1992; Meyer-Reil and Köster, 1992).

The near seabed region or benthic boundary layer is one of strong vertical gradients of flow velocity and particle concentration (Nowell and Jumars, 1984; Sternberg, 1986). The processes that laterally distribute and sort the material falling out of the water column are as important as vertical settling in determining the availability of this material as food. Benthic organisms often rely on advection to supply food (LaBarbara, 1984; Miller *et al.*, 1984; Graf, 1992). They are dependent on the fluid medium for transport of this material and, in return, can influence these transport processes (Grant, 1983; Eckmann and Nowell, 1984; Jumars and Nowell, 1984; Miller *et al.*, 1984). Apart from *in situ* measurements of suspended particle concentrations and particle settling velocities (Kineke and Sternberg, 1989) and grain-size analyses of suspended particles within distinct water layers close to the sea-floor (Cacchione and Drake, 1979; Sternberg *et al.*, 1986; Townsend *et al.*, 1992), there is little information about the organic content and composition of particles within the benthic boundary layer [BBL]. Moreover, detailed studies of vertical structures in the BBL in the deep sea have been few. Many of the previous studies have generally been carried out at depths of several tens of metres above the sea floor, and not, as in the case of the present study, from depths of only a few centimetres above the bottom.

Based on flume experiments, a hydrodynamic sorting of particles in a 10-cm water layer above the sediment was reported by Muschenheim (1987); effects of benthos on sediment transport were described by Nowell *et al.* (1980); and stimulated bacterial growth was reported by Wainwright (1987, 1990). Based on *in situ* measurements, increased microbial biomass in the benthic turbidity zone after resuspension and vertical gradients of particulate matter in shallow waters were demonstrated by Ritzrau and Graf (1992).

The aims of this study of the Barents Sea Continental Margin were: (1) to characterize and quantify the particulate matter in a gradient very close to the sea-floor; (2) to determine whether similar patterns of particle distributions are to be found at different sites on the continental margin; and (3) to inquire whether hydrodynamic sorting can explain particle stratification.

METHODS

During Meteor cruise 13 in July 1990, Poseidon cruise 181 in February 1991 and Meteor cruise 17 in July 1991, bottom-water samples were taken from 10 stations at 5 locations on a 170 km long transect across the continental slope of the western Barents Sea. This transect extended in a line between 74°50'N, 16°E and 75°20'N, 10°E and covered water depths between 370 and 2500 m (Fig.1).

Sampling

An *in situ* bottom water sampler (Thomsen *et al.*, 1994), modified for deep-sea deployments, was used to collect 8-15 l of water at each of four distinct heights above the sea-floor. The sampling system consisted of four cylindrical polyethylene bottles. Below each bottle, a tube was mounted which enlarges to a cone (diameter 8 cm) with a

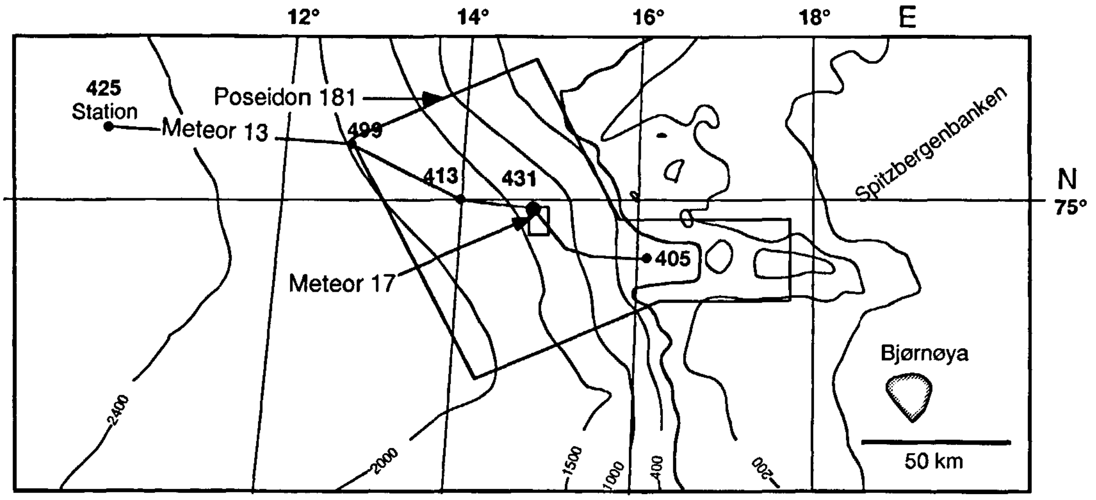

Figure 1

Location of stations on the Barents Sea Continental Margin.

2 mm wide horizontal slit as a water inlet (Fig. 2). A ball valve was located between each water inlet and tube. The water inlets were located 10, 15, 25 and 40 cm above the sea-floor. The water inlets were omnidirectional pointed into the approaching flow. The bottles and the electronic system were located well above the boundary-layer sampling section, at least 30 cm above the highest water inlet. The bottles were connected to a centrifugal pump in the upper part of the instrument. During the sampling procedure, fresh water in the four bottles was replaced by near-bottom water from the station. Pumping time was long enough for a total exchange of water and the pump-timer was calibrated by adding fluorescent dye into the fresh water before a test-deployment. Once the bottles were filled, the ball valves closed. A normal launch involved lowering the instrument system to the sea floor using a simple wire cable (10 mm diameter, 200 g/m in water). Two buoys (Benthos, 25 kg net buoyancy each) were tied to the wire cable 30 and 80 m above the instrument. The approach and position on the sea-floor of the water sampler were monitored by means of a pinger attached to the wire 30 m above the instrument system. Immediately after touching down, 50 m more of the wire cable were paid out so that the wire was slack enough to prevent disturbance by ship movements. The penetration depth of the instrument was determined by means of a lead, filled with fat or by photographs of a ver-

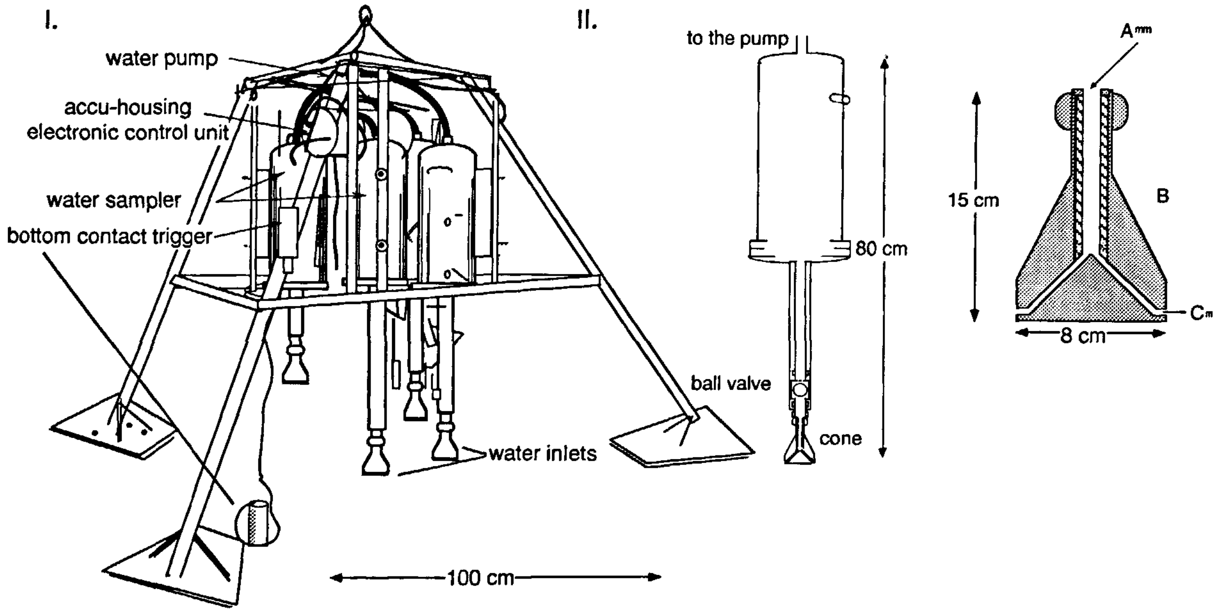

Figure 2

(I) The bottom water sampler containing water samplers, pump, accu-housing with electronic control unit, bottom contact trigger. (II) Schematic drawing of one water sampler with multidirectional water inlet (Eversberg 1991) A = inner tubing; B = cone; C = water inlet.

tical rod, which penetrates the sea bed. The pinger and the additional cable were suspended by the two buoys.

During Meteor cruise 17, replicate sampling over 24 hours around station 431 was carried out and flow velocity was measured by two thermistor flow meters mounted on the vertical rod within the instrument cage of the bottom water sampler. The sensors were located at distances of 20 and 65 cm to the sea-floor (assuming 2 cm penetration depth of the device). Flow direction was obtained through photographs of a Benthos deep-sea compass with a vane. During Meteor cruise 13, a waiting period of 12 min. was kept before sampling to allow material resuspended during deployment to drift away with the current.

Flow velocity data from the literature (Pfirman and Solheim, 1989; Blaume, 1992), as well as our own measurements of bottom currents in later deployments in the same area, suggest that the waiting period of 12 minutes was adequate. Transmissiometer readings in later years revealed that after 5 minutes (flow velocity 5 cm s^{-1} at z_{20}) the sampling errors due to artificial resuspension can be excluded.

During deployments the navigation systems of the research vessel and the pinger control display unit helped to maintain a position directly above the instrument system. Detailed description of the sampling procedures and the instrument are given by Thomsen *et al.* (in press). Water samples from 500 cm and 50 m above the sea-floor were taken with 15 l Niskin bottles on a CTD cast.

Analysis

Water samples were deep-frozen and after 1-2 month analyzed for the following parameters: particulate organic carbon [POC] and particulate organic nitrogen [PON] of water were measured with a Heraeus CHN-Analyzer. Chlorophyll a [Chl a.] and chlorophyll equivalents [Chl.] were analyzed spectralfluorometrically with a Turner Fluorometer and calculated using the equations of Lorenzen (1967). Total particulate matter [TPM], was determined using the method of Bodungen *et al.* (1991). Oxygen was measured according to Grasshoff (1976). Water samples (100 ml) for bacterioplankton were preserved with 2 % buffered, particle-free formalin. Bacterial numbers and bacterial organic carbon [BOC] were determined by the Acridine Orange epifluorescence direct counting technique of Hobbie *et al.* (1977) using a Zeiss Standard fluorescence microscope. Cell volumes of 100 to 150 bacteria of each sample were determined from photographs using methods described by Thomsen (1991) and carbon was estimated from biovolumes using a conversion factor of 0.11 pg C μm^{-3} (Meyer-Reil, 1983), using the image analysis program "Image 1.37" for Macintosh computers.

A correlation matrix and a dependent t.-test with pairing of all variables were computed with $P. \leq 0.01$, $P. \leq 0.05$ and $P. \geq 0.01$. Statistics were evaluated using the statistical software "Stat View II" for Macintosh computers.

RESULTS

For a closer view of the benthic boundary layer characteristics, detailed observations of concentration profiles and bacterial-volume size spectra of 5 stations of the Meteor 13 transect in summer 1990 are presented in Figures 3 and 4.

At station 405 (373 m, shelf edge) chlorophyll equivalent content, POC and TPM of the bottom water decreased from 10 to 15 cm with increasing values beween 15 cm and 40 cm and lower values at 500 cm above the sea-floor (Fig. 3A).

Compared to the other stations, the concentration profile of bacterial abundance showed a strong increase from 25 to 40 cm a.b (Tab. 1). Median cell volumes of bacteria shifted to higher values from 0.08 μm^3 to 0.15 μm^3 from 10 to 40 cm above the sea-floor, where highest bacterial organic carbon was found. (Tab. 1, Fig. 4).

At station 431 (1 340 m, upper slope), chlorophyll equivalent content of the bottom water decreased into the water column while POC and TPM increased into the near-bottom water column (Fig. 3B). At this station median cell volumes and carbon content of bacteria showed an extreme shift to higher values between 10 and 25 cm above bottom (a.b.) (Tab. 1, Fig. 4).

At station 413 (1750 m, mid slope), chlorophyll equivalent content of the bottom water decreased into the water column up to 25 cm a.b. while POC increased from the sea-floor up to 40 cm a.b., whereas TPM did not show any particular gradient (Fig. 3C). At this station, again median cell volumes of bacteria and bacterial organic carbon showed a shift to higher values between 10 and 40 cm above the sea-floor (Tab. 1, Fig. 4).

At station 499 (1970 m, mid slope) again chlorophyll equivalent content and TPM of the bottom water decreased into the water column while POC showed increasing values (Fig. 3D). At this station median cell volumes of bacteria showed no distinct shift to higher values while bacterial organic carbon was highest at 40 cm a.b. (Tab. 1, Fig. 4).

At station 425 (2537 m, lower slope), profiles of chlorophyll and POC appear to be inversely correlated, and again TPM showed no obvious trend (Fig. 3E). Median cell volumes of bacteria shifted to higher values between 10 and 25 cm above the sea-floor, where highest bacterial organic carbon was found (Tab. 1, Fig. 4).

Compared to values higher in the water column (50 m a.b.), chlorophyll, POC and TPM concentrations within the 10 - 40 cm water layers were always higher (Fig. 3).

For a general view of the benthic boundary layer characteristics across the transect, measured values and ratios are presented in Table 1. The table also shows results from Poseidon cruise 181 in February 1991 and Meteor cruise 17 in July 1991.

Oxygen varied between 266 and 376 µmol l^{-1} and did not correlate with height above the sea-floor ($P. > 0.1$). Chlorophyll equivalent concentrations ranged from 0.0 to 0.13 µg l^{-1} with a median value of 0.05 µg l^{-1}. Chlorophyll equivalent was negatively correlated with height up to 40 cm above the sea-floor ($P. < 0.01$). Chlorophyll a [median value 0.02 µg l^{-1}], which was associated with intact phytoplankton cells, accounted for a high proportion (32 % mean value) of the chlorophyll equivalents in the water samples. Particulate organic carbon [POC] concentrations

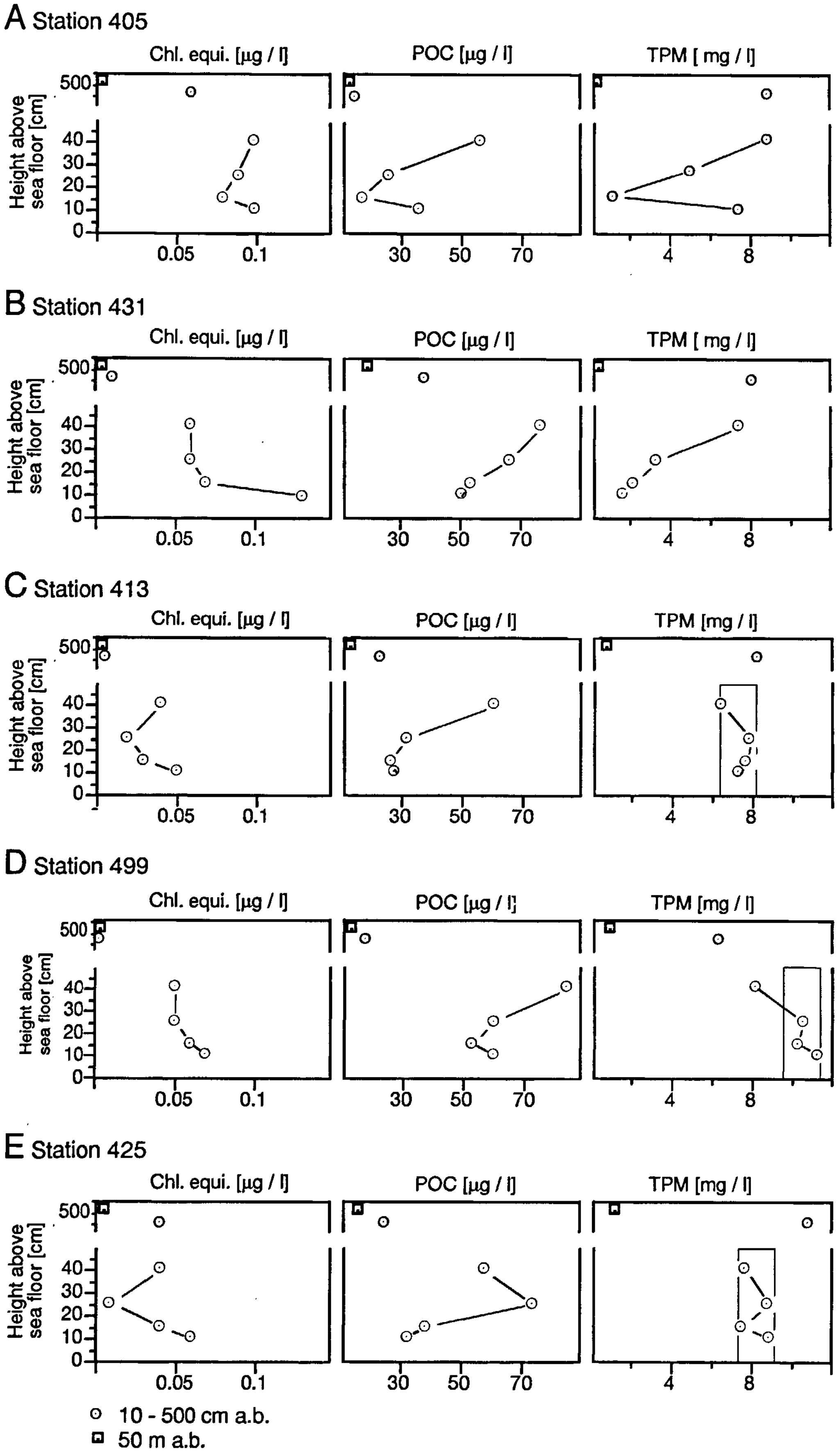

Figure 3

Concentration profiles of chlorophyll equivalents, particulate organic carbon and total particulate matter in the near-bottom water of stations of Meteor cruise 13 in July 1990. Boxes represent the 95 % confidence limits for vertical TPM profiles for stations 413, 499 and 425. Small boxes [_] represent concentration values at 50 m height above sea floor.

Table 1

Oxygen and particle concentrations in near-bottom water samples taken during Meteor cruise 13 in July 1990, Poseidon cruise 181 in February 1991 and Meteor cruise 17 in July 1991 from 10 stations across the continental margin of the western Barents Sea.

CONCENTRATIONS

METEOR 13	Height above sea-floor [cm]	Oxygen [µM]	Chlorop. *a* [µg/l]	POC / PON	Bacterial organic carbon (BOC) [µg/l]	Bacterial number [x10⁷/l]
Station 405 373m	500	376	0.008	16	0.44	4.00
	40	375	0.029	19	2.07	9.00
	25	320	0.016	26	0.57	3.00
	15	317	0.025	17	0.55	2.60
	10	318	0.033	13	0.29	2.60
Station 431 1340m	500	315	0.006	20	0.15	1.10
	40	315	0.037	9	0.38	0.84
	25	316	0.025	15	0.96	3.30
	15	319	0.037	23	0.56	3.90
	10	317	0.082	16	0.05	0.79
Station 413 1750m	500	316	0.003	35	0.31	3.60
	40	316	0.012	14	0.68	2.10
	25	315	0.008	7	0.59	2.90
	15	315	0.008	9	0.24	1.90
	10	315	0.016	9	0.34	1.80
Station 499 1993m	500	316	0.000	35	0.12	12.00
	40	309	0.016	8	0.28	14.00
	25	310	0.016	8	0.12	12.00
	15	308	0.016	11	0.11	11.00
	10	266	0.020	12	0.17	17.00
Station 425 2537m	500	320	0.015	27	0.17	1.70
	40	320	0.016	23	0.17	2.40
	25	324	0.000	8	0.33	2.40
	15	322	0.016	31	0.33	2.30
	10	325	0.024	32	0.22	2.70

METEOR 17	Height above sea-floor [cm]	Chlorophyll equivalents [µg/l]			Particulate organic carbon (POC) [µg/l]		
Stations 384/386 1370 m	40	0.10	0.07	0.06	61.00	78.00	85.00
	25	0.09	0.05	0.05	70.00	90.00	106.00
	15	0.14	0.09	0.07	65.00	65.00	66.00
	10	0.18	0.13	0.09	46.00	52.00	63.00
					replicate sampling over 24 h		
Poseidon 181 Stations 225, 245 400, 1350m	40	0.05	0.01		52.37	48.96	
	25	0.04	0.03		23.86	36.43	
	15	0.06	0.05		24.32	23.55	
	10	0.06	0.04		17.35	20.19	

ranged from 16 to 107 µg l^{-1} with a median value of 52 µg l^{-1}. POC was positively correlated with height up to 40 cm above the sea-floor (P. < 0.01).

Total particulate matter concentrations ranged from 1.2 to 11.3 mg l^{-1}. There was a change from increasing concentrations of TPM at the shallower stations to uniform distributions at the deeper stations.

POC/PON ratios ranged from 5 to 35 with a median value of 15. There was no significant correlation between height above the sea-floor and POC/PON values (P. > 0.1). Chl./POC [%] ratio ranged from 0.01 to 0.5 % with a median value of 0.12 %. It generally decreased from the sea bed into the water column (P.< 0.01). POC/TPM [%] ratio ranged from 0.2 to 3.2 % with a median value of 0.5 %.

Bacterial numbers in the benthic boundary layer measured during Meteor cruise 13 ranged from 0.08 to 1.7×10^8 cells l^{-1} with a median value of 0.28×10^8 cells l^{-1}. There was no significant correlation between height above sea-floor and bacterial numbers (P. > 0.1). BOC estimated for the 5 stations of Meteor cruise 13 ranged from 0.05 to 2.07 µg l^{-1} with a median value of 0.3 µg l^{-1} and highest values at 25 and 40 cm above the sea-floor. BOC was correlated with POC ($P \leq 0.05$). Size spectra of bacteria showed distinct differences with height above the seabed. From 10 to 25 and 40 cm above the sea-floor the distribution of individual bacterial volume shifted to larger bacteria. Between 10 to 40 cm above the bed, 35 to 65 % of the bacteria were particle-associated, while more than 85 % of the bacteria were free-living 500 cm above the sea-floor . BOC/POC [%] ratio ranged from 0.1 and 3.7 % with a median value of 0.8 %. During replicate sampling over 24 hours at station 431 (Meteor 17, Tab.1) these distinct chlorophyll and POC patterns of distribution were also recorded . The shape of each particle component concentration curve was similar at the three stations and similar to those from the Meteor cruise 13 (Tab.1). The average values

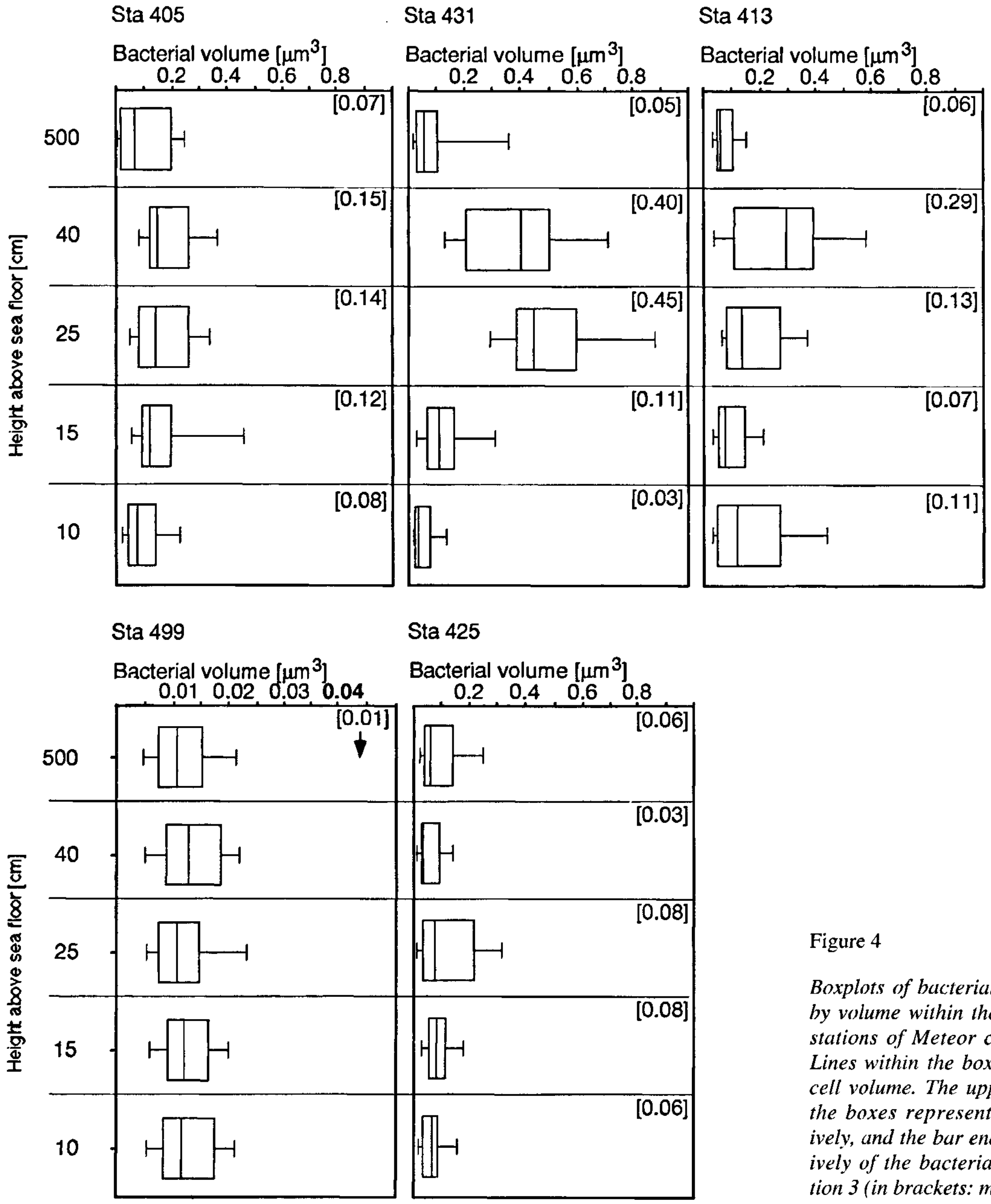

Figure 4

Boxplots of bacterial size class distribution by volume within the near-bottom water of stations of Meteor cruise 13 in July 1990. Lines within the boxes indicate the median cell volume. The upper and lower limits of the boxes represent 25 and 75% respectively, and the bar ends 10 and 90% respectively of the bacterial volume size distribution 3 (in brackets: median values).

of 15 min measurements of flow velocity (sampling rate 1 s^{-1}) at the upper and lower flow meters were 28.3 cm s^{-1}, and 22.5 cm s^{-1} respectively at distances of 65 and 20 cm to the sea-floor. Estimated bottom shear velocity, assuming a logarithmic velocity profile, ranged from 1.7 to 2.4 cm s^{-1}. The bottom current direction was northwesterly, approximately parallel to the bathymetry.

DISCUSSION

Despite their different positions on the continental margin, at all stations concentration profiles of chlorophyll, POC and BOC were similar and showed significant correlations ($P \leq 0.05$). Therefore the median concentration values of chlorophyll equivalents (accounting for phytodetritus), POC and BOC of all the 10 stations of the transect measured on all cruises were computed from corresponding sampling heights to show the characteristic particle concentration profiles in the near bottom waters (Fig. 5).

The following trends were apparent:

Chlorophyll equivalent decreased from the seabed into the water column.

POC increased from the seabed into the water column with decreasing concentrations between 40 and 500 cm above the sea-floor.

The low Chl./POC ratios (~ 0.1 %) in this POC maximum suggests that the material was not enriched in high chlorophyll phytodetritus but of mainly organic debris with high C/N ratios.

The general shape of the concentration curve of C/N ratios showed no significant trend in the near-bottom waters. This particulate organic matter in the near-bottom water was either refractory material (≈ C/N 15) that had passed many resuspension loops or mainly of terrestrial origin. Up to 60 % of identifiable organic matter in sediments sam-

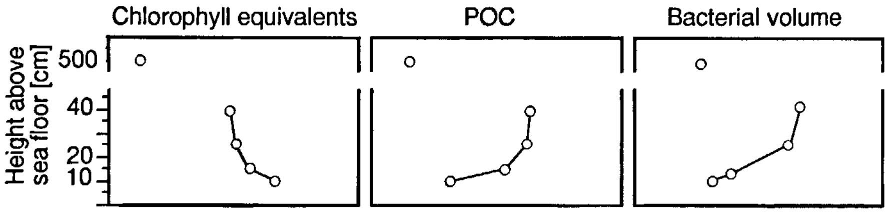

Figure 5

Benthic boundary layer characteristics of median values (dimensionless) of chlorophyll equivalents, particulate organic carbon and bacterial volume computed from corresponding sampling heights of all the 10 stations of the transect.

pled at the Barents Sea site were of terrestrial origin (Wagner, 1993).

The low Chl./POC ratios at the Barents Sea site indicate that the direct nutritional value of the organic material found at this site was probably low, but that the bacterial epiflora found on the suspended detritus could be important for animals feeding on these particles.

BOC was correlated with POC. The bacterial biomass and size class distribution data show that maximum biomass and higher individual size classes occur within the upper near-bottom boundary layer (25 to 40 cm), where high POC concentrations were found.

The ratio of BOC to POC of 0.3 to 3.7 % suggests the importance of the bacteria as a food source. Applying a frequently used carbon-conversion factor of 0.4 pg C μm^{-3} cell volume (Bjørnsen, 1986) bacteria would contribute up to 15 % to the POC pool. Patching (1991) showed that there was evidence of a barophilic bacteria community living within the benthic boundary layer (sediment-contact water of multicorer samples), indicating a special adapted bacteria flora not of benthic origin. To what degree this additional carbon source is accessible to the benthic community depends on the hydrodynamic behaviour of the bacteria-attached POC. No general trend in the distribution pattern of TPM in the near-bottom waters was apparent.

Hydrodynamic sorting of the particulate organic fraction

Vertical profiles produced by hydrodynamic sorting

The slopes of particle concentration profiles are determined by the settling velocity of the particles and the bottom shear velocity, determining whether sediments are transported in suspension or as bedload (Rouse, 1937; McCave, 1972). Muschenheim (1987b) showed that there exists a distinct hydrodynamic sorting of particles within the benthic boundary layer, producing flux profiles, which were simultaneously "top-heavy" for the lighter fraction (less dense) with low settling velocities (organic detritus) and "bottom-heavy" for the heavier (denser) fraction with higher settling velocities. In most natural environments hydrodynamic sorting is possible (Middleton and Southard, 1984). The Rouse number ($z = w / \beta \kappa u^*$) (w is the settling velocity of the particle, β is a numerical constant, κ is the Kármán constant and u* is the bottom shear velocity) is a suitable criterion for suspension. Because both β (~ 1) and κ (~ 0.4) are supposed to be constants it is expected that the main factor that determines the distribution of suspended sediment with height above the bed is the ratio of the settling velocity to the shear velocity (w/u*) (Rouse, 1937; Middleton and Southard, 1984). Particles with low settling velocities (small, light or low density particles) will have a rather uniform distribution with height above the bottom (this corresponds very roughly to $w \leq 0.1\ u^*$ and $z \leq 0.25$). Particles with higher settling velocities are more concentrated closer to the bottom ($w \geq 0.4\ u^*$ and $z \geq 1$) or transported as bedload ($w \geq 1\ u^*$). Increase in shear velocity will also result in a more uniform distribution of suspended sediment in the vertical section (Eisma, 1993).

Thus for small Rouse numbers [<< 1] the particle concentration will be uniform with depth. As Rouse number increases [≈1], concentration will increase towards the sea floor.

Comparison of theory and data

Data on suspended particulate matter in the near- bottom waters from the Barents Sea Continental Margin (1 to 10 g m^{-3}) suggest that hydrodynamic sorting within the particulate organic fraction occured. Chlorophyll equivalents monotonically decreased above the seabed. (Fig. 5). Aggregated phytodetritus, which is associated with chlorophyll and is formed in surface waters, has high settling velocities of 0.1-0.2 cm s^{-1} (Aldrege and Silver, 1988). Once concentrated and further aggregated on the sediment surface by currents, experimental-estimated settling rates of the resuspended fluff increased up to 0.35-1.2 cm s^{-1} (Lampitt, 1985). At the Barents Sea site, decreasing concentrations of chlorophyll equivalents above the sea-floor were consistent with these previous findings, suggesting packaging in relatively large aggregates. Rouse numbers of the material could not be determined because it is very difficult to measure settling velocities of natural samples. Flocs are fragile and notoriously hard to sample without breaking (Krank and Milligan, 1985). They will break up in the shear field of the water-inlets of the sampling system and/or are modified within the sampling bottles during sampling procedures. Taking Lampitt's (1985) data into account the chlorophyll profiles during replicate sampling during Meteor cruise 17 with u* of 1.7 to 2.4 cm s^{-1} would result in increasing chlorophyll concentrations towards the sea floor with settling velocities ($w \geq 0.4\ u^*$) of the phythodetritus of 0.7 to 1 cm s^{-1}.

The POC data suggest that this organic fraction has at least low settling velocities with low Rouse numbers. Contrary to expectations the POC profiles were not uniform with height above the sea floor. Concentrations increased off the bed. It is very difficult to interpret this phenomena, which cannot be explained with a simple hydrodynamic model. Sampling errors (oversampling of the finer fraction away from the bottom) could result in increasing POC concentrations. Sternberg *et al.* (1986) reported that a suspended sediment size fraction of ≤ 62 µm can cause sampling errors of max. 1.6 % if the isokinetic flow into the water sampler is not guaranteed. Average particle size on all stations of the Meteor and Poseidon cruises was < 12 µm, so this problem is considered as minor and the oversampling could not result in different size distributions of bacteria within the different water bottles. Colby (1963) showed that particles of the 63 to 125 µm size range produced increasing concentration profiles off the sediments of the Mississippi river. Stolzenbach *et al.* (1992) discussed whether POC could be scavanged during turbulent transport through the fluff layer. At present, the best explanation for a POC sink near the sea floor seems to be that the POC within the lower near-bottom boundary layer (10 to 15 cm) was scavenged by the fast-sinking phytodetritus either in the near-bottom waters or in the course of transport through the fluff layer.

With an average particle size of < 12 µm for the whole TPM fraction, profiles of TPM should be uniform. The sinking velocities of these particles (10^{-3}-10^{-2} cm s^{-1}, McCave and Gross, 1991), which only belong by less than 0.1% to the "heavy" phytodetritus fraction, are expected to be very low. Thus even under low flow velocities with u* of 0.1 to 0.01 cm s^{-1} Rouse numbers are << 1. At the deeper stations at the Barents Sea site, TPM profiles were more or less uniform (95 % confidence limits) but on the upper slope strong gradients occurred. This could be a result of a shift from suspension-feeding towards deposit-feeding macrofauna. Studies of biodeposition showed that macrofauna can have a enormous influence on near-bottom particle transport (Asmus and Asmus, 1990; Muschenheim and Newell, 1989; Muschenheim, 1987). At the shelf edge station 405, macrofauna were very abundant and mainly dominated by sedentary polychaetes (1024 ind. m^{-2}, Juterzenka, pers. comm.) and large epibenthic megafauna. The feeding height of suspension-feeding macrofauna was 10 to 30 cm due to the presence of stones. Data suggest that TPM and bacterial abundances were minimized and oxygen consumption was enhanced within the near-bottom water due to the influence of the interface feeders (Tab. 1). The abundant macrofauna on the slope station 431 (1250 ind. m^{-2}, mainly polychaetes, Juterzenka, pers. comm.) with an average tube height of 2-4 cm above sediment surface, intercepts suspended particles travelling past, influencing the near-bottom water up to a height of 25 cm. The low concentrations of TPM 10 to 25 cm above the bed (Fig. 3) suggest this interaction. Studies of the depletion of TPM above a high abundant suspension-feeding macrofauna at mid-slope revealed the immense influence of the animals on the near-bottom waters (Thomsen *et al.*, subm.) So both the less abundant macrofauna and the shift towards deposit feeding at deeper stations could explain the differences of the TPM concentration profiles from these shallower to the deeper stations.

Implication for benthic community structure and cycling of organic matter within the benthic boundary layer

Data suggest that particulate organic matter derived from phytodetritus generally had higher settling velocities and thus contributed little to the total organic carbon pool in near-bottom waters (Chl./POC ≤ 0.5 %, Tab.1). These particles remained suspended for short periods of time and hence the state of the boundary layer becomes less important in their dispersion. With high Rouse numbers, the dense material will be transported in the near-bed region either in contact with or a few centimetres above the bottom, and thus often within reach of benthic organisms. In case of resuspension due to increasing current velocities the material will rapidly resettle under lower flow conditions and can be deposited. This mechanism could explain the fast downslope transport of phytodetritus described by Walsh and Gardner (1992). The inclination of the continental slope results in rapid near-bed lateral transport of this heavy material to the deep sea faster even than vertical sedimentation. There is evidence that at the Barents Sea site material from the shelf can reach deep water in rapid pulses of cold and dense bottom water in cross-slope direction (Blaume, 1992).

The POC fraction with low Rouse numbers tends to follow streamlines in flow, remains suspended for a longer time and hence the "state of the boundary layer" becomes more important in its dispersion. The bacterial biomass and size class distribution data (Table 1) show that maximum biomass and higher individual size classes occur within the upper near-bottom boundary layer (25 to 40 cm), where the high POC concentrations and high percentages of particle associated bacteria were found.

Low settling velocities and high residence times within the benthic boundary layer would result in long-term horizontal fluxes of POC. Resuspension of sediments and turbulence were shown to stimulate bacterial activity significantly (Wainwright, 1987; Ritzrau and Deming, subm.) As bacteria were bound to particles, carbon input of this material to the benthos could occur via aggregate -and fecal pellet formation (Kranck, 1984; Gibbs, 1985; Biddanda, 1985; Muschenheim *et al.*, 1989; Kineke and Sternberg, 1989).

Acknowledgements

The authors wish to thank B. v. Bodungen, D. Boesch and W. Ritzrau for careful review of the manuscript. Thanks to the crew of RV *Meteor* and RV *Poseidon* for their help during the cruise. This is publication of GEOMAR and publication no. 231 of the Sonderforschungsbereich 313, Kiel University.

REFERENCES

Alldredge A.L. and M.W. Silver (1988). Characteristics, dynamics and significance of marine snow. *Progress in Oceanography* , **20**, 41-82.

Altenbach A.V. (1992). Short term processes and patterns in foraminiferal response to organic flux rates. *Marine Micropalaeontogy*, in press.

Asmus, R.M. and H. Asmus (1992). Mussel beds: limiting or promoting phytoplankton ? *Jour. of Exp. Mar. Biol. Ecol.*, **148**, 215-232.

Biddanda A.B. (1985). Microbial synthesis of macroparticulate matter. *Marine Ecology Progress Series*; 20, 241-251.

Bjørnsen P.K. (1986). Automatic determination of bacterioplankton biomass by image analysis. *Applied Environmental Microbiology*, **51**,6, 1199 -1204.

Blaume F. (1992). Hochakkumulationsgebiete am norwegischen Kontinentalhang. Ber. SFB 313, **36**, Kiel University, ISSN 0942-119X.

Bodungen B.v., M. Wunsch and H. Fürderer (1991). Sampling and analysis of suspended and sinking particles in the North Atlantic. *Geophysical Monograph*, **63**, 47-56.

Cacchione D.A. and D.E. Drake (1979). A new instrument system to investigate sediment dynamics on continental shelves. *Marine Geology*, **30**, 299-312.

Colby B.R. (1963). Fluvial sediments. Geological Survey Bulletin, **1181-A** Washington, 47 pp.

Eisma D. (1993). Suspended Matter in the Aquatic Environment. Verlag Springer, Heidelberg, 312 pp.

Ekman J.E. and A.R.M. Nowell (1984). Boundary skin friction and sediment transport about an animal tube mimic. *Sedimentology*, **31**, 851-862.

Gibbs R.J. (1985). Estuarine flocs: Their size, setting velocity and density. *Journal of Geophysical Research*, **90**, 3249-3251.

Graf G. (1989). Benthic pelagic coupling in a deep-sea benthic community. *Nature*, **341/6241**, 437-439.

Graf G. (1992). Benthic pelagic coupling: A benthic view. *Oceanography and Marine Biology Annual Review* , **30**, 149-190.

Grant J. (1983). The relative magnitude of biological and physical sediment reworking in an intertidal community. *Journal of Marine Research*, **41**, 673-689.

Grasshoff K. (1976). Methods of seawater analysis. Verlag Chemie, Weinheim, 317 pp.

Hobbie J.E., R.J. Daley and S. Jasper (1977). Use of Nucleopore filters for counting bacteria by fluorescense microscopy. *Applied and Environmental Microbiology* , **33**, 1225-1228.

Jumars P.A. and A.R.M. Nowell (1984). B. Effects of benthos on sediment transport: difficuties with functional grouping. *Continental Shelf Research*, **3**, 115-130.

Juterzenka K.v. (pers. comm.). Inst. f. Polarökologie, Kiel university, 24148 Kiel, FRG.

Kineke G.C. and R.W. Sternberg (1989). The effect of particle settling velocity on computed suspended sediment concentration profiles. *Marine Geology*, **90**, 159-174.

Kranck K. (1984). The role of flocculation in the filtering of particulate matter in estuaries. In: *The estuarie as a filter*, Kennedy, V.S. editor. Academiv press, New York: 159-175.

Kranck K. and **T.G. Milligan** (1985). Origin of grain size spectra of suspension deposited sediment. *Geological Marine Letters*, **5**, 61-66.

LaBarbera M. (1984). Feeding currents and particle capture mechnisms in suspension feeding animals. *Amer. Zoology*, **24**, 71-84.

Lampitt R.S. (1985). Evidence for seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Research*, **32**, 885-879.

Lorenzen C.J. (1967). Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnology and Oceanography*, **12**.

McCave I.N. (1972). Transport and escape of fine grained sediment from shelf areas. In: *Shelf sediment transport. process and pattern*, Swift, D.J.P., Duane, D.B. and O.H. Pilkey, editors, Dowden, Hutchinson and Ross: 225-248.

McCave I.N. (1984). Size spectra and aggregation of suspended particles in the deep ocean. *Deep-Sea Research*, **31**, 329-352.

McCave I.N. and T.F. Gross (1991). In-situ measurements of particle settling velocity in the deep sea. *Marine Geology*, **99**, 403-413.

Meyer-Reil L.A. (1983). Benthic response to sedimentation events during autumn to spring at a shallow water station in Western Kiel Bight. II Analysis of benthic bacterial populations. *Marine Biology*, **77**, 247-256.

Meyer-Reil L.A. and M. Köster (1992). Microbial life in pelagic sediments: the impact of environmental parameters on enzymatic degradation of organic materials. *Marine Ecology Prog. Ser.*, **81**, 65-72.

Middleton G.V. and J.B. Southard (1984). In: Mechanics of sediment movement. S.E.P.M. Short course Number 3, 2nd Edition, Providence.

Miller, D.C., P.A. Jumars and A.R.M. Nowell (1984). Effects of sediment transport on deposit feeding: scaling arguments. *Limnology and Oceanography*, **29**, 1202-1217.

Muschenheim D.K. (1987). The dynamics of near-bed seston flux and suspension-feeding benthos. *Journal of Marine Research*, **40**, 473-497.

Muschenheim D.K. (1987)B. The role of hydrodynamic sorting of seston in the nutrition of a benthic suspension feeder, Spio setosa (Polychaeta: Spionidae). *Biological Oceanography*, 265-288.

Muschenheim, D.K., P.E. Kepkay and K. Kranck (1989). Microbial growth in turbulent suspension and its relation to marine aggregate formation. *Netherland Journal of Sea Research*, **23**, 283-292.

Muschenheim, D.K. and C.R. Newell (1992). Utilization of seston over a mussel bed. *Mar. Ecol. Prog. Ser.*, **85**,131-136.

Nowell A.R.M., P.A. Jumars and J.E. Ekman (1980). Effects of biological activity on the entrainment of marine sediments. *Marine Geology* , **42**, 133-153.

Nowell A.R.M. and P.A. Jumars (1984). Flow environments of aquatic benthos. *Annual Review of Ecology Systems*, **15**, 303-328.

Patching J.W. (1991). Biomass and activity of a deep ocean bacterial population - evidence of a barophilic community. 6th Deep-Sea Biology Symposium, Copenhagen 1991, Abstracts.

Pfirman S.L. and A. Solheim (1989). Subglacial meltwater discharge in the open-marine tidewater glacier environment: observations from Nordaustlandet, Svalbard Archipelago. *Marine Geology* 86, 265-281.

Rice A.L., D.S.M Billett, J. Fry, A.W.G. John, R.S. Lampitt, R.F.C. Mantoura and R.J. Morris (1986). Seasonal deposition of phytodetritus to the deep-sea floor. T*he oceanography of the Rockall Channel*, 265-279.

Ritzrau W. and G. Graf (1992). Increase of microbial biomass in the benthic turbidity zone BTZ of Kiel Bight, Baltic Sea, after resuspension by a storm event. *Limnology and Oceanography*, **37**, 5, 1081-1086.

Ritzrau W. and J. Deming (subm.). Effects of resuspension and turbulence on bacterial activity. *Marine Ecology Progress Series.*

Rouse H. (1937). Modern conception of mechanics of turbulence. *Trans American Society of Civil English* , **102**, 436-505.

Sternberg R.W., R.V. Johnson, D.A. Cacchione and D.E. Drake (1986). An instrument system for monitoring and sampling suspended sediment in the benthic boundary layer. *Marine Geology* **71**, 187-199.

Stolzenbach K.T., K.A. Newman and C.S. Wong (1992). Aggregation of fine particles at the sediment-water interface. *Journal of Geophysical Res.*, **97**, 889-989.

Thiel H., O. Pfannkuche, G. Schriever, K. Lochte, A.J. Gooday, C. Hemleben, R.F.C. Mantoura, C.M. Turley, J.W. Patching and F. Riemann (1989). Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. Biological Oceanography, **6**, 203-239.

Thomsen L. (1991). Treatment and splitting of samples for bacteria and meiofauna biomass determinations by means of a semi-automatic image analysis system. *Marine Ecology Progress Series*, **71**, 301-306.

Thomsen L. , G. Graf, V. Martens and E. Steen (1994). An instrument for sampling water from the benthic boundary layer. *Continental Shelf Research*. **14**, 7/8, 871-882.

Thomsen L. , G. Graf, K. v. Juterzenka and U. Witte (in press). An *in situ* experiment to investigate the depletion of seston above an interface feeder field on the continental slope of the western Barents Sea. *Marine Ecol. Prog.Ser.*

Townsend D.W., L.M. Mayer, D. Dotch and R.W. Spinrad (1992). Vertical structure and biological activity in the bottom nepheloid layer of the Gulf of Maine. *Contin. Shelf Res.*, **12**, 367-387.

Wainright S.C. (1987). Stimulation of heterotrophic microplankton production by resuspended marine sediment. *Science*, **238**, 1710-1711.

Wainright S.C. (1990). Sediment-to-water fluxes of particulate material and microbes by resuspension and their contribution to the planctonic food web. *Marine Ecology Progress Series*, **62**, 271-281.

Walsh I.D. and W.D. Gardener (1992). A comparison of aggregate profiles with sediment trap fluxes. *Deep Sea Res.*, **39**, 11/12a, 1817-1834.