

Sedimentological and biological differences across a deep-sea ridge exposed to advection and accumulation of fine-grained particles

Sedimentology
Benthic ecology
Deep-sea ridge
Vøring Plateau
Norwegian Sea

Sédimentologie
Écologie benthique
Dorsale profonde
Plateau de Vøring
Mer de Norvège

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ABSTRACT

Large amounts of clay and silt particles from the northern Vøring Plateau (Norwegian Sea) accumulate on a ridge (Vøring Plateau escarpment) situated at 1 245-1 310 m depth on the northern Vøring Plateau. Calculated Holocene sedimentation rates are up to 18 cm ky⁻¹, while amounting to less than 1 cm ky⁻¹ on the slope south of the ridge. Six stations were sampled - three on each side of the ridge - to obtain quantitative information of different biological components and relate these observations to the environmental conditions. Pronounced biological differences between the southern and northern sites are evident in terms of oxygen consumption, meio- and macrofauna composition, meiofauna biomass and meiofauna depth distribution. A specific fauna consisting of pogonophorans and nematode assemblages of relatively large-sized animals inhabits areas on Vøring Plateau which are characterized by high sedimentation rates and high organic carbon content. Accumulation of particles larger than 63 µm in sediment horizons between 6-10 cm depth is possibly due to vertical particle transports by a burrowing enteropneust.

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RÉSUMÉ

Différences sédimentologiques et biologiques d'un côté à l'autre d'une dorsale profonde exposée à l'advection et à l'accumulation de fines particules

D'importantes quantités de particules argileuses et de vase en provenance du plateau continental de la Mer de Norvège se sont accumulées sur une dorsale, l'escarpement du plateau Vøring, à 1 245-1 310 m de profondeur. Les taux de sédimentation calculés pour l'Holocène y atteignent 18 cm par millénaire alors que, plus au sud, sur le talus continental, ils sont inférieurs à 1 cm par millénaire. Six stations ont été échantillonnées (trois de chaque côté de la dorsale) afin de quantifier les constituants biologiques et de comparer ces observations aux caractéristiques de l'environnement. Des différences notables entre les stations du nord et celles du sud sont observées dans la consommation de l'oxygène, dans la composition de la macrofaune et dans la composition, la biomasse et la répartition verticale de la méiofaune. Des populations de pogonophores et de nématodes, constituées d'ani-

maux de tailles relativement grandes, forment la faune spécifique qui occupe, sur le plateau Vöring, des zones caractérisées par une forte sédimentation et par une teneur élevée en carbone organique. L'accumulation de particules de tailles supérieures à 63 μm , observée dans le sédiment entre 6 et 10 cm de profondeur, résulte probablement de l'apport vertical par un entéropeuste fouisseur.

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INTRODUCTION

A large-scale interdisciplinary research programme in the Norwegian-Greenland Sea was launched in 1985 by the Sonderforschungsbereich 313, a special research unit at the University of Kiel, Germany (cf. Thiede *et al.*, 1985). The aim has been to investigate the particle flux to the sea bed and to determine the palaeo-oceanographic history of water masses. The present study focuses on the benthic environment and more specifically on sedimentary processes and organisms living on a profile across a ridge located at 1 245-1 424 m water depth on the Vöring Plateau off the Norwegian continental shelf. Prior to this

study, one of us (J.R.) had obtained preliminary results which indicated large lateral transport of fine sediments across the ridge. This process could possibly help to explain the faunal differences observed between the top and the foot of the ridge (Jensen, 1988).

We selected six sampling stations, three on each side of the ridge, and examined regional grain-size distribution, sedimentation rates, and water content down to 16 cm sediment depth; the biological parameters analyzed down to 10 cm depth were oxygen consumption, chlorophyll *a*, and the metazoan fauna. The paper presents detailed information on the most abundant metazoan taxon, the nematodes. Vertical transport processes of pelagic material mediated by benthic macrofauna are discussed.

Some studies have been conducted in recent years on the influence of sediment type and associated parameters on metazoan meiofauna and small-sized macrofauna in the deep-sea (Shirayama, 1983; 1984; Tietjen, 1984; 1989; Pfannkuche, 1985; Thistle and Sherman, 1985; Woods and Tietjen, 1985; Aller and Aller, 1986; Shirayama and Swinebanks, 1986; Carmen *et al.*, 1987; Pfannkuche and Thiel, 1987; Alongi and Pichon, 1988; Tietjen *et al.*, 1989). Results of benthic studies on metazoan fauna below 1 000 m depth in the Norwegian Sea derive from 13 investigations only (Thiel, 1971; Zaptsepin and Rittikh, 1976; Dahl *et al.*, 1977; Dinet, 1979; Laubier and Sibuet, 1979; Romero-Wetzel, 1987; 1989 *a; b*; Jensen, 1988; in press; Köster *et al.*, 1991; Jensen *et al.*, in press; Romero-Wetzel and Gerlach, in press). Only Thiel (1971) and Zaptsepin and Rittikh (1976) included the sedimentological aspect. Graf (1989) discussed benthic-pelagic coupling at our site, and Bathman *et al.* (1990) and Bathman *et al.* (1991) summarized the quality and quantity of vertical particle flux of pelagic material.

SITE, MATERIALS AND METHODS

Study site

The Vöring Plateau is a terrace situated off the Norwegian continental shelf and slope at 65-68°N and at water depths of 1 200-1 600 m (Fig. 1A). The flow of surface water from the south into the Norwegian Sea is an extension of the North Atlantic current. The prevailing bottom currents are from the West; salinity of the bottom water is 35 and the bottom temperature below 1 000 m is -0.7°C. Six stations across a ridge were sampled; they are at 1 245-1 424 m depth; the outermost stations are some 28 km distant from

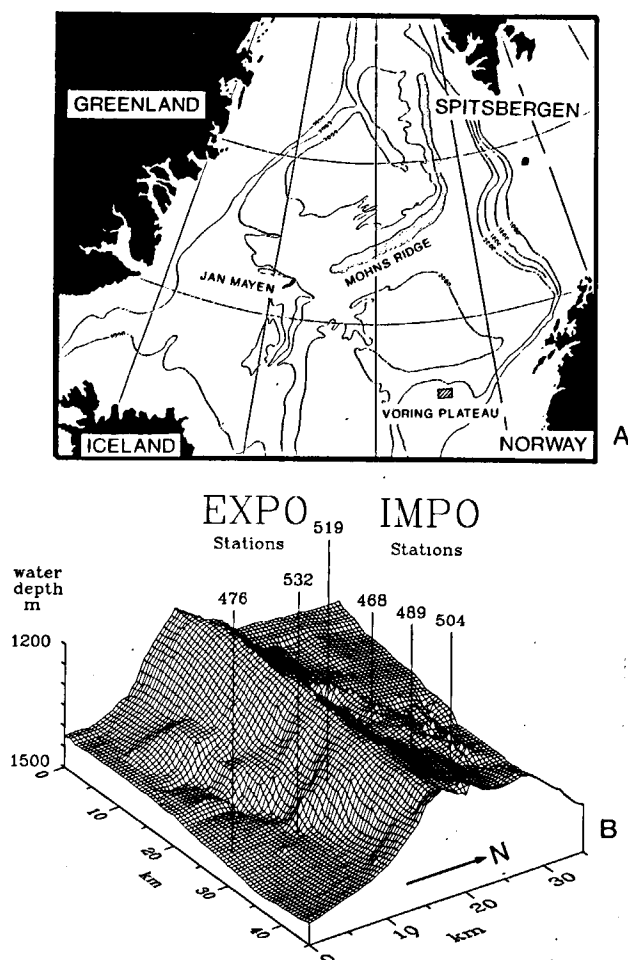


Figure 1

A) Map of Norwegian Sea with sampling area on the Vöring Plateau indicated; isobaths in metres; B) map of ridge with sampling stations. Stations 476, 532 and 519 are herein referred to as the Expo-stations opposed to the Impo-stations (stations 468, 489 and 504).

Table 1

Station data across a deep-sea ridge in the Norwegian Sea (Meteor cruise 7/4). #) Registration number for sedimentological samples in the Geological Institute, University of Kiel, Germany.

Sta.	Date (1988)	Coordinates		Depth (m)	GIK no. #
		Lat. (°N)	Long. (°E)		
476	21.8	67°39,2'	05°47,1'	1 424	16 068
532	30.8	67°40,4'	05°49,9'	1 400	23 024
519	27.8	67°41,4'	05°51,8'	1 325	16 055
468	19.8	67°44,1'	05°55,0'	1 245	23 004
489	23.8	67°46,5'	06°00,1'	1 286	16 054
504	25.8	67°48,3'	06°01,2'	1 310	23 328

each other (Fig. 1 B, Tab. 1). Three of the stations located at the southern slope of the ridge, are referred to as Expo-stations (stations 476, 532 and 519), signifying advection (Export) of pelagic material; the three other stations (stations 468, 489 and 504), located at the top and on the northern slope of the ridge, are called Impo-stations, signifying accumulation (Import) of pelagic material.

Sampling procedures and laboratory analyses

Samples for sedimentological analyses were taken at each station with a high-momentum corer (Meischner and Rumohr, 1974) equipped with a 100 cm-long plexiglass tube, 8 cm in diameter. Additional samples were taken with a USNEL box corer (50 x 50 cm), penetrating to a depth of about 40 cm in the sediments. Box-core samples were sub-sampled with a 40 cm long plexiglass tube, 8 cm in diameter. Sediments of the short cores were sliced at 1 cm intervals for sediment texture analysis; in this paper only the uppermost 16 cm will be discussed. Grain-size analysis was performed by wet sieving (63-125 µm and 125-2 000 µm) and the Atterberg sedimentation method [< 6.3 µm, 6.3-20 µm and 20-63 µm (*in von Engelhardt, 1964*)]. Water content was determined for each centimetre interval as the loss of weight of wet sediments dried at 70°C.

The regional extension of the area of high Holocene sediment accumulation, where sediments were thicker than 1 m, was mapped by means of 3.5 kHz sub-bottom profiling an area of 50 x 35 km (Fig. 1 B). A Kastenlot sediment core [Kögler, 1963 (30 x 30 cm, 9.6 m long)] from the centre of high accumulation revealed the Holocene age of sediment above the mapped sandy acoustic reflector (Rumohr *et al.*, in prep.). Sedimentation rates for advected grain size fractions were calculated from the local thickness and the local Holocene mean grain size composition (7-10 down-core samples).

Samples for biological analyses were taken at each station with a multiple corer (Barnett *et al.*, 1984) modified to attach eight 63 cm-long cylindrical tubes (10 cm inner diameter) which penetrated some 30 cm into the sediments. One large box-core sample was taken on each station for the analysis of the macrofauna. Meiofaunal analyses were restricted to the uppermost 10 cm of sediments which were sliced at 1 cm intervals. Three samples of 1 cm³ sediment per cm were extracted for chlorophyll *a* and analyzed according to Jeffrey and Humphrey (1975).

From each station, three tubes from the multiple corer were directly used as incubation chambers for determination of oxygen consumption. These cores were kept in darkness and at *in situ* temperature in the laboratory and were incubated for 48 hours. They were closed by a piston equipped with a magnetic stirrer. The covers had two connections for a flow-through system (6 mm inner diameter) as well as a small outflow (3 mm inner diameter) for taking water samples for oxygen determinations. Oxygen determinations were carried out as described by Grasshoff (1976).

Meiofauna analyses from each station are based on three 10 cm³ samples from each centimetre layer down to 5 cm depth and three 20 cm³ samples from each centimetre layer from 5 to 10 cm depth. These samples were preserved in 4 % formalin and stained with Rose Bengal. In the laboratory, sediments were gently washed on a sieve with a mesh size of 45 µm. All stained metazoans were sorted under a dissection microscope. All nematodes were identified to species level applying a Leitz Dialux microscope; a species list is available upon request to P. J. In order to show similarities of nematode assemblages between the six stations, the abundance of each species found per station was plotted in a matrix and an Euclidean cluster analysis was performed. Such an analysis considers presence-absence as well as abundance information. Biomass of meiofauna was derived from measurements of body volume, assuming a specific weight of 1.1. Carbon content of nematodes was calculated as 12.4 % of wet weight (Jensen, 1984). Sediments for macrofauna analysis were searched for fragile animals such as enteropneusts prior to sieving, after which the fauna was concentrated in a sieve with a mesh size of 1 mm. The retained animals were sorted under a dissection microscope and their biomass is given as formalin wet weight, after blotting on filter paper.

RESULTS

Sediment characteristics

Regional sediment composition

Holocene sediments at the Expo-stations are between 10 cm (stations 532 and 519) and 18 cm thick (station 476), in contrast with those at the Impo-stations where the Holocene column is up to 2 m thick. The Holocene sediment column in all six stations is mainly composed of clay (fraction < 6.3 µm), in amounts varying from 52 % in the Expo-stations to 73-77 % in the Impo-stations. On the other hand, the sand fraction (63-2 000 µm, mainly foraminifera) is a characteristic feature in the Expo-stations with values between 26 and 30 %, while the sand fraction of Impo-stations accounts for only 1-5 % of the sediments. The silt fractions vary little between the six stations and comprise 23-30 % (Fig. 2).

Regional sedimentation rates

High sedimentation rates of fine silt (fraction 6.3-63 µm) and clay (fraction < 6.3 µm) are evident at the Impo-sta-

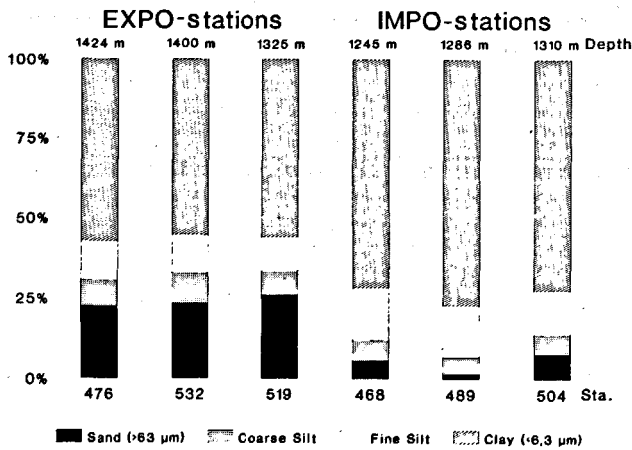


Figure 2

Regional grain-size distribution of the Holocene sediment column at six stations across a deep-sea ridge in the Norwegian Sea. Mean values of 7-10 samples. For station data, see Table 1 and Figure 1.

tions with maximum rates (station 489) of 150 mm ky⁻¹ for clay, 32 mm ky⁻¹ for fine silt (6.3-20 μm) and 10 mm ky⁻¹ for coarse silt (20-63 μm), totalling a rate of 191 mm ky⁻¹. Sand particles here (mainly foraminifera) accumulate with only 2.7 mm ky⁻¹. This is in contrast with the findings in the Expo-stations, which give higher rates for sand (2.7-4.6 mm ky⁻¹) but only 8.9-15.4 mm ky⁻¹, an equivalent of 5-8 % of the maximum Impo-rates for particles < 63 μm (Fig. 3, station 489). This is in good agreement with other places on the Vøring Plateau (Vogelsang, 1990). A calculation of the accumulated volume in the area of investigation results in 0.53 km³. There is no significant evidence of a decrease of Holocene sediment thickness surrounding the high accumulation area that would indicate nearby erosion, and no argument for a local sediment source, *e. g.* mud volcanoes.

Vertical grain-size distribution

The vertical distribution pattern down to 16 cm depth of the five grain-size classes; *i. e.* < 6.3 μm, 6.3-20 μm, 20-63 μm, 63-125 μm and 125-2 000 μm, is separated into regional groups related to the Expo-stations and the Impo-stations (Fig. 4 A-E). Particles > 2 000 μm, probably advected by ice or drifting macroalgae, were excluded from the calculation. The vertical distribution pattern of the grain-size class 20-63 μm is similar in all six stations down to 4 cm depth comprising 5-7.5 % (Fig. 4 C); the relative amounts of the 20-63 μm grain-size class increase with increasing sediment depth in the Expo-stations because of bioturbation which mixes Holocene and glacial time sediments (unpublished δ¹⁸O data), whereas they remain rather constant in the Impo-stations (pure Holocene sediments). The relatively constant vertical distribution pattern of the other grain-size classes down to 16 cm depth (and deeper) is a striking regional feature of the Impo-stations. In contrast, the distribution patterns in the Expo-stations in the uppermost 2 cm of sediments are characterized by a very low content in clay and silt (< 6.3 μm

and 6.3-20 μm) and high sand content (63-125 μm and 125-2 000 μm) compared to respective contents down-core. Moreover, the vertical distribution of grain sizes is similar down to 8-10 cm depth in the Expo-stations, below which the curves diverge strongly (Fig. 4 A-E). There appears, however, to be an accumulation of 63-125 μm and partly also of 125-2 000 μm grains in 4-10 cm depth at the Expo-stations as well as a distinct increase in 4-6 cm depth at station 489 (Fig. 4 D-E).

Water content

The water content of the sediments at the six stations is clearly separated into two regional groups, *i. e.* sediments comprising the Expo-stations with 40-60 % water in the uppermost 10 cm; and sediments from the Impo-stations which have a water content of 60-75 % with highest values in stations 489 and 504 (Fig. 4 F). The vertical distribution pattern of water content in the sediments shows the trivial feature of highest values in the uppermost 2 cm and a more or less downcore decrease. The sediments in station 468 are, however, unique in an almost constant water content profile throughout the column down to 16 cm depth (Fig. 4 F).

Biological characteristics

Oxygen consumption and chlorophyll a content

Oxygen consumption differs by a factor of almost six between stations, *i. e.* 0.9 ml O₂ m⁻² h⁻¹ in station 504 and up to 5.3 ml O₂ m⁻² h⁻¹ in station 532; other stations have values varying between 1.2-2.5 ml O₂ m⁻² h⁻¹ (Tab. 2). Highest oxygen consumptions appear at the slope of the Expo-stations.

Chlorophyll *a* profiles were nearly constant down to 10 cm depth and between stations; hence only integrated values are given (Tab. 2). Most chlorophyll *a* values are between 31.0-33.2 mg m⁻²; stations 519 and 468 have slightly lower values, 24.2 and 28.2 mg m⁻², respectively.

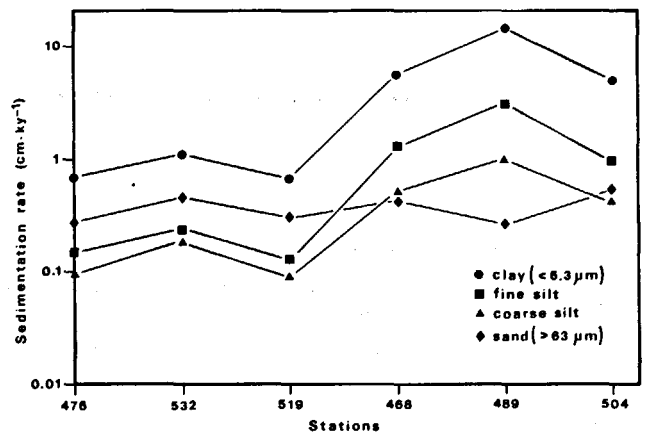


Figure 3

Regional sedimentation rates (log scale) of the Holocene sediment grain-size fractions at six stations across a deep-sea ridge in the Norwegian Sea (northern Vøring Plateau). Mean values of 7-10 samples. For station data, see Table 1 and Figure 1.

Figure 4

Vertical distribution of Holocene sediment grain-size fractions (< 6.3-2,000 µm) (A-E) and water content (F) down to 16 cm sediment depth at six stations across a deep-sea ridge in the Norwegian Sea (northern Vøring Plateau). For station data, see Table 1 and Figure 1.

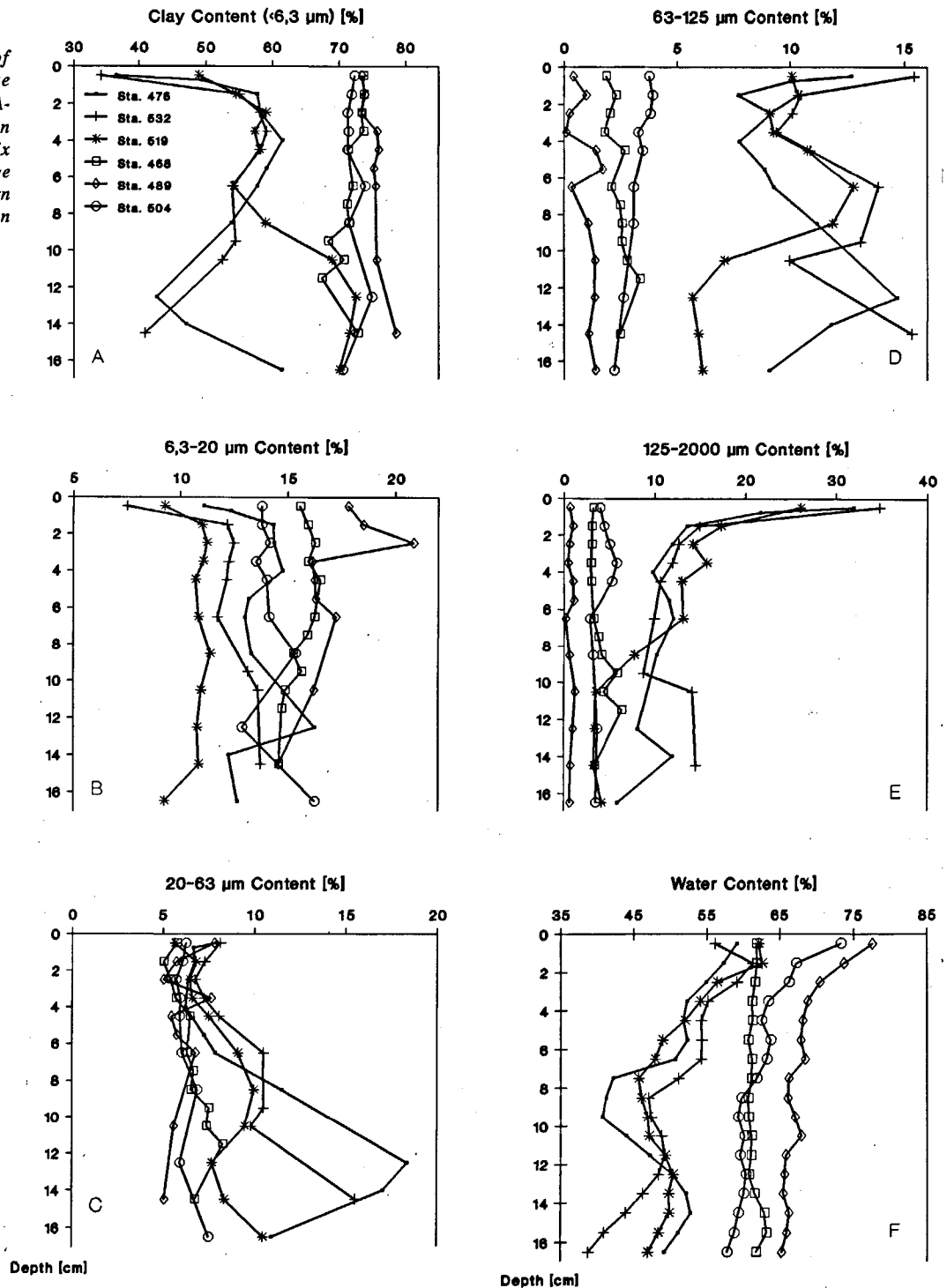


Table 2

Oxygen consumption ($\text{ml O}_2 \text{ m}^{-2} \text{ h}^{-1}$) with standard deviation and chlorophyll a content (mg m^{-2}) down to 10 cm depth at six stations across a ridge in the Norwegian Sea.

	476	532	519	468	489	504
Oxygen consumption ($\text{ml O}_2 \text{ m}^{-2} \text{ h}^{-1}$)	1.4	5.3	2.5	1.2	1.8	0.9
± 1 SD	0.2	0.1	0.1	0.3	0.1	0.4
Chl. a (mg m^{-2})	32.3	33.2	24.2	28.2	33.2	31.0

Meiofauna

More than 96 % of the biomass of multicellular meiofaunal organisms are made up by nematodes and harpacticoid copepods. Biomass values are generally higher in the Impo-stations than in the Expo-stations, *i. e.* 0.55-1.00 g WW m^{-2} vs. 0.20-0.57 g WW m^{-2} down to 10 cm depth (Tab. 3). Harpacticoid copepods are most numerous in the uppermost 0-1 cm layer in all stations with 10-24 ind. 10 cm^{-2} . They are distinctly different in their vertical distribution pattern, *i. e.* maximum depth of penetration in Expo-stations is 2-4 cm opposed to 6-8 cm in Impo-stations.

The biological characteristics of the nematode fauna were analyzed in detail (Fig. 5, 6 and 7, Tab. 4). Results of

Table 3

Total biomass (g WW m⁻²) of benthic metazoan fauna down to 10 cm depth retained on a 45 µm sieve (meiofauna) and on a 1 mm sieve (macrofauna, at six stations across a ridge in the Norwegian Sea: 1) mainly Kinorhyncha; 2) mainly (y) fragments of Spongia and Hydrozoa and (x) Pogonophora and other unidentified worms; 3) Enteropneusta were hand-picked from box corers.

	476	532	519	468	489	504
MEIOFAUNA						
Nematoda	0.34	0.25	0.15	0.42	0.36	0.89
Harpacticoid	0.22	0.03	0.03	0.17	0.18	0.10
Copepoda						
Others ¹	0.01	0.01	0.02	0.01	0.01	0.01
TOTAL (g WW m ⁻²)	0.57	0.29	0.20	0.60	0.55	1.00
MACROFAUNA						
Polychaeta	0.24	0.16	0.23	0.70	0.12	1.14
Mollusca	0.23	0.08	0.04	0.02	0.05	0.02
Crustacea	0.01	0.04	0.24	0.26	0.02	0.09
Sipunculida	0.66	0.58	0.88	0.00	0.02	0.00
Echinodermata	0.34	0.20	1.00	1.12	1.00	0.85
Enteropneusta	24.00	12.00	12.00	30.00	16.00	16.00
Others ²	0.00	0.00	0.00	0.22	0.47	0.23
	(y)	(y)	(y)	(x)	(x)	(x)
TOTAL (g WW m ⁻²)	25.48	13.06	14.39	32.10	17.21	18.10

Euclidean cluster analysis show two distinct faunal groups (Fig. 5) representing a regional separation of Expo-stations and of Impo-stations. The Expo-stations are inhabited by an abundant population of *Pararaeolaimus rumohri* (exclusively found there) and high abundances of many different desmoscolecids. This is in contrast with the Impo-stations, which are primarily united by the presence of *Rhabdodemanina* sp., *Desmodora pilosa* (both exclusively found in stations 489 and 504), *Acantholaimus elegans* and *Sabatieria* sp. There is a trend showing higher species number and abundance at the Expo-stations than at the Impo-stations (Tab. 4), i. e. 39-43 spp. and 259-393 ind. 10 cm⁻² vs. 37-40 spp. and 248-298 ind. 10 cm⁻². Conversely, mean body weight of nematodes shows animals are larger at Impo-stations than at Expo-stations (152-448 ng C vs. 72-119 ng C). The species diversity (H') and evenness (J) are high at each station (4.49-4.86 bits and 0.86-0.90, respectively) without obvious regional differences.

The vertical distribution pattern of nematode abundances indicates decreasing numbers with increasing depth (Fig. 6). Nematodes occur at least down to 10 cm depth in the Impo-stations and this is mainly due to the deep-dwelling *Sabatieria* sp. [*S. pulchra* group of species (Fig. 7)]; the nematodes in the Expo-stations penetrate down to only 5-8 cm depth. The abundance of *Sabatieria* sp. (Fig. 7) differs greatly between Expo- and Impo-stations, e. g. most are concentrated in shallow layers in the former station. But the population maximum is found at between 2 and 5 cm depth in all stations. The vertical distribution pattern of nematode biomass generally follows the same trend as the abundance pattern (Fig. 6). Deviating from this trend is station 504 with an exceptionally high value between 1-2 cm depth (330 µg C 10 cm⁻²), the cause of which is mainly the pre-

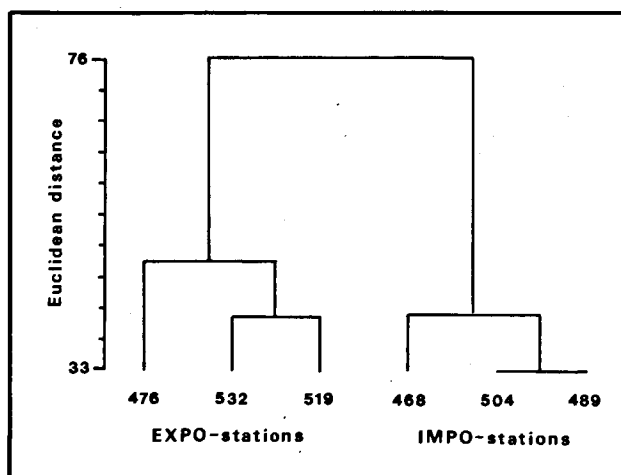


Figure 5

Cluster analysis (Euclidean distance) of 73 nematode species and their abundances down to 10 cm depth at six stations across a deep-sea ridge in the Norwegian Sea.

sence of the large *Rhabdodemanina* sp. with an adult weight of 3.4 µg C. An increase in biomass in 4-5 cm depth in stations 532 is also unusual. This is due to the relatively high abundance of the medium-sized *Syringolaimus renaudae*.

Macrofauna

Macrofaunal biomass down to 10 cm depth (Tab. 3) varies between 13.06 g WW m⁻² (station 532) and 32.10 g WW m⁻² (station 468). The biomass values are heavily influenced by the presence of up to four specimens of the enteropneust *Stereobalanus canadensis* in one sample (1/4 m²), which has an adult weight of about 2 g WW. When the enteropneusts are excluded, biomass values vary only from ca. 1 to 2 g WW m⁻² between the six stations. Some macrofaunal groups show distinct distribution patterns, e.g. sipunculans (*Golfingia* sp.), sponges and hydroids inhabit mainly the Expo-stations and molluscs are mainly found in sediments of station 476. In contrast the pogonophorans *Siboglinum brevicephalum*, *Nereilinum murmanicum* and at least two other still unidentified species (Flügel, pers. comm.) are found exclusively in the Impo-stations.

Table 4

Five biological characteristics of the nematode fauna down to 10 cm depth at six stations across a ridge in the Norwegian Sea.

	476	532	519	468	489	504
No. species	41	43	39	37	38	40
Abundance (No. 10 cm ⁻²)	356	393	259	298	295	248
Mean body weight (ng C)	119	80	72	176	152	448
Diversity (H')	4.78	4.86	4.63	4.49	4.55	4.57
Evenness (J)	0.89	0.90	0.88	0.90	0.87	0.86

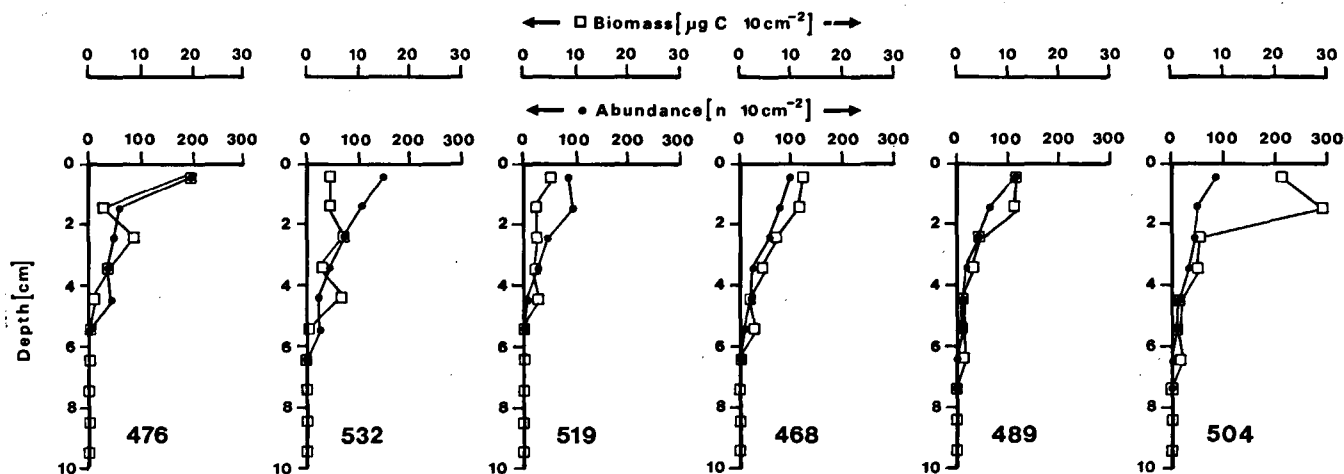


Figure 6

Vertical distribution of nematode abundance and biomass down to 10 cm depth at six stations across a deep-sea ridge in the Norwegian Sea.

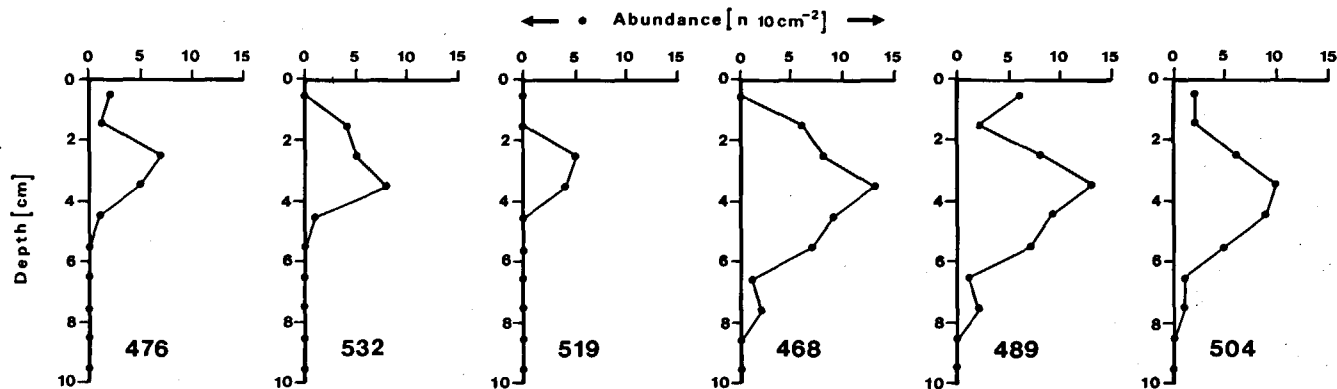


Figure 7

Vertical distribution of the deep-dwelling nematode *Sabatieria* sp. (*S. pulchra* group of species) at six stations across a deep-sea ridge in the Norwegian Sea.

DISCUSSION

Advection and sediment accumulation

Taking the regional sedimentation rates of fine and coarse-grained sediments into consideration, there is strong evidence - without applying statistical tests - indicating the existence of a pronounced advection of clay and silt particles from and across the area represented by the Expo-stations. This is contrasted by an abundant accumulation of such grains in the Impo-stations (Fig. 3) because there is no indication for a local sediment source applying for a regional surplus of more than 0.5 km³ of sediment. Bottom current measurements (Rumohr, 1990) are in good agreement with the concept of the occurrence of topographically related strong westerly bottom currents along the southern slope across the Expo-stations during times with upslope components (several days every 20-40 days), *i. e.* the effect of a Taylor column structure (*cf.* Brechner and Hoog, 1980). This mechanism may account for the limited amount of fine material (< 63 µm) deposited on the southern slope (Fig. 3) and also explains the great fallout of such particles on the

ridge and on the northern slope - the calm centre of a suspected temporary anticyclonic vortex. As deduced from the abundant accumulation of fine-grained material resulting in high sedimentation rates in the Impo-stations (0.53 km³) and the good agreement of the sediment thickness on the southern slope with other places on the Vøring Plateau, the bottom area exporting this material must be several times larger than the accumulation area. The suggested source area, assuming an export equivalent of 5 cm sediment thickness (approximately 25 % Holocene sediment thickness on the Vøring Plateau), should be in the magnitude of 10,000 km², which corresponds to a circle of 120 km in diameter. A prevailing direction of sediment transport by near-bottom currents parallel to the depth contours suggests transport distances up to 100 km or more (Rumohr, 1990).

Biological activity

Chlorophyll *a* in the sediment of Vøring Plateau was regarded as a short-lived tracer for freshly settled pelagic material such as fecal pellets (Graf, 1989). Recently, a half-life of three weeks was calculated for this pigment in

sediments from the above area (Abele-Oeschger, 1991). Compared to the irregular grain-size distribution along the profile, the even chlorophyll *a* distribution indicates that food supply is not directly linked to the slower near bottom advective processes, which determine the final deposition area. Most likely the chlorophyll *a* - perhaps contained within fecal pellets - is already degraded to phaeopigments, when the fine-grained material is transported to the deposition areas. Future investigations should confirm this hypothesis by analyzing degradation products of chlorophyll *a* in bottom-near transported particles. The biological communities across the ridge respond differently in terms of oxygen consumption to the almost constant sedimentation of chlorophyll *a*. This cannot be explained by observed regional differences in faunal composition, *e. g.* suspension and surface deposit-feeding organisms (such as hydroids, sponges and sipunculans predominating) on the southern slope as opposed to mostly infaunal worms (polychaetes, nematodes and pogonophorans) on the northern slope (Tab. 3). Hydroids and sponges were so low in abundance that they could not exert a large influence on oxygen consumption, and deep-dwelling pogonophorans are known to utilize oxygenated water from the surface for their chemoautotrophic endo-symbionts (Southward, 1989). This leaves sipunculans which in the present study occur in densities of up to 4 ind. 78 cm⁻² at the Expo-stations (*see also* Romero-Wetzel, 1987), tiny polychaetes (*cf.* Romero-Wetzel, 1989 *b*) and nematodes for consideration. Further studies should reveal their metabolic capacities as well as the bacterial oxygen consumption. At all events, it is likely that the processes causing the sediment transport from the slope of the Expo-stations (stations 532 and 519) - for example bottom currents - stimulate benthic oxygen consumption of small-sized organisms.

Present results show higher nematode biomass values on the northern slope with high sedimentation rates than on the southern slope. This is rather similar to results obtained by Thiel (1971) from the Norwegian Sea slope of the Iceland-Faroe-Ridge *vs.* the Atlantic slope of the ridge influenced by strong bottom currents and less sedimentation. On the other hand, and in contradiction with findings by Thiel (1971), abundances of nematodes on the northern slope were in general lower than on the southern slope. Dinert (1973) also studied the abundances of meiofauna organisms (mainly composed of nematodes) on two opposite slopes of the Walvis ridge off South-East Africa which were suggested to be influenced by same set of factors as those prevailing on the Iceland-Faroe ridge; yet, lowest nematode abundances were obtained on the slope suggested to be influenced by strongest bottom currents and less sedimentation rates in accordance with results obtained by Thiel (1971). The observed differences between the present study and Thiel (1971) and Dinert (1973) can not be explained by employed methods: extraction and concentration methods were similar in all three studies. Other characteristics of the nematode fauna from the Iceland-Faroe-Ridge and the Walvis Ridge remain to be studied.

In terms of assemblage, the nematode fauna exhibited a

strong relationship with regional differences related to lateral advection and accumulation of fine material, *i. e.* Expo-stations on the southern slope *vs.* Impo-stations on the northern slope, respectively. This example highlights the importance of identifying the fauna to the lowest possible taxon, *i. e.* species level (*see also* Thistle and Sherman, 1985; Tietjen, 1989), and utilizing the information as a tool to demonstrate the influence of physico-chemical parameters on the fauna. The nematodes in station 489 (maximum accumulation rate) and station 504 are both closely related to the fauna at the foot of the Norwegian continental shelf at 970 m depth (station 70); the latter area is regarded by Jensen (1988) to be unique in terms of species composition and large biomass. Rumohr (*in press*) has also shown that the locality of station 70 is characterized by an exceptionally large sedimentation of fine particles - from the shelf and upper slope - comparable to the situation on the northern slope of the ridge. These observations, together with the specific occurrence of pogonophorans in all these stations, lead to the conclusion that there exists a fauna association on Vöring Plateau which specifically inhabits areas with high sedimentation rates of fine material at different water depths and caused by different sedimentation events. Rumohr (*in press*) shows that these areas also are characterized by high carbon contents.

The depth distribution of the nematode and harpacticoid copepod fauna also shows a distinct regional pattern which appears to be related to differences in pore water content in Expo- and Impo-stations (Fig. 4 F); *i. e.* the pore water content in Impo-stations is higher than 60 % throughout the sediment column. Harpacticoid copepods and nematodes penetrate down to 6-8 cm and at least 10 cm, respectively depth in Impo-stations. This compares with the vertical distribution of harpacticoid copepod and nematode fauna which is limited to 2-4 cm and 6-8 cm depths, respectively in Expo-stations where pore water content is 50-60 % in the uppermost 6 cm of sediments and further decreases with increasing depth. The oxygen concentration in the pore water also delineates the vertical distribution of the fauna in the deep-sea (Shirayama and Horohoski, 1982). It is noteworthy that the nematode *Sabatieria sp.* is the most abundant and deep-dwelling species of the three *Sabatieria* species occurring at all three stations. From an evolutionary point of view it is interesting that this *Sabatieria* species - related to the *S. pulchra* group of species - is the inhabitant of the deep sediment horizons. It has been suggested (Jensen, 1981) that the *S. pulchra* group of species inhabits muddy sediments in meso- and polyhaline waters and exhibits the unique characteristic of being able to inhabit deep sediment horizons with very low oxygen concentration in pore water. The abundance and vertical distribution of the present deep-sea *Sabatieria* species is thus in accordance with observations from shallow waters. The observations indicate that this distribution pattern and, consequently, the specific physiological nature of the *S. pulchra* group of species may be a general rule.

Recent results of macrofaunal studies on Vöring Plateau (Romero-Wetzel, 1989 *a*; Jensen, *in press*) have also shown that the enteropneust *Stereobalanus canadensis*

occurs in branched burrow systems down to 10 cm depth. Freshly sedimentated pelagic material (intact coccolithospheres and Loricae of tintinnids) lines its burrow wall in considerable numbers, and its fecal pellets - consisting of crushed pelagic material and clay particles - are deposited in large patches in the burrow system. Hence, both behavioural traits of this enteropneust cause a significant input of pelagic material into deep sediment horizons which may explain *e. g.* the distinct accumulation of grains larger than 63 μm in deep sediment horizons at the Expo-stations (*cf.* Fig. 4 C, E). A detailed study of the deep-dwelling polychaetes *Notomastus latericeus* and *Myriochele* spp. and the sipunculan *Golfingia* sp. could also reveal that some of these species are responsible for a vertical particle transport down to 4-6 cm depth, as a result of processes related to feeding or tube-construction (*cf.* Romero-Wetzel, 1987; 1989 *b*; Graf, 1989).

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REFERENCES

- Abele-Oeschger D. (1991). Potential of some carotenoids in two recent sediments of Kiel Bight as biogenic indicators of phytodetritus. *Mar. Ecol.-Prog. Ser.*, **70**, 83-92.
- Aller J.Y. and R.C. Aller (1986). Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the Hebble site, western North Atlantic. *Deep-Sea Res.*, **33**, 755-790.
- Alongi D.M. and M. Pichon (1988). Bathyal meiobenthos of the Western Coral Sea: distribution and abundance in relation to microbial standing stocks and environmental factors. *Deep-Sea Res.*, **35**, 491-503.
- Barnett P.B.O., J. Watson and D. Conolly (1984). A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanologica Acta*, **7**, 4, 399-408.
- Bathmann U.V., R. Peinert, T. Noji and B. von Bodungen (1990). Pelagic origin and fate of sedimenting particles in the Norwegian Sea. *Prog. Oceanogr.*, **24**, 117-125.
- Bathmann U.V., T. Noji and B. von Bodungen (1992). Sedimentation of pteropods in the Norwegian Sea in autumn. *Deep-Sea Res.*, **38**, 1341-1361.
- Brechner W.O. and N.G. Hoog (1980). Oceanic observations of stratified Taylor columns near a bump. *Deep-Sea Res.*, **27**, 1029-1045.
- Carmen K.R., K.M. Sherman and D. Thistle (1987). Evidence that sediment type influence the horizontal and vertical distribution pattern of nematodes at a deep-sea site. *Deep-Sea Res.*, **34**, 45-53.
- Dahl E., L. Laubier, M. Sibuet and J.-O. Strömberg (1977). Some quantitative results on benthic communities of the deep Norwegian Sea. *Astarte*, **5**, 61-79.
- Dinet A. (1973). Distribution quantitative du méiobenthos profond dans la région de la dorsale de Walvis (Sud-Ouest africain). *Mar. Biol.*, **20**, 20-26.
- Dinet A. (1979). A quantitative survey of meiobenthos in the deep Norwegian Sea. *Ambio Spec. Rep.*, **6**, 75-77.
- von Engelhardt W. (1964). *Methoden der Sedimentuntersuchungen*. Schweitzerbarth, Stuttgart, 303 pp.
- Graf G. (1989). Benthic-pelagic coupling in a deep-sea benthic community. *Nature*, **341**, 437-439.
- Grasshoff K. (1976). *Methods of sea water analysis*. Verlag Chemie, Weinheim, 317 pp.
- Jeffrey S.W. and G.F. Humphrey (1975). New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*₁, and *c*₂ in higher plants, algae and natural phytoplankton. *Biochem. Physiol.*, **167**, 191-197.
- Jensen P. (1981). Species, distribution and a microhabitat theory for marine mud-dwelling Comesomatidae (Nematoda) in European waters. *Cah. Biol. mar.*, **22**, 231-244.
- Jensen P. (1984). Measuring carbon content in nematodes. *Helgoländer Meeresunters.*, **38**, 83-86.
- Jensen P. (1988). Nematode assemblages in the deep-sea benthos of the Norwegian Sea. *Deep-Sea Res.*, **35**, 1173-1184.
- Jensen P. (1992). An enteropneust's nest: results of the burrowing traits by the deep-sea acorn worm *Stereobalanus canadensis*. *Sarsia*, in press.
- Jensen P., R. Emrich and K. Weber (1992). Brominated metabolites and reduced numbers of meiofauna organisms in the burrow wall lining from the deep-sea enteropneust *Stereobalanus canadensis*. *Deep-Sea Res.*, in press.
- Kögler F.C. (1963). Das Kastenlot. *Meyniana*, **17**, 1-7.
- Köster M., P. Jensen and L.-A. Meyer-Reil (1991). Hydrolytic activity associated with organisms and biogenic structures in deep-sea sediments, in: *Microbial enzymes in aquatic environments, Chapter 19*, R.J. Chrost, editor. Springer Verlag, Berlin, 298-310.
- Laubier L. and M. Sibuet (1979). Ecology of the benthic communities of the deep North East Atlantic. *Ambio Spec. Rep.*, **6**, 37-42.
- Meischner D. and J. Rumohr (1974). A light-weight, high-momentum gravity corer for subaqueous sediments. *Senckenberg. marit.*, **6**, 105-117.
- Pfannkuche O. (1985). The deep-sea meiofauna of the Porcupine seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stocks. *Oceanologica Acta*, **8**, 343-353.
- Pfannkuche O. and H. Thiel (1987). Meiobenthic stocks and benthic activity on the NE-Svalbard shelf and in the Nansen Basin. *Polar Biol.*, **7**, 253-266.
- Romero-Wetzel M.R. (1987). Sipunculans as inhabitants of very deep, narrow burrows in deep-sea sediments. *Mar. Biol.*, **96**, 87-91.
- Romero-Wetzel M.R. (1989 *a*). Branched burrow-systems of the enteropneust *Stereobalanus canadensis* (Spengel) in deep-sea sediments of the Vöring Plateau, Norwegian Sea. *Sarsia*, **74**, 85-89.

- Romero-Wetzel M.R. (1989 b). Struktur und Bioturbation des Makrobenthos auf dem Vöring Plateau (Norwegische See). *Ber. Sonderforschungsb. 313*, **13**, 1-204.
- Romero-Wetzel M.R. and S.A. Gerlach (1992). Abundance, biomass, size-distribution and bioturbation potential of deep-sea macrozoobenthos on the Vöring Plateau (1 200-1 500 m, Norwegian Sea). *Meeresforschung (Repts mar. Res.)*, in press.
- Rumohr J. (1990). Eine topographische Sedimentfalle auf dem nördlichen Vöring Plateau. *Sonderforschungsb. 313*, **1**, 338-343.
- Rumohr J. (1992). A high accumulation area on the continental slope off Northern Norway and sediment transport by cascading winter water. *Deep-Sea Res.*, in press.
- Shirayama Y. (1983). Size structure of deep-sea meio- and macrobenthos in the Western Pacific. *Int. Revue ges. Hydrobiol.*, **68**, 799-810.
- Shirayama Y. (1984 a). The abundance of deep-sea meiobenthos in the Western Pacific in relation to environmental factors. *Oceanologica Acta*, **7**, **1**, 113-121.
- Shirayama Y. (1984 b). Vertical distribution of meiobenthos in the sediment profile in bathyal, abyssal and hadal deep-sea systems of the Western Pacific. *Oceanologica Acta*, **7**, **1**, 123-129.
- Shirayama Y. and M. Horikoski (1982). Vertical distribution of smaller macrobenthos and larger meiobenthos in the sediment profile in the deep-sea system of Suruga Bay (Central Japan). *J. oceanogr. Soc. Japan*, **38**, 273-280.
- Shirayama Y. and D.D. Swinebanks (1986). Oxygen profile in deep-sea calcareous sediment calculated on the basis of measured respiration rates of deep-sea meiobenthos and its relevance to manganese diagenesis. *La Mer*, **24**, 75-80.
- Southward A.J. (1989). Animal communities fuelled by chemo-synthesis: life at hydrothermal vents, cold seeps and in reducing sediments. *J. Zool., Proc. zool. Soc. Lond.*, **217**, 705-709.
- Thiede J., S.A. Gerlach and G. Wefer (1985). Sedimentation im Europäischen Nordmeer. Organisation und Forschungsprogramm für die Zeitraum 1985-87. *Ber. Sonderforschungsb. 313*, **1**, 1-101.
- Thiel H. (1971). Häufigkeit und Verteilung der Meiofauna im Bereich des Islands-Färöer-Rückens. *Ber. dt. Wiss. Komm. Meeresforsch.*, **22**, 99-128.
- Thistle D. and K. Sherman (1985). The nematode fauna of a deep-sea site exposed to strong near-bottom currents. *Deep-Sea Res.*, **32**, 1077-1088.
- Tietjen J.H. (1984). Distribution and species diversity of deep-sea nematodes in the Venezuela Basin. *Deep-Sea Res.*, **31**, 119-132.
- Tietjen J.H. (1989). Ecology of deep-sea nematodes from the Puerto Rico trench area and Hatteras abyssal plain. *Deep-Sea Res.*, **36**, 1579-1594.
- Tietjen J.H., J.D. Deming, G.T. Rowe, S. Macko and R.J. Wilke (1989). Meiobenthos of the Hatteras abyssal plain and Puerto Rico trench: abundance, biomass and associations with bacteria and particulate fluxes. *Deep-Sea Res.*, **36**, 1567-1577.
- Vogelsang E. (1990). Palaeo-Ozeanographie des Europäischen Nordmeeres an hand stabiler Kohlenstoff- und Sauerstoffisotope. *Ber. Sonderforschungsb. 313*, **23**, 1-136.
- Woods D.R. and J.H. Tietjen (1985). Horizontal and vertical distribution of meiofauna in the Venezuela Basin. *Mar. Geol.*, **68**, 233-241.
- Zaptsepin V.I. and L.A. Rittikh (1976). Quantitative distribution of macrobenthos in the Norwegian Sea and southern part of the Greenland Sea. *Oceanology*, **16**, 397-400.