

BENTHIC MACROFAUNAL COMMUNITY STRUCTURE IN THE NORWEGIAN TRENCH, DEEP SKAGERRAK

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ABSTRACT

Benthic communities were studied at 15 stations along two transects at between 144 and 682 m depth in the Norwegian Trench. Communities of the deep accumulation bottoms generally exceeding 400 m depth, and 65 nautic miles apart, had a high similarity in species-dominance composition (Bray-Curtis index). The faunal composition on the slopes also showed high similarities, but was less homogeneous. The average number of species per 0.1 m² was significantly higher at the shallow-slope stations (mean 28.6) than at the deep-trench stations (mean 19.8). Among all stations abundance varied between 455 and 6660 ind·m⁻² and biomass was generally low, <40 g wet wt·m⁻² (excluding some large individuals). Dominant faunal groups were polychaetes and molluscs followed by crustaceans. The tube-building polychaete *Spiochaetopterus bergensis* was numerically dominant at all deep-trench stations, where the bivalves *Thyasira eumyaria* and *Kelliella miliaris* were also abundant. Sediment characteristics, transport and accumulation rates are discussed as structuring factors for the benthic communities.

Key words: abundance, biomass, species numbers, transport, accumulation, feeding groups, *Spiochaetopterus*, *Thyasira*, *Kelliella*, *Amphilepis*

1. INTRODUCTION

The Norwegian Trench is a deep (≈250-700 m) part of the Skagerrak surrounded by the shallow Kattegat in the southeast (mean depth ≈23 m) and the North Sea in the west (mean depth ≈50 m) and extends northwards along the south-central Norwegian coast to form a deep-water connection with the Norwegian Sea. The Norwegian Trench is the largest accumulation area for suspended matter entering the North Sea from the Atlantic Ocean and the English Channel (Eisma & Kalf, 1987). The annual deposition is about 30·10⁹ kg (dry weight). This corresponds to a sedimentation of more than 4.0 mm·y⁻¹ in the northeastern Skagerrak, about 2.0 mm·y⁻¹ on the southern and northern slopes, and about 1.0 mm·y⁻¹ in the central basin (Van Weering *et al.*, 1987; Dennegård *et al.*, 1992). From the North Sea rather strong bottom currents, up to 20 m·s⁻¹, enter the Skagerrak and occur down to 500 m, especially on the south side of the trench (Rodhe, 1987). These currents are likely to resuspend and distribute the suspended matter on the slopes. The near-bottom vertical transport of organic and inorganic particles in some areas, and the accumulation of such particles in others, are likely

to have significant effects on the structure of the benthic system.

The macrofauna in the deeper Skagerrak was first described by Petersen (1915) and characterized as an *Amphilepis norvegica* - *Pecten vitreus* community. However, Petersen took samples only at three deep (275-670 m) stations, where he found *A. norvegica* to be present at all three. Apart from a few stations studied by Rosenberg *et al.* (1987) and Rosenberg *et al.* (1990), most information on macrofaunal communities has been presented by Josefson (1981, 1985). He has described the macrofaunal distribution in the eastern part of the Skagerrak at seven stations sampled quantitatively at depths between 200 m and 620 m.

Early studies of the benthic meiofauna of the deeper Skagerrak in the 1930s focused on species distribution of ostracods (Elofson, 1941), amphipods (Enequist, 1950), cumaceans (Forsman, 1940), and foraminiferans (Höglund, 1947). Recent studies of meiofauna (De Bovée *et al.*, 1996) and foraminiferans have also been conducted (Bergsten *et al.*, 1996; Moodley *et al.*, 1993, and references therein).

In the present study we have sampled the macrofauna along two transects. Ten stations were sampled

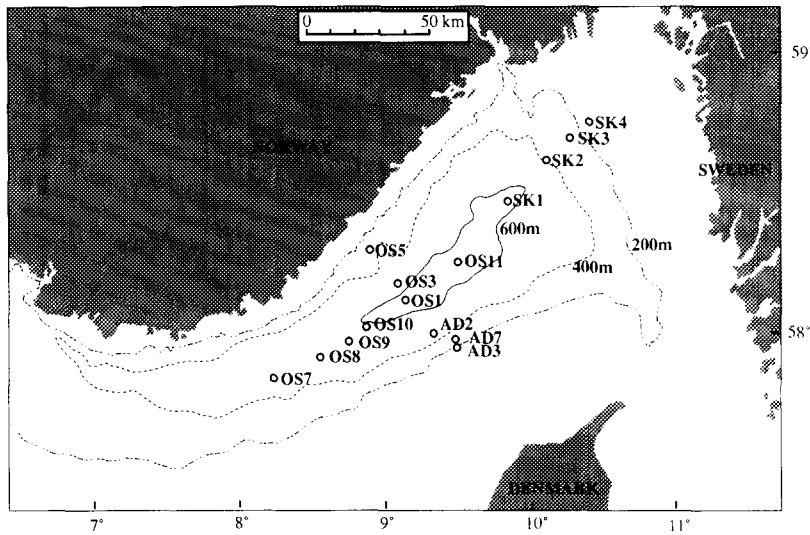


Fig. 1. The Skagerrak with sampling stations and depth contours.

in the Norwegian Trench from southwest to northeast and five stations on the Danish and Norwegian slope sides of the Trench from southeast to northwest (Fig. 1). The aim of this study is to describe the benthic communities in relation to depth and sediment characteristics. This is the first comparative study of benthic macrofauna from the western and central parts of the deep Skagerrak.

The main bottom-water inflow to the Skagerrak is of North Atlantic origin. The salinity below 100 m depth in the Skagerrak is constant and exceeds 35 psu, the temperature is between 5.5 and 6.5°C, and the oxygen concentration is more than 5 ml·dm⁻³ (North Sea Task Force, 1993). The sediment in the investigated area is predominantly clay with an organic carbon content of more than 2% (Van Weering & Qvale, 1983; Moodley *et al.*, 1993). In the 1930s, Enequist (1950) found the clay sediment in the deep part of the Norwegian Trench to be largely changed into coprogen (pelletized) material.

2. MATERIAL AND METHODS

The benthic macrofauna was sampled from 1992 to 1994; positions and depths are given in Table 1. Three hauls were taken down to ≈18 cm sediment depth at each station with a 0.1 m² Smith-McIntyre grab. The residue retrieved on a 1 mm sieve was preserved in ≈80% ethanol and the animals were later sorted out at 6x magnification. Biomass is ethanol wet weight with shells, and for the polychaetes *Myriochele oculata* and *Spiochaetopterus bergensis* including that part of the tubes where the worms were present inside. Sediment profile pictures (22x12 cm) were taken close to station SK1 and SK2 with an *in*

situ camera described in Rosenberg & Diaz (1993). Sediment grain-size structure and percent organic C and total N (dry weight, analysed by a Carlo Erba, model 1106) (Table 1) were analysed at Göteborg University, department of Geology (Stevens *et al.*, 1996). Numerical classification of the benthic communities including all species was made based on the group-average sorting algorithm (Bray & Curtis, 1957). Separation into feeding groups was mainly based on information by Fauchald & Jumars (1979) and Josefson (1986). *S. bergensis* was, however, treated as a suspension feeder based on observations by Barnes (1965). Differences in number of species between stations were tested by ANOVA where sample replicates were nested. Abundance-to-depth relations were tested by regression analysis.

3. RESULTS

The Bray-Curtis similarity index, based on abundance data, grouped all stations deeper than 400 m, except station AD2 on the eastern slope, into one unit with a similarity above 55% (Fig. 2). The distance between these stations, the western station OS7 and the eastern station SK1, is about 65 nautical miles. Among the deep-trench stations, OS1 and OS10, and OS8 and OS11, were paired tightly with similarities above 85%. All other stations shallower than 350 m had lower similarities. The similarity between the deeper group of stations and the shallower group was 22%. Station AD3 had low similarity with the rest, only 7%. In the following, the cluster of eight stations with similarities above 55% are called deep-trench stations, and the other seven stations are called shallow-slope stations.

TABLE 1
The benthic stations with depths, positions, sampling dates and sediment characteristics.

station	depth (m)	position		sediment (0-2 cm)					date
		N	E	Clay (%)	Silt (%)	Org C (%)	Tot N (%)	C/N (%)	
AD 2	455	58°00,00'	9°21,25'						Aug-92
AD 3	177	57°56,20'	9°27,30'						Aug-92
AD 7	294	57°58,38'	9°23,90'						Aug-92
OS 1	637	58°08,00'	9°10,99'	31.1	60.1	2.4	0.29	8.3	May-93
OS 3	411	58°12,00'	9°05,01'	38.5	60.7	2.3	0.27	8.5	May-93
OS 5	252	58°20,00'	8°52,99'	43.9	53.6	2.1	0.24	8.8	May-93
OS 7	507	57°50,01'	8°17,00'	54.2	45.4	2.3	0.31	7.4	May-93
OS 8	521	57°53,01'	8°32,01'	43.3	51.9				May-93
OS 9	538	57°59,00'	8°43,99'	38.7	58.5	2.4	0.25	9.6	May-93
OS 10	573	58°00,88'	8°52,49'	46.2	52.9				May-93
OS 11	682	58°16,53'	9°30,57'	36.9	61.7	2.9	0.31	9.4	May-93
SK 1	482	58°29,08'	9°52,88'						May-94
SK 2	350	58°36,50'	10°09,61'						May-94
SK 3	260	58°39,37'	10°15,60'						May-94
SK 4	144	58°44,20'	10°27,20'						May-94

Numerically dominant faunal groups at all stations were polychaetes (23-73% of the total abundance) and molluscs (4-49%) followed by crustaceans (2-20%) (Fig. 3). Echinoderms and sipunculids were represented at 9 stations each, with 1 to 6% of the total abundance.

Total number of species, abundance, biomass and feeding categories are listed in Table 2. The average number of species per 0.1 m² was significantly ($p < 0.05$, $F = 6.20$) higher at the shallow-slope stations, between 12 and 40 (mean 28.6, $SE = 2.2$), than at the deep-trench stations, between 11 and 25 (mean 19.8, $SE = 1.1$). Abundance and number of species were highest at station AD3 and lowest at stations SK1 and SK3. The abundance at the deep-trench stations varied between 820 and 2887 ind·m⁻², and at the shallow-slope stations between 455 and 6660 ind·m⁻².

Total biomass at the stations varied between 12.2 and 140.5 g·m⁻². A few large specimens at stations AD2 (*Funiculina quadrangularis*, 13.1 g·m⁻²), AD7 and SK4 (*Brissopsis lyrifera*, 116.0 and 76.3 g·m⁻²), and AD3 (*Cerianthus lloydii*, 28.9 and *Ophiura sarsi*, 10.1 g·m⁻²) made large contribution to the total biomass. If these weights are subtracted, all stations have biomass values lower than about 40 g·m⁻², except station AD3 (87.4 g·m⁻²). At the latter station *Myriochele oculata* weighed 26.4 g including tubes. *Spiochaetopterus bergensis* had the highest biomass (3.4 to 14.9 g·m⁻²) at the deep-trench stations, except at station OS7 where *Terebellides stroemi* weighed 11.5 g·m⁻². *Orbinia norvegica* and *Abra nitida* had high biomass values at several shallow-slope stations.

Sub-surface deposit feeders and surface deposit feeders were the dominant feeding categories at the shallow-slope stations. At these stations suspension feeders made up less than 16% numerically, whereas at all deep-trench stations they dominated at most stations and contributed 28 to 66%. Predators made up between 2 and 20% of the total numbers at all stations.

Spiochaetopterus bergensis ranked first by number at all eight deep-trench stations with abundances between 293 and 1740 ind·m⁻² (Table 3). The abundance was significantly ($p < 0.001$, $F = 18.81$) positively correlated with depth. The tubes were about 1 mm in diameter and up to about 120 mm long. *Thyasira eumyaria* and *Kelliella miliaris* were among the top three dominants at most deep-trench stations, and their densities were also significantly ($p < 0.001$, $F = 25.21$; $p < 0.01$, $F = 16.34$) positively correlated with depth.

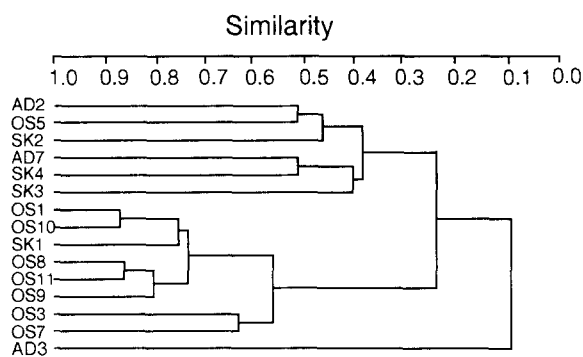


Fig. 2. Benthic community similarity based on species-dominance composition (Bray-Curtis index) in the deep Skagerrak.

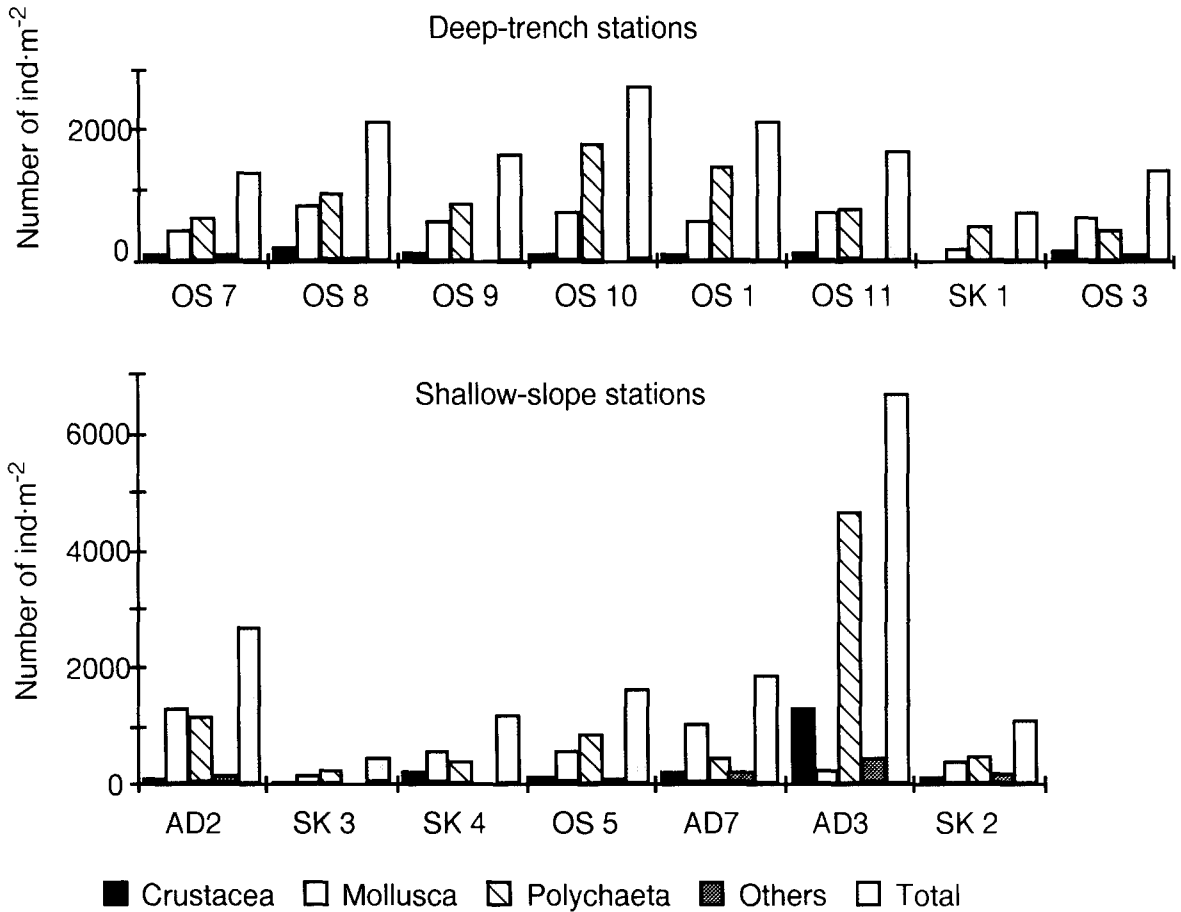


Fig. 3. Total and faunal-group abundance per m^2 at the deep-trench and shallow-slope stations in the Skagerrak.

The eight first listed species in Table 3 and *Thyasira equalis* occurred at all deep-trench stations. *T. equalis* and *Heteromastus filiformis* occurred at all stations sampled, and *Paramphinoe jeffreysi* and *Nuculoma tenuis* were only missing at one station. All four *Thyasira* species listed in Table 3 were found at most stations.

On the shallow-slope stations the dominance was more variable between species. *Heteromastus filiformis*, *Abra nitida*, and *Thyasira equalis* were conspicuous species at several stations. Species occurring in high numbers at single stations were *Maldane sarsi*, *Myriochele oculata*, *Praxillella affinis*, *Arcturella dilatata* and *Tharyx mcintoshi*. The crustacean *Calocaris macandreae* was found at stations OS5, SK2, SK3 and SK4, indicating deep burrowing activity at these stations. Of the two type species (*sensu* Petersen, 1915) of the deep Skagerrak, *Amphilepis norvegica* was collected at stations AD7; OS3, OS5, OS7, OS8, OS9, OS10, SK2 and SK3 (abundance 43, 3, 27, 73, 23, 3, 3, 37 and 7 $ind \cdot m^{-2}$, respectively), and *Delectopecten vitreus* (= *Pecten vitreus*) at station OS9 (a single find).

The sediment profile image from station SK1 showed considerable activity down to about 7 cm depth, where the apparent redox potential discontinuity (RPD) was also found. At that level about 7 oxidized pockets or feeding voids were seen, and vertical stripes of slightly lighter colour than in the surrounding sediment also extended down to more than 12 cm depth (end of image). Some of these structures may be associated with the tubes and activity of *Spiochaetopterus bergensis*. Indication of activity at this station was found down to at least 10 cm. The upper 4 cm of the sediment showed indications of strong reworking activity and part of the sediment was pelletized material. The sediment profile image at station SK2 showed reworking activity down to about 7 cm depth and the apparent RPD was (at least partly) found there. Sediment pockets were seen between 3 and 15 cm depth. A pink worm appeared in a vertical position between 13 and 19.5 cm depth. The upper part of that worm was clearly segmented and it appeared to be *Heteromastus filiformis*, a head-down sub-surface feeder (Clough & Lopez, 1993). The top sediment at the OS stations was predominantly

TABLE 2

Number of species, abundance, biomass and feeding categories at the deep-trench and shallow-slope stations in the Skagerrak.

	Deep-trench stations							
	OS11	OS1	OS10	OS9	OS8	OS7	SK1	OS3
number of species per 0.3 m ²	29	27	34	35	35	29	22	32
number of individuals per m ²	1843	2350	2887	1790	2350	1470	820	1513
biomass per m ² (g wet wt·m ⁻²)	15.4	25.1	22.9	20.5	25.8	30.0	16.4	15.9
subsurface deposit feeders (%)	37	26	26	30	27	40	25	36
deposit feeders (%)	10	4	6	10	16	22	5	20
predators (%)	2	3	2	6	5	9	7	7
suspension feeders (%)	50	66	65	51	50	28	62	35
unknown (%)	1	1	1	2	2	1	1	2

	Shallow-slope stations						
	AD2	SK2	AD7	SK3	OS5	AD3	SK4
number of species per 0.3 m ²	46	43	49	25	61	62	47
number of individuals per m ²	2673	1097	1837	455	1637	6660	1183
biomass per m ² (g wet wt·m ⁻²)	47.9	12.2	140.5	16.0	29.7	126.4	123.2
subsurface deposit feeders (%)	57	50	33	47	31	38	35
deposit feeders (%)	19	15	56	27	51	43	58
predators (%)	9	19	4	20	15	5	3
suspension feeders (%)	13	15	3	4	3	13	4
unknown (%)	2	1	4	2	1	1	0

clay-silt (Table 1). Organic C varied between 2.1 and 2.9% and total N between 0.24 and 0.31%.

4. DISCUSSION

The study has shown a high similarity between the benthic communities in the deep (>400 m) part of the Skagerrak, except at station AD2. That station, situated at the southern slope, may be more influenced by down-slope water and sediment transport than the stations in the deeper part of the Norwegian Trench. The high faunal similarity in the deep trench suggests that the environmental conditions here are similar over large areas. This applies not only to temperature, salinity and sediment grain size, but most likely also to an even horizontal distribution of food to the benthic fauna. The accumulation rate on the slopes are high (Van Weering *et al.*, 1987), which may be associated with a consistent down-slope transport in some areas (Stevens *et al.*, 1996), and the organic C and total N are rather even in the top sediment (Table 1). The C/N ratios of 7.4 to 9.6 are indicative of rather labile sediment (Gray, 1992). Pingree *et al.* (1982) have shown that the cyclonic water transport in the Skagerrak can, at least in summer, create high concentrations of phytoplankton in the open eastern part. Most of this algal biomass is channelled through the pelagic microbial food chain and only a minor part will eventually serve as food for the deep-trench benthic system (Rosenberg *et al.*, 1990). It seems more likely that energy to the deeper parts of the Skagerrak is channelled through near-bottom horizontal transport

and resuspension processes as shown by Stevens *et al.* (1996) and Van Weering *et al.* (1987).

Biomass in the deep trench was low compared to that in coastal areas of the Skagerrak (Rosenberg & Möller, 1979), but in agreement with what Josefson (1985) obtained in the deeper eastern Skagerrak. Also the numbers of species were similar to Josefson's records, but he sampled a larger area. Abundances were similar or higher in Josefson's investigation.

From sediment profile pictures at the two deep-trench stations it is evident that the upper 4 to 7 cm is bioturbated and has oxic sediment pockets, and that the RPD appears to be at about that depth. In addition, apparent tubes, feeding voids and a worm were found at the bottom of the images, *i.e.* down to 12 to 19.5 cm in the sediment. These structures are indicative of strong biogenic activity deep in the sediment. Also other species, *e.g.* *Thyasira* spp. (Dando & Southward, 1986) and *Calocaris macandreae* (Anderson *et al.*, 1991) are known to have significant effects on sediment chemistry. Thus, several of the dominant species that burrow deep into the sediment will have a significant impact on the geochemical processes and on the fate of organic contaminants in the deep Skagerrak.

The benthic infauna at the shallow-slope stations was more heterogeneous than in the deep-trench. As temperature and salinity are similar to the levels in the deeper areas, the greater variability is suggested to be due to differences in near-bottom water transport, coarser sediment (Van Weering & Qvale, 1983) and

TABLE 3

Abundance per m² of the six dominant species at each station. Animal group belonging: P=polychaetes, M=molluscs, C=crustaceans, E=echinoderms, S=sipunculans. Feeding categories: S=suspension, Ss=subsurface deposit, D=deposit, P=predator.

species	Anim. group	Feed. categ	Deep-trench stations (depth below)								Shallow-slope stations (depth below)						
			OS11	OS1	OS10	OS9	OS8	OS7	SK1	OS3	AD2	SK2	AD7	SK3	OS5	AD3	SK4
			682	637	573	538	521	507	482	411	455	350	294	260	252	177	144
<i>Spiochaetopterus bergensis</i>	P	S	633	1367	1740	763	830	310	407	293	210	7	0	3	0	0	0
<i>Thyasira eumyaria</i>	M	Ss	323	227	450	243	310	110	50	117	83	13	7	0	23	0	0
<i>Kelliella miliaris</i>	M	S	290	180	123	153	340	87	103	230	93	160	0	13	17	0	0
<i>Yoldiella lucida</i>	M	Ss	103	137	77	110	93	87	23	130	147	43	13	0	37	0	0
<i>Terebellides stroemi</i>	P	D	83	37	93	50	117	153	30	40	67	0	70	0	7	13	0
<i>Heteromastus filiformis</i>	P	Ss	80	80	30	27	73	127	87	87	150	207	40	120	80	130	87
<i>Philomedes lilljeborgi</i>	C	D	73	40	50	63	143	57	10	17	3	3	0	0	3	0	0
<i>Thyasira ferruginea</i>	M	Ss	33	3	27	23	30	150	0	37	37	10	0	0	43	3	0
<i>Thyasira obsoleta</i>	M	Ss	30	50	43	77	47	0	0	7	43	10	7	0	7	0	0
<i>Eriopisa elongata</i>	C	Ss	30	33	17	0	3	7	3	0	40	63	7	3	33	0	33
<i>Paramphinome jeffreysi</i>	P	Ss	27	23	3	10	13	7	10	0	57	33	10	3	10	57	53
<i>Lumbrineris latreilli</i>	P	P	23	40	47	60	70	80	43	0	53	100	3	0	100	0	0
<i>Abra nitida</i>	M	D	17	0	10	17	30	10	0	53	350	53	500	95	193	23	357
<i>Thyasira equalis</i>	M	Ss	13	63	67	27	47	60	10	57	380	87	300	17	190	73	117
<i>Orbinia norvegica</i>	P	Ss	10	3	3	0	7	10	3	7	23	23	23	40	27	0	17
<i>Nuculoma tenuis</i>	M	Ss	7	3	7	3	17	27	0	67	137	23	123	20	37	60	20
<i>Lumbrineris gracilis</i>	P	P	0	7	0	0	0	0	0	40	0	7	0	65	0	0	0
<i>Onchnesoma steenstrupi</i>	S	D	0	3	0	7	3	10	0	80	47	40	37	7	23	3	0
<i>Maldane sarsi</i>	P	Ss	0	0	3	0	0	0	0	0	0	0	0	0	0	1380	7
<i>Arcturella dilatata</i>	C	S	0	0	0	0	0	0	0	0	0	0	3	0	0	667	0
<i>Diastylis lucifera</i>	C	D	0	0	0	0	0	0	0	0	0	3	140	5	3	7	23
<i>Diplocirrus glaucus</i>	P	D	0	0	0	0	0	0	0	0	0	0	10	0	0	23	87
<i>Myriochele oculata</i>	P	D	0	0	0	0	0	0	0	0	0	0	150	3	3	2033	13
<i>Ophiura</i> sp. juv.	E	P	0	0	0	0	0	0	0	0	30	0	0	0	0	183	10
<i>Philomedes globosus</i>	C	D	0	0	0	0	0	0	0	47	0	0	0	0	0	560	0
<i>Praxillella affinis</i>	P	Ss	0	0	0	0	0	0	0	0	427	7	7	0	0	0	0
<i>Praxillella praetermissa</i>	P	Ss	0	0	0	0	0	0	0	0	0	0	0	0	0	750	20
<i>Spiophanes kroeyeri</i>	P	D	0	0	0	0	0	0	0	0	10	0	7	0	50	63	30
<i>Tharyx mcintoshii</i>	P	D	0	0	0	0	0	0	0	0	0	0	0	0	410	0	0
Total at station			1843	2350	2887	1790	2350	1470	820	1513	2673	1097	1837	455	1637	6660	1183

higher accumulation rates than in deeper areas (Van Weering *et al.*, 1987). Differences in food availability and competition including predation pressure may also be involved. At some of the slope stations the percentage of predators was higher than at the deep-trench stations.

The rich benthic community at the station on the southern slope, AD3, had the highest biomass and abundance. This may indicate an important horizontal carbon transport close to the bottom. Such high biomass and high abundance have been noticed also in other slope areas in the Kattegat (Rosenberg, 1995) and in the SW Baltic (Arntz *et al.*, 1976). Metazoan meiofauna sampled at the same times as the macrofauna in this study also had the highest densities on the slopes and declining numbers with depth (De Bovée *et al.*, 1996).

Josefson (1985) argued that the differing hydrographical regime in deep and shallow areas of the eastern Skagerrak had a significant influence on macrofaunal dispersion and on benthic community diversity. Josefson (1985) also recorded major divi-

sions in the faunal community distributions between 40-200 m, 200-360 m and 360-650 m depth in the eastern Skagerrak. The present study suggests that a vertical discontinuity in faunal distribution occurs at 400 m and that it continues towards the west of the Norwegian Trench. Also the recent study of foraminiferan species composition (Bergsten *et al.*, 1996), conducted at the same time and in many cases at the same stations as in the present study, suggests that the distributions of different foraminiferan taxa are also strongly influenced by water transport, depth and sediment structure.

As for benthic macrofauna, demersal fish communities in the shallow-slope areas are also significantly different from those of the deep-trench below 250 to 300 m (Bergstad, 1990). The dominant species in the deep-trench is the roundnose grenadier (*Coryphaenoides rupestris*). This suggests that the bathymetry and the Atlantic inflow largely determine the species composition in the deep Skagerrak. How the fish communities affect the infauna is not known in detail as most fish species caught by bottom trawls feed on

pelagic or semi-pelagic crustaceans and fish (Bergstad, 1991).

It is suggested that the benthic fauna in the deep trench is dominated by suspension feeders. The dominance of *Spiochaetopterus bergensis* contributes to this pattern. Detailed studies by Barnes (1965) have shown such a feeding behaviour. However, Fauchald & Jumars (1979) have found that *Spiochaetopterus* sp., under conditions of low particle concentrations, can feed on particles on the sediment surface. Thus, perhaps *Spiochaetopterus bergensis* switches between these two modes of feeding and, thus, the percent of animals suggested to be suspension feeding in Table 2 may, at times, be lower. Josefson (1985) designated *S. bergensis* as a deposit feeder, and he concluded that sub-surface feeders had highest densities on the lower shelf where sedimenting organic matter was highest.

Petersen (1915) described the deep Skagerrak benthic community as characterized by *Amphilepis norvegica* and *Delectopecten vitreus* since these species were found only in these deep waters. In the present study we have found *A. norvegica* to be common at several stations, but the dominant species was always *Spiochaetopterus bergensis*. As the latter species was ubiquitous and *Delectopecten vitreus* only found at one station, it is suggested that *A. norvegica* and *S. bergensis* may be more qualified to be designated as type species for the benthic community of the deep trench of the Skagerrak. Petersen (1915) did not identify the worms to species level in his investigation. Among the bivalves he found three *Thyasira* (= *Axinus*) species: *T. flexuosa*, *T. croulinensis* and *T. ferruginea*. We did not record *T. croulinensis*, but found *T. eumyaria*, *T. equalis* and *T. obsoleta*. Thus, several *Thyasira* species occur in the deep Norwegian Trench.

Several benthic macrofaunal studies conducted in the 1980s have suggested recently elevated biomasses in the northeastern areas of the Kattegat and the Skagerrak compared to results obtained in 1911/12 (Pearson *et al.*, 1985; Rosenberg *et al.*, 1987) and in the 1970s (Josefson, 1990). These increases in biomass have been attributed mainly to increased inputs of nutrients. However, such a temporal comparison cannot be made for the stations sampled in this study, as these stations have not been sampled before.

5. CONCLUSIONS

This study of the macrofauna in the Norwegian Trench has designated two different communities with similar faunal composition, one in the deeper parts of the trench generally below 400 m depth, and one on the slopes generally found at 140 to 400 m depth. The faunal distribution is suggested to be related to sediment characteristics, transport and accumulation rates. The polychaete *Spiochaetop-*

terus bergensis was the dominant macrofaunal species at all deep stations and its density was positively correlated with the depth.

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6. REFERENCES

- Anderson, S.J., R.J.A. Atkinson & A.C. Taylor, 1991. Behavioural and respiratory adaptations of the mud-burrowing shrimp *Calocaris macandreae* Bell (Thalassinidea: Crustacea) to the burrow environment.—*Ophelia* **34**: 143-156.
- Arntz, W. E., D. Brunswig & M. Sarnthein, 1976. Zonierung von Mollusken und Schill im Rinnensystem der Kieler Bucht (Westliche Ostsee).—*Seckenberg. marit.* **8**: 198-269.
- Barnes, R.D., 1965. Tube-building and feeding in chaetopterid polychaetes.—*Biol. Bull.* **129**: 217-233.
- Bergsten, H., K. Nordberg & B. Malmgren, 1996. Recent benthic foraminifera as tracers of water masses along a transect in the Skagerrak, north-eastern North Sea.—*J. Sea Res.* **35**: 111-121.
- Bergstad, O.A., 1990. Ecology of the fishes of the Norwegian Deep: Distribution and species assemblages.—*Neth. J. Sea Res.* **25**: 237-266.
- , 1991. Distribution and trophic ecology of some gadoid fish of the Norwegian Deep. 1. Accounts of individual species.—*Sarsia* **75**: 269-313.
- Bray, J.R. & J.T. Curtis, 1957. An ordination of the Upland forest communities of Southern Wisconsin.—*Ecol. Monogr.* **27**: 325-349.
- Clough, L.M. & G.R. Lopez, 1993. Potential carbon sources for the head-down deposit-feeding polychaete *Heteromastus filiformis*.—*J. mar. Res.* **51**: 595-616.
- Dando, P.R. & A.J. Southward, 1986. Chemoautotrophy in bivalve molluscs of the genus *Thyasira*.—*J. mar. biol. Ass. U.K.* **66**: 915-929.
- De Bovée, F., P.O.J. Hall, S. Hulth, G. Hulthe, A. Landén & A. Tengberg, 1996. Quantitative distribution of metazoan meiofauna in continental margin sediments of the Skagerrak (northeastern North Sea).—*J. Sea Res.* **35**: 189-197.
- Dennegård, B., A. Jensen, A. Kuijpers & T.C.E. Van Weering, 1992. Quaternary sediment accumulation and recent sedimentary processes in the Skagerrak and northern Kattegat, an overview. In: B. Dennegård & A. Kuijpers. Marine geological environmental investigations in the Skagerrak and northern Kattegat. Univ. Göteborg, Dept. Mar. Geol., Rep. 7: 1-12.
- Eisma, D. & J. Kalf, 1987. Dispersal, concentration and dep-

- osition of suspended matter in the North Sea.—J. Geol. Soc. Lond. **144**: 161-178.
- Elofson, O., 1941. Zur Kenntnis der marinen Ostracoden Schwedens.—Zool. Bidr. Uppsala **19**: 215-534.
- Enequist, P., 1950. Studies on the soft-bottom amphipods of the Skagerak.—Zool. Bidr. Uppsala **28**: 297-493.
- Fauchald, K. & P. Jumars, 1979. The diet of worms; a study of polychaete feeding guilds.—Oceanogr. mar. biol. ann. Rev. **17**: 193-284.
- Forsman, B., 1940. Untersuchungen über die Cumaceen Skageraks.—Zool. Bidr. Uppsala **18**: 1-162.
- Gray, J. S., 1992. Eutrophication in the sea. In: G. Colombo, I. Ferrari, V.U. Ceccherelli & R. Rossi. Marine eutrophication and population dynamics. Olsen & Olsen, Fredensborg, Denmark: 3-15.
- Höglund, H., 1947. Foraminifera in the Gullmar Fjord and the Skagerak.—Zool. Bidr. Uppsala **26**: 1-329.
- Josefson, A.B., 1981. Persistence and structure of two deep macrobenthic communities in the Skagerrak (west coast of Sweden).—J. exp. mar. Biol. Ecol. **50**: 63-97.
- , 1985. Distribution of diversity and functional groups of marine benthic infauna in the Skagerrak (eastern North Sea) - can larval availability affect diversity?—Sarsia **70**: 229-249.
- , 1986. Temporal heterogeneity in deep-water soft-sediment benthos. An attempt to reveal temporal structure.—Est. coast. Shelf Sci. **23**: 147-169.
- , 1990. Increase of benthic biomass in the Skagerak-Kattegat during the 1970s and 1980s - effects of organic enrichment?—Mar. Ecol. Prog. Ser. **66**: 117-130.
- Moodley, L., S.R. Troelstra & T.C.E. Van Weering, 1993. Benthic foraminiferal response to environmental change in the Skagerrak, northeastern North Sea.—Sarsia **78**: 129-139.
- North Sea Task Force, 1993. North Sea Subregion 8. Assessment Report 1993. State pollution control authority, Oslo: 1-79.
- Pearson, T.H., A.B. Josefson & R. Rosenberg, 1985. Petersen's benthic stations revisited. I. Is the Kattegat becoming eutrophic?—J. exp. mar. Biol. Ecol. **92**: 157-206.
- Petersen, C.G.J., 1915. On the animal communities of the sea bottom in the Skagerak, the Christiania Fjord and the Danish waters.—Rep. Dan. biol. Stn **23**: 1-28.
- Pingree, R.D., P.M. Holligan, G.T. Mardell & R.P. Harris, 1982. Vertical distribution of plankton in the Skagerrak in relation to doming of the seasonal thermocline.—Cont. Shelf Res. **1**: 209-219.
- Rodhe, J., 1987. The large-scale circulation in the Skagerrak; interpretation of some observations.—Tellus **39A**: 245-253.
- Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability.—Neth. J. Sea Res. **34**: 303-317.
- Rosenberg, R. & R.J. Diaz, 1993. Sulfur bacteria (*Beggiatoa* spp.) mats indicate hypoxic conditions in the inner Stockholm Archipelago.—Ambio **22**: 32-36.
- Rosenberg, R. & P. Möller, 1979. Salinity stratified benthic macrofaunal communities and long-term monitoring along the west coast of Sweden.—J. exp. mar. Biol. Ecol. **37**: 175-203.
- Rosenberg, R., J.S. Gray, A.B. Josefson & T.H. Pearson, 1987. Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched?—J. exp. mar. Biol. Ecol. **105**: 219-251.
- Rosenberg, R., E. Dahl, L. Edler, L. Fyrberg, E. Granéli, W. Granéli, Å. Hagström, O. Lindahl, M.O. Matos, K. Pettersson, E. Sahlsten, P. Tiselius, V. Turk & J. Wikner, 1990. Pelagic nutrient and energy transfer during spring in the open and coastal Skagerrak.—Mar. Ecol. Prog. Ser. **61**: 215-231.
- Stevens, R.L., H. Bengtsson & A. Lepland, 1996. Textural provinces and transport interpretations with fine-grained sediments in the Skagerrak.—J. Sea Res. **35**: 99-110.
- Van Weering, T.C.E. & G. Qvale, 1983. Recent sediments and foraminiferal distribution in the Skagerrak, northeastern North Sea.—Mar. Geol. **52**: 75-99.
- Van Weering, T.C.E., G.W. Berger & J. Kalf, 1987. Recent sediment accumulation in the Skagerrak, northeastern North Sea.—Neth. J. Sea Res. **21**: 177-189.