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Some quantitative results on benthic communities of the deep Norwegian Sea*

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In July–August 1975 a joint French-Swedish expedition (NORBI) with Norwegian participation explored the abyssal benthic fauna of the Norwegian sea about which previous knowledge was fragmentary. Sampling was carried out in depths between 2465 and 3718 m at 11 stations located in all four deep basins, viz. the Norwegian (3), Lofoten (2), Spitsbergen (1), and Greenland (5) basins. The gears used were box corer, epibenthic sled, beam trawl, baited trap, and camera sled.
The bulk of the collection, comprising over 430,000 specimens, has now been sorted as to higher taxa. Macrofaunal densities from core samples range from 40 to 6440 individuals per m^2, with a mean value of 1584 ind. Approximate densities obtained from sled and trawl samples are much lower: from 1.76 to 40.65 ind./m^2 for the epibenthic sled samples, and from 0.48 to 3.17 ind./m^2 for the trawl samples. Judging from a few duplicated samples, results from the trawl appear more homogeneous than those from the sled. The baited trap caught only lysianassid amphipods, varying in number from nearly 2000 individuals to 1. For all gears except the baited trap, densities are much higher in the Greenland basin than at corresponding depths in the Norwegian basin. The Lofoten basin shows large variations possibly due to influence from productive surface waters and nearby coastal banks. The only station from the Spitsbergen basin indicates an intermediate situation. The high densities in the Greenland basin could be due to the vertical convection phenomenon.
The faunal composition is discussed only with respect to higher taxa. Nematoda, Polychaeta, Bivalvia, Ostracoda, Tanaidacea, and Holothuroidea, mentioned in order of total numbers obtained, dominate the box core samples. For the sled samples the dominance order is slightly different, viz.: Nematoda, Bivalvia, Polychaeta, Holothuroidea, and Peracarida. The traw catches show a picture similar to the sled samples, with an obvious dominance of Holothuroidea and larger Polychaeta and Bivalvia.
Compared with the open oceans the number of species from the deep basins in the Norwegian Sea appears to be very low. There are only 13 species of echinoderms, 3 fishes, and about 30 amphipods. Of Crustacean groups common in the deep world ocean Anomura (pagurids, galatheids, lithodids) and Penaeid prawns are lacking in the deep Norwegian Sea. No macrurid fish was caught in our trawl samples. Ophiuroids are unusually rare. Large carnivorous species seem to be restricted to Amphipoda.
Compared with other areas of the North Atlantic and the Pacific, the Norwegian Sea deep benthic fauna appears richer with respect to density but poorer with respect to diversity.

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INTRODUCTION

History of exploration

Sporadic samples of Norwegian Sea deep water benthos were first taken in the northern part of the area by Swedish polar expeditions in 1861 and 1868. These samples attracted attention by establishing records, e.g. for Cumacea, at greater depths than investigated by any earlier expedition (Sars 1873). The

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British 'Lightning' and 'Porcupine' expeditions in 1869 and 1870 contributed further information on the southernmost part of the area and gave a very first indication of a difference between Norwegian Sea and North Atlantic deep sea faunas.

Inspired by these results and those from other fields of oceanography, the Norwegian scientists H. Mohn and G. O. Sars took the initiative to mount the Norwegian North-Atlantic Expedition which, on board the ship 'Vøringen', investigated the whole area during the summers 1876–1878 (Wille 1882). Numerous stations were investigated and by the standards of its time the expedition was highly successful. However, deep sea dredging was still in its infancy and greatly hampered by all sorts of technical difficulties, and the number of benthic stations in depths exceeding 2500 m was limited to 6 only. The information obtained concerning the bottom fauna down to about 2000 m was fairly extensive, but for greater depths it remained very incomplete. Thus, dredgings on six stations at depths exceeding 2500 m yielded only 16 species of invertebrates, representing the groups Hydrozoa, Anthozoa, Mollusca, Crustacea, Pycnogonida, and Echinodermata. As will be shown later in this paper, these findings give a very fragmentary picture of the faunal composition.

Nevertheless the Norwegian North-Atlantic Expedition remained the main source of information on the bottom fauna of the deep Norwegian Sea. Subsequent samplings were more peripheral and less extensive. The most important one was made by the Danish 'Ingolf' Expedition 1895–96, which worked for some time in the waters between Iceland and Jan Mayen and dredged successfully in depths down to 2465 m (Wandel 1898). A few samples were also taken by Swedish expeditions in the deep areas between Spitsbergen and Greenland (Nathorst 1900, Kolthoff 1901). The comprehensive research programs carried out in the Polar Sea by expeditions from the Soviet Union have barely touched the northernmost part of the Norwegian Sea (Professor I. Tokin, pers. comm.).

A survey of the literature on the cold water bottom fauna of the area was made by Ekman (1935). After that time additions to the knowledge of this fauna have been few and scattered. An important meiofauna study by Thiel (1971) includes the southernmost part of the deep Norwegian Sea.

Theoretical background and aims of the NORBI expedition

During the two latest decades techniques for the sampling and study of deep sea benthos have been much improved. A great volume of data concerning the world ocean benthos has accumulated and permitted certain conclusions concerning faunal composition, diversity, and quantitative distribution (Menzies et al. 1973).

The Norwegian Sea is geographically isolated from the world ocean by shallow sills, and its hydrography is very different (Mosby 1972, with references). As shown by Ekman (1935) it is also faunistically isolated, with numerous endemics at the species level. This isolation is probably closely connected with the geological history of the region (Dahl 1972).

The formation of the deep Norwegian Sea seems to have started about 60 million years B.P. (Vogt 1972). There appear to be indications that the outflow from the Norwegian Sea – Polar Basin area into the Atlantic was much smaller in early Tertiary times than from the Miocene onwards, a condition possibly connected with a gradual subsidence of the Greenland – Iceland – Faroe ridge (Vogt loc. cit.). This would seem to imply an even higher degree of early faunistic isolation than presumed by Dahl (loc. cit.).

The whole deeper part of the Norwegian Sea is filled by homoiohaline water of negative temperatures, the boundary against positive temperature surface waters lying deeper in the East than in the West where it comes close to the surface even in summer. Formation of cold bottom water takes place by means of vertical convection in winter, especially in the area between Jan Mayen and Spitsbergen (Helland-Hansen & Nansen 1909, Mosby 1972). Negative temperature bottom water could not be formed until the late Tertiary cooling of the Arctic region had proceeded so far that negative surface temperatures occurred at least during winter. Some recent evidence (Herman et al. 1971) indicates that ice formation at high latitudes in the Polar Basin could take place as early as 3.3 million years B.P., i.e. slightly earlier than indicated by the sources quoted by Dahl

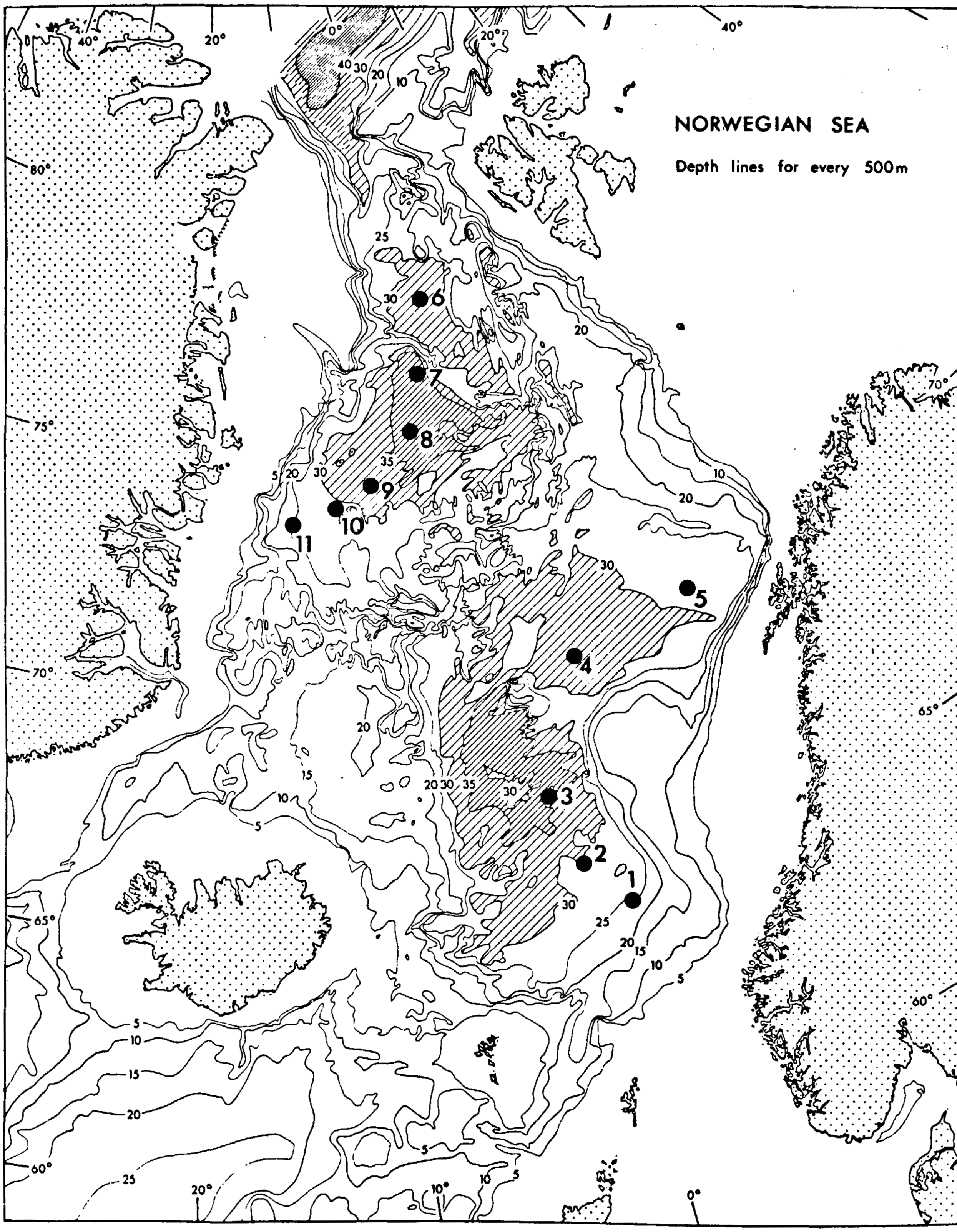

Fig. 1. Location of the NORBI sampling stations.

(loc. cit.). However, temperatures were probably lower in the centre of the Polar Basin than in the Norwegian Sea.

The isolation and cooling of the deep Norwegian Sea might explain the absence of a deep sea fauna of cosmopolitan type, as indicated by the scanty information available. However, in the light of the facts and considerations briefly presented above it appeared desirable to elucidate the points enumerated below.

1. The qualitative and quantitative composition of the deep sea communities, especially in depths below 2500 m.
2. The degree of diversity of the fauna as compared with that of the world ocean.
3. The degree and level of endemism of the fauna and its implications with respect to the time scale of evolution at the species and possibly higher levels.
4. The degree of ecological affinity with faunas of other areas and other bathymetric levels.

For all these reasons, the project of a further exploration of the deep benthic communities of the Norwegian Sea appeared very interesting. The program itself was developed as a French-Swedish collaboration since late 1973, and a one month cruise on board N. O. 'Jean Charcot' was planned for the summer of 1975: NORBI (Norwegian Sea Biology) between the Centre National pour l'Exploitation des Océans (CNEXO, Paris) and the Swedish Natural Science Research Council (NFR, Stockholm). The cruise itself took place from July 18 to August 12, 1975. The scientific team comprised French, Swedish, and Norwegian scientists from several institutions. The cruise was led by two of us (L. L. and E. D.).

The aim of the present paper is to give the main preliminary results which appear at the end of the sorting and counting of the samples. We wish to express our thanks to the National Sorting Center for Biological Oceanography (CENTOB, COB, Brest) for sorting the material collected during NORBI.

METHODS

Sampling gears

Modern investigations in the deep sea after World War II began in the Soviet Union and semi-quantitative and quantitative gears slowly developed. For the NORBI cruise, we decided to follow a practice applied since 1973 in the Bay of Biscay, which consists in the use of several gears, each of them being well fitted to catch a given category of the fauna: the Reineck box-corer slightly modified from the original design (Reineck 1958, 1963) for sediment analysis, microflora, meiofauna, and macrofauna; the epibenthic sled from Woods Hole Oceanographic Institution (Hessler & Sanders 1967) equipped with a closing device working by hydrostatic pressure (Bervas, Potin & Reyss 1973) and a posterior bag made of 0.5 mm nylon net for macrofauna; a model of commercial single beam trawl of 5 metres width with a posterior bag of 0.5 cm mesh for large macrofauna and megafauna; and a large baited trap fitted with a flash-camera system and an ultrasonic release developed at COB for the capture of carnivorous species.

The Reineck box-corer

The box-corer is operated without pinger, and the wire speed is slowed down to 10–15 m/min when the sampler is about 100 m above the bottom. The contact is seen from the tension recorder, and a security length of about 10 m of wire is paid out before bringing in the sampler. A good discussion of the method has been given by Hessler & Jumars (1974). The surface of the box is 600 cm^2 (1/16.7 of a m^2). During NORBI, 22 samples have been obtained from a total number of 23 operations (one failure).

The epibenthic sled and the beam trawl

Basically, these two devices are operated in the same way, which has been fully described (Laubier, Martinais & Reyss 1971). Based on satellite navigation system and ultrasonic pinger, this method permits an evaluation of the length of the haul on the bottom with an accuracy of some 20%. However, it gives a maximum length compared with the true working path of the gear, which means that faunal densities obtained are minimum values. During NORBI, 17 samples have been obtained from 18 epibenthic sled operations (one failure), and 17 samples from 17 trawlings.

Sled and trawl samples cannot be considered quantitative, but can be used for comparisons with the same gears in different places.

The baited trap

The trap we used during NORBI is made of a large cubic frame (aluminium and magnesium alloy, 2 × 2 × 2 m) supporting the ultrasonic release, the Edgerton flash camera system, and the floats which give buoyancy when a weight is released. The trap is covered with a nylon net of 1.2 cm size mesh; the entrance to the trap is located at mid-height, and its minimum diameter is 24 cm. Within the trap, 8 to 10 plastic bottles, with the entrance cut out and fixed in reverse position, work as smaller traps adapted for small organisms. The bait consisted of Labrid fishes. A small flash and goniometric system facilitate the recovery of the trap when it comes back to the surface. The trap was set on the bottom during about 10 hours (9 to 14 hours) at 7 stations during NORBI. The results are given in absolute numbers and expressed as catch (in number of individuals) per unit of effort (10 hours of fishing).

Post sampling procedures

From the box-corer, surface sub-samples (20–30 cm^2) are taken and frozen for laboratory analysis of carbon and nitrogen. The amounts of organic carbon and total nitrogen are determined respectively by combustion methods with LECO analyzer after HCl treatment of dry sediment and with COLEMAN analyzer. Sub-samples for meiofauna are also taken with small corers. Then, the remaining surface (520–580 cm^2) over a thickness of some 20 cm is washed through a 250 μm screen and preserved in buffered formalin.

The samples from the epibenthic sled are washed with the same method, but three screens are used (2 mm, 1 mm, and 0.5 mm.) An elutriation technique similar to the Sanders, Hessler & Hampson method (1965) is used. The samples from the trawl receive a similar treatment.

A very small part of the material has been sorted out on board for staining and fixation for special purposes. The major part has been preserved and was sorted out by zoological groups at Brest. Meiofauna has not yet been sorted. For macrofauna and megafauna, all trawl and core samples and 12 sled samples have been sorted, and yielded a provisional total of 436.658 individuals, exclusive of colonial groups such as Protozoa, Porifera, Hydrozoa, and Bryozoa.

Sampling sites

Eleven stations have been investigated during NORBI. Their locations were chosen to give a general idea of the main deep basins of the Norwegian Sea from about 2500 m depth downwards (Fig. 1): sts. 1, 2, and 3 in the Norwegian basin, sts. 4 and 5 in the Lofoten basin, both in the eastern part; st. 6 in the Spitsbergen basin and sts. 7, 8, 9, 10, and 11 in the Greenland basin, both in the western part. Depths vary from 2465 to 3718 m. The total number of samples per station varies from 7 to 5. Location of all samples, together with depths and length of hauls, are given in Table I. All sample sites are located by satellite navigation and pinger graphic method, and relate to the true bottom positions of the gears. Depths recorded by echosounder are corrected by use of Matthews' hydrographic tables. In the case of traps, time spent on the bottom is given in hours.

RESULTS

Organic matter

Analyses have been conducted on 18 box-corer samples. Results are given in Table II.

In the four deep basins of the Norwegian Sea, the amounts of organic carbon and nitrogen decrease with increasing depth. Norwegian, Lofoten, and Spitsbergen basins show values of organic carbon from 0.90 to 0.37 % of dry sediment weight, while nitrogen varies from 0.12 to 0.05 %. The C/N ratio increases slightly with depth, but remains below 10. In the Greenland basin, organic carbon and nitrogen values show a wider range of variation within a given station and reach the highest absolute figures for depths of 2500–2900 metres. For instance, sample KR 21 gives a percentage for organic carbon of 1.08 and of 0.13 for nitrogen. The C/N ratio varies also greatly in the Greenland basin. For the deepest station of this basin, the C/N ratio reaches rather high values (9.5 and 12.9).

Faunal densities

Total densities for counted organisms have been calculated for box-corer, sled, and trawl. For the sled and the trawl, the area sampled is the length of the haul by the width of the

List of stations

Table I

Gear Code: CP - Beam trawl, DS - Epibenthic sled, KR - Reineck corer, NA - Baited trap, TR - Camera sled

Station	Date	Gear Code and no.	Position	Depth, m	Length of haul on bottom, m
1	19.07	CP 01	64°24',3N, 01°43',9E - 64°23',5N, 01°44',7E	2 615 - 2 577	1 665
	19.07	CP 02	64°26',5N, 01°35',1E - 64°25',2N, 01°36',0E	2 714 - 2 668	2 315
	19.07	DS 01	Wire tangled		
	20.07	DS 02	64°24',6N, 01°36',3E - 64°23',8N, 01°36',4E	2 653 - 2 653	1 230
	20.07	DS 03	64°13',9N, 01°39',8E - 64°19',4N, 01°40',5E	2 538 - 2 529	1 405
	20.07	KR 01	64°26',0N, 01°38',3E -	2 707	-
	20.07	KR 02	64°26',0N, 01°37',1E -	2 725	-
2	21.07	CP 03	65°15',6N, 00°01',8W - 65°15',3N, 00°06',3W	2 904 - 2 904	3 785
	21.07	CP 04	65°13',6N, 00°05',6W - 65°12',5N, 00°03',8W	2 913 - 2 866	2 500
	20.07	DS 04	65°29',0N, 00°02',5E - 65°28',5N, 00°02',3E	3 016 - 3 016	905
	21.07	DS 05	65°22',9N, 00°02',1E - 65°22',4N, 00°02',2E	2 970 - 2 970	815
	21.07	KR 03	65°24',9N, 00°01',3E -	2 992	-
	21.07	KR 04	65°24',2N, 00°00',1W -	2 988	-
	21.07	NA 01	65°16',5N, 00°02',7E -	2 910	-
3	22.07	CP 05	66°45',9N, 02°01',9W - 66°46',1N, 01°58',4W	3 369 - 3 369	2 590
	22.07	CP 06	66°45',2N, 01°44',9W - 66°45',5N, 01°42',2W	3 522 - 3 645	2 090
	23.07	DS 06	66°46',7N, 01°33',1W - 66°46',5N, 01°31',2W	3 672 - 3 658	1 405
	23.07	DS 07	66°45',2N, 01°26',6W - 66°45',4N, 01°25',6W	3 612 - 3 612	778
	23.07	KR 05	66°45',4N, 01°33',2W -	3 665	-
	23.07	KR 06	66°45',6N, 01°32',4W -	3 665	-
	22.07	NA 02	66°46',6N, 01°35',0W -	3 699	-
	23.07	TR 01	66°47',3N, 01°21',4W - 66°48',8N, 01°20',2W	3 559 - 3 522	2 960
4	25.07	CP 07	69°04',8N, 04°41',6E - 69°05',3N, 04°43',7E	3 213 - 3 213	1 805
	25.07	CP 08	69°07',5N, 04°39',9E - 69°07',2N, 04°36',6E	3 213 - 3 213	2 560
	25.07	DS 08	69°14',3N, 04°18',4E - 69°13',8N, 04°20',2E	3 213 - 3 210	1 500
	25.07	DS 09	69°09',8N, 04°32',2E - 69°09',4N, 04°33',0E	3 211 - 3 211	970
	24.07	KR 07	69°18',2N, 04°06',8E -	3 155	-
	25.07	KR 08	69°16',3N, 04°11',6E -	3 213	-
	25.07	NA 03	69°06',4N, 04°39',0E -	3 213	-
	25.07	TR 02	69°06',7N, 04°36',6E - 69°06',8N, 04°38',6E	3 213 - 3 213	1 370
5	26.07	CP 09	69°42',6N, 10°43',0E - 69°41',9N, 10°39',9E	2 930 - 2 930	2 390
	27.07	CP 10	69°21',9N, 10°25',2E - 69°20',6N, 10°28',0E	2 966 - 2 966	3 130
	26.07	DS 10	69°38',4N, 10°28',6E - 69°37',8N, 10°28',3E	2 939 - 2 939	1 035
	26.07	DS 11	69°32',9N, 10°22',3E - 69°32',5N, 10°21',1E	2 957 - 2 957	1 140
	27.07	KR 09	69°29',2N, 10°11',6E -	2 957	-
	27.07	KR 10	69°28',0N, 10°12',5E -	2 957	-
	27.07	TR 03	69°27',8N, 10°13',3E - 69°26',6N, 10°16',1E	2 966 - 2 966	2 960
6	02.08	CP 12 *	77°00',7N, 00°57',6E - 77°00',1N, 01°04',0E	3 193 - 3 195	3 190
	02.08	DS 12	76°54',4N, 01°44',6E - 76°54',0N, 01°46',3E	3 200 - 3 200	1 390
	02.08	DS 13	76°54',3N, 01°49',0E - 76°54',0N, 01°50',6E	3 193 - 3 193	790
	03.08	KR 11	76°52',5N, 02°02',9E -	3 208	-
	03.08	KR 12	76°53',7N, 01°33',0E -	3 203	-
	02.08	NA 04	76°55',4N, 01°35',0E -	3 193	-
	02.08	TR 04	76°57',0N, 01°21',4E - 76°56',8N, 01°26',3E	3 193 - 3 193	3 140
7	03.08	CP 13	76°01',4N, 01°49',4W - 76°02',5N, 01°41',1W	3 709 - 3 709	4 565
	04.08	DS 14	76°02',7N, 01°47',0W - 76°02',5N, 01°43',2W	3 709 - 3 709	1 095
	04.08	KR 13	76°03',7N, 01°26',8W -	3 709	-
	04.08	KR 14	76°04',7N, 01°29',8W -	3 713	-
	04.08	KR 15	76°04',3N, 01°28',5W -	3 718	-
	03.08	NA 05	76°03',8N, 01°27',8W -	3 713	-
	03.08	TR 05	76°04',2N, 01°27',0W - 76°04',0N, 01°20',8W	3 690 - 3 230	3 330
8	04.08	CP 14	74°42',0N, 03°03',6W - 74°42',8N, 03°05',6W	3 617 - 3 524	3 650
	05.08	DS 15	74°42',9N, 03°27',6W - 74°43',1N, 03°30',6W	3 595 - 3 595	1 500
	05.08	KR 16	74°45',5N, 03°25',8W -	3 606	-
	05.08	KR 17	74°44',8N, 03°25',3W -	3 608	-
	05.08	TR 06	74°43',7N, 03°47',7W - 74°44',2N, 03°52',6W	3 595 - 3 585	2 590
9	06.08	CP 15	73°33',0N, 07°37',9W - 73°32',8N, 07°39',2W	3 210 - 3 210	700
	06.08	DS 16	73°35',3N, 07°26',0W - 73°34',9N, 07°27',7W	3 266 - 3 257	1 150
	06.08	KR 18	73°37',9N, 07°26',3W -	3 306	-
	06.08	KR 19	73°37',2N, 07°26',3W -	3 294	-
	06.08	NA 06	73°39',2N, 07°23',0W -	3 325	-
	06.08	TR 07	73°39',9N, 07°24',3W - 73°38',6N, 07°27',9W	3 290 - 3 270	3 200
10	07.08	CP 16	73°28',2N, 10°06',6W - 73°28',3N, 10°02',6W	2 937 - 2 937	2 145
	07.08	DS 17	73°27',9N, 09°50',5W - 73°28',1N, 09°53',4W	2 941 - 2 941	1 550
	07.08	KR 20	73°28',1N, 09°48',0W -	2 904	-
	07.08	KR 21	73°27',8N, 10°06',8W -	2 941	-
	07.08	NA 07	73°28',5N, 10°06',0W -	2 906	-
	07.08	TR 08	73°28',0N, 10°03',1W - 73°28',2N, 09°58',3W	2 933 - 2 933	2 590
11	08.08	CP 17	73°30',7N, 13°39',6W - 73°32',3N, 13°39',0W	2 502 - 2 475	2 900
	08.08	DS 18	73°36',3N, 13°35',1W - 73°35',9N, 13°35',8W	2 470 - 2 470	885
	08.08	KR 22	73°37',0N, 13°38',9W -	2 465	-
	08.08	KR 23	73°37',3N, 13°35',9W -	2 492	-
	08.08	TR 09	73°32',0N, 13°41',1W - 73°31',1N, 13°41',2W	2 493 - 2 493	1 665

* CP 11, a shallow-water station omitted here

Table II. Organic matter in per cent of dry sediment weight

St.	Box core sample	Depth m	C. total	C. organ.	N. total	Proteins	C/N
1	01	2707	6.16	0.897	0.123	0.107	7.292
1	02	2725					
2	03	2992					
2	04	2988	6.83	0.597	0.1	0.088	5.97
3	05	3665					
3	06	3665	7.42	0.477	0.052	0.031	9.17
4	07	3155	6.67	0.462	0.065	0.027	7.10
4	08	3213	1.48	0.375	0.049	0.01	7.65
5	09	2957	4.75	0.69	0.09	0.065	7.66
5	10	2957	5.01	0.72	0.098	0.073	7.34
6	11	3208	4.64	0.825	0.11	0.064	7.5
6	12	3203					
7	13	3709	6.16	0.228	0.024	0.012	9.5
7	14	3713					
7	15	3718	1.86	0.453	0.035	0.026	12.9
8	16	3606	3.29	0.661	0.073	0.054	9.05
8	17	3608	3.66	0.612	0.078	0.04	7.8
9	18	3306	2.71	0.963	0.121	0.068	7.95
9	19	3294	2.51	0.645	0.087	0.023	7.41
10	20	2904	1.92	0.712	0.098	0.032	7.26
10	21	2941	2.68	1.083	0.129	0.081	8.39
11	22	2465	1.78	0.711	0.1	0.041	7.11
11	23	2493	2.18	0.853	0.099	0.06	8.6

gear. As said above, this gives only a minimum value for the density.

Densities obtained by the three gears are not comparable: the Reineck box-core retains all macrofauna, and the samples are significantly screened on 0.25 mm mesh. The epibenthic sled selects larger organisms, and the samples are screened on 0.5, 1.0, and 2.0 mm mesh. Some small animals may be lost through the anterior part of the net of the sled (1 mm size mesh). The trawl retains megafaunal organisms, and a fairly good number of large macrofaunal individuals which cannot pass through the posterior bag (5 mm size mesh).

Table III shows organisms sampled in the Reineck box-core arranged by main zoological groups. Corresponding densities are expressed in number of individuals per 10 cm². Although variations of density within the same station are rather large, the Norwegian basin shows the highest density (6.440/10 cm²) in one sample from st. 1 and a clear decrease of density with increasing depth (minimum density of 0.054 ind./10 cm² for a depth of 3665 m). In the Lofoten basin, densities are relatively low. The minimum value observed in the shallower station falls within the range of intra-station variation. The Greenland basin shows densities often increasing with depth, while the absolute values remain low for the western shallow stations (10 and 11). The range of variation from all samples is extremely high: from 54 to 6440 ind. per m².

The densities calculated for the epibenthic sled samples are given in Table IV, together

Table III. Box core samples

Stations	1	2	2	3	3	4	5	5	6	6	7	8	9	9	10	10	11	11	Tot.
Sample	KR02	KR03	KR04	KR05	KR06	KR08	KR09	KR10	KR11	KR12	KR15	KR16	KR18	KR19	KR20	KR21	KR22	KR23	
Actiniaria								1								1			2
Nemertinea	1		1														2		4
Nematoda	316	78	30	1	1	1	3	2	119	2	122	3	205	40	53	16	4	16	1013
Polychaeta	31	19	16		1	17	5	3	25	17	99	9	22	10	21	12	6	12	325
Echiuria											1				1				2
Gastropoda		1			1												1		3
Bivalvia	6	3	4		1	2	6	2	10		15	7	1	9	7	3	1	8	86
Acarina	2	1																	3
Ostracoda	4	2	2								1		1	2	1				13
Copepoda	7		3						3		10		3	2	8	5		2	43
Amphipoda																		3	3
Tanaidacea	1			1				1	5		5		5	9	9	4		3	43
Isopoda	1					1							1					1	4
Holothuroidea	11	6	3	1		2			7		2	2		1	3		2	1	41
Tunicata								1							2				3
Total	380	110	59	3	4	23	14	10	169	19	255	21	239	73	105	41	16	46	1588
Ind./10 cm²	6,440	1,848	1,026	0,054	0,074	0,422	0,264	0,187	3,188	0,355	4,654	0,388	4,509	1,292	1,944	0,759	0,288	0,829	

TABLE IV a Epibenthic sled samples: Number of individuals obtained (no. ind.) and density calculated as number of individuals per hectare (ind./ha).

Station no.		1	2	3	3	4	5	6	7	8	9	10	11
Sample no.		DS 02	DS 04	DS 06	DS 07	DS 09	DS 11	DS 13	DS 14	DS 15	DS 16	DS 17	DS 18
Actiniaria	no. ind.	43	192	14	7	33	552	9	3314	936	7	36	231
	ind./ha	436	2651	124	112	425	6052	142	22950	7800	76	288	3263
Nemertinea	no. ind.	1	2	3	-	-	10	38	2	45	1	18	25
	ind./ha	-	-	-	-	-	4	-	-	-	-	-	-
Nematoda	no. ind.	14	1069	22	17	203	409	6250	4201	32785	721	4101	538
	ind./ha	142	14765	195	273	2616	4484	98892	29093	273208	7837	32861	7599
Polychaeta	no. ind.	548	738	943	312	281	1653	3234	1845	1511	416	1124	1618
	ind./ha	5569	10193	8389	5013	3621	18125	51170	12777	12591	4522	9006	22853
Echiura	no. ind.	-	-	-	-	-	4	48	26	174	-	6	7
	ind./ha												
Aplacophora	no. ind.	15	7	4	2	15	873	98	37	89	27	16	21
	ind./ha	152	97	35	32	193	9572	1551	256	741	293	128	297
Gastropoda	no. ind.	154	997	729	481	29	538	107	33	50	15	11	58
	ind./ha	1565	13771	6485	7728	373	5899	1693	228	416	163	88	819
Bivalvia	no. ind.	373	5237	1841	821	886	18401	3588	5114	2786	428	306	885
	ind./ha	3790	72334	16379	13191	11417	201765	56772	35415	23216	4652	2451	12500
Acarina	no. ind.	-	1	-	-	-	2	-	1	-	-	-	-
	ind./ha												
Pycnogonida	no. ind.	19	32	116	30	5	362	218	483	158	45	84	529
	ind./ha	193	442	1032	482	64	3969	3449	3345	1316	489	673	7472
Ostracoda	no. ind.	2	10	100	50	5	27	7	73	100	48	53	11
	ind./ha	-	-	-	-	-	-	-	-	833	522	-	-
Copepoda	no. ind.	4	39	3	1	14	109	437	119	132	391	928	108
	ind./ha	-	-	-	-	-	1195	6914	824	1100	4250	7435	1525
Cirripedia	no. ind.	-	-	-	-	-	-	-	-	-	-	-	1
	ind./ha												
Mysidacea	no. ind.	1	-	-	-	-	1	-	-	-	11	-	3
	ind./ha	-	-	-	-	-	-	-	-	-	120	-	-
Amphipoda	no. ind.	79	49	194	68	27	319	293	580	934	155	132	1195
	ind./ha	803	677	1726	1092	348	3498	4636	4016	7783	1685	1057	16879
Cumacea	no. ind.	292	-	-	-	-	-	-	-	-	-	-	46
	ind./ha	2967	-	-	-	-	-	-	-	-	-	-	650
Tanaidacea	no. ind.	33	212	122	104	111	557	1717	463	812	326	411	969
	ind./ha	335	2928	1085	1671	1430	6107	27167	3206	6766	3543	3293	13686
Isopoda	no. ind.	113	373	66	23	7	659	757	2492	1568	513	474	1724
	ind./ha	1148	5152	587	369	90	7226	11978	17257	13066	5576	3798	24350
Macrura	no. ind.	1	2	3	2	-	-	-	4	-	4	7	6
	ind./ha												
Crinoidea	no. ind.	10	1	-	-	-	14	-	-	-	-	9	54
	ind./ha	-	-	-	-	-	-	-	-	-	-	-	763
Holothuroidea	no. ind.	33	137	249	128	79	1296	982	4370	6697	561	357	1305
	ind./ha	335	1892	2215	2056	1018	14210	15538	30263	55808	6098	2861	18432
Asteroidea	no. ind.	2	-	-	-	-	-	-	-	-	-	-	28
	ind./ha	-	-	-	-	-	-	-	-	-	-	-	395
Ophiuroidea	no. ind.	-	5	1	-	-	-	-	-	-	-	-	-
	ind./ha												
Echinoidea	no. ind.	-	3	-	-	-	8	-	-	-	-	1	7
	ind./ha												
Tunicata	no. ind.	1	-	11	3	1	69	21	1	6	4	193	41
	ind./ha	-	-	-	-	-	-	-	-	-	-	1546	579
TOTAL		1738	9106	4421	2049	1696	25863	17804	23158	48783	3673	8268	9410
NUMBER IND./M^2		1.76	12.57	3.93	3.29	2.18	28.35	28.17	16.03	40.65	3.99	6.625	13.29
NUMBER IND./M^2 > 2 mm		0.75	1.24	0.32	0.05	0.34	2.11	3.98	8.59	7.19	0.81	0.57	2.96
NUMBER IND/M^2 < 2 mm		1.015	11.33	3.61	3.23	1.84	26.24	24.19	7.44	33.45	3.17	6.04	10.33
RATIO $\frac{No. < 2\ mm}{No. > 2\ mm}$		1.35	9.13	11.20	61.11	5.42	12.43	6.07	0.86	4.64	3.91	10.48	3.48

TABLE IV b Epibenthic sled samples: Dominance values for major animal groups in per cent of total number of individuals. Values below 0.1 % not included.

Station no.	1	2	3	3	4	5	6	7	8	9	10	11
Sample no.	DS 02	DS 04	DS 06	DS 07	DS 09	DS 11	DS 13	DS 14	DS 15	DS 16	DS 17	DS 18
Actiniaria	2.5	2.11	0.3	0.3	1.9	2.1	0.05	14.3	1.9	0.2	0.4	2.4
Nemertinea												
Nematoda	0.8	11.7	0.5	0.8	12	1.6	35.1	18.1	67.2	19.6	49.6	5.7
Polychaeta	31.5	8.1	21.3	15.2	16.6	6.4	18.2	8	3.07	11.3	13.5	17.2
Echiura												
Aplacophora	0.9	0.07	0.1	0.1	0.9	3.4	0.6	0.2	0.18	0.7	0.19	0.2
Gastropoda	8.9	10.9	16.5	23.5	1.7	2.1	0.6	0.1	0.1	0.4	0.13	0.6
Bivalvia	21.5	57.5	41.5	40.1	52.3	71.1	20.2	22	5.7	11.7	3.7	9.4
Acarina												
Pycnogonida	1.1	0.3	26	1.5	0.3	1.4	1.2	2.1	0.3	1.2	1	5.6
Ostracoda	-	-	-	-	-	-	-	-	0.2	1.3	-	-
Copepoda	-	-	-	-	-	0.4	2.45	0.5	0.3	10.6	11.2	1.1
Cirripedia												
Mysidacea	-	-	-	-	-	-	-	-	-	0.3	-	-
Amphipoda	4.5	0.5	4.4	3.3	1.6	1.2	1.6	2.5	1.9	4.2	1.6	12.7
Cumacea	16.8	-	-	-	-	-	-	-	-	-	-	0.5
Tanaidacea	1.9	2.3	2.7	5.1	6.6	2.2	9.6	2	1.6	8.9	4.9	10.3
Isopoda	6.5	4.1	1.5	1.1	0.4	2.5	4.3	10.7	3.2	14	5.7	18.3
Macrura												
Crinoidea	-	-	-	-	-	-	-	-	-	-	-	0.6
Holothuroidea	1.9	1.5	5.6	6.2	4.7	5	5.5	18.8	13.7	15.3	4.3	13.9
Asteroidea	-	-	-	-	-	-	-	-	-	-	-	0.3
Ophiuroidea												
Echinoidea												
Tunicata	-	-	-	-	-	-	-	-	-	-	2.3	0.4

with partial densities for larger macrofauna (retained on 2 mm screen) and smaller macrofauna (passing through 2 mm screen and retained on 0.5 mm screen). For the main zoological components, number of individuals, density per hectare, and relative dominance as percentage of the total number of individuals are given.

Sts. 5, 6, 7, and 8 show very high densities. St. 8 shows the highest value for the Norwegian Sea with 40 ind. per m^2.

In the Norwegian basin rather low densities were found, the exception being the sample from st. 2 which showed the moderately high figure of about 12 ind./m^2. The figure for the shallowest station, no. 1, is notably low. The Lofoten basin shows a remarkable difference between the samples from st. 4 (3200 m) and st. 5 (2900 m). The samples from the Spitsbergen basin (st. 6, 3200 m) and from the two deepest stations in the Greenland basin (st. 7, 3700 m and st. 8, 3600 m) were rich, while the three stations on the Western slope of the Greenland basin, i. e. st. 9 (3300 m), st. 10 (2900 m), and st. 11 (2500 m), showed lower figures although with an apparent tendency to increase with decreasing depth. For some general comments on the sled samples cf. the discussion at the end of this section.

The densities calculated from the trawl samples are given in Table V. As for the sled, number of individuals, density per hectare, and relative dominance as percentage of the total sample are given for the main zoological components.

The Norwegian basin appears relatively poor with densities of 0.73 to 1.65 ind. per m^2, and an intra-station variation of about 1 to 2. The Lofoten and Spitsbergen basins show still

TABLE V a Beam trawl samples: Number of individuals obtained (no. ind.) and density calculated as number of individuals per hectare (ind./ha)

Station no.		1	1	2	2	3	3	4	4	5	5	6	7	8	9	10	11
Sample no.		CP 01	CP 02	CP 03	CP 04	CP 05	CP 06	CP 07	CP 08	CP 09	CP 10	CP 12	CP 13	CP 14	CP 15	CP 16	CP 17
Actiniaria	no. ind.	135	332	1028	343	165	236	105	189	263	619	334	10979	1094	15	1062	2526
	ind./ha	162	286	543	274	127	226	116	148	220	396	209	4810	599	-	990	1742
Nemertinea	no. ind.	10	4	-	2	2	1	-	-	1	-	4	6	1	-	17	74
	ind./ha																
Nematoda	no. ind.	1104	92	192	336	10	97	11	-	13	5	28	14700	38877	39	10934	2864
	ind./ha	1326	79	101	269	7	92	12	0	10	3	17	6440	21302	-	10195	1975
Polychaeta	no. ind.	6598	8032	1550	2702	191	292	177	130	238	377	454	2796	910	63	2788	2757
	ind./ha	7925	6939	819	2161	147	279	196	101	199	241	284	1224	499	-	2600	1901
Sipuncula	no. ind.	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	ind./ha																
Echiura	no. ind.	-	-	-	-	-	-	-	-	-	-	1	12	5	1	24	26
	ind./ha																
Aplacophora	no. ind.	-	1	3	7	-	-	-	-	5	-	1	7	4	-	12	18
	ind./ha																
Gastropoda	no. ind.	72	296	362	161	53	52	75	97	270	315	57	198	154	-	788	862
	ind./ha	86	255	191	129	41	49	83	76	226	201	36	87	84	-	735	594
Scaphopoda	no. ind.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	10
	ind./ha																
Bivalvia	no. ind.	292	309	2146	7262	17	63	32	29	59	306	13	3352	435	1	1558	3391
	ind./ha	350	266	1133	5809	13	60	35	22	49	195	8	1468	238	-	1453	2339
Cephalopoda	no. ind.	1	-	-	1	2	-	2	2	-	2	1	4	2	-	-	1
	ind./ha																
Acarina	no. ind.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	ind./ha																
Pycnogonida	no. ind.	18	36	230	125	64	206	273	38	78	47	285	1346	64	20	941	717
	ind./ha	21	31	124	100	49	197	302	30	65	30	179	590	36	-	877	494
Ostracoda	no. ind.	7	-	2	5	-	-	-	-	-	-	-	15	1	-	4	11
	ind./ha																
Copepoda	no. ind.	14	9	6	8	-	-	-	-	-	3	-	19	51	1	87	711
	ind./ha																
Cirripedia	no. ind.	-	1	-	1	-	-	-	-	-	-	17	-	2	-	-	2
	ind./ha																
Mysidacea	no. ind.	17	25	77	65	4	-	17	1	90	1	4	-	1	-	26	70
	ind./ha																
Amphipoda	no. ind.	19	28	14	14	205	148	69	139	70	60	556	1762	1493	97	188	925
	ind./ha	23	24	9	11	158	142	76	108	59	32	349	771	818	-	175	638
Cumacea	no. ind.	9	7	-	-	-	-	-	-	-	-	-	-	-	-	-	60
	ind./ha																
Tanaidacea	no. ind.	39	20	25	58	1	10	2	-	1	3	10	208	270	7	476	1042
	ind./ha	46	17	13	46	0	9	2	0	1	2	6	91	148	-	444	718
Isopoda	no. ind.	122	136	96	44	6	4	43	73	257	54	25	1075	342	-	296	1089
	ind./ha	146	117	51	35	4	4	48	57	215	35	15	471	187	-	276	751
Macrura	no. ind.	67	129	49	76	153	146	69	157	166	176	164	130	213	68	88	54
	ind./ha																
Crinoidea	no. ind.	79	32	41	72	-	-	-	-	2	5	-	-	-	-	23	226
	ind./ha																
Holothuroidea	no. ind.	314	186	8021	8903	20504	7258	3441	6409	8300	6448	9228	18865	13962	105	7679	8491
	ind./ha	377	160	4238	7122	15833	6945	3812	5007	6945	4120	5785	8265	7650	-	7160	5855
Asteroidea	no. ind.	29	81	8	14	-	-	-	1	-	7	10	-	-	1	37	285
	ind./ha																
Ophiuroidea	no. ind.	-	1	-	1	-	-	-	-	-	4	5	-	-	-	5	-
	ind./ha																
Echinoidea	no. ind.	2	9	9	33	-	-	-	-	74	51	-	-	-	-	397	174
	ind./ha																
Tunicata	no. ind.	4	-	7	3	1	1	-	-	-	-	-	-	-	-	103	263
	ind./ha																
TOTAL		8968	9766	13866	20237	21378	8514	4316	7265	9887	8483	11197	55470	57880	418	27533	26649
NUMBER IND./M^2		1.077	0.843	0.732	1.618	1.650	0.814	0.478	0.567	0.827	0.542	0.702	2.430	3.171	0.119	2.567	1.837

TABLE V b Beam trawl samples: Dominance values for major animal groups in per cent of total number of individuals. Values below 0.1 % not included.

Station no.	1	1	2	2	3	3	4	4	5	5	6	7	8	9	10	11
Sample no.	CP 01	CP 02	CP 03	CP 04	CP 05	CP 06	CP 07	CP 08	CP 09	CP 10	CP 12	CP 13	CP 14	CP 15	CP 15	CP 17
Actiniaria	1.5	3.3	7.4	1.7	0.3	2.7	2.4	2.6	2.7	7.2	2.8	19.8	1.9	-	3.3	9.5
Nemertinea																
Nematoda	12.3	0.9	1.4	1.6	0.0	1.1	0.3	0.0	0.1	0.0	0.2	26.5	67.2	-	30.7	10.7
Polychaeta	73.5	82.1	11.2	12.3	0.9	3.4	4.1	1.8	2.4	4.4	4.0	5.0	1.6	-	20.1	10.3
Sipuncula																
Echiura																
Aplacophora																
Gastropoda	0.8	3	2.6	0.8	0.2	0.6	1.7	1.3	2.7	3.7	0.5	0.4	0.2	-	2.8	3.2
Scaphopoda																
Bivalvia	3.2	3.1	15.5	35.8	0.1	0.7	0.7	0.3	0.6	3.6	0.1	6.0	0.7	-	5.6	12.7
Cephalopoda																
Acarina																
Pycnogonida	0.2	0.3	1.7	0.6	0.3	2.4	6.3	0.5	0.8	0.5	2.5	2.4	0.1	-	3.4	2.7
Ostracoda																
Copepoda																
Cirripedia																
Mysidacea																
Amphipoda	0.2	0.3	0.1	0.0	1.0	1.7	1.6	1.9	0.7	0.5	5.0	3.2	2.6	-	0.7	3.5
Cumacea																
Tanaidacea	0.4	0.2	0.2	0.2	0.0	0.1	0.0	0.00	0.00	0.00	0.1	0.4	0.4	-	1.7	3.9
Isopoda	1.4	1.4	0.7	0.2	0.0	0.0	1.0	1.0	2.6	0.5	0.2	1.9	0.6	-	1.0	4.1
Macrura																
Crinoidea																
Holothuroidea	3.5	1.9	57.8	43.9	95.9	85.2	79.7	88.3	80.8	75.9	82.4	34.0	24.1	-	27.9	31.8
Asteroidea																
Ophiuroidea																
Echinoidea																
Tunicata																

lower figures ranging from 0.48 to 0.83 ind. per m^2. In the Greenland basin, the densities are much higher, except for st. 9, where the trawl dug into the sediment soon after it reached the bottom. The range of variation with depth for each of the basins sampled is rather low. In particular, the reduction of density does not follow the increase in depth. The main feature of this series of trawl samples is the relative richness of the Greenland basin.

The baited traps were used in 7 stations only. The results are shown in Table VI; comparisons can be made using the catch in number of individuals caught per 10 hours on the bottom.

Compared with other types of samples, the abundance of carnivorous amphipods as expressed by the catch in the trap is curiously very low in the Greenland basin (especially for sts. 9 and 10). The highest value comes from st. 2 in the Norwegian basin. Sts. 3, 4, 6, and 7 (between 200 and 650 individuals per 10 hours) approximate the mean value (455). The main feature from trap samples is the very meagre catches in the western part of the Greenland basin compared with the richness of this area as shown by catches with other types of gear.

As seen from this brief survey the over-all picture of the densities as obtained by all kinds of gear shows interesting traits which may be due to different forces acting in different parts of the area and in the different deep basins.

The general impression of the Norwegian basin is one of low densities. This is in spite of the fact that the single Reineck core sample from st. 1 included in this report is the richest one of all. In the Reineck samples the densities decrease consistently with increasing depth, while the sled and trawl

Table VI. Baited trap samples

Station no.	Gear code	Time on bottom	Individuals captured	Individuals/ 10 h
2	NA 01	11 h 55'	1825	1520
3	NA 02	11 h 59'	785	654
4	NA 03	9 h 00'	182	202
6	NA 04	9 h 30'	305	321
7	NA 05	12 h 18'	508	413
9	NA 06	13 h 54'	4	2.8
10	NA 07	11 h 40'	1	0.08

samples from st. 2 and st. 3 are, on the whole, richer than those from st. 1. St. 3 is definitely poorer than st. 2, although a high abundance of *Elpidia glacialis* in one trawl sample results in a value above the average. It should be noted, however, that the baited traps at sts. 2 and 3 gave the highest catches of carnivorous amphipods.

In the Lofoten basin, practically all samples gave low or very low densities, the exception being the sled from st. 5, which owing to high numbers of Bivalvia, shows a density of 28.36 ind. per m^2, one of the highest values obtained. The apparent poverty of the deep sea fauna of the Lofoten basin is somewhat surprising considering the proximity of particularly st. 5 to the rich coastal banks with their steep continental slope. Possibly the high density of small bivalves at st. 5 (20 ind. per m^2) may reflect this proximity. The amphipod catch at st. 4 is less than half the average.

The single station, no. 6, in the Spitsbergen basin with one rich and one poor Reineck sample, a rich sled, and a poor trawl, hardly permits any general conclusion concerning that basin. The catch of trapped amphipods is somewhat below the average.

The most striking feature of all with respect to faunal densities are the very high values obtained in the Greenland basin and especially in the two deep eastern stations nos. 7 and 8. In these stations all values, except one Reineck core from st. 8 are above, in most cases much above, the averages. The more westerly stations show if not low, so at least lower values. The tendency to lower densities is, however, very evident in the case of carnivorous amphipods. A trap at st. 7 yielded 508 specimens as compared with 4 at st. 9 and 1 at st. 10. No obvious explanation could be found.

As already pointed out above (p. 62) deep water formation by means of vertical convection in winter takes place on a very large scale in the waters between Jan Mayen and Spitsbergen, i.e. in the Greenland and Spitsbergen basins. This will also lead to a downward transport of organic matter, most pronounced in the areas where sts. 7 and 8 are situated. The effects of drifting ice may be both positive and negative. Melting ice sets nutrients free, while an ice-cover, by shutting out light, lowers production in the lighted zone. Logically the first-mentioned effect should be proportionally stronger in the eastern, the other one in the western part of the Greenland basin. The stations 9–11 form a section up the lower part of the western continental slope, but here as elsewhere in the Norwegian Sea there exists no definite trend towards an increased density of the deep sea fauna with decreasing depth.

In the Norwegian basin, body size as expressed by the ratio in the sled samples between animals retained by the 2 mm and finer screens, shows a clear decrease with increasing depth, thus supporting the hypothesis of individual size decreasing with depth (Rome & Menzel 1971, Thiel 1975). In the Lofoten basin and the two Western basins this is not the case. The extreme value is found at st. 8 (3600 m) where the ratio between organisms not retained and those retained by a 2 mm screen is 0.866 as compared with 61.113 at st. 3 (3600 m) in the Norwegian basin. This means that more than 50% of the specimens at st. 8 were more than 2 mm, a very exceptional figure for such depths.

Faunal composition

General remarks

Although only a small fraction of the material has hitherto been dealt with systematically by specialists, the sorting into higher taxa of various rank, different for different phyla, reveals important differences in the faunal composition of the deep basins East and West of the Midatlantic ridge (Tables IV and V). Differences in North-South direction between the two Eastern abyssal basins are small and cannot yet be fully estimated. On the Western side, however, the Spitsbergen basin, judging from the few samples available, seems to be slightly different from

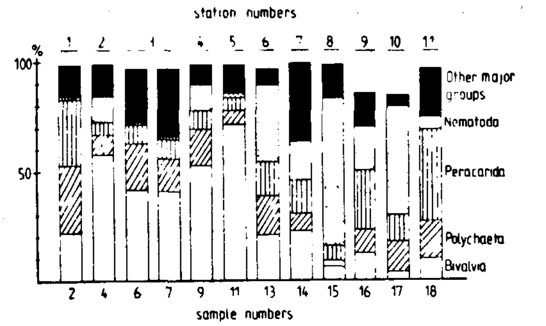

Fig. 2. Dominance values for more important higher taxa in 12 epibenthic sled samples. Bivalves dominate at sts. 2–5, nematodes at sts. 6, 8, and 11. At the shallower sts. 1 and 11 peracarids are relatively more numerous. 'Other major groups' comprise Actiniaria, Aplacophora, Gastropoda, Pycnogonida, and Holothuroidea. If copepods were added at sts. 9 and 10 approximately 95% of the fauna would be covered also at those stations.

the Greenland basin in some respects. Especially judging from the single trawl haul, it shows closer affinities with the fauna of the Lofoten and Norwegian basins. The sled samples, however, indicate a closer relationship with the abyssal fauna of the Greenland basin. It should be stressed that these statements do not take into account the specific composition but only the dominance figures for higher taxa.

In the sled samples 11 higher taxa constitute more than 97% of all the animals. These taxa are the Actiniaria, Nematoda, Polychaeta, Aplacophora, Gastropoda, Bivalvia, Pycnogonida, Amphipoda, Tanaidacea, Isopoda, and Holothuroidea. In three samples they reach a lower percentage (DS 02, st. 1; DS 16, st. 9; DS 17, st. 10), viz. 82, 87, and 85% respectively. If the Cumacea are added in the former case and the Copepoda and Ascidiacea in the latter ones, the sum in all cases represents more than 97%. The dominating groups are undoubtedly the Nematoda, Bivalvia, Polychaeta, Holothuroidea, and Peracarida mentioned in order of numbers appearing in our samples.

The trawl samples give approximately the same picture, but with the obvious dominance of larger animals, such as large polychaetes, bivalves, and nematodes and with an absolute dominance of holothurians in sts. 3 to 6 (about 90% in the samples from st. 3, more than 80% in sts. 4 and 6, and more than 75% in st. 5). Trawl samples from st. 2 also show a high percentage of holothurians (about 50%).

Since the mentioned taxa form such a large proportion of the fauna, it seems justified to deal with them separately before looking at other groups of animals.

Actiniaria

Sea anemones are present in all samples, but show a low abundance in sts. 1–4 and 6. From comparisons of sled and trawl data, it is evident that small specimens are abundant at sts. 5, 7, and 8 and larger ones at sts. 7, 10, and 11. The abundance seems to be highest at st. 7 (up to 23,000 ind./ha) with dominance values of about 20 for the trawl sample and 14 for the sled sample. Generally speaking, actinians are more common in the Greenland basin than in the other ones. The low figures for the Spitsbergen basin cannot be accounted for at present.

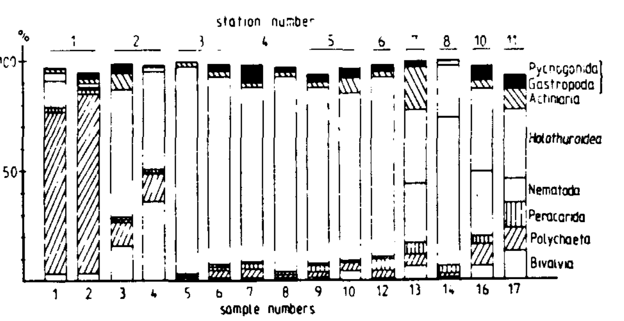

Fig. 3. Dominance values for more important higher taxa in 16 beam trawl samples. Polychaetes are dominating at st. 1, while Holothuroidea show a massive dominance at sts. 3–6. Large sized nematodes are particularly important at sts. 1 and 7–11.

Nematoda

The nematodes are most common in the Spitsbergen and Greenland basins and especially in the deep areas of the latter, although the figures obtained (abt 273,000 ind./ha) are not particularly high. At sts. 6 to 10 nematodes constitute an important part of the fauna and at st. 8 they represent 67% of the animals caught both by the trawl and the sled. The relatively large numbers of nematodes caught by the trawl at sts. 7, 8, and 10 are notable and distinguish the Greenland basin from the Eastern basins (sts. 2–5), where practically no large-sized nematodes were caught. In the Eastern basins, our samples show that about 1% or less of the fauna is made up by nematodes, the exceptions being the sled samples from sts. 2 and 4. In shallower waters (2500 m) on both sides of the Norwegian Sea (sts. 1 and 11), nematodes constitute slightly more than 10% of the fauna in the samples.

Polychaeta

Like the nematodes, the polychaetes are represented in practically all samples taken. The highest numbers in the box-core samples were recorded from sts. 1, 2, 6, and 7 (31, 19, 21, and 99 ind./sample, respectively).

The sled consistently collected high numbers of polychaetes, especially at sts. 5–8, with a maximum of 51,170 ind./ha in the Spitsbergen basin (st. 6).

The trawl catches were largest at sts. 1, 2, 10, and 11. Fairly small numbers were recorded at the stations where the sled showed great numbers (sts. 5, 6, 7, and 8).

The polychaetes are well represented by large specimens in the shallowest station in the Norwegian basin (st. 1), where the group has its highest dominance value (31% in a sled sample, 73.5 and 82.1 % respectively in the two trawl samples). Small-sized polychaetes are best represented in the shallowest station of the Lofoten basin (st. 5, 2950 m) and in the deep part of the Spitsbergen and the Greenland basins.

Bivalvia

Bivalves are present in practically all the samples from the 11 stations. In the trawl samples, most specimens were found at st. 2 (Norwegian basin, 5809 ind./ha), but a fair number also from sts. 7, 10, and 11 in the Greenland basin (up to 2339 ind./ha). At st. 2 the large number was accounted for mainly by one species, *Hyalopecten frigidus*.

Small bivalves were most common at the deep stations of all the basins, and particularly in the Spitsbergen basin. The peak number was, however, found in the Lofoten basin in a sled from st. 5 (201,765 ind./ha), where the trawl caught only very few bivalves.

The dominance picture gained from the sled samples shows high bivalve figures for the two Eastern basins (sts. 3–5, 41, 52, and 71% respectively) and declining importance in the Spitsbergen and Greenland basins.

Holothuroidea

All kinds of gears have collected holothurians. However, they are rare in the cores. Trawl and sled samples show high densities of holothurians in the Norwegian Sea, with a clear-cut dominance of the eurybathic

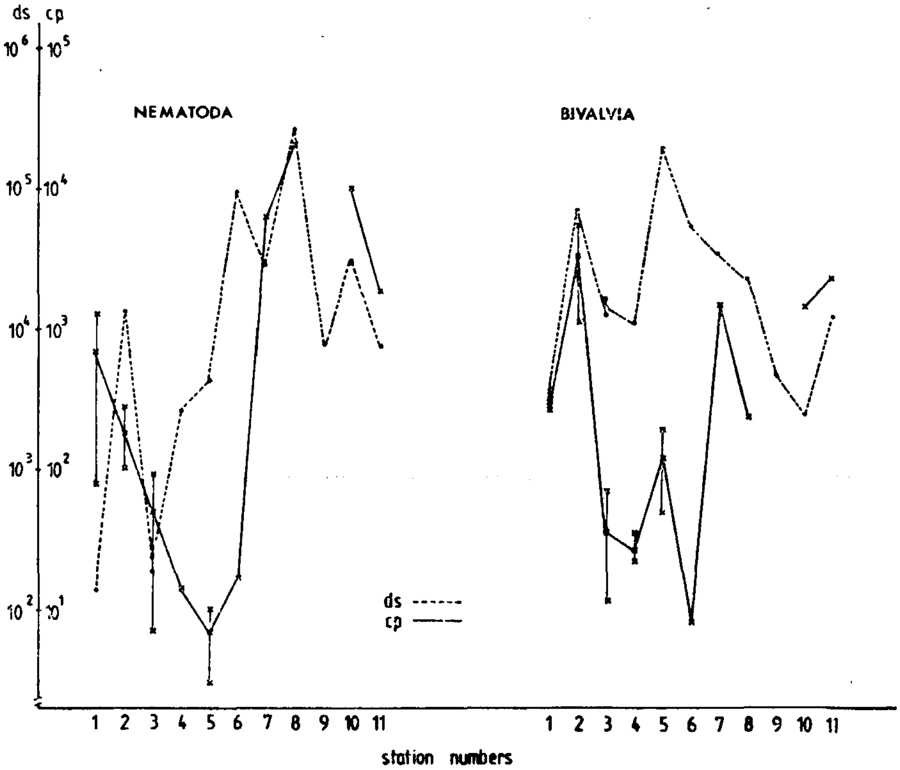

Fig. 4. The variation in absolute numbers of nematodes (left) and bivalves (right). Solid lines represent beam trawl samples (cp) and broken lines epibenthic sled samples (ds).

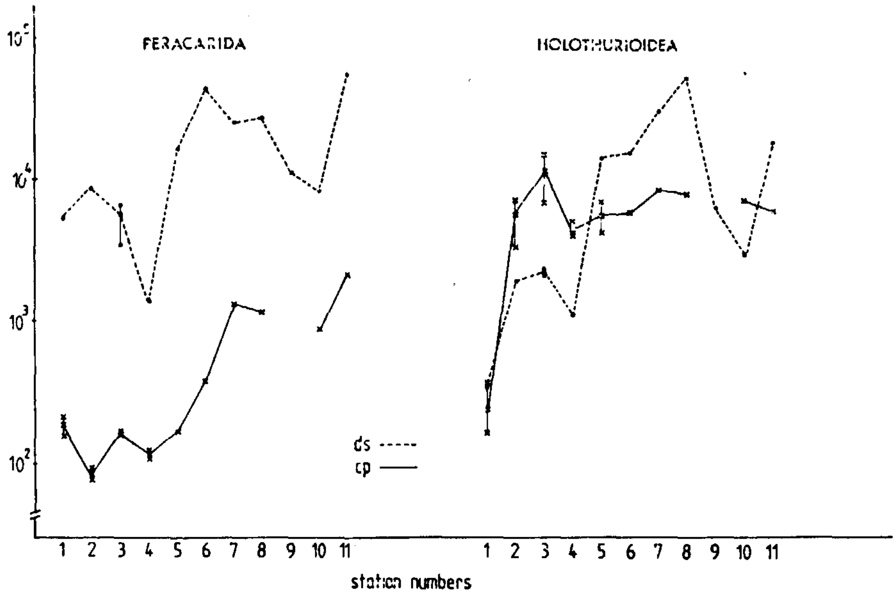

Fig. 5. Variation in absolute numbers of peracarids, comprising Amphipoda, Isopoda, Cumacea, and Tanaidacea (left) and holothurians (right). Solid lines represent beam trawl samples (cp) and broken lines epibenthic sled samples (ds).

species *Elpidia glacialis.* In the Norwegian basin, *E. glacialis* has been mostly collected in the trawls, and dominates at st. 3 (11.389 ind./ha). In the North, *E. glacialis* tends to dominate in the sled samples, and this fact can be related to a decrease in the mean size of the individuals (maximum value at st. 8, 55,808 ind./ha).

Peracarida

The three orders Amphipoda, Isopoda, and Tanaidacea show approximately the same picture in terms of abundance and distribution.

The sled samples gave the highest number of animals at sts. 5–8 (i.e. the three Northern basins) with a peak for amphipods in the Greenland basin (st. 8, 7783 ind./ha), for isopods in the same basin (st. 7, 17,257 ind./ha), and for tanaids in the Spitsbergen basin (st. 6, 27,167 ind./ha).

The trawl samples contained more animals of all three taxa in the Western basins, especially the Greenland basin. In the case of the isopods, a large proportion of the specimens caught in the Eastern basins belonged to the one species *Chiridothea megalura*, and among the big tanaids *Sphyrapus serratus* was dominating.

The amphipods collected with the trawl in the Western basins were dominated by *Halirages* spp. and *Phippsiella* sp.

The trap samples showed a picture which was very different from the one mentioned above. Most animals (mostly *Eurythenes gryllus)* were caught in the Norwegian basin (sts. 2 and 3) and a fair number also at three stations in the other three basins (sts. 4, 6, and 7). It is notable that only 4 were collected at st. 9 and 1 at st. 11, although a few specimens were still caught in the trawls.

The Cumacea were found only at sts. 1 and 11, i.e. the shallowest of the stations. At st. 1, the Cumacea showed a dominance figure of 16.8%, while it was very low at st. 11 (less than 1%).

In terms of dominance, the peracarids (Amphipoda, Isopoda, Tanaidacea) have approximately the same position at all the stations (approximately 10%).

Gastropoda

The gastropods seem to play a more important part in the faunal composition of the Norwegian and Lofoten basins than in the other two basins. Especially the sled samples from sts. 2, 3, and 5 show considerable numbers of gastropods (about 13.700, 7000, and 5900 ind./ha respectively). Sts. 1 and 6 show one fourth to one third of that number, while the other stations showed rather small numbers (less than 400 ind./ha).

The trawl samples contained relatively few gastropods except for the shallower stations in the Greenland basin (sts. 10 and 11) where 735 and 594 ind./ha were recorded.

Pycnogonida

The numbers of pycnogonids caught by the sled showed the same distribution in general terms as those of the actinians, i.e. with peak numbers in the Lofoten, Spitsbergen, and Greenland basins (sts. 5 to 8).

The trawl catches increased slightly in the Western basins, but the absolute numbers were consistently rather low.

Other taxa

Sponges have been collected in fairly large quantities, especially in the trawl samples from the Greenland basin. The colonies are often broken into pieces, and for that reason they have not been taken into account in the numerical data, although they must contribute materially to the total biomass.

The copepods show a very marked increase in numbers in the Western basins as compared to the Eastern ones. For the sled samples, this is especially notable for sts. 6, 9, and 10 (the Spitsbergen and Greenland basins). At the last station, the dominance figure for copepods was as high as 11.2% for the sled sample. Relatively high numbers were also recorded at sts. 10 and 11 in the trawl samples (81 and 490 ind./ha respectively). The core samples reinforce the impression of greater abundance of copepods in the Lofoten and Greenland basins.

The decapod crustaceans (Macrura) show no specific tendencies in their abundance. Macrurans were caught in all trawl samples. Other groups of decapod crustaceans common in the Atlantic are totally absent from the Norwegian sea: Anomura (pagurids, galatheids, and lithodids) and penaeid Macrura.

Echiuroids were caught by the trawl only in the Spitsbergen and Greenland basins and the great majority of specimens obtained by the sled was found in the same areas. The only echiuroids from the Eastern basins were 4 specimens from st. 5. The highest number was found at st. 8 (the Greenland basin; 1450 ind./ha).

Ophiuroids are extremely rare in the deep Norwegian Sea basins, which is very unusual compared with other oceans.

Fishes are limited to three species only in our catches (two Liparids and one Zoarcid) and were never caught below 3000 m depth. No macrurid fish was collected in our samples.

DISCUSSION

Despite the fact that deep sea benthic communities have been studied since about a century ago, quantitative evaluations were first achieved during the Galathea expedition (Spärck 1951). Complete reviews of such quantitative studies have been given by Sanders et al. (1965) and Hessler & Jumars (1974).

The main difficulty comparing existing results lies in the screening problem, in other words the distinction of faunal categories from the average size of the animals or from zoological considerations. Nematodes are usually considered as a major part of the meiofauna (McIntyre 1969); in the case of the Norwegian Sea, they appear to be exceptionally large, and an important part of the nematofauna has been retained on the 1 mm screen. From such examples, it seems more convenient for quantitative comparisons to take into account the number of animals retained on a given screen, irrespective of the category to which the group normally belongs. This point is specially true for the deep sea benthos, which generally shows a clear decrease in average size with depth (Rowe & Menzel 1971).

In the case of the Reineck samples, they have been sorted on a 0.25 mm screen, and they can be compared with results from Hessler & Jumars (1974) in the central North Pacific Ocean, although the latter come from an oligotrophic area and a depth of 5500 m. On the average, the Norwegian Sea appears only four times richer than the North Pacific (mean value of 1584 ind. per m^2 versus 374 ind. per m^2). The ratio between meiofauna (Nematoda, Copepoda, and Ostracoda) and macrofauna numbers is very similar: 2.3 in the North Pacific, and 2.06 in the Norwegian Sea. The range of variation is low in the North Pacific, and very high in the Norwegian Sea. This could be due either to the different size of the samplers (600 versus 2500 cm^2) or to the geographical and bathymetric variation. Data from Sanders et al. (loc. cit.) and Rowe & Menzel (loc. cit.) obtained with the anchor dredge can hardly be compared with our box-corer results, even if Gage (1975) recently evaluated the quantitative significance of results from this kind of gear in shallow water samples. On the whole, however, a comparison with the North West Atlantic shows similarity except for the Norwegian basin deepest station which is extremely poor. For comparable depth, the Norwegian Sea looks slightly richer than the North West Atlantic; this is especially the case with sts. 1, 7, and 9.

As pointed out by Sanders et al. (loc. cit.), the organic carbon content of the sediment does not reflect the density of the fauna; the value of 0.23 % at the rich st. 7 (KR 13) is much lower than the 0.48 % value for the poor st. 3. This situation can be explained by assuming that the analytical method does not differentiate between labile and refractory organic carbon compounds as trophic sources.

Comparisons with unpublished data from the Bay of Biscay in the North East Atlantic obtained by two of us (L.L., M.S.) using the same sampling and sorting procedures show clear similarities when mean values are considered. The mean values from 21 core samples are 1726 ind. per m² for 3000 m depth and 892 ind. per m² for 4100 m depth near the slope; in the central part of the Bay, at 4700 m, the density falls at 494 ind. per m². However, station values from the Norwegian Sea show a very great range of variation of about two orders of magnitude (10^2). Data from the Bay of Biscay are much more homogeneous.

Comparison with the Polar basin deep sea fauna collected with a sphincter-type corer and sorted on a 0.149 mm mesh sieve (Paul & Menzies 1974) shows great differences from the Norwegian Sea. From depths between 1060 and 2530 m, densities varied from 22 to 194 ind./m², with an average of 63 ind./m². These very low values of density are much below even those from the oligotrophic North Pacific area reported upon by Hessler & Jumars (loc. cit.), despite the fact that the arctic samples were washed on a finer sieve. In the southernmost part of the Norwegian Sea, Thiel (1971) found much higher values than Paul & Menzies (loc. cit.). In 4 samples from depths of 1685 and 1825 m sieved on 0.15 mm mesh size, the average density of Nematoda (except Desmoscloecida) was 52,000 ind./m². The Nematoda in question made up an average of about 82 % of the total meiofauna retained on screens down to a mesh size of 0.042 mm. The densities found by Thiel may be roughly 1000 times higher than those recorded from the Polar basin by Paul & Menzies. They are about 10 times higher than those from our own richest samples from the deeper parts of the Norwegian Sea, but being screened on 0.15 instead of 0.25 mm mesh size they are not directly comparable. In Thiel's samples the number of nematodes increases rapidly in fractions from mesh sizes smaller than 0.15 mm, the fraction 0.15–0.10 mm giving 141,400 nematodes/m² and the fraction 0.10–0.042 mm 783,200 nematodes/m². These figures suggest that the difference between the 0.25 and 0.15 mm fractions may be substantial.

Data from sled samples are difficult to compare with previous studies. Hessler & Sanders (1967) did not consider epibenthic sled samples as quantitative samples. The total number of individuals for four samples between 1330 and 2864 m in the North West Atlantic varies from 5897 to 25,242 individuals, and this agrees with the range of variation of our data from the Norwegian Sea. The mean density for sled samples in the Norwegian Sea is 13.40 ind./m². From unpublished data obtained by two of us in the Bay of Biscay using the same sampling and sorting procedures, the mean density value for eleven sled samples in depths between 2800 and 3200 m is 1.76 ind./m², i.e. eight times lower than in the Norwegian Sea. The mean ratio between Reineck core and sled densities is 118/1; this high difference is partly due to the samplers, partly due to the washing procedure (0.25 mm mesh sieve for the core, 0.50 mm for the sled).

To our knowledge comparable quantitative data from deep sea beam trawl samples have never been published. The results of our trawl samples in the Norwegian Sea are clearly more homogeneous than the sled data. Except for st. 9, the range of variation lies between 0.47 and 3.17 ind./m², with a mean of 1.32 ind./m². The larger range of variation within sled samples could be due partly to repeated lifts off the bottom during some hauls. The mean ratio between sled and trawl densities is 10.1/1. For a few dominant species such as *Elpidia glacialis*, the density computed from trawl samples reaches nearly one holothurian per m² in the Greenland basin. From unpublished data obtained in the Bay of Biscay, the mean density value for eight trawl samples between 2700 and 3200 m is 0.024 ind./m², the ratio between sled and trawl mean densities being of 73.3/1. This figure probably demonstrates a higher biomass in the Norwegian Sea than in the Bay of Biscay, although it should again be stressed that sled and trawl samples are not quantitative and give only minimum values, which need not in themselves be directly comparable from sample to sample.

Trap samples from the Norwegian Sea can be compared with data obtained in the central Pacific in 5720 m of water by Shulenberger & Hessler (1974). Two sets of three-chambered fish traps were placed on the bottom during 2 and 96 hours respectively. The catch per 10 hours in number of individuals (adding to the longest trapping 196 individuals represented only by fragments) was 320 and 200 ind./10 h, figures which are very similar to those from sts. 4 and 6 in the Lofoten and Spitsbergen basins. As in the case of the Norwegian Sea, all amphipods caught in the Pacific belonged to the family Lyssianassidae. No mature *E. gryllus* have been collected in the Norwegian Sea. This can be related to a change of trophic behaviour of mature females (Shulenberger & Hessler 1974). The poorness of the trap catches from the Greenland basin, as compared with the richness of sled and trawl samples from the same area, cannot at present be accounted for. Our samples confirm the hypothesis of the importance of large mobile scavengers within the abyssal benthic communities.

From sled and trawl samples only, the number of species appears extremely low in the Norwegian Sea. For instance, Echinoderms comprise 13 species only, and fishes three species, while for amphipods, hitherto only provisionally sorted, the number of species may lie around 30. For a similar span of depth in a limited area such as the Bay of Biscay, the number of species is about eight times higher, for amphipods perhaps 5 to 6 times higher. Although definite evaluations cannot yet be made, diversity seems to be extraordinarily low in the Norwegian Sea compared with other regions and similar depths. If well established through further studies of our samples, this very low diversity combined with the peculiar faunistic composition strongly supports the hypothesis of a rather young deep sea fauna inhabiting the Norwegian Sea basins, well isolated from North East Atlantic faunal influence (Dahl 1972).

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REFERENCES

Bervas, J. Y., Potin, L. & Reyss, D. 1973. Réalisation d'une drague epibenthique à fermeture automatique. Document interne CNEXO, Brest (unpublished report).

Dahl, E. 1972. The Norwegian Sea deep water fauna and its derivation. *Ambio Spec. Rep. 2*, 19–24.

Ekman, S. 1935. *Tiergeographie des Meeres.* Akad. Verlagsges., Leipzig, 542 p.

Gage, J. D. 1975. A comparison of the deep-sea epibenthic sledge and anchor-box dredge samplers with the van Veen grab and hand coring by diver. *Deep-Sea Res. 22*, 693–702.

Helland-Hansen, B. & Nansen, F. 1909. The Norwegian Sea: Its physical oceanography based upon the Norwegian researches 1900–1904. *Rep. Norw. Fish. Marine Inv. 2*, 1.

Herman, Y., Grazzini, C. V. & Hooper, C. 1971. Arctic paleotemperatures in late Caenozoic Time. *Nature 232*, 466–469.

Hessler, R. R. & Jumars, P. A. 1974. Abyssal community analysis from replicate box-cores in the Central North Pacific. *Deep-Sea Res. 21*, 185–209.

Hessler, R. R. & Sanders, H. L. 1967. Faunal diversity in the deep sea. *Ibid. 14*, 65–78.

Kolthoff, G. 1901. *Till Spetsbergen och Nordöstra Grönland år 1900.* Stockholm, Skoglunds. 227 p.

Laubier, L., Martinais, J. & Reyss, D. 1972. Deep-sea trawling and dredging using ultrasonic techniques. pp. 175–187 in R. W. Brauer (ed.) *Barobiology and the Experimental Biology of the Deep Sea.* Univ. North Carolina.

McIntyre, A. D. 1951. Ecology of marine meiobenthos. *Biol. Rev. 44*, 245–290.

Menzies, R. J., George, R. Y. & Rowe, G. T. 1973. *Abyssal Environment and Ecology of the World Oceans.* Wiley. 488 pp.

Mosby, H. 1972. Basic problems in the Norwegian Sea. *Ambio Spec. Rep. 2*, 7–10.

Nathorst, A. G. 1901. *Två somrar i Norra Ishafvet* Stockholm, Beijers. 1: 414 p. 2: 352 p.

Paul, A. L. & Menzies, R. J. 1974. Benthic ecology of the high arctic deep sea. *Mar. Biol. 27*, 251–262.

Reineck, H. E. 1958. Kastengreifer und Lotröhre 'Schnepfe'. *Senckenb. lethaea 39*, 42–48, 54–56.

Reineck, H. E. 1963. Der Kastengreifer. *Natur Mus. 93*, 102–108.

Rowe, G. T. & Menzel, D. W. 1971. Quantitative benthic samples from the deep Gulf of Mexico with some comments on the measurements of deep-sea biomass. *Bull. Mar. Sci. 12*, 845–867.

Sars, G. O. 1873. Om Cumaceer fra de store dybder i Nordishafvet. *K. Sv. Vet. Ak. Handl. 11* (6), 1–12.

Shulenberger, E. & Hessler, R. R. 1974. Scavenging abyssal amphipods trapped under oligotrophic Central North Pacific gyre waters. *Mar. Biol. 28*, 185–187.

Spärck, R. 1951. Density of bottom animals on the ocean floor. *Nature 168*, 112–113.

Thiel, H. 1971. Häufigkeit und Verteilung der Meiofauna im Bereich des Island-Färöer-Rückens. *Ber. Deutsche Wiss. Komm. Meeresf. 22*, 99–128.

Thiel, H. 1975. The size structure of the deep-sea benthos. *Int. Rev. ges. Hydrobiol. 60*, 575–606.

Vogt, P. R. 1972. The Faeroe-Iceland-Greenland aseismic ridge and the Western boundary undercurrent. *Nature 239*, 79–81.

Wandel, C. F. 1898. Report of the voyage. *Den Danske Ingolf-Exp. 1*, 1–21.

Wille, C. 1882. Historical account. *The Norw. North-Atl. Exp. 1876–1878 1*, 1–54.

RÉSUMÉ

Les communautés benthiques des quatre bassins de la Mer de Norvège au-delà de 2000 m de profondeur ont été étudiées en utilisant quatre engins de prélèvement: le carottier Reineck de 600 cm^2, la drague épibenthique, un chalut à perche, et une grande nasse appatée fonctionnant en engin libre. Onze stations comprises entre 2465 et 3718 m ont été explorées dans les bassins de Norvège, des Lofoten, du Spitsberg et du Groenland.

Les densités de macrofaune dans les carottiers varient de 54 à 6440 individus au m^2, avec une valeur moyenne de 1584 ind./m^2. Les densités obtenues à partir des dragages et des chalutages sont beaucoup plus faibles: de 1,76 a 40,65 ind./m^2 dans les dragages, et de 0,48 a 3,17 ind./m^2 dans les chalutages. D'après quelques prélèvements en double, les prélèvements réalisés avec le chalut sont plus homogènes que ceux obtenus avec la drague. La nasse appatée a capturé seulement des Amphipodes Lyssianassides, en nombre variant de près de 2000 à 1 individus. A l'exception des nasses, les autres types d'engins fournissent des densités plus fortes à profondeur comparable dans le bassin du Groenland que dans le bassin de Norvège. Le bassin des Lofoten montre d'importantes variations en partie liées à la forte productivité des eaux de surface. Le bassin du Spitsberg constitue une zone de transition. Les fortes densités du bassin du Groenland sont peut-être liées au phénomène de convection verticale.

La composition faunistique est étudiée par grands groupes zoologiques. Dans l'ordre du nombre total d'individus dans les prélèvements, les Nématodes, les Polychètes, les Bivalves, les Ostracodes, les Tanaidacés et les Holothuries dominent les carottiers. Pour la drague épibenthique, les résultats diffèrent légèrement: Nématodes, Bivalves, Polychètes, Holothuries et Péracarides. Les coups de chalut présentent à peu près la même composition faunistique générale, avec une dominance élevée des grands individus comme les Holothuries, les Polychètes et les Bivalves. Les nasses n'ont capturé que des Amphipodes Lyssianassides.

Le nombre d'espèces des bassins profonds de la Mer de Norvège est extrêmement faible. Les Echinodermes comprennent 13 espèces, les Poissons 3. Des groupes communs dans l'océan mondial profond comme les Anomoures (pagures, galathéides et lithodes) et les Penaeides sont totalement absents de la Mer de Norvège d'après nos prélèvements. Aucun poisson Macrouridé n'a été capturé. Les Ophiures sont inhabituellement rares. Les grands carnivores paraissent limités aux Amphipodes et aux Isopodes.

Comparée à d'autres zones de l'Atlantique Nord et du Pacifique, la faune benthique profonde de la Mer de Norvège est plus riche au point de vue densité, mais la richesse en espèces est beaucoup plus faible. La diversité spécifique est vraisemblablement très faible également.

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