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Macrofauna standing stock of the Dogger Bank. A comparison: III. 1950–54 versus 1985–87. A final summary

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ABSTRACT: The macrofauna communities on the Dogger Bank in April/May 1985–87 were compared with those in April/May 1950–54 (Ursin, 1960). Unpublished data from Birkett on the central and western Dogger Bank from April/May 1952–54 were also used for the comparison. The changes in the communities from the fifties to the eighties were made clear by the increasing species numbers and in an increase or dominance of short-living opportunistic species. In contrast, a decrease in long-living bivalves was found. The total biomass in 1985–87 was 2.5 to 8 times higher than in 1950–54. Similarities between stations were below 20 %. Some hypotheses concerning natural and anthropogenic impacts are given to interpret the observed changes.

INTRODUCTION

Long-term changes in benthic communities have been documented for several coastal and nearshore European regions (cf. Pearson & Barnett, 1987). For a long time, offshore regions in the North Sea, such as the Dogger Bank, were expected to be unaffected by anthropogenic environmental changes.

The Dogger Bank is a shallow water area in the southern central North Sea, 300 km long. 8000 years ago, the Bank was the southern border of the North Sea. The depths range between 18 and 40 m.

The basis of this investigation was a comparison between recent data and data by Ursin (1960) on echinoderms, Kirkegaard (1969) on polychaetes, and Petersen (1977) on bivalves. Also unpublished data from Birkett (in Kröncke, 1991) for the western and central Dogger Bank from 1952–54 were used for comparison.

This work was part of the German interdisciplinary project "Biogeochemistry and the distribution of suspended matter in the North Sea and implications to Fisheries Biology" (= TOSCH) investigating the situation in the southern North Sea with respect to the distribution of pollutants in water, sediment, invertebrate macrofauna and fish. Preliminary results have been published by Kröncke (1988, 1990).

MATERIAL AND METHODS

Area of investigation

An example of Ursin's station nets (1960) in April/May 1950–54, the most complete one of 1952, is given in Figure 1a. Due to limitations in ship time in April/May 1985–87, only parts of the total Ursin station map were revisited (Fig. 1b; Table 1). Figure 2 and Table 2 show stations investigated by Birkett in April/May 1952–54.

Table 3 gives the sediment structure of the area under investigation in 1951–52 and 1985–87 as observed by sight, Figure 3 by grain size analysis of samples from July 1986 (Figge, pers. comm.). The depth of the area under investigation ranges from 30 to 35 meters.

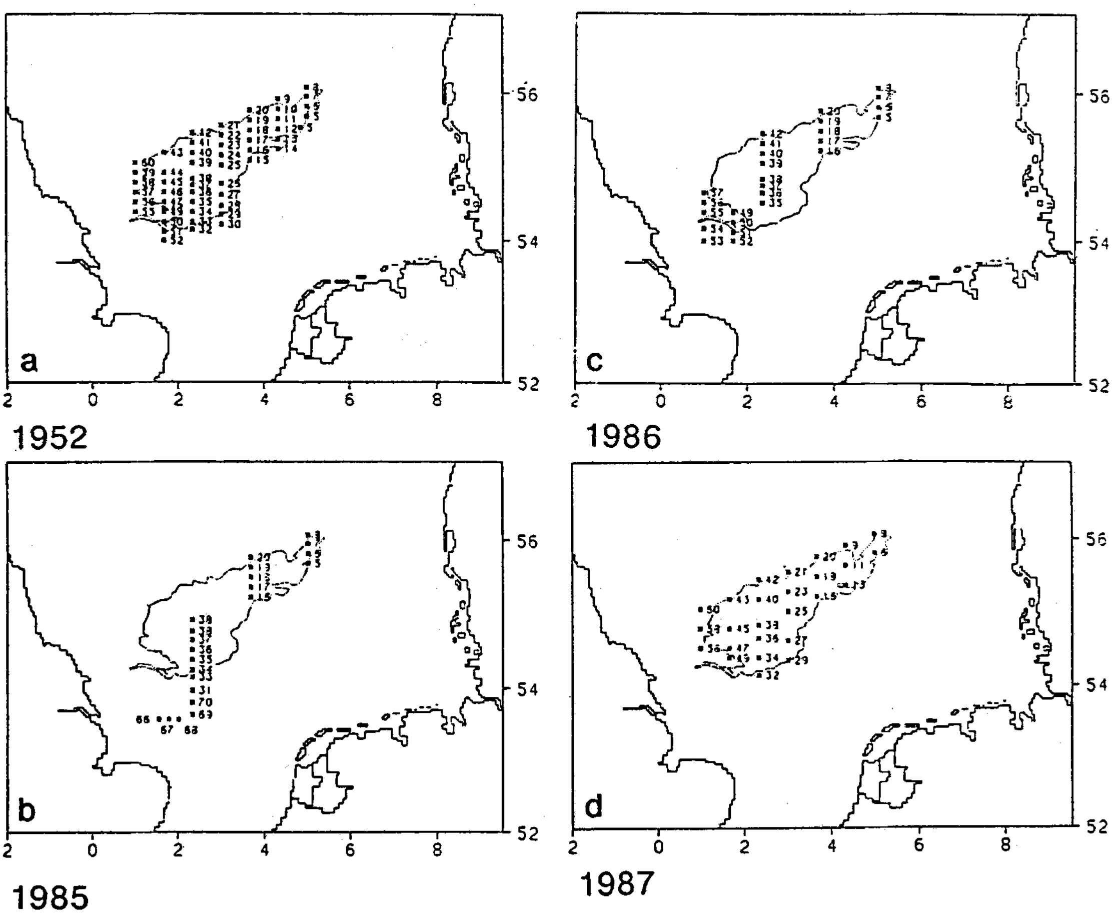


Fig. 1. Station maps. a: Ursin's station map of April/May 1952, as exemplar of the years 1950 to 1954; b, c, d: station maps for April/May 1985 to 1987

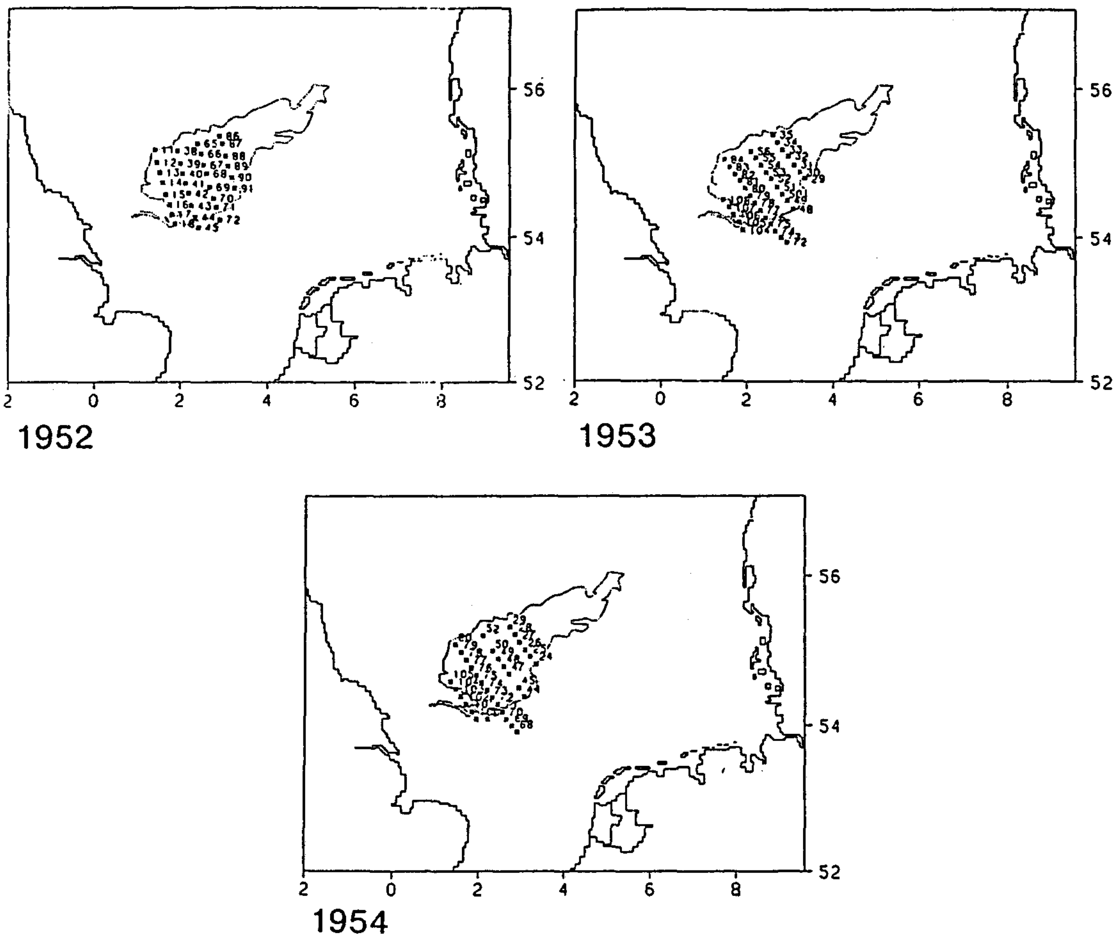


Fig. 2. Birkett's station maps for 1952 to 1954

Sampling

A 0.2 m^2 Van Veen grab was used, similar to that described in Ursin (1960). Ursin's grab weighed 60 kg (Ursin, 1954), whereas the one used in 1985–87 had a weight of 150 kg. A penetration of about 10 cm was achieved, which is a volume of about 10–12 l of sediment. Ursin obtained about 8–10 l in his grabs. Two grabs per station were taken. In contrast to Ursin, who sieved the samples through a mesh of 1.8 mm, a sieve with a mesh size 1 mm was used during the recent investigations. All residue from the sieve was fixed in 4 % formalin buffered with tetraborate. In the laboratory, the samples were stained with rose bengal to aid sorting. Birkett's 0.2 m^2 Van-Veen grab weighed 116 kg; the sieves he used had a mesh size of 1.5 mm.

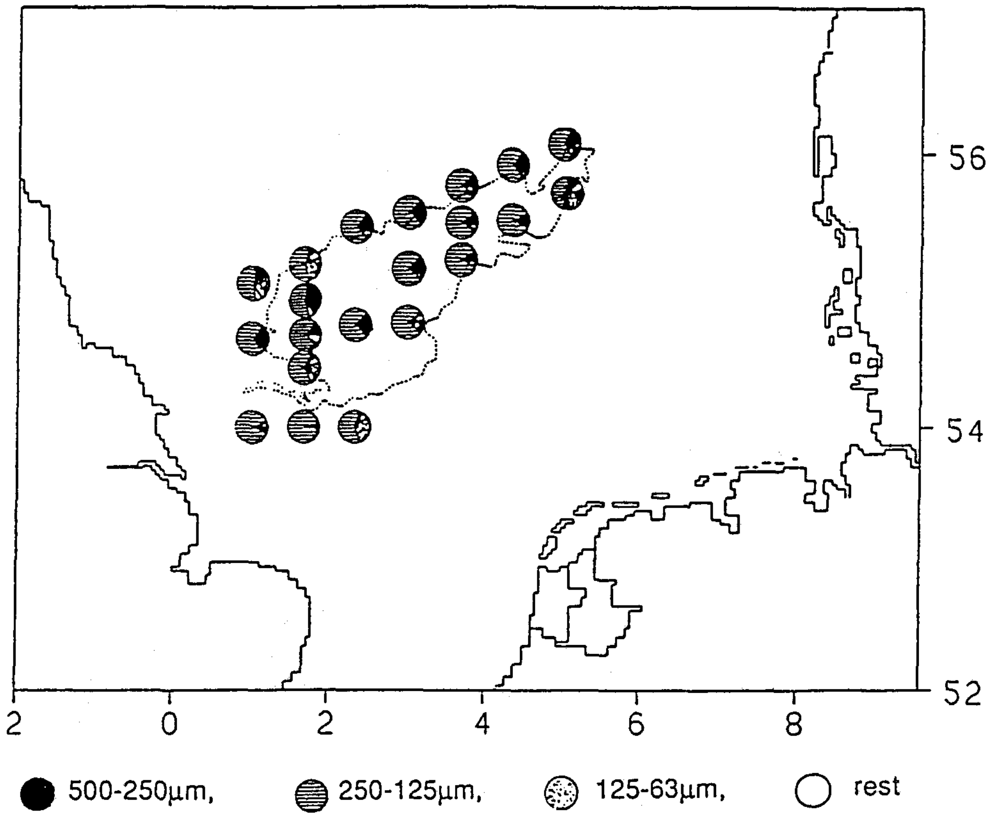


Fig. 3. Sediment classification according to grain size analysis (Figge, pers. comm.)

Methodological comparison

To assess the influence of the different grabs (150 kg = G-150; 90 kg = G-90) and mesh sizes (1.8 mm = M-1.8; 1 mm = M-1) on the comparability of the data, a methodological comparison was carried out in March 1988 at two stations on the Dogger Bank with different sediments: Station 6 with muddy fine sand and Station 18 showing fine sand with shells (Table 3). Five replicates per station were taken of each grab and mesh size. The fine material, washed through 1.8 mm mesh, was collected with the 1 mm mesh to assess the losses of individuals and species numbers using the 1.8 mm mesh.

Biomass

In the recent investigation, the biomass of the samples collected in April/May 1987 only was measured, because during that cruise the most complete station grid was investigated. In the former investigations, the biomass was determined per nautical square (30 × 60 nautical miles) in the North Sea (Petersen, 1977).

Table 1. Station list for April/May 1950–54 (Ursin) and 1985–87

Stat. Nr.	N	E	Depth (m)	Sampling year							
				1950	1951	1952	1953	1954	1985	1986	1987
5	55°40′	05°00′	40	*	*	*	*	*	*	*	
5.1	55°31′	04°51′	40		*	*	*				
6	55°48′	04°51′	34	*	*	*	*	*	*	*	*
7	55°56′	04°51′	37	*	*	*		*	*	*	
8	56°04′	04°51′	43	*	*	*	*	*	*	*	*
9	55°54′	04°20′	43	*	*	*	*	*			*
10	55°46′	04°20′	40	*	*	*	*	*			
11	55°38′	04°20′	32	*	*	*	*	*			*
12	55°30′	04°20′	34	*	*	*	*	*			
13	55°22′	04°20′	42	*	*	*	*	*			*
14	55°14′	04°20′	40		*	*	*	*			
15	55°05′	03°40′	40	*	*	*	*	*	*		
16	55°13′	03°40′	32	*	*	*	*		*	*	*
17	55°21′	03°40′	26	*	*	*	*	*	*	*	
18	55°29′	03°40′	31	*	*	*	*	*	*	*	*
19	55°37′	03°40′	36	*	*	*	*	*	*	*	
20	55°45′	03°40′	47	*	*	*			*	*	*
21	55°33′	03°00′	40	*	*	*	*	*			*
22	55°25′	03°00′	32	*	*	*	*	*			
23	55°17′	03°00′	29	*	*	*	*	*			*
24	55°09′	03°00′	25	*	*	*	*	*			
25	55°01′	03°00′	23		*	*	*	*			*
27	54°37′	03°00′	33	*	*	*	*	*			*
28	54°28′	03°00′	35		*		*	*			
29	54°21′	03°00′	39	*		*	*	*			*
30	54°13′	03°00′	42			*	*				
31	54°00′	02°20′	50								*
32	54°09′	02°20′	51		*	*					*
33	54°15′	02°20′	30		*	*			*		
34	54°23′	02°20′	27		*	*			*		
35	54°31′	02°20′	20		*	*			*	*	
36	54°39′	02°20′	18		*	*			*	*	*
37	54°45′	02°20′	22		*	*			*	*	
38	54°50′	02°20′	27		*	*			*	*	*
39	55°03′	02°20′	35		*	*				*	
40	55°11′	02°20′	32		*	*				*	*
41	55°19′	02°20′	37		*	*				*	
42	55°27′	02°20′	44		*	*				*	*
43	55°11′	01°40′	36		*	*					*
45	54°47′	01°40′	23		*	*					*
46	54°39′	01°40′	20	*	*	*	*	*			
47	54°31′	01°40′	18		*	*					*
49	54°23′	01°40′	48		*	*				*	*
50	54°15′	01°40′	48		*	*				*	
51	54°07′	01°40′	68		*	*				*	
52	54°00′	01°40′	37			*				*	
53	54°00′	01°00′	46							*	
54	54°10′	01°00′	45							*	
55	54°23′	01°00′	46		*	*				*	
56	54°31′	01°00′	55		*	*				*	*
57	54°39′	01°00′	60		*	*				*	
58	54°47′	01°00′	50		*	*					*
60	55°03′	01°00′	61		*	*					*

Table 2. Birkett's station list for 1952–1954

1952 Stat. Nr.	N	E	1954 Stat. Nr.	N	E
11	55° 09′	01° 25′	26	55° 00′	03° 06′
12	54° 59′	01° 27′	27	55° 06′	02° 58′
13	54° 51′	01° 31′	28	55° 12′	02° 52′
14	54° 43′	01° 35′	29	55° 18′	02° 44′
15	54° 33′	01° 39′	44	54° 23′	03° 04′
16	54° 25′	01° 44′	45	54° 30′	02° 57′
17	54° 17′	01° 48′	47	54° 41′	02° 43′
18	54° 10′	01° 52′	48	54° 47′	02° 36′
38	55° 08′	01° 56′	49	54° 53′	02° 28′
39	54° 58′	02° 00′	50	54° 59′	02° 20′
40	54° 50′	02° 03′	51	54° 05′	02° 13′
41	54° 42′	02° 07′	52	55° 11′	02° 06′
42	54° 34′	02° 11′	68	53° 56′	02° 55′
43	54° 24′	02° 15′	69	54° 00′	02° 48′
44	54° 15′	02° 20′	70	54° 05′	02° 40′
45	54° 07′	02° 25′	71	54° 11′	02° 34′
65	55° 14′	02° 24′	72	54° 17′	02° 27′
66	55° 06′	02° 29′	73	54° 22′	02° 19′
67	54° 57′	02° 32′	74	54° 28′	02° 12′
68	54° 50′	02° 36′	75	54° 34′	02° 04′
69	54° 39′	02° 40′	76	54° 40′	01° 57′
70	54° 30′	02° 45′	77	54° 46′	01° 50′
71	54° 23′	02° 49′	78	54° 52′	01° 43′
72	54° 13′	02° 54′	79	54° 58′	01° 36′
86	55° 20′	02° 53′	80	55° 04′	01° 28′
87	55° 14′	02° 58′	100	54° 05′	01° 57′
88	55° 04′	03° 02′	101	54° 11′	01° 50′
89	54° 56′	03° 05′	102	54° 17′	01° 42′
90	54° 47′	03° 10′	103	54° 23′	01° 35′
91	54° 38′	03° 14′	104	54° 29′	01° 28′
			105	54° 35′	01° 21′
1953 Stat. Nr.	**N**	**E**			
29	54° 48′	03° 21′	74	54° 05′	02° 40′
30	54° 53′	03° 14′	75	54° 11′	02° 33′
31	54° 59′	03° 06′	76	54° 16′	02° 26′
32	55° 06′	02° 58′	77	54° 22′	02° 19′
33	55° 11′	02° 50′	78	54° 28′	02° 11′
34	55° 17′	02° 43′	79	54° 34′	02° 05′
35	55° 23′	02° 36′	80	54° 50′	01° 58′
48	54° 23′	03° 04′	81	54° 46′	01° 51′
49	54° 30′	02° 56′	82	54° 51′	01° 44′
50	54° 35′	02° 49′	83	54° 57′	01° 36′
51	54° 51′	02° 42′	84	55° 03′	01° 29′
52	54° 48′	02° 34′	104	54° 06′	01° 55′
53	54° 53′	02° 27′	105	54° 12′	01° 49′
54	54° 59′	02° 20′	106	54° 18′	01° 41′
55	55° 05′	02° 13′	107	54° 24′	01° 35′
56	55° 10′	02° 06′	108	54° 30′	01° 27′
72	53° 57′	02° 56′			
73	54° 00′	02° 48′			

Table 3. Sediment types for 1950–1954 (Ursin) and 1985–1987

Stat. Nr.	(m)	1950–1954	1985–1987
5	40	Fine sand	Fine sand
6	34	Fine sand	Fine sand
7	37	Fine sand	Fine sand
8	43	Coarse sand, stones	Fine sand
9	4	Fine sand, dead shells	Fine sand, dead shells
11	32	Fine sand, dead shells	Fine sand, dead shells
13	42	Muddy fine sand	Fine sand, dead shells
15	40	Muddy fine sand	Fine sand, dead shells
16	32	Fine sand	Fine sand, dead shells
17	26	Fine sand, dead shells	Fine sand, dead shells
18	31	Fine sand, dead shells	Fine sand, dead shells
19	36	Fine sand, dead shells	Fine sand, dead shells
20	47	Fine sand, dead shells	Fine sand
21	40	Fine sand, dead shells	Fine sand, dead shells
23	29	Fine sand, dead shells	Fine sand, dead shells
25	23	Fine sand, dead shells	Fine sand, dead shells
27	33	Muddy fine sand	Fine sand, dead shells
29	39	Muddy fine sand	Fine sand, dead shells
31	50	Muddy fine sand	Muddy fine sand
32	51	Mud. f. s., dead shells, stones	Fine sand
33	30	Coarse sand	Fine sand
34	27	Coarse sand	Fine sand, dead shells
35	20	Fine sand, dead shells	Fine sand, dead shells
36	18	Fine sand, dead shells	Fine sand, dead shells
37	22	Fine sand, dead shells	Fine sand, dead shells
38	27	Fine sand, dead shells	Fine sand, dead shells
39	35	Fine sand, dead shells	Fine sand, dead shells
40	32	Fine sand, dead shells	Fine sand, dead shells
41	37	Fine sand, dead shells	Fine sand, dead shells
42	44	Fine sand	Fine sand, dead shells
43	36	Fine sand	Fine sand, dead shells
45	23	Coarse sand, stones	Fine sand
47	18	Fine sand	Fine sand
49	48	Muddy fine sand	Fine sand
50	48	Muddy fine sand	Fine sand
51	68	Muddy fine sand	Fine sand
52	37	Muddy fine sand	Muddy fine sand
53	46	Muddy fine sand	Muddy fine sand
54	45	Muddy fine sand	Muddy fine sand
55	46	Fine sand	Muddy fine sand
56	55	Muddy fine sand	Muddy fine sand
57	60	Muddy fine sand	Muddy fine sand
58	50	Muddy fine sand	Muddy fine sand
60	61	Muddy fine sand	Muddy fine sand

To determine the total biomass, the ash-free dry weight (24 h at 80 °C and 6 h at 480 °C, respectively) of organisms was determined. Using the conversion rates for wet weight and ash-free dry weight given by Salzwedel et al. (1985), the total wet weight per nautical square was determined.

Cluster analyses

The cluster analyses were performed with the "percentage similarity" coefficient after Whittaker & Fairbanks (1958), where $\dot{s} = \Sigma \min p_i(x\log_2)$, p_i = percentage species abundance.

Similarities between stations

The percentage species similarity defined as $(c \times 100)/(a + b - c)$ (Greig-Smith, 1964), where a = the number of species present in the first sample, b = the number of species present in the second sample, and c = the number of common species present in both samples, deals with the absence and presence of species per station. Concerning the different species abundances per station, the similarity coefficient of Whittaker & Fairbanks (1958) was also used.

Abundance-Biomass-Comparison curves

For this method, introduced by Warwick (1986), the species are ranked in order of importance on the x-axis (logarithmic scale) with percentage dominance on the y-axis (cumulative scale).

Under stable undisturbed conditions, the biomass is dominated by a few large species, each represented by few individuals. In this case, the biomass curve is above the abundance curve. Under moderate disturbances, the large dominants are eliminated from the community, and the inequality in size between the numerical and biomass dominants is reduced. The ABC curves are close together. As disturbance becomes more severe, benthic communities become dominated numerically by small species. Then the abundance curve moves above the biomass curve.

RESULTS

Sediment comparison

Table 3 shows the sediment characterization, judged by sight, during the periods 1950–54 (only Ursin) and 1985–87. During both investigations, the sediments of the Dogger Bank proper were characterized as fine sands with a varying amount of dead shells, whereas the sediments of the deeper parts were said to be muddy fine sands. Discrepancies are limited to stations 8, 33, 34 and 45, with Ursin finding coarse sands and myself finding fine sands. Figure 3 confirms that sediments of the Dogger Bank proper were mainly fine sands, whereas at greater depths muddy sands were found.

Methodological comparison

Different grab weights

In comparing the different grab weights (G-90 and G-150), no differences regarding the percentage of individuals per species (Fig. 4), presence/absence of species (Table 4), species numbers (Table 5) and diversities and evenness (Table 6), could be discerned between station 6 with muddy fine sands and station 18 with fine sands, using several

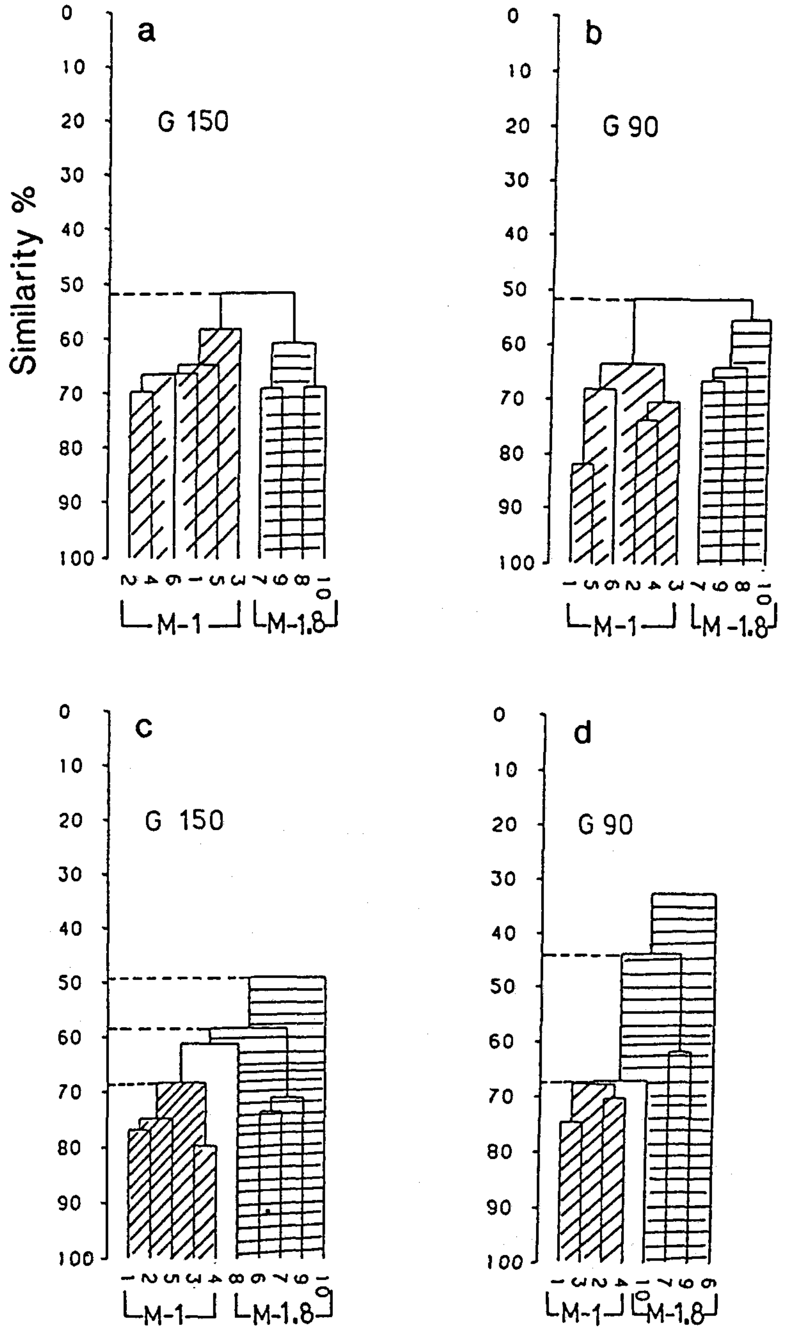


Fig. 4. Similarities between samples sieved over the mesh sizes 1 mm (M-1) and 1.8 mm (M-1.8) and between samples taken with grab weights of 150 kg (G-150) and of 90 kg (G-90) at station 6 (a, b) and 18 (c, d)

Table 4. Similarities (%, Greig-Smith coefficient) between samples taken with grabs of different weights (150 kg = G-150 and 90 kg = G-90) and sieved over different mesh sizes (1 mm = M-1 and 1.8 mm = M-1.8)

Station 6	G-150/M-1	G-150/M-1.8	G-90/M-1	G-90/M-1.8
G-150/M-1	37.5	40.3	38.0	35.3
G-150/M-1.8		38.7	36.5	34.7
G-90/M-1			40.5	37.9
G-90/M-1.8				34.4
Station 18	**G-150/M-1**	**G-150/M-1.8**	**G-90/M-1**	**G-90/M-1.8**
G-150/M-1	53.3	51.7	42.3	44.8
G-150/M-1.8		55.4	45.8	44.6
G-90/M-1			46.3	45.1
G-90/M-1.8				46.2

Table 5. Significance of difference in species numbers due to different grab weights (G-150 and G-90) and mesh sizes 1 mm and 1.8 mm (M-1 and M-1.8). ns = not significant

	G-150/M-1	G-150/M-1.8	G-90/M-1	G-90/M-1.8	a
Stat. 6	*	*			ns
		*		*	ns
			*	*	ns
	*		*		ns
Stat. 18	*	*			<0.01
		*		*	ns
			*	*	<0.01
	*		*		ns

methods. All calculations showed that the natural variation within the 5 replicates taken per grab was similar to the variation which occurred when different grab weights were used.

Different mesh sizes

The community structure was not affected by using different mesh sizes (Fig. 5; Table 4), nor did species numbers (Table 5), diversities and evenness (Table 6) show any significant differences. Again, the natural variation within the 5 replicates sieved per mesh size was similar to that using different mesh sizes. One significant difference using the two mesh sizes was the loss of small individuals through the bigger mesh size M-1.8 during 1950–54. It appeared that almost all of the amphipods were lost through the M-1.8. Therefore, this order was disregarded in the long-term comparison. For other ecologically important species or for species which had been found to increase in occurrence during the eighties, the individual numbers in 1985–87 were corrected by the loss through mesh size 1.8 mm (M-1.8) (Table 7). Only corrected data were used for the long-term comparison.

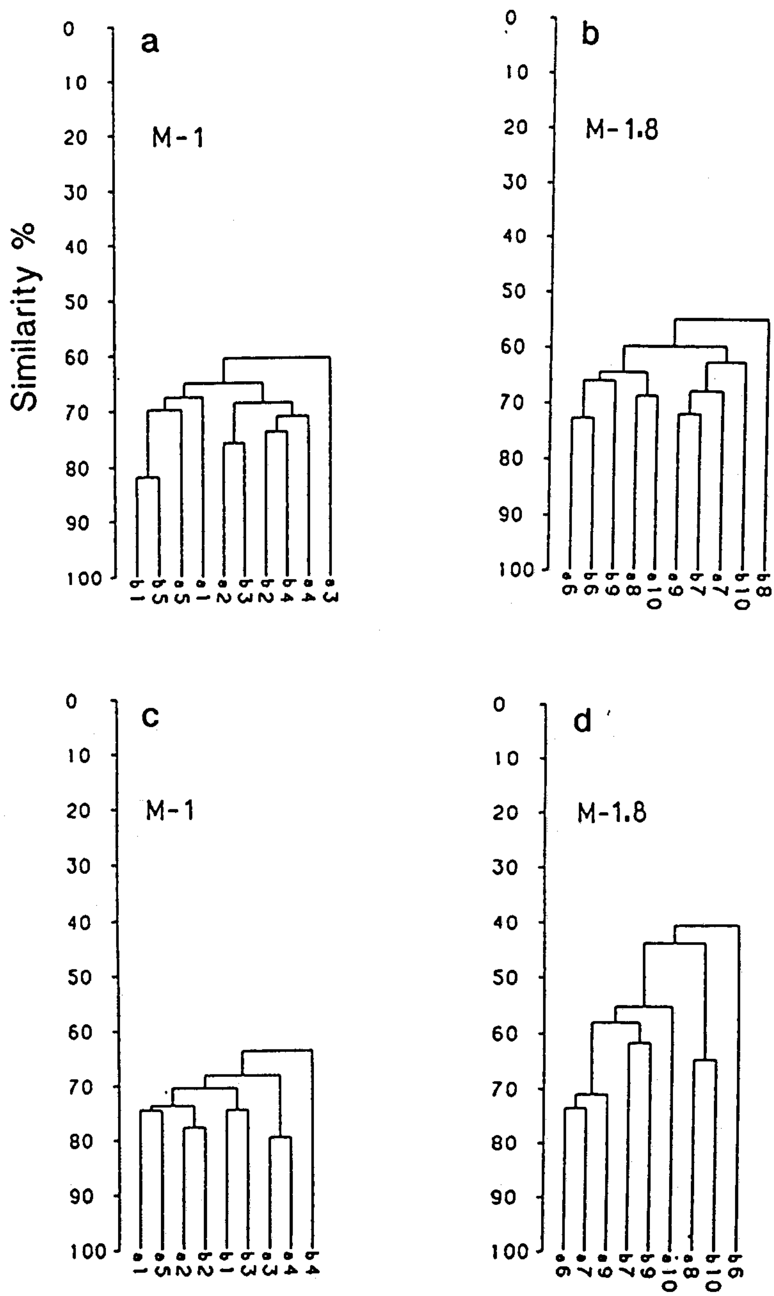


Fig. 5. Similarities between samples (a taken with G-150, b with G-90) sieved over mesh size 1 mm (M-1) and 1.8 mm (M-1.8) at station 6 (a, b) and 18 (c, d)

Table 6. Mean diversities (H) and evenness (J) for M-1, M-1.8, G-150 und G-90 of samples from stations 6 and 18

Station	6		18	
	H	J	H	J
G-150/M-1	3.4	0.7	4.0	0.8
G-150/M-1.8	3.6	0.9	4.2	0.9
G-90/M-1	3.5	0.8	4.0	0.8
G-90/M-1.8	3.6	0.8	3.7	0.8

The methodological comparison had been completed before the unpublished data of Birkett became available. Since Birkett employed intermediate grab weight (116 kg) and mesh size (1.5 mm), his results fall into the same range of similarities observed when using the sampling techniques of Ursin and myself.

Faunistic comparison

The following results refer only to polychaetes, echinoderms and bivalves.

Species numbers, diversities and evenness

During the fifties, the mean species numbers were 12 to 14 per 0.2 m^2 (Tables 8, 9). In 1985–87, I found 23 to 29 per 0.2 m^2. The mean diversities calculated from Ursin's data range between 2.5 and 2.7 (Table 10); those calculated from Birkett's data amount to 2.9 (Table 9). During the eighties the mean diversities ranged between 3.2 and 3.4 (Table 10).

During 1950–54 the mean evenness was 0.8 (Tables 9, 11), whereas during 1985–87 an evenness of 0.7 was calculated (Table 11).

Species abundance

Comparison of the abundance data between the fifties and the eighties (Table 12) revealed a considerable increase in numbers of the opportunistic short-living, deposit-feeding polychaetes such as *Nephtys cirrosa, Spiophanes bombyx* and *Scoloplos armiger*, the ophiurid *Amphiura filiformis* and the bivalve *Montacuta bidentata*. Similarly, the individual numbers of the carnivorous polychaetes, e.g. the genus *Nephtys* and *Goniada maculata*, increased. Other short-living, deposit-feeding species such as the bivalves *Abra prismatica* and *Tellina fabula*, and the polychaetes *Chaetozone setosa* and *Magelona* spp. showed similar abundances. In contrast, the individual numbers of long-living bivalves such as *Ensis ensis, Mactra c. cinerea* and *Spisula subtruncata* decreased. During the eighties, the sea-urchin *Echinocardium cordatum* occurred in the same numbers as during the fifties.

Cluster analyses

The cluster analyses derived from Ursin's (1951/52), Birkett's (1953/54) and my data (1985–87) resulted in two main communities: one on the Dogger Bank proper and another one at its south-western boundary (Fig. 6).

Table 7. Constant occurrence (K), individual numbers (NI m^{-2}), percentage of loss (L) through meshsize 1.8 mm and converted individual numbers for 1985–87 (NI*) for species which went into the long-term comparison

	1985				1986				1987			
Stations per cruise	22				26				26			
Species	K (%)	NI m^{-2}	L (%)	NI* m^{-2}	K (%)	NI m^{-2}	L (%)	NI* m^{-2}	K (%)	NI m^{-2}	L (%)	NI* m^{-2}
Chaetozone setosa	77	20	70	6	85	11	70	3	85	13	70	4
Goniada maculata	77	21	30	15	69	15	30	10	88	19	30	13
Magelona spp.	91	80	50	40	85	45	50	22	96	47	50	24
Nephtys hombergii	91	28	30	19	85	17	30	12	100	23	30	16
Nephtys caeca	64	32	40	19	69	14	40	9	73	7	40	3
Nephtys cirrosa	55	42	45	23	54	22	45	12	54	40	45	22
Nephtys longosetosa	9	18	15	15	–	–	–	–	38	6	15	5
Ophelia limacina	73	113	55	51	65	28	55	13	69	52	55	23
Owenia fusiformis	68	41	30	21	81	42	30	21	69	44	50	22
Spiophanes bombyx	86	141	33	95	96	182	33	122	92	281	33	189
Abra prismatica	36	22	80	4	77	23	80	5	88	46	80	9
Cultellus pellucidus	46	10	0	10	23	4	0	4	73	13	0	13
Donax vittatus	5	3	0	3	12	40	0	40	15	12	0	12
Ensis ensis	18	4	0	4	31	5	0	5	23	7	0	7
Gari fervescens	36	7	80	1	42	4	80	1	50	6	80	1
Mactra c. cinerea	9	17	0	17	12	3	0	3	8	4	0	4
Mysella bidentata	41	43	60	17	69	39	60	16	65	66	60	26
Montacuta ferruginosa	27	6	20	5	31	5	20	4	62	9	20	7
Spisula subtruncata	5	13	40	8	8	3	40	2	27	6	40	4
Tellina fabula	73	44	10	40	85	46	10	41	58	88	10	79

Table 8. Mean species number for 1985–1987 and 1950–1954 (Ursin)

Stat.	Species number/0.2 m^2			Species number/0.2 m^2				
	1985	1986	1987	1950	1951	1952	1953	1954
5	28	30		7	3	19	15	12
6	18	24	34	14	18	11	6	15
7	33	26		9	12	18	11	16
8	24	18	34	4	21	4	6	7
9			36	13	15	19	20	11
11			31	15	12	13	9	16
13			33	16	11	13	13	12
16	23	23	26	7	15	12	9	
17	28	24		6	10	9	9	5
18	27	32	25	2	12	21	8	8
19	23	29		2	16	19	11	12
20	31	26	34	3	20	16		
21			32	4	20	19	19	10
23			35	9	10	10	4	9
25			22	8	3	9	3	3
27			38	7	6	8	8	9
29			29	6		15	12	4
32			25		9	14		
33	22				18	8		
34	23		30		4	14		
35	22	15			10	9		
36	15	24	17		8	9		
37	18	20			8	9		
38	19	21	25		5	3		
39		27			10	16		
40		27	32		8	9		
41		34			14	19		
42		30	33		14	9		
43			33		17	17		
45			20		7	7		
47			19		10	9		
49		29	30		23	20		
50			23		12	12		
51		18			19	17		
52		12			10	9		
55		22			10	14		
56		22	29		9	23		
57		27			7	17		
58					6	15		
60					18	12		

In the fifties (Ursin), the Dogger Bank proper community was dominated by suspension feeding polychaetes such as *Myriochele oculata* and *Owenia fusiformis*, long-living bivalves such as *Spisula subtruncata* and *Spisula elliptica*, and ophiurids such as *Ophiura albida* and *Acrocnida brachiata* (Fig. 6; Table 13). During the eighties, however, this community was dominated by opportunistic, short-living polychaetes, bivalves and the ophiurid *Amphiura filiformis*. Birkett found the polychaetes *Magelona* spp., *Scololepis*

Table 9. Species numbers, diversities and evenness for Birkett's data

Stat. Nr.	N. of species	H	J	Stat. Nr.	N. of species	H	J	Stat. Nr.	N. of species	H	J
11	17	3.8	0.9	29	15	3.3	0.9	24	18	3.6	0.9
12	16	3.2	0.8	30	19	3.4	0.8	25	13	2.8	0.7
13	11	2.3	0.7	31	19	2.1	0.5	26	11	3.2	0.9
15	3	1.6	1	32	22	2	0.5	27	5	2.2	0.9
16	6	2.5	1	33	15	1.2	0.3	28	14	3.5	0.9
17	10	3.2	1	34	16	3.1	0.8	29	15	3.6	0.9
38	17	3.6	0.9	35	21	3.8	0.9	44	13	2.9	0.8
39	7	2.4	0.9	48	18	3.7	0.9	45	11	3	0.9
40	16	3.8	0.9	49	22	3.5	0.8	47	12	3.5	1
41	7	2.6	0.9	50	12	2.3	0.6	48	7	2.4	0.9
42	5	2.1	0.9	51	18	1.5	0.4	49	17	3.7	0.9
43	17	3.5	0.9	52	11	2.6	0.7	50	19	3.1	0.7
44	7	2.2	0.8	53	17	3.6	0.9	51	15	3.5	0.9
45	6	1.3	0.5	54	8	2.1	0.7	52	23	4	0.9
66	15	3.5	0.9	55	19	3.8	0.9	68	13	2.7	0.7
67	21	3.6	0.8	56	24	4	0.9	69	10	2.4	0.7
68	13	3.2	0.9	72	19	3.2	0.7	70	11	3.1	0.9
69	13	2.7	0.7	73	15	3.1	0.8	71	14	3.1	0.8
70	6	2.3	0.9	74	7	2.6	0.9	72	11	3.3	1
71	11	3	0.9	75	2	0.7	0.7	73	11	2.9	0.8
72	14	2.8	0.7	76	10	2.7	0.8	74	19	4	0.9
86	14	2.6	0.7	77	14	2.4	0.6	75	11	3.2	0.9
87	23	3.9	0.9	78	14	3.4	0.9	76	12	2.9	0.8
88	11	2.8	0.8	79	15	3.6	0.9	77	12	3.5	1
89	12	3.2	0.9	80	13	3.4	0.9	78	15	2.6	0.7
90	14	2	0.5	81	5	2.3	1	79	18	3.5	0.8
91	16	3.7	0.9	82	9	2.1	0.7	80	10	3.1	0.9
				83	19	3.7	0.9	100	11	2.8	0.8
				84	16	3.9	1	101	7	2.6	0.9
				104	13	3.4	0.9	102	20	3.8	0.9
				105	15	3.6	0.9	103	18	3.2	0.8
				106	16	3.4	0.9	104	16	3.4	0.9
				107	17	3.4	0.8	105	43	4.9	0.9
				108	10	2.9	0.9				

Table 10. Mean diversities for 1985–1987 and 1950–1954 (Ursin)

Stat.	Diversity/m²			Diversity/m²				
	1985	1986	1987	1950	1951	1952	1953	1954
5	3.4	4.1		2.1	0.6	3.0	2.7	3.2
6	3.2	3.5	3.4	3.6	3.6	2.8	2.0	1.7
7	3.8	2.5		2.9	1.3	1.6	2.8	3.8
8	3.9	3.7	3.4	2.0	2.0	1.8	2.5	2.4
9			4.0	3.0	3.3	2.3	1.6	1.4
11			4.0	3.3	2.7	3.4	3.1	3.5
13			3.4	3.2	2.4	2.0	3.3	1.3
16	2.1	3.1	3.5	2.5	2.3	3.1	3.1	
17	3.8	2.9		2.4	3.1	2.2	2.9	2.2
18	3.5	3.2	3.9	1.0	2.7	3.9	2.5	2.9
19	3.3	3.0		1.0	3.1	3.4	3.0	3.1
20	3.5	3.8	3.6	1.4	3.5	3.4		
21			2.8	1.9	3.4	3.3	4.1	3.2
23			3.2		2.9	3.0	1.8	3.0
25			4.0	2.9	1.5	2.8	0.2	1.6
27			4.1	2.3	2.4	2.8	2.2	2.5
29			2.9	1.7		3.6	3.0	1.0
32			3.0		0.6	3.1		
33	2.8				3.4	1.9		
34	3.4		3.3		1.8	3.3		
35	3.2	2.9			2.6	2.9		
36	3.1	3.4	3.1		2.8	2.7		
37	3.2	3.1			2.9	2.8		
38	3.2	3.4	4.1		1.7	1.5		
39		3.7			2.6	3.1		
40		3.5	3.3		2.5	3.0		
41		2.9			3.6			
42		2.8	3.0		3.0	3.0		
43			1.6		3.5	3.6		
45			3.2		2.7	2.1		
47			3.4		3.1	2.9		
49		2.6	3.3		3.3	3.6		
50		3.5			2.4	1.6		
51		2.2			2.8	3.0		
52		3.0				2.9		
55		3.0			3.1	3.0		
56		3.8	3.5		2.6	3.6		
57		3.8			1.6	2.7		
58			3.8		1.6	2.4		
60			4.4		3.6	3.2		

ciliata and *Chaetozone setosa* in higher abundances than Ursin did, in combination with generally low species numbers; thus, these species dominated his community. The remaining species composition is also different from the recent one.

In all the investigations, the community at the south-western border was dominated by *Amphiura filiformis*. In the recent community, more short-living species became dominant than in the fifties.

Table 11. Mean evenness for 1985–1987 and 1950–1954 (Ursin)

Stat.	Evenness/m^2			Evenness/m^2				
	1985	1986	1987	1950	1951	1952	1953	1954
5	0.7	0.8		0.8	0.4	0.7	0.9	0.9
6	0.8	0.8	0.7	0.9	0.9	0.8	0.8	0.4
7	0.8	0.5		0.9	0.4	0.4	0.8	1.0
8	0.8	0.9	0.7	1.0	0.4	0.9	1.0	0.9
9			0.8	0.8	0.9	0.5	0.4	0.4
11			0.8	0.9	0.8	0.9	1.0	0.9
13			0.7	0.8	0.7	0.5	0.9	0.4
16	0.5	0.7	0.7	0.9	0.6	0.9	1.0	0.3
17	0.8	0.6		0.9	0.9	0.7	0.9	0.9
18	0.7	0.6	0.8	1.0	0.7	0.9	0.9	1.0
19	0.7	0.6		1.0	0.8	0.8	0.9	0.9
20	0.8	0.8	0.7	0.9	0.8	0.9		
21			0.6	1.0	0.8	0.8	1.0	1.0
23			0.6	1.0	0.9	0.9	0.9	1.0
25			0.9	1.0	1.0	0.9	0.1	1.0
27			0.8	0.8	0.9	0.9	0.7	0.8
29			0.6	0.7		0.9	0.9	1.0
32			0.7		0.2	0.8		
33	0.6				0.8	0.6		
34	0.8		0.7		0.9	0.9		
35	0.7	0.8			0.8	0.9		
36	0.8	0.8	0.8		0.9	0.9		
37	0.8	0.7			1.0	0.9		
38	0.8	0.8	0.9		0.7	0.9		
39		0.8			0.8	0.8		
40		0.7	0.7		0.8	1.0		
41		0.6			1.0	0.9		
42		0.6	0.6		0.8	1.0		
43			0.3		0.9	0.9		
45			0.8		1.0	0.7		
47			0.8		0.9	0.9		
49		0.5	0.7		0.7	0.8		
50		0.8			0.7	0.5		
51		0.5			0.7	0.7		
52		0.8				0.9		
55		0.7			0.9	0.8		
56		0.8	0.7		0.8	0.8		
57		0.8			0.6	0.7		
58			0.7		0.6	0.6		
60			0.8		0.9	0.9		

Only in 1985–87 was a separate community observed to occur in the northeastern part that was characterized by the presence of the polychaetes *Ophelia limacina* and *Goniada maculata*, species that were predominant in the earlier investigations on the whole Dogger Bank.

Table 12. Mean individual numbers per m² (NI) from the Danish (D), Birkett's (B), and the 1985–1987 investigations

Species / Stations per cruise	1951 (D) 50 NI/m²	1952 (D) 54 NI/m²	1952 (B) 55 NI/m²	1953 (B) 72 NI/m²	1985 22 NI/m²	1986 26 NI/m²	1987 26 NI/m²	
Chaetozone setosa	9	5	–	16	6	3	4	=
Goniada maculata	11	9	9	8	15	10	13	+
Magelona spp.	6	6	23	25	40	22	24	=
Nephtys hombergii	10	15	–	–	19	12	16	=
Nephtys caeca	6	6	–	–	19	9	3	+
Nephtys cirrosa	10	6	15	15	23	12	22	+
Nephtys longosetosa	7	8	–	–	15	–	23	+
Ophelia limacina	33	22	28	11	51	13	23	=
Owenia fusiformis	17	17	5	7	8	5	12	–
Scoloplos armiger	10	10	–	–	21	21	22	+
Spiophanes bombyx	6	6	–	–	95	122	189	++
Abra prismatica	8	15	5	18	4	5	9	=
Cultellus pellucidus	10	9	19	7	10	4	13	=
Donax vittatus	5	15	12	14	3	40	12	=
Ensis ensis	10	14	21	19	4	5	7	–
Gari fervescens	5	6	29	6	1	1	1	–
Mactra c. cinerea	5	8	7	393	17	3	4	–
Mysella bidentata	7	35	10	13	17	16	26	+
Montacuta ferruginosa	6	10	8	8	5	4	7	=
Spisula subtruncata	65	203	32	8	8	2	4	–
Tellina fabula	47	2	41	47	40	41	79	=
Amphiura filiformis	123	72	8	9	67	121	355	+
Echinocardium cordatum	14	13	13	14	9	13	18	=

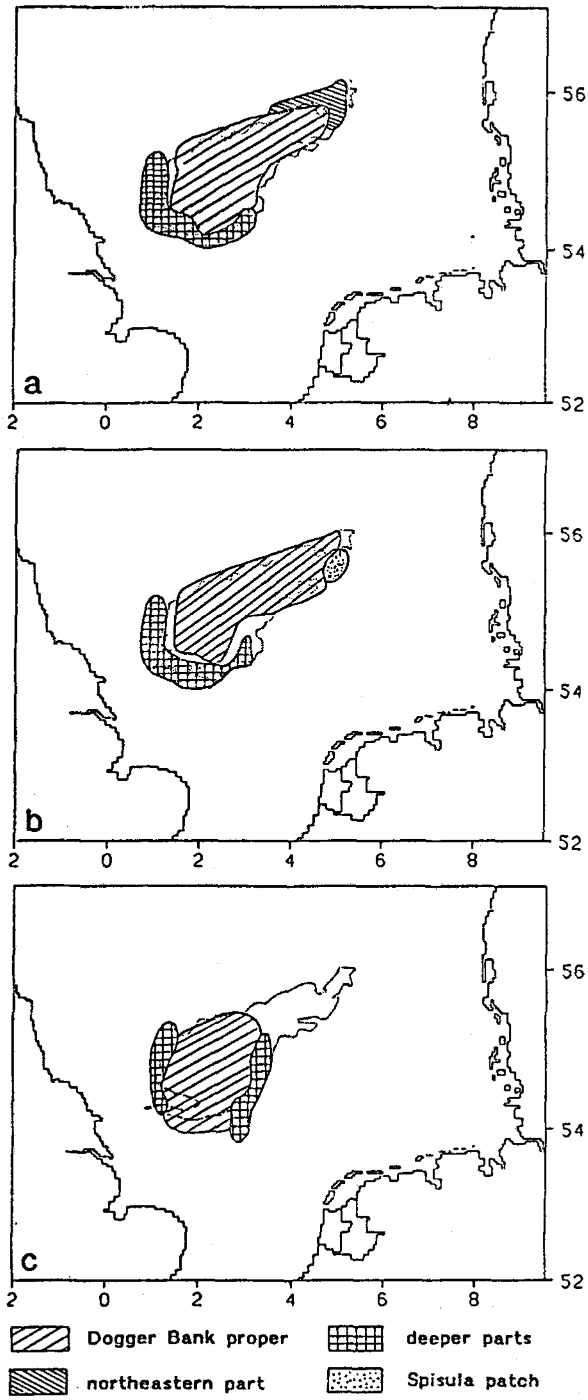


Fig. 6. Macrofauna communities in (a) 1985–87, (b) 1951–52 after Ursin and (c) 1953–54 after Birkett

Table 13. Ten dominant species within the communities in the Dogger Bank area

1985–1987	1951–1952 (Danish)	1953–1954 (Birkett)
Dogger Bank proper	Dogger Bank proper	Dogger Bank proper
Spiophanes bombyx	*Myriochele oculata*	*Magelona* spp.
Paraonis fulgens	*Acrocnida brachiata*	*Scolelepis ciliata*
Amphiura filiformis	*Tellina fabula*	*Chaetozone setosa*
Nucula tenuis	*Ophiura albida*	*Nepthys* spp.
juv. *Ophiuroidea*	*Ophelia limacina*	*Glycinde nordmanni*
Phoronis spp.	*Spisula subtruncata*	*Ophelia limacina*
Tellina fabula	*Echinocyamus pusillus*	*Eteone lactea*
Scoloplos armiger	*Owenia fusiformis*	*Anaitides subulifera*
Magelona spp.	*Spisula elliptica*	*Myriochele oculata*
Donax vittatus	*Goniada maculata*	*Anaitides maculata*
Deeper Parts	Deeper Parts	Deeper Parts
Amphiura filiformis	*Amphiura filiformis*	*Magelona* spp.
juv. *Amphiura*	*Acrocnida brachiata*	*Scolelepis ciliata*
Montacuta bidentata	*Amphiura chiajei*	*Nephtys* spp.
Pholoe minuta	*Lumbrinereis* spp.	*Myriochele oculata*
juv. *Ophiuroidea*	*Pectinaria auricoma*	*Pectinaria auricoma*
Phoronis spp.	*Echinocardium cordatum*	*Glycinde nordmanni*
Spiophanes bombyx	*Montacuta bidentata*	*Eumida sanguinea*
Thyasira flexuosa	*Tellina fabula*	*Eteona lactea*
Nucula nitida	*Nucula nitida*	*Ophelia limacina*
Nucula tenuis	*Echinocyamus ousillus*	*Owenia fusiformis*
Northeastern part		
Spiophanes bombyx		
Ophelia limacina		
juv. *Ophiuroidea*		
Scoloplos armiger		
Abra prismatica		
Phoronis spp.		
Goniada maculata		
Myriochele oculata		
Thracia phaeseolina		
Amphiura filiformis		

Biomass

In 1987, the total biomass in most of the nautical squares was 2.5 to 8 times higher than in 1950–54 (Fig. 7); however, a reduction in biomass of 30 % was found for the northeastern squares. Polychaetes doubled their biomass within the last 30 years. The biomass of echinoderms increased 3 to 5 times on the central Dogger Bank, and 7 to 15 times in the southern nautical squares. In the northeastern squares, it decreased as their total biomass did. Mollusca biomass increased 2- to 5-fold, except in the northeastern squares where it decreased by about 30 %.

Similarities between stations

A mean similarity of only 17.4 % between Ursin's and the recent data (Table 14) for the whole Dogger Bank was calculated by the presence/absence of species (Greig-Smith, 1964). Similarities per species between the present and Ursin's data set varied from 7 to 23 %; between the present and Birkett's set from 9 to 13 % (Figs 8, 9).

Abundance-Biomass-Comparison curves

Although no biomass data per species exist for the fifties, the ABC-method was applied to assess the amount of biological disturbance in the communities of the Dogger Bank during the eighties. Figures 10 and 11 give the abundance (A) and biomass (B) per species for several stations in 1985 and 1986. Most of the curves indicate undisturbed communities, but in both years the curves for stations 16 and 18 from the northeastern Dogger Bank are close together indicating moderately disturbed communities. The biomass at stations 35 to 52 is dominated by the sea-urchin *Echinocardium cordatum.*

DISCUSSION

Methodological comparison

The different grab weights had no influence on the comparability of the data sets (Fig. 4; Tables 5, 6), nor did the different mesh sizes produce any differences in the species numbers, diversity, evenness and species composition (Fig. 5; Tables 5, 6). Thus, the main difference observed was the different number of small individuals, and this was due to the loss of individuals through the larger mesh size used in 1950–54. As the percentage of loss was estimated and the data of 1985–87 were first converted with this percentage (Table 7) and then used for the long-term comparison, the comparability of the data sets is guaranteed.

Long-term comparison

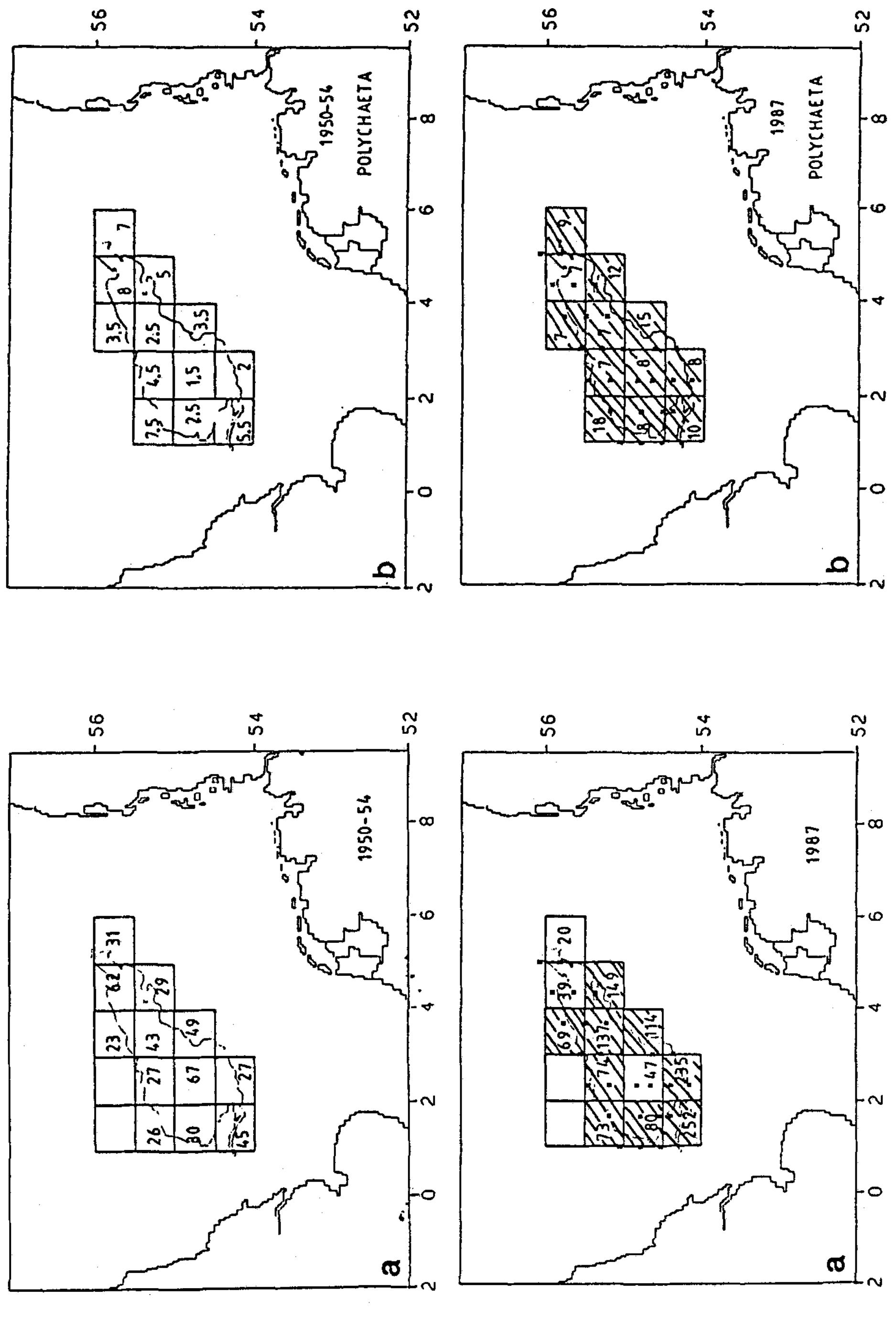
The changes found between the macrofauna communities of 1950–54 and 1985–87 can be described as follows:

- higher species numbers
- diversity decline
- increase of opportunistic, short-living species
- decrease of long-living bivalves
- 2.5 to 8-fold increase in biomass
- low similarity between stations from the fifties and the eighties

The question arose whether these changes have been caused by natural changes in the environment or by anthropogenic impact?

Natural changes

Changing water temperature, current systems and weather conditions may play a role, but North Sea surface temperatures from 1902–54 and from 1971–80 (Tomczak &


1950-54
POLYCHAETA
b
1987
POLYCHAETA
b
1950-54
a
1987
a

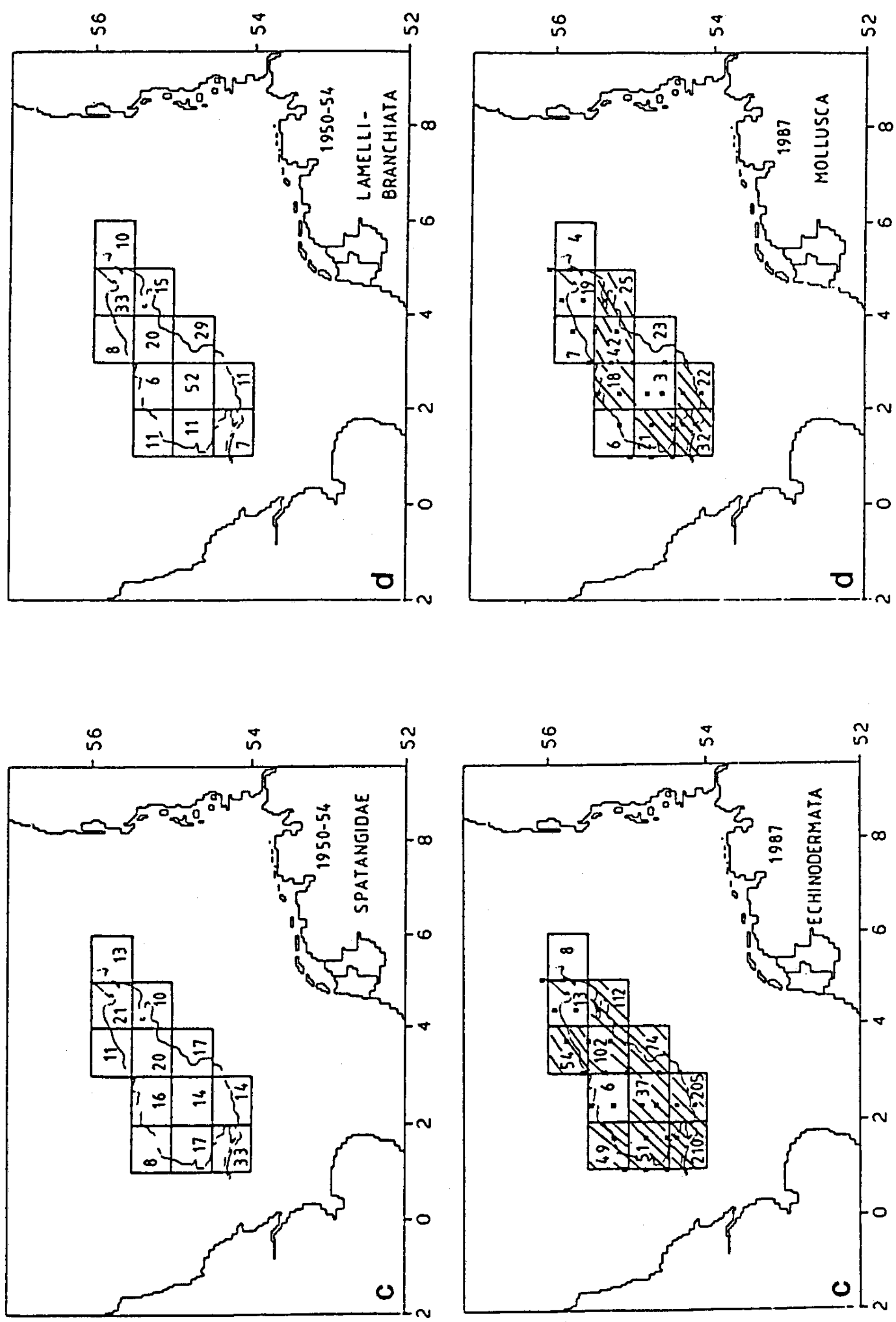


Fig. 7. Biomass per nautical squares (wet weight g/m^2) for (a) total biomass, (b) Polychaetes, (c) Echinoderms and (d) Molluscs for 1950–54 and 1987

Table 14. Similarities between stations from 1985–1987 and 1951–1952 (Ursin) after Greig-Smith (1964)

St.	1985		1951		1952	
	6–20	31–40	6–20	31–40	6–20	31–40
1985						
6–20	41.8		24.0		18.8	
31–40		33.3		18.1		15.7
1951						
6–20			26.5			
31–40				18.4		
1952						
6–20					26.7	
31–40						20.1

St.	1986			1951			1952		
	6–20	35–50	51–57	6–20	35–50	51–57	6–20	35–50	51–57
1986									
6–20	49.9			22.4			19.8		
35–50		37.6			15.5			16.7	
51–57			33.6			12.0			21.1
1951									
6–20				28.3					
35–50					20.0				
51–57						19.6			
1952									
6–20							26.7		
35–50								18.2	
51–57									23.1

St.	1987			1951			1952		
	6–20	21–40	42–60	6–20	21–40	42–60	6–20	21–40	42–60
1987									
6–20	48.1			23.5			20.8		
21–40		40.0			12.3			14.9	
42–60			33.9			16.6			20.0
1951									
6–20				32.1					
21–40					11.4				
42–60						17.0			
1952									
6–20							28.0		
21–40								12.8	
42–60									20.4

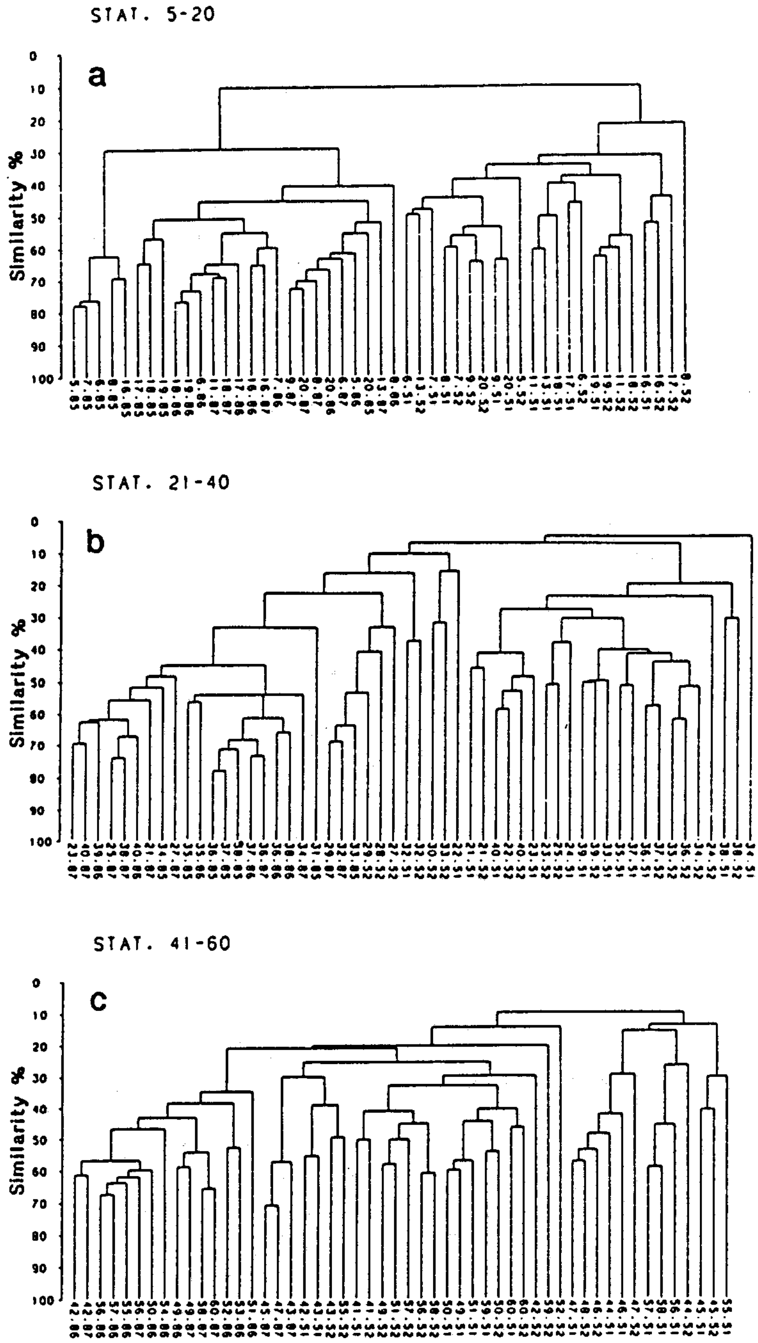


Fig. 8. Similarities between the stations of 1985–87 and 1951–52 (Ursin)

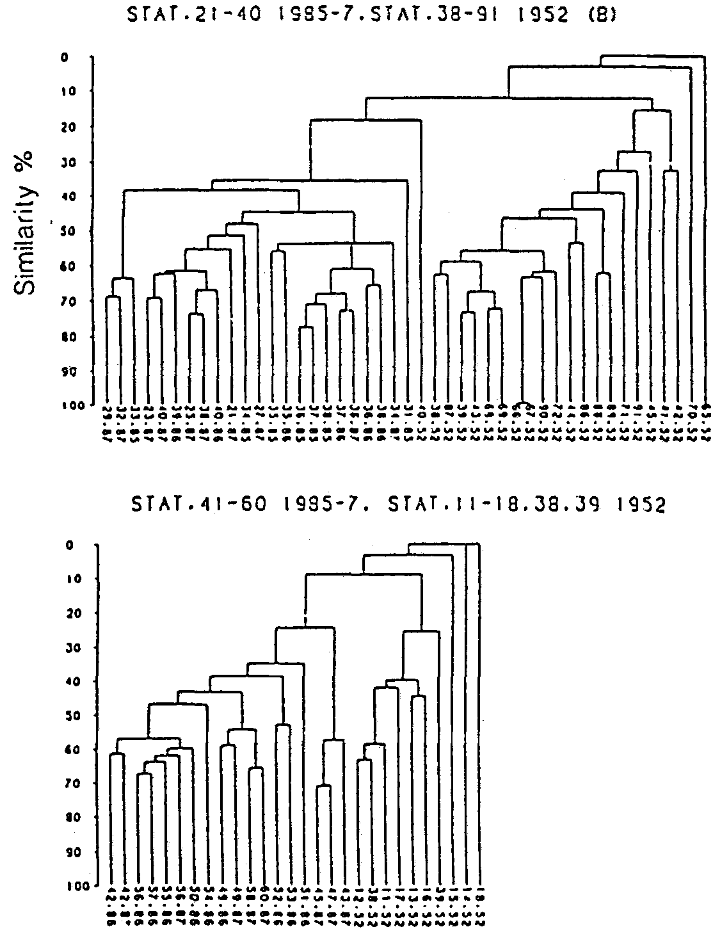


Fig. 9. Similarities between the stations of 1985–87 and 1952 (Birkett)

Goedecke, 1962; Becker et al., 1986) do not show any significant increase. Taylor & Stephens (1983) mentioned a small increase of surface temperatures in winter and spring in the Southern Bight of 0.3 °C from 1961 to 1976. However, no data for bottom temperatures are available, and their impact on changes in the benthos may be neglected. No information on changing current activities in the Dogger Bank area is available. Wind data (Seewetteramt Hamburg, pers. comm.) do not show higher frequencies of heavy storms during the fifties than during the eighties.

Besides natural environmental changes, anthropogenic influences on the macrofauna communities of the Dogger Bank have to be considered.

Anthropogenic impact

Purdom & Garrod (1990) indicated an increase in fishery for haddock, cod and plaice on the Dogger Bank since 1950. On the other hand, well-known fisheries biologists such

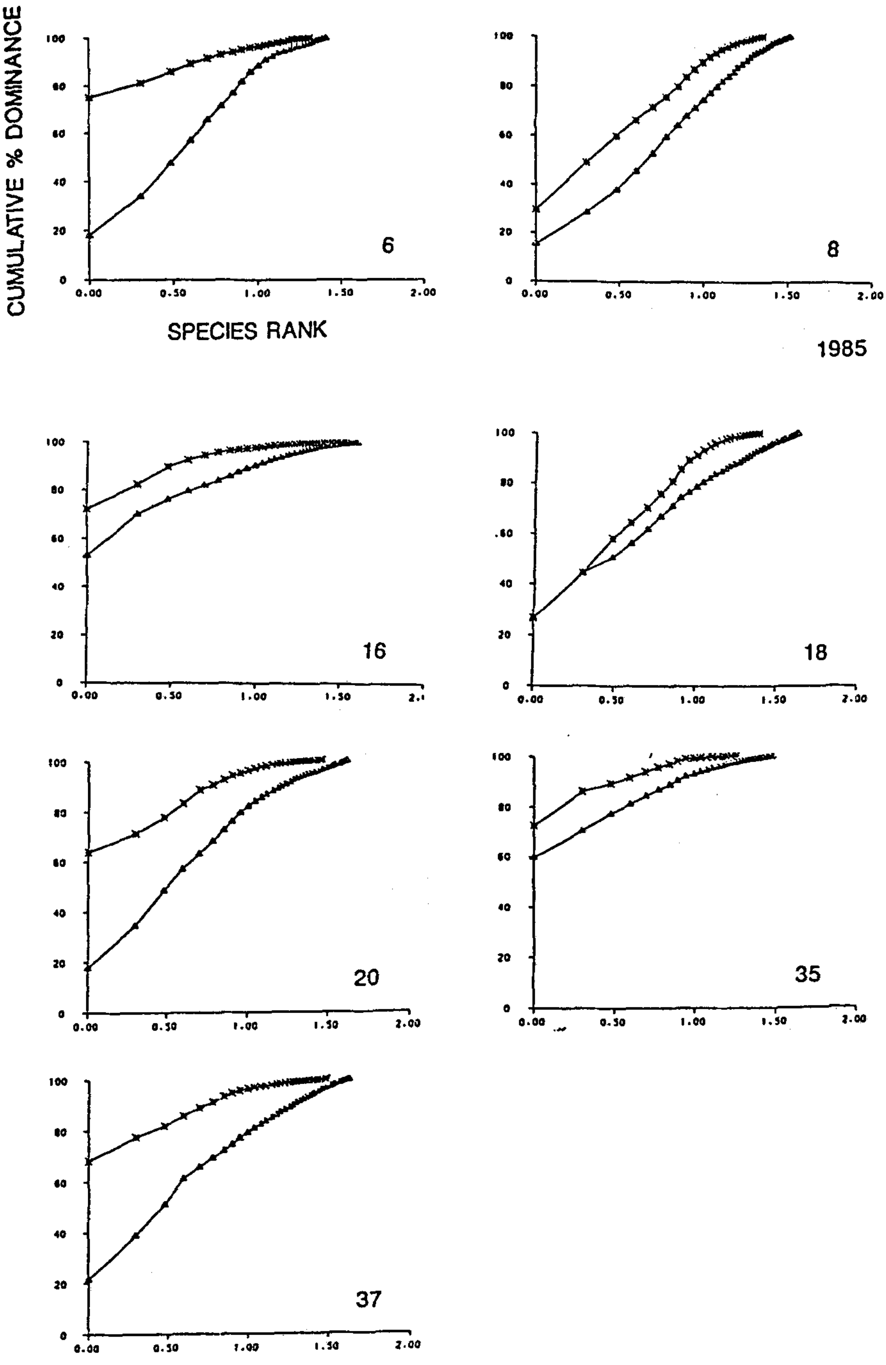


Fig. 10. ABC curves for the few stations of April/May 1985. Δ = abundance, * = biomass

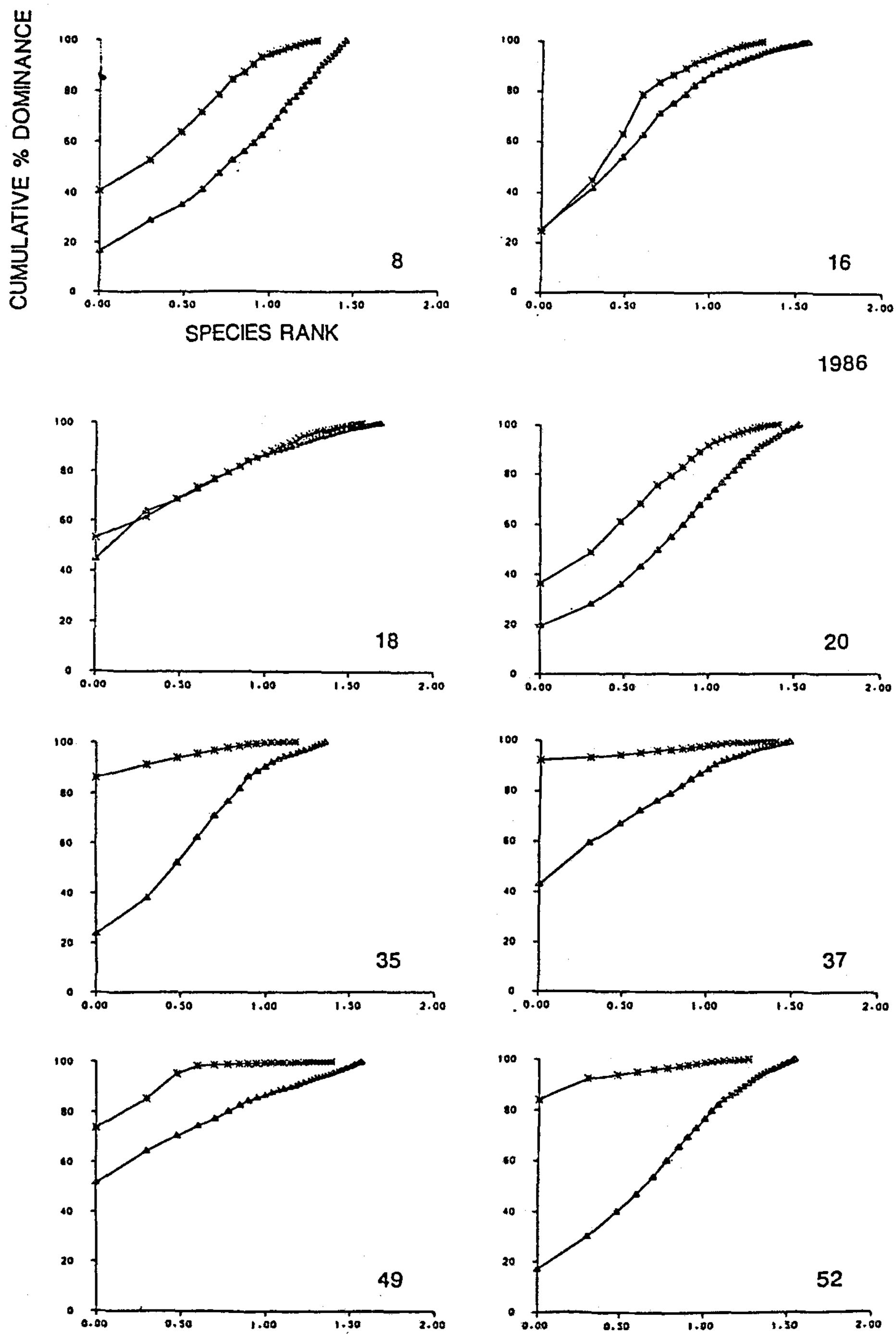


Fig. 11. ABC curves for the few stations of April/May 1986. Δ = abundance, * = biomass

as Rauck, Daan and Pope (pers. comm.) think the Dogger Bank has been unimportant for commercial fisheries for the past 10 years, and the above mentioned increase is negligible in relation to the whole North Sea. Sand-eel fishery takes place in spring around the Dogger Bank with light gear that should not damage the sea floor (Popp Madsen, pers. comm.). The stable distribution of the sea-urchin *Echinocardium cordatum* on the whole Dogger Bank in comparison with the former investigations seems to support the idea that damage by fisheries is an unimportant factor with regard to benthic community changes since this species is severely suffering under fishery pressure in other areas (Redant, 1987).

Concerning other anthropogenic impacts, the changes in the macrofauna communities of the Dogger Bank generally fit well into the model given by Pearson & Rosenberg (1978) for communities under increasing eutrophication of the environment. The changes are confirmed by other investigations as well. From the fifties to the eighties the number of species increased from 12 and 14 to 23 and 29 per 0.2 m^2, which is a 100 to 150 % increase (Tables 8, 9). Pearson & Rosenberg (1978) described a general increase of species number under increasing eutrophication, which was also found by Rosenberg & Möller (1979) and Riesen & Reise (1982). The extreme increase in the number of species should have caused a higher rise in diversity than that calculated (Tables 9, 10). The lower evenness in 1985–87 (Tables 9, 11) indicates a dominance of less species during the eighties than during the fifties, which explains the rather low increase in diversity. Polychaete species such as *Spiophanes bombyx* and *Scoloplos armiger* which increased in numbers from 1950–54 to 1985–87 (Table 12), are said to be opportunistic and tolerant of bad environmental conditions (Pearson & Rosenberg, 1978; Rachor, 1982; Reise, 1982; Pearson et al., 1983; von Westernhagen et al., 1986). The increase of predators such as *Nephtys hombergii* and *Nephtys caeca* may be due to the increase of small polychaete species, for example *Scoloplos armiger* (Table 12). As Schubert & Reise (1986) and Beukema (1987) have shown, *N. hombergii* feeds mainly on *S. armiger*.

The ophiurid *Amphiura filiformis* was found in increasing densities during several investigations related to enrichment of organic matter (Rosenberg & Möller, 1979; Pearson et al., 1985, 1986; Rosenberg et al., 1987). Duineveld et al. (1987) mentioned a drastic increase of this species in the southern North Sea due to enrichment of organic matter. For the bivalve species a recent dominance of small, short-living species is obvious. They represented r-selective species that are known to be more tolerant of changing environmental conditions. Species such as *Ensis ensis*, *Mactra c. cinerea* and *Spisula subtruncata* which can become quite old have been drastically reduced (Table 12). No patch as during the fifties (Petersen, 1977; Birkett, unpubl. data in Kröncke, 1991) could be found and all specimens found measured a few millimetres only.

The total benthic biomass (g/m^2 wet weight) in most of the nautical squares on the Dogger Bank was 2.5 to 8 times higher in 1987 than in 1951–52 (Fig. 7). Increasing biomass is often described as resulting from the enrichment of organic matter in the environment, e.g. investigations in the Skagerrak and Baltic Sea by Cederwall & Elmgren (1980) and Rosenberg et al. (1987), and in the German Bight by Rachor (1990). The reduced biomass of about 30 % in 1987 in the northeastern part of the Dogger Bank is mainly due to the lack of bivalves, i.e. to the lack of the *Spisula* patch Petersen (1977) found in the fifties, but even polychaetes and echinoderms show decreased weights.

Calculated similarities between the stations of the fifties and the eighties of 7 to 23 %

(Figs 8, 9; Table 14) are lower than those found by Pearson et al. (1985) and Rosenberg et al. (1987) with 30 % and 27 %, respectively, when comparing their recent data from Kattegat and Skagerrak with Petersen's from 1911–12. The cluster analyses of all data sets revealed two sediment-dependent communities (Fig. 6; Table 12): one on the Dogger Bank proper in fine sands with shells, and another one in the deeper boundary parts on muddy fine sands. The community in the deeper parts was dominated by *Amphiura filiformis* during all investigations, but during the eighties more short-living species were found. There was a clear shift in dominance to short-living, deposit-feeding species in the community on the Dogger Bank proper. This confirms that communities on muddy sands that have a higher content of organic matter show less effects following possible eutrophication than those on fine sands with a lower content of organic matter.

An assessment of the amount of biological disturbance by the ABC-method by Warwick (1986) revealed that only the communities from the northeastern part of the Dogger Bank seem to be moderately disturbed (Figs 10, 11). The shape of the curves for the central and western stations is characteristic of unpolluted communities on muddy sands (Warwick et al., 1987). As the sediment of the central Dogger Bank is sand with only a small amount of mud, the high biomass curve indicates a better food resource than is otherwise typical for sand areas.

Evidence of increasing eutrophication as is available for the coastal parts of the North Sea where increasing nutrient concentrations, increasing phytoplankton biomass (Gerlach, 1984; Hickel et al., 1989; Radach & Bohle-Carbonell, 1990) and corresponding macrofauna changes (Rachor, 1990) have been reported, is not available for the Dogger Bank area. Nevertheless, it is a region of high phytoplankton production during winter (Brockmann & Wegner, 1985; Richardson & Olsen, 1987). As Duineveld et al. (1987) discovered that adjacent areas of the Dogger Bank are also enriched, there is evidence that the changes in the macrofauna communities might be due to increasing eutrophication of the Dogger Bank. As this area is influenced by residual currents (Hainbucher et al., 1986), rather coarse sediments are found. On the other hand, however, it is a region of high production due to continual sedimentation and resuspension.

Another anthropogenic impact might be the increasing pollution of the central North Sea. In contrast to the prevailing opinion of undisturbed offshore regions, highest concentrations of lead and cadmium were found in the fine fraction (< 20 µm) of sediments (Albrecht 1987; Irion & Müller, 1987; Kersten & Klatt, 1988), in macrofauna species (Kröncke, 1987; Karbe et al., 1988; Everaarts & Fischer, 1989) and in dab (*Limanda limanda*) (Claussen, 1988) on the Dogger Bank compared with the concentrations found in the German Bight and Danish coastal waters. Irion & Müller (1990) could show by dating sediment cores that on the eastern part and south of the Dogger Bank within the uppermost 10 cm depth there is an increase in lead concentration of 100–150 %. Kersten & Kröncke (1992) give evidence that the fine fraction (< 20 µm) of the Dogger Bank sediments are twice as toxic as those from the German Bight. Some macrofaunal species prefer to feed on particles smaller than 20 µm – highly contaminated particles Brown (1986) –, which might prevent long-living bivalve species from becoming old and large, for these species are known to accumulate, for example, large amounts of cadmium (Ray, 1984).

At the moment, it is impossible to say which factor or which combination of factors might have caused the changes in the Dogger Bank benthic communities. All that can be said is that even in offshore populations long-term changes can be detected. This fact contradicts the prevailing opinion of unaffected offshore communities in contrast to often highly affected nearshore ones.

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