STRUCTURE OF MEIOFAUNA COMMUNITIES IN THE SOUTHERN BIGHT OF THE NORTH SEA

BY

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INTRODUCTION

The consequences of the human activities on the North Sea ecosystem are not always directly measurable. A method to evaluatie the human impact is to follow the evolution of benthic communities (Gray *et al.*, 1980 ; Heip, 1980). Nowadays, meiobenthos is well recognized as an important compartment within the benthic systems and has some properties in advantage of the macrobenthos (Herman & Heip, 1986 ; Heip *et al.*, 1988).

The meiobenthos comprises one of the most dominant groups of higher metazoans in soft-bottom communities. They are mainly very small animals separated from the macrobenthos either on a methodological basis (size passing a 1 mm-sieve ; biomass < 0.45 µg dry weight) or on a taxonomical basis. Many so called "meiofauna taxa" are animal groups of higher taxonomical level (order to phylum) and consist of small organisms which mainly have their live cycle in or upon the sediments or related substrates. Typical meiofauna taxa are e.g. Nematoda, Harpacticoida, Turbellaria, Kinorhyncha, Tardigrada, Gnathostomulida, Halacarida.

In spite of the awareness of the importance of the meiofauna in marine sediments, little is known about factors controlling its development and distribution. Gerlach (1971) already postulated that meiofauna is energetically more important than macro-fauna due to size, higher turn-over rates and shorter generation times. Due to a faster response capacity, ecological processes within meiofauna are on a smaller scale and shorter time period (Warwick, 1984 ; Gee et al., 1985b).

Although field studies increase exponentially in the last decades, large efforts are concentrated on easily accessible locations in estuaria, salt marshes and littoral fringes (Herman & Heip, 1985 ; Reise, 1984 ; Herman *et al.*, 1985 ; Gee *et al.*, 1985a). In the last decade experimental field and laboratory work was set up to study auto-ecological and interactive relationships within or among specific meiofaunal taxa (e.g.

Alongi, 1985 ; Gee *et al.*, 1985b ; Chandler & Fleeger, 1987 ; Decho, 1986 ; Decho & Castenholz, 1986).

Besides the growing consciousness about the important role in benthic ecology, there is also an increasing interest in meiofaunal composition and distribution patterns in less accessible subtidal areas. In the early seventies the study of the benthic communities of the Southern Bight of the North Sea started with the "Mathematical model of the North Sea'-project (Govaere *et al.*, 1980). Recently Vincx (1986 ; in press a, b, c) described the nematode communities in this area, and Vanreusel (1989) analysed the nematode communities in the highly dynamic Delta area off the Dutch coast. These detailed studies of the Nematoda revealed well defined communities related to specific environmental characteristics.

In our study, the characteristics of the higher meiofaunal taxa were analysed. The aim was i) to identify typical assemblages according to certain environmental parameters on the basis of quantitative data and ii) to distinguish different communities within environments with nearly identical properties.

In this study only the mean values of all variables in each locality are considered. The temporal variation of meiobenthic communities in different types of sediment will be the subject of following publications.

MATERIAL AND METHODS

The meiobenthic community structure was examined from 52 localities in the Southern Bight of the North Sea. The position of these stations is shown in Fig. 1. Off the Belgian coastal area 18 localities were sampled seasonally from June 1977 till December 1979 (loc. 101-118 ; Herman *et al.*, 1985). Six of these localities were continuously sampled till December 1984. Station 250 was studied from January 1983 till January 1984 (see Huys, Herman & Heip, 1986). 26 stations are located in and around an TiO_2-waste disposal area off the Dutch coast (loc. 401-426). Seven stations were sampled during a R. V. Aurelia cruise, four of these are located north of Texel (loc. 501-513).

All meiofauna samples were collected by subsampling gear with standard plastic cores (inner surface = 10.2 cm^2). In the Belgian coastal zone the 1977 samples were collected out of a 0.1 m^2 Van Veen grab. From April 1978 onward, a modified Reineck boxcorer (surface 170 cm^2) (Farris & Crezée, 1976) was used. From October 1984 onward, a spade boxcorer was operated on board of the R. V. BELGICA (sampling surface : 0.25 m^2). Off the Dutch coast a 600 cm^2 boxcorer was used. Four to six subsamples up to a depth of 10 cm were taken from each box. Two cores for chemical and sediment analyses were frozen. All samples for meiofauna were fixed with hot formalin (70°C) to a final concentration of 4% formaldehyde.

The extraction technique of the meiofauna differs with sediment type. For medium to coarse sands with low amounts of silt and detritus simple decantation on

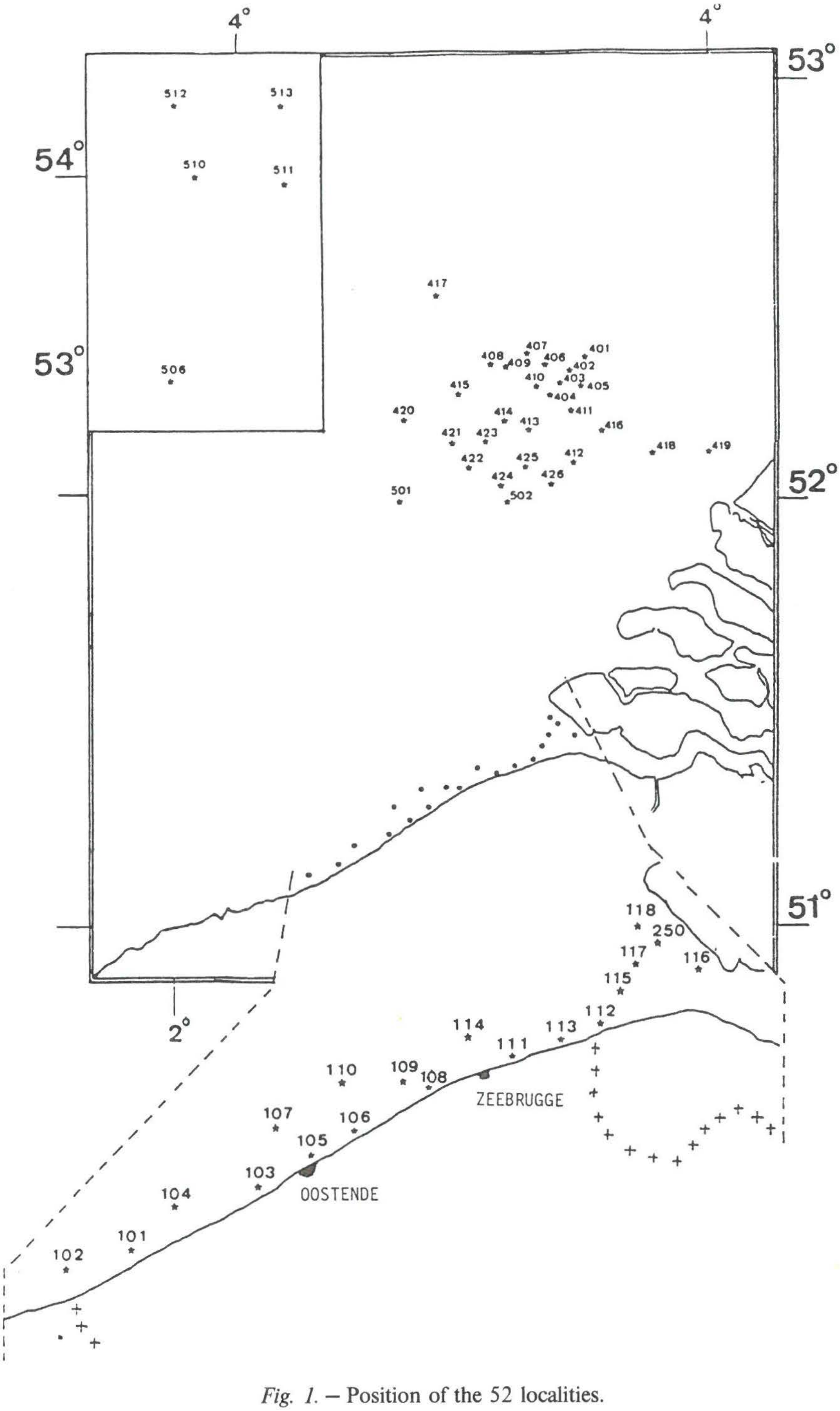


Fig. 1. – Position of the 52 localities.

a 38 µm-sieve is sufficient (Pfannkucke & Thiel, 1988). The through-method (Barnett, 1968) is highly efficient for fine to medium pure sands. The fauna extraction from muddy or detritus rich sediments is done using a density gradient centrifugation technique (Heip *et al.*, 1985). Characteristics of the sediment and the grain size distribution of the sand fraction was determined following Buchanan and Kain (1971).

The elutriated meiofauna was stained with rose bengal and the major taxa were counted. The Copepoda Harpacticoida were separated for identification to species and grouping in one of the five following biomass classes :

- class 1 : 4 µg, large epibenthic or phytal forms
- class 2 : 2 µg, mostly epibenthic or phytal forms and larger endobenthic species
- class 3 : 1 µg, smaller epi- and endobenthic forms, very large interstitial species
- class 4 : 0.5 µg, mostly cylindrical interstitial forms
- class 5 : 0.2 µg, very small interstitial forms

200 nematodes were selected randomly for biomass determination. This was done with a Mettler ME 2/BA 25 microbalance up to an accuracy of 0.1 µg.

A wide range of diversity and evenness indices was used, following Heip *et al.* (1988), to express the complexity of the meiobenthic communities.

Two multivariate analysis methods were used in order to find relationships between the communities of the 52 localities : Detrented Correspondence Analysis (DCA) (Hill, 1979b ; Hill & Gauch, 1980) as ordination technique and TWINSPAN (Two-way Indicator Species Analysis), a polythethic divisive classification technique proposed by Hill (1979a). Spearman rank correlation and Kruskal-Wallis analysis of variance was done according to Siegel (1956). An *a posteriori* test to distinguish variance within localities from variance between localities has performed according to Sokal & Rohlf (1981).

RESULTS

Environmental characteristics

The mean depths and the mean values of the sediment characteristics of the 52 localities are given in Table 1. Three depth zones are distinguished : i) close to the Belgian-Dutch coast with a mean depth varying from 0.7 m to 13.4 m (loc. 101-250) ; ii) the area off the Dutch coast (loc. 401-502) with mean depth ranging from 27 m to 35 m (and a maximum depth of 45 m) ; iii) the most northern area with depths from 43 m to 50 m (loc. 510-513).

The median grain size of the sand fraction varies between 88 µm to 643 µm ; which classifies the sediments, according to the Wenthworth scale, as very fine to coarse sands. The distribution of the classes in the different localities is illustrated in Fig. 2A. The northern part of the study area is characterised by very fine sand, which is also present in the Zeebrugge area. Fine sands are dominant off the Belgian-Dutch coast, while in the open sea, more medium sands occur. In this study, coarse sand (> 500 µm) is found sporadically. Most of these sands are well to very well sorted with a trend towards the finer fractions (symmetrical to negative skewness).

The mud content of the different localities is shown in Fig. 2B. In the coastal region as well as in the northern part of the study area, important amounts of very fine material is present. In nearly half of the localities, the mean mud content is higher than 10%. All the sedimentological parameters are correlated with each other and with their geographic position (Table 2). The strong correlation between most sediment charactistics and depth shows significant differences in the southern, central and northern parts of the study area (Fig. 2). The central open sea zone is characterized by medium sands with low mud content. Towards the northern area, the mud content increases significantly. Off the Belgian coast one notes the same gradient : sands in the south-western zone and high concentrations of silty sediments in the north-eastern zone.

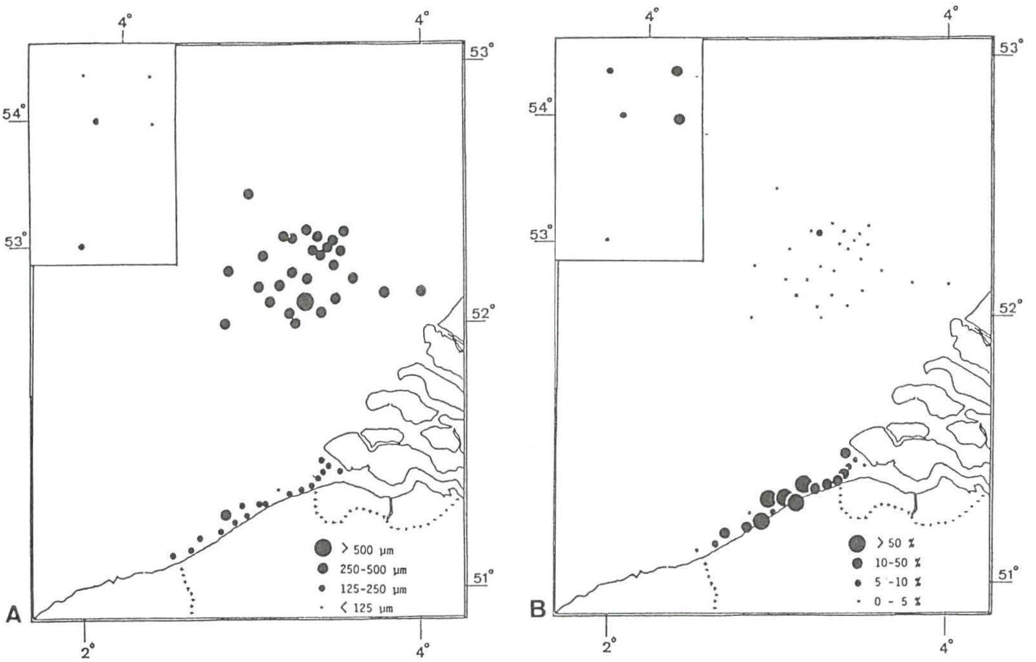


Fig. 2A. – Distribution of the mean median grain size Mdµm of the sand fraction in the 52 localities.
B. – Distribution of the mud content (% particles < 62 µm) in the 52 localities.

TABLE 1

Mean depth and mean values of the sediment characteristics per station.
(Mdμm : median grain size of the sand fraction ; Sort Φ and Skew Φ :
sorting and skewness of the sand fraction in Φ-units and the percentages sand, mud and gravel)

Locality	D(m)	Mdμm	Sort Φ	Skew Φ	% Sand	% Mud	% Gravel
101	7.4	205	0.40	0.237	94.2	5.80	0.00
102	11.2	226	0.41	0.056	96.3	2.72	1.03
103	8.6	151	0.38	0.231	79.1	20.70	0.14
104	11.9	190	0.46	0.090	86.2	12.50	1.20
105	9.0	167	0.50	0.183	49.1	50.10	0.75
106	8.7	173	0.37	0.227	90.9	9.09	0.00
107	10.4	300	0.48	0.007	93.6	5.15	1.20
108	8.9	172	0.58	0.278	36.5	63.40	0.00
109	8.6	171	0.49	0.138	41.3	58.60	0.00
110	10.6	148	0.52	0.133	55.1	44.80	0.01
111	9.1	205	0.41	0.190	70.1	27.60	2.19
112	10.2	156	0.57	0.188	55.0	44.90	0.00
113	8.9	184	0.43	0.168	68.5	30.90	0.40
114	11.0	130	0.65	- 0.062	22.2	77.20	0.50
115	11.8	215	0.44	0.212	73.8	26.00	0.22
116	13.1	217	0.42	0.229	97.4	2.57	0.00
117	8.8	186	0.35	0.110	92.0	7.78	0.13
118	11.1	175	0.46	0.184	80.1	18.70	0.82
250	7.0	230	0.37	0.015	98.6	1.31	0.00
401	30.8	290	0.37	- 0.020	98.6	1.37	0.04
402	31.0	281	0.33	0.001	98.5	1.46	0.02
403	30.2	303	0.34	0.025	99.3	0.57	0.15
404	29.2	291	0.33	0.008	98.8	1.07	0.16
405	28.2	304	0.35	0.006	98.4	1.60	0.00
406	30.5	283	0.28	0.020	98.8	1.15	0.06
407	36.8	280	0.41	0.004	99.0	0.84	0.16
408	35.3	272	0.35	- 0.016	98.1	1.06	0.83
409	45.0	277	0.60	- 0.011	88.7	6.75	4.50
410	31.5	292	0.36	0.008	98.9	1.07	0.04
411	38.5	285	0.39	0.014	95.7	0.96	3.24
412	28.5	269	0.36	0.002	98.3	1.16	0.51
413	29.7	362	0.46	0.004	98.0	1.35	0.69
414	34.1	300	0.37	0.000	98.3	1.29	0.38
415	34.0	314	0.34	0.017	80.8	4.76	14.41
416	26.5	307	0.38	- 0.006	97.3	2.44	0.30
417	32.0	284	0.35	- 0.041	99.7	0.28	0.00
418	29.0	301	0.73	- 0.009	99.4	0.55	0.00
419	32.0	324	0.57	0.157	99.7	0.24	0.00
420	39.5	283	0.29	0.027	96.8	2.12	1.06
421	37.2	261	0.33	- 0.018	97.6	2.26	0.04
422	36.2	282	0.32	0.015	97.0	2.85	0.09
423	29.3	327	0.42	0.024	97.3	2.57	0.08
424	35.8	643	0.73	0.171	96.2	2.48	1.29
425	31.3	315	0.48	- 0.012	97.0	2.63	0.29
426	27.3	395	0.58	- 0.089	95.4	2.48	2.12
501	32.0	358	0.36	- 0.015	99.8	0.18	0.00
502	34.0	385	0.43	- 0.006	99.7	0.21	0.00
506	31.0	239	0.35	- 0.039	99.7	0.22	0.00
510	46.0	132	0.31	0.038	89.7	10.20	0.00
511	43.0	119	0.25	0.021	87.3	12.60	0.00
512	46.0	115	0.66	- 0.039	90.7	9.20	0.00
513	50.0	88	0.20	0.005	74.7	25.20	0.00

TABLE 2

Spearman's rank correlation between depth and sediment characteristics
(* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

	Depth	Md µm	Sort Φ	Skew Φ	% Sand	% Mud	% Gravel
Md µm	0.2848 0.41*	–	–	–	–	–	–
Sort Φ	-0.3395 .14*	0.0044 .975	–	–	–	–	–
Skew	-0.5017 .001***	-0.3608 .009**	0.0821 .563	–	–	–	–
% Sand	0.3518 .011*	0.6659 .001***	-0.3513 .011*	-0.4588 .001***	–	–	–
% Mud	-0.4319 .001***	-0.7165 .001***	0.3202 .021*	0.4918 .991***	-0.9600 .001***	–	–
% Gravel	0.0457 .758	0.2508 .073	0.1473 .298	-0.0674 .635	-0.2473 .077	0.0912 .520	–
NB	0.7937 .001***	0.2245 .110	-0.4943 .001***	-0.5426 .001***	0.4588 .001***	-0.4882 .001***	-0.1316 .352
EL	0.2760 .048*	0.0447 .735	-0.1674 .235	-0.1880 .182	0.2522 .071	-0.2358 .092	-0.2776 .046*

General composition of the meiofauna communities

– *Spatial distribution of the meiofauna taxa*

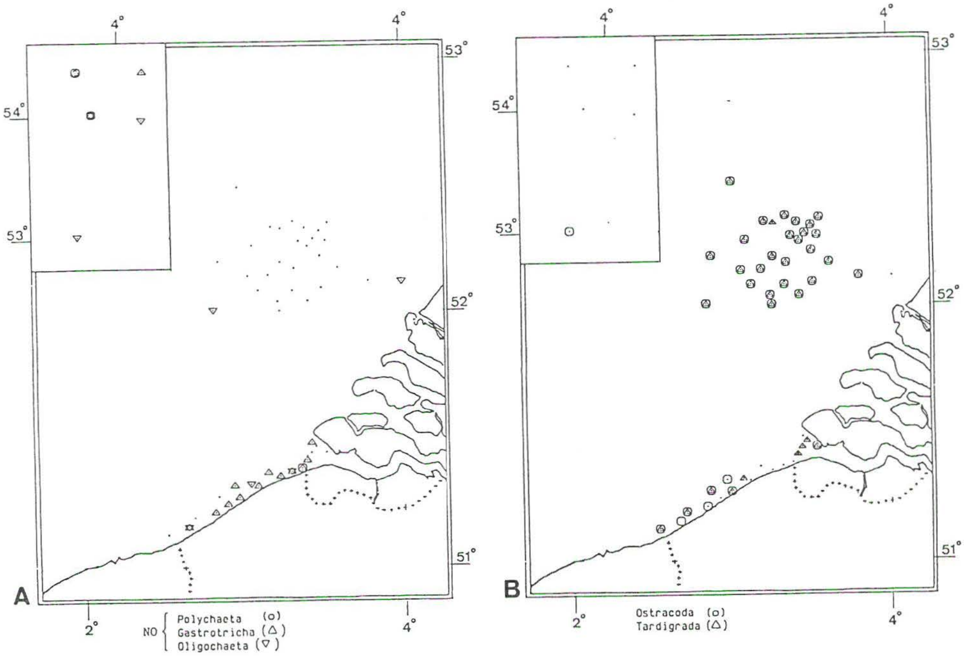
A total of seventeen higher meiobenthic taxa are found in the 52 localities. In 10% of the samples a mean of ten to twelve taxa per sample occur. In 38% of the samples, five to nine taxa are present. In the poorest communities one to maximum four taxa are present. Nematoda, Copepoda Harpacticoida and Turbellaria occur in all the localities. Interstitial Polychaeta are lacking in three localities, Oligochaeta in eight and Gastrotricha in fifteen localities, as illustrated in Fig. 3A. The distribution of other taxa is shown in Fig. 3B-F. Ostracoda and Tardigrada occur in 36 localities (Fig. 3B). Interstitial Hydrozoa and Halacarida are found in respectively 35 and 37 localities (Fig. 3C). Seven taxa have a more restricted distribution. Nemertinea and Kinorhyncha are found in resp. eleven and nine localities (Fig. 3D). Bryozoa scarcely occur in six localities, while Rotifera are restricted to five localities off the Belgian coast only (Fig. 3E). Sipunculida, Priapulida and interstitial Mollusca occur very sporadically in resp. four, three and one locality (Fig. 3F).

– *Density of the meiofauna*

The mean density of each meiofauna taxon for all 52 localities is summarized in table 3. The mean total density varies from 210 ind. 10 cm^{-2} to 4633 ind. 10 cm^{-2}, with an overall mean of 1594 ind. 10 cm^{-2}. The mean density is less than 1000 ind. 10^{-2} in twelve sampling stations. In 24 localities a mean abundance between 1000 and 2000 ind. 10 cm^{-2} and in sixteen localities more than 3000 ind. 10 cm^{-2} are found.

The overall mean density of the most dominant taxon, the Nematoda, is 1394 ind. 10 cm^{-2} and varies from 203 (loc. 110) to 4631 ind. 10 cm^{-2} (loc. 112). A maximum density of 19020 ind. 10 cm^{-2} is noted at loc. 112, a minimum of 13 ind. 10 cm^{-2} in loc. 111 and loc. 114. In 5% of the samples, the nematode density is less than 100 ind. 10 cm^{-2} and in 6% of the samples it is more than 6000 ind. 10 cm^{-2} occur.

For the second most abundant taxon, the Copepoda Harpacticoida, the overall mean density is 99 ind. 10 cm^{-2}. In some localities (loc. 112, 113 and 115) this group is very rare (1 ind. 10 cm^{-2}). Maximal abundances vary between 250 and 800 ind. 10 cm^{-2}. An extreme high value is noted for loc. 114 (6633 ind. 10 cm^{-2}). For the Turbellaria, the mean abundance is between 0.3 and 162 ind. 10 cm^{-2}, with an overall mean of 47 ind. 10 cm^{-2}. Maximal densities are noted in sandy localities off the Belgian coast and may reach up to 558 ind. 10 cm^{-2} (loc. 102) and 478 ind. 10 cm^{-2} (loc. 104). Gastrotricha also may attain high densities (206 ind. 10 cm^{-2} in loc. 406 ; 182 ind. 10 cm^{-2} in loc. 416 and 156 ind. 10 cm^{-2} in loc. 107). Their mean abundance is 33 ind. 10 cm^{-2}.



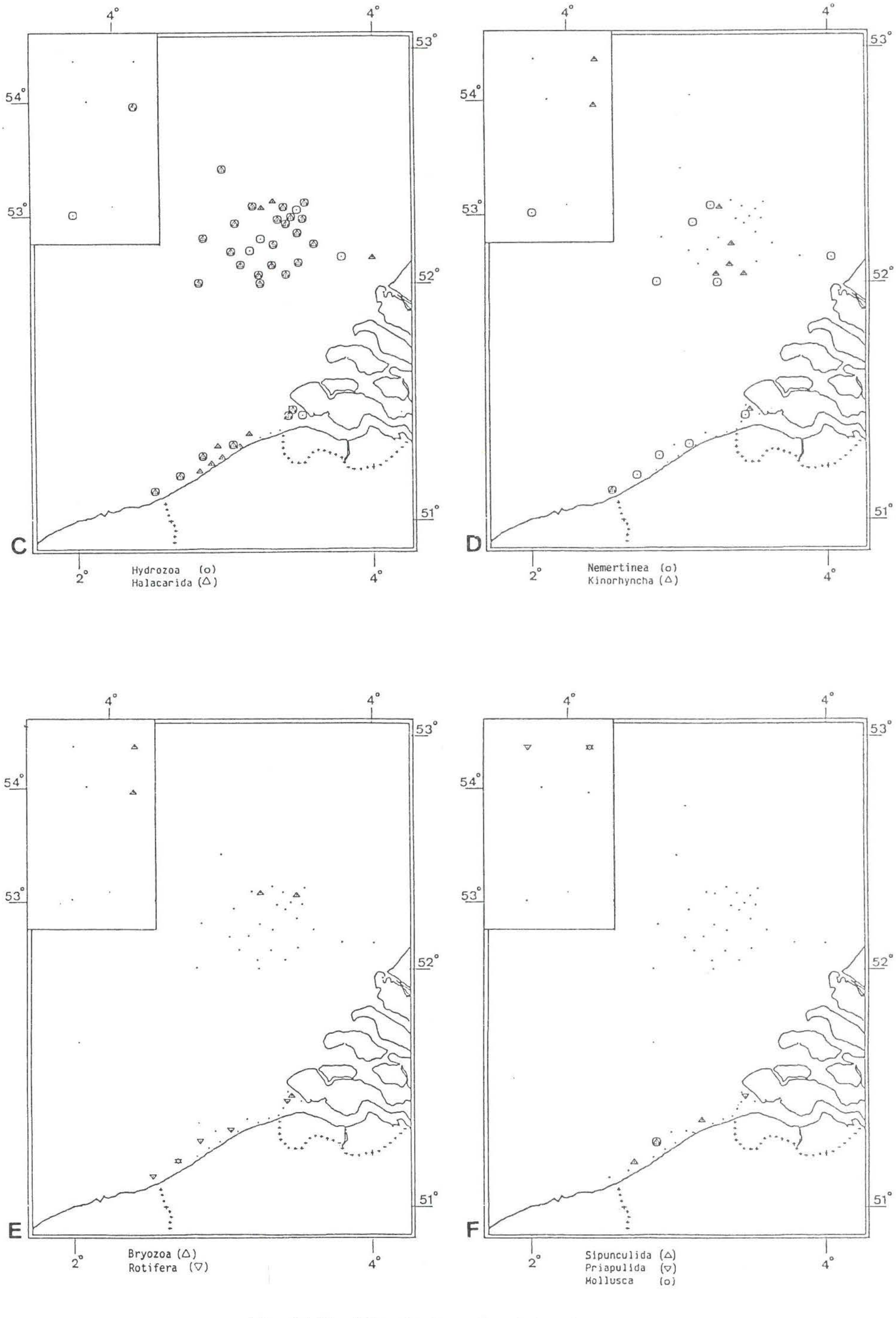


Fig. 3A-F. – Distribution of meiobenthic taxa.

TABLE 3

Mean density per taxon and mean total meiofauna density for 52 localities in the Southern Bight of the North Sea ($N.10\ cm^{-2}$)

Taxon/Loc.	101	102	103	104	105	106	107	108	109	110	111	112	113
Nematoda	706.1	2047.0	1877.6	2052.3	1890.2	2758.0	383.1	2285.0	773.6	203.2	1337.1	4631.4	1368.0
Harpacticoida	30.9	57.2	16.6	32.0	103.7	27.1	121.2	9.4	34.5	4.4	8.0	1.1	1.5
Turbellaria	9.6	65.8	5.6	69.1	1.9	4.8	28.3	1.5	3.9	0.7	0.9	0.6	1.4
Polychaeta	2.2	6.7	2.4	4.3	3.6	3.1	11.4	0.5	1.0	1.0	1.2	–	0.7
Gastrotricha	–	8.7	–	10.0	–	–	33.9	–	*	–	–	–	–
Ostracoda	0.9	0.5	0.3	4.1	–	0.1	7.3	–	–	0.1	–	–	–
Tardigrada	–	1.0	–	0.7	–	1.7	5.0	–	*	–	–	–	–
Hydrozoa	–	0.5	–	0.1	–	–	5.8	–	0.1	–	–	–	–
Halacarida	–	0.4	0.1	0.2	0.2	0.1	6.4	0.2	0.2	0.1	–	–	–
Oligochaeta	–	1.3	0.4	3.2	0.2	0.2	0.6	0.1	–	0.2	0.2	0.2	–
Nemertini	–	1.0	–	0.9	–	–	0.1	–	*	–	–	–	–
Sipunculida	–	–	–	0.8	–	–	*	–	–	–	–	–	–
Bryozoa	–	–	–	*	–	–	–	–	–	–	–	–	–
Rotifera	–	0.2	–	*	–	–	0.7	–	*	–	–	–	–
Kinorhyncha	–	*	–	–	–	–	–	–	–	–	–	–	–
Mollusca	–	–	–	–	–	–	0.4	–	–	–	–	–	–
Total	749.7	2190.2	1903.0	2177.7	1999.8	2795.1	604.4	2296.7	813.5	209.7	1347.4	4633.3	1371.6

Taxon/Loc.	114	115	116	117	118	250	401	402	403	404	405	406	407
Nematoda	481.8	546.1	1932.4	1729.5	3046.8	1411.1	1022.3	1061.0	830.3	823.3	925.3	1032.5	1007.0
Harpacticoida	33.5	0.9	24.0	16.9	7.6	31.3	178.5	138.5	101.8	134.5	148.5	372.0	89.8
Turbellaria	8.2	2.9	10.9	23.9	5.4	44.8	80.0	104.0	28.0	102.3	91.0	131.3	101.3
Polychaeta	0.6	2.1	5.4	3.3	23.0	5.7	19.3	7.5	9.5	10.5	8.3	11.0	2.8
Gastrotricha	–	–	1.6	4.9	–	18.8	67 8	67.3	57.5	56.3	83.8	116.8	25.8
Ostracoda	–	–	0.1	–	–	–	3.3	4.3	6.3	1.0	3.0	0.8	0.3
Tardigrada	–	0.1	0.2	1.4	–	6.9	20.5	4.3	2.3	2.5	10.0	5.0	1.5
Hydrozoa	–	0.1	1.2	0.2	–	1.2	11.3	6.5	2.8	8.3	1.3	3.8	–
Halacarida	0.1	–	–	0.3	–	0.7	1.3	–	0.5	0.8	0.3	0.3	0.8
Oligochaeta	0.1	0.1	0.7	0.4	4.5	1.4	10.5	3.3	2.8	3.5	1.0	7.5	2.0
Nemertini	–	–	–	*	–	–	–	–	–	–	–	–	–
Sipulculida	–	–	–	–	–	–	–	–	–	–	–	–	–
Priapulida	–	–	–	–	–	*	–	–	–	–	–	–	–
Bryozoa	–	–	–	–	–	0.5	–	1.3	–	–	–	–	–
Rotifera	–	–	–	*	–	–	–	–	–	–	–	–	–
Kinorhyncha	–	–	–	–	–	0.3	–	–	–	–	–	–	–
Total	524.3	552.3	1976.5	1780.8	3087.3	1522.6	1414.5	1397.8	1041.5	1142.8	1272.3	1680.8	1231.0

* < 0.1

Taxon/Loc.	408	409	410	411	412	413	414	415	416	417	418	419	420
ematoda	582.0	1942.5	874.8	1152.3	394.8	1319.6	1991.5	574.3	1005.5	486.0	2669.0	1005.0	1672.0
Harpacticoida	105.5	18.5	75.3	77.5	187.0	143.1	73.0	72.3	81.8	90.5	29.0	13.0	213.0
Turbellaria	39.3	29.0	58.8	122.5	79.0	67.1	82.3	21.3	96.0	27.5	28.5	5.5	162.0
Polychaeta	6.8	3.5	4.3	6.0	8.8	8.3	11.3	5.0	4.8	5.0	11.0	1.5	17.0
Gastrotricha	18.5	5.8	24.8	39.8	109.8	71.8	37.5	17.3	132.3	30.5	14.0	–	60.0
Ostracoda	0.8	–	0.5	0.5	0.8	5.1	0.3	2.0	1.5	0.5	2.0	–	3.0
Tardigrada	2.5	3.3	11.0	3.0	0.8	2.2	9.3	3.5	12.3	18.5	13.5	–	6.5
Hydrozoa	1.0	–	1.5	18.8	6.3	4.6	8.3	2.0	2.3	0.5	0.5	–	7.0
Halacarida	1.3	0.3	0.3	0.3	0.8	1.4	–	1.0	0.3	3.0	–	0.5	0.5
Oligochaeta	1.8	1.0	1.0	6.3	1.5	2.8	7.0	1.8	6.5	2.5	4.5	–	2.0
Nemertini	0.3	–	–	–	–	–	–	0.3	–	–	–	0.5	–
Bryozoa	–	3.5	–	–	–	–	–	–	–	–	–	–	–
Kinorhyncha	–	3.3	–	–	–	0.5	–	–	–	–	–	–	–
Total	759.5	2010.5	1052.0	1426.8	789.3	1626.5	2220.3	700.5	1343.0	664.5	2772.0	1026.0	2143.0

Taxon/Loc.	421	422	423	424	425	426	501	502	506	510	511	512	513
Nematoda	1715.5	979.0	1555.5	1872.5	1485.5	1324.5	1003.0	443.3	344.5	2645.0	2362.5	1946.0	1381.5
Harpacticoida	117.0	80.5	80.5	233.5	146.5	600.0	260.5	121.0	66.5	13.3	9.8	15.3	67.0
Turbellaria	110.0	73.5	151.5	89.9	67.0	90.5	23.0	25.3	28.0	0.3	3.5	2.8	6.0
Polychaeta	1.5	9.5	23.0	72.0	12.5	31.0	14.0	29.0	16.0	–	1.3	–	3.0
Gastrotricha	47.5	130.0	86.5	58.0	65.5	105.5	19.5	21.0	10.5	–	0.3	–	–
Ostracoda	1.5	2.5	1.0	63.0	4.5	14.0	7.5	8.7	0.5	–	–	0.3	1.5
Tardigrada	4.0	0.5	3.5	40.0	7.0	12.0	3.0	1.3	–	–	–	–	–
Hydrozoa	5.0	0.5	6.0	33.5	3.0	38.5	6.5	0.7	2.0	–	0.8	–	–
Halacarida	1.5	0.5	–	4.5	2.0	2.5	3.5	4.7	–	–	0.3	–	–
Oligochaeta	1.0	0.5	1.5	8.5	6.0	7.0	–	0.3	–	–	–	0.3	1.5
Nemertini	–	–	–	–	–	–	0.5	2.3	1.5	–	–	–	–
Sipunculida	–	–	–	–	–	–	–	–	–	–	–	–	0.5
Priapulida	–	–	–	–	–	–	–	–	–	–	–	0.3	1.0
Bryozoa	–	–	–	–	–	–	–	–	–	–	0.3	–	2.5
Kinorhyncha	–	–	–	1.0	0.5	2.5	–	–	–	–	0.5	–	0.5
Total	2004.5	1277.0	1909.0	2475.5	1800.0	2228.0	1341.0	657.7	469.5	2658.7	2379.0	1964.8	1465.0

For the less abundant taxa – Polychaeta, Oligochaeta, Tardigrada, Halacarida, Hydrozoa and Ostracoda – the mean density is usually less than 5 ind. 10 cm^{-2}, although their maximum scores may reach several tens per sample. The density of the rare taxa, i.c. the Nemertinea, Sipunculida, Priapulida, Bryozoa, Rotifera, Kinorhyncha and Mollusca can be neglected. They totalize an overall mean abundance of 0.6 ind. 10 cm^{-2}.

Multivariate analysis of the meiofauna communities

– *TWo-way INdicator SPecies ANalysis*

For the TWINSPAN classification we used the standard parameters proposed by Hill (1979a), except for the cutlevels of which the best results are obtained with the following series :

$$0 - e^2 - e^4 - e^6$$
$$0 - 7.4 - 54.6 - 403$$

The first TWINSPAN division selects 29 localities in which taxa occur with strong preference for pure sands, such as Gastrotricha, Ostracoda, Tardigrada and Hydrozoa. The other 23 localities, mainly silty sediments, constitute a second group. The 52 localities are classified into four TWINSPAN groups illustrated by the dendrograph in Fig. 4.

Taxa can be characteristic for more than one group, but often have different importance. Within the four groups we find the following differential taxa.

TWIN 1 : Nemertinea (NERT), Rotifera (ROTI) en Ostracoda (OSTR).
TWIN 2 : Tardigrada (TARD), Hydrozoa (HYDR), Gastrotricha (GAST) en Turbellaria (TURB).
TWIN 3 : Gastrotricha, Tardigrada, Hydrozoa, Nemertinea, Bryozoa (BRYO), Rotifera, Kinorhyncha (KINO) en Turbellaria.
TWIN 4 : Nematoda (NEMA), Copepoda Harpacticoida (HARP), Turbellaria, Polychaeta (POLY), Ostracoda, Halacarida (HALA) en Oligochaeta (OLIG).

Sipunculida (SIPU), Priapulida (PRIA) and interstitial Mollusca (MOLL) do not appear as differential taxa. Well distributed and dominant meiofauna groups are not always acting as the most preferential taxa. For each dichotomy, TWINSPAN selects one or more indicator species. Gastrotricha and Copepoda Harpacticoida act as indicator taxa for the first division. Nemertinea and Gastrotricha are indicator taxa to distinguish respectively TWIN 1-2 and TWIN 3-4. Within the four TWINSPAN groups the indicator taxa are :

TWIN 1 : Rotifera, Ostracoda
TWIN 2 : Ostracoda, Gastrotricha, Tardigrada

TWIN 3 : Kinorhyncha
TWIN 4 : Sipunculida, Halacarida, Harpacticoida.

– *Detrended Correspondence Analysis (DCA)*

The results of the ordination of the taxa and the localities is given in two dimensional diagrams (Figs 5 and 6). The same symbols and abbreviations as for the TWINSPAN analysis are used. Fig. 5 gives the ordination of all localities for the three most important DCA-axes (Fig. 5A : Ax1-Ax2 ; Fig. 5B : Ax1-Ax3). Downweighting of the less important taxa results in similar ordination, both for localities as for taxa. DCA-Ax1 clearly separates the four TWINSPAN locality groups. Nor DCA-Ax2 (Fig. 5A), nor DCA-Ax3 (Fig. 5B) allow to distinguish clearly TWIN 3 from TWIN 4, but they do well separate TWIN 1 from TWIN 2.

The ordination of the seventeen meiofauna groups along the first three DCA-axes is plotted in Fig. 6. Taxa with high preference for silty sediments only (Priapulida, Sipunculida and Bryozoa) are situated in the negative values of Ax 1 of the graphs. The other taxa are more or less randomly distributed in the positive values of Ax 1.

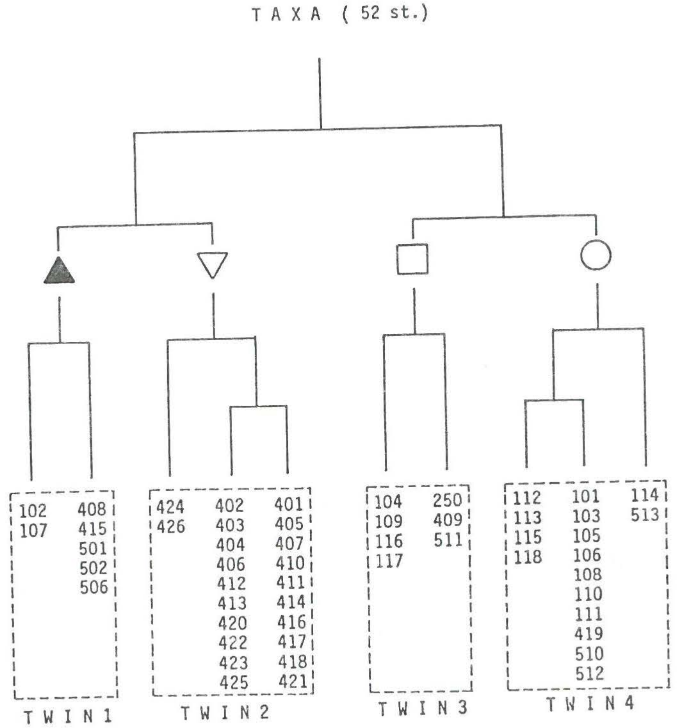


Fig. 4. – Dendrograph of the TWINSPAN classification of the 52 localities. TWIN 1 (▲) ; TWIN 2 (∇) ; TWIN 3 (□) ; TWIN 4 (○).

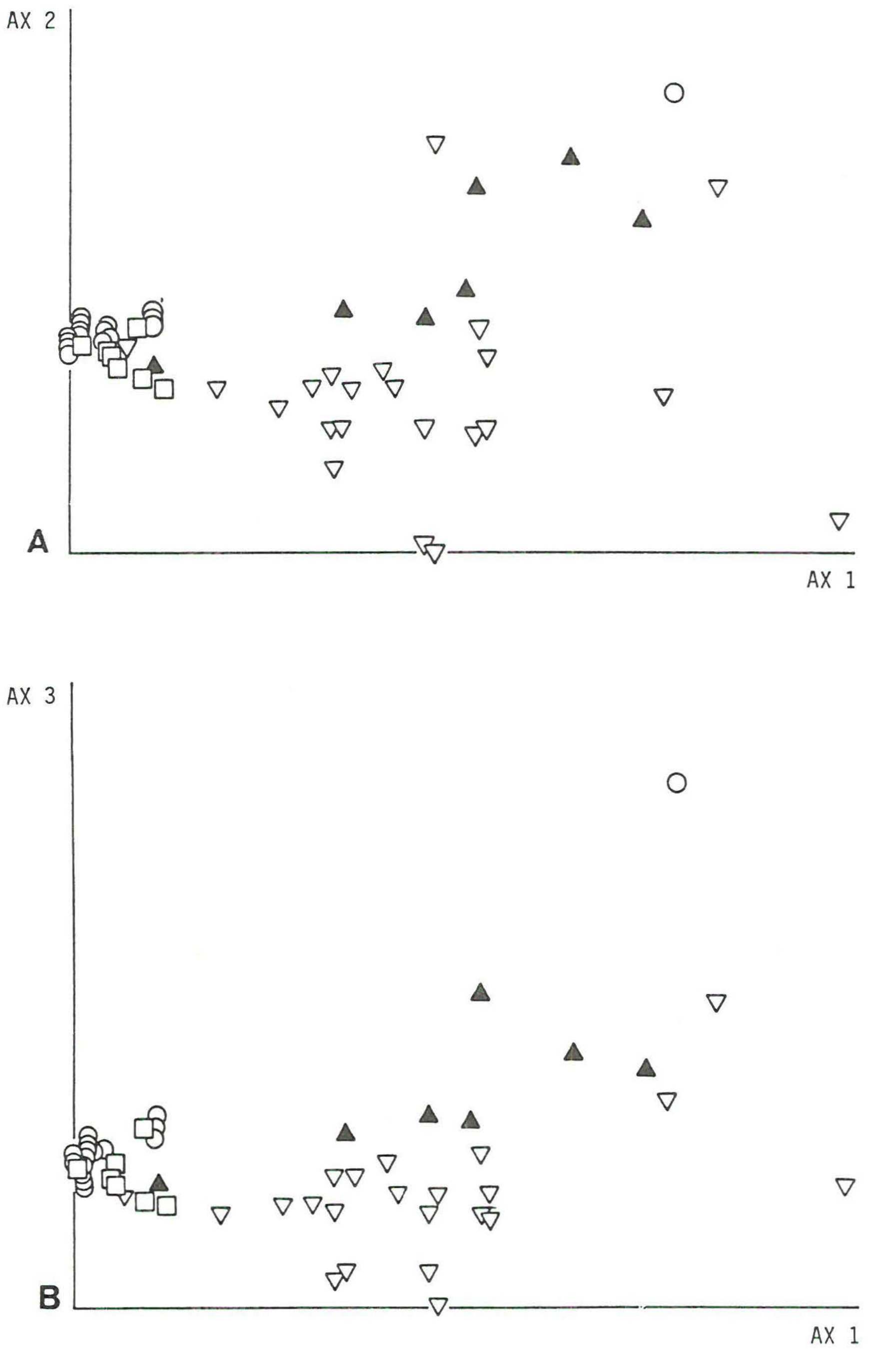


Fig. 5. – Two dimensional DCA-plots for the 52 localities. A : Ax1-Ax2 ; B : Ax1-Ax3. (symbols as in Fig. 4).

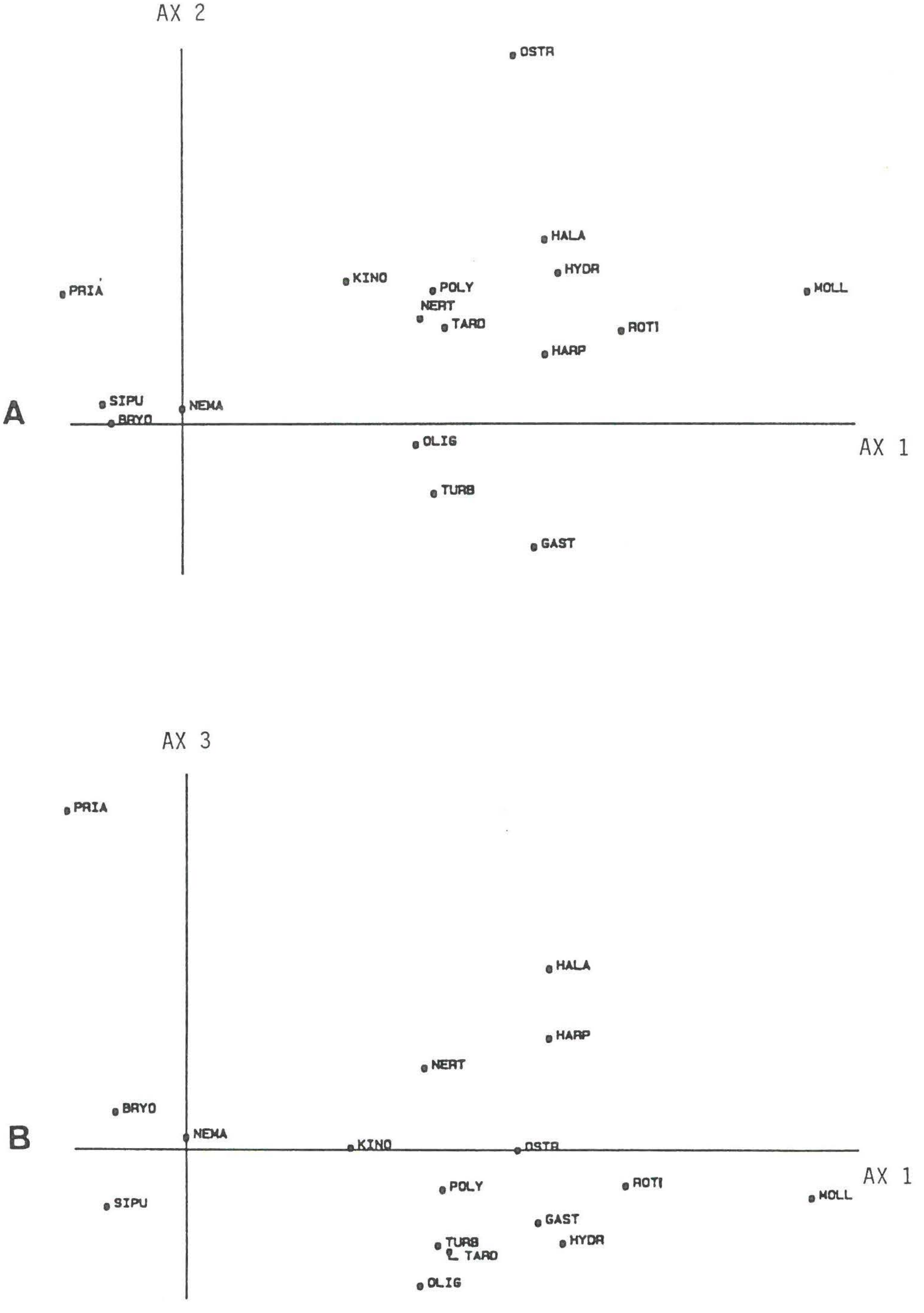


Fig. 6. – Two dimensional DCA-plots for 17 taxa. A : Ax1-Ax2 ; B : Ax1-Ax3. (symbols as in Fig. 4 ; for abbreviations see text).

The TWINSPAN-classification and the DCA-ordination indicate that the locality groups TWIN 1 to TWIN 4 can be considered as entities. Their distribution in the field is illustrated in Fig. 7. Except for two, all localities of the TWIN 1 and the TWIN 2 group are situated in the central part of the study area. TWIN 3 consists of five localities of the Belgian-Dutch coastal zone, one of the central area and one of the northern zone. TWIN 4 groups thirteen localities near the coast and the three most northern ones.

Relation between meiofauna composition and environmental characteristics within the locality groups

– *The environmental characteristics*

The mean values of the environmental parameters for each of the TWINSPAN groups are given in Table 4. As mentioned above there is a strong correlation between these variables. A Kruskall-Wallis analysis of variance results in a significant difference between the four locality groups, except for the sorting and gravel content of the sediments. The ordination of the TWINSPAN groups along the four most principal DCA-axes is also significantly different.

TABLE 4

Mean and standard error for the environmental parameters and for the DCA Ax1-Ax4 for the different TWINSPAN groups and their χ^2 with the significance of the Kruskal-Wallis anova (** p< 0.01 ; *** p<0.001 ; symbols as in table 1)

		TWIN 1 n = 7	TWIN 2 n = 22	TWIN 3 n = 7	TWIN 4 n = 16	χ^2 + sign.
Depth	$\bar{x}$	26.8	31.9	19.6	18.1	8.998
	S.E.	4.2	0.8	6.3	3.9	**
Md µm	$\bar{x}$	299	315	199	173	31.857
	S.E.	22	17	19	13	***
Sort Φ	$\bar{x}$	0.39	0.40	0.42	0.46	5.568
	S.E.	0.02	0.03	0.04	0.03	0.135
Skew Φ	$\bar{x}$	0.001	0.01	0.07	0.15	15.799
	S.E.	0.01	0.01	0.03	0.03	***
% sand	$\bar{x}$	95.5	97.9	84.6	70.8	24.615
	S.E.	2.6	0.3	7.4	5.5	***
% mud	$\bar{x}$	2.0	1.6	14.6	28.9	28.515
	S.E.	0.8	0.2	7.5	5.5	***
% gravel	$\bar{x}$	2.5	0.5	0.8	0.3	3.077
	S.E.	2.0	0.2	0.6	0.1	0.380
DCA ax1	$\bar{x}$	35.4	33.6	4.7	5.9	30.295
	S.E.	5.8	3.3	1.2	3.6	***
DCA ax2	$\bar{x}$	27.6	15.2	19.0	23.4	23.710
	S.E.	2.8	1.9	0.8	1.9	**
DCA ax3	$\bar{x}$	24.1	12.7	15.1	20.0	21.915
	S.E.	2.7	1.6	1.2	2.7	***
DCA ax4	$\bar{x}$	22.7	11.8	14.1	19.0	21.257
	S.E.	2.7	1.5	1.2	2.6	***

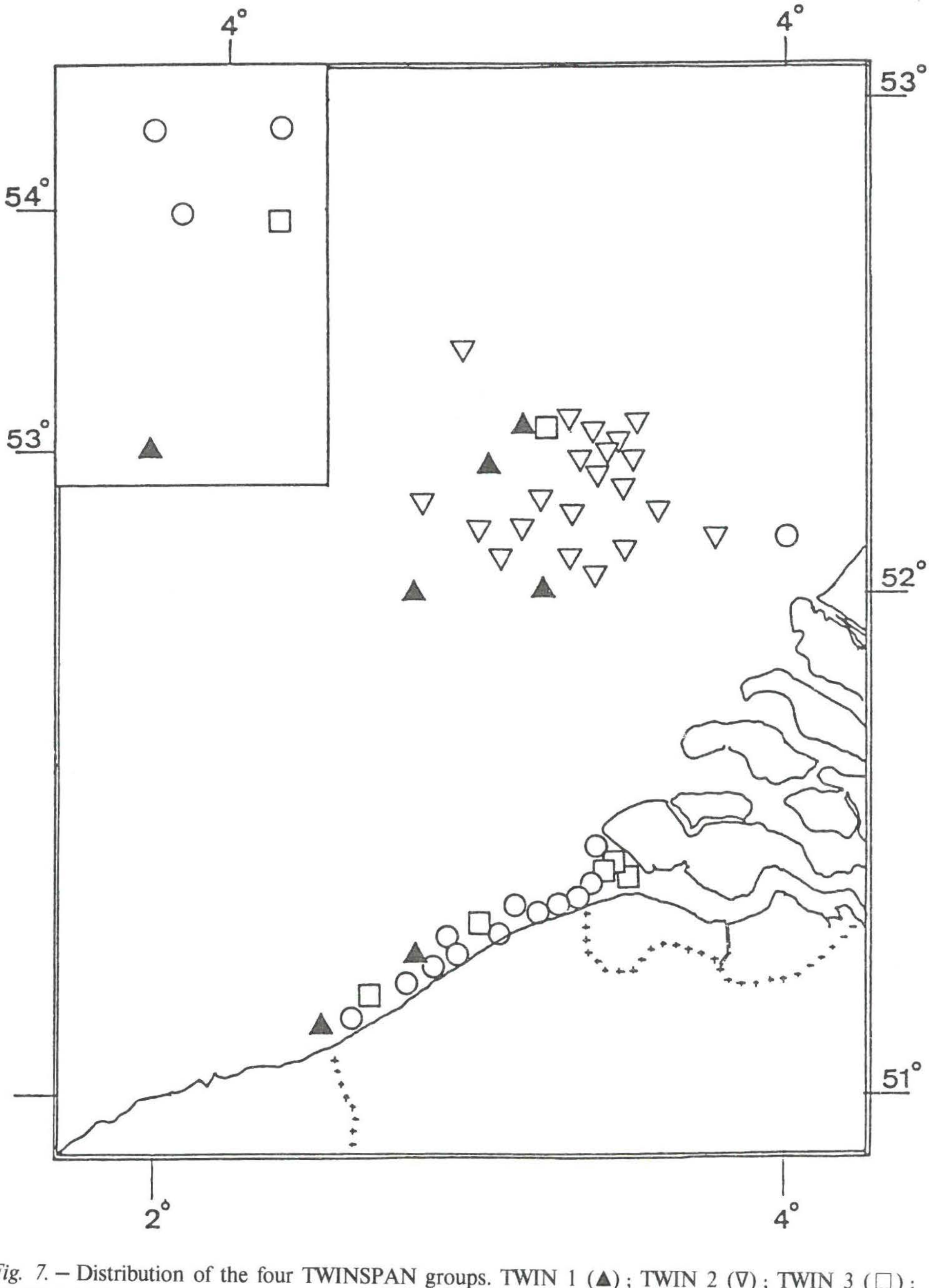


Fig. 7. – Distribution of the four TWINSPAN groups. TWIN 1 (▲) ; TWIN 2 (▽) ; TWIN 3 (□) ; TWIN 4 (○).

Multiple comparison of these observations in pairs between the four groups (after Conover, 1971) is done to define to most important environmental parameter (Table 5). TWIN 1 and TWIN 2 are significantly separated along DCA-Ax2, Ax3 and Ax4. The same is true for their geographic position. TWIN 3 and TWIN 4 cannot be distinguished from each other with one of the abiotic parameters. TWIN 1 and TWIN 2 differ significantly from TWIN 4, and also from TWIN 3. The multiple comparison shows that the median of the sand fraction, the sand and silt content contribute most to separate the TWINSPAN groups from each other, which is mainly visualized along the DCA-Ax1. The geographic position, the sorting and skewness of the sand fraction are less important parameters.

TABLE 5

Multiple comparison of the Kruskal-Wallis one-way anova between the four TWINSPAN groups for the environmental parameters, the DCA Ax1-Ax4 and the community parameters (* : significantly different ; – : not sign. different ; N = mean total density per sample : N_o = S = number of taxa ; Shannon-Wiener index H' ; Brillouin's index H ; Simpson's dominance index SI ; Hill's diversity indices N_1 and N_2 ; evenness indices J, E_{10}, E'_{10}, E_{21} and E'_{21})

	TWIN 1 - TWIN 2	TWIN 1 - TWIN 3	TWIN 1 - TWIN 4	TWIN 2 - TWIN 3	TWIN 2 - TWIN 4	TWIN 3 - TWIN 4
Depth	–	–	–	–	*	–
Md µm	–	*	*	*	*	–
Sort Φ	–	–	–	–	*	–
Skew Φ	–	–	*	–	*	–
% sand	–	*	*	*	*	–
% mud	–	*	*	*	*	–
% gravel	–	–	–	–	–	–
NB	–	–	–	–	*	–
OL	*	–	–	–	–	–
DCA ax1	–	*	*	*	*	–
DCA ax2	*	*	–	–	*	–
DCA ax3	*	*	–	–	*	–
DCA ax4	*	*	–	–	*	–
N	*	*	*	–	–	–
N_o	–	*	*	*	*	*
H'	–	*	*	*	*	*
H	–	*	*	*	*	*
SI	–	*	*	*	*	–
N1	–	*	*	*	*	–
N2	–	*	*	*	*	*
J	–	*	*	*	*	–
N_{10}	–	–	–	–	*	*
N'_{10}	–	*	*	*	*	–
N_{21}	–	*	*	*	*	*
N'_{21}	–	*	*	*	*	–

– *The composition of the meiobenthos in the TWINSPAN groups*

The mean density per meiobenthic taxon, the mean total density and the average number of taxa found per sample is given in Table 6A for each TWINSPAN group. The lowest total density is found in TWIN 1 with an average of 960 ind. 10 cm^{-2}. In the three other groups, densities have about the same magnitude and vary from 1600 ind. 10 cm^{-2} to 1800 ind. 10 cm^{-2}. In TWIN 1 and TWIN 2, a mean of eight to nine taxa per sample is found. In the TWIN 3 and TWIN 4 localities, respectively a mean of 5.3 and 3.4 taxa per 10 cm^2 are present. Table 6B gives the relative abundance for each taxon within the four TWINSPAN groups. Fifteen meiofauna taxa are found in TWIN 1 and twelve in TWIN 2. Nematoda and Harpacticoida contribute respectively about 80% and 10% of the total meiofauna community in these TWIN groups. Turbellaria, Gastrotricha and Polychaeta are regularly present in these localities. Other taxa represent in both locality groups less than 2% of the total meiofauna. In TWIN 3 there are sixteen taxa and in TWIN 4 fourteen. In these locality groups, the Nematoda represent more than 96% of the total meiofauna. Except for Copepoda Harpacticoida and Turbellaria, other taxa are scattered over the localities and their densities are very small.

Diversity of the meiofauna communities

For each sample eleven diversity and evenness indices were calculated. Several localities from the Belgian coastal zone were followed for a long period and show that temporal variability of the diversity within the same locality is rather small (see Herman *et al.*, 1985 and Vincx & Herman, 1989). In the multivariate analysis, we used the mean values for each diversity parameter in the 52 localities.

The overwhelming dominance of one taxon, i.c. the Nematoda, results in rather low diversity values : the mean of the commonly used Shannon-Wiener diversity H' varies between zero and 2,25 bits/ind. The Brillouin's diversitt H varies from zero to 2,21 bits/ind. The highest value noted for Hill's diversity N_1 is 4,76 (loc. 107) (Detailed diversity values are available on request).

Table 7 presents the mean and the standard error for each of the eleven community parameters for the four locality groups. The Kruskal-Wallis analysis of variance demonstrates again significant differences between the four TWINSPAN groups. The mean diversity and evenness indices in TWIN 1 and TWIN 2 are significantly higher than in the other two groups. This is clearly illustrated by multiple comparison (Table 5). Both TWIN 3 and TWIN 4 are significantly different from the other two groups. TWIN 1 and TWIN 2 only have significantly different densities, while TWIN 3 and TWIN 4 differ significantly for the number of taxa, the diversity indices H', H, N_1 and the evenness indices N_{10} and N_{21}. Some differences between the TWINSPAN groups are illustrated in Fig. 8, where the results of the one way anova with an *a posteriori test* for the mean total density N, the mean number of taxa N_0 and Hill's diversities N_1 and N_2 is graphically represented.

TABLE 6

Density per taxon and mean total density (N.10 cm^{-2}) and mean number of taxa per sample for the four TWINSPAN groups

A	TWIN 1	TWIN 2	TWIN 3	TWIN 4
Nematoda	768.0	1236.0	1743.0	1757.0
Harpacticoida	114.88	154.16	23.85	22.08
Turbellaria	32.99	88.31	26.44	3.62
Polychaeta	12.68	13.39	3.49	2.81
Gastrotricha	18.48	67.65	5.90	–
Ostracoda	3.90	5.43	0.60	0.20
Tardigrada	2.33	8.63	1.77	0.11
Hydrozoa	2.64	7.72	0.52	0.01
Halacarida	2.45	0.96	0.27	0.08
Oligochaeta	0.82	4.05	0.95	0.50
Nemertini	0.85	–	0.14	0.03
Sipunculida	0.006	–	0.12	0.03
Priapulida	–	–	0.005	0.08
Bryozoa	–	0.06	0.62	0.16
Rotifera	0.12	–	0.009	–
Kinorhyncha	0.003	0.20	0.58	0.03
Mollusca	0.05	–	–	–
Total	960	1587	1809	1787
Taxa (mean/sample)	8.0	8.6	5.3	3.4

Mean relative abundance per taxon per TWINSPAN group (%)

B	TWIN 1	TWIN 2	TWIN 3	TWIN 4
Nematoda	80.00	77.88	96.35	98.32
Harpacticoida	11.97	9.71	1.32	1.24
Turbellaria	3.44	5.56	1.46	0.20
Polychaeta	1.32	0.84	0.19	0.16
Gastrotricha	1.93	4.26	0.33	–
Ostracoda	0.41	0.34	0.03	0.01
Tardigrada	0.24	0.54	0.10	0.01
Hydrozoa	0.28	0.49	0.03	*
Halacarida	0.26	0.06	0.01	*
Oligochaeta	0.09	0.26	0.05	0.03
Nemertini	0.09	–	0.01	*
Sipunculida	*	–	0.01	*
Priapulida	–	–	*	*
Bryozoa	–	*	0.03	0.01
Rotifera	0.01	–	*	–
Kinorhyncha	*	0.01	0.03	*
Mollusca	0.01	–	–	–
Total (N.10cm^{-2})	960	1587	1809	1787
Taxa taxa/sample)	8.0	8.6	5.3	3.4

* < 0.01%

TABLE 7

Mean and standard error for the different community parameters for the four TWINSPAN groups and their χ^2 with the significance of the Kruskal-Wallis anova (** $p < 0.01$; *** $p < 0.001$; symbols as in Table 5)

		TWIN 1 n = 7	TWIN 2 n = 22	TWIN 3 n = 7	TWIN 4 n = 16	χ^2 + sign.
N	$\bar{x}$	960	1587	1803	1790	7.571
	S.E.	230	118	196	279	**
N_0	$\bar{x}$	9.0	8.6	5.3	3.5	36.061
	S.E.	0.5	0.2	0.7	0.4	***
H'	$\bar{x}$	1.16	1.15	0.35	0.17	37.837
	S.E.	0.11	0.07	0.07	0.03	***
H	$\bar{x}$	1.13	1.14	0.34	0.15	37.873
	S.E.	0.10	0.07	0.07	0.03	***
SI	$\bar{x}$	0.61	0.63	0.90	0.95	36.804
	S.E.	0.04	0.03	0.02	0.01	***
N_1	$\bar{x}$	2.34	2.31	1.32	1.13	36.127
	S.E.	0.17	0.11	0.08	0.02	***
N_2	$\bar{x}$	1.74	1.70	1.16	1.06	37.482
	S.E.	0.10	0.08	0.04	0.01	***
J	$\bar{x}$	0.38	0.37	0.14	0.09	35.878
	S.E.	0.03	0.02	0.03	0.01	***
N_{10}	$\bar{x}$	0.30	0.27	0.31	0.43	11.682
	S.E.	0.03	0.01	0.05	0.04	**
N'_{10}	$\bar{x}$	0.19	0.18	0.07	0.05	33.095
	S.E.	0.02	0.02	0.02	0.01	***
N_{21}	$\bar{x}$	0.75	0.74	0.89	0.94	38.239
	S.E.	0.02	0.01	0.02	0.01	***
N'_{21}	$\bar{x}$	0.51	0.49	0.35	0.30	34.916
	S.E.	0.02	0.02	0.02	0.02	***

The relationship between the diversitt indices and the environmental characteristics is examined by means of a Spearman rank correlation (Table 8). It shows that the total meiofauna density is not correlated with any environmental parameter. No correlation is found between the gravel content, eastern length (EL) position and the biological parameters examined. On the other hand, the geographical position on the South-North-axis is significantly correlated with the meiofauna composition. All community parameters, except for the evenness E_{10}, are strongly correlated with the following three, related environmental parameters : median grain size of the sand fraction, silt and sand content.

Biomass of the meiofauna communities

Biomass of the meiofauna communities is determined by summation of taxon biomasses per locality. When, for nematodes, density is too small for biomass

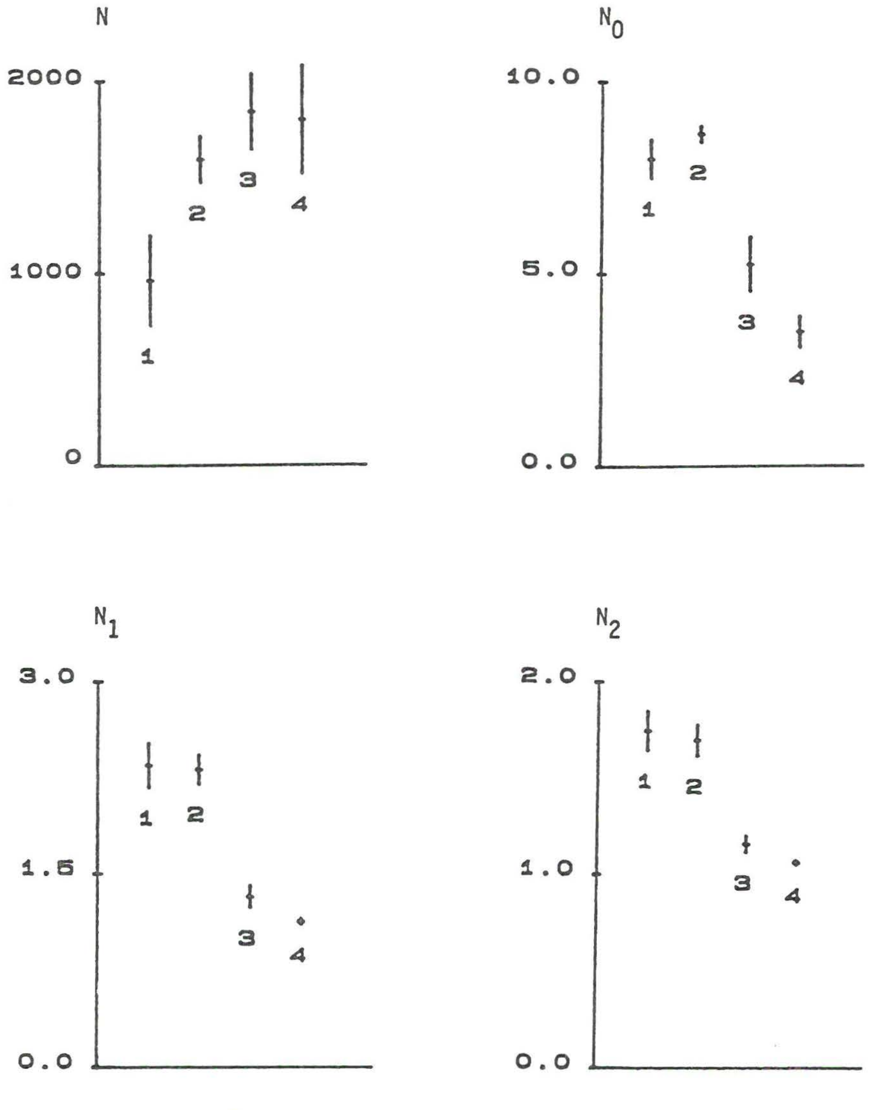


Fig. 8. – Mean total meiofauna density N and mean Hill's diversity numbers N_0, N_1 and N_2 for the four TWINSPAN groups (symbols as in Table 5).

TABLE 8

Spearman rank correlation r_s with their significance between environmental characteristics and the community parameters (symbols as in Table 5)

		N	N_0	H'	H	SI	N_1	N_2	J	E_{10}	E'_{10}	E_{21}	E'_{21}
Depth	rs	0.0530	0.5732	0.2738	0.2732	- 0.2353	0.2690	0.2209	0.2182	- 0.5032	0.1631	- 0.4476	0.2399
	sign	.668	.001***	.024**	.024**	.053	.027**	.070	0.74	.001***	.184	.001***	.049**
Md µm	rs	- 0.1394	0.7732	0.6798	0.6784	- 0.6496	0.6750	0.6376	0.6431	- 0.2449	0.5704	- 0.7212	0.5796
	sign	.257	.001***	.001***	.001***	.001***	.001***	.001***	.001***	.015***	.001***	.001***	.001***
Sort Φ	rs	0.0809	- 0.2070	- 0.2493	- 2554	0.2174	- 0.2440	- 0.2539	- 0.2743	0.1313	- 0.2163	0.2300	- 0.4008
	sign	.512	.090***	.040**	.036**	.022**	.045**	.037**	.024**	.286	.031**	.059	.001***
Skew Φ	rs	0.1908	- 0.4887	- 0.3976	- 0.4002	0.3878	- 0.3881	- 0.3661	- 0.3659	0.4560	- 0.3129	0.4475	- 0.4016
	sign	.119	.001***	.001***	.001***	.001***	.001**	.002**	.002**	.003**	.009**	.001***	.001***
% sand	rs	- 0.1394	0.6450	0.5490	0.5502	- 0.5327	0.5404	- 0.5020	0.5196	- 0.3490	0.4657	- 0.6299	0.5588
	sign	.257	.001***	.001***	.001***	.001***	.001***	.001***	.001***	.004**	.001***	.001***	.001***
% mud	rs	0.1540	- 0.6922	- 0.5779	- 0.5791	0.5608	- 0.5697	- 0.5296	- 0.5444	0.3766	- 0.4981	0.6698	- 0.5678
	sign	.210	.001***	.001***	.001***	.001***	.001***	.001***	.001***	.002**	.001***	.001***	.001***
% gravel	rs	0.473	0.2203	0.2207	0.2178	0.2141	0.2334	0.2300	0.2119	- 0.0523	0.2205	- 0.2230	0.1250
	sign	.702	.071	.070	.074	.080	.017	.059	.083	.672	.071	.068	.310
NB	rs	- 0.0319	0.6020	0.3614	0.3639	- 0.3334	0.3533	0.3067	0.3257	- 0.4919	0.2559	- 0.5094	0.3671
	sign	.796	.001***	.002**	.002**	.005**	.003**	.011**	.007**	.001***	.035**	.001***	.002**
EL	rs	0.0477	0.1023	0.0751	0.0752	0.0565	0.0724	0.0521	0.0702	- 0.1261	0.0431	- 0.0477	0.0835
	sign	.699	.406	.543	.542	.647	.558	.673	.570	.305	.727	.699	.498

determination with a microbalance, it is calculated from individual dry weight per season. This is only necessary for some localities off the Belgian coast. In summer the mean individual dry weight is 0,325 µg dwt. ind^{-1}, for the winter samples the mean biomass is 0,441 µg dwt. ind^{-1}. The average nematode dry weight in TWIN 1, TWIN 2 and TWIN 3 is approximately 0.5 µg dwt. ind^{-1} and 0.31 µg dwt. ind^{-1} in TWIN 4.

Biomass estimations of the Copepoda Harpacticoida are based on the selection of each specimen into one of the five biomass classes, resulting in an accurate estimation of the harpacticoid biomass. The average individual copepod biomass for TWIN 1 to TWIN 4 is respectively 0.55 µg dwt, 0.36 µg dwt, 0.76 µg dwt and 1.02 µg dwt.

For all other meiofauna taxa, the individual biomass is defined from literature data (Dumont *et al.*, 1975 ; Hummon, 1976 ; McIntyre, 1978 ; Ankar & Elmgren, 1978 ; Van Damme *et al.*, 1980 ; Faubel, 1982 ; McLachlan *et al.*, 1981 ; Faubel *et al.*, 1983 ; Widbom, 1984 ; Grant en Swinghamer, 1987). Following individual dry weights were used : Turbellaria (3.5 µg dwt), Gastrotricha (0.7 µg dwt), Ostracoda (7,8 µg dwt), Tardigrada (0,5 µg dwt), Hydrozoa (1,6 µg dwt), Halacarida (0,6 µg dwt), Bryozoa (5 µg dwt), Rotifera (0,1 µg dwt) and Kinorhyncha (1,2 µg dwt). Polychaeta, Nemertinea and Mollusca are estimated on 10 µg dwt per individual, for Oligochaeta, Sipunculida and Priapulida we used a mean of 20 µg dwt per individual.

The mean biomass for each taxon is given per TWINSPAN group in Table 9A. The total mean biomass differs significantly between the locality groups (χ^2 = 24,87 ; $p < 0{,}001$). The highest value is noted for TWIN 2 with a mean total biomass of 1416 µg dwt. 10 cm^{-2}, due to the higher number of taxa such as Turbellaria, Polychaeta, Oligochaeta and Hydrozoa. In TWIN 3, the mean of 1062 µg dwt. 10 cm^2 is due to the high score of the Nematoda (872 µg dwt. 10 cm^{-2}). Turbellaria, Polychaeta and Harpacticoida are less important in this locality group. The same is true for TWIN 1 with a mean total biomass of 803 µg dwt. 10 cm^{-2}. The lowest value of 623 µg dwt. 10 cm^{-2} is found in TWIN 4.

The relative propostion of each taxon in the four groups is given in Table 9B. In TWIN 1 and TWIN 2, the Nematoda represent respectively 46,15% and 43,64% of the total biomass ; in TWIN 3 and TWIN 4 this is respectively 82,11% en 87,48%. The biomass of the five most dominant taxa in TWIN 1 is 84,43%, in TWIN 2 82,19%, in TWIN 3 and TWIN 4 respectively 96,40% and 97,63%. The importance of Nematoda is reduced and Harpacticoida are surpassed by Turbellaria or Polychaeta in terms of biomass. This shift is clearly illustrated in Fig. 9. This is obvious for TWIN 1 and TWIN 2, in which other meiofauna taxa clearly reduce the dominant role of the Nematoda. In the silty localities of TWIN 3 and TWIN 4 the overdominance of the nematode density is more or less reduced in terms of biomass by the Harpacticoida. Turbellaria and Polychaeta.

TABLE 9

Mean biomass per taxon and total biomass per sample for the four TWINSPAN groups (μ dwt.10 cm^{-2})

A	TWIN 1	TWIN 2	TWIN 3	TWIN 4
Nematoda	384	618	872	545
Harpacticoida	63.18	55.50	18.13	22.52
Turbellaria	115.47	309.09	94.54	12.67
Polychaeta	126.90	133.90	34.90	28.10
Gastrotricha	12.94	47.36	4.13	–
Ostracoda	30.42	42.35	4.68	1.56
Tardigrada	1.17	4.32	0.88	0.06
Hydrozoa	42.24	123.52	8.32	0.16
Halacarida	1.47	0.58	0.16	0.05
Oligochaeta	16.40	81.00	19.00	10.00
Nemertini	8.50	–	1.40	0.30
Sipunculida	0.12	–	2.40	0.60
Priapulida	–	–	0.10	1.60
Bryozoa	–	0.30	3.10	0.80
Rotifera	0.01	–	*	–
Kinorhyncha	*	0.24	0.70	0.04
Mollusca	0.50	–	–	–
Total	803	1416	1062	623

* < 0.01 μg dwt

Mean relative biomass per taxon per TWINSPAN group (%)

B	TWIN 1	TWIN 2	TWIN 3	TWIN 4
Nematoda	46.15	43.64	82.11	87.48
Harpacticoida	7.59	3.92	1.71	3.61
Turbellaria	13.88	21.83	8.90	2.03
Polychaeta	15.25	9.46	3.29	4.51
Gastrotricha	1.56	3.34	0.39	–
Ostracoda	3.66	2.99	0.44	0.25
Tardigrada	0.14	0.31	0.08	0.01
Hydrozoa	5.08	8.72	0.78	2.57
Halacarida	0.18	0.04	0.02	0.01
Oligochaeta	1.97	5.72	1.79	1.61
Nemertini	1.02	–	0.13	0.05
Sipunculida	0.01	–	0.23	0.10
Priapulida	–	–	0.01	0.26
Bryozoa	–	0.02	0.29	0.13
Rotifera	*	–	*	–
Kinorhyncha	*	0.02	0.07	0.01
Mollusca	0.06	–	–	–
Total (mg dwt.m^{-2})	803	1416	1062	623

* < 0.01%

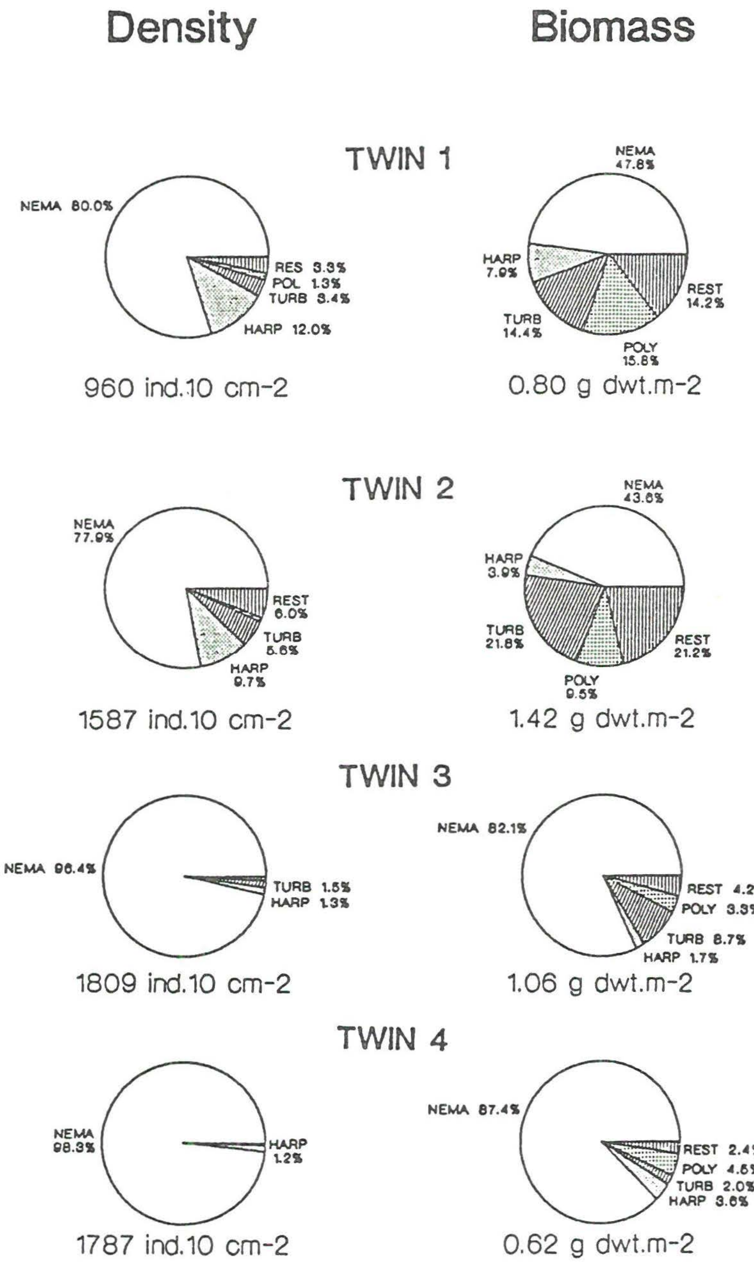


Fig. 9. – Mean relative abundance and biomass of the four most dominant taxa : Nematoda (NEMA). Harpacticoida (HARP), Turbellaria (TURB), Polychaeta (POLY) and the remainder (REST) of the meiofauna in the four TWINSPAN groups.

DISCUSSION

The results presented above are an attempt to use more objective data analysis techniques for a better approach to define meiofauna communoity structures. The overall mean values for all variables have been used for the analysis in order to exclude the time induced variability (e.g. seasonality, reproductive activity) and physical induced changes (e.g. wave action, storms and gales). Remane (1933) already postulated that meiobenthic species are more stenotopic than macrobenthic ones and consequently are more suitable to characterize benthic communities. Later on, Por (1964), Coull & Herman (1970), Fenchel (1978), McLachlan *et al.* (1981) and Hicks & Coull (1983) confirm these findings and demonstrate that the most diverse and heterogeneous meiofauna communities are found in sandy sediments. Meiofauna is characterized by a high number of cosmopolitic genera, while the species composition is strongly regionally dependent.

Nematoda, Copepoda Harpacticoida and Turbellaria occur in all localities of the Southern Bight of the North Sea. The fact that Sipunculida, Priapulida and interstitial Mollusca are sporadically found in the study sites may be related to their scarceness and the sampling methods used. The distribution of the other taxa is correlated with the sediment type, mainly medium to coarse sands, in which the presence of interstitial space may enhance the development of diverse meiofauna communities. The most dominant taxa are in decreasing order of importance : Nematoda, Copepoda Harpactocoida, Turbellaria, Gastrotricha and Polychaeta. The same sequence is found in littoral zones (Schmidt, 1969 ; Renaud-Debyser & Salvat, 1963 ; Reise, 1987 ; Armonies & Hellwig-Armonies, 1987), in sublittoral areas (McIntyre, 1978 ; Faubel *et al.*, 1983 ; Heip *et al.*, 1984), and in the deep sea (Thiel, 1979 ; Dinet, 1980 : Rutgers van de Loeff & Lavaleye, 1986).

As in nearly all marine environments the meiofauna community is dominated by nematodes. In sandy habitats exceptional dominance of Gastrotricha (Coull, 1973) and Turbellaria (Martens & Schockaert, 1981 ; Martens *et al.*, 1985) may occur. On algae the meiofauna is regularly dominated by Copepoda Harpacticoida (Coull & Wells, 1983).

The mean total meiofauna density is about $1{,}6.10^6$ ind. m^2 and is agreement with the values found in temporate boreal areas (Heip *et al.*, in press). The very high values (12 and 19.10^6 ind. m^{-2}) recorded in this study are not exceptional. Warwick & Price (1070) found a peak density of 22.10^6 ind. m^{-2}, Van Damme *et al.* (1980) 17.10^6 ind. m^{-2} and Lasserre *et al.* (1975) a maximum of 12.10^6 ind. m^{-2}.

The lack of sufficient interstitial spaces results in changes of the community composition, because meiofauna is able to adapt to changing environmental conditions (Levy & Coull, 1977). The optimal size of interstitial organisms can be reduced to spheres of 0.5 to 1 mm, once this size surpassed they start a burrowing life (Schwinghamer, 1981). In soft sediments there is no size limit for burrowing organisms. This is clearly demonstrated in the composition of the meiofauna communities of the four TWINSPAN groups and their relation to the environmental characteristics. An increasing silt content results in super dominance of the Nematoda. In extreme situations, nematodes may be the only surviving taxon. This phenomenon is also found in Dutch waters (Smol *et al.*, 1986 ; Huys, Vanreusel & Heip, 1986), in the German Bight (Juario, 1975) and in the North of France (Bodin, 1984).

Apart from the sediment characteristics, other factors such as food availability and quality, light and turbidity, may be important in the development of meiobenthic communities. Wollast (1976) found in the Belgian coastal area a high concentration of organic material, of which an important amount incorporates into the sediment. Bouquegneau *et al.* (1985) recorded organic material from planktonic origin (e.g organic nitrogen and chlorophyl a) up to several centimeters into the sediment. The bulk of this material is remineralized by bacterial activity (up to 78% ; Billen & Lancelot, 1988). The high concentration of organic material and the related bacterial biomass in the Belgian coastal area increases the number of bacterivorous Nematoda (Vinx, 1986 ; Vincx, in press, b). Moreover, high turbidity and poor light conditions in this area are not favourable for development of other Metazoa.

The complexity of the meiofauna communities is also illustrated in the diversity indices. This information, combined with the results of the multivariate analysis of the community composition, gives a qualitative approach of the meiofauna communities within each locality group. The relative low number of taxa (max. 17) enhances the importance of their relative proportions in the qualitative appreciation of the meiofauna communities. In spite of the very high dominance of the Nematoda, the different diversity indices can separate the meiofauna communities in the four locality groups.

The importance of the Nematoda in terms of biomass is significantly lower than in terms of density. This is clearly reflected in the sandy sites of TWIN 1 and TWIN 2, where the nematode biomass is less than half of the total biomass, which is mainly due to the presence of specimens with high individual biomass, such as Turbellaria, Polychaeta, Oligochaeta and Hydrozoa.

It is clearly demonstrated that the number of meiobenthic taxa, their relative abundance and their biomass are strongly related to environmental characteristics. This is reflected in their community structures. One of the main characteristics of the meiofauna is that a large number of species have a high turn-over rate, so that they may quickly respond to environmental changes. The shift towards dominance of one meiobenthic group may indicate the presence of more opportunistic species within that group.

Between the locality groups, differences in density, biomass and especially in diversity are more pronounced than in other areas investigated as e.g. Heip *et al.* (1983) ; Vanreusel (1989). This indicates that environmental characteristics, others than those related to sediment may be involved, directly or indirectly, in structuring meiofauna communities. Although, factors controlling this differentation are hard to define. To distinguish on the one hand, effects of changing environmental conditions (light, input of nutrients, sediment composition) and on the other hand effects of anthropogenic origin, the fauna has to be analysed at a lower taxonomic level (preferably at species level). Besides this, more autoecological information and experimental work about the reactions of organisms to natural and anthropogenic effects is needed to fully understand the structuring of meiobenthic communities.

SAMENVATTING

In de periode 1977-1985 hebben we van 52 localiteiten in de Zuidelijk Bocht van de Noordzee de algemene meiofaunasamenstelling in relatie tot de omgevingsfactoren onderzocht. De sedimentsamenstelling is duidelijk gecorreleerd met de geografische ligging : het sublittoraal van de Belgische Westkust is gekenmerkt door zandige substraten, terwijl voor de Oostkust slibrijke sedimenten domineren ; de mediane korrelgrootte van de zandfraktie neemt af naar het Noorden van het studiegebied.

In totaal zijn er 522 monsters onderzocht, verdeeld over 322 staalnames, waarbij vertegenwoordigers uit 17 verschillende hogere taxonomische groepen of meiobenthos-taxa zijn aangetroffen. De vier taxa die vrijwel in elke localiteit voorkomen zijn de Nematoda, de Copepoda Harpacticoida, de Turbellaria en de Polychaeta. Een aantal groepen hebben soms hoge dominanties en worden in meer dan 2/3 van de localiteiten aangetroffen : de Oligochaeta, de Gastrotricha, de Tardigrada, de Halacarida, de Hydrozoa en de Ostracoda. Andere taxa worden sporadisch in minder dan 20% van de lokaliteiten aangetroffen. Tot deze groep behoren de Nemertinea, de Rotifera, de Kinorhyncha, de Bryozoa, de Sipunculida, de Priapulida en tenslotte de interstitiële Mollusca.

De gemiddelde totaaldensiteit bedraagt 1594 ind. 10 cm^{-2}. De gemiddelde abundantie van de Nematoda schommelt tussen de 13 ind. 10 cm^{-2} en 19000 ind. 10 cm^{-2}. De densiteit voor de andere dominante taxa bedraagt gemiddeld 99 ind. 10 cm^{-2} (Copepoda Harpacticoida), 47 ind. 10 cm^{-2} (Turbellaria), 33 ind. 10 cm^{-2} (Gastrotricha), 9 ind. 10 cm^{-2} (Polychaeta) en 2 ind. 10 cm^{-2} (Oligochaeta). Tardigrada, Halacarida, Hydrozoa en Ostracoda worden regelmatig aangetroffen. Hun gemiddelde abundantie is meestal lager dan 5 ind. 10 cm^{-2}. De bijdrage van de andere taxa in de totale densiteit is vrijwel te verwaarlozen.

Door het toepassen van multivariate analysemethoden (TWINSPAN en DCA) zijn de 52 localiteiten in vier groepen onderverdeeld.

– Een eerste groep (TWIN 1) wordt door zeven localiteiten gevormd waarvan twee voor de Belgische Westkust en de andere vijf in open zee liggen. Het substraat is door medium zanden gekenmerkt die kleine hoeveelheden grind (2,5%) en slib (2%) bevatten. De meiofaunagemeenschappen bestaan uit gemiddele acht hogere taxa per staal. De gemiddelde totaaldensiteiten zijn significant lager dan in de andere TWIN-

SPAN-groepen. Als karakteristieke meiofaunataxa treden Nemertinea en in mindere mate de Ostracoda naar voren.

– De tweede groep (TWIN 2) bestaat uit 22 localiteiten die alle in het centrale, open zee gedeelte van het studiegebied liggen. Het sediment bestaat hoofdzakelijk uit gemiddelde zanden met een zeer laag slib- en grindgehalte (resp. 1,6% en 0,5%). Hier treft men gemiddeld meer dan acht verschillende hogere taxa per staal aan, waarbij de Tardigrada, de Hydrozoa, de Gastrotricha en de Turbellaria kenmerkend zijn.

– De derde groep (TWIN 3) bestaat eveneens uit zeven localiteiten, waarvan vijf dicht tegen de Belgische kust aanliggen. Het sediment bestaat uit fijn zand met een gemiddeld slibgehalte van 14,6%. Meestal wordt een intermediair aantal hogere taxa aangetroffen. Tot de kenmerkende taxa behoren de Nemertinea, de Bryozoa, de Kinorhyncha, de Rotifera en de Turbellaria.

– De vierde groep (TWIN 4) bestaat uit zestien localiteiten waarvan er drie in het dieper noordelijk deel van het studiegebied zijn gesitueerd. De andere liggen tegen de Belgisch-Nederlandse kust aan. Ze zijn door fijne substraten gekarakteriseerd die bestaan uit een mengeling van zeer fijne tot fijne zanden met een vrij hoog gehalte aan slib (28,9%). Hierin worden de armste meiofaunagemeenschappen aangetroffen. Deze bestaan uit gemiddeld 3,4 hogere taxa, waarvan de Nematoda, de Copepoda Harpacticoida, de Turbellaria, de Polychaeta en de Halacarida de meest kenmerkende zijn .

Voor elk van de 322 staalnames werden in totaal elf verschillende diversiteits- en evennessindices berekend. De hoge dominantie van de Nematoda, vooral in de kustlocaliteiten, maakt dat diversiteitswaarden zeer laag zijn. De Shannon-Wiener diversiteit H' schommelt tussen nul en 2,25 bits/ind. De Brillouin's diversiteit H varieert van nul tot 2,21 bits/ind. Alle gemeenschapsparameters zijn hoog significant met de volgende sterk gerelateerde omgevingsparameters gecorreleerd : mediane korrelgrootte (Mdµm), slibgehalte en zandgehalte. Alleen de evenness E_{10} vertoont een iets mindere correlatie. De vier localiteitengroepen zijn op basis van de diversiteit duidelijk van elkaar te onderscheiden. TWIN 1 en TWIN 2 hebben beduidend hogere diversiteiten dan TWIN 3 en TWIN 4 (en dit voor alle indices). De biomassa van de gemeenschappen, bepaald door de sommatie van de biomassa's van de taxa per localiteit, zijn tussen de TWINSPAN-groepen significant verschillend. De totale biomassa heeft de hoogste waarde in TWIN 2 met gemiddeld 1416 µg dwt. 10 cm^{-2}. In TWIN 3 is de gemiddelde biomassa 1062 µg dwt. 10^{-2}, 803 µg dwt. 10 cm^{-2} in TWIN 1 en 623 µg dwt. 10 cm^{-2} in TWIN 4. In zandige sedimenten vermindert het belang van de Nematoda in termen van biomassa . In de localiteiten van TWIN 1 en TWIN 2 maken de Nematoda respectievelijk 46% en 44% van de totale biomassa uit. In de slibrijkere localiteiten van TWIN 3 en TWIN 4 is deze bijdrage respectievelijk 82% en 87%.

De samenstelling van de meiofaunagemeenschappen in de Zuidelijke Bocht van de Noordzee is in overeenstemming met deze gevonden in gematigde boreale wateren (zoals de Engelse kustwateren en Duitse Bocht). Het aantal meiofauna-taxa, de relatieve abundantie en de biomassa wordt vooral door strukturele fysische parameters bepaald en is duidelijk met deze gecorreleerd. Dit bevestigt de algemene stelling dat de samenstelling van het sediment één van de belangrijkste factoren in de struktureering van de bodemgemeenschappen is.

Binnen de entiteiten *zand* en *slib* treden verschillen in densiteit, biomassa en vooral in diversiteit sterker naar voren dan in tot nu toe onderzochte biotopen. Dit kan erop wijzen dat antropogene invloeden meer impact uitoefenen op de gemeenschapsstruktuur op het niveau van het taxon dan de natuurlijke omgevingsvormen. Deze differentiële uiting kan eventueel worden gebruikt om een onderscheid te maken tussen, enerzijds de effecten van wisselende omgevingsvariabelen (zoals samenstelling van het sediment, licht, diepte ...) en anderzijds de effecten veroorzaakt door een of ander vorm van pollutie.

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