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FREE-LIVING MARINE NEMATODES
FROM THE SOUTHERN BIGHT
OF THE NORTH SEA

BY

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INTRODUCTION

Free-living marine nematodes are bottom-living organisms which occur in a wide range of habitats, often numbering millions per m^2 ; they are small worms (mostly between 1 and 2 mm long) and structurally rather simple; they are the most abundant animals (mean dominance approximates 90%) of the meiobenthos. The meiobenthos comprises small organisms, mainly metazoans, which are separated from the larger macrobenthos either on a methodological basis (i.e. all animals passing a 1 mm or a 0.5 mm sieve) or a taxonomic basis (i.e. particular animal groups such as Nematoda, Harpacticoida, Turbellaria, Gastrotricha, Kinorhyncha, Tardigrada, Foraminifera etc. which consist exclusively or mainly of small species living in and on the sediments). Meiobenthos comprises one of the most numerous groups of organisms in littoral and sublittoral soft-bottom communities. In spite of their large numbers and ubiquitous presence in marine sediments, little is known about the factors controlling abundance and distribution of the meiobenthos. Gerlach (1971) postulated that meiofauna may be five times more important energetically than macrofauna in benthic systems due to their small size and higher turnover rates. However, the trophic role of the meiofauna is not well established. Some studies have suggested that meiofauna is food for higher trophic levels (Sibert *et al.*, 1977), yet other studies pretend that meiofauna acts primarily in nutrient regeneration (Tenore *et al.*, 1977). Coull & Bell (1979) have suggested that the specific role of the meiofauna may vary according to habitat. In muds, meiofauna is restricted to surface layers and is probably available as food, while in sands the meiofauna lives at greater depths and is not grazed upon. Some theories of meiofauna control have focused on intrameiofaunal predation (McIntyre, 1971; McIntyre & Murison, 1973; Heip & Smol, 1975) or physical factors (Coull, 1969; Hullings & Gray, 1976). More recent studies indicate that meiofauna-macrofauna associations must be evaluated in benthic systems (e.g. Bell, 1980). Although the meiofauna seems to share many ecological

properties with the macrofauna, processes operate on a much smaller and shorter time scale within the meiofauna (e.g. Warwick, 1984).

Despite their basically uniform morphology, nematodes occupy very different trophic positions within the meiobenthos. The diversity in feeding is reflected in species diversity. The number of nematode species in most sites is much higher than that of any other metazoan taxon (Platt & Warwick, 1980). In all, about 4000 species of free-living marine nematodes, belonging to some 450 genera have been described to date.

Until about 1950, the knowledge of free-living marine nematodes from European waters was restricted to their taxonomy. Taxonomic research on marine nematodes started in the intertidal zone as this environment can be sampled more easily than the subtidal region. The study of the nematodes from the sublittoral area of the Southern Bight of the North Sea is the aim of this study.

Ecological work of sublittoral nematode communities (at the species or genus level) in and near to the North Sea is limited to less than ten studies: British coast (Warwick & Buchanan, 1970, 1971; Ward, 1973, 1975), French coast (Boucher, 1980; Gourbault, 1981) and German Bight (Lorenzen, 1974; Juario, 1975). The study of the benthos in the Southern Bight of the North Sea started in 1971 with the "Mathematical Model of the North Sea" and was continued from 1976 on with the "Concerted Actions in Oceanography".

MATERIAL AND METHODS

The nematode communities from 102 stations in the Southern Bight of the North Sea, sampled between 1972 till 1984 are examined in this study. The position of the stations is shown in Fig. 1 and the geographic position is given in Table 1. (exact sampling dates are available on request).

56 stations were sampled during 1971-1975 within the framework of the "Projekt Zee" (all stations with prefix 'M' in Table 1). All stations were sampled in 1972 (2 to 3 times) but in the other years samples were taken on an irregular basis. Since sampling during different seasons was only done in 1972 for most stations, I decided to examine all the samples of 1972 in order to get a survey of species occurrence over the whole area. From 1976 on, 16 new stations were examined on a seasonal basis (stations 10061 to 11315 in Table 1 and Fig. 1). In September 1978, the meiofauna of the Kwintebank (stations with prefix 'SB') was examined (see Willems *et al.*, 1982a & b). In June 1984 the meiofauna of the stations with prefix 'H' was analysed.

The meiofauna samples collected from 1971-1975 were taken by subsampling a 0.1 m² Van Veen grab, pushing the plastic cores through a small hatch at the upper side of the grab into the collected sediment to a depth of minimum 10 cm. From April 1978 on, a modified Reineck-boxcorer (surface 170 cm²) (Farris & Crezee, 1976)

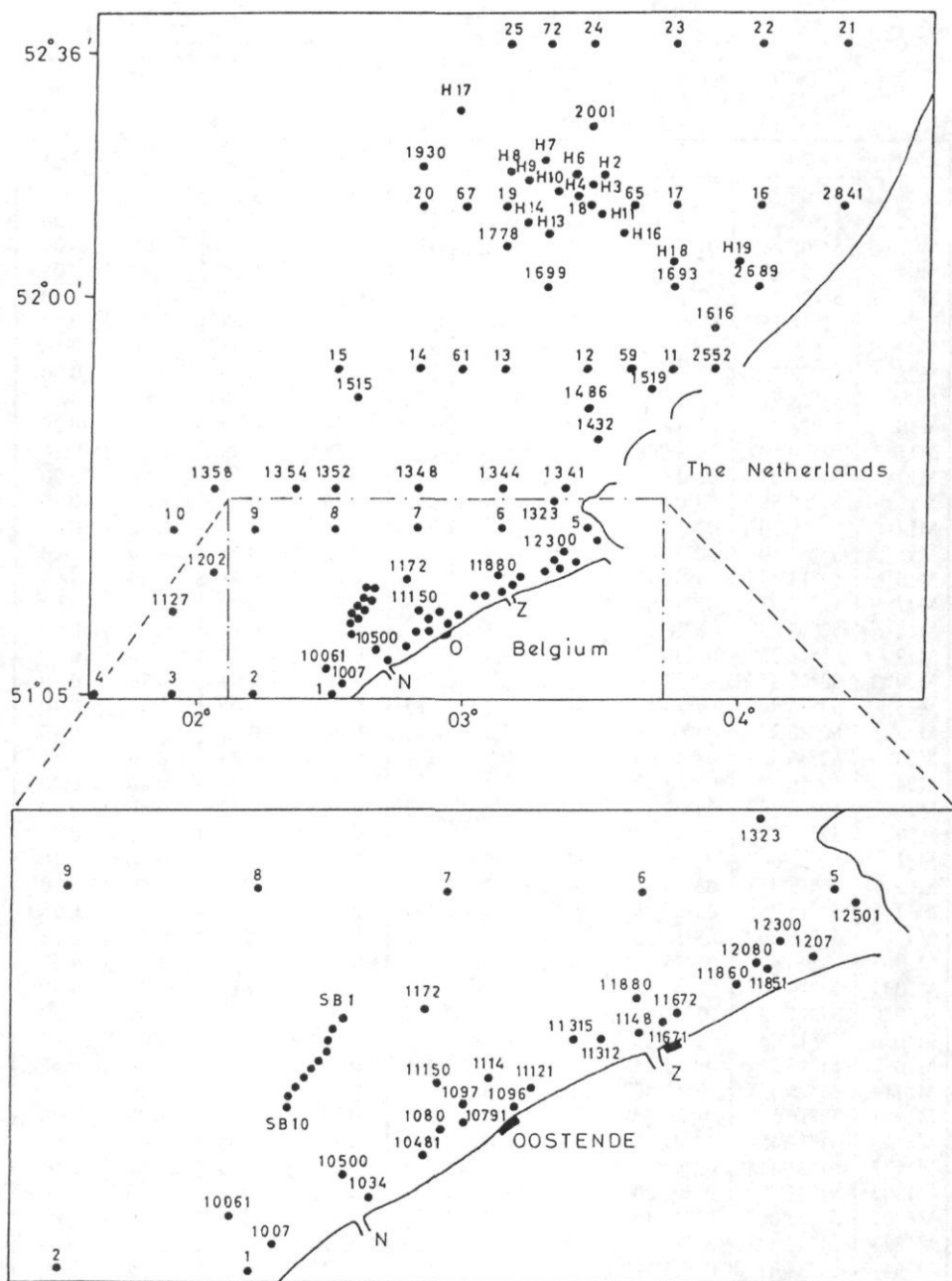


Fig. 1. - Position of the sampling stations.

TABLE I

List of the sampling sites with their coordinates (NB, EL,
depth (D in m) and sediment characteristics (% gravel ;

Md = median of the sand fraction (μm) ;

Sc = sorting coefficient (Φ) ;

Sk = skewness (Φ) ; % silt and % org. C).

Station	NB	EL	D	Gravel	Md	Sc	Sk	Silt	Org C
M01	51°05'20"	02°33'00"	12	1.0	154	0.0	5.15	0.30	
M02	51°05'20"	02°15'00"	26	4.1	236	0.37	-0.18	0.82	0.00
M03	51°05'20"	01°57'00"	35	45.3	325	0.41	?	0.06	0.00
M04	51°05'20"	01°38'50"	37	50.0	372	0.28	0.00	0.00	0.05
M05	51°28'25"	03°28'10"	8	1.3	159	0.50	0.03	41.12	1.50
M06	51°28'25"	03°09'15"	12	2.8	259	0.48	-0.08	2.73	0.10
M07	51°28'25"	02°52'00"	25	34.2	291	0.48	-0.07	2.50	0.10
M08	51°28'25"	02°33'00"	32	15.3	255	0.36	-0.09	0.93	0.00
M09	51°28'25"	02°15'00"	31	34.4	496	0.45	-0.10	2.00	0.30
M10	51°28'25"	01°57'00"	29	9.0	392	0.29	-0.04	0.30	0.20
M11	51°50'50"	03°47'00"	9	0.3	215	0.38	-0.08	0.60	0.20
M12	51°50'50"	03°28'10"	23	3.5	376	0.43	-0.11	0.00	0.20
M13	51°50'50"	03°09'15"	32	0.3	400	0.33	-0.04	0.00	0.10
M14	51°50'50"	02°52'00"	35	2.6	346	0.35	-0.05	0.50	0.00
M15	51°50'50"	02°33'00"	43	7.4	406	0.33	-0.01	0.40	0.00
M16	52°13'35"	04°04'45"	21	0.4	283	0.44	-0.01	2.00	0.00
M17	52°13'35"	03°47'00"	24	0.4	303	0.36	-0.09	2.10	0.00
M18	52°13'35"	03°28'10"	30	1.1	287	0.41	-0.11	1.00	0.00
M19	52°13'35"	03°09'15"	36	0.8	281	0.34	-0.06	2.80	0.00
M20	52°13'35"	02°52'00"	31	2.1	299	0.30	-0.04	0.90	0.00
M21	52°36'30"	04°24'10"	41	0.2	233	0.22	-0.05	0.90	0.10
M22	52°36'30"	04°04'45"	23	0.6	277	0.30	-0.01	1.40	0.10
M23	52°36'30"	03°47'00"	25	0.2	219	0.25	-0.03	0.80	0.10
M24	52°36'30"	03°28'10"	30	2.3	227	0.30	-0.05	1.40	0.30
M25	52°36'30"	03°09'15"	34	1.7	257	0.31	-0.12	0.80	0.10
M59	52°50'50"	03°37'15"	14	2.4	300	0.28	?	1.00	0.10
M61	52°50'50"	03°01'05"	32	2.8	421	0.36	?	0.50	0.10
M65	52°13'35"	03°37'15"	28	0.7	279	0.35	?	0.50	0.10
M67	52°13'35"	03°01'05"	37	3.5	287	0.33	?	0.50	0.15
M72	52°36'30"	03°18'15"	22	0.6	242	0.25	?	0.30	0.07
M1007	51°06'47"	02°35'16"	?	0.5	158	0.31	?	42.50	1.20
M1034	51°10'50"	02°44'05"	7	0.3	150	0.25	-0.17	60.00	1.70
M1080	51°14'34"	02°45'42"	5	0.1	182	0.21	?	0.00	0.30
M1096	51°15'25"	02°57'56"	6	0.3	173	0.22	?	7.00	0.45
M1097	51°15'25"	02°53'24"	8	0.0	140	0.84	?	90.00	1.35
M1114	51°16'52"	02°55'40"	39	9.0	417	0.50	-0.44	1.00	0.20
M1127	51°16'52"	01°57'00"	30	10.0	360	0.24	?	1.00	0.20
M1148	51°19'45"	03°09'15"	?	0.0	171	0.37	1.00	68.00	2.00
M1172	51°21'11"	02°48'52"	?	1.0	213	0.53	1.00	26.00	2.00
M1202	51°22'38"	02°06'00"	33	39.0	338	0.39	?	1.50	0.10
M1207	51°24'04"	03°25'45"	12	0.0	?	?	?	90.00	2.00
M1323	51°32'37"	03°21'02"	6	2.1	216	0.37	?	0.50	0.05
M1341	51°34'01"	03°23'24"	?	1.0	163	0.32	?	2.00	0.20
M1344	51°34'01"	03°09'15"	30	12.3	263	0.54	?	4.00	0.40
M1348	51°34'01"	02°51'08"	35	7.0	342	0.34	?	1.00	0.30
M1352	51°34'01"	02°33'00"	28	16.5	382	0.43	?	1.00	0.20
M1354	51°34'01"	02°24'00"	28	1.5	366	0.29	?	1.00	0.10

Station	NB	EL	D	Gravel	Md	Sc	Sk	Silt	Org C
M1358	51°34'01"	02°06'00"	42	32.0	426	0.51	?	1.50	0.05
M1432	51°41'01"	03°30'28"	?	0.2	179	0.46	?	2.00	0.10
M1486	51°45'13"	03°28'07"	18	0.4	257	0.24	0.03	0.00	0.23
M1515	51°46'37"	02°39'48"	26	5.0	412	0.32	?	0.00	0.00
M1519	51°46'37"	02°24'00"	?	2.0	204	0.46	?	0.00	0.20
M1616	51°55'06"	02°33'00"	?	0.0	140	0.55	?	242.0	1.00
M1693	52°02'12"	03°47'00"	24	2.0	235	0.35	?	1.70	0.30
M1699	52°02'12"	03°18'41"	25	1.5	319	0.49	- 0.12	0.50	0.15
M1778	52°07'53"	03°09'15"	33	1.0	373	0.44	?	0.00	0.05
M1930	52°19'19"	02°51'08"	40	1.0	332	0.37	?	0.00	0.15
M2001	52°25'03"	03°28'07"	33	0.3	311	0.35	?	1.00	0.10
M2552	51°50'50"	03°56'28"	?	?	?	?	?	?	?
M2689	52°02'12"	04°05'56"	13	0.0	142	0.86	- 0.26	5.90	0.09
M2841	52°13'35"	04°24'25"	?	?	?	?	?	?	?
10061	51°08'21"	02°31'40"	8	0.0	193	0.41	0.36	4.30	?
10481	51°12'20"	02°50'14"	?	0.2	148	0.43	0.39	31.4	?
10500	51°11'06"	02°42'04"	14	0.5	177	0.42	0.29	22.7	?
10791	51°14'25"	02°54'50"	8	1.1	157	0.42	0.37	57.7	?
11121	51°16'40"	03°00'30"	9	0.0	174	0.41	0.35	14.2	?
11312	51°19'10"	03°06'00"	8	0.0	149	0.43	0.38	61.8	?
11671	51°21'00"	03°12'40"	9	0.0	151	0.36	?	46.0	?
11672	51°21'00"	03°14'00"	8	0.0	179	0.41	0.36	21.7	?
11851	51°23'02"	03°22'56"	10	0.1	129	0.43	0.39	37.1	?
12080	51°24'04"	03°21'02"	?	?	?	?	?	?	?
12300	51°24'31"	03°23'24"	13	0.1	196	0.30	0.33	33.9	2.22
12501	51°27'17"	03°31'33"	16	0.0	198	0.40	0.34	0.50	?
11860	51°22'38"	03°18'41"	9	0.5	88	2.24	0.32	46.3	?
11880	51°22'00"	03°09'15"	11	2.2	99	0.50	0.27	95.3	?
11150	51°07'10"	02°31'00"	12	0.5	338	?	0.21	0.20	?
11315	51°19'30"	03°03'00"	8	0.0	163	0.42	0.37	42.0	?
H2	52°18'46"	03°28'49"	31	0.2	289	0.30	+ 0.01	0.00	?
H3	52°17'04"	03°26'59"	29	0.27	322	0.32	+ 0.04	0.03	?
H4	52°15'13"	03°24'47"	27	0.0	297	0.32	- 0.01	0.00	?
H6	52°19'35"	03°23'19"	30	0.0	287	0.27	- 0.02	0.12	?
H7	52°21'03"	03°18'26"	37	0.23	292	0.46	+ 0.03	0.01	?
H8	52°19'59"	03°10'41"	34	1.11	300	0.39	- 0.04	0.11	?
H9	52°19'08"	03°13'56"	44	0.30	302	0.47	0.01	0.10	?
H10	52°16'15"	03°21'10"	31	0.00	292	0.31	0.01	0.03	?
H11	52°12'52"	03°29'12"	31	6.13	290	0.41	0.01	0.00	?
H13	52°09'48"	03°19'55"	30	1.27	437	0.52	- 0.01	0.10	?
H14	52°11'29"	03°13'52"	33	0.67	306	0.34	- 0.02	0.10	?
H16	52°10'07"	03°35'44"	29	0.54	335	0.36	- 0.01	0.45	?
H17	52°29'02"	02°58'57"	32	0.00	284	0.35	- 0.04	0.25	?
H18	52°06'46"	03°46'30"	29	0.00	301	0.73	- 0.01	0.55	?
H19	52°06'46"	04°00'00"	32	0.00	324	0.57	+ 0.16	0.24	?
SB1	51°20'30"	02°41'40"	15	6.84	234	0.38	- 0.19	1.61	3.94
SB2	51°19'45"	02°41'00"	16	10.62	375	0.38	+ 0.25	0.00	7.16
SB3	51°19'20"	02°40'45"	15	3.42	654	0.28	+ 0.07	0.30	3.51
SB4	51°18'40"	02°40'45"	16	1.13	402	0.30	+ 0.02	0.05	1.81
SB5	51°18'00"	02°40'10"	14	0.24	517	0.24	- 0.11	0.00	2.92
SB6	51°17'30"	02°39'30"	15	2.21	281	0.36	+ 0.25	0.14	1.69
SB7	51°16'42"	02°38'57"	10	0.00	188	0.41	+ 0.37	0.12	4.64
SB8	51°16'20"	02°38'15"	14	0.00	205	0.40	+ 0.36	0.00	1.00
SB9	51°15'35"	02°37'35"	14	0.00	211	0.39	+ 0.32	0.15	1.99
SB10	51°14'48"	02°37'08"	14	0.00	230	0.38	+ 0.33	0.36	1.39

was used. Four subsamples were taken from each Reineck-box. Two replicates for meiofauna were fixed with warm (70 °C) formaldehyde to a final concentration of 4%. The two other cores for chemical and sediment analysis were immediately frozen. Two hundred nematodes from each subsample were picked out at random and identified to species level. From October 1984 on, meiofauna was sampled using a box-corer (sampling area = 0.25 m², from which a 10.16 cm²-cores were taken on board of the Belgian Oceanographic Research Vessel 'Belgica').

The extraction techniques of nematodes from sediments differ with sediment type. Simple decantation on a sieve (38 µm) is satisfactory when the sediment is a sand with low amounts of detritus or silt (Hulings & Gray, 1971). The through-method (Barnett, 1968; Heip, 1976) is also applicable for sand samples. The extraction from muds or detritus is done using a density-gradient centrifugation technique (Heip *et al.*, 1974; Heip *et al.*, 1985).

The grain size distribution of the sediment, organic matter, temperature, salinity and suspended matter was determined (Holme & McIntyre, 1971 and 1984).

Non-parametric statistics (Kruskal-Wallis one-way analysis of variance and Spearman rank correlation coefficient) were used (Siegel, 1956; Conover, 1971).

Different diversity measures proposed by Heip *et al.* (1988) have been calculated (see Vincx, in press).

Multivariate analysis (Ordination (DCA) and Twinspan-classification) are used to examine the species distributions of the different stations (Hill, 1979a & b; Hill & Gauch, 1980 and Gauch, 1982).

RESULTS

Environmental parameters

Depth and sediment characteristics (percentage gravel, median of the sand fraction; sorting coefficient; skewness; percentage silt and percentage organic carbon) of the 102 stations are summarized in Table 1.

Figs 2-5 show the most important sedimentological characteristics. These parameters are correlated with each other (Table 2). This strong correlation between most of the measured parameters shows that sediment composition differs significantly from south to the north. The median of the sand fraction increases significantly from the south to the north, while the silt content, org C content and the skewness decrease significantly from the south to the north (this is mainly because of the high number of fine sand and silt stations along the Belgian coast). Only the median of the sand fraction and the gravel content have a significant negative correlation with EL, i.e. the offshore stations from the southern part have significantly coarser sediments than the coastal stations and the off-shore stations in the north.

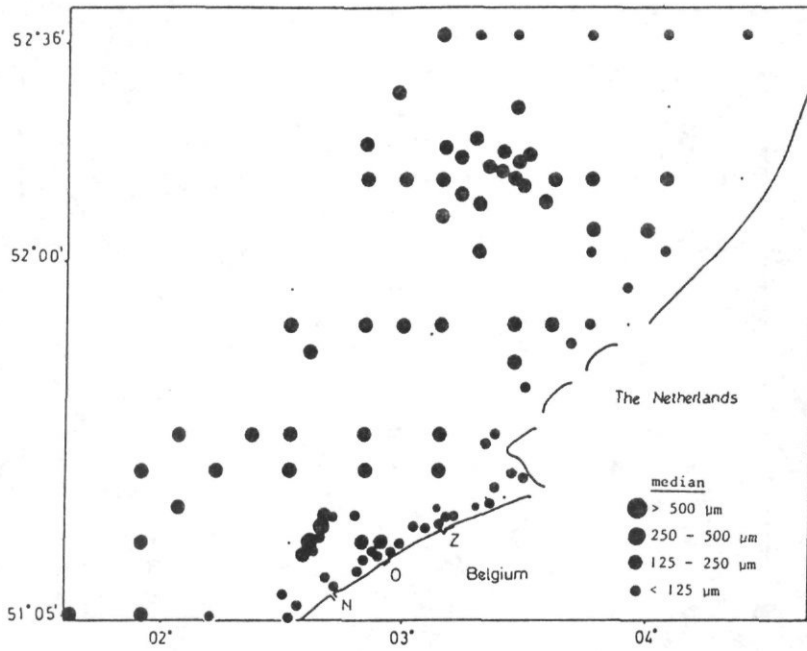


Fig. 2. — Distribution of the sandy stations in the Southern Bight.

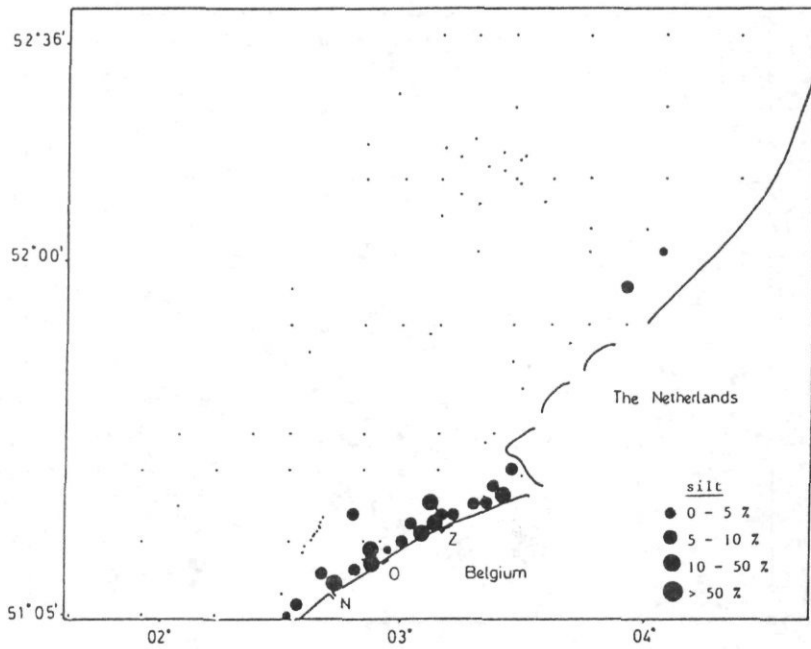


Fig. 3. — Distribution of the silty sediment stations in the Southern Bight.

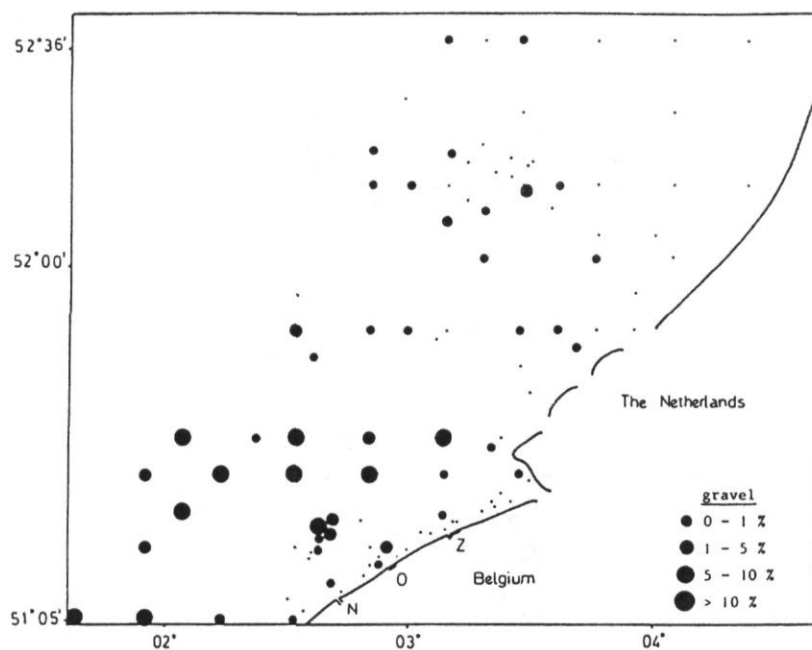


Fig. 4. — Distribution of the gravel content of the stations in the Southern Bight.

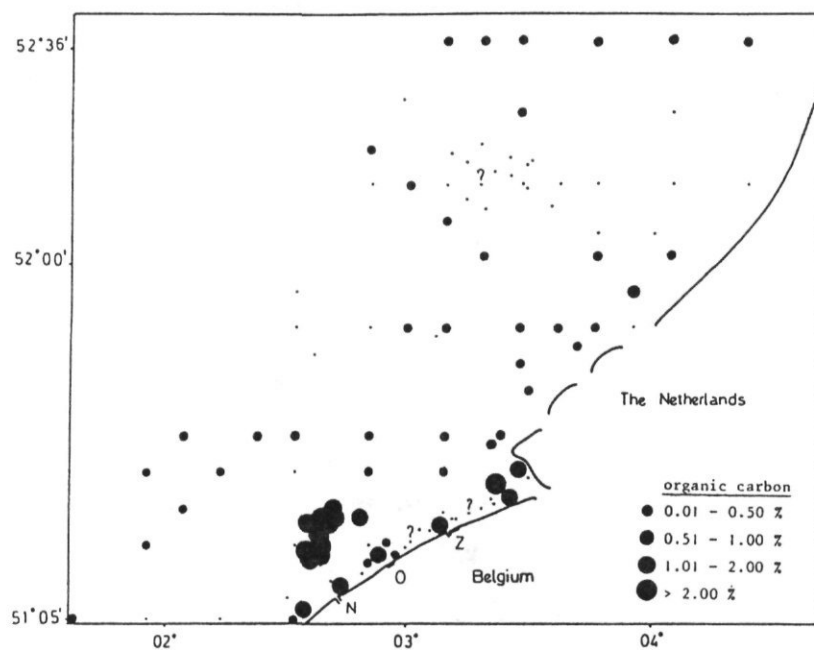


Fig. 5. — Distribution of the organic carbon in the stations of the Southern Bight.

TABLE 2

Spearman rank correlation coefficient (r_s) between different environmental parameters of the 102 stations (abbreviations are as in Table 1).

** : $p < 0.01$, highly significant

*** : $p < 0.001$, very highly significant

	N	r_s	sign.
Md with silt	98	- 0.6198	0.001 ***
Md with Sc	97	- 0.1772	0.041 **
Md with Org C	69	- 0.2950	0.007 **
Md with NB	98	0.2966	0.002 **
Md with EL	98	- 0.1748	0.043 **
Md with Sk	70	- 0.4584	0.001 ***
Md with depth	90	0.6555	0.001 ***
Md with gravel	98	0.5096	0.001 ***
Silt with Sc	97	0.3025	0.001 ***
Silt with Org C	70	0.1430	0.119
Silt with NB	99	- 0.2960	0.001 ***
Silt with EL	99	0.0447	0.330
Silt with Sk	70	0.2018	0.047 **
Silt with depth	91	- 0.4320	0.001 ***
Silt with gravel	99	- 0.1125	0.134
Sc with Org C	69	0.0272	0.412
Sc with NB	97	- 0.1314	0.100
Sc with EL	97	0.0569	0.290
Sc with Sk	69	0.1426	0.121
Sc with depth	89	- 0.868	0.209
Sc with gravel	97	- 0.0299	0.389
Org C with NB	70	- 0.4941	0.001 ***
Org C with EL	70	- 0.1289	0.144
Org C with SK	42	- 0.4586	0.001 ***
Org C with depth	63	- 0.5499	0.001 ***
Org C with gravel	70	- 0.2995	0.006 **
Sk with NB	70	- 0.3499	0.001 ***
Sk with EL	70	- 0.1166	0.168
Sk with depth	67	- 0.4417	0.001 ***
Sk with gravel	70	- 0.4279	0.001 ***
Depth with NB	91	0.5417	0.001 ***
Depth with EL	91	- 0.0394	0.355
Gravel with NB	99	- 0.0272	0.395
Gravel with EL	99	- 0.3802	0.001 ***

Density of the nematode community

The mean nematode densities vary between 35 ind./10 cm² and 2860 ind./10 cm². I will not discuss density values in more detail, because too many sampling procedures have been used over the 13 years of sampling. Therefore I will only deal with relative characteristics of the nematode communities, i.e. the relative abundance (%) of each species within the stations.

Species composition

The examination of the 102 stations revealed 456 nematode species belonging to 159 genera and 37 families. (A complete species list is available on request).

The mean relative abundances of all 456 nematode species from each station (mean values are calculated for all the samples of each station) were analysed by means of a two-way indicator species analysis (TWINSPAN). The classification dendrogram of the 102 stations is shown in Fig. 6. Characteristics of the analysis are as follows: five pseudospecies cut levels were used in the analysis: 0-5-10-25-50; this means that if the relative abundance of one species differs from 1 to 50% (as an example) the species will be split up in "pseudospecies" according to the noted relative abundances. Six station groups (TWIN 1 to TWIN 6) are considered as entities because of the following reasons: TWIN 6 is obviously distinct from the others and a further division of this group will split off only one (or a small number of) station(s). The other station groups, TWIN 1, TWIN 2-3, TWIN 4 and TWIN 5 are determined at the level of the fourth dichotomy; from this point on, only TWIN 2-3 has been split up at the level of the fifth dichotomy because too many stations were left within the combined station group. The location of the six station groups is shown in Fig. 7.

Two DCA ordinations have been calculated: DCA1 including all species and all stations (Fig. 8) and DCA2 downweighting rare species for all stations (Fig. 9). Only Axis 1 to Axis 2 and Axis 3 are presented. Higher axes do not show any particular pattern in the position of the different stations. Stations from each of the six Twinspan-groups are indicated by a single symbol in order to obtain a better overview on the position of the different station groups.

DCA1 and DCA2 show a similar position of the 102 stations in a two-dimensional space determined by Axis 1 and Axis 2. The stations of TWIN 6 and TWIN 5 are more close together (especially along Axis 2) in DCA2 than in DCA1. This indicates that the stations of both groups are especially different on the basis of their rare species (less common than 1/5 of the commonest frequency). No remarkable difference is present between DCA1 and DCA2 in the Axis 1-scores.

Figs 10-11 present the iso-lines of respectively DCA1-Axis1 scores and DCA1-Axis 2 scores in the study area (similar areas are delineated for DCA2). A superposition of both figures gives more or less the same station groups as those defined by Twinspan-classification.

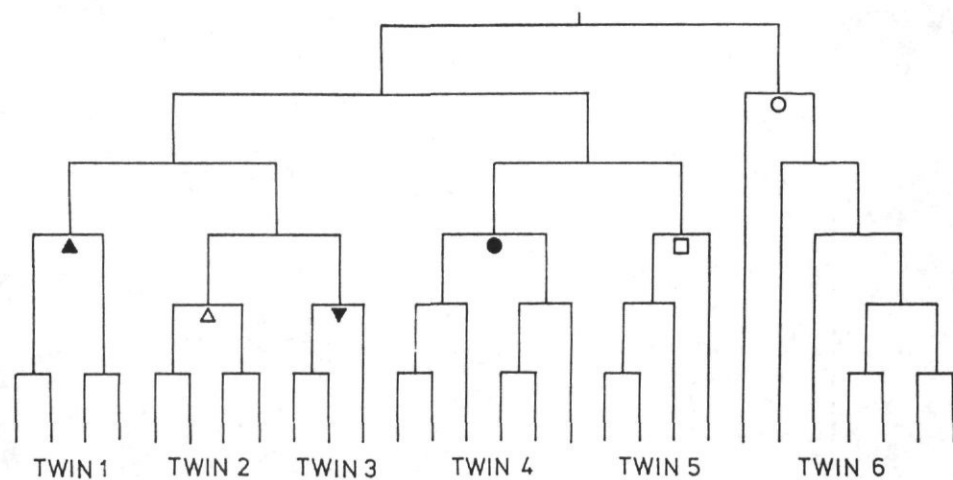


Fig. 6. - Dendrogram of the Twinspan classification.

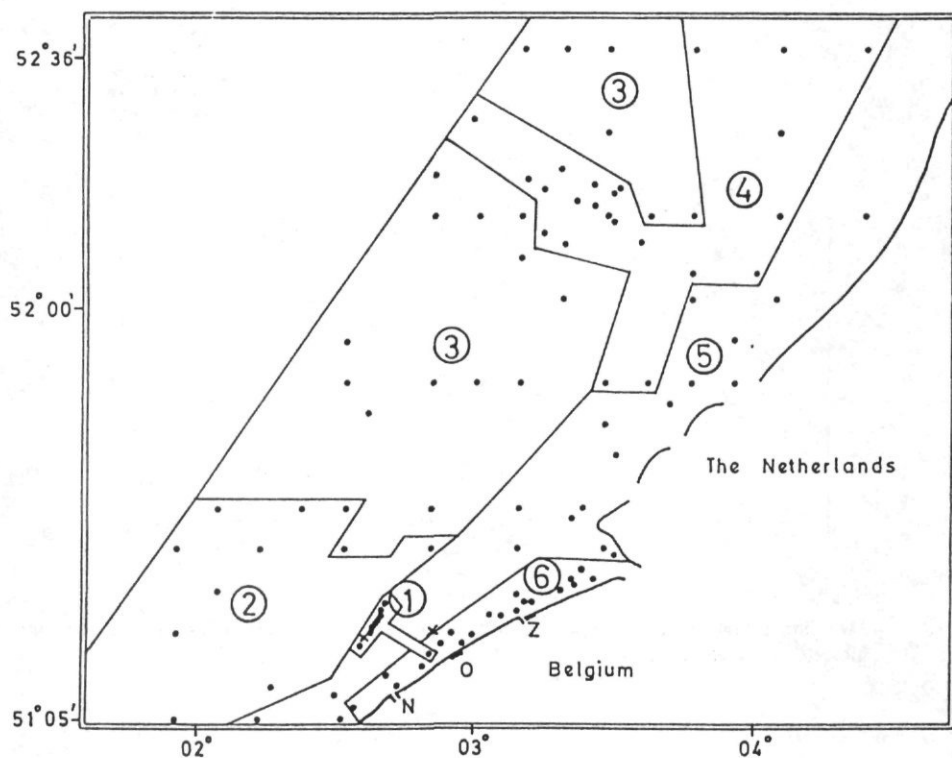


Fig. 7. - Position of the six Twinspan-station groups in the Southern Bight.

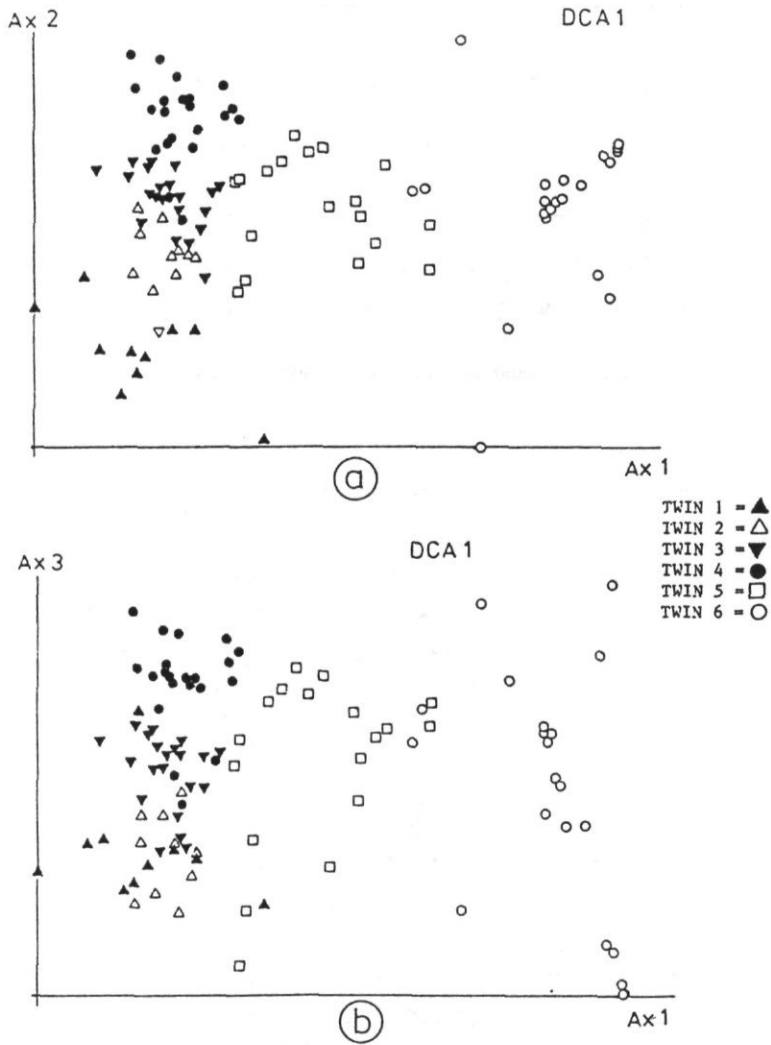


Fig. 8. — Two-dimensional plots of the DCA1-ordination (stations of the six Twinspan-groups are indicated by a single symbol); a : Ax1-Ax2 ; b : Ax1-Ax3.

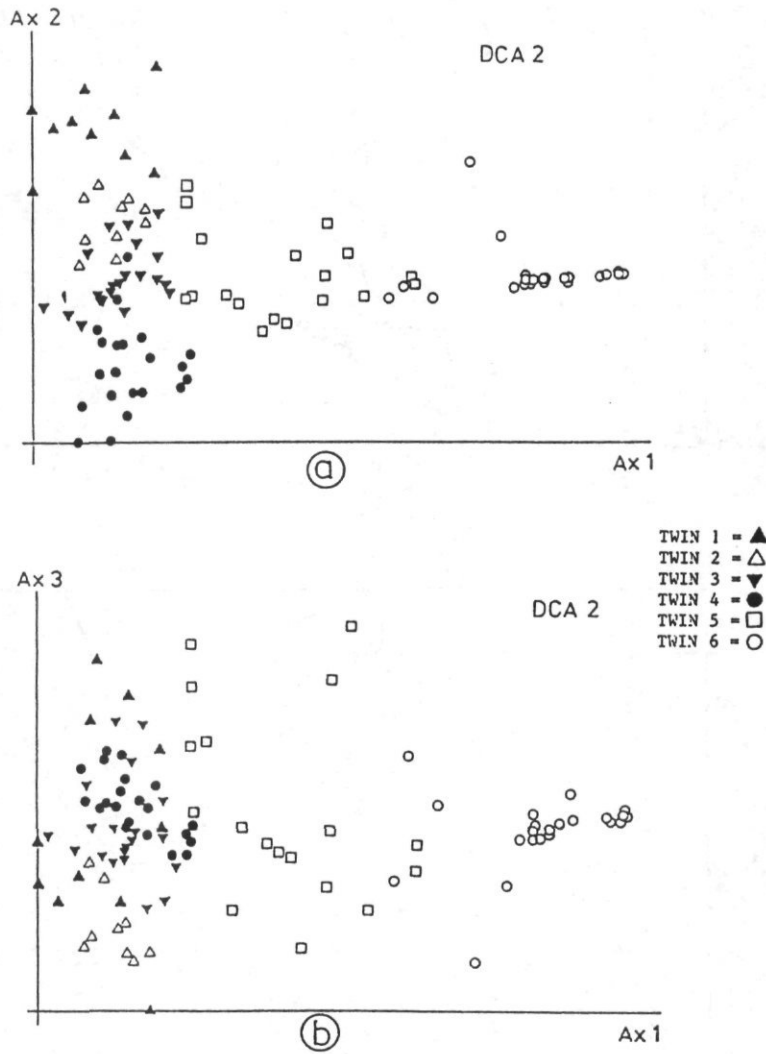


Fig. 9. - Two-dimensional plots of the DCA2-ordination (stations of the six Twinspace-groups are indicated by a single symbol); a: Ax1-Ax2; b: Ax1-Ax3.

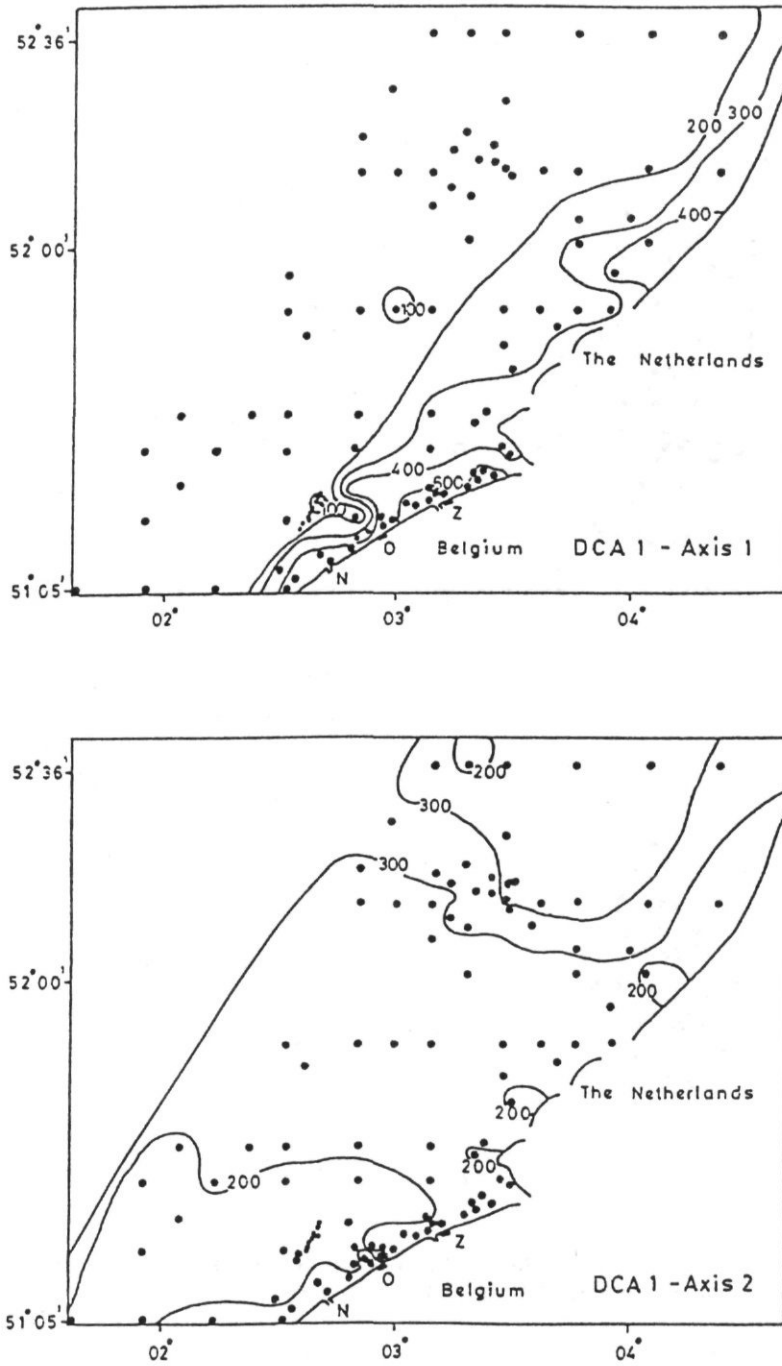


Fig. 10. — Areas demarcated by iso-lines of DCA1-Axes1 and Axes2 scores of the stations in the Southern Bight.

TABLE 3

Summary of the sedimentological characteristics per station group
as defined by the TWINSPAN-classification
(TWIN 1 → TWIN 6)
(Abbreviations as in Table 1)

		TWIN 1	TWIN 2	TWIN 3	TWIN 4	TWIN 5	TWIN 6
Md (μm)	\bar{x}	326.8	374.8	315.1	299.8	211.5	168.6
	SE	49.6	17.7	13.5	10.3	11.7	14.5
	n	10	10	21	21	16	20
Silt (%)	\bar{x}	0.26	1.09	0.69	0.39	4.52	44.60
	SE	0.15	0.25	0.15	0.12	2.48	5.73
	n	10	10	21	21	16	21
Sc (φ)	\bar{x}	0.33	0.38	0.35	0.38	0.42	0.52
	SE	0.02	0.03	0.01	0.03	0.04	0.09
	n	10	10	20	21	16	20
Org C (%)	\bar{x}	2.84	0.13	0.18	0.10	0.27	1.41
	SE	0.64	0.03	0.10	0.03	0.10	0.22
	n	10	10	20	6	14	10
Sk (φ)	\bar{x}	0.15	- 0.03	- 0.01	0.003	0.02	0.48
	SE	0.07	0.03	0.04	0.01	0.07	0.17
	n	9	4	13	20	9	15
Depth (m)	\bar{x}	13.4	31.8	30.0	29.8	16.5	11.2
	SE	1.07	1.58	1.67	1.45	2.49	1.93
	n	10	10	21	21	13	16
Gravel (%)	\bar{x}	2.46	27.19	2.74	0.85	1.86	0.85
	SE	1.13	5.22	0.77	0.33	0.76	0.43
	n	10	10	21	21	16	21

Environmental characteristics of the different station groups (TWIN 1 to TWIN 6) are presented in Table 3. All parameters differ significantly between the six groups; however, most parameters are also significantly correlated with one another (see Table 2).

Multiple comparison between pairs of the Twinspan station groups shows that the median (Md) of the sand fraction is the most important environmental factor in characterizing the different station groups; only TWIN 1, TWIN 3 and TWIN 4 are not significantly different on the basis of the Md. Highly significant correlation exists between Md, silt content, sorting coefficient, geographic position (NB), skewness, depth and gravel content along Axis 1 of both DCA1 and DCA2. Organic carbon and geographic position (EL) seem to determine Axis 2.

Generally, the Southern Bight can be divided into six main areas on the basis of the nematode species composition (Fig. 7):

1) The Belgian coast (TWIN 6), except a few stations on the west coast. This area is characterized by fine-medium sand with a high amount of silt (44.6%) and of

organic carbon (1.4%); the depth is about 10 m. Only three differential species (taken out of the Twinspan) in this area have a mean relative abundance $> 5\%$, i.e. *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Sabatieria punctata*.

2) The Dutch coast and the western part of the Belgian coast (TWIN 5). The area is characterized by fine-medium sands, low amount of silt ($< 5\%$) and gravel (1.9%). Depth is about 16 m. Five differential nematode species have a mean relative abundance $> 5\%$: *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* and *Sabatieria celtica*.

The southern off-shore area is characterized by two types of "communities" localised in a rather patchy distribution (in relation with the heterogeneous topography of the different sandbanks in the area).

3) The crests of the sand banks (example Kwinte Bank, TWIN 1) are about 10-15 m deep, and are characterized by medium sands with almost no silt. The amount of organic carbon is very high (2.8%). Four differential species have a mean relative abundance $> 5\%$, i.e. *Bathylaimus parafilicaudatus*, *Desmodora schulzi*, *Leptonemella aphanothecae* and *Onyx perfectus*.

4) Station group TWIN 2 is situated in the deepest zone (> 30 m) with the coarsest sediment. In this area, only the channels between the sand banks have been sampled. Only five species have a mean relative abundance $> 5\%$: *Hypodontolaimus* n. sp. 1, *Onyx perfectus*, *Rhys ornata*, *Rhynchonema quemer* and *Spilophorella paradoxa*.

Species of the Epsilonematidae and the Draconematidae are also characteristic of the southern part.

The northern off-shore area is split up in two station groups TWIN 3 and TWIN 4.

5) TWIN 3 stations are characterized by clean medium sand with some gravel (2.8%). Five differential species have a mean relative abundance $> 5\%$: *Chromaspirina parapontica*, *Chromaspirina pellita*, *Dichromadora cucullata*, *Karkinochromadora lorenzeni* and *Xyala striata*.

6) TWIN 4 stations have no significantly different sediment from TWIN 3 except for the gravel content which is higher in TWIN 4. This area is surrounded by TWIN 3 stations. Differences in the biotic data of the last two station groups are not very obvious. Five differential species of TWIN 4 have a mean relative abundance $> 5\%$, i.e. *Chromaspirina parapontica*, *C. pellita*, *Karkinochromadora lorenzeni*, *Molgolaimus turgofrons* and *Neochromadora munita*. Only two of these are different from the five species in TWIN 3. Some of the differential species of both groups TWIN 3 and TWIN 4 are the same, i.e. *Gonionchus heipi*, *Leptonemella aphanothecae*, *Microlaimus ostracion*, *Paramesonchium belgicum* and *Valvaelaimus major*.

Feeding types

Wieser (1953) defined an ethological classification of the free-living marine nematodes, derived from the structure of the buccal cavity and the gut content. The

morphological division of the genera proposed by Wieser is assumed to represent different types of feeding mechanisms. These four groups are :

1A : selective deposit-feeders ; 1B ; non-selective deposit-feeders ; 2A : epigrowth-feeders and 2B : predators-omnivores.

The partitioning of the species over the four main feeding types can be summarized in a trophic index $\Sigma\theta^2$ (θ = the % of each feeding type), varying between 0.25 and 1.00 $\Sigma\theta^2 = 1$ indicates that only one trophic type is present (this has only been found when that trophic type was 1B).

The mean relative abundances of the feeding parameters per Twinspan station group (TWIN 1 to TWIN 6) are noted in Table 4, together with the overall mean for the whole area. In general, non-selective deposit-feeders (1B) and epigrowth-feeders (2A) are equally abundant, while predators-omnivores (2B) and selective deposit-feeders (1A) are less numerous. However, important significant differences exist between the six station groups. Fig. 11 presents the relative abundances of the feeding types for the six station groups.

TABLE 4

Summary of the mean relative abundances of the four feeding-types (θ) and the trophic diversity ($\Sigma\theta^2$) in the station groups as defined by the TWINSpan-classification (TWIN 1 \rightarrow TWIN 6) and overall mean of each parameter for the whole area. (SE = standard error ; n = number of observations).

θ		TWIN 1	TWIN 2	TWIN 3	TWIN 4	TWIN 5	TWIN 6 mean	Overall
1A	\bar{x}	18.48	9.04	10.72	11.74	5.62	1.45	8.63
	SE	3.69	1.65	1.17	1.62	1.25	4.43	0.78
	n	10	10	21	21	18	22	102
1B	\bar{x}	23.46	19.11	21.26	14.80	40.19	92.87	38.72
	SE	4.08	1.51	1.43	1.25	5.10	2.64	3.17
	n	10	10	21	21	18	22	102
2A	\bar{x}	31.15	50.05	45.90	52.20	33.18	4.27	34.93
	SE	5.27	2.18	2.63	3.07	4.11	2.22	2.19
	n	10	10	21	21	18	22	102
2B	\bar{x}	26.70	21.80	22.24	21.27	20.19	1.36	17.57
	SE	5.07	2.38	1.75	2.45	2.53	0.49	1.26
	n	10	10	21	21	18	22	102
$\Sigma\theta^2$	\bar{x}	32.53	35.70	34.39	39.28	39.44	89.06	48.03
	SE	3.25	1.63	1.54	2.30	3.26	3.17	2.41
	n	10	10	21	21	18	22	102

The number of selective deposit-feeders (1A) is higher in open sea areas (TWIN 1 to TWIN 4) ; the number of predators-omnivores (2B) varies around 20% in the whole area, except for the Belgian coast where a very low number is noted

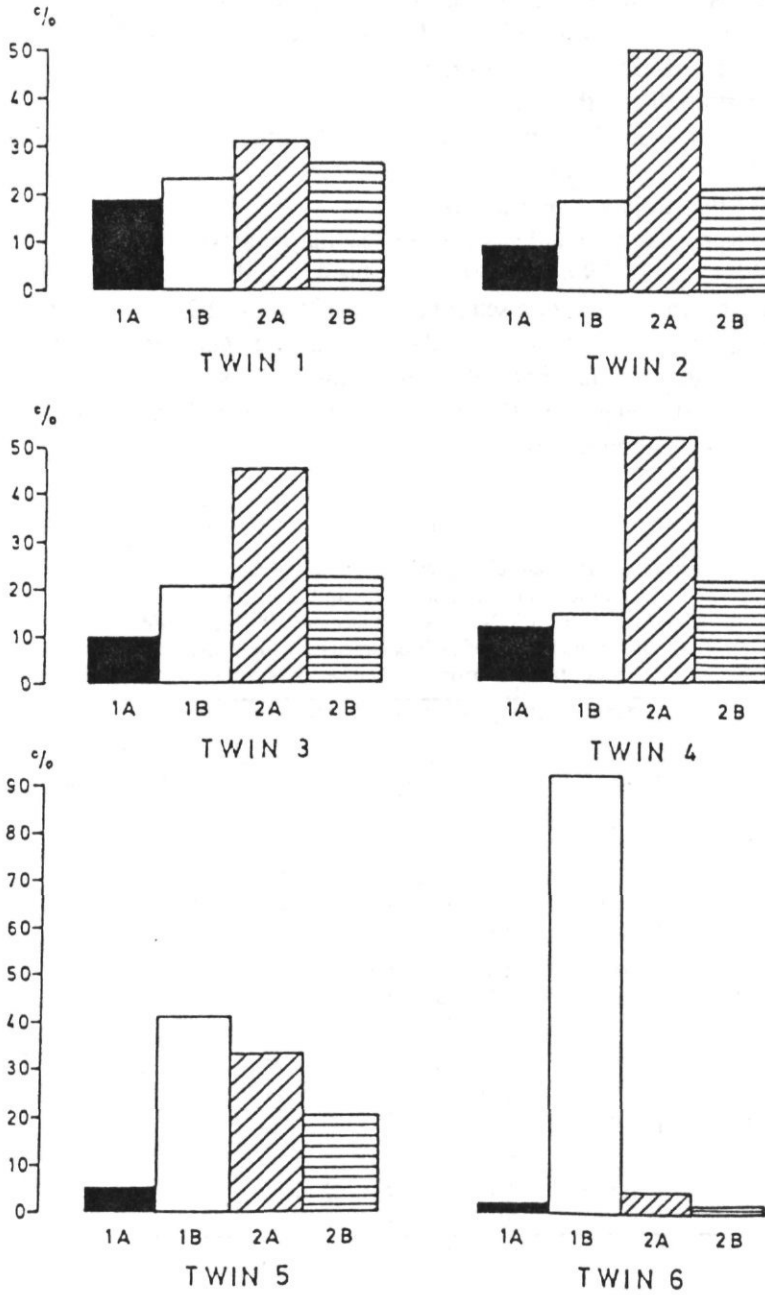


Fig. 11. — Mean relative abundance of the four feeding types for the six TWIN station groups.

(TWIN 6). The relative abundance of epigrowth-feeders (2A) is highest in the open sea area (TWIN 1 to TWIN 4), while non-selective deposit-feeders (1B) are more numerous along the coast (TWIN 5 and TWIN 6).

The distribution of the feeding types is influenced by sediment characteristics with the following trends :

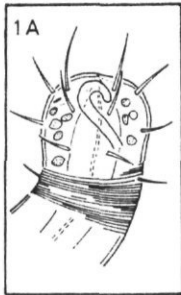
- the proportion of 1A is larger in well sorted, clean sand ;
- the proportion of 1B decreases in coarser sediment and is very high in silty bottoms, much loaded with organic carbon ;
- the proportion of 2A increases with the median grain size of the sand fraction and decreases with increasing silt content and organic carbon ;
- the proportion of 2B increases in sandy, well sorted sediments not much loaded with organic carbon.

The most important differential species per feeding type for each TWIN station group are shown in Fig. 12.

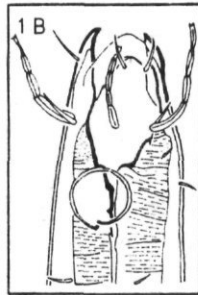
The four most dominant differential species of TWIN 1 are distributed over the four feeding types ; i.e. *Leptonemella aphanothecae* is considered to be a selective deposit-feeder (1A) ; it has a very small buccal cavity and the species is characterized by a coat of Cyanobacteria around the whole body which is supposed to be a source of food ; *Bathylaimus paraflicaudatus* is considered as a non-selective deposit-feeder (1B) ; this species has a big, unarmed buccal cavity (only small denticles are present in the posterior part of the buccal cavity) ; the gut contains always a variety of detritus ; diatoms were never observed ; *Desmodora schulzi* is an epigrowth-feeder (2A) : its buccal cavity is provided with prominent teeth ; by means of a well developed pharynx it is possible to swallow epigrowth particles from the sediment surface ; the very mobile lips are separated from the cephalic capsule and allow these animals to "attach" themselves to the sediment and to scrape of the grains ; the gut contains also a lot of diatoms ; *Onyx perfectus* is a predator (2B) which is characterized by a very big dorsal tooth in the buccal cavity (connected with a well developed pharyngeal gland). Gut content is never very obvious (e.g. no parts of other nematodes or other meiobenthic groups were found), indicating that the species does not swallow entire prey.

The distribution of the feeding types of the dominant differential species in TWIN 2 is as follows : *Rhynchonema quemer* is a non-selective deposit-feeder (1B) with a rather small unarmed buccal cavity ; the lips however are very mobile and can open the buccal cavity widely. *Hypodontolaimus* n.sp.1, *Rhps ornata* and *Spilophorella paradoxa* are epigrowth-feeders (2A) ; these three species are chromadorids with well developed buccal teeth. They contain often diatoms and other small debris particles in the gut. *Onyx perfectus* is the dominant predator (2B) (cf. TWIN 1). In TWIN 3, the five dominant differential species are distributed over three feeding types (1A is lacking) ; *Xyala striata* is the most important non-selective deposit-feeder (1B) which is a species from the Xyalidae with a common distribution in the open sea area. The species has a big unarmed buccal cavity and has a very well ornamentated cuticle.

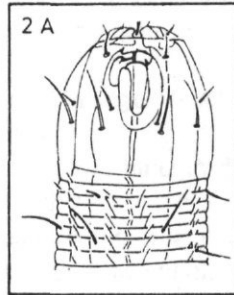
TWIN 1



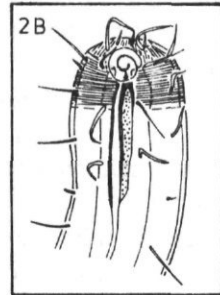
Leptonemella aphanothecae



Bathylaimus parafilicaudatus

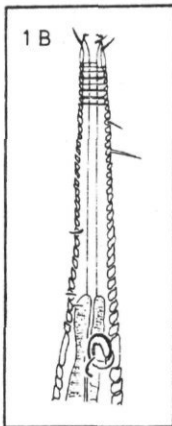


Desmodora schulzi

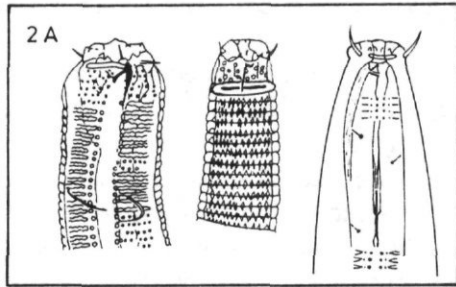


Onyx perfectus

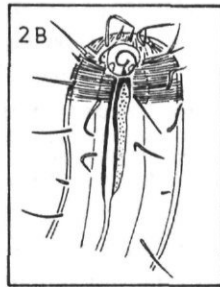
TWIN 2



Rhynchonema quemer

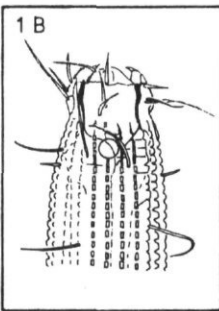


Hypodontolaimus n. sp. 1
Rhips ornata
Spilophorella paradoxa

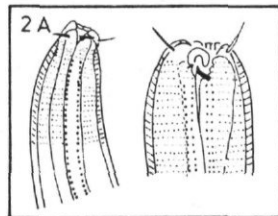


Onyx perfectus

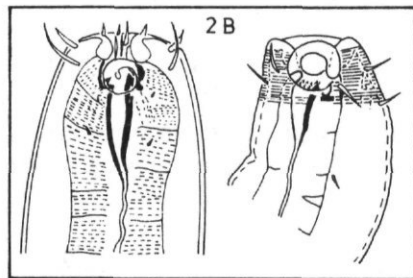
TWIN 3



Xyala striata



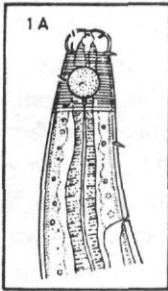
Dichromadora cucullata
Karkinochromadora lorenzeni



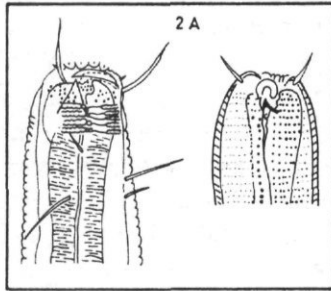
Chromaspirina parapontica
Chromaspirina pellita

Fig. 12. — Important differential species per feeding type for each TWIN station group.

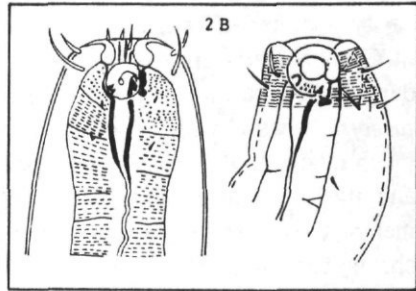
TWIN 4



Molgolaimus turgoifrons

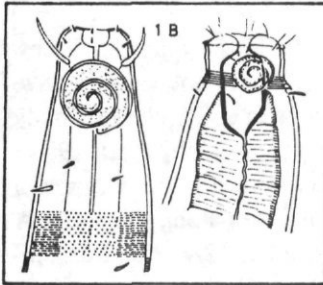


Neochromadora munita
Karkinochromadora lorenzeni

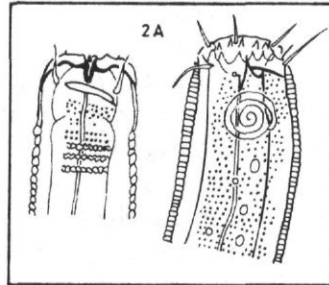


Chromaspirina parapontica
Chromaspirina pellita

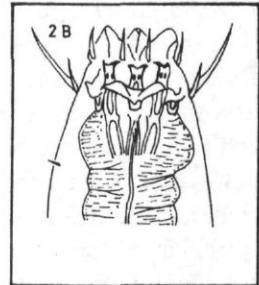
TWIN 5



Sabatieria celtica
Richtersia inaequalis

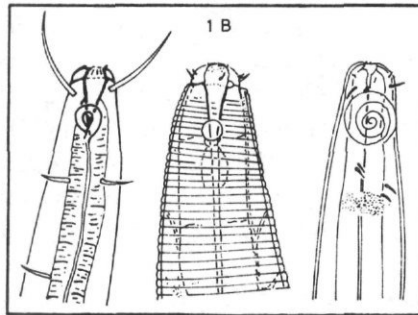


Prochromadorella attenuata
Paracyatholaimus pentodon



Enoploides spiculohamatus

TWIN 6



Ascolaimus sp.1
Daptonema tenuispiculum
Sabatieria punctata

Fig. 12. - (cont.).

Two chromadorids, *Dichromadora cucullata* and *Karkinochromadora lorenzeni* are the important epigrowth-feeders (2A); both species are small (± 1 mm) and have a small buccal cavity provided with small teeth. They co-occur in a lot of stations. Two congeneric desmodorids, *Chromaspirina parapontica* and *C. pellita* are the most important predators (2B); these are bigger animals (± 2 mm) with a large buccal cavity surrounded by a very large muscular pharynx; *C. pellita* has always a "coat" of Cyanobacteria around the whole body. In station group TWIN 4, non-selective deposit-feeders with a mean relative abundance $> 5\%$ are lacking. *Molgolaimus turgofrons* is the most important selective deposit-feeders (1A); this species is very much related to the *Microlaimus* species (2A). Because of the very small buccal cavity and the pronounced pharyngeal bulb, *Molgolaimus turgofrons* is considered as a member of the 1A-group (Juario, 1975 considered this species as 2A). Two chromadorids, *Karkinochromadora lorenzeni* and *Neochromadora munita* are the important epigrowth-feeders (2A); *N. munita* is the bigger species which is also quite common in the northern open sea area. The predators are the same as in TWIN 3: *Chromaspirina parapontica* and *C. pellita*.

In TWIN 5, 1A-species are not present among the most important ones. *Richtersia inaequalis* and *Sabatieria celtica* are the most important non-selective deposit-feeders. *R. inaequalis* is a small, aberrant nematode with a very clumpy body and a large unarmed buccal cavity (*R. inaequalis* is considered as 2A by Platt, 1977; however, the gut content of these animals is always very diverse). *S. celtica* is a comesomatid that is very abundant in the silty sand communities along the coast. A cyatholaimid and a chromadorid are important epigrowth-feeders (2A); i.e. *Paracyatholaimus pentodon* and *Prochromadorella attenuata* respectively. *P. pentodon* is a larger species with a well armed buccal cavity; gut contents a lot of diatoms. *P. attenuata* is a smaller species with very minute teeth in the buccal cavity. The predator (2B) is a large enoplid *Enoploides spiculohamatus*. This species has well developed teeth and mandibles in the buccal cavity. In TWIN 6 only non-selective deposit-feeders are present among the most important differential species, i.e. *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Sabatieria punctata*. They all belong to a different family, respectively Axonolaimidae, Xyalidae and Comesomatidae.

Table 5 presents the distribution of the feeding types of all the differential species (list obtained in the Twinspan classification) within the six TWIN station groups. I summarize this as follows:

- TWIN 1 is differentiated from the other groups by the high proportion of 1A (about 50% of the differential species).
- TWIN 2 and TWIN 3 are differentiated from the other groups by the high proportion of 2B (about 50% of the differential species).
- TWIN 4 is characterized by a more or less even distribution of the feeding types among the differential species
- TWIN 5 is differentiated from the others by the combination of a high proportion of 1B ($\pm 60\%$) and 2B ($\pm 30\%$).

– TWIN 6 is differentiated from the five others by the high proportion of 1B ($\pm 80\%$).

From this and the overall relative abundance of the feeding types within the six groups, we may conclude that the distribution of the feeding types is mainly determined by the distribution of the differential species within each station group. The non-differential species are more or less equally spread over the four feeding types and do not cause important changes in the general distribution of the feeding types.

TABLE 5

Number of differential species in each feeding type
in the different Twinspan station groups
(N = the total number of the differential species per TWIN group)

	1A	1B	2A	2B	N
TWIN 1	8	2	5	2	17
TWIN 2	5	6	16	6	33
TWIN 3	3	6	7	6	22
TWIN 4	2	2	13	5	22
TWIN 5	1	15	3	7	26
TWIN 6	1	7	–	1	9

Diversity

A typical feature of nematode communities, perhaps the most important is understanding their ecological success, is the large number of species present in any one habitat.

Diversity is determined at different levels of the nematode community ; i.e. species diversity of the whole community, species diversity of eight dominant families (Chromadoridae, Comesomatidae, Cyatholaimidae, Desmodoridae, Microlaimidae, Oncholaimidae, Thoracostomopsidae and Xyalidae), species diversity of the four feeding types, family diversity and trophic diversity within the whole community (Vincx, in press).

Diversity data can be summarized as follows :

the open sea stations are characterized by nematode communities which are comparable in terms of species diversity ; the number of species S is about 30-35 per sample with the Shannon-Wiener diversity index H' between 4.00-4.50 bits/ind.. The communities in the coastal stations are less diverse ($S = 7-22$; $H' = 1.4-3.5$ bits/ind.). The stations along the Belgian east coast have communities with low diversity ($S = 7$; $H' = 1.41$ bits/ind.) and with a pronounced dominance of a few species (Simpson index = 0.54) ; the diversity within the eight families is also low.

The station groups of the *southern* part of the area do not differ in overall species diversity but they differ in species diversity within the Chromadoridae, Cyatholaimi-

dae, Microlaimidae and Xyalidae. For these families, the diversity is higher in the station group with the most coarse sediment (i.e. in the channels between the sand banks).

Differences between the two open sea areas in the *northern* part are reflected in the diversity of the Oncholaimidae and the Xyalidae (both highest in the station group with the finest sediment) and the species evenness of the total nematode community.

In the *open sea area* (south + north), the diversity in each feeding type increases with the total diversity. The non-selective deposit-feeders are most abundant in the area off the Belgian east coast, their species diversity being nevertheless significantly lower than in the other areas.

The station group in the northern open sea region which is characterized by clean medium sands with some gravel (< 3%), is localised in a dumping area of TiO₂-waste. The lower diversity in trophic structure in this area (in comparison with adjacent open sea areas) possibly indicates the effect of irregular environmental disturbance caused by pollution.

Species diversity of the whole community increases as the sediment becomes more coarse; the same correlation is found between the species diversity within the Chromadoridae, Demsodoridae, Microlaimidae and Xyalidae. The family diversity and trophic groups diversity is correlated in the same way with the sediment characteristics. The Comesomatidae, Oncholaimidae and Thoracostomopsidae have low diversity values in all types of sediments.

DISCUSSION

Zoogeographical and ecological analysis of marine benthic communities was first established on the basis of the macrobenthos.

Petersen (1914) was the first in studying this kind of problem and his definition of a community is as follows: "two dominant species from different taxonomic groups should be used to designate a community". Petersen's communities were conceived as descriptive statistical entities and not as biocoenoses, which implies ecological units. Therefore, Thorson (1957) stated that a community must be composed of species which interact with each other and the environment and a community has, therefore, an ecological basis.

Thorson (1957) defined "isocommunities" or "parallel-level bottom-communities" as ecological parallels since the same type of bottoms is inhabited by species of "parallel" animal communities in which different species of the same genera replace one another as the "characterizing species".

This concept was first established for the macrofauna, but it seems now that homogeneity and parallelism are even more pronounced at the meiofauna level (Remane, 1933; Por, 1964; Coull & Herman, 1970; cf. review Hicks & Coull, 1983).

As far as the nematodes are concerned, the existence of isocommunities is particularly clear for silty, coastal areas. These habitats are characterized by a reduced number of families and species, which seem to have a world-wide distribution. This community is characterized by the following genera : *Sabatieria* (mainly *S. punctata*), *Dorylaimopsis*, *Spirinia* (mainly *S. parasitifera*), *Terschellingia* (mainly *T. longicaudata*), *Metalinhomoeus* and *Sphaerolaimus*.

The nematode communities in the sandy substrates of the European waters are very uniform in their species composition too. However, the diversity of this kind of community is so high that it is very difficult to list a workable number of characteristic species. The species composition of the isocommunities on sand substrates is very diverse and the relative abundance of the different species is determined by factors that are still unknown. The parallel-level bottom communities of sandy substrata are mainly determined by the overall presence of Desmodoridae, Microlaimidae, Chromadoridae, Cyathoalimidae, ...

While much of this "parallelism" in community structure around the world is partly the result of certain families being interstitial (and thus confined to sandy sediment), others being burrowers and gliders (and thus confined to muds), others being strictly epiphytic (and thus in the phytal), the specificity of the assemblages in most cases is remarkable. However, in marine nematodes, some families are so highly diversified that they occur in high abundance in almost every habitat, be it with different species or genera (e.g. *Daptonema stylosum* is confined to sand while *D. tenuispiculum* is confined to sandy silt). On the other hand, the Epsilonematidae and the Draconematidae are only present in very coarse substrata.

The state of the knowledge of the subtidal meiofauna of the North Sea has been recently reviewed by Heip *et al.* (1983) and Heip *et al.* (1988). A more general review of the ecology of marine nematodes is presented by Heip *et al.* (1985). Nematodes appear to be more sensitive to slight changes in sediment composition than either macrofauna or harpacticoid copepods (Warwick & Buchanan, 1970). Govaere *et al.* (1980) recognized only three zones in our area of investigation in the Southern Bight based on macrofauna and harpacticoid assemblages. These areas are : a coastal zone, a transition zone and an open sea area. Buchanan (1963) found that the macrofauna of the Northumberland coast is poorly correlated with the granulometric composition of the sediment, but depends largely on the water depth.

Nematode species distribution changes with sediment type (Wieser, 1959 ; Warwick & Buchanan, 1970 ; Tietjen, 1971, 1977 ; Warwick, 1971 ; Scheibel, 1976 and this study). Tietjen (1977) suggested that changes in food are responsible for changing species distributions. Warwick (1971), Platt (1977) and Nichols (1980) suggested that morphological adaptations may be important in determining species presence in a given sediment type. The size of the interstices determines which type of locomotion may be utilised by interstitial organisms. Sediment porosity (as a measure of interstitial space) decreases with the degree of sorting in sediments of the same median grain size. This implies that increased variation in particle size permits

closer packing, and results in smaller interstitial spaces (Ruttner-Kolisko, 1961). Levy & Coull (1977) suggested that interstitial meiofauna must be of convenient size to fit into existant interstices. Schwinghamer (1981) found that benthic animals with a spherical diameter of 0.5 and 1.0 mm define the upper limit of the interstitial meiofauna. A shift from interstitial to burrowing lifestyles with a class of intermediate sized animals capable of neither is present in most substrates. In fluid muds however, there is no restriction on the size of organisms that are capable of burrowing (Warwick, 1984). The split between macro- and meiobenthos occurs at 45 μg because many life history and feeding characteristics switch more or less abruptly at about this body size, compromise traits being either non-viable or disadvantageous (Warwick, 1984). Meiofauna and macrofauna therefore comprise two separate evolutionary units each with an internally coherent set of biological characteristics.

It has been shown for macrobenthic organisms that the distribution of trophic groups is affected by food source and bottom stability (see for a review : Gray, 1974 ; Rhoads, 1974). The deposit-feeding and suspension-feeding macrobenthos show a marked spatial separation ; suspension-feeders are largely confined to sandy or firm muddy bottoms while deposit-feeders attain high densities on soft muddy substrata (Rhoads & Young, 1970). The low proportion of suspension-feeders on unstable muddy bottoms is related to the instability of the surface, which may clog their filtering structures. The incompatibility of deposit- and suspension-feeding populations has been termed "trophic group amensalism". Amensalism is an interaction between two populations where one population is inhibited and the other is not. Rhoads and Young (1970) predicted that the macrobenthic animals in Buzzard's Bay, would be of three types, namely : (1) homogeneous suspension-feeders, where deposit-feeders are excluded by inadequate food source ; (2) homogeneous deposit-feeders, where suspension-feeders are excluded by reworking and resuspension of sediments (partly by the deposit-feeders) ; (3) mixed trophic groups where a diverse suspension- and deposit-feeding community thrives due to the physical stability of the bottom.

Although the meiofauna seems to share many ecological properties with the macrofauna, processes operate on a much smaller spatial and shorter time scale within the meiofauna. Since changes in meiofauna populations exposed to manipulation appear to occur more quickly than in macrofauna (see Bell, 1980 for a review), the meiofauna may represent a special group of benthic organisms which can be used to test ideas on long-term community changes and succession within a feasible period of time. Meiofauna may structure macrofaunal communities too (Watzin, 1983). When macrofaunal larvae and juveniles recruit into the benthos, they are of the same size category as the meiofauna ; therefore competition for shared space and food may become important. There exists an affect of macrobenthic feeding activities, especially of deposit-feeders, on the trophic structure of the meiobenthic community as well. Govaere *et al.* (1980) described three macrobenthic communities in the Southern Bight of the North Sea. Deposit-feeders are especially abundant along the Belgian

coast ; but along the Dutch coast and the Southern sand bank area, carnivores dominate the deposit-feeders and omnivores and filter-feeders increase in number. The open sea area is characterized by a more even distribution of the macrobenthic trophic groups, with the filter-feeders very abundant in most of the stations ; the complexity of the trophic chain is highest within this area (Govaere, 1978). The detailed distribution (and hence the activity) of the different macrobenthic animals is not known at present within the area ; it is very probable that especially in "the more stable open sea area" the activity of the macrobenthos in reworking the sediment is more important (cf. high abundance of deposit-feeding macrobenthos in some stations) than in the coastal area, where the effects of e.g. tidal currents and pollution is to enhance the settling of fine particles within the sediment. Nevertheless, the similarity between the trophic group separation of macrobenthos and nematodes is striking. The trophic group separation within the nematodes probably exists between non-selective deposit-feeders (1B) and epigrowth-feeders (2A). In TWIN 2, 3 and 4 the 2A feeding type is two to three times more abundant than the 1B ; in TWIN 5 both groups are equally numerous ; in TWIN 6, 1B is the dominant feeding type with 2A almost absent ; in TWIN 1, the distribution of the four feeding types is rather even, with a high proportion of 1A. For the nematodes, there is no incompatibility between feeding groups because the deposit-feeders are not capable of reworking the substrata in such a way that it becomes unattractive to epigrowth-feeders. The lower amount of food in the open sea sediments is perhaps not sufficient for the deposit-feeding nematodes, which are therefore not able to survive in quite high numbers. But perhaps there exists some incompatibility between high densities of macrobenthic deposit-feeders and epigrowth-feeders and harpacticoid copepods. Only 2A nematodes are dependent on the same food source as the copepods (Warwick, 1981). Interstitial copepods browse on the surface of sand grains, scraping off the epiflora (Noodt, 1971 ; Feller, 1980). The interstitial spaces may be filled by fine resuspended and reworked material which can partly be caused by deposit-feeding activities of the macrobenthos. Epigrowth-feeders among the nematodes may be unable to feed unless suitable surfaces are available (Alongi & Tietjen, 1980). If the interstices are filled with fine material (f.i. in the case of heterogeneous sediment, i.e. high median of the sand fraction with some (or a lot of) silt, high sorting coefficient, cf. TWIN 5 and 6), the sand grain surfaces are no longer surrounded by rather large interstices and therefore less available to be scraped off ; the movement of specialized interstitial animals is also inhibited by the filling up of the interstitial space. From all this, I conclude that the availability of food, heterogeneity of the sediment and the abundance of the deposit-feeding macrobenthos are the main limiting factors for the number of epigrowth-feeding nematodes.

SAMENVATTING

De nematodengemeenschappen van de Zuidelijke Bocht van de Noordzee, bemonsterd in 102 stations tijdens de periode van 1972 tot 1984, werden bestudeerd. In totaal zijn er 456 soorten gevonden die behoren tot 159 genera en 37 families.

Op basis van de nematodensoortensamenstelling kan de Zuidelijke Bocht van de Noordzee verdeeld worden in zes grote gebieden :

1) De Belgische kust (met uitzondering van enkele stations langs de westkust). Dit gebied is gekenmerkt door fijn tot gemiddeld zand met een hoog percentage (45%) slib en organische koolstof (1.4%) ; de diepte bedraagt gemiddeld 10 m. Belangrijke soorten zijn : *Ascolaimus* sp. 1., *Daptonema tenuispiculum* en *Sabatieria punctata*.

2) Het gebied langs de Nederlandse kust en de Belgische westkust. Dit gebied wordt gekenmerkt door fijn tot gemiddeld zand met een kleine hoeveelheid slib (< 5%) en grint (< 2%) ; de diepte bedraagt gemiddeld 16 m. Belangrijke soorten zijn : *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* en *Sabatieria celtica*.

De zuidelijke open zee-zone kan verdeeld worden in twee gebieden :

3) De ruggen van de zandbanken (10-15 m diep) met een bodem die bestaat uit gemiddeld zand met een zeer laag slibgehalte maar met een hoog percentage aan organische koolstof (> 2%). Belangrijke soorten zijn : *Bathylaimus parafilicaudatus*, *Desmodora schulzi*, *Leptonemella aphanothecae* en *Onyx perfectus*.

4) De geulen tussen de zandbanken (25-35 m diep) hebben een zeer grof sediment (> 25 % grint). Belangrijke soorten zijn : *Hypodontolaimus* n. sp. 1, *Onyx perfectus*, *Rhips ornata*, *Rhynchonema quemer* en *Spilophorella paradoxa*. De Epsilonematidae en de Draconematidae zijn eveneens karakteristiek voor deze zuidelijke zone.

5) Een gebied gekenmerkt door zuiver gemiddeld zand met een laag grintgehalte (< 3%). Belangrijke soorten zijn : *Chromaspirina parapontica*, *C. pellita*, *Dichromadora cucullata*, *Karkinochromadora lorenzeni* en *Xyala striata*.

6) Een gebied gekenmerkt door zuiver gemiddeld zand met een hoger grintgehalte (> 3%). Belangrijke soorten zijn : *Chromaspirina parapontica*, *C. pellita*, *Karkinochromadora lorenzeni*, *Molgolaimus turgofrons* en *Neochromadora munita*.

De vier voedingstypes van de nematoden zijn als volgt verspreid : selectieve deposit-eters (type 1A) zijn belangrijker in de open zee-zone (in vergelijking met de kustzone) ; de gemiddelde relatieve abundantie is echter niet hoger dan 20% ; de omnivore-predatoren (Type 2B) hebben een relatieve abundantie die varieert rond 20% over het gehele gebied (met uitzondering van de Belgische oostkust die minder dan 20% omnivoren-predatoren herbergt). De relatieve abundantie van de epistatum-eters (type 2A) is het hoogst in het open zeegebied (tussen 30 en 52%), terwijl de niet-selectieve deposit-eters (type 1B) talrijker voorkomen in het kustgebied (tussen 40 en 93%).

De verspreiding van de verschillende voedingstypes (en in het bijzonder de epistratum-eters) wordt bepaald door de heterogeniteit van het sediment en door het voorkomen van de macrobenthische deposit-eters.

De invloed van de sedimentsamenstelling op de verspreiding van de voedingstypes kan als volgt worden samengevat :

- het aandeel van type 1A is groter in goed gesorteerd, zuiver zand ;
- het aandeel van type 1B daalt in grovere sedimenten maar ze komen zeer talrijk voor in slibbige sedimenten met een hoog gehalte aan organische koolstof ;
- het aandeel van type 2A neemt toe met de mediaan van de zandfractie en vermindert met een stijgend gehalte aan slib en organische koolstof ;
- het aandeel van type 2B neemt toe in zandige, goed gesorteerde sedimenten met een laag gehalte aan organische koolstof.

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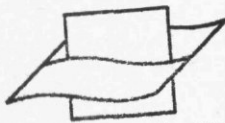
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Invloed van het wassen op de houdbaarheid van schol



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W. VYNCKE

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SAMENVATTING

Met een roterende trommelwasmachine werden wasproeven op schol (*Pleuronectes platessa* L.) uitgevoerd. Het wassen verlengde de houdbaarheid met 1 à 2 dagen, doch werkte een grijze verkleuring van de donkere zijde in de hand. Tussen 0,5 - 1 en 2 min wasduur werd geen verschil genoteerd.

Er kon worden besloten dat het wassen van schol alleen nut heeft vóór het fileren of panklaar maken (ontkopen, verwijderen van vinnen en staart, portioneren) van de vis.

1. INLEIDING

In vorige publikaties (1) (2) (3) werd de problematiek van het wassen van vis behandeld en werden resultaten van wasproeven op kabeljauw (*Gadus morhua* L.) gegeven. Met een trommelwasmachine werd een geringe verlenging van houdbaarheid van 1 à 2 dagen bekomen.

De proeven werden met schol (*Pleuronectes platessa* L.) verdergezet.

2. EXPERIMENTELE GEGEVENS

2.1. Vis

Schol (*Pleuronectes platessa* L.) afkomstig uit de Zuidelijke Noordzee, gevangen in de periode maart tot mei met een gewicht van 200 à 300 g en een versheid van 4 à 7 dagen. Op te merken valt dat de vis reeds aan boord onmiddellijk na het strippen werd gewassen.

2.2. Wasmachine

Trommelwasmachine LeBa (Hoogwoud, Nederland). De trommel draait aan 25 toeren per minuut en heeft een diameter van 53 cm voor een lengte van 60 cm. De machine werd aan een centrifugaalpomp aangesloten. Het waterdebiet uit de 54 sproei-openingen van 5 mm bedroeg 180 l/min bij 0,5 kg druk.

2.3. Laboratoriumbepalingen.

— Elektrische weerstand : met een « Intelectron Fish-Tester » (Dethlof Electronics, Hamburg).

— Totale vluchtige basische stikstof (TVB), trimethylamine (TMA), totale vluchtige zuren (TVZ), totaal aantal bacteriën (TAB) van de huid en van het visvlees en organoleptische keuring : volgens de vroeger vermelde methoden (3). Bij deze laatste keuring werd evenwel alleen rekening gehouden met de versheidsgraad van de vis. Grijsz verkleuringen (zie verder) werden niet in aanmerking genomen.

2.4. Werkwijze

De machine werd telkens met 20 kg vis gevuld. Wastijden van 0,5, 1 en 2 min werden onderzocht. Langere wastijden werden niet beproefd daar werd vastgesteld dat met de betrokken machine de vis licht beschadigd werd wanneer langer dan 2 min werd gewassen.

De vis werd in ijs opgeslagen en bij 0°C bewaard. Na respectievelijk 0, 2, 7 en 10 dagen werden van ieder monster vijf vissen voor chemische, bacteriologische en organoleptische analyses genomen.

Alle proeven werden vijfmaal op verschillende tijdstippen herhaald.

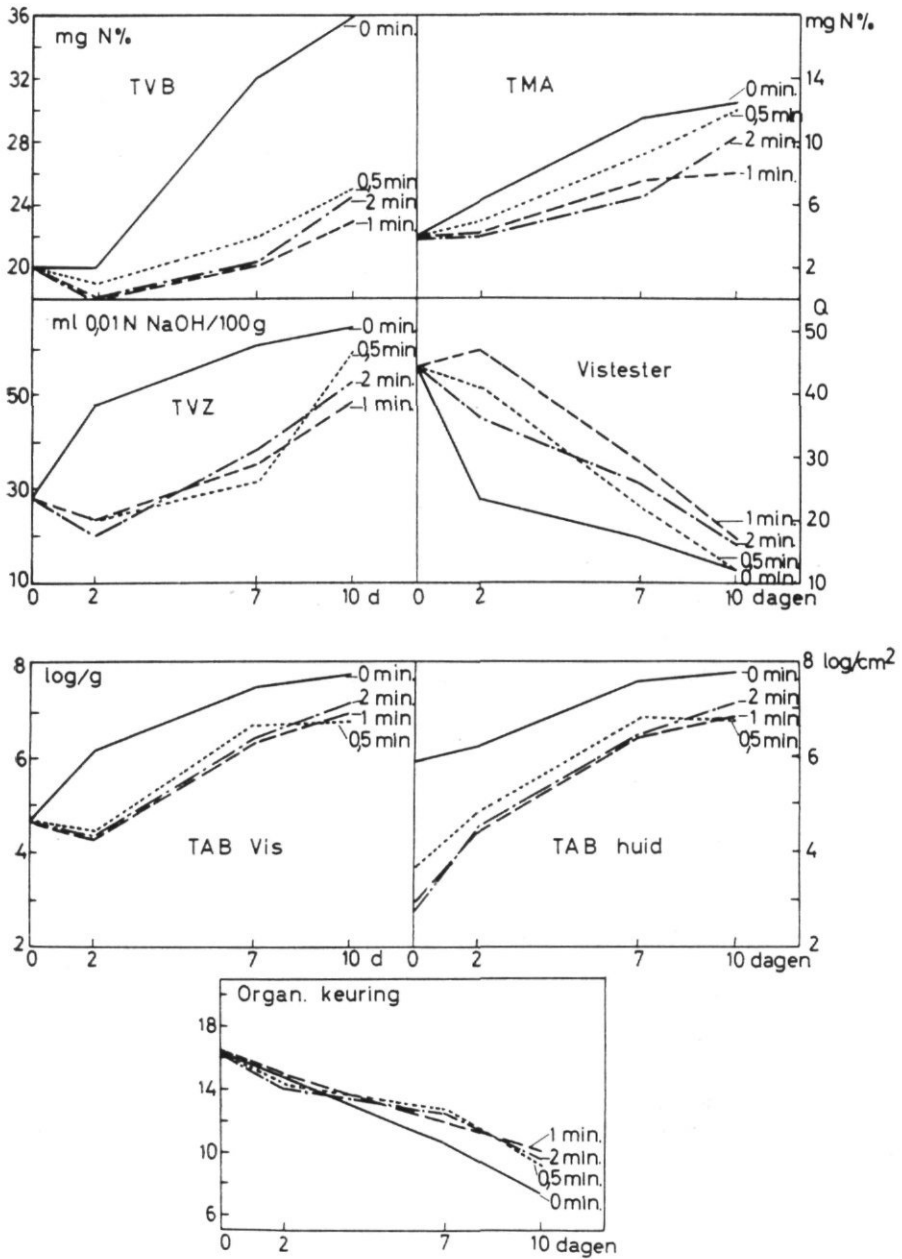
3. RESULTATEN EN DISKUSSIE

De gemiddelde resultaten zijn grafisch in figuur 1 weergegeven.

Het totaal aantal bacteriën van de huid werd door het wassen sterk gereduceerd. Voor een wastijd van 2 min bedroeg de reductie 99,9 %; voor 0,5 en 1 min was dit meer dan 99,5 %. Het kiemgetal steeg dan opnieuw, maar bereikte nooit dit van ongewassen vis terug. Het aantal bacteriën in het visvlees bleef eveneens gedurende gans de bewaarperiode lager in de gewassen schol. Deze verlaging van kiemgetal bleek echter niet voldoende om het bederf van gewassen vis voldoende te remmen.

Uit de evolutie van de vistesterwaarden, TVB, TMA, TVZ en de organoleptische scores bleek dat er de eerste 5-6 dagen praktisch geen verschil in bederf tussen gewassen en ongewassen schol te noteren viel. Vanaf dit tijdstip werd wel een verschil in het voordeel van de gewassen vis vastgesteld. De ongewassen vis had de grens van bederf na 9 d (± 1 d) bereikt,

FIGUUR 1. — Invloed van 0, 0,5, 1 en 2 min wassen op de evolutie van TVB, TMA, TVZ, Vistesterwaarden, TAB en organoleptische scores van schol



terwijl dit voor de gewassen vis 1 à 2 dagen later plaats greep. Tussen 0,5, 1 en 2 min wasduur kwam weinig verschil voor.

Deze resultaten zijn in overeenstemming met deze van Obdam (4).

Zoals voor het wassen van kabeljauw (3) kan men betwijfelen of een verlening van houdbaarheid van 1 à 2 dagen voor de praktijk belangrijk is. Daarenboven kwam een ander verschijnsel de resultaten beïnvloeden. Bij drie proeven op de vijf werd vastgesteld dat de donkere zijde van de vis na 1 of 2 dagen opslag in ijs grijs werd. Dit was slechts matig het geval voor de ongewassen vis, maar de gewassen vis werd sterk verkleurd.

Dit fenomeen kan wellicht als volgt worden uitgelegd. Schol, zoals andere platvissoorten, wordt zeer dikwijls met de *bokkervisserij* gevangen, daar hierdoor een hoger rendement wordt bereikt. Deze manier van vissen kan echter gemakkelijk huidbeschadigingen veroorzaken. De graad van beschadiging hangt van een aantal factoren af waarvan de weersomstandigheden, de aard van de bodem, het gewicht van de wekkerkettingen en de duur van de sleep de voornaamste zijn.

Wanneer de huidbeschadiging een zekere graad heeft bereikt worden de vissen vlug grijs. Dit werd ook in Nederland vastgesteld waar de invloed van het « zwaar » of « licht » vissen werd bestudeerd (5).

De huid, en meer bepaald het dermis bevat chromatoforen die gemodificeerde cellen zijn die pigment bevatten (zwart, geel, rood of wit) (6). Men kan aannemen dat deze pigmenten door de mechanische beschadiging van de huid gemakkelijker geoxydeerd worden waardoor de grauwe kleur domineert. Door het wassen in een trommelwasmachine wordt de beschadiging groter waardoor de verkleuring nog toeneemt. Anders uitgedrukt kan men vooropstellen dat wanneer een schol door de vangstomstandigheden neiging tot grijsworden vertoont, deze neiging door het wassen nog zal worden versterkt.

4. BESLUITEN

Deze proeven hebben aangetoond dat het niet aan te raden is schol die nog enkele dagen moet worden bewaard vooraleer bewerkt en/of gekommercialiseerd te worden, te wassen.

Daar de temperatuur de voornaamste faktor is die de bederfsnelheid bepaalt, dient de vis daarentegen na de veiling zo spoedig mogelijk opnieuw afgeijsd en in koelkamer bij 0°C voor verdere bewaring te worden geplaatst.

Het wassen van de vis is anderzijds een noodzakelijkheid vóór het fileren of het panklaar maken van het produkt (ontkopen, verwijderen van vinnen

en staart en portioneren). Zoals werd aangetoond, wordt in de eerste plaats het kiemgetal zeer sterk verlaagd. Dit kan op het gebied van de volksgezondheid van belang zijn daar eventueel aanwezige schadelijke kiemen eveneens sterk in aantal worden gereduceerd. Verder wordt de presentatie van het produkt verbeterd en wordt tenslotte de bezoedeling van oppervlakten waarmede de vis in aanraking komt, sterk verminderd.

SUMMARY

Washing experiments were carried out on plaice (*Pleuronectes platessa* L.) using a rotary washing machine. Shelf life was improved by 1 or 2 days but washing enhanced a grey discolouration of the dark side of the fish. No difference was noted between washing times of 0,5 - 1 and 2 minutes.

It could be concluded that washing plaice is useful only before filleting or dressing (beheading, removal of fins and tail, portioning) the fish.

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