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The distribution of Nematodes communities in the Southern Bight of the North Sea.

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Abstract : The nematode communities from 102 stations in the Southern Bight of the North Sea, sampled between 1972 and 1984, are examined. On the whole, 456 species, belonging to 159 genera and 37 families were found.

Multispecies patterns are analysed by means of cluster analysis (Bray-Curtis dissimilarity coefficient), Twinspan classification and DCA ordination.

Generally, the Southern Bight can be divided into six main areas on the base of nematode species composition.

Sediment structure was found to be the determining environmental factor in the species composition of nematode communities. Also several other environmental factors, (temperature, salinity, chlorophyll a, $NO3^{-}$, $NH4^{+}$) seem to influence the distribution of the nematode species.

One of the most striking features of the coastal ecosystemS, and of the Belgian coastal zone in particular, is the importance of the role of the bacteria. A general increase of the level of primary production in the coastal area, as a result of increasing nutrient input, does not necessarily lead to an increase of pelagic or demersal fish production, but could induce a modification of the food web, in particular the enhancement of microbiological activity at the expense of long trophic chains dominated by macroorganisms.

The near absence of nematode-predators in the region off the Belgian east coast, the dominance of bacterivores, the very low species diversity of the nematode community and the paucity of higher metazoans within the area, can be partly explained on the basis of the increase in nutrient input within the area, and partly on the basis of the high amount of "mixed" pollution.

Résumé : Identification des assemblages de nématodes de 102 stations de la partie sud de la mer du Nord où des prélèvements ont été effectués de 1972 à 1984 : 456 espèces ont été répertoriées, appartenant à 159 genres et 37 familles.

Interprétation des communautés par l'analyse des groupements d'espèces (coefficient de dissimilarité de Bray-Curtis et classification polythétique Twinspan) et par l'analyse factorielle des correspondances (DCA).

Globalement, le bassin du sud de la mer du Nord peut être divisé en six zones principales définies par la composition spécifique des nématodes.

La structure sédimentaire apparaît comme le facteur du milieu déterminant de la composition spécifique de la nématocoenose ; cependant, d'autres facteurs (température, salinité, chlorophylle a, $N03^{-}$, NH4+) semblent également influer sur la distribution des espèces.

L'importance du rôle des bactéries représente l'un des caractères les plus remarquables des écosystèmes côtiers et, en particulier, de celui de la côte belge. Dans cette région, un accroissement du taux de production primaire, lié à une intensification de l'apport de nutriments, n'entraîne pas nécessairement l'augmentation de la production en poissons pélagiques ou démersaux ; mais il pourrait provoquer des modifications des réseaux trophiques, notamment la stimulation de l'activité microbiologique aux dépens des chaînes trophiques longues dominées par les macro-organismes.

Au large de la côte est de Belgique, la dominance des nématodes bactérivores, la quasi-absence des prédateurs, la très faible diversité spécifique des communautés de ce groupe et la pauvreté des métazoaires supérieurs peuvent trouver leur explication d'une part dans l'augmentation de l'apport en nutriments et d'autre part dans la grande quantité de pollution diffuse.

INTRODUCTION

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).

In the Southern Bight, studies started in 1971. Some of the data on nematodes were already published (Heip *et al.* (1979), Vincx (1981), Vincx *et al.* (1982), Heip *et al.* (1983), Vincx (1983), Herman *et al.* (1985),Vincx (1986 a & b) and Vincx (in press).

This work concentrates on the description of characteristic Species-assemblages of the nematodes within the area and their correlation with environmental parameters.

MATERIAL AND METHODS

Study area

All samples originate from the area bordered to the south by 51°05'20"N and to the north by 52°36'30"N, to the east by the Belgian and Dutch border and to the west by a border extending 60 km from the Belgian coast in the south to 105 km from the Dutch coast in the north (Fig.1), commonly called the Southern Bight of the North Sea.

The tidal current system, determined by the funnel-shaped Channel, organizes the sedimentation in the Southern Bight. The currents are parallel with the Belgian coast with a decreasing velocity to the north. These currents distribute the sediments (gravels, sand and mud) in the area and maintain its topography.

In the southern part, the area is characterized by several sand banks, in the northern part decreasing current velocities result in decreasing grain size of the sand. The topography is characterized by large sand waves and sand ribbons.

Mud is brought into the North Sea mainly by rivers and through the Channel in the order of 5-10x10^6 ton/year (Veenstra, 1970 ; McCave, 1973). Near the Belgian coast, sedimentation of mud is influenced by features of the incoming water from the rivers. Mud is transported from the Scheldt into the sea ; this mud is mainly of marine origin but it may be enriched with pollutants from the Scheldt.

Sampling stations and dates

The nematode communities from 102 stations in the Southern Bight sampled between 1972 till 1984 are examined in this study.

56 stations were collected during 1971-1975. Sampling occurred in different seasons (four times a year) (station numbers 1 to 2841 in Fig. 1).

From 1976 on, 16 new stations were examined (along the Belgian coast ; station numbers 10061 to 11315 in Fig. 1).

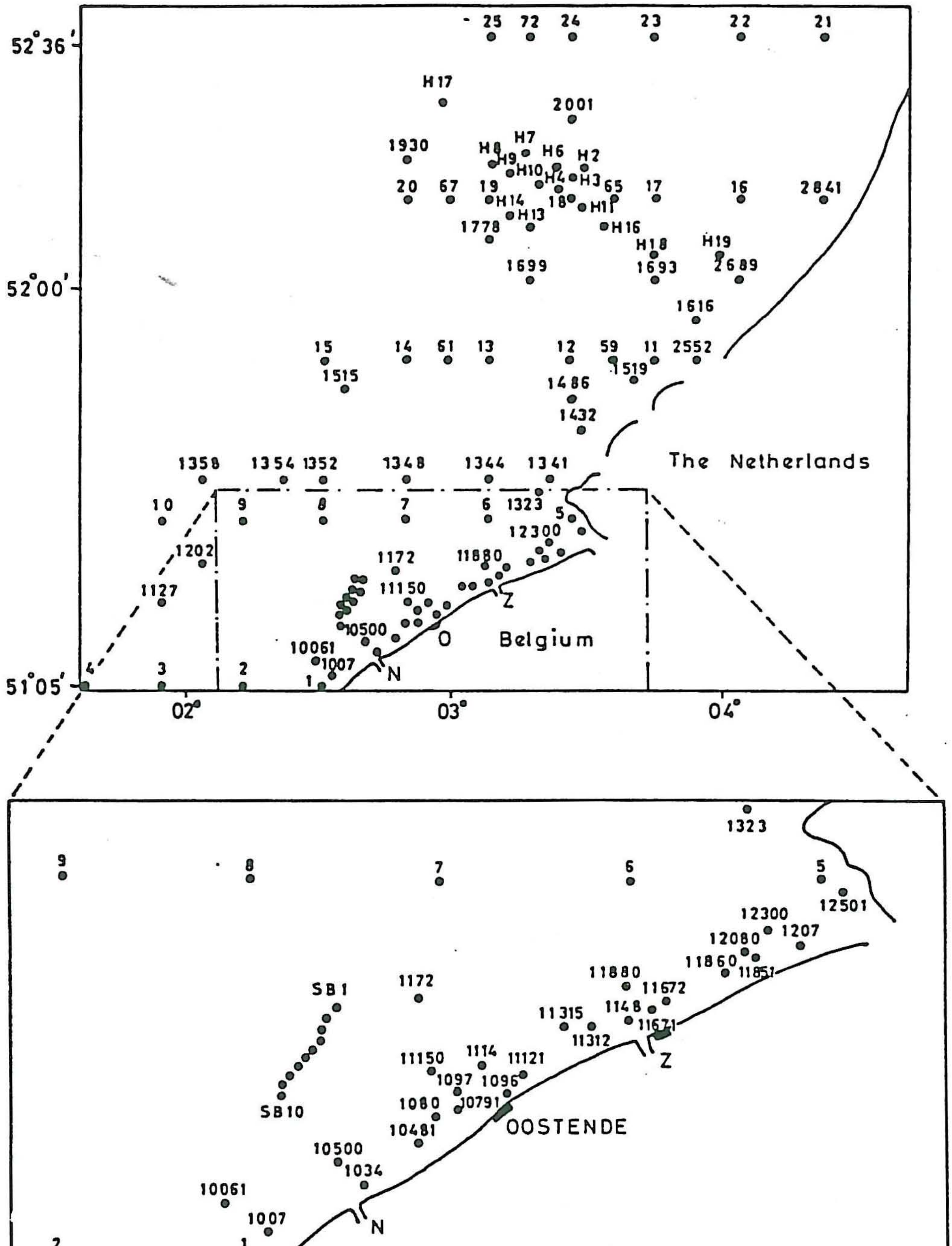

Fig. 1 : Position of the sampling stations.

In September 1978, the meiofauna of the Kwintebank (stations with prefix 'SB' in Fig.1) (see Willems *et al.*, 1982 a & b) and in June 1984, the meiofauna of the stations with prefix 'H' have been analysed (Fig. 1).

Sampling methods

The meiofauna samples collected from 1972-1975 were taken by subsampling a 0.1 m^2 Van Veen grab. From April 1978 on, a modified Reineck-boxcorer (surface 170 cm^2) (Farris & Crezee, 1976) was used.

Four subsamples (10.16 cm^2) were taken : two replicates for meiofauna were fixed with warm formalin (70°C) to a final concentration of 4 %. The two other cores for chemical and sediment analysis were immediately frozen.

From October 1984 onwards, meiofauna was sampled using a box-corer (sampling area = 0.25 m^2) from which subsamples were taken from the Belgian Oceanographic Research Vessel "Belgica".

Extraction techniques

The extraction techniques of nematodes from sediments differ with sediment type.

Simple decantation on a sieve (38 µm) is satisfactory for sand with low amounts of detritus or silt (Hulings & Gray, 1971). The trough-method (Barnett, 1968 ; Heip, 1976) is also applicable for sand samples. The extraction from muds or detritus (after the sand has been removed by decantation or other methods) is done using a density-gradient centrifugation technique (Heip *et al.* 1985).

Microscopical examination and determination.

Two hundred nematodes from each subsample were identified to species level.

Numerical methods

A) Association measures and accompanying classifications.

Field e*t al.* (1982) recommend the Bray-Curtis coefficient (Bray & Curtis, 1957) for marine data because it is not affected by joint absences and it gives more weight to abundant species (in comparing samples) than- to the rare ones.

B) Ordination

For ordination we used DCA (Detrended Correspondence Analysis). Technical details of it are given in Hill (1979 b), Hill & Gauch (1980) and Gauch (1982).

C) Twinspan-classification

The Twinspan (Two-way indicator species analysis) -classification technique is a polythetic divisive classification technique (Hill, 1979 a). First the samples, and secondly the species are classified, using the classification of the samples as a basis. In this way, the species are classified according to their ecological preferences. The two classifications are then used together to obtain an ordered two-way table that expresses the species "synecological relations as succinctly as possible".

RESULTS

Environmental parameters

The position, depth and sediment characteristics of all sampling stations are summarized in Table 1.

The median grain size, percentage silt and percentage gravel for each station is plotted in Figs 2-4.

From the Spearman rank correlations between the different parameters, we conclude that the median grain size of the sand fraction increases significantly from the south to the

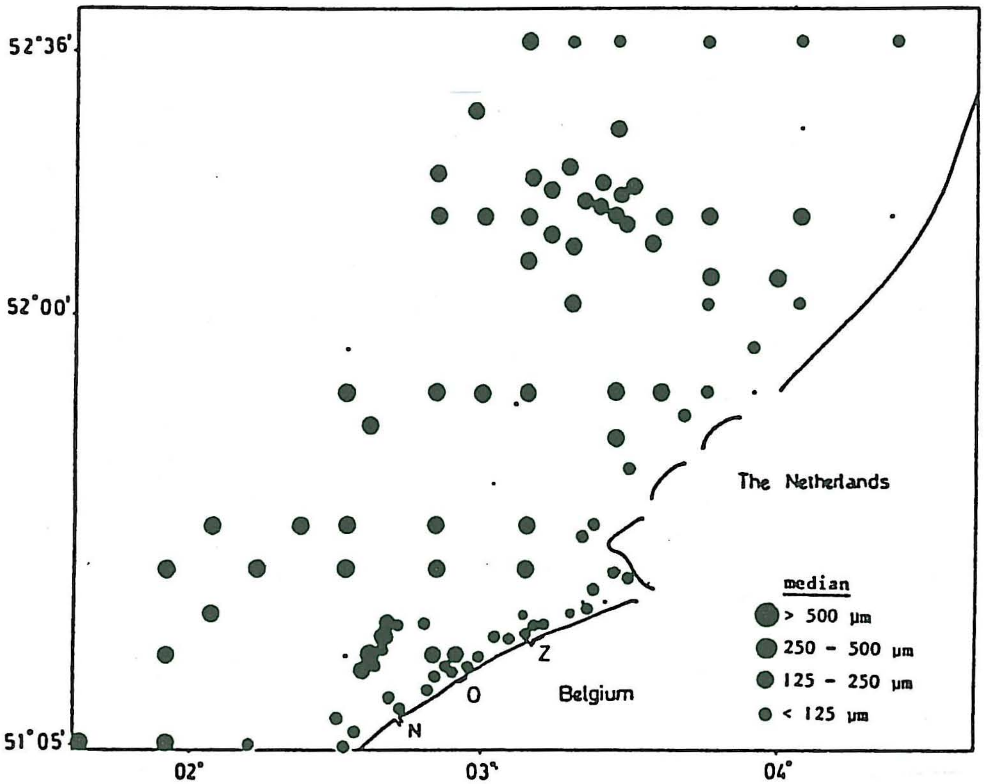

Fig. 2 : Distribution of the sandy stations in the Southern Bight.

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 (ø) ; Sk = skewness (ø); % 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	0.26	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°05'20n	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	227	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
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	10.24	0.03	0.00	0.23

Station	NB	EL	D	Gravel	Md	Sc	Sk	Silt	Org C
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	?	?42.0	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	0.10
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	2.5	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°25'31"	03°23'24"	13	0.1	196	0.40	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	0.0	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	-0.001	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

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 grain size of the sand fraction and the gravel content have a significantly negative correlation with EL, i.e. the offshore stations from the southern part (i.e. those stations between 1°57'and 3° EL) have significantly coarser sediments than the coastal stations and the off-shore stations in the north (east of 3° EL).

Density

The sampling procedure in the early years (1972-1975) is only adequate to give information on the species composition and the relative abundance of the most common species within the community. Densities of nematode communities of the study area were already published by Van Damme & Heip (1977) ; they calculated for the period 1971-1975 the mean nematode density in the Southern Bight for subsequent summer and winter periods. These authors distinguished three zones in the Southern Bight : a coastal zone, an intermediate zone and an open sea zone. These zones were mainly defined on the distribution of the macrobenthos and the harpacticoid copepods (cf. also Govaere *et al.*, 1980). The coastal zone has a mean nematode value of 1196 ind./10 cm^2 the intermediate zone a mean density

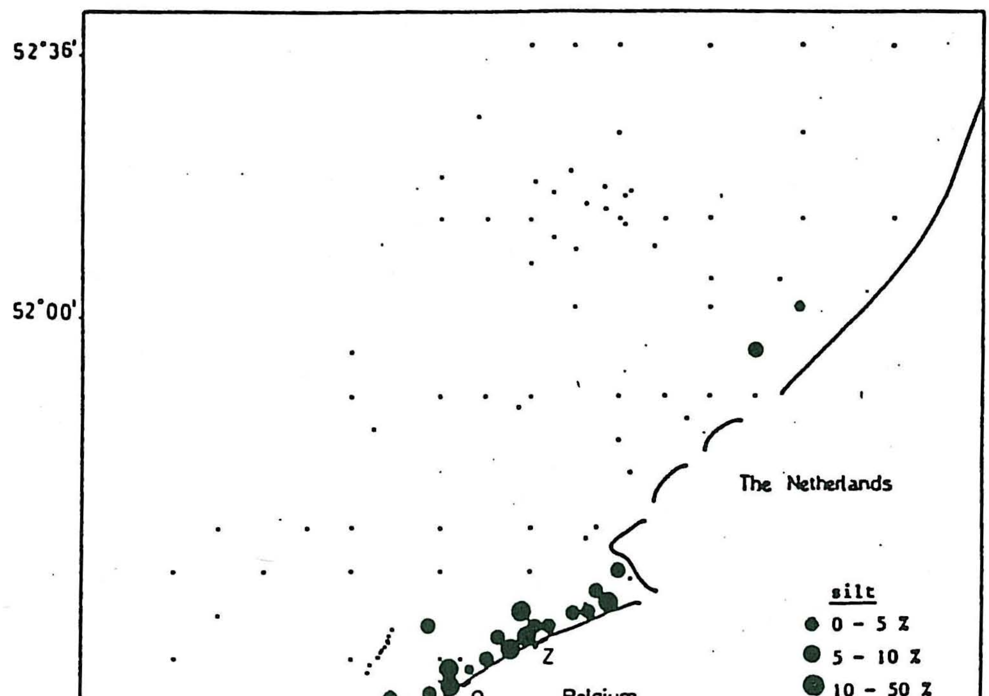

Fig. 3 : Distribution of the silty sediment stations in the Southern Bight.

of 1071 ind./10 cm^2 and the open sea zone a mean density of 963 ind./10 cm^2 ; this results in an overall mean of 1000 ind./10 cm^2 for the whole area. Differences between the three areas are not statistically significant. As already mentioned, these values should be treated with caution because sampling was not well adjusted for quantitative meiobenthic research.

Species composition

The examination of the 102 stations revealed 456 nematode species, belonging to 159 genera and 37 families. Complete species lists are available on request from the first author.

Following species are considered as very common, because they occur in more than 50 % of the stations (in decreasing order of frequency) :

Prochromadorella attenuata, Dichromadora cucullata, Onyx perfectus, Enoploides spiculohamatus, Chromaspirina parapontica, Microlaimus marinus, Sabatieria celtica, Neochromadora munita, Paracyatholaimus pentodon, Xyala striata, Chromaspirina pellita and Viscosia franzii.

146 species are very rare, i.e. they are found in only one station. These species occur also in very low numbers.

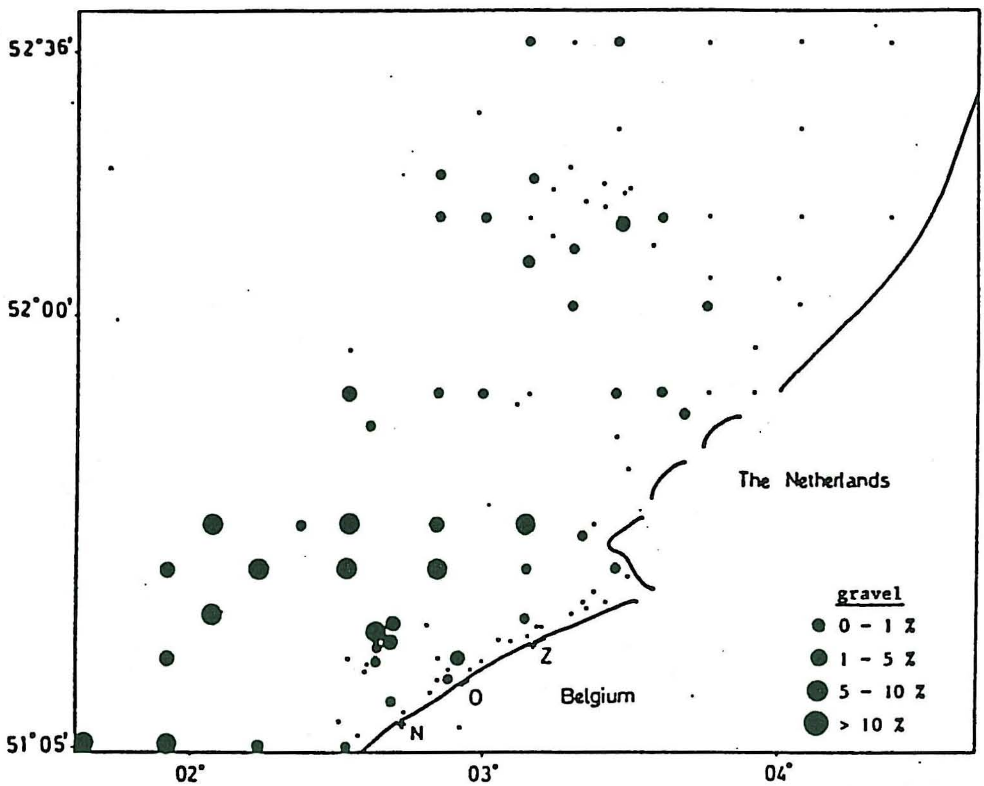

Fig. 4 : Distribution of the gravel content of the stations in the Southern Bight.

29 species have a mean relative abundance higher than 1 % ; these are in decreasing order of occurrence :

Sabatieria punctata, Daptonema tenuispiculum, Karkinochromadora lorenzeni, Prochromadorella attenuata, Paracyatholaimus pentodon, Sabatieria celtica, Chromaspirina parapontica, Neochromadora munita, Chromaspirina pellita, Onyx perfectus, Enoploides spiculohamatus, Microlaimus conothelis, Dichromadora cucullata, Monhystera disjuncta, Molgolaimus turgofrons, Microlaimus marinus, Desmodora schulzi, Paracanthonchus thaumasius, Xyala striata, Richtersia inaequalis, Spirinia parasitifera, Daptonema normandicum, Leptonemella aphanothecae, Chromadorita sp.3, Rhynchonema quemer, Tubolaimoides aff. *tenuicaudatus) Viscosia franzii, Calomicrolaimus honestus and Monoposthia mirabilis.*

Multivariate-Analysis of the multispecies patterns

In a cluster analysis, only 185 out of the 456 species (with an overall mean relative abundance > 0.5 %) were taken into account. Six station groups are recognized (CLUS 1 to CLUS 6) (Fig .5).

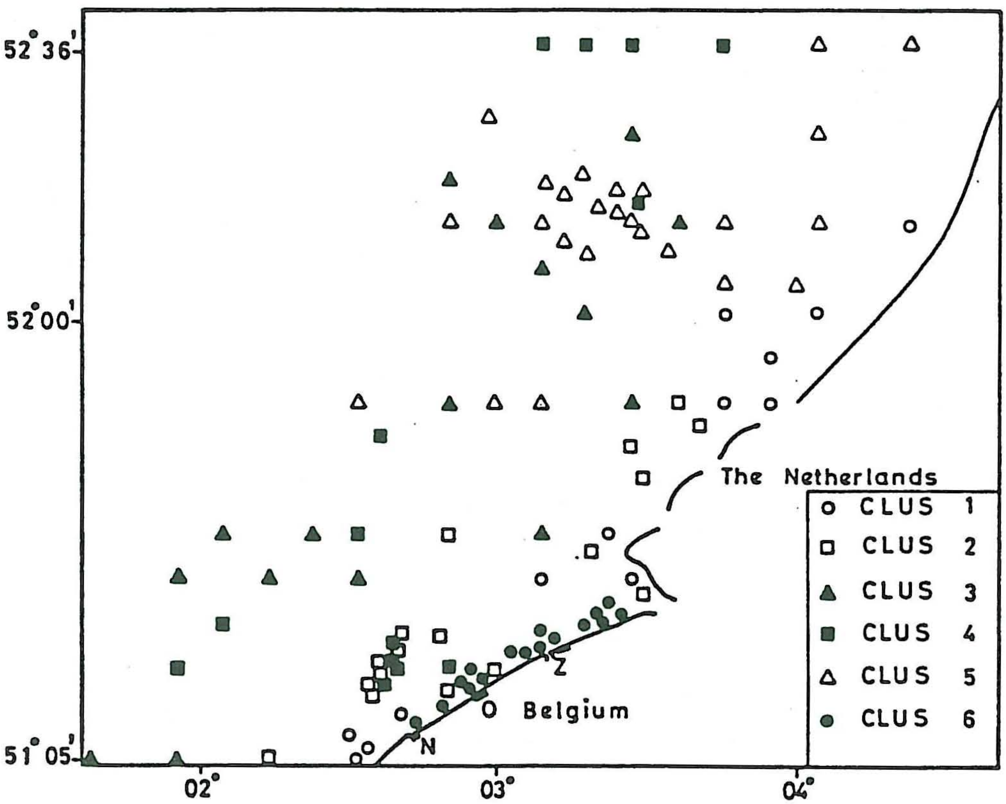

Fig. 5 : Distribution of the six station groups of the cluster analysis in the Southern Bight.

CLUS 1 contains stations along the Dutch coast and the Belgian west coast. CLUS 2 contains stations of the southern offshore part of the area and the area before the Dutch Delta. CLUS 3 and CLUS 4 contain open sea stations from the south to the north in the area. CLUS 5 is restricted to the northern open sea area. CLUS 6 contains stations along the middle and east part of the Belgian coast.

For the Twinspan-analysis all 456 species were taken into account. From the resulting classification (Fig. 6), we consider the six station groups 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 following differential species (with a mean relative abundance > 5 %) are selected during the classification :

TWIN 1 (10 stations) : *Bathylaimus parafilicaudatus, Desmodora schulzi, Leptonemella aphanothecae, Onyx perfectus.*

TWIN 2 (10 stations) : *Hypodontolaimus* n.sp.1, *Onyx perfectus, Rhips ornata, Rhynchonema quemer, Spilophorella paradoxa.*

TWIN 3 (21 stations) : *Chromaspirina parapontica, Chromaspirina pellita, Dichromadora cucullata, Karkinochromadora lorenzeni, Xyala striata.*

TWIN 4 (21 stations) : *Chromaspirina parapontica, Chromaspirina pellita, Karkinochromadora lorenzeni, Molgolaimus turgofrons, Neochromadora munita.*

TWIN 5 (18 stations) : *Enoploides spiculohamatus, Paracyatholaimus pentodon, Prochromadorella attenuata, Richtersia inaequalis, Sabatieria celtica.*

TWIN 6 (22 stations) : *Ascolaimus* sp.1, *Daptonema tenuispiculum, Sabatieria punctata.*

The species list per station group is important in the comparison with the closest station group within the classification. It is not allowed to compare the differential species of one subdivision with the species of a station group that is far apart in the classification.

Two DCA ordinations have been done :

DCA 1 : including all species and all stations

DCA 2 : downweighting of rare species and all stations

The two-dimensional plots are presented in Figs 7-8.

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 most common frequency). No other remarkable difference are present between DCA1 and DCA2.

In Figs 7-8 the results of the Twinspan analysis are superimposed on the plots of DCA.

The greatest distance is present between TWIN 6 and TWIN 1 on Axis 1 although the differences between TWIN 1 to TWIN 6 are not so clearly separated along Axis 2. Axis 2 however shows the largest distance (dissimilarity) between TWIN 4 and TWIN 1 while TWIN 2, 3, 5 and 6 have intermediate positions.

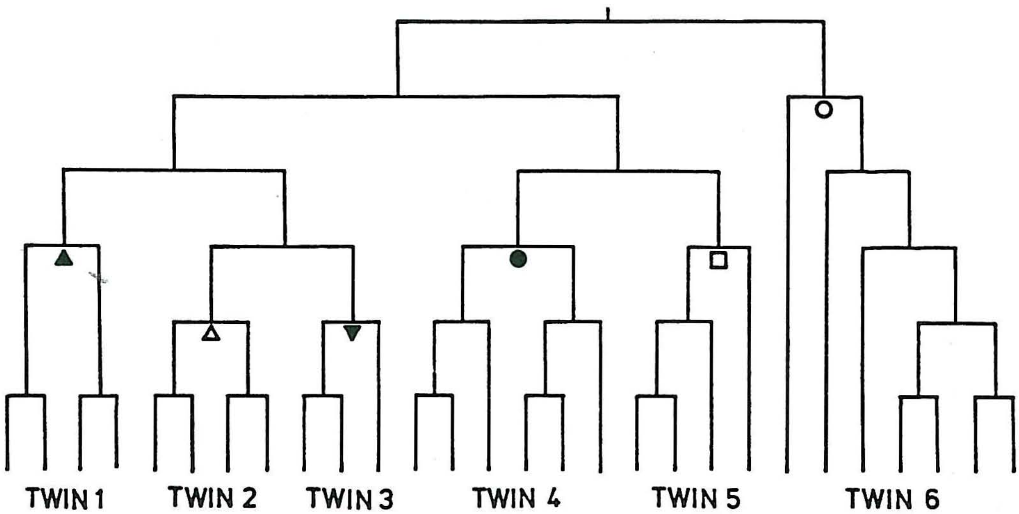

Fig. 6 : Dendrogram of the Twinspan classification.

Figs 9-10 present the iso-lines of respectively DCA1-Axis 1 scores and DCA1-Axis 2 scores in the area (similar areas are delineated for DCA2).

The subdivision of the stations from the coast to the open sea along Axis 1 and from the south to the north along Axis 2 is very obvious. A superposition of both figures gives more or less the same station groups as those defined by the Twinspan-classification.

The distribution of the station groups within the field is given in Fig. 11. TWIN 1 combines 9 stations on the Kwinte Bank and one Station along the Belgian west coast.

TWIN 2 groups 10 stations west of the Kwinte Bank.

TWIN 3 groups the offshore stations off the Dutch Delta together with some offshore stations in the north; also one Kwinte Bank station (SB9) and one station a few miles off Ostend is included.

TWIN 4 groups the northern offshore stations which are situated in a dumping area of TiO2.

TWIN 5 combines the coastal stations along the Dutch coast, together with three stations along the Belgian west coast.

TWIN 4 groups all remaining stations along the Belgian coast.

Conclusion

The Twinspan-classification agrees in most aspects with the Clustan-classification, except for the open sea area, where the different zones are not geographically separated from each other. CLUS 3 and CLUS 4 are distributed over the whole area, while CLUS 5 is restricted to the northern part.

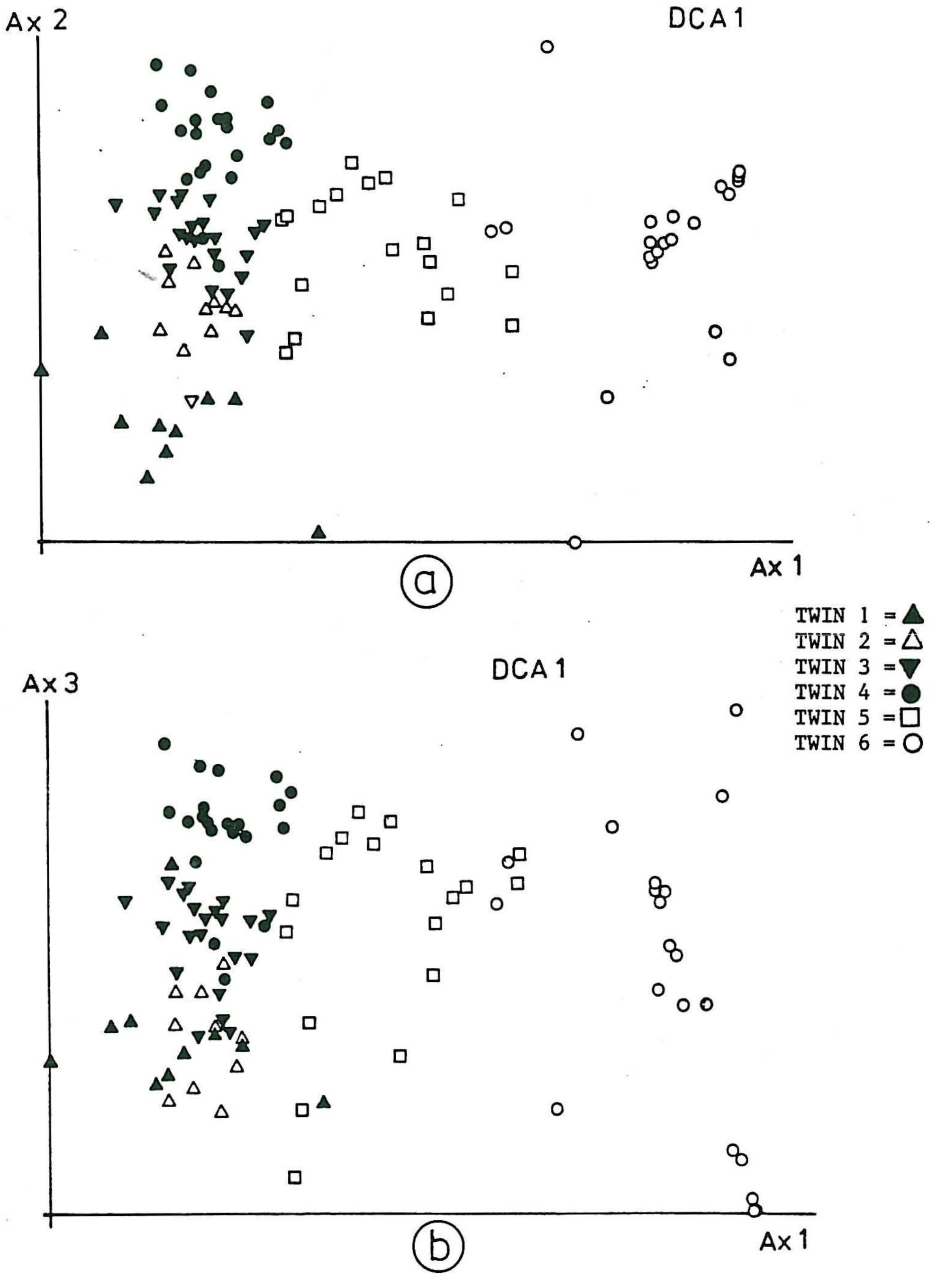

Fig. 7 : Two-dimensional plots of the DCA1- ordination (stations of the six Twinspan-groups are indicated by a single symbol) ; a : Ax1-Ax2 ; b : Ax1-Ax3.

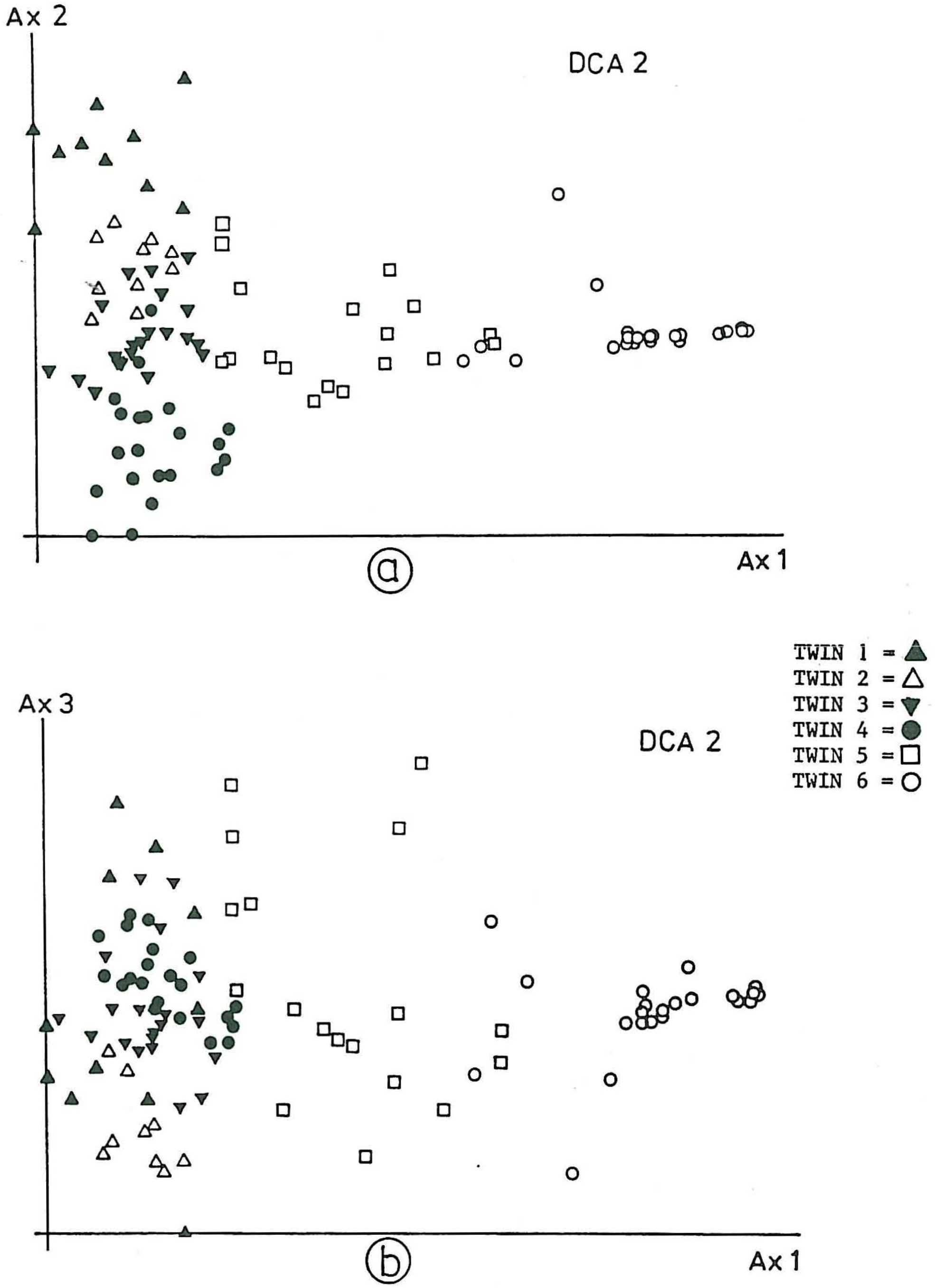

Fig. 8 : Two-dimensional plots of the DCA2-ordination (stations of the six Twinspan-groups are indicated by a single symbol) ; a : Ax1-Ax2 ; b : Ax1-Ax3.

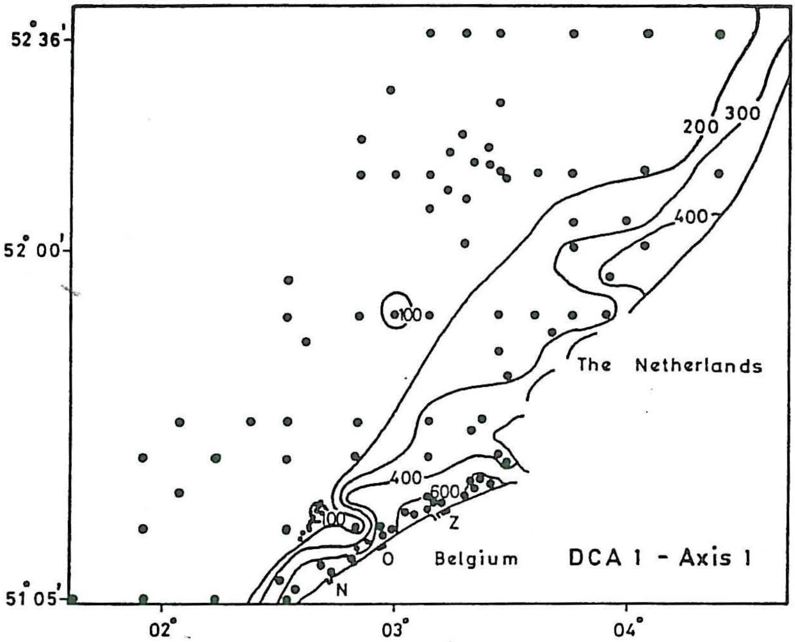

Fig. 9 : Areas demarcated by iso-lines of DCA1-Axis A scores of the stations of the Southern Bight.

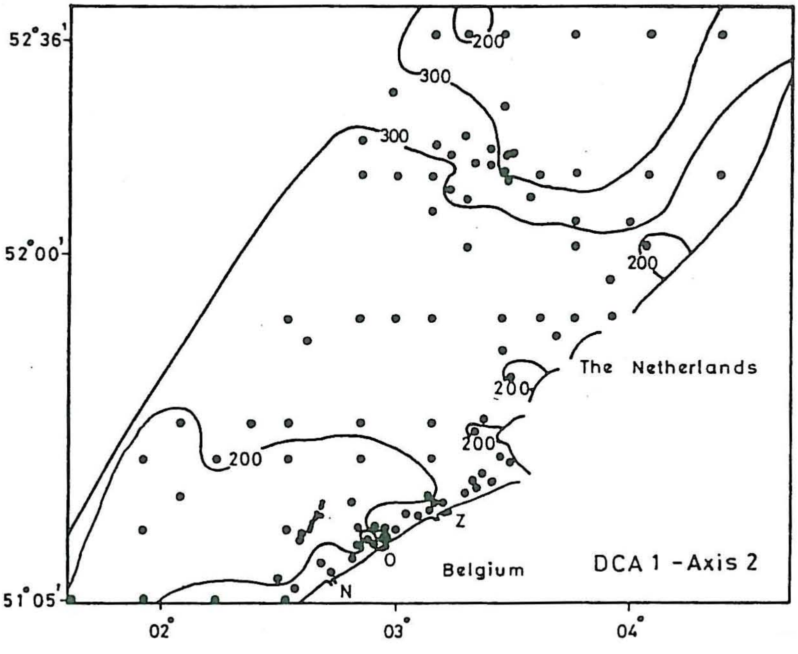

Fig. 10 : Areas demarcated by iso-lines of DCA1-Axis 2 scores of the stations of the Southern Bight.

The following comparisons between the two classifications can be made :

TWIN 1 is split up in two sets of stations which have affinities with CLUS 2 and CLUS 4.

TWIN 2 is split up in two sets of stations too, *i.e.* CLUS 4 and CLUS 3. The northern stations of CLUS 3 and CLUS 4 are not present in TWIN 2, but are classified separately in TWIN 3. However, TWIN 2 and TWIN 3 are the result of the fifth dichotomy while the other station groups are the result of the fourth dichotomy in the Twinspan-classification.

TWIN 4 is, except for a few stations, similar to CLUS 5.

TWIN 5 consists of the coastal stations of CLUS 5 ; the region before the Dutch Delta is part of CLUS 2 and shows affinities with the SB (sandbank) stations.

TWIN 6 is similar to CLUS 5 except for a few stations west of Nieuwpoort.

The Twinspan-classification (in combination with the DCA-ordination) gives information on the relationship between the different station groups; station groups which are more different from each other are father apart in the DCA-ordination; taking this distance into account, the Twinspan-dendrogram is produced in the most realistic way possible (e.g. TWIN 1 and TWIN 6 are farthest apart as well in the ordination as in the TWIN-dendrogram). In the Clustan-classification, station groups may turn around their dividing point and the neighbour station group is therefore not necessarily the most similar one (cf. CLUS 1 with CLUS 6).

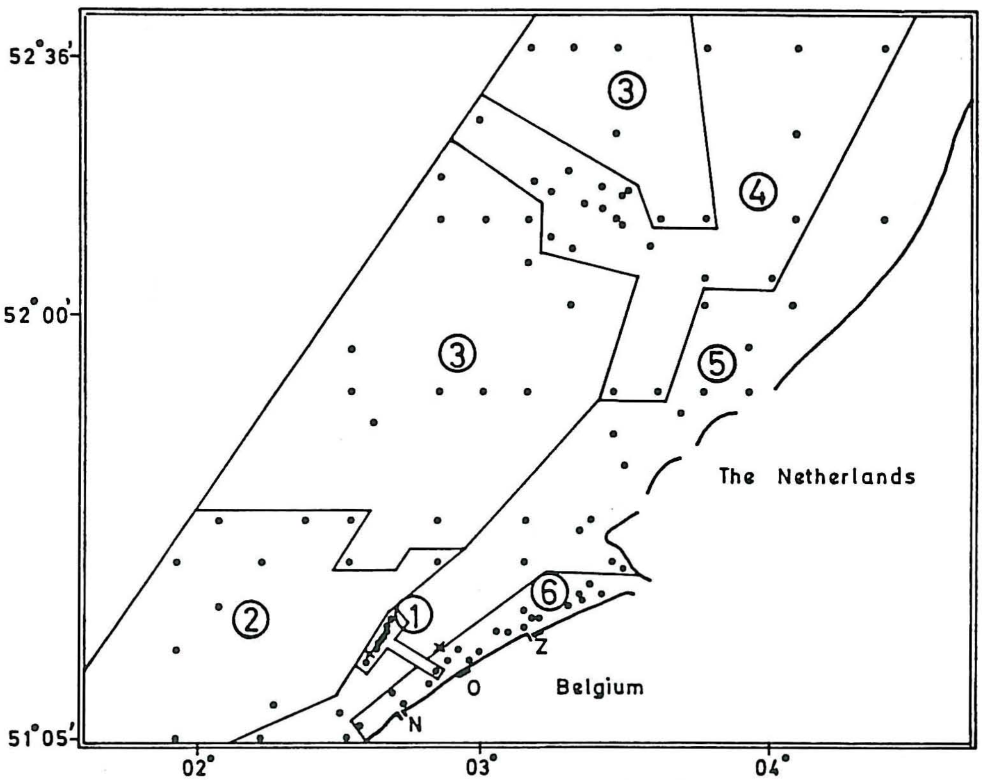

Fig. 11 : Position of the six Twinspan-station groups in the Southern Bight.

The importance of the very high number of species with a low abundance in this heterogeneous area, cannot be neglected in the comparison of the different stations. For the classification of the communities in the open sea more particularly, the number of species per station is very high. Especially the southern area is split up in a different way in both classifications : rare (mean relative abundance < 0.5%) but differential species of "isolated and aberrant areas" (e.g. sandbanks) are not included in the Clustan analysis (e.g. Epsilonematidae and Draconematidae in the coarse sediments).

From this point on, the interpretation of the community parameters of the nematodes in the Southern Bight of the North Sea will be examined by means of differences between the six Twinspan (=TWIN) station groups.

Relationship between species composition and environmental characteristics

Environmental characteristics of the different station groups (TWIN 1 to TWIN 6) are presented in Table 2.

All parameters differ significantly between the six groups (Table 3). However, most parameters are also significantly correlated with one another.

TABLE 2

Summary of the sedimentological characteristics per station group as defined by the TWINSPAN-classification (TWIN 1 ⇒ TWIN 6). (Abbreviations as in Table 2).

		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 (ø)	$\bar{x}$	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 (ø)	$\bar{x}$	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

Multiple comparison between pairs of the Twinspan station groups (Table 3) shows that the median grain size of the sand fraction is the most important environmental factor in characterizing the different station groups (12 from the 15 couples of station groups are significantly different in this parameters) ; only TWIN 1, TWIN 3 and TWIN 4 are not significantly different on the basis of the Md.

The *silt* content is similar in TWIN 1 and TWIN 4 ; TWIN 2 and TWIN 3 & TWIN 5 ; TWIN 3 and TWIN 4 ; only TWIN 5 is significantly different from all the other station groups.

The *other parameters* are less indicative, except for the difference between TWIN 1 and TWIN 4 (Kwinte Bank an Ti02-dumping) where only the amount of org C and depth is different ; these two station groups are also separated by their geographic position (NB and EL).

Highly significant correlations exist between Md, silt content, sorting coefficient, geographic position (NB), skewness, depth and gravel content along Axis 1 of both DCA 1 and DCA 2. Organic carbon and geographic position (EL) seem to determine Axis 2.

Several other environmental factors (e.g. temperature, salinity, chlorophyll a, $NO3^-$, $NH4^+$) have been determined in the Southern Bight in June 1985 (P. Herman, unpublished results).

Temperature was highest in the coastal area (between 13.9° C and 15.4° C) and decreases gradually towards the open sea area (12.6°C- 14.5°C).

TABLE 3

Results of the multiple comparisons of the Kruskal-Wallis one-way anova of the different Twinspan-station groups, based on the environmental parameters. (+ is signif. doff. ; - not signif. diff. at the p = 0 05 level).

	Md	Silt	Sc	Org C	NB	EL	Sk	Depth	Gravel
TWIN 1 and TWIN 2	+	+	-	+	-	-	-	+	+
TWIN 1 and TWIN 3	-	+	-	+	+	+	+	+	-
TWIN 1 and TWIN 4	-	-	-	+	+	+	-	+	-
TWIN 1 and TWIN 5	+	+	-	+	+	+	-	-	-
TWIN 1 and TWIN 6	+	+	+	-	-	+	-	-	-
TWIN 2 and TWIN 3	+	-	-	-	+	+	-	-	+
TWIN 2 and TWIN 4	+	+	-	-	+	+	-	-	+
TWIN 2 and TWIN 5	+	-	-	-	-	+	-	+	+
TWIN 2 and TWIN 6	+	+	-	+	-	+	+	+	+
TWIN 3 and TWIN 4	-	-	-	-	+	+	-	-	+
TWIN 3 and TWIN 5	+	+	-	-	+	+	-	+	-
TWIN 3 and TWIN 6	+	+	+	+	+	-	+	+	+
TWIN 4 and TWIN 5	+	+	-	-	+	-	-	+	-
TWIN 4 and TWIN 6	+	+	+	+	+	+	+	+	-
TWIN 5 and TWIN 6	+	+	-	+	+	+	+	-	+
X^2	55.621	58.745	11.563	40.942	64.153	52.674	20.597	49.303	36.163
p	0.000	0.000	0.041	0.000	0.000	0.000	0.001	0.000	0.000

Salinity was lowest in the coastal area (Belgian east coast and region north of the Dutch Delta) (21.1 ‰ - 30.0 ‰) and increases gradually towards the open sea area (> 35.0 ‰). The Dutch Delta (with exception of the Western Scheldt) has less outflow of fresh water into the North Sea ; the influence of the Western Scheldt, Meuse and Rhine on the salinity of the coastal area is obvious.

The content of chl a in the sediment is very high along the Belgian east coast (20-40 $\mu g.cm^{-2}$) before the Dutch Delta, values are much lower (10-23 $\mu g.cm^{-2}$) and the chl a content decreases drastically along the Dutch coast, north of the Delta. The chl a content of the open sea area is very low (< 4 $\mu g.cm^{-2}$).

The $NO3^{-}$ content was similar along the whole coast ; a decrease in $NO3^{-}$ content was found from the coast to the open sea area.

The $NH4^{+}$ content was especially high before the Dutch Delta. Values off the Belgian coast were much lower than those of the northern coastal area.

The distribution of these environmental factors within the area is remarkably similar to the distribution of the nematode species; especially the chl a content shows the aberrant situation along the Belgian east coast (TWIN 6), the similarity between the Dutch coast and the Belgian west coast (TWIN 5); the distribution in the open sea area is rather uniform; the high amount of chl a on the Kwintebank in the southern part of the area indicates however the isolated situation within the area (notice similar difference between TWIN 1 and TWIN 2). However, values in the open sea area are rather scarce and differences in chl a content are perhaps too small to be responsible for the differences noted in the nematode species composition.

DISCUSSION

Thorson (1957) defined "isocommunities" or "parallel-level bottom communities" as ecological parallels since the same types of bottoms are 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 parallel-level bottom-communities of sandy substrata are mainly determined by the overall presence of Desmodoridae, Microlaimidae, Chromadoridae, Cyatholaimidae,... While much of this "parallelism" (*sensu* Thorson, 1957) in community structure around the world is partly the result of certain families being interstitial (and thus confined to sands), 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 biotope, be it with different species or genera (e.g. *Daptonema stylosum* is confined to sand while *Daptonema tenuispiculum* is confined to sandy silt).

Wollast (1976) examined the distribution of sediment organic matter in the Southern Bight of the North Sea. The geographic distribution of ignition loss of the bottom sediments indicates a higher flux of sediment organic matter in the coastal zone than in the offshore area. This is particularly true in a region of mud accumulation just in front of the Belgian coast (cf. TWIN 6). The quantitative importance of the benthos (micro-and meiobenthos) in recycling organic matter in the Belgian coastal zone indicates that an important part of primary production settles down on the sediment. Faecal pellets and zooplankton corpses can only make up a small fraction of this flux: it is therefore very likely that phytoplankton cells and phytoplankton detritus constitute the bulk of the organic matter flux to the sediment.

A direct confirmation was obtained in the area of mud accumulation off the coast, where vertical distribution of chl a and particulate nitrogen in the sediment were determined, showing the importance of benthos in the recycling of the organic phytoplankton matter (Bouquegneau *et al.*, 1985).

In the Southern North Sea between 52°30'N and 55°N (north of our investigation area), a persistent chlorophyll maximum coincides with an enriched benthic zone (Creutzberg, 1984). In this area, a gradient of tidal current velocities is decreasing from south to north; where the current velocities drop below a critical value, mud and detritus are deposited on the bottom. In this particular area, the benthic fauna is very rich and biomass values are comparable with those in the Wadden Sea. The zone of increased biomass coincides with a maximum of chl a and can be attributed to the accumulation of organic matter, which is mineralized in that enriched zone and mixed with the overlying water masses.

One of the most striking features of coastal ecosystems, and of the Belgian coastal zone in particular, is the importance of the role of bacteria, both in the planktonic and in the benthic phases, in the utilization of primary production (Bouquegneau *et al.*, 1985 ; Billen & Somville, 1985).

Billen & Somville (1985) suggest that the importance of bacterial activity versus macroorganisms activity is a characteristic of enriched, or concentrated media - *i.e.* media where the production or input of organic matter is high per unit volume - versus oligotrophic, diluted environments. A general increase of the level of primary production in the coastal area, as a result of increasing nutrient input, does not necessarily lead to an increase of pelagic or demersal fish production~ but could induce a modification of the food web resulting in the enhancement of microbiological activity at the expense of long trophic chains dominated by macroorganisms.

The near absence of nematode-predators in the region off the Belgian east coast, the dominance of the deposit-feeders (most of them bacterivores), the very low species diversity of the nematode community (see Vincx, in press) and the paucity of higher metazoans within the area, can be partly explained on the basis of the increase in nutrient input within the area.

Nematode species living in the coastal area of the Belgian east coast, are the same as those living in the tidal mud flats, where the redox layer is situated at a few millimeters from the top of the bottom. These species are *Sabatieria* spp., *Daptonema* spp., *Terschellingia* spp..

Braeckman *et al.* (1984) determined the amount of heavy metals (Cu, Zn, Pb, Cd and Hg) in three stations (one mud and two sand stations) along the Belgian coast. The concentrations of heavy metals in the two sandy stations are quite similar, while the mud station has significantly higher levels of heavy metals. An emperical enrichment factor is calculated as the ratio of the mean concentration in the mud station, and the mean concentration in the sand station. The enrichment factors are for Cu : 10.3 ; Zn : 9.1 ; Pb : 2.9 ; Cd : 2.7 and Hg : 24.

The nematode species composition of the polluted Belgian east coast is correlated with an increase in heavy metal concentration and an increase in the silt content of the sediment (Heip *et al.*, 1984 and Vincx, 1986b).

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REFERENCES

BARNETT, P.R.O., 1968. Distribution and ecology of harpacticoid copepods of an intertidal mudflat. Int. Revue ges. Hydrobiol., 53 (2), 177-209.

BILLEN, G.& M. SOMVILLE, 1985. Utilization of primary products by planktonic and benthic bacteria. In : Concerted Actions Oceanography. Final Report, vol. 3 : Biological Processes and Translocations. C. Heip & P. Polk (Eds). Ministry of Scientific Policy, Brussels, Belgium, 175-198.

BOUCHER, G., 1980. Facteurs d'équilibre d'un peuplement de Nématodes des sables sublittoraux. Mem.Mus.natn.Hist.nat. A, 114 : 1-81.

BOUQUEGNEAU, J.M., G. BILLEN, C. JOIRIS, M.H. DARO, C. LANCELOT,.H. HECQ, A. BERTELS, M. BOSSICART, M. SOMVILLE, J.P. MOMMAERTS, J. WIJNANT, & J.C. WEHREN, 1985. Carbon cycling in the Belgian coastal zone and adjacent areas. General structure of the ecosystem. In : Biological Processes and Translocations. C.M. 1982/L : 31. C. Heip & Polk (Eds).

BRAECKMAN, A., C. HEIP, H. DEDEURWAERDER, G. DECADT, 1984. Heavy metals (Cu, Zn, Pb, Cd and Hg) in sediments of the Southern Bight of the North Sea. In : Ecological and ecotoxicological studies of benthos of the S.B. of the N.S. Progress Report, 1983, 48-55.

BRAY, J.R. & J.T. CURTIS, 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr., 27 : 325-349.

COULL, B.C. & S.S. HERMAN, 1970. Zoogeography and parallel level bottom communities of the meiobenthic harpacticoida (Crustacea, Copepods) of Bermuda. Oecologia (Berl.), 5 : 392-399.

CREUTZBERG, F., 1984. A persistent chlorophyll a maximum coinciding with an enriched benthic zone. Proceedings of the 19th European marine Biology Symposium, Plymouth, Devon, U.K. (Ed. P.E. Gihb), 109-122.

FARRIS, R.A.& M. CREZEE, 1976. An improved Peineck box for sampling coarse sand. Int. Pevue ges.Hydrobiol. , 61 : 703-705.

FIELD, J.G., K.R. CLARKE & R.M. WARWICK, 1982. A practical strategy for analysing multispecies distribution patterns. Mar.Ecol.-Prog.Ser., 8 : 37-52.

GAUCH, H.G., 1982. Multivariate analysis in community ecology. Cambridge University Press, 298 pp.

GOURBAULT, N., 1981. Les peuplements de Nematodes du chenal de la Baie de Morlaix (premières données). Cah.Biol.mar., 22 : 65-82.

GOVAERE, J.C.R., D.VAN DAMME, C. HEIP & L.A.P. DE CONINCK, 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helg. wiss. Meeresunters., 33 : 507-521.

HEIP, C., 1976. The life-cycle of Cyprideis torosa (Crustacea, Ostracoda). Oecologia (Berl.), 24 : 229-245.

HEIP, C., R. HERMAN, G. BISSCOP, J. GOVAERE, M. HOLVOET, D.VAN DAMME, C. VANOSMAEL, K. WILLEMS & L.A.P. DE CONINCK. 1979. Benthic studies of the Southern Bight of the North and itS adjacent continental estuaries. Progress Report I. ICES CM L/9 : 133-163.

HEIP, C., R. HERMAN & M. VINCX, 1983. Subtidal meiofauna of the North Sea : A review. Biol. Jb. Dodonaea, 51 : 116-170.

HEIP, C., R. HERMAN & M. VINCX, 1984. Variability and productivity of meiobenthos in the Southern Bight of the North Sea. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 183 : 51-56.

HEIP, C., M. VINCX & G. VRANKEN, 1985. The ecology of marine nematodes. Oceanogr. Mar.Biol.Ann.Rev., 23 : 399-389.

HERMAN, R., M. VINCX & C. HEIP, 1985. Meiofauna of the Belgian coastal waters : spatial and temporal variability and productivity. In : Concerted Actions Oceanography Heip & Polk (Eds), Ministry of Scientific Policy, Brussels, Belgium, 65-80.

HICKS, G.R.F. & B.C. COULL, 1983. The ecology of marine meiobenthic harpacticoid copepods. Oceanogr.Mar.Biol.Ann.Rev., 21 : 67-175.

HILL, M.O., 1979a. TWINSPAN - A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systelatics. Cornell University, Thaca, N.Y., 48 pp.

HILL, M.C., 1979b. DECORANA - A Fortran program for detrended correspondance analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, N.Y., 30 pp.

HILL, M.O. & H.G. GAUCH, 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio, 42 : 47-58.

HULINGS, N.C. & J.S. GRAY, 1976. Physical factors controlling abundance of meiofauna on tidal and atidal beaches. Mar. Biol.., 34 : 77-83.

JUARIO, J.V., 1975. Nematode species composition and seasonal fluctuation of a sublittoral meiofauna community in the German Bight. Veröff.Inst.Meeresforsch.Bremerh., 15 : 283-337.

LORENZEN, S., 1974. Die Nematodenfauna der sublittoralen Region der Deutschen Bucht, insbesondere im Titan-Abwässergebiet bei Helgoland. Veroff.Inst. Meeresforsch. Bremerh., 14 : 305-327.

MC CAVE, I.N., 1973. Mud in the North Sea. In : North Sea Science. NATO North Sea Conference, Aviemore, Scotland, (Ed. E.D. Goldberg). MIT Press, 75-100.

POR, F.D., 1964. A study of the Levantine and Pontic Harpacticoida (Crustacea, Copepoda). Zool.Verh., 64, 1.

REMANE, A., 1933. Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. Wiss.Meeresunters., N.F., 21 : 161-221

THORSON, G., 1957. Bottom communities (sublittoral or shallow shelf) Mem. geol. Soc. Amer., 67 : 461-534.

VAN DAMME, D. & C. HEIP, 1977. Het meiobenthos in de Zuidelijke Noordzee. In : Nationaal onderzoeks-en ontwikkelingsprogramma-Projekt Zee, C.F. Nihoul & L.A.P. De Coninck (eds), 17 : 1-114.

VEENSTRA, H.J., 1970. Sediments of the southern North Sea. In : F.M. Delany (Ed.), The Geology of the East Aylantic Continental Margin, 3, Europe, Report 70/15 (Institute of Geological Sciences, London).

VINCX, M., 1981. New and little known nematodes from the North Sea. Cah.Biol.mar., 22 : 431-451.

VINCX, M. 1983. Redescription and ontogenetic study of Desmodora schulzi Gerlach, 1950. Biol.Jb. Dodonaea, 51 : 171-179.

VINCX, M., 1986a. Free-living marine nematodes from the Southern Bight of the North Sea. I. Notes on species of the genera Gonionchus Cobb, 1920, Neochromadora Micoletzky, 1924 and Sabatieria Rouville, 1903. Hydrobiologia, 140 : 255-286.

VINCX, M., 1986b. Free-living marine nematodes from the Southern Bight of the North Sea. Ph.D. Thesis, State Univ. Gent : 1-618.

VINCX, M. (in press). Diversity of nematode communities in the Southern Bight of the North Sea. Neth.J. Sea Res.

WARD, A.R., 1973. Studies on the sublittoral free-living nematodes of Liverpool Bay. I. The structure and distribution of the nematode populations. Mar. Biol. 22 : 53-66.

WARD, A.R., 1975. Studies on the sublittoral marine nematodes from sublittoral sediments in Liverpool Bay. Mar. Biol., 30 : 217-225.

WARWICK, R.M. & J.B. BUCHANAN, 1970. The meiofauna off the caast of Northumberland. I. The structure of the nematode population. J.mar.biol.Ass.U.K., 50 : 129-146.

WARWICK, R.M. & J.B. BUCHANAN, 1971. The meiofauna off the coast of Northumberland. II. Seasonal stability of the nematode population. J.mar.biol.Ass.U.K, 51 : 355-362.

WILLEMS, K.A., M. VINCX, D. CLAEYS, C. VANOSMAEL & C. HEIP, 1982a. Meiobenthos of a sublittoral sandbank in the Southern Bight of the North Sea. J.mar.biol.Ass.U.K. 62 : 535-548.

WILLEMS, K.A., C. VANOSMAEL, D. CLAEYS, M. VINCX & C. HEIP, 1982b. Benthos of a sublittoral sandbank in the Southern Bight of the North Sea : general considerations. J.mar.biol.Ass.U.K., 62 : 549-557.

WOLLAST, R. 1976. Transport et accumulation de polluants dans l'estuarire de l'Escaut. In : L'Estuaire de l'Escaut. Programma national de recherche et de développement. Environnement Eau, Projet Mer, vol. 10, J.C.J. Nihoul & R. Wollast (Eds), Brussels, 191-218.