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Ecology of the free-living marine nematodes from the Voordelta (Southern Bight of the North Sea). I. Species composition and structure of the nematode communities.

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Abstract : The structure of nematode communities (species composition and abundance) of twenty stations in the Voordelta (Southern Bight of the North Sea) was investigated in relation to the sediment composition, the bottom morphology, the hydrodynamical forces, the salinity and the chlorophyll-a content. Similarities between stations were determined using classification (TWINSPAN) and ordination (DCA) techniques.

Changes in the structure and the composition of the nematode communities are mainly correlated to the sedimentological gradient. Apart from the sediment composition, the salinity also determines the species composition of these communities. Finally, a correlation between the ecophysiological characteristics of the species present, the environmental stability and the food supply is hypothesized. However, further investigations are required to support these results.

Résumé : La structure des communautés de nématodes (composition et abondance des espèces) de vingt stations du Woordelta (Mer du Nord) est étudiée en relation avec la composition du sédiment, la morphologie du fond, les forces hydrodynamiques, la salinité et la teneur en chlorophylle-a. Des similarités entre les stations ont été établies à partir des techniques de classification (TWINSPAN et DCA).

Des changements dans la structure et la composition des communautés de nématodes sont essentiellement liés au gradient sédimentologique.

En dehors de la composition du sédiment, la salinité détermine également la composition spécifique des communautés de nématodes. Finalement, une relation entre les caractéristiques écophysiologiques des espèces existantes, la stabilité de l'environnement et l'apport nutritif est hypothétique. Des recherches ultérieures sont nécessaires pour compléter les résultats.

Introduction

The Voordelta is the sublittoral region along the coast of The Netherlands, from the Belgian border in the south to the Hoek van Holland in the north. Offshore, the area is arbitrarily limited by the 15 meter water depth line. From north to south, the Nieuwe Waterweg, the Haringvliet, the lake Grevelingen, the Eastern Scheldt and the Western Scheldt open into this part of the Southern Bight of the North Sea (Fig. 1). As a result of the tidal currents and the transport of sediments, a heterogeneous pattern of banks and channels is present. Moreover the hydrodynamical regime and the bottom morphology have been (and still are) changing drastically since the start of the Delta project (1970) (Elgershuizen, 1981 ; Van den Bergh, 1984). The Delta project resulted in the closure of the lake Grevelingen (1971) and the Haringvliet (1970), and the construction of a storm surge barrier in the Eastern Scheldt (1986) (Fig. 1). Correlated with the changes of the environment, alterations in the biota of the Voordelta are expected.

This study is part of a general research program, which aims to evaluate the effect of the Delta project on the ecosystem of the Voordelta region. Before any changes in biotic parameters are evaluated, a base line study of the biological environment is required. In several projects (Huys *et al*, 1986 ; Vanreusel *et al.*, 1986, & Seip & Brand, 1987) the benthos is examined. This study deals with an important component of the marine benthic ecosystem : the free-living nematodes, which have not previously been studied in this area.

The relationship between the structure of the nematode communities (especially the species composition and the species abundance distributions) and the present environmental gradients is also investigated. The Voordelta region is characterized by several physical and chemical gradients (*i.e.* depth, hydrodynamics, sediment composition, chlorophyll-a content) which might be important for the determination of the structure of the nematode communities.

MATERIAL AND METHODS

Sampling

Based on the geographic position of the estuarine mouths and the information on the abiotic characteristics of the study area, twenty sampling stations were selected (Fig. 1). Sampling was performed within three periods (*i.e.* Autumn 1984, Spring 1985 and Autumn 1985) by means of a box corer (0.07 m^2 sampling surface).

Each sample was subsampled by taking four cores of 10 cm^2 to a depth of minimum 15 cm into the sediment. For one or two subsamples (see further), 200 nematodes were randomly picked out and determined to species level. The mean individual biomass was determined on the third subsample. Two hundred nematodes were transferred to an aluminium vial, after rinsing them several times with distilled water. Following two hours of drying and 30 minutes of cooling, the nematodes were weighed on a Mettler ME22/BA22 microbalance (with an accuracy of 0.1 µg). From the fourth subsample, a sedimentological analysis (median of the sand fraction (mm), silt fraction (%), gravel fraction (%) and sorting (ø) was carried out. All the subsamples used for the study of the nematodes were fixed in 4 % formalin (for a detailed description of the extraction procedure of the nematodes see Heip *et al.*, 1985).

Measurements of the current velocities (Vmin. and Vmax.), the chlorophyll-a content of the water column and the salinity (in % fresh water) were obtained from Rijkswaterstaat DGW Middelburg (The Netherlands).

Statistics

Two multivariate analysis were applied to show the affinities between the stations and/or the species : Twinspan and Detrended correspondance analysis.

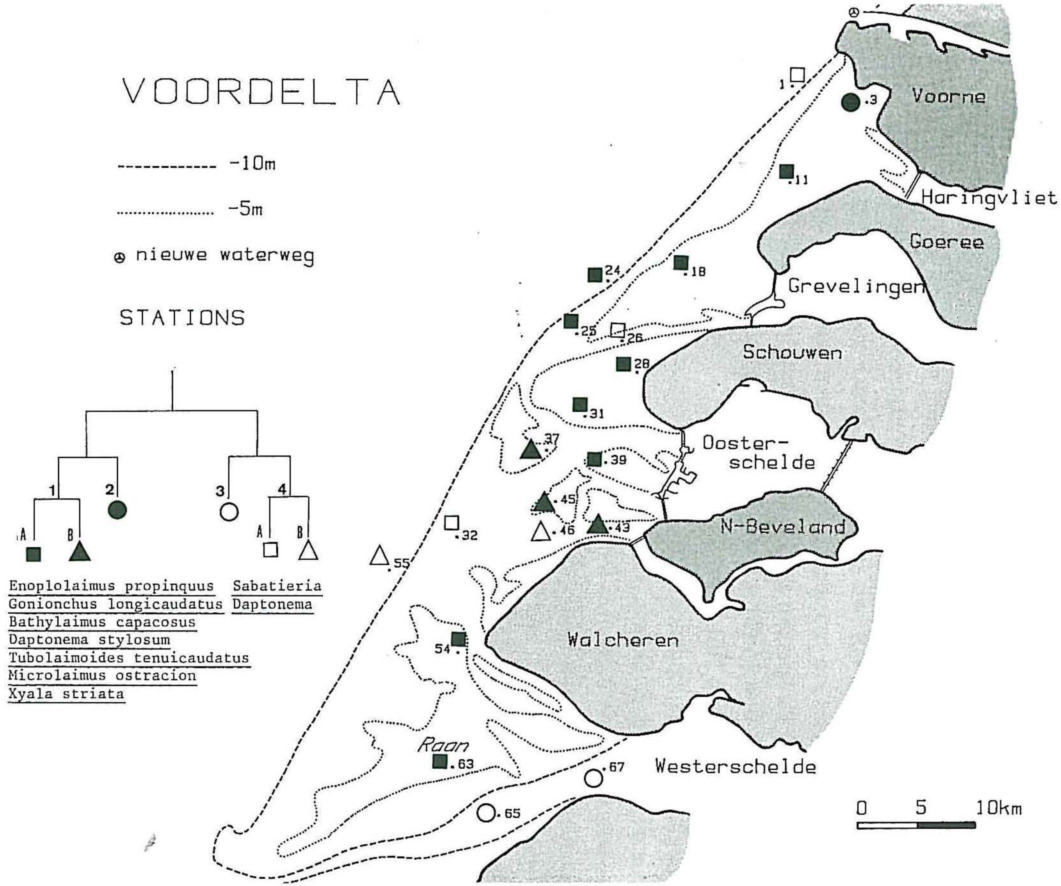

Fig. 1 : The Dutch Delta region with indication of the 20 stations and the twingroups. The indicated species are the differential species of the two twingroups, formed after the first dichotomy.

The Twinspan (Hill, 1979) or Two-Way INdicator SPecies ANalysis is an hierarchical, polythetic, divisive technique of classification. Not only the samples, but also the species are classified with the result that the similarities between the stations are immediately shown through the selection of several characteristic (or differential) species, and the species are selected on the basis of their ecological preferences.

Ninty nine subsamples have been investigated of which 40 (two subsamples per station) come from the first sampling period (Autumn 1984), 36 (for four of the 20 stations no second subsample was studied) from the second sampling period (Spring 1985) and the remaining 23 (only for three stations a second subsample was studied) from the third sampling period (Autumn 1985). During the two sampling periods of 1985 the number of subsamples, studied on species level, have been often reduced to one (instead of 2), because of the high similarity between the two subsamples of each station during the first sampling period (1984). All species are considered. The Twinspan was carried out on the basis of the relative abundances of the species. As pseudo-species cut levels, the Braun-Blanquet scale (0 %, 5 %, 26 %, 51 % and 76 %) is used (Mueller-Dombois & Ellenberg, 1974 ; Westhoff & Van der Maarel, 1973 : in Hill 1979).

The Detrended Correspondance Analysis (DCA) is an improved version of the correspondance analysis (Hill & Gauch, 1980). As rare species may distort the analysis (they often have an extreme position over the first two axes), their weight was reduced. If Cmax is the frequency of the commonest species , Fj the frequency of species j, and Aij the abundance of species j in sample i, and if Fj is smaller than Cmax/5, then Aij is replaced by Aij * Fj / Cmax/5. All 99 subsamples are considered.

The non-parametric Kruskall Wallis one-way analysis of variance was used to test the mutual independency of samples (or twingroups). An a posteriori test (Conover, 1971) was used to detect which stations or twingroups had significantly different characteristics.

Correlations were calculated by means of the non-parametric Spearman rank correlation coefficient.

Species diversity is expressed by N_1 (Hill, 1973), representing the reciprocal of the Shannon Wiener index. N_1 forms part of a set of 'diversity numbers' of different order (N_a with a = O -> + ∞). Heip *et al.* (1988) preferred the use of indices of different orders, which probe different aspects of the community.

RESULTS

Abiotic factors

Depth and hydrodynamics

The Voordelta is characterized by an heterogeneous bottom pattern of banks and channels (Fig. 1). Eight of the twenty selected stations are located in the channels (the stations 1, 26, 32, 43, 46, 55, 65 and 67 : 12 - 30 m), twelve are situated on, or on the border of the banks. This bottom profile is associated with strong tidal currents. The highest (Vmax.> = 100 cm/s) as well as the lowest velocities (Vmin.= < 5 cm/s) are measured in the Western Scheldt (stations 65 and 67 ; Table I). Station 43, situated near the storm surge barrier in the mouth of the Eastern Scheldt, is also characterized by a high maximum current velocity (91 cm/s) and by a large difference between the minimum and the maximum current velocity (85 cm/s). In the remaining stations the maximum current velocity amounts only 42 to 66 cm/s (Table I).

TABLE I

The maximum and minimum current velocities and the difference between the two (Vmax., Wmin. and ΔV : in cm/s), the depht (in m), the chlorophyll-a content (in µg/101) and the percentage fresh water in the 20 stations of the Dutch Delta region. All values are measured during Spring '85, with exception of the depth, determined for the three sampling periods.

st	Vmax.	Vmin.	ΔV	depth			Chl a	% fresh water
				camp 1	camp 2	camp 3		
1	55	6	49	12.8	12.7	14.2	65.3	16.2
3	-	-	-	1.8	3.0	3.0	90.3	33.2
11	42	7	35	2.6	3.4	5.8	134.5	26.0
18	45	16	29	3.0	14.7	4.6	106.2	12.4
24	63	14	49	12.0	14.7	18.2	84.3	11.4
25	58	17	41	10.0	10.2	10.8	71.8	9.6
26	49	20	29	11.5	13.0	10.5	91.7	11.0
28	63	4	59	-	8.9	3.0	122.1	12.4
31	49	15	34	5.0	5.5	4.0	92.4	10.2
32	58	30	28	15.4	16.6	14.4	71.8	9.5
37	59	18	41	11.2	6.2	10.4	72.3	9.3
39	52	28	24	6.5	6.3	5.2	96.1	9.7
43	91	6	85	12.0	16.2	12.5	90.0	11.5
45	62	22	40	6.5	8.2	6.4	61.8	9.5
46	66	11	55	11.5	12.0	11.7	64.0	9.7
54	57	29	28	6.5	6.0	8.4	106.4	11.4
55	63	26	37	17.5	17.2	16.4	51.2	8.0
63	59	13	46	10.4	10.0	5.0	126.6	11.0
65	102	4	98	18.1	17.8	16.5	86.8	13.0
67	120	5	115	30.2	28.2	29.9	69.7	15.9

Sediment composition

The sand fraction of the sediment always consists of fine to medium sand (Table II). The finest sediments are present in the northern part of the study area, from the mouth of the Grevelingen up to the Nieuwe Waterweg (the stations 1, 3, 11, 18 and 26), and in station 32,

TABLE II

The median grain size of the sand fraction, the sorting of the sediment, the silt fraction and the gravel fraction in the 20 stations of the Dutch Delta region.

	median grain size (mm)				sorting - phi				silt (%)				gravel (%)			
st.	camp 1	camp 2	camp 3	mean	camp 1	camp 2	camp 3	mean	camp 1	camp 2	camp 3	mean	camp 1	camp 2	camp 3	mean
1	0.129	0.141	0.148	0.139	0.326	0.441	0.252	0.339	14.43	20.10	9.21	14.58	0.39	0.14	0.15	0.22
3	0.168	0.157	0.143	0.156	0.280	0.332	0.180	0.264	3.27	1.30	3.49	2.68	0.36	1.52	0.81	0.89
11	0.170	0.170	0.178	0.173	0.405	0.432	0.315	0.384	1.08	4.06	2.02	2.38	0.18	6.58	0.16	2.30
18	0.183	0.205	0.186	0.191	0.220	0.278	0.191	0.229	0.65	3.70	1.60	1.98	0.00	0.22	0.84	0.35
24	0.261	0.278	0.274	0.271	0.382	0.361	0.306	0.346	1.54	2.89	3.43	2.62	0.16	0.00	0.41	0.19
25	0.233	0.246	0.261	0.246	0.335	0.312	0.270	0.305	1.16	1.74	2.04	1.64	0.04	0.10	0.02	0.05
26	0.163	0.158	0.156	0.159	0.303	0.306	0.204	0.272	4.91	3.02	7.96	5.29	0.39	0.26	1.09	0.58
28	0.193	0.230	0.202	0.208	0.286	0.386	0.281	0.317	1.75	0.88	1.34	1.32	0.00	0.98	0.46	0.48
31	0.238	0.254	0.204	0.232	0.314	0.325	0.264	0.301	0.66	1.77	1.59	1.34	0.30	0.00	0.09	0.13
32	0.164	0.164	0.154	0.160	0.320	0.347	0.231	0.299	1.87	3.29	17.81	7.65	0.03	0.00	0.35	0.12
37	0.263	0.313	0.266	0.280	0.407	0.740	0.329	0.492	2.48	1.20	4.39	2.69	1.47	4.06	5.78	3.77
39	0.218	0.199	0.205	0.207	0.286	0.334	0.278	0.299	1.85	2.57	1.80	2.07	0.00	0.01	0.00	0.00
43	0.310	0.221	0.237	0.256	0.254	0.327	0.279	0.286	5.06	0.67	2.82	2.85	0.30	0.00	0.03	0.11
45	0.357	0.241	0.367	0.321	0.548	0.336	0.313	0.399	0.77	1.90	0.92	1.19	5.16	0.66	2.37	2.73
46	0.233	0.243	0.210	0.228	0.340	0.508	0.161	0.336	6.31	2.64	3.95	4.30	1.70	1.19	1.25	1.38
54	0.191	0.196	0.314	0.233	0.334	0.326	0.565	0.408	2.71	1.15	2.64	2.16	0.00	0.67	10.89	3.85
55	0.331	0.308	0.343	0.327	0.889	0.611	0.377	0.625	3.36	5.06	3.53	3.00	1.24	2.07	1.87	1.72
63	0.203	0.180	0.182	0.188	0.240	0.205	0.153	0.199	0.76	1.93	2.11	1.60	0.00	0.00	0.00	0.00
65	0.327	0.348	0.336	0.337	0.472	0.834	0.375	0.560	1.68	9.93	1.28	4.29	0.69	4.55	2.12	2.45
67	0.284	0.210	0.181	0.225	0.400	0.261	0.285	0.315	1.05	21.40	66.20	29.55	2.44	0.14	0.04	0.87

situated off the mouth of the Eastern Scheldt (Md > 0.200 mm). The coarsest sediments are found in some other stations near the mouth of the Eastern Scheldt (stations 37, 45 and 55) and in station 65 off the Western Scheldt (Md >= 0.280 mm).

In most of the stations the percentage of silt is very low (< 3 % ; Table II). The largest silt fractions (3 - 30 % mean) are found in the channels (the stations 1, 26, 32, 46, 55, 65 and 67). Only station 1 is characterized by a silt fraction which amounts more than 5 % (max. 20 %) during all sampling periods. The stations of the Western Scheldt are characterized by temporal accumulations of silt (respectively from 1 % up to 9 %, and even up to 66 % (in Autumn 1985) ; Table II).

In general the sediment is very well sorted (sort Ø < 0.35 ; Table II). In the stations 37, 45, 55 and 65, and to a lesser extent in the stations 46 and 54, the sorting is only good or moderate (0.35 > sort Ø < 0.850).

Most of the granulometric parameters are mutually correlated. Fine sand is often characterized by a very good sorting, a small percentage of gravel and a high silt fraction. Medium sand is often associated with a high percentage of gravel and a moderate sorting of the sediment (Table III).

TABLE III

Significant (P = < 0.05) Spearman rank correlation coefficients between the sedimentological factors.

		Autumn '84 (n = 20)		Spring '85 (n = 20)		Autumn '84 (n = 20)		3 periods (n = 20)	
		r_S	p	r_S	p	r_S	p	r_S	p
Md(ø)	- Sorting	- 0.534	0.008	- 0.388	0.045	- 0.696	0.001	- 0.492	0.001
	- Gravel	- 0.487	0.015	—	—	- 0.520	0.009	- 0.413	0.001
	- Silt	—	—	—	—	0.500	0.012	0.275	0.017
	- Depth	—	—	—	—	—	—	- 0.284	0.014
Sorting	- Gravel	0.670	0.001	0.606	0.002	0.476	0.017	0.488	0.001
	- Depth	0.429	0.029	—	—	—	—	0.290	0.012
Silt	- Depth	—	—	0.416	0.034	—	—	0.362	0.002
Gravel	- Depth	0.424	0.031	—	—	—	—	—	—

Chlorophyll-a content

The highest chlorophyll-a values (> 106 µg/10 1) are found at the level of the shallow banks (the stations 11, 18, 28, 54 and 63 ; Table I). Low values (< 65 µg/10 l) are associated with some of the deeper stations mainly those in the seaward offshoots of the Eastern Scheldt (the stations 45, 46 and 55). All chlorophyll-a values are measured at the surface of the water column, and not near the bottom as usually done for the determination of the phytoplanktonic and phytobenthic biomass available to the benthic organisms. However, in the

Voordelta region no stratification occurs due to the high water turbulence. Besides, a high chlorophyll-a content in the water column is often correlated with high chlorophyll-a values in the bottom (especially in shallow waters with a high turbidity) because the production depends on the light penetration and on the nutrient supply. For that reason it is assumed that the chlorophyll-a content on the surface of the water column is representative for that near the bottom.

Salinity

The fresh-water input in the Delta region influences the salinity only to a low degree (Table I). Only station 3, and to a lesser extent station 11, both situated off the Haringvliet sluices, are characterized by a fresh-water fraction, which amounts respectively 33.2 and 26 %. This is high in comparison to the 13 to 16 % off the Western Scheldt mouth and the Nieuwe Waterweg, and to the 8 to 12 % fresh water in the remaining stations.

The nematode communities

Species composition

In total 242 species, belonging to 90 genera and 29 families are found. A detailed species list is available on request. The amount of species is relatively large considering the limited study area. All species are known : most of them are also present along the Belgian coast (Heip *et al.*, 1983 ; Vincx, 1986). Two species (*Monoposthia mirabilis* and *Terschellingia longicaudata*) have been redescribed (Vanreusel & Vincx, 1989, & Vincx & Vanreusel, 1989).

Multivariate analysis of the species composition of the stations

Twinspan classification.

Fig. 2 shows the twinspan classification of the 20 stations. As soon as subsamples of the same station and the same sampling period are subdivided into different twinspan-groups (or twingroups), this dichotomy is no longer considered. As the separation of these subsamples takes place on different hierarchical levels, the twingroups finally considered are also formed on different levels. Subsamples of the same station, but sampled during different periods, are also characterized by a relatively high affinity for each other. Only the subsamples of the stations 37, 45, 46 and 67 become separated from each other before the fourth dichotomy. For further discussion these four stations are linked to these twingroups which contain at least the samples of two sampling periods. The reliability of this simplification is supported by the results of the DCA (see further).

The differential species, causing the important dichotomies, are selected. One of the two sample groups (TWIN 1+2), discerned after the first dichotomy (all stations indicated with a black symbol : see Fig. 1), is characterized by the presence of *Enoplolaimus propinquus*, *Gonionchus longicaudatus*, *Bathylaimus capacosus*, *Daptonema stylosum*, *Tubolaimoides tenuicaudatus*, *Microlaimus ostracion* and *Xyala striata*. In the second group (TWIN 3+4 : all stations with an open symbol, Fig. 1), the dominant species belong to the genera *Sabatieria* and *Daptonema*.

After a second and a third dichotomy the first group is split up in three twingroups (Figs. 1 and 2), with following species being characteristic :

TWIN 1A (■) : According to the station, one of the following species is more or less dominant : *Daptonema stylosum* (Xyalidae), *Bathylaimus capacosus* (Tripyloididae), *Metadesmolaimus aduncus* (Xyalidae), *Microlaimus ostracion* (Microlaimidae) and *Onyx perfectus* (Desmodoridae).

TWIN 1B (▲) : *Dichromadora hyalocheile* (Chromadoridae) is dominant, while *Siphonolaimus ewensis* (Siphonolaimidae), *Sigmophoranema rufum* (Desmodoridae) and *Prochromadorella attenuata* (Chromadoridae) are the subdominant species.

TWIN 2 (●) : These communities are dominated by *Hypodontolaimus setosus* (Chromadoridae), *Metadesmolaimus pandus* (Xyalidae) and *Theristus pertenuis* (Xyalidae). *Eleutherolaimus stenosoma* (Linhomoeidae) and *Leptolaimus elegans* (Leptolaimidae) are the subdominant species.

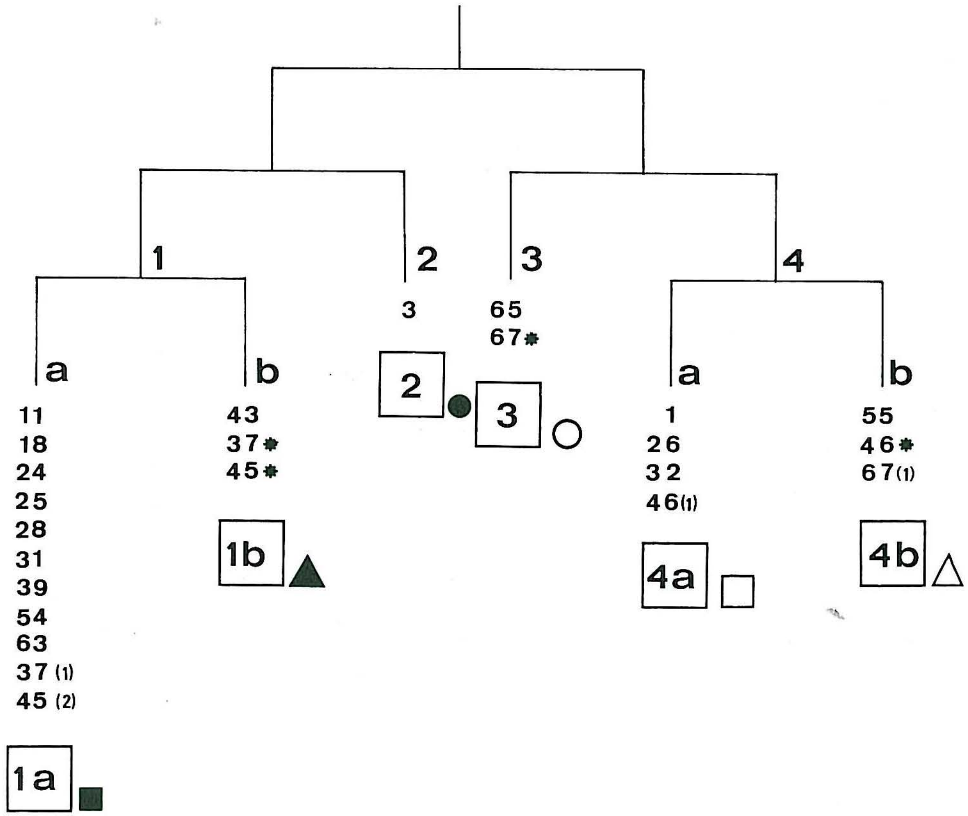

Fig. 2 : The twinspan-classification of the 20 stations ; (1) and (2) indicate the replicates of a station sampled respectively during the first and the second sampling period ; * indicates the remaining replicates of the same station (the symbols, by wich each twingroup is indicated, are the same as in the figures 1, 3 and 4).

Within the second group of stations three types of *Sabatieria* assemblages can be distinguished :

TWIN 3 (○) : *Daptonema tenuispiculum* is the dominant species, while *Sabatieria punctata, Ascolaimus elongatus* and *Sigmophoranema rufum* are subdominant.

TWIN 4A (□) : Beside the dominance of several *Sabatiera* (*S. celtica* and *S. punctata*), and *Daptonema* species (*D. kornoeense, D. riemanni* and *D. xyaliforme*), these stations are characterized by the subdominance of *Odontophora rectangula, Prochromadorella attenuata* and *P. longicaudata.*

TWIN 4B (Δ) : *Sabatieria punctata, Metoncholaimus scanicus, Spirinia parasitifera* and *Microlaimus conothelis* are the dominant species.

Detrended Correspondance Analysis

Fig. 3. shows the results of the DCA with indication of the different twinqroups. The twingroups are easy to distinguish in the two- dimensional DCA space. However, in some cases the distance is smaller between twingroups than within (= between subsamples belonging to the same group). This is mainly so for subsamples which are separated early in the hierarchy of the twinspan classification from the other subsamples of the same station (for example some of the subsamples of the stations 37, 45, 67 and 46 (respectively indicated with A, B, C and D in Fig. 3).

Correlation with the environmental factors

The two twingroups 1 + 2 and 3 + 4 differ significantly ($p < 0.05$) for the silt fraction, the depth, and the chlorophyll-a content (Tables IV and V).

The four twingroups 1, 2, 3 and 4, formed after the second dichotomy, are significantly different for the silt fraction, the depth and the median grain size (Tables IV and V).

TABLE IV

Kruskal Wallis test between the twingroups (for different hierarchical levels) ont he basis of environmental factors and on the basis of the diversity index (n = 60 or n = 20 (*) ; K = the Kruskal Wallis coefficient ; p = significance).

	2 twingroups		4 twingroups		6 twingroups	
	K	p	K	p	K	p
Sorting	1.805	0.170	2.939	0.401	5.001	0.174
Median (mm)	0.691	0.400	11.882	0.008	35.676	0.000
Silt	16.188	0.000	16.886	0.001	18.478	0.002
Gravel	3.290	0.070	5.108	0.164	14.542	0.013
Depth	30.203	0.000	35.213	0.000	37.568	0.000
Chl a *	6.440	0.011	6.666	0.080	10.901	0.053
% freshwater *	0.014	0.900	5.016	0.170	8.008	0.156
Vmax. *	2.162	0.140	7.202	0.066	12.282	0.030
N_1	9.705	0.002	20.723	0.000	22.865	0.000

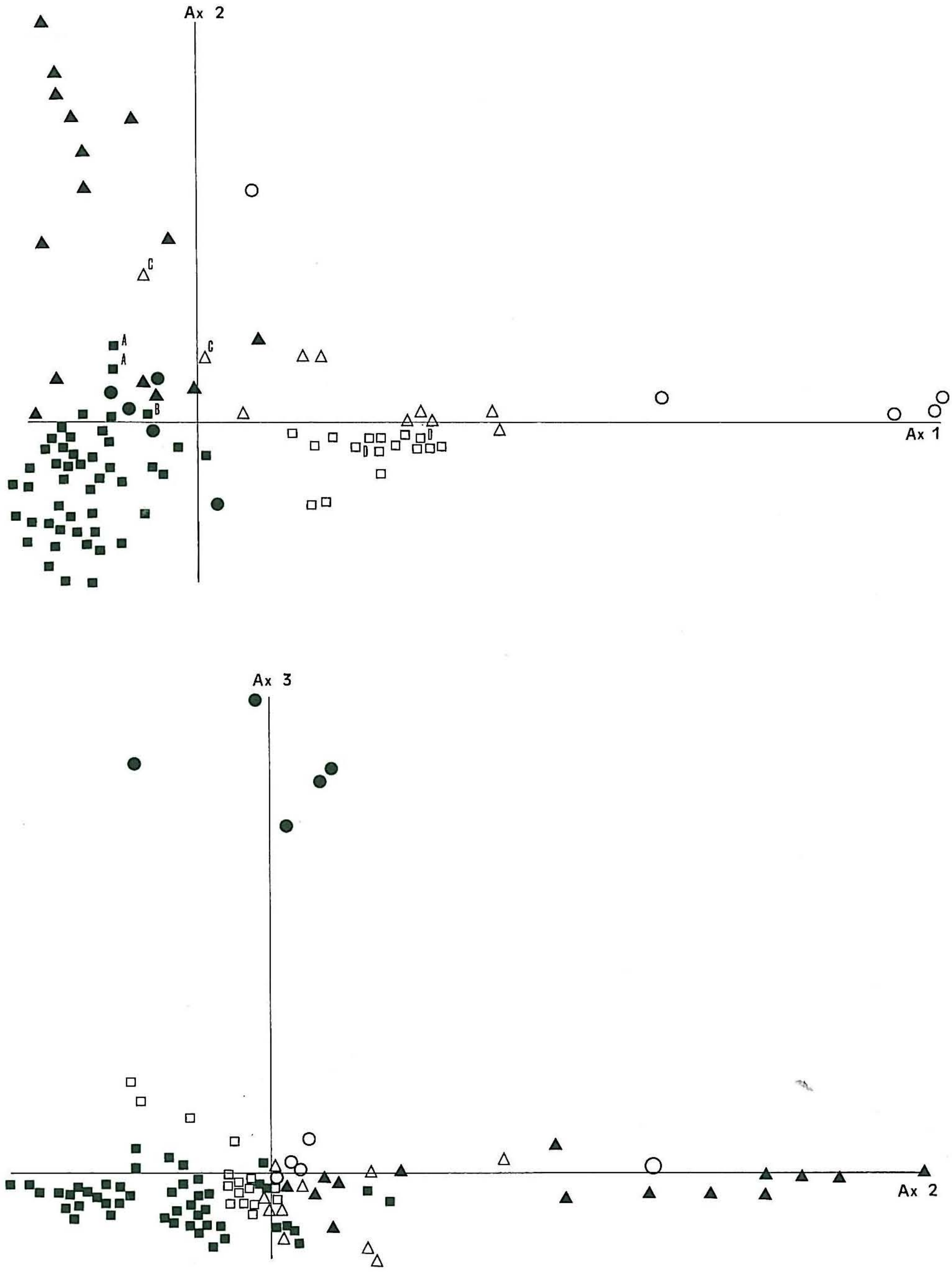

Fig. 3 : The DCA ordination of the replicates of the 20 stations, with indication of the six twingroups of Fig. 1. A, B, C and D indicates the replicates of respectively the stations 37, 45, 67 and 46, which are separated relatively early in the hierarchy of the twinspan classification of the remaining replicates of those stations.

The six twingroups 1a, 1b, 2, 3, 4a and 4b, which are finally considered for further analysis, differ significantly for the median grain size, the depth, the silt and the gravel fraction, and the maximum current velocity (Tables IV and V).

TABLE V

Mean and standard error of the environmental factors which differ significantly between the different twingroups.

twin		1+2	3+4	1	2	3	4	1a	1b	2	3	4a	4b
Silt	mean	2.00	9.80	3.00	3.50	20.00	6.00	2.00	2.00	2.50	20.00	8.50	2.50
	S.E.	0.25	3.25	0.40	0.90	14.00	2.00	0.50	0.70	0.70	13.00	2.50	0.50
depth	mean	7.00	16.50	7.50	2.50	23.00	13.50	7.50	10.00	3.00	22.50	13.00	17.50
	S.E.	1.15	2.30	1.50	-	5.00	1.00	1.00	1.70	0.50	2.50	0.70	3.00
chl a	mean	88.00	73.00	-	-	-	-	-	-	-	-	-	-
	S.E.	6.60	4.75	-	-	-	-	-	-	-	-	-	-
Md.	mean	-	-	0.23	0.17	0.28	0.21	0.22	0.29	0.16	0.27	0.16	0.27
	S.E.	-	-	0.01	0.01	0.04	0.02	0.01	0.02	0.01	0.05	0.01	0.04
Vmax	mean	-	-	-	-	-	-	54.00	71.00	-	111.00	53.00	62.00
	S.E.	-	-	-	-	-	-	2.50	9.50	-	9.00	3.00	1.50

The DCA graph in Fig. 4 shows the similarities between the stations on the basis of sedimentological and bottom morphological factors (Median (ø), sorting (ø), silt (%), gravel (%) and depth (m)).

Especially a silt-gravel gradient is important along axis 1 (Eigen value of axis 1 = 0.335 ; E.V. of axis 2 = 0.041). Although each twingroup (indicated on the graph) is characterized by a more or less pronounced tendency, they are not unequivocally separated along one of the two first axes, or both axes together.

In summary, it is found that the six twingroups are mostly distinguished on the basis of the median grain size, the silt fraction and the water depth (which is correlated with the silt fraction and the chlorophyll-a content). However the discrimination is not unequivocal on the basis of only sedimentological and bottom morphological characteristics (see DCA graph Fig. 4). Therefore the impact of others factors must not be neglected.

Diversity

The mean diversity index N_1 for each station varies between 5 and 36 (Fig. 5) The N_1 indices differ significantly for the six twingroups (Table IV).

Biomass

The mean biomass per individual and per station varies between 0.085 and 2.460 µg dry weight (dwt). The mean individual biomass over the 20 stations amounts 0.402 µg dwt (Table VI).

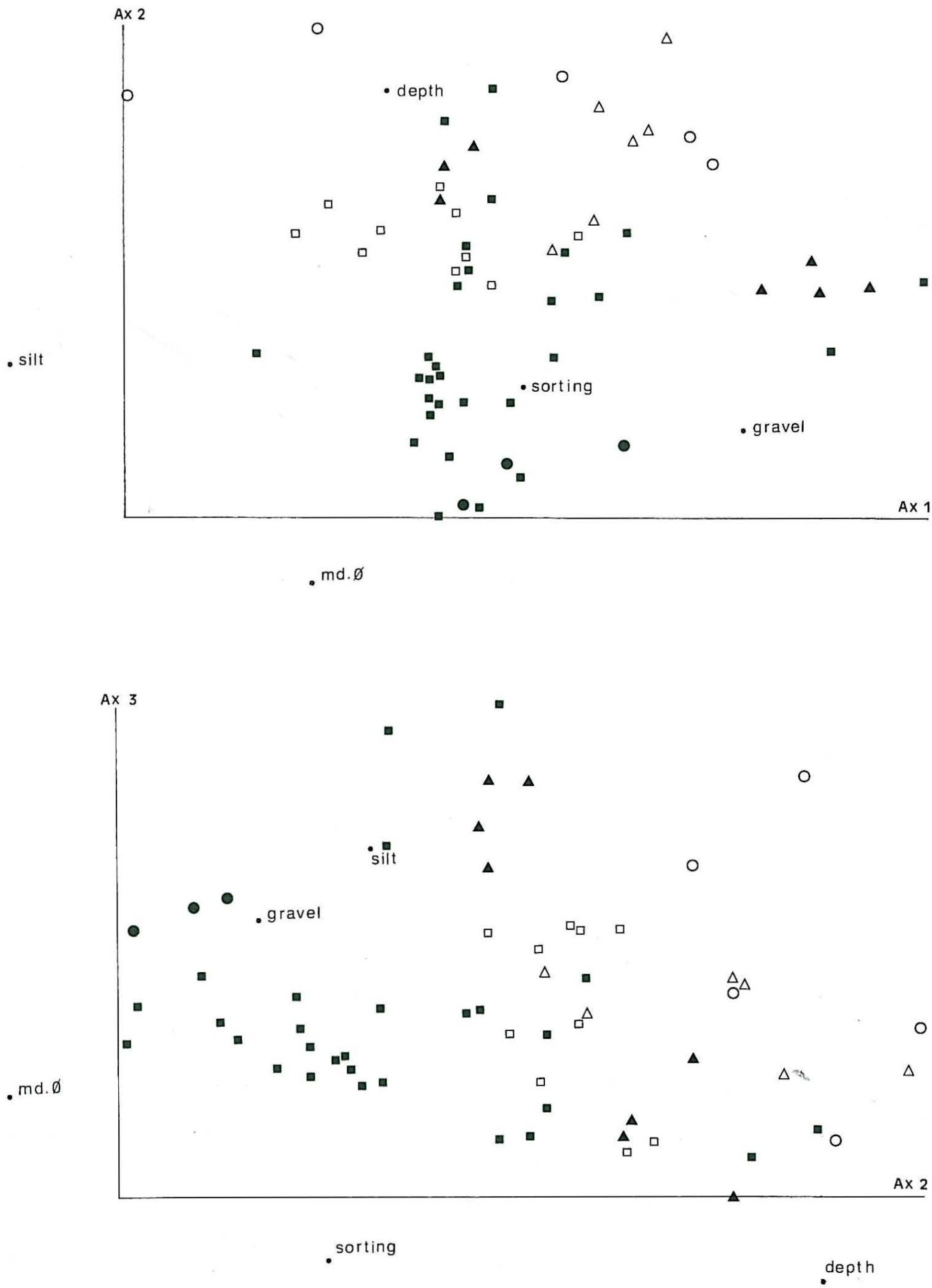

Fig. 4 : The DCA ordination of the 60 replicates (20 stations over three sampling periods) based upon the sedimentological and bottom morphological characteristics (with indication of the six twingroups).

TABLE VI

The mean biomass (in µg dwt) per individual in the 20 stations during the three sampling periods.

	biomass per individual		
st.	Autumn'84	Spring'85	Autumn'85
1	0.248	0.409	0.229
3	0.291	0.249	0.085
11	0.162	0.435	0.156
18	0.176	0.353	0.183
24	0.348	0.528	0.284
25	0.184	0.204	0.184
26	0.185	0.371	0.167
28	0.190	0.555	0.291
31	0.248	0.328	0.340
32	0.192	0.329	0.350
37	0.275	0.700	0.154
39	0.251	0.282	0.205
43	0.383	0.804	0.387
45	0.297	1.400	0.347
46	0.541	2.459	0.600
54	0.260	0.176	0.385
55	0.816	0.443	0.588
63	0.157	0.410	0.541
65	0.261	0.500	1.349
67	0.354	0.543	0.251

DISCUSSION

The structure of a biological community is characterized by a temporal and spatial variability, which results from several biotic and abiotic structuring factors. A primary objective of community ecology is gaining insight in these causal relationships as well as in the relative importance of the different structuring factors.

The Voordelta region is rather a unique study area due to its position off the different estuary mouths. In this heterogeneous and unstable area, there are many physical and chemical gradients, which could be important for the structure of the present nematode communities. These gradients are mainly formed by the sediment composition, the salinity, the chlorophyll-a content and the hydrodynamical forces. All these factors may contribute to the presence of different types of nematode communities. Nothwithstanding the fact that the different twingroups do not differ significantly on the basis of salinity, this factor is still considered in the discussion, as the only station with a low salinity (in comparison to the other stations) forms a twingroup on its own on the basis of its species composition (= station 3 or TWIN 2).

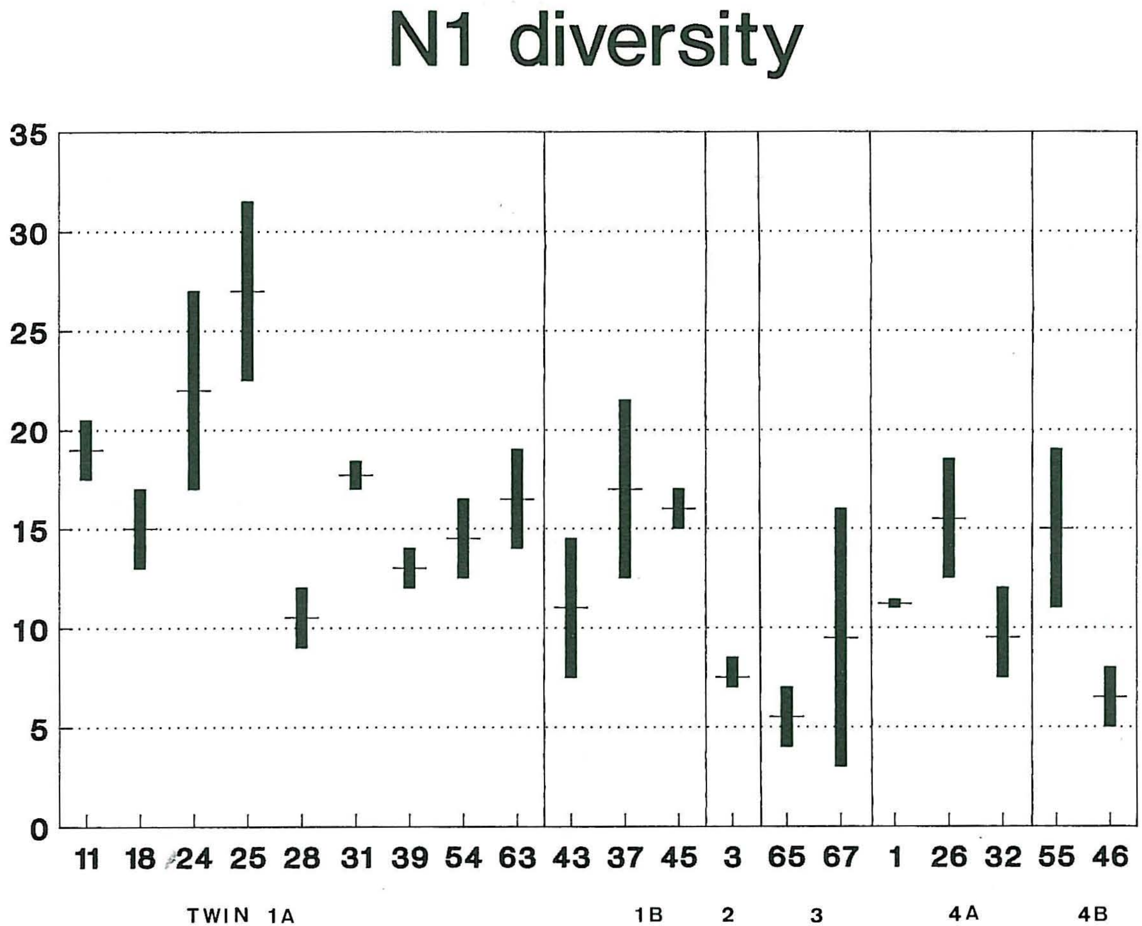

Fig. 5 : Mean and variation (S.E.) of the diversity index N_1 for the 20 stations which are ordered in twingroups.

Sediment composition

The different nematode assemblages of the Voordelta region are distinguished by the median grain size of the sand fraction and the silt content of the sediment.

The sand communities

From the literature it is known that medium sand and/or less sorted sediments with a high gravel fraction (> 1 %) are often characterized by the dominance of Chromadoridae and the subdominance of Desmodoridae (Wieser, 1960 ; Tietjen, 1969 ; 1977 ; 1980 ; Ward 1975). In well sorted, fine sandy sediments Desmodoridae and also Linhomoeidae, Comesomatidae, Xyalidae and Tripyloididae are dominant (Wieser, 1960 ; Tietjen, 1969 & Ward, 1975).

In the Voordelta region the same tendency is noticed for the three types of sand communities :

TWIN 1A : The dominant species belong to one of the following families : Xyalidae, Tripyloididae, Microlaimidae and Desmodoridae. This twingroup consists of almost all the shallow stations of the study area (the stations 11, 18, 24, 25, 28, 31, 39, 54 and 63). These stations are characterized by a silt poor, well sorted, fine sandy and stable substrate.

TWIN 1B : Species belonging to the families of the Chromadoridae and Siphonolaimidae are dominant, while the subdominant species belong to the Desmodoridae and the Chromadoridae. These stations are not explicitly characterized by the same sediment composition. The stations 37 and 45, both shallow stations, situated near the mouth of the Eastern Scheldt, have a less sorted, medium sandy sediment with a higher gravel fraction, while the substrate of station 43, situated near the storm surge barrier, consists of very well sorted, medium sand.

TWIN 2 : These communities are dominated by species of the Chromadoridae and the Xyalidae. The Linhomoeidae and the Leptolaimidae contain the subdominant species. Only station 3, situated off the sluices of the Haringvliet, belongs to this twingroup. Nevertheless, the fine sandy sediment of this station is not unique in the Voordelta region.

The silt and silty sand communities

The communities which are common in silt and silty sand of brackish as well as marine environments are the most striking example of parallellism within marine nematode communities (see review Heip *et al* , 1985). According to Ward (1975) the relative abundance of the genus *Sabatieria* is positively correlated with the amount of silt. Juario (1975) comes to the same conclusions for *S. pulchra*. According to this author, *S. celtica* is a subdominant species in silty sand, while it is less abundant in pure silt or sand. Comparing the known data on dominant species of the silt and the silty sand substrates, it is concluded that along a gradient of pure silt to silty sand different species assemblages are found, for which the dominance of the genus *Sabatieria* is often the most common characteristic.

TWIN 3 : These stations are characterized by an unstable sediment composition, especially concerning the silt fraction. This twingroup is formed by the two stations, situated in the mouth of the Western Scheldt (the stations 65 and 67).

TWIN 4A : Concerning their habitat, these stations are discriminated by their relatively large and (especially) stable silt fraction (5 - 15 %) and by fine sandy sediments (0.14 mm < Md. < 0.16 mm) : the stations off the Nieuwe Waterweg (station 1, the mouth of the lake Grevelingen (station 26) and a part of the mouth of the Eastern Scheldt (station 32).

TWIN 4B : These stations have, in comparison to the stations of TWIN 4A, a higher percentage of gravel and a smaller silt fraction. Their substrate consists of medium sand. This twingroup is formed by two stations situated in the seaward offshoots of the Eastern Scheldt (the stations 46 and 55).

A community, similar to that of TWIN 3, is present more downstream of the Western Scheldt (Heip *et al.*, 1984). Here this community is also associated with the very unstable (or flocculent), superficial silt layers. On one hand probably good swimming species, like *Daptonema tenuispiculum*, survive in these unstable sediments. On the other hand eurytopic, non-selective detritus feeders are more tolerant to the pollution in this estuary (Heip *et al.*, 1984).

The communities of TWIN 4A are characterized by the dominance of species with an affinity to silt and silty sand (= *Sabatieria spp.*. However, the subdominance of species belonging to the Xyalidae is rather characteristic for fine sand (Tietjen, 1977 ; 1980). In accordance with the sediment composition, these assemblages represent a transition situation between silt and sand communities. A similar community (with besides *Dorylaimopsis metatypicus,* as most important subdominant species *Sabatieria pulchra*, *Odontophora setosa, Theristus problematicus*, *Daptonema normandicum* and *Daptonema rusticum*) was found in fine sand off the Long Island sound by Tietjen (1977).

Concerning TWIN 4B, parallel communities are found elsewhere, but in more silty sediments in comparison to our study area : silty sand off the Dutch Bight is characterized by a *Microlaimus* - *Sabatieria* community (Lorenzen, 1974 ; Juario, 1975). In silty sand off the intertidal zone of Strangford Lough (N. Ireland) *Spirinia parasitifera* is dominant, while *Microlaimus zosterae* is subdominant (Platt, 1977). In the silty surface sediments of a subtropical seagrass community *Daptonema fistulatum* is dominant, while *Metoncholaimus scissus* and *S. parasitifera* are the subdominant species (Hopper and Meyers, 1967). Wieser and Kanwisher (1961), found a similar community in Penzance Marsh (Woods Hole), characterized by the dominance of *Spirinia parasitifera* and *Metoncholaimus pristiuris.*

Salinity

Almost 50 % of the differential species of TWIN 2 (= station 3) is euryhaline with a distribution extending to the mesohaline zone (*Theristus pertenuis, Paralinhomoeus lepturus, Oncholaimus brachycercus, Enoploides labiatus* and *E. spiculohamatus*), and for some species even to the oligohaline zone. (*Eleutherolaimus stenosoma, Hypodontolaimus setosus, Ascolaimus elongatus, Sphaerolaimus gracilis, Viscosia viscosa, Dichromadora cephalata, Oncholaimus oxyuris* and *Calomicrolaimus honestus*) (Heip *et al.*, 1985). Only three differential species of TWIN 1 (to which station 11 belongs) are euryhaline (*Odontophora rectangula, Sigmophoranema rufum* and *Tubolaimoides tenuicaudatus*), with a distribution which is limited up to the poly- or mesohaline zone.

Chlorophyll-a content

According to several authors (Warwick, 1971 ; Brenning, 1973 ; Elmgren, 1976 ; Platt, 1977 ; Willems *et al.*, 1982 ; Bouwman, 1983 & Jensen, 1984) meiobenthic communities are structurally, numerically as well as functionally organised in relation to the food richness of their habitat, and more specifically to the amount of available organic matter and microphytobenthos.

Pearson and Rosenberg (1987) postulated a general hypothesis on the structuring of benthic communities in relation to the food supply : in the case of a sufficient food supply, communities are dominated by species with a maximal turnover, or r-strategists with a fast growth and a high reproductive activity. In the case of a continuous or predictable lack of food, especially species with a small growth rate and a minimal turnover survive. According to Schiemer (1983, 1985) r-strategists prefer a high food supply because their high growth rate and assimilation coefficient are associated with high costs of maintenance. Species with a low metabolic activity however, are competitively inferior in the case of a large food supply.

Consideration of the life cycle and the biomass of the dominant species of the 20 stations in the Voordelta region in relation to the chlorophyll-a content confirms the hypothesis of Pearson and Rosenberg (1987). For instance, the mean individual biomass per station is negatively correlated with the chlorophyll-a content (r_S = -0.440 ; n = 20). The stations of TWIN 4B (station 55 and 46), situated in the seaward offshoots of the mouth of the Eastern Scheldt and characterized by a very low chlorophyll-a content (< 65 µg/10 l) in comparison to the remaining stations (see Table I), are qualitatively as well as quantitatively dominated by bigger species belonging to the Thoracostomopsidae and the Oncholaimidae (*Metoncholaimus scanicus, Enoploides spiculohamatus, Enoplolaimus propinquus E. denticulatus, Oncholaimellus calvadosicus* and *Oxyonchus dentatus*, by large predators (*Onyx perfectus* and *Sigmophoranema rufum)* or by *Sabatieria spp.* (Comesomatidae). Experimental and field studies have shown that species, belonging to the Enoplidae, the Oncholaimidae and the Comesomatidae, have often a conservative reproductive strategy (Wieser & Kanwisher, 1960 ; Hopper & Meyers, 1966 a and b ; von Thun, 1968 : in Bouwman, 1983 ; Smol *et al* , 1980 ; Vincx, 1989). Their life cycle varies between a few months up to more than one year, while their production often amounts only 25 eggs per female. In general, larger species should have a lower reproduction potential than small species (Heip *et al.*, 1985).

In the stations of TWIN 1A, 50 % of the differential species belong to the Xyalidae or the Cyatholaimidae. Only three differential species are large predators. With the exception of the Autumn-samples of station 25, 28 and 39, the Xyalidae and or the Cyatholaimidae are always dominant in the stations belonging to this twingroup. These stations are characterized by the highest chlorophyll-a values for the Voordelta region (Table I). The life cycle of the Chromadoridae, Cyatholaimidae and Xyalidae is, in comparison to that of the preceding families, much shorter (1 to 2 months), while their reproduction potential is higher (Vranken *et al.*, 1981 ; Romeyn *et al.*, 1983).

However, observations of mass aggregations especially from *Pontonema vulgare*, but also from several other Oncholaimidae species in organically enriched areas, seem not to be in accordance with the above hypothesis (Gerlach, 1958 ; Moore, 1971 ; Meyers and Hopper, 1967 ; Lorenzen *et al.*, 1987 ; Prein, 1988). But, according to Pearson and Rosenberg (1987), to correlate the distribution of a species with the food supply, not only the size of this supply, but also the fluctuations, and the predictability of these fluctuations has to be taken into account. Therefore when the food supply is unpredictable, again the slow growing species, but also the species which can maximize their biomass, are favoured (Pearson & Rosenberg, 1987). These species are more able to survive starvation periods (Schiemer, 1987).

Pontonema vulgare for example is a common species on shallow water soft bottoms of protected coastal areas, containing high amounts of organic substances. In such enclosed areas upwelling of oxygen depleted water may create sudden anoxia throughout the water column and causes mass mortalities of benthic and pelagic organisms. According to Prein (1988), *P. vulgare* survives these situations and takes advantages of the sharp increase of food. The author also suggest that the wide range of feeding strategies and possible food types permits *P. vulgare* to react flexibly to changes in quality and quantity of food. The sudden availability of considerable amounts of food can support large populations of this species (Prein, 1988). However, this example also shows that oncholaimid species not always have a conservative reproductive strategy. Notwithstanding that the hypothesis of Pearson and Rosenberg is not contradicted by the present results, definite conclusions cannot be drawn as only little information on the reproductive strategy of particular species is available.

Physical disturbance and stability of the environment

In sublittoral areas with a heterogeneous bottom morphology, like the Voordelta, a distinction has to be made between the shallow banks, influenced by the wave action, and the deeper channels, often characterized by unpredictable minimum and maximum current velocities.

In the Western Scheldt the fluctuating current velocities give rise to temporal accumulations of silt. Once the current velocity decreases to a certain critical value, the silt particles can be deposited (Creutzberg, 1984 ; Wollast, 1976). These unstable silt layers are characterized by the extremely high dominance (> 75 %) of three very tolerant species (*Sabatieria punctata, Daptonema tenuispiculum* and *Ascolaimus elongatus*), which seem to be adapted to such unstable environments.

Nothwithstanding the fact that the current velocities at station 43 are similar to the Western Scheldt, this station is not characterized by temporal accumulations of silt. It is remarkable that this station shows the largest affinity for two near-by situated, but shallow and thus silt poor stations (the stations 37 and 45). The sorting of the sediment at these two stations is variable in comparison to the remaining shallow stations. The most similar characteristic for the stations 37, 43 and 45 is probably the hydrodynamical stress, which is evident in station 43 by the direct measurements of the fluctuating current velocities, and which is indicated by the variability over time of the sorting of the sediment at the stations 37 and 45.

Mechanical disturbance, associated with predictable or unpredictable environmental fluctuations, is one of the most important factors, which determines the structure of a nematode community (Warwick, 1971 ; Brenning, 1973 ; Platt, 1977 ; Govaere *et al.*, 1980 ; Bouwman *et al.*, 1983 ; Alongi, 1986). According to Warwick and Gee (1984), communities, which are disturbed by the activity of macrobenthic organisms and by fluctuations In the abiotical environment, are dominated by opportunistic species (with a short generation time and a high respiration rate). In the absence of such population reducing mechanisms, conservative species (with a low respiration rate and a long generation time : = climax community) are more favoured. An example of such a climax community is, still according to Warwick and Gee (1984), the *Terschellingia spec. -Sabatieria pulchra* community, often associated with silty sediments and characterized by a low species diversity. A disturbed community is more diverse and is, for example in Clifton, dominated by three Chromadoridae species among which *Ptycholaimellus ponticus* (Warwick & Gee, 1984).

According to these authors, these results support the stability-diversity hypothesis of Huston : "The apparent anomaly of a higher diversity at Clifton than Neal point is consistent with Huston (1979) dynamic equilibrium hypothesis... Under stable conditions, where population reductions are infrequent, competive equilibrium is approached and diversity decreased". According to Platt and Lambshead (1983), who suggested to combine the preceding hypothesis with that of Connel (1979), one has to distinguish different gradations of disturbance : diversity is higher in the case of disturbance, unless the impact of the disturbance is so catastrophic that species disappear.

Examples of such 'catastrophic' communities in the Voordelta are probably the *Daptonema-Sabatieria-Ascolaimus* communities of the hydrodynamically disturbed and heavily polluted stations in the mouth of the Western Scheldt. An example of an intermediary disturbed community, comparable to the opportunistic community of Clifton, is probably present in the hydrodynamically disturbed stations off the mouth of the Eastern Scheldt (TWIN 1B). These communities are dominated by *Dichromadora hyalocheile.*

Besides, the above mentioned presence or absence of opportunistic and conservative species is also connected to the food supply in the Voordelta. The hypothesis of Pearson and Rosenberg (1987) can even be connected with the one of Warwick and Gee (1984) : Elmgren (1978) showed that predation and disturbance caused by macrobenthic organisms is more important in the case of a higher food supply.

However, if the *Sabatieria-Terschellingia* community on the one hand, and the Chromadoridae community on the other hand are indeed specific examples of respectively a climax and a pioneer community, one has to take care not to generalize the hypothesis of Warwick and Gee (1984) to all forms of population-reducing mechanisms. For instance, the chromadorid *Dichromadora hyalocheile* is indeed very abundant in the hydrodynamically disturbed stations of TWIN 1B. But the dominant species of the opportunistic community in Clifton (Warwick & Gee, 1984), *Ptycholaimellus ponticus*, is in the Forth estuary limited to the clean, unpolluted and undisturbed, sandy sediments (Moore, 1987). In an experimental study on the effect of Pentachlorophenol on the structure of marine nematode communities by Cantelmo and Rao (1978), first of all a reduction of the Chromadoridae and the Desmodoridae was observed.

Moreover, *Sabatieria pulchra*, the dominant species of the so called climax community, is often very abundant in disturbed environments, independent of the sediment composition. It is suggested by several authors that *Sabatieria pulchra* is extremely physiologically adapted to stressed life conditions (Heip & Decraemer, 1974 ; Tietjen, 1980 & Heip *et al.*, 1984). This species even survives as a facultatively anaerobic species in deoxygenated sediments (Jensen, 1984).

CONCLUSIONS

The nematode communities of the banks poor in silt, and those of the silty channels are clearly distinguished on the basis of the dominance of *Sabatieria spp.* Three types of communities, typically for silty sand sediments are present : (1) a *Sabatieria spp. - Daptonema spp.* community, at the level of the Nieuwe Waterweg, the lake Grevelingen, and in the channel of the Eastern Scheldt ; (2) Communities with higher abundances of larger, mostly conservative species, are typical for the chlorophyll-a poor regions of the channel of the Eastern Scheldt ; and (3) a species poor community, containing eurytope and tolerant species is typical for the unstable silty bottom layer of the Western Scheldt.

For the silt poor, sandy stations, three types of communities may be discerned as well. Two of them are typical for well sorted fine sands, in which mainly Xyalidae, Tripyloididae and Desmodoridae are abundant. The two fine sandy station groups can be discerned from each other on the base of the higher input of fresh water at the level of the sluices of the Haringvliet. The third community is found in dynamically disturbed habitats, characterized by poorly sorted medium sands, in which the chromadorids are the dominant, and the desmodorids the subdominant group.

It is remarkable that, notwithstanding the fact that the Voordelta region is a heterogeneous and unstable area, characterized by several large environmental gradients, the relatively small sedimentological gradient is most strongly correlated with changes in the structure and the composition of the nematode communities. In the past ecological field studies of sublittoral nematode communities were often limited to the evaluation of correlations with the sediment composition, assuming that such information was sufficient to gain insight in the ecology of this group (see review Heip *et al.*, 1985). However, recently more authors have found, on an experimental basis as well as in the field , both a relationship between the ecophysiology of species and the structure of the nematode communities, and a relationship with environmental factors other than sedimentological. In this paper some evidence for similar correlations are suggested : e.g. the relation between the species composition and the mean individual biomass of the nematodes, and the chlorophyll-a content, the hydrodynamical forces and the stability of the environment.

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REFERENCES

ALONGI, D.M., 1986. Population structure and trophic composition of the free-living nematodes inhabiting carbonate sands of Davies reef, Great Barrier reef, Australia. *Aust. J. Mar. Freshw. Res.*, 37 : 609-619.

BOUWMAN, L.A., 1983. A survey of nematodes from the Ems estuary. Part 2 : Species assemblages and associations. *Zool. Jb. (Syst.)*, 110 : 345-376.

BOUWNAN, L.A., K. ROMEYN & W. ADMIRAAL, 1983. On the ecology of meiofauna in an organically polluted estuarine mudflat. IN : Systematics, ecology and feeding biology of estuarine nematodes. Bouwman, L.A., Diss., Wageningen, Biologisch onderzoek Eems-Dollard Estuarium, *Publicaties en Verslagen*, N 3, 6 : 128-155.

BRENNING, U., 1973. The distribution of littoral nematodes in the Wismarburcht. *Oikos, Suppl.* 15 : 98-104.

CANTELMO, F.R. & K.R. RAO, 1978. Effects of pentachlorophenol on the meiobenthic nematodes in an experimental system. In : Pentachlorophend. K.R.R., Plenum Publ. Corporation New York : 165-174.

CONNEL, J.H., 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. *Symp. Brit. Ecol. Soc.*, 20 : 141-163.

CONOVER, W.J., 1971. Practical non-parametric statistics. John Wiley & Sons, New York : 1-462.

CREUTZBERTG, F., 1984. A persistent chlorophyll a maximum coinciding with an enriched benthic zone. In : Proceedings of the 19 th E.M.B.S. Gibbs, B.E., Cambridge University Press : 109-122.

ELGERSHUIZEN, H.B., 1981. Some environmental impacts of a storm surge barrier. *Mar. Pollut. Bull.*, 12 : 265-271.

ELMGREN, R., 1976. Baltic benthos communities and the role of meiofauna. Contribution from the Asko Laboratory, University of Stockholm, Sweden (Ed. Janson, A.M.), 14 : 1-32.

ELMGREN, R., 1978. Structure and dynamics of baltic benthos communities with particular reference to the relationship between macro and meiofauna. *Kieler Meeresforsch.*, 4 : 1-22.

GERLACH, S.A., 1958. Die Nematodenfauna der sublittoralen Region in der Kieler Bucht. *Kieler Meeresforsch.* 14 : 64-90.

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. *Helgolander wiss. Meeresunters.*, 33 : 507-521.

HEIP, C. & W. DECRAEMER, 1974. The diversity of nematode communities in the Southern North Sea. *J. mar. biol. Ass. U.K.*, 54 : 251-255.

HEIP, C., R. HERMAN & M. VINCX, 1983. Subtidal meiofauna of the North sea. *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. Reun. Cons. int. Explor. Mer.*, 183 : 51-56.

HEIP, C., P. HERMAN & K. SOETAERT, 1988. Data processing, evaluation and analysis. In : Introduction to the study of the meiofauna. Higgings, R.P. & H. Thiel, The Smithsonian Institution Press, Washington D.C. London, 197-231.

HEIP, C., M. VINCX & G. VRANKEN, 1985. The ecology of marine nematodes. *Oceanogr. Mar. Biol. Ann. Rev.*, 23 : 399-489.

HILL, M.O., 1973. Diversity and eveness : a unifying notation and its consequences. *Ecology*, 54 : 427-432.

HILL, M.O., 1979. Twinspan - a fortran program for arranging multivariate data in an ordered two way table by classification of the individuals and attributes. Ithaca, N.Y. Cornell University. *Ecology & Systematics* : 1-48.

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

HOPPER, B.E. & S.P. MEYERS, 1966 a. Observations on the bionomics of the marine nematode *Metoncholaimus sp.*, *Nature*, 209 : 899-900.

HOPPER, B.E. & S.P. MEYERS, 1966 b. Aspects of the life cycle of nematodes. *Helgolander wiss. Meeresunters.*, 13 : 444-449.

HOPPER, B.E. & S.P. MEYERS, 1967. Population studies on benthic nematodes within a subtropical seagrass community. *Mar. Biol.*, 1 : 85-96.

HUSTON, M., 1979. A general hypothesis of species diversity. *Amer. Nat.*, 113 : 81-101.

HUYS, R., A. VANREUSEL & C. HEIP, 1986. Het meiobenthos van de Voordelta. Final report (Summary) BOVO project Rijkswaterstaat DGW Middelburg (N1.) 40 pp.

JENSEN, P., 1984. Ecology of benthic and epiphytic nematodes in brackish waters. *Hydrobiologia*, 108 : 201-217.

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

LORENZEN, S., 1974. Die Nematodenfauna der sublittoralen Region der Deutschen Bucht, ins besondere im Titanabwasser-gebiet bei Helgoland. *Veroff. Inst. Meeresforsch. Bremerh.*, 14 : 305-327.

LORENZEN, S., M. PREIN & C. VALENTIN, 1987. Mass aggregations of the free-living marine nematode *Pontonema vulgare* (Oncholaimidae) in organically polluted fjords. *Mar. Ecol. - Prog. Ser.* 37 : 27-34.

MEYERS, S.P. & B.E. HOPPER, 1967. Studies on marine fungal - nematode associations and plant degradation. *Helgol. Wiss. Meeresunters.* 15 : 270-281.

MOORE, P.G., 1971. The nematode fauna associated with holdfasts of kelp (*Laminaria hyperborea*) in North-East Britain. *J. mar. biol. Ass. U.K.* 51 : 589-604.

MOORE, C.G. 1987. Meiofauna of the industrialised estuary and Firth of Forth, Scotland. *Proc. R. Soc. Edinb.*, 93B : 415-430.

MUELLER-DOMBOIS, D. & H. ELLENBERG, 1974. Aims and methodes of vegetation ecology. Wiley New York.

PEARSON, T.H. & R. ROSENBERG, 1987. Feast and famine : structuring factors in marine benthic communities. In : Organisation of communities. Past and present. Gee, H.R. & P.S. Giller, Blackwell Scientific publications, 373-375.

PREIN, M., 1988. Evidence for a scavenging lifestyle in the free-living Nematode *Pontonema vulgare* (Enoplida, Oncholaimidae. *Kieler Meeresforsch., Sonderh.* 6 : 389-394.

PLATT, H.M. & P.J.D. LAMBSHEAD, 1985. Neutral model analysis of patterns of marine benthic species diversity. *Mar. Ecol. Prog. Ser.*, 24 : 75-81.

PLATT, H.M., 1977. Ecology of free-living marine nematodes from an intertidal sand flat in Strangford Lough, Northern Ireland. *Estuar. cstl. mar. sci.*, 5 : 685-693.

ROMEYN, K., L.A. BOUWMAN & W. ADMIRAAL, 1983. Ecology and cultivation of the herbivorous brackisch-water nematode *Eudiplogaster pararmatus. Mar. Ecol. - Prog. Ser.*, 12 : 145-153.

SCHIEMER, F., 1983. Comparative aspects of food dependence and energetics of free-living nematodes. *Oikos*, 41 : 32-42.

SCHIEMER, F., 1985. Bioenergetic differentiation of aquatic invertebrates. *Verh. Internat. Verein. Limnol.*, 22 : 3014-3018.

SCHIEMER, F., 1987. Nematoda. *Animal energetics*, 1 : 185-215.

SEIP, P.A. & R. BRAND, 1987. Inventarisatie van macrobenthos in de Voordelta. *Nioz rapport 1 - Texel (N1).*

SMOL, N., C. HEIP & M. GOVAERT, 1980. The life cycle of *Oncholaimus oxyuris* in its habitat. *Annls Soc. r. zool. Belg.*, 110 : 87-103.

THUN, W. VON, 1968. Autökologische Untersuchungen an freilebenden Nematoden des Brackwassers. *Ph. D thesis Kiel university*, 72 pp.

TIETJEN, J.H., 1969. The ecology of shallow water meiofauna in two New England estuaries. *Oecologia (Berl.)*, 2 : 251-291.

TIETJEN, J.H., 1977. Population distribution and structure of the free-living nematodes of Long Island Sound. *Mar. Biol.*, 43 : 123-136.

TIETJEN, J.H., 1980. Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight apex. *Estuar. coast. Mar. Sci.* 10 : 61-73.

VAN DEN BERG, J.H., 1984. Morphological changes of the ebb - tidal delta of the Eastern Scheldt during recent decades. *Geol. & Mijnbouw*, 63 : 363-375.

VANREUSEL, A., R. HUYS, G. DE SMET & C. HEIP, 1986. Het meiobenthos van de Voordelta. Final report BOVO project Rijkwaterstaat DGW Middelburg (Nl.) 450 pp.

VANREUSEL, A. & M. VINCX, 1989. Free-living marine nematodes from the Southern Bight of the North sea. III Notes on species of the Monoposthiidae, Filipjev 1934. *Cah. Biol. Mar.* 30 : 69-83.

VINCX, M., 1986. Free-living marine nematodes from the Southern Bight of the North Sea. Ph. D. Thesis State University Ghent (Belgium). 618 pp.

VINCX, M., 1989. Seasonal fluctuations and production of nematode communities in the Belgian coastal zone of the North Sea. Verhandelingen van het symposium "Invertebraten van Belgie" : 57-66.

VINCX, M. & A. VANREUSEL, 1989. Free living marine nematodes from the Southern Bight of the North sea. II Notes on species of the Trefusiidae, Lorenzen, 1981. *Hydrobiologia*. 175 : 213-221.

VRANKEN, G., L.K. THIELEMANS & M. VAN DIJCKE, 1981. Aspects of the life cycle of *Monhystera parelegantula* (Nem. Monhysteridae). *Mar. ecol. - Prog. Ser.*, 6 : 67-72.
WARD, A.R., 1975. Studies on the sublittoral free-living nematodes of the Liverpool Bay. II. Influence of sediment composition on the distribution of marine nematodes. *Mar. Biol.*, 30 : 217-225.
WARWICK, R.M. 1971. Nematodes associations in the Exe estuary. *J. mar. biol. Ass. U.K.*, 51 : 439-454.
WARWICK, R.M. & J.. GEE, 1984. Community structure of estuarine meiobenthos. *Mar. Ecol. - Prog. Ser.*, 18 : 97-111.
WESTHOFF, V & E. VAN DER MAAREL, 1973. The Braun Blanquet approach. In : Ordiantion and classification of communities. *Whitaker, R.A., Junk, The Hague*, 617-726.
WIESER, W., 1960. Benthic studies in Buzzards bay. II. The meiofauna. *Limnol. Oceanogr.*, 5 : 121-137.
WIESER, W. & J.W. KANWISHER, 1960. Growth and metabolism in a marine nematode *Enoplus communis, Bastian. Z. vergl. Physiol.*, 43 : 29-36.
WIESER, W. & J.W. KANWISHER, 1961. Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusettes. *Limnol. Oceanogr.*, 6 : 262-270.
WILLEMS, K.A., C. VANOSMAEL, D. CLAEYS. M. VINCX & C. HEIP, 1982. Benthos of a sublittoral sand bank 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'estuarie de l'Escaut. In : L'estuarie de l'Escaut. Programme national de recherche et de développement environnement, eau projet mer. Volume 10 Nihoul, J.C.J. & R. Wollast, Bruxelles, 191-219.