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DIVERSITY OF THE NEMATODE 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. Overall, 456 species, belonging to 159 genera and 37 families were found.

Sediment structure and chlorophyll a content were found to be determining environmental factors in the species composition of the nematode communities.

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

The open sea stations are characterized by nematode communities which are comparable in terms of species diversity; the number of species S is about 30-35 per sample (sample size is about 100) with H' between 4.00-4.50 bits/ind. The communities in the coastal stations are less diverse (S=7-22); H'=1.4-3.5 bits/ind.). The stations along the Belgian east coast have communities with low diversity (S=7; H'=1.41 bits/ind.) and with a pronounced dominance of a few species (Simpson index=0.54); the diversity within the eight families is also very low.

The relationship between environmental stability (or disturbance) and stability and diversity of the nematode communities can be explained by the following factors: habitat heterogeneity, food availability, productivity, density and population growth rates.

1. INTRODUCTION

The study of the benthos in the Southern Bight of the North Sea started in 1971, and is still going on (GOVAERE *et al.*, 1980; VANOSMAEL *et al.*, 1982; WILLEMS *et al.*, 1982a, b; HEIP *et al.*, 1979; VINCX, 1981; HEIP *et al.*, 1983; VINCX, 1983 and VINCX, 1986a). Nematodes are numerically the most important meiobenthic taxon within the area (VINCX, 1986b). The description of characteristic species assemblages of the nematodes within the area and their correlation with environmental parameters is discussed in VINCX *et al.* (in press).

An important feature of nematode communities, perhaps the most important in understanding their ecological success, is the large number of species present in any one habitat - usually an order of magnitude greater than for any other major taxon (HEIP *et al.*, 1985). However, species richness varies much among habitats.

Diversity indices have been particularly popular because of the presumed relationship between species diversity and environmental quality. However, any index involves an inevitable loss of information compared to the data from which it was calculated. In the case of species diversity measures, the information lost includes the identity of the species in the community. For this reason, diversity indices should never be used alone and must be coupled with population data or multivariate analysis, which reflect qualitative community composition.

Diversity within ecological groups of communities is interesting to examine because overall diversity may increase by addition of new ecological groups or by diversifying the already present ecological unit in the low-diversity community.

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2. MATERIAL AND METHODS

The nematode communities from 102 stations in the

Southern Bight of the North Sea sampled between 1972 and 1984 are examined in this study. The position of the stations, sampling methods and extraction techniques are given in VINCX *et al.* (in press).

Calculation of the most frequently used diversity and evenness indices was performed in order to compare my own data with values from communities described in the literature. The various measures of diversity and the difficulties involved in dealing with them have been discussed in HURLBERT (1971), PEET (1974) and HEIP *et al.* (1988). Following indices have been calculated : 1. number of species (=S or N0); 2. Shannon-Wiener diversity index H'(SHANNON & WEAVER, 1949); 3. Brillouin index H (PIELOU, 1969); 4. Simpson index SI; 5. Hill's number N1 (=e H' in ln) (HILL, 1973); 6. Hills's number N2 (= 1/SI) (HILL, 1973); 7. Evenness index J (=H/Hmax) (PIELOU, 1969); 8. Evenness index E1,0 (=N1/N0) (HILL, 1973) 9. Evenness index E2,1 (=(N2/N1) (HILL, 1973); 10. E'1,0 (= N1- 1/N0-1) (HEIP, 1974) and 11. E'2,1 (=N2-1/N1-1) (ALATALO, 1981).

HEIP *et al.* (1988) recommend the diversity number N1 over H' and H because it is approximately normally distributed, and because it gives an equivalent number of species; this is N1=S (number of species) when all the species have an equivalent number of individuals.

The diversity indices thus far considered take no account of the relative differences between species (*e.g.* taxonomic differences above the species level; groups of species based on their trophic requirements (feeding types). If in one community all the species belong to a single genus and in the other, every species belongs to a different genus, it would be reasonable to regard the latter community as functionally the more diverse of the two. Therefore, it would be desirable to be able to split the total diversity measure of a community in a hierarchical way: a higher (*e.g.* generic) component and a lower (*e.g.* specific) component. PIELOU (1977) shows that H' and H can be subdivided in a hierarchical way. ROUTLEDGE (1979) discussed the hierarchical subdivision of diversity and concluded that the only diversity indices which can be divided are the diversity numbers of HILL (1973), from which H' can be considered as a member. For the calculation of the hierarchical diversity, *i.e.* species diversity within separate

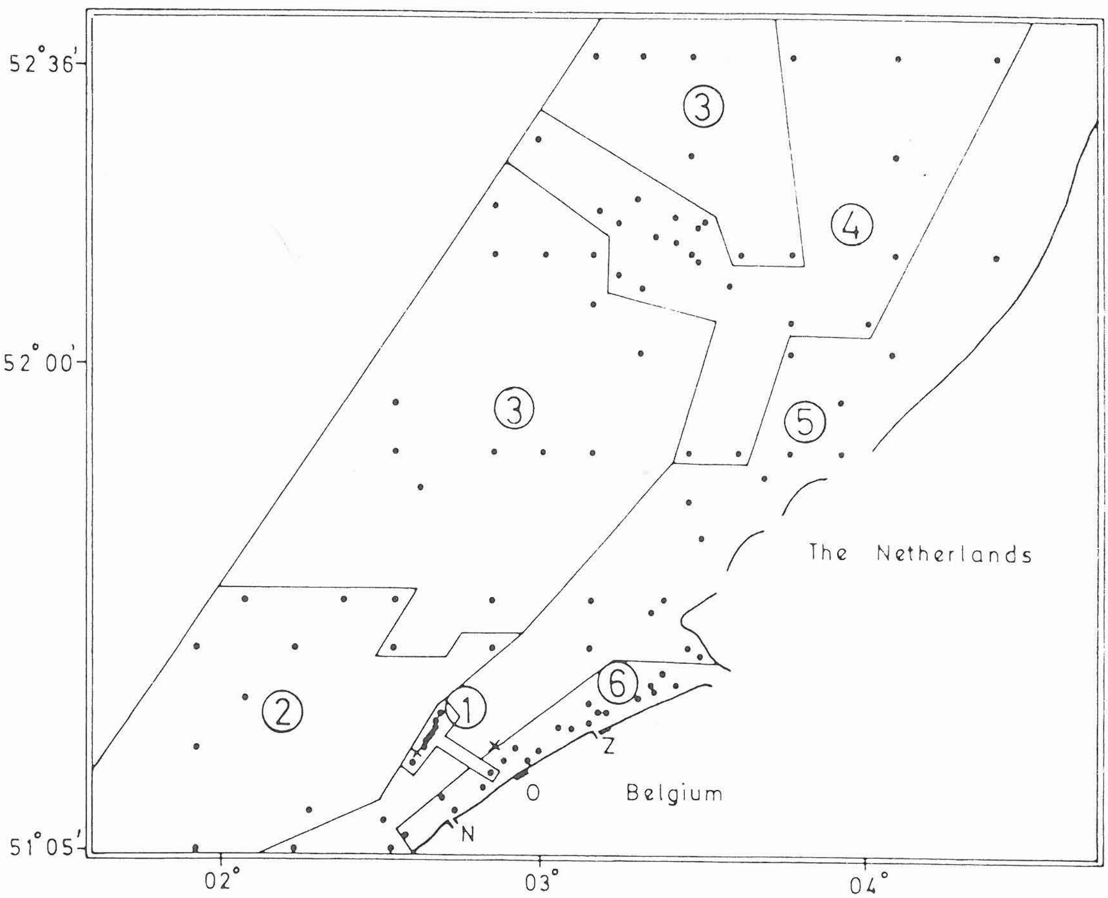

Fig. 1. Position of the six Twinspan-station groups in the Southern Bight.

families and within feeding types, I have used the N1-index. N2 gives more weight to the abundance of common species than N1, and gives therefore less weight to rare species. N1 gives in turn less importance to the rare species than N0 which counts all species as equivalent, independent of their abundance.

3. RESULTS

According to VINCX *et al.* (in press), six areas (=groups of stations, named from now on TWIN 1 to TWIN 6) can be delineated within the Southern Bight of the North Sea, based on the nematode species composition (Fig. 1). These groups of stations have been calculated from multivariate analysis of the species occurrence data (both Twinspan analysis and DCA, *cf.* HILL, 1979a and b).

The coastal region is divided into two main areas:
1. The Belgian coast (TWIN 6), except a few stations on the west coast. Important species are: *Ascolaimus* sp.1, *Daptonema tenuispiculum* and *Sabatieria punctata.*
2. The Dutch coast and the western part of the Belgian coast (TWIN 5). Important species are: *Enoploides spiculohamatus, Paracyatholaimus pentodon, Prochromadorella attenuata, Richtersia inaequalis* and *Sabatieria celtica.* The southern off-shore region consists of two areas showing a patchy distribution. The distribution is correlated with the topography of the sand banks in that region:
3. The crests of the sand banks (TWIN 1) are characterized by *Bathylaimus parafilicaudatus, Desmodora schulzi, Leptonemella aphanothecae* and *Onyx perfectus.*
4. The channels between the sand banks (TWIN 2) are characterized by *Hypodontolaimus* n.sp.1, *Onyx perfectus, Rhips ornata, Rhynchonema quemer, Spilophorella paradoxa, Epsilonematidae* spp. and *Draconematidae* spp.. The northern off-shore area is quite homogeneous, although two regions are distinguished on the amount of gravel within the sediment: TWIN 3 in Fig. 1 is characterized by *Chromaspirina parapontica, Dichromadora cucullata, Karkinochromadora lorenzeni* and *Xyala striata;* TWIN 4 is situated in a TiO_2 dumping area (SPAANS, 1987) and is characterized by *Chromaspirina parapontica, C. pellita, K. lorenzeni,* Molgolaimus turgofrons and *Neochromadora munita.*

The species diversity of the nematode communities of the different samples are available on request. Mean values of the diversity and evenness indices per station group are noted in Table 1. The mean values must be considered with caution because most of these coefficients are not distributed normally and therefore no basic statistics are allowed. However, non-parametric statistics and correlations may show some trends in differences which exist between the different station groups. The overall diversity of the nematode community for the whole area is calculated as 3.48 bits/ind.(H') or 3.05 bits/ind.(H). An average number of 25.3 species per sample (sample size is about 100, see N in Table

TABLE 1

Diversity indices (mean value and SE) of the six Twinspan station groups.

	H	*H*	*SI*	*J*	N_1	N_2
TWIN 1	4.05±0.24	3.53±0.20	0.11±0.03	0.83±0.03	18.40±2.41	12.18±1.70
TWIN 2	4.35±0.18	3.76±0.14	0.08±0.02	0.87±0.02	21.88±1.87	15.39±1.44
TWIN 3	4.34±0.85	3.74±0.07	0.08±0.01	0.87±0.01	21.39±1.19	14.51±1.20
TWIN 4	4.05±0.12	3.61±0.11	0.12±0.01	0.81±0.02	17.95±1.38	11.47±1.07
TWIN 5	3.53±0.11	3.12±0.24	0.15±0.01	0.79±0.02	12.58±0.99	8.33±0.74
TWIN 6	1.41±0.16	1.28±0.14	0.54±0.04	0.52±0.04	3.15±0.44	2.33±0.29
Overall mean	3.48±0.06	3.05±0.05	0.20±0.01	0.76±0.01	14.95±0.52	10.02±0.42

	E10	*E´10*	*E21*	*E´21*	*S*	*N*
TWIN 1	0.59±0.04	0.58±0.04	0.66±0.03	0.63±0.03	30.3±3.5	103± 2.8
TWIN 2	0.64±0.03	0.63±0.03	0.68±0.02	0.67±0.03	33.0±2.0	97± 2.9
TWIN 3	0.65±0.02	0.64±0.02	0.70±0.02	0.69±0.02	32.3±1.4	92± 1.4
TWIN 4	0.54±0.03	0.51±0.01	0.61±0.02	0.58±0.02	33.2±2.0	149± 8.9
TWIN 5	0.54±0.03	0.65±0.02	0.61±0.02	0.61±0.02	22.7±1.3	109±13.7
TWIN 6	0.45±0.03	0.35±0.04	0.77±0.02	0.58±0.03	7.6±0.9	124±12.7
Overall mean	0.56±0.01	0.52±0.01	0.68±0.01	0.62±0.01	25.3±0.7	115± 4.1

TABLE 2

Multiple comparison (after a significant Kruskal-Wallis oneway analysis of variance) of the different diversity coefficients between the six Twinspan station groups.

	H´	*H*	*SI*	*J*	N_1	N_2	*E10*	*E´10*	*E21*	*E´21*
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	63.84	62.55	61.54	50.48	63.95	57.87	32.31	36.83	33.09	18.99
sign.	***	***	***	***	***	***	***	***	***	***

1) is present. The dominance index is generally low (SI=0.20) and the evenness indices vary around 0.50 (*i.e.* E1,0=0.56; E'1,0=0.52; E2,1=0.68; E'2,1=0.62).

Nematode communities from TWIN 1,2,3 and 4 have the highest diversity and evenness coefficients; TWIN 5 has an intermediate position, while TWIN 6 has very low diversity values and a high Simpson dominance index.

Kruskall-Wallis test shows that all coefficients are significantly different between the six station groups (Table 2). Multiple comparison between pairs of station groups shows that especially TWIN 5 and 6 are significantly different from the others for most diversity and evenness indices. The open sea stations (TWIN 1 to TWIN 4) are comparable in terms of species diversity. The evenness of the nematode communities of station

TABLE 3

Mean values (±SE) of the N_1-species diversity coefficient for the species composition of eight important families per Twinspan station group (CHROM = Chromadoridae; COMES = Comesomatidae; CYATH= Cyatholaimidae; DESMOD = Desmodoridae; MICROL = Microlaimidae; ONCHOL = Oncholaimidae; THORAC = Thoracostomopsidae; XYAL = Xyalidae). ´Fam´ is the mean N_1-diversity of the nematode community on the basis of the family composition.

	CHROM	*COMES*	*CYATH*	*DESMOD*	*MICROL*	*ONCHOL*	*THORAC*	*XYAL*	*Fam.*
TWIN 1	3.39±0.89	1.13±0.38	1.70±0.47	2.64±0.45	1.69±0.41	1.00±0.21	1.54±0.41	3.01±0.61	7.25±1.02
TWIN 2	4.68±0.45	1.00±0.00	3.22±0.47	2.75±0.33	2.54±0.29	1.25±0.05	1.67±0.21	4.21±0.42	7.15±0.48
TWIN 3	3.67±0.20	1.33±0.14	2.14±0.17	3.34±0.16	2.48±0.23	1.61±0.14	2.06±0.12	4.38±0.25	7.42±0.45
TWIN 4	3.40±0.20	1.30±0.08	2.70±0.15	3.53±0.25	2.35±0.17	1.23±0.09	1.94±0.13	3.29±0.40	6.59±0.38
TWIN 5	2.13±0.24	1.29±0.09	1.79±0.15	2.09±0.26	1.51±0.17	1.49±0.08	1.84±0.12	2.55±0.25	7.12±0.37
TWIN 6	1.24±0.16	1.15±0.62	1.35±0.24	1.12±0.13	1.25±0.25	1.02±0.02	1.00±0.00	1.20±0.09	2.75±0.23
Overall mean	3.11±0.16	1.24±0.06	2.26±0.10	2.81±0.11	2.09±0.10	1.31±0.06	1.83±0.08	3.00±0.13	6.17±0.19

group TWIN 4 is significantly lower than for TWIN 2 and TWIN 3.

The N1-species diversity for the eight dominant families, together with the N1-family diversity of the nematode community in the six station groups are presented in Table 3. Species diversity is highest in the Chromadoridae, followed by the Xyalidae, Desmodoridae, Cyatholaimidae, Microlaimidae, Thoracostomopsidae, Oncholaimidae and Comesomatidae.

Significant differences between the six station groups are noted in Table 4. The species diversity within eight families shows significant differences between station groups, which are not different in their overall species diversity. The station groups of the southern part of the area (TWIN 1 and TWIN 2) are not different in terms of species diversity but differ on the basis of the species diversity within the Chromadoridae, the Cyatholaimidae, the Microlaimidae and the Xyalidae. For the four families, diversity is higher in TWIN 2 (station group with the most coarse sediment : Md=375 μm and 27% gravel).

The open sea area of the south (TWIN 2) differs from the open sea area in the north (TWIN 3) mainly on the basis of species diversity within the Chromadoridae and the Cyatholaimidae, which is highest in TWIN 2.

Differences between the two open sea areas in the north (TWIN 3 and TWIN 4) are reflected in the diversity of the Oncholaimidae and the Xyalidae (both highest in TWIN 3) and the species evenness of the total nematode community.

The coastal stations (TWIN 5 and TWIN 6) differ in diversity from the open sea stations. However, the diversity within the Thoracostomospidae and the Xyalidae is similar for TWIN 5 and the open sea stations (TWIN 1 to TWIN 4).

The stations along the Belgian east coast (TWIN 6) are characterized by very low diversity, as well for the whole community as for the diversity within the eight important families.

The N1 species diversity within the four feeding types (1A: selective deposit-feeders; 1B: non-selective deposit-feeders; 2A: epigrowth-feeders; 2B: predators/omnivores) was calculated for the different samples and mean values for the six station groups are given in Table 5.

The diversity of the epigrowth-feeders (2A) is highest (see also WARWICK, 1982), followed by the diversity of the non-selective deposit-feeders, the predators-omnivores and the selective deposit-feeders. This general trend is mainly caused by the distribution of the species within the four feeding types of the com-

TABLE 4

Multiple comparison (after a significant Kruskal-Wallis oneway analysis of variance) of the N_1-diversity coefficients of eight families between the six Twinspan station groups.

	CHROM	*COMES*	*CYATH*	*DESMOD*	*MICROL*	*ONCHOL*	*THORAC*	*YXAL*	*Fam.tot.*
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	41.37	62.40	20.73	32.07	16.79	20.48	10.23	53.07	47.20
cases	89	85	80	86	83	76	78	101	102
sign.	***	***	***	***	**	***	***	***	***

munities in the open sea area (TWIN 1 to TWIN 4). The overall trophic diversity (F.T.) of the communities is similar for TWIN 1 to TWIN 4, intermediate for TWIN 5 (because of a low diversity of 1A) and very low in TWIN 6 (because of a high dominance of 1B). Significant differences between the six station groups are noted in Table 6. The N1 total species diversity is very highly significantly positively correlated with the diversity within the four feeding types separately; *i.e.* the total diversity increases with an increasing diversity within the feeding types.

The high species diversity of the nematode communities in the open sea area of the Southern Bight is reflected in a high trophic diversity too; *i.e.* the diversity in each feeding type increases with the total diversity. The non-selective deposit-feeders are most successful in the area off the Belgian coast, in comparison with the other trophic groups which are nearly absent in this area, where the total species diversity is also very low. But, the species diversity within 1B in TWIN 6 is nevertheless significantly lower than in the other areas.

The N1 species diversity of the total community and the N1 species diversity within each of the four feeding types is significantly correlated with the median of the sand fraction and the amount of silt *i.e.* diversity increases as the median of the sand fraction increases and with a decreasing silt content (Spearman rank correlation coefficient at the 0.001 level). The same trends are present in the diversity within the Chromadoridae, Cyatholaimidae, Desmodoridae, Microlaimidae and Xyalidae. The family diversity is also correlated in the same way with the sediment characteristics. The Comesomatidae, Oncholaimidae and the Thoracostomopsidae (all three families have low diversity values in all stations) are not much influenced by the sediment characteristics.

4. DISCUSSION

The highest known species diversity for nematode communities is recorded from deep sea areas in the Golf of Gascogne (DINET & VIVIER, 1977; H'= 5.24-6.67 bits/ind.); lowest values are found in polluted subtidal muddy communities of the Southern Bight (H'=0.00 in some stations of TWIN 1).

The similar diversity within one region (*e.g.* similar total species diversity in the four off-shore station groups TWIN 1 to TWIN 4) and between geographically disjunct regions (compare E. Atlantic or European values (*e.g.* WARWICK & BUCHANAN, 1970; LORENZEN, 1974; JUARIO, 1975; BOUCHER, 1980; GOURBAULT, 1981) with W Atlantic or American values (*e.g.* TIETJEN, 1977) suggests that comparable diversities can be anticipated in most shallow sedimentary biotopes. Perhaps there is a standard range which most shallow-water nematode communities may be expected to attain structurally.

In the open sea area of the Southern Bight of the North Sea, it is very probable that the nematode communities are in a state of nonequilibrium, where a dynamic balance is established between the rate of competitive displacement and the frequency of population reduction, which results in a constant level of species diversity. The four trophic types are rather numerous and diverse within the area. However, there are small but interesting differences between the four station groups in the open sea area. TWIN 1, 2 and 3 have communities with the highest mean trophic diversity, while TWIN 4 has a less diverse trophic structure. TWIN 4 stations are localized in a dumping area of TiO_2waste. It is possible that the lower diversity in trophic structure in this area (in comparison with adjacent areas) may indicate the effect of irregular environmental disturbance caused by pollution. The trophic structure of a community has been used to

TABLE 5

Mean values (±SE) of the N_1-diversity coefficient for the species composition of the different feeding types (1A to 2B); FT indicates the N_1-diversity for the community based on the relative abundance of the four feeding types; the N_1-species diversity is also included.

	1A	*1B*	*2A*	*2B*	*FT*	*Species*
TWIN 1	4.88±0.88	5.84±0.61	5.96±1.05	4.30±0.55	3.41±0.17	18.40±2.44
TWIN 2	4.78±0.89	5.22±0.61	9.26±0.99	5.06±0.65	3.21±0.12	21.88±1.89
TWIN 3	4.52±0.41	5.33±0.23	7.85±0.55	5.79±0.46	3.27±0.09	21.39±1.20
TWIN 4	3.23±0.32	5.75±0.53	7.63±0.42	4.81±0.36	3.06±0.10	17.67±1.32
TWIN 5	2.01±0.30	4.97±0.39	4.74±0.53	4.50±0.49	2.86±0.14	12.53±1.00
TWIN 6	1.00±0.17	2.36±0.21	1.32±0.21	1.02±0.21	1.27±0.14	3.17±0.44
Overall mean	3.10±0.23	4.71±0.17	5.81±0.24	4.09±0.17	2.73±0.10	14.95±0.52

TABLE 6

Multiple comparison (after a significant Kruskal-Wallis oneway analysis of variance) of the N_1-diversity coefficient of the four feeding types and the relative abundance of the four feeding types (FT) between the six Twinspan station groups. (+ is sign. diff. at the p=0.05 level).

	1A	*1B*	*2A*	*2B*	*FT*
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	-	+	+	+	+

predict stability (MAY, 1973); a trophically more diverse community would be more stable.

The coastal area is in several aspects (environmental and biological) divided in two distinct regions: the coastal area off the Dutch coast together with a few stations on the Belgian west coast (TWIN 5) and the rest of the Belgian coast (TWIN 6).

The relationship between environmental stability (or disturbance), stability and species diversity of the nematode communities in the Southern Bight can be stated as follows. The following characteristics may be responsible for the higher diversity in the open sea area (TWIN 1 to TWIN 4) compared with the coastal zone: - habitat heterogeneity (clean well sorted fine to coarse sand) (following the arguments of PAINE, 1966 and CONNELL, 1975) - reduced availability of food (*cf.* HUSTON, 1979) - low productivities (low densities; low population growth rates) (*cf.* HUSTON, 1979).

The reduced species diversity in the coastal areas is probably caused by a combination of factors opposite to those in the open sea area habitat heterogeneity is very much reduced, which is reflected in the higher sorting of the sand fraction and the increased amount of fine particles (especially along the Belgian coast); food enrichment (esp. org C and chl a, see VINCX *et al.*, in press) is also much higher along the coast, with extreme high values off the Belgian coast.

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