Jan Vanaverbeke, Maaike Steyaert, Wendy Bonne & Magda Vincx

3. Three decades of meiobenthos research on the Belgian Continental Shelf: an overview

3.1. Introduction and definition

Meiofauna are benthic organisms passing a 1mm sieve and being retained on a 38µm sieve. Dominant taxa within the meiobenthos are nematodes and harpacticoid copepods, which reach very high densities in soft sediments. Other taxa include kinorhynchs, turbellarians, interstitial polychaetes and many others (Plate 1). Meiobenthos samples are usually collected using boxcorers or reineck boxcorers. These are subsequently subsampled using smaller cores (surface 10cm^2), from which the top 10-20 centimetres are studied.

Plate 1. Meiofauna taxa

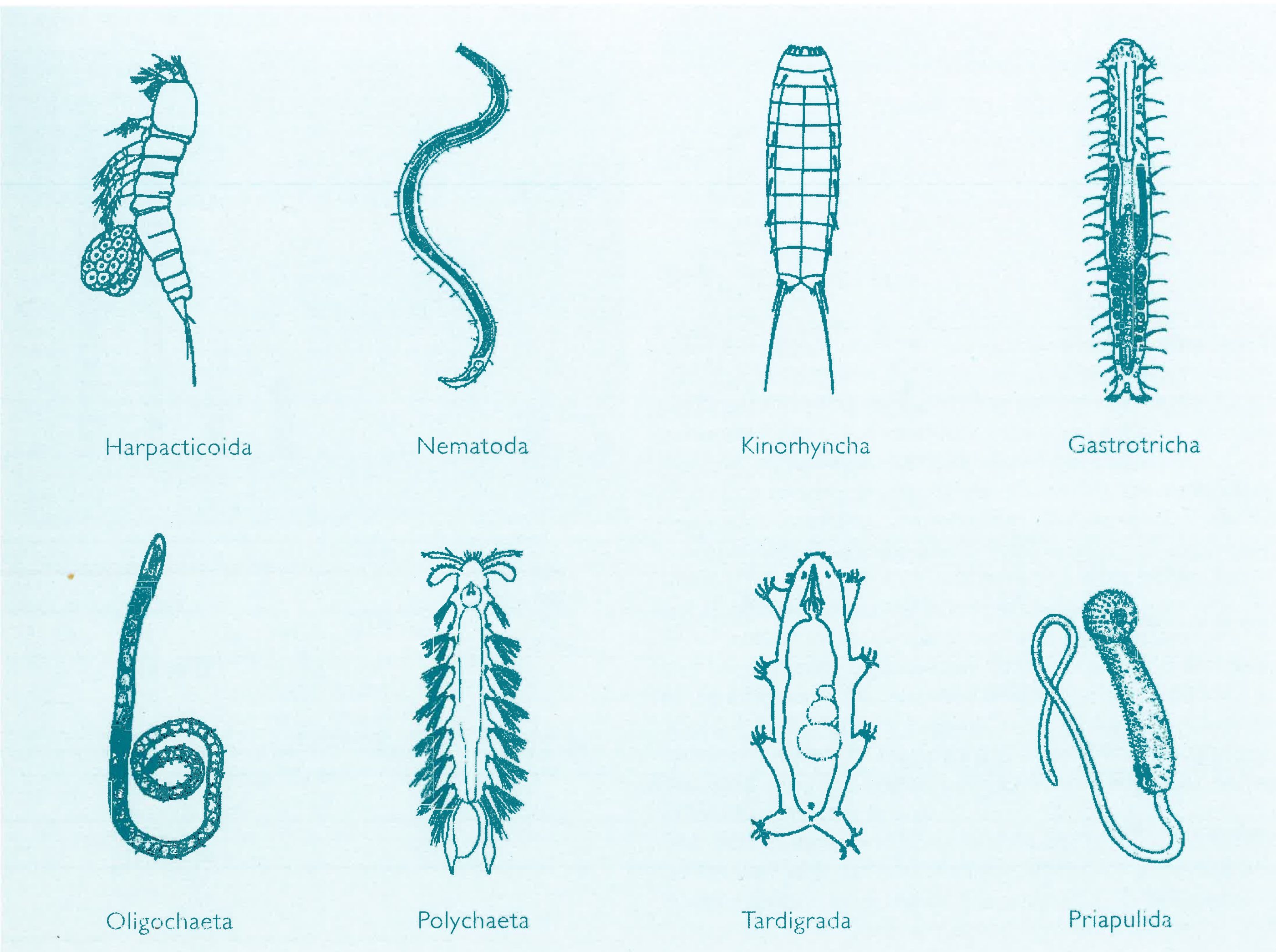

Table 1. Summary of meiobenthos literature of the BCS. Maximum and minimum densities, biomass and diversity numbers N_0 and N_1 are given per zone and per taxonomic group. (nema = nematodes; harp = harpacticoid copepods; total = total meiobenthos)

Reference	**Zone**	**Taxa**	**Density (ind./10cm²)**	**Biomass (gC/m²)**	**N_0**	**N_1**
Decraemer 1972	2	nema			2-38	1.12-9.20
Heip & Decraemer 1974	1	nema			13-74	2.33-18.13
Jensen 1974	2	nema			25-31	13.80-18.40
Claeys 1979	3	nema	107-1836	0.083-2.696	21-58	
		harp	34- 577	0.001-0.004	4-18	
Govaere et al. 1980	1-9	harp			0.89/st.(1,2)	1.15 (1,2)
					8.9/st (3)	3.94 (3)
					13.7/st (4-6)	6.63 (4-6)
		total	934-1261(1,2)			
			623-2735(4)			
			757-1640 (5,7)			
Heip et al. 1980	1,2	nema	300-4220(2)	0.290-0.353	4-30	
Heip et al. 1982	1,2,3	nema	2175 (1,2)	0.239 (1,2)		
			628(3)	0.071 (3)		
Willems et al. 1982	3	nema	134-1095		25-54	
		harp	35-342		5-37	
		total	186-1234			
Willems et al. unpubl. report	3	nema	58-1095		25-54	
		harp	25-342		5-37	
		total	186-1234			
Heip et al. 1983	1-9	nema	1190-1920(1,2)	0.160-0.239(1,2)	1-16/st(1,2)	
		harp			13.7/st(3)	6.49(3)
Heip et al. 1984	1,2	nema	706-2472(1)	0.090-0.250(1)	3.8-23.5(1)	
			1337-2285(2)	0.130-0.220(2)	2-11(2)	
		harp	6-45.1(1)		0.005-0.036	10(1)
			1.6-10.8(2)		7(2)	
Heip et al. 1985	1,2	nema	336-2710(1)	0.160-0.239(1)	11-16(1)	
			203-4631(2)	0.189(2)	3-8(2)	
		harp			2-8(1)	
					0-1(2)	
Huys et al. 1986	2	harp			8-20	
Chen 1987	1,2,3,6,9	nema	787(1)	0.149(1)	38(1)	15.83(1)
			1934(2)	0.260(2)	9(2)	4.95(2)
			173-454(3)	0.020-0.028(3)	32-55(3)	7.19-37.76(3)
			639(6)	0.101(6)	55(6)	33.85(6)
			254(9)	0.026(9)	65(9)	40.58(9)
		harp	315(1)		11(1)	2.42(1)
			63(2)		1(2)	1.00(2)
			120-267(3)		9-25(3)	6.20-14.90(3)
			50(6)		12(6)	6.58(6)
			207(9)		33(9)	18.95(9)
		total	1417(1)			
			2318(2)			
			441-806(3)			
			767(6)			
			551(9)			
Vandenberghe 1987	6	nema	358-3781		37-56	
		harp	44-260			
		total	819-4727			
Herman 1989	1,2	nema	706-2758(1)			
			383-4631(2)			
		harp	16.6-121.1(1)	0.010-0.070(1)	1.4-11.95(1)	1.09-2.89(1)
			0.9-121.2(2)	0.001-0.010(2)	1.3-3.8(2)	1.03-1.51
		total	750-2795(1)			
			210-3087(2)			
Vincx 1989	2	nema	55-5610		3-16	
Vincx & Herman 1989	1,2,3,4	nema	948-1509	0.092-0.231		
	6,8,9	harp	20-70	0.004-0.020		
Heip et al. 1990	1-9	nema	1350(1+2)	0.070	5(2)	
		harp		0.008		
Vincx 1990	1,2,3,4	nema			7.6/st(1,2)	3.15-88.00
	6,8,9				30.3(3)	
					22.7(4)	
					32.3-33(6,9)	
Huys et al. 1992	North Sea	harp				5-29
Steyaert et al. 1994	1,2	nema	2528-3268(1)			
			346-1083(2)			
Steyaert et al. 1996	1,2	nema				2.00-7.00(1)
						1.50-6.50(2)

Table 1 shows literature data collected up to present on the BCS. Densities are expressed as ind./10cm². Diversity is expressed as Hill's numbers N_0 and N_1 (Hill 1973). These numbers were calculated from the original data when possible. The Shannon-Wiener diversity index H' was often used in earlier studies, but Heip et al. (1988) preferred the use of Hill's numbers to express benthic diversity. Total biomass values are listed (or recalculated) in gC/m². The C-content of a nematode was assumed to be 0.42*dry weight, the estimated conversion factor for harpacticoid copepods was 0.4*dry weight (C. Neira, pers. comm.).
For some studies, it was not possible to find out which area has been investigated. These studies were therefore not included in Table 1. Some of the listed results not only apply for the BCS but also include data from stations outside the BCS.

3.2. Results

Figure 3 shows that most studies were conducted in the near coastal area. During the history of Belgian meiobenthos research, 68 stations were visited in zone 1 and 58 stations in zone 2. In zone 3, only 10 stations, all on the Kwinte Bank, were investigated while in deeper areas even less research was conducted. No data were found from zone 5 and 7.

NUMBER OF MEIOFAUNA STATIONS PER ZONE

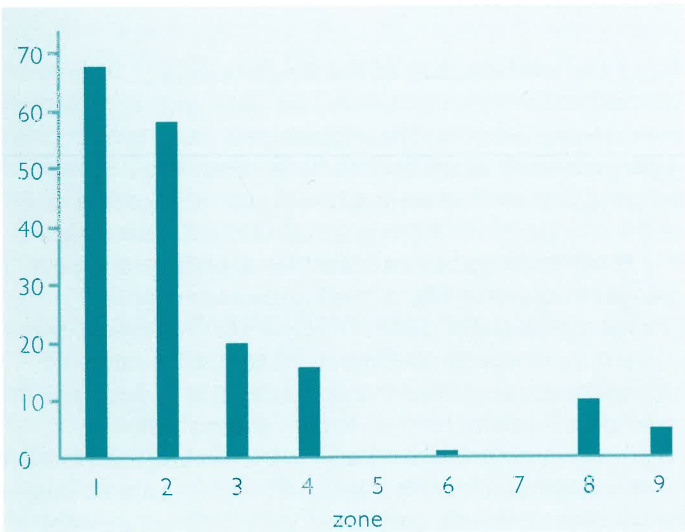

Figure 3. Intensity of meiobenthos studies on the BCS.

Mean meiobenthos densities don't differ much and fluctuate between 1000 and 1500 ind./10cm² (Fig. 4). The mean densities on the Kwinte Bank (zone 3) are however much lower.
Despite the absence of any density related trend, a clear pattern in diversity could be found. Diversity within the nematode communities clearly increases with increasing distance from the shore (Fig. 5). A fivefold increase in average species number per station was observed between the inshore and "offshore" zones. The harpacticoid copepod diversity showed a similar pattern (Fig. 6). Here, the data suggest an increase in the mean number of species per station with a factor 30 between zone 1 and 9.

AVERAGE MEIOBENTHOS DENSITY PER ZONE

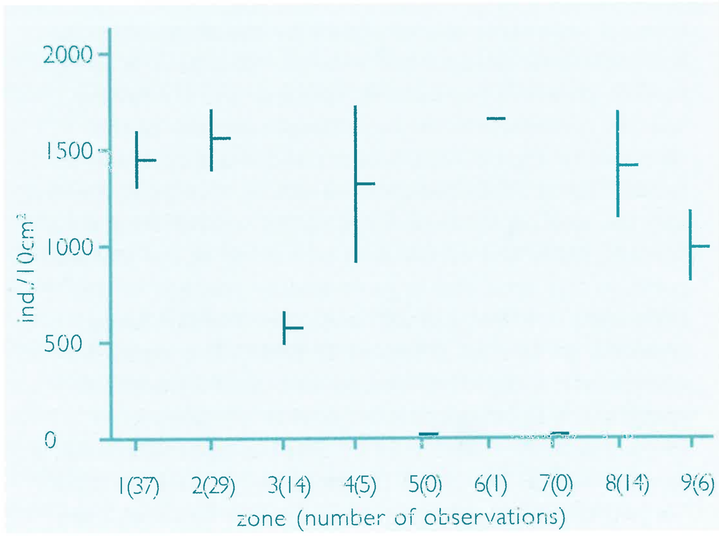

Figure 4. Average meiobenthos densities (±standard error).
The total number of observations is indicated between brackets.

3.3. Discussion

Care is needed when comparing densities, biomass values and species richness reported by several authors. Different sampling methods (e.g. Van Veen grab, Reineck boxcorer) yield incomparable data (certainly for absolute densities). However, the data used here still allow detecting general trends. Diversity indices are depending upon total sampling size, which in turn depends upon the methodology (sampling equipment, number of stations, number of replicates,...) but form the most objective criterion for comparing different areas.
The increase in species diversity within the nematode and harpacticoid communities from zone 1 to 9 still has to be confirmed by new data originating from stations in zones 4 to 7. Figure 5 suggests that the highest values for nematode diversity are reached in zone 6. In addition, copepod diversity might reach its maximum closer to the coast than in zone 9.
The lack of a pattern in meiofauna density (Fig. 4) should be treated with caution. Mean densities for zone 4, 8 and 9 were mainly collected by Govaere et al. (1980) who used a Van Veen Grab, a method underestimating

meiobenthos density. The absence of a density zonation pattern could further be due to the sampling methodology applied by Willems et al. (1982) for the Kwinte Bank (zone 3). These authors investigated only the sediment down to a depth of 10 cm, while in these kind of well-aerated sediments the fauna can penetrate the sediment down to a depth of 20 cm or more. When comparing their values with cores investigated to 20cm sediment depth, it seemed that they only found 65% of the total fauna.
Based on harpacticoid communities, Van Damme & Heip (1977), followed by Govaere et al. (1980), subdivided the BCS in three zones: a coastal area (< 10 m depth) with a relatively poor community (0.89 species/station, N_1=1.13), an open sea community (> 20 m) with a rich community (13.7 species/station, N_1=6.63) and a transition zone in between with intermediate values (8.9 species/station, N_1=3.94).
Coastal sediments are inhabited by the *Microarthridion littorale-Halectinosoma herdmani*-community. The large surface-dwellers (epibenthic species) and burrowing species (some endobenthic ectinosomatids) of this community are detritus feeders and most common in muddy sands. *Halectinosoma herdmani*, a large epibenthic species, and *Leptastacus laticaudatus*, a small interstitial species, typify the community occurring in the transition zone. In this area, the organic matter content of the sediments is lower, but stations often contain large amounts of detritus (Heip et al. 1983). The open sea community is characterised by two small interstitial species: the *Leptastacus laticaudatus- Paramesochra helgolandica*-community. Since small species dominate, a low biomass is recorded (Huys et al. 1984). Interstitial harpacticoids are grazers, require clean sands and are completely absent in sediments with mud content (Heip 1980). These typical interstitial species of the families Paramesochridae and Cylindropsyllidae form a homogeneous ecological group together with some species of Ectinosomatidae, Diosaccidae and Ameiridae (Heip et al. 1990).
Heip et al. (1984) used both the harpacticoid and nematode community data to subdivide the coastal area in an eastern and a western part, coinciding with the coastal areas used for this synthesis. The eastern area showed less species-rich nematode and copepod communities. Several authors (Herman et al. 1985, Herman 1989, Vincx & Herman 1989) confirmed this. Meiobenthos communities are very well related to the sediment structure. Fine to medium coarse sand dominate the heterogeneous west coast, while at the eastern part the sediment consists of fine to very fine sands with a high mud content. Yet, the copepod community of the coastal zone is not closely associated with sediment characteristics (Heip 1980).
Comparing the nematode diversity of comparable sediments of other European coastal areas, it became clear that the nematode community of the east coast is extremely impoverished. Sediment composition cannot act as the sole responsible factor for this pattern (Vincx & Herman 1989). The high mud content in the east coast sediments originates from the Westerschelde estuary causing a high amount of organic and inorganic pollution (Vincx & Herman 1989). At the muddy stations of the eastern Belgian coastal area, less than five copepod species are found, all being large epibenthic species.

AVERAGE NUMBER OF NEMATODA SPECIES PER ZONE

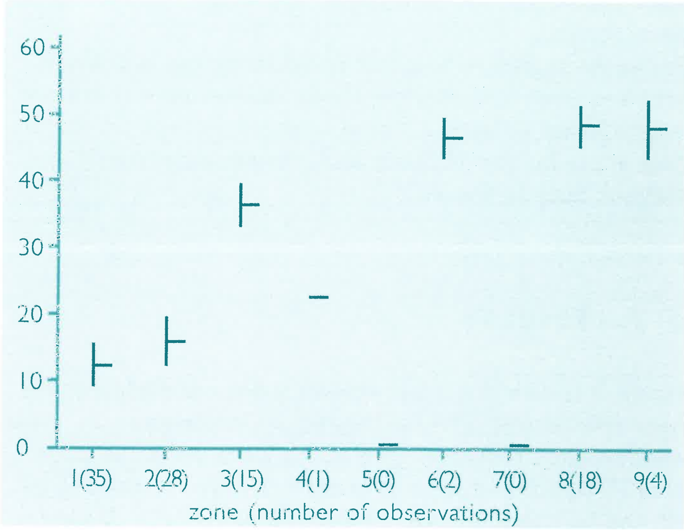

FIGURE 5. AVERAGE NUMBER OF NEMATODE SPECIES PER STATION PER ZONE (±STANDARD ERROR). THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

Along the western part of the Belgian coast, *Microarthridion littorale* is often the only species recorded from muddy localities. The harpacticoid fauna is also impoverished in sandy sediments on both sides of the Belgian coast and corresponds well with the community of the transition zone (Heip et al. 1990). Recent research in a few coastal stations allowed for assessing long-term changes in the diversity of nematode communities (Steyaert et al. 1994, 1995, 1996, 1999). The overall trend was still valid: coarser sediments, with a wide range of microhabitats, contained more species than finer grained sediments. However, the diversity of nematode communities on a microscale (e.g. the vertical distribution of nematode communities within 10cm²) in an east coast station was positively correlated with the mud content of the sediment. This is due to the higher diversity within non-selective deposit feeders. These species react on an elevated deposition of organic matter associated with fine sediments. This correlation was only established in spring, when oxygen penetrates deeper into the sediment. The relationship disappeared when the sediment turned anaerobic. These findings demonstrate the seasonality of nematode diversity in fine-grained sediments. In contrast, there is a constant high diversity in coarse sediments, since oxygen is always present in the large interstitia. The most surprising result however, was the fact that near the Westerschelde mouth, a shift towards richer nematode communities occurred when compared to the reports written in the eighties (cf. Vincx 1986).

AVERAGE NUMBER OF HARPACTICOIDA SPECIES PER ZONE

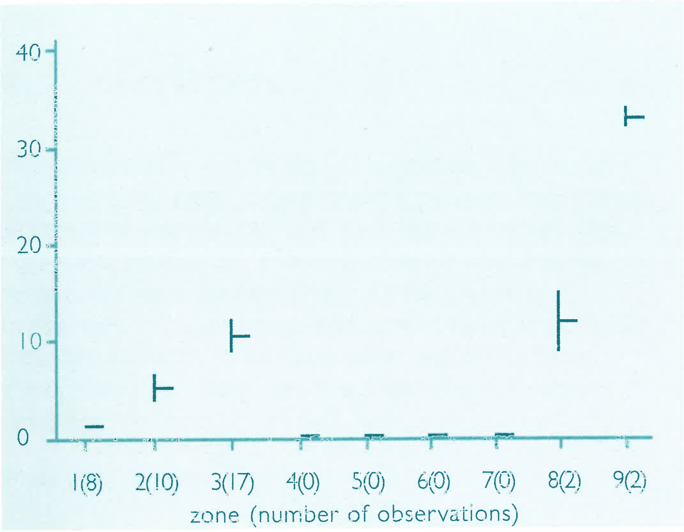

Figure 6. Average number of harpacticoid species per station per zone (±standard error). The total number of observations is indicated between brackets.

Vincx et al. (1990) and Vincx (1990) studied the nematode communities of 120 stations in the Southern Bight of the North Sea including both the Belgian and the Dutch Continental Shelf. According to these studies, the BCS should be divided into 5 areas. A coastal area, coinciding with zones 1 and 2, is separated from a transition area, covering zones 4 and 6, which extends onto the Dutch coast. The Kwinte Bank area (zone 3) had a separate community and formed an island within the transition area. Further offshore, 2 areas were distinguished from west to east, the latter one continuing into the deeper coastal waters in front of the Dutch Delta (the Voordelta-area). The coastal area is characterised by a low nematode diversity compared to the other areas (N_0=7.6). The nematode community here was dominated by *Ascolaimus* sp.1, *Daptonema tenuispiculum* and *Sabatieria punctata*. In the transition area, 22.7 species/station were counted, with *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* and *Sabatieria celtica* being the most important nematode species, whereas the stations in the offshore area harboured at least 30 species. The western offshore area was characterised by a nematode community dominated by *Ptycholaimellus vincxae*, *Onyx perfectus*, *Rhips ornata*, *Rhynchonema quemer*, *Spirophorella paradoxa*, Epsilonematidae spp. and Draconematidae spp., while in the eastern part the most important species were *Chromaspirina parapontica*, *Dichromadora cucullata*, *Karkinochromadora lorenzi* and *Xyala striata*. On the Kwinte Bank, situated in the transition area, a mean number of 30.3 species per station was found. The different nematode communities were related to a specific sediment type, however, other environmental variables (e.g. temperature, salinity, chl *a* content, NO^{3-}, NH^{4+}) influenced the distribution of nematode communities as well. The prevailing clean coarse sands in both the open sea area and at the Kwinte Bank explain the high diversity. The high species diversity is reflected in the distribution of the individual nematodes over the four feeding types as defined by Wieser (1953): diversity within feeding types increases when total diversity increases. The coastal area shows a different pattern: low species diversity combined with a loss on trophic diversity. This can partly be explained by the lower habitat heterogeneity (better sorting of the sediments and a high amount of small particles), but it mainly suggests a strong organic pollution in that area.

Within zone 3, only the Kwinte Bank was studied in detail. Claeys (1979) and Willems et al. (1982) give data on the nematode and copepod communities from 10 stations on this sandbank. Harpacticoids are more diverse and more numerous in the coarse sands at the northern end of the sandbank than in the fine sands at the southern end. A total of 65 copepod species were identified.
Vincx et al. (1990) and Vincx (1990) considered the Kwinte Bank as a separate unit on the BCS, characterised by *Bathylaimus parafilicaudatus*, *Desmodora schulzi*, *Leptonemella aphanothecae* and *Onyx perfectus*. A more detailed analysis by Claeys (1979) and Willems et al. (1982) revealed the existence of three different nematode communities on the sandbank. Again, these communities reflect differences in sediment granulometry along the sandbank. Two groups show close similarity, while the third community is characterised by a high relative abundance of the nematode families Epsilonematidae and Draconematidae. This is exceptional for European 'offshore' nematode communities. Both families are adapted to an instable environment and are mostly found on beaches with strong hydrodynamic regimes. Willems et al. (1982) stated that it should be questioned whether a true sandbank community exists. In such high energetic environments, it could be possible that many species are to be considered as erratic "guests" (Wieser 1959). However, during recent research (Vanaverbeke unpubl.) on the Kwinte Bank, more or less the same nematode communities were found, including the Epsilonematidae spp. and the Draconematidae spp.. Therefore, the existence of a "Kwinte Bank nematode community", being totally different from the communities in the surrounding areas can be accepted. Claeys (1979) and Willems et al. (1982) used only 100 nematodes from each of 10 stations, originating from 1 sampling campaign. The Kwinte Bank nematode community has consequently not been fully characterised. Chen (1987) studied the nematodes from two stations on the Kwinte Bank and found significant differences in total biomass values between his stations and the ones reported in Claeys (1979) and Willems et al. (1982). Single sampling campaigns are indeed inadequate to gain a complete picture of nematode communities of a highly instable environment.

The harpacticoid copepod communities on the Kwinte Bank show high affinities with the communities from the open sea area. Food input in both systems is low as a consequence of a strong turbulence around the sandbank or of a low input from a nutrient-poor water column in the open sea. Two communities could be discerned on the Kwinte Bank. The first community is typical for coarse sandy sediments, while the other community, including many interstitial harpacticoids is usually found in well-sorted sand. The number of species recorded here is again quite variable: Claeys (1979) reports 4-18 species, Willems et al. (1982) found 5-37 species while Chen (1987) ended up with 9-25 copepod species.
Vincx (1990) found a mean value of 22.7 nematode species per station in zone 4. The channels in between the sandbanks can probably be considered as a transition zone between the species poor coastal area and the more diverse open sea area.
Vandenberghe (1987) studied one station from zone 6. In two replicates, 41 and 52 nematode species were found making the species richness in the channels between the Zeeland Banks comparable with the diversity of the deeper parts of the BCS. This station was situated north of the Thornton Bank at a greater depth than the channel stations in zone 4, explaining the difference in nematode species richness between these two zones.
Little research has been conducted in the offshore parts of the BCS (zone 8 and 9). Only Govaere et al. (1980), Chen (1987), Vandenberghe (1987), Vincx (1990) and Vincx et al. (1990) studied the meiobenthos in these areas. Their data show that the nematode diversity there is higher when compared to the coastal and transition areas. Vandenberghe (1987) recorded 37-56 species in zone 8, whereas Chen (1987) found 55 nematode species in the same area and 93 in zone 9. Chen (1987) also found the harpacticoid communities to be more diverse with increasing depth (12 harpacticoid species in zone 7, 33 species in zone 8). Based on nematode community structure, Vincx et al. (1990) divided the deeper areas in an eastern and western part. Diversity in both areas is however quite similar (east: 32.3 species/station; west: 33 species/station), but a multivariate analysis revealed major differences in the nematode community composition.
Summarising it can be stated that the BCS can be subdivided into areas with different meiobenthos species richness and community composition. The communities reflect both differences in sediment granolumetry and the high organic loading of the sediments near the Westerschelde mouth. Standardised research ought to complete the picture. Temporal variation of the meiobenthos communities has not sufficiently been reported making changes in pollution levels and their effects on benthos difficult to evaluate. The nematode community in front of the Westerschelde estuary has seemingly changed since the beginning of the 1990's, but long-term studies still need to prove this.

BIODIVERSITY OF THE BENTHOS AND THE AVIFAUNA OF THE BELGIAN COASTAL WATERS