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Spatial variation of the macrobenthos species and communities of the Belgian Continental Shelf and the relation to environmental variation.

Ine Moulaert, Kris Hostens, Hans Hillewaert and Jan Wittoeck

Macrobenthos data for the Belgian Continental Shelf were used (1) to give an overview of the spatial pattern of the different macrobenthic species and communities of the Belgian Continental Shelf and (2) to examine the influence of different environmental variables on the spatial distribution of the macrobenthos species and communities on different spatial scales. The Belgian part of the North Sea is a highly dynamic area with a continuous succession of gullies and sandbanks. A variety of human activities like sand extraction, dredge dumping and fishing also affect the ecosystem. Samples were collected in the framework of different monitoring programs during 2004 and 2005 using the same sampling techniques. Total abundance, number of species and diversity indices were calculated and used for spatial comparison. The differences in community structure were investigated through multivariate analyses. Several a-biotic variables were measured and used in statistical tests to investigate the relation with the macrobenthos on different spatial scales. Multivariate analysis distinguished five major community groups, with a clear separation between the coastal and the offshore samples. The groups were characterised by the presence and/or absence of certain species and the relative abundance of the different taxonomic and feeding type groups. The average density, species richness and diversity were highly variable within each group. The distribution patterns of certain species were clearly related to the environmental variability. Univariate measures correlated best with depth and salinity, whereas multivariate analysis identified median grain size, mud content and salinity as the major environmental variables influencing the faunal patterns.

key words: spatial variation, macrobenthos, Belgian Continental Shelf, environmental variation, spatial scale

Contact author: Moulaert Ine, ILVO-Fisheries, Institute for Agriculture and Fisheries Research, Unit Animal Sciences, Fisheries, Ankerstraat 1, 8400 Oostende, Belgium TEL: +32 059 569847
Email: ine.moulaert@ilvo.vlaanderen.be

Introduction

The macrobenthos in marine sediments plays an important role in ecosystem processes such as nutrient cycling, pollutant metabolism, dispersion and burial, and in secondary production (Snelgrove, 1998). Understanding the patterns and processes associated with this diversity is therefore of great importance for coastal zone management and conservation (Snelgrove, 1998). Identifying the processes that are important in determining the spatial patterns is complicated by a variation apparent on different scales (Thrush 1991). At the larger scale, physical environmental factors determine the broad distributional patterns of benthic organisms (Barry & Dayton, 1991). General circulation, tidal currents, sediment grain size, depth and food supply are thought to be the driving forces behind the distributions of macro-invertebrates in soft-sediment habitats (e.g. Gray 1974; Thrush, 1991; Constable, 1999; Rees et al., 1999; Sanvicente-Añorve et al., 1996; Ellingsen, 2002). At smaller scale, spatial patterns are not only modified by a-biotic but also by biotic factors (life cycle characteristics, predation, competition) or interactions between them (Trush, 1991; Sanvicente-Añorve et al., 2002). Information about the magnitude of variability at multiple spatial scales has potentially profound implications for our views on the relative importance of ecological processes structuring benthic populations and assemblages, the design of tools and guidelines for monitoring, as well as for management and conservation (Norén K & Lindegarth M, 2005).

The Belgian Continental Shelf (BCS) is a highly dynamic area, due to strong currents and wave action, with a mix of different sediment types, a continuous succession of gullies and sandbanks and an inflow of

freshwater from the Schelde. This results in a high variation of benthic communities and species (Degraer et al., 2006). Apart form these natural factors influencing the biodiversity, many anthropogenic activities take place all over the BCS (sand extraction, dredge dumping, fisheries,…). In order to understand the effects caused by these human activities, the natural variation, both spatial and temporal, needs to be understood. Therefore knowledge of the spatial variation and the factors causing this variation are needed on different scales, as speculations about the importance of a certain process in terms of its influence on local density and composition of a community are only meaningful with respect to certain specific spatial scales.

The macrobenthos of the BCS has been studied several times (e.g. Govaere et al., 1980; Vanosmael et al., 1982; Willems et al, 1982; Van Hoey et al., 2004). These studies mainly focused on the western coastal area and the top of the Flemish banks. Currently four subtidal communities are distinguished in the soft substrates of the BCS (Degraer et al., 2003; Van Hoey et al, 2004).

The aim of this study was (1) to give an overview of the spatial pattern of the different macrobenthic species and communities present on the BCS and (2) to examine the influence of different environmental variables on the spatial distribution of the macrobenthos on different spatial scales.

Materials and methods

Sampling

Samples were collected within the framework of different monitoring programs and thus, sampling locations are irregularly scattered over the Belgian Continental Shelf (Fig 1). Certain areas like the Hinderbanken, Thorntonbank and the Gootebank were sampled in more detail. Sampling was conducted mainly in September/October 2005. Samples from the Gootebank and the Thorntonbank were sampled in September/October 2004 and the samples from the Hinderbanken in March 2005. At every location one or three replicates were taken with a Van Veen grab (0.1m²). The macrobenthic samples were fixed in a formaldehyde-seawater solution before being washed over a 1 mm sieve in the lab and subsequently coloured with eosine. Macrobenthic specimens were sorted and identified, if possible up to species level. The sieving of the samples after fixation, implies that many small benthic invertebrates are found (e.g. Nematoda, Oligochaeta) (Degraer et al., 2007). The densities of

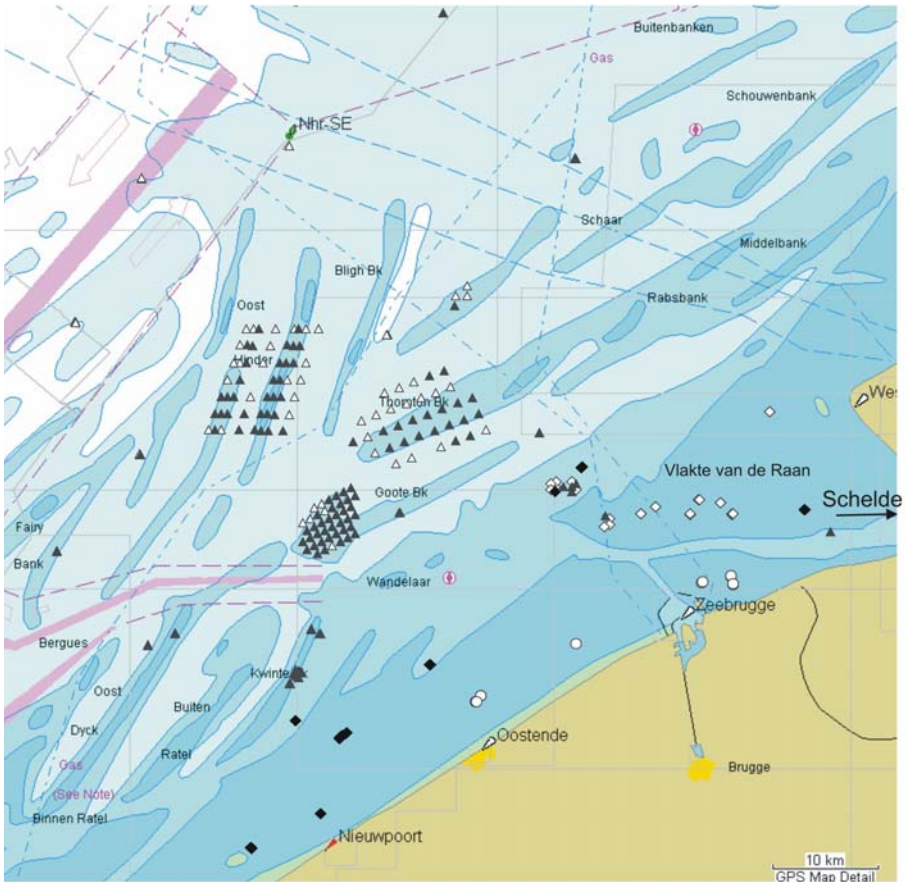


Figure 1: Map of the BCS with the sampling locations and the indication of the different groups (◇: group I; ◆: group II; ○: group III; △; group IV; ▲: group V).

these species might be largely underestimated as a major part of the individuals is even smaller. Therefore Nematoda and Oligochaeta are in this study limited to the large individuals, captured using the above mentioned sampling and processing techniques.

The main community characteristics, total abundance (/m²), number of species (/0.1m²) and Shannon-wiener diversity index, were used for spatial comparisons. Nemertina species (because of the incorrect counting) and rare taxa (species which occurred in less then 10 samples) were excluded from the dataset. Certain taxa were lumped because of difficulties with the identification (*Cirratulidae* and *Capitellidae*). Samples with only 1 or no species at all, were excluded from the data. This resulted in a dataset with 281 samples and 85 species.

Apart from the macrobenthos samples, a-biotic data were collected. Depth and salinity (Practical Salinity Scale) at the different sampling locations were measured. The depth was corrected for the tide. From every Van Veen grab a subsample was taken for further sediment analysis. Particle size distribution of sediment was analysed by dry sieving the sediment through a stack of Wentworth sieves. The sediment was characterised by the percentage of silt (<63µm), the median grain size and sorting coefficient. The amount of coarse material (>2mm) was also used in a single correlation. Geographical location (longitude and latitude) and the distance offshore were also taken into account.

Data analysis

The relationship between the abundance, number of species and diversity versus the different a-biotic parameters was tested using the Spearman Rank correlation. Because multiple tests were calculated on the same data, the Bonferroni-correction was used to adjust the significance level.

The community structure was investigated through different multivariate analyses using the reduced dataset. Two Way INdicator SPecies ANalysis (TWINSPAN) was used for grouping the samples according to their species composition (cutlevels: 0, 3, 10, 25, 100). Indicator species for each of the groups were identified through Indicator Species Analysis and the significance was tested by a Monte Carlo Test (Dufrêne and Legendre, 1997). The similarity between the samples of 1 group and dissimilarity between samples of different groups were analysed through SIMPER. Canonical Correspondence Analysis (CCA) was performed using square root transformed abundance data.

A Spearman's rank correlation was calculated between the similarity matrix based on the faunal data (4th root transformed, Bray-Curtis similarity) and the similarity matrix calculated from the set of environmental data (untransformed data, Normalised Euclidian distance). To identify the best explaining variables from the whole set of environmental data, the calculation of this correlation was repeated for all combinations of variables (Primer BIOENV-routine: Clarke & Warwick 1994). The analyses were performed using PCord (McCune and Mefford 1999), Primer (v 4.0, Plymouth Marine Laboratory, Plymouth, UK) and Statistica (Statsoft, 2003).

Results

The a-biotic environment

The depth ranged from 5 m down to 41 m. Salinity ranged from 30.93 till 34.72 with lowest values in the vicinity of the estuary and highest values recorded in the offshore and western coastal areas. Salinity had a bimodal distribution with a first peak between 31.5 and 32 and a second peak between 33.5 and 34.5. The median grain size ranged from 17 µm to 1100 µm with most stations between 100 and 400 µm. More than 50% of the samples had a median grain size between 250 and 300 µm, but this is biased because of the high number of samples in the offshore sandbank area (Hinderbanken, Gootebank and Thorntonbank). The coarser grained sediments are mainly found further offshore, but occur also in some parts of the coastal zone. More than 90% of the samples had a mud content lower than 5%. The other 10% were all recorded in the eastern coastal zone, between the harbour of Oostende and the estuary of the Schelde. The sorting coefficient of the grain size varied between 1.1 and 4.2 and showed no geographical gradient or pattern. All a-biotic parameters were significantly correlated with each other, except for the sorting of the sediment that was only significantly correlated to mud content, distance offshore and latitude (table 4).

General characterisation of the macrobenthos

Species richness per sample varied between 0 and 40 species (taking into account the whole dataset). Fortyseven or 23.5% of the total number of species were uniques (restricted to a single site). Forty-one of these unique species (87%) were singletons (only 1 individual at a site). Sixteen species occurred in more then 20% of the samples. The most common species

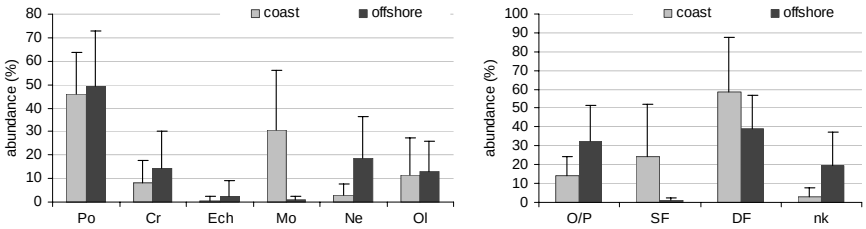


Figure 2: Relative abundance of the coastal and offshore area for the 6 major taxonomic groups (left) and for the different feeding groups (right). Po: Polychaeta; Cr: Crustacea; Ech: Echinodermata; Mo: Mollusca; Ne: Nematoda; Ol: Oligochaeta; O/P: Omnivore/Predator; SF: Suspension feeder; DF: Deposit feeder; nk: not known)

in all samples were juvenile *Nephtys* species (determined as *Nephtys* species with a maximum length of 1 cm) and Oligochaeta (both 76%), Nematoda (74%) and *Nephtys cirrosa* (64%). *Spiophanes bombyx* and *Hesionura elongata* were also very common inhabitants of the BCS with their presence in respectively 60% and 58% of the samples.

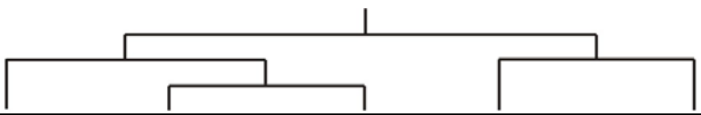
Macrobenthic density varied between 0 and 7260 ind.m^{-2}. In 37 % of the samples total abundance was higher than 1000 ind.m^{-2} and in 58% of the samples the abundance was between 100 and 1000 ind.m^{-2}. Polychaeta were the most abundant taxa.

The highest species richness and densities were found in the zone running from the western coastal area to the area 15-20 km offshore in the eastern part of the BCS. High species richness and densities were also found in the gullies of the further offshore area. The top of the sandbanks as well as the eastern coastal area had generally lower densities and diversity.

Macrobenthic species assemblages of the Belgian Continental Shelf

TWINSPAN primarily divided all samples based on the presence/absence of *Hesionura elongata, Polygordius appendiculatus, Urothoe brevicornis, Echinocyamus pussilus* and *Abra alba* (eigenvalue first division: 0.38). This resulted in an almost perfect separation of the samples from the area maximum 15km offshore (coastal zone) from samples from the more offshore part of the BCS (> 15km). In the coastal zone, Polychaeta account for 46% of the total density and mollusca 30% (Fig 2). In the offshore area, Polychaeta were also the most important taxa (49%) but Mollusca represented only 1% of the total density. Respectively 19%, 15% and 13% of the density in the offshore area was taken up by Nematoda, Crustacea and Oligocheata. In the coastal area, abundance was dominated by deposit feeders (59%). Suspension feeders represented 25% of the total abundance. The offshore area on the other hand, was dominated by deposit feeders (39%) and omnivores/predators (32%), whereas the abundance of suspension feeders was very low (1%). Because Nematoda were not determined to species level, the feeding type can therefore not be established, resulting in a high number of 'not known'.

Table 1: Characterisation of the different groups: percentage of similarity, number of samples per group, mean density (ind.m^{-2}), mean number of species per sample and mean diversity (Shannon-wiener) and the environmental variables (mean ± standard deviation).



	GROUP I	GROUP II	GROUP III	GROUP IV	GROUP V
% of similarity	46.9	51.4	45.6	50.0	40.9
number of samples in group	31	27	16	66	138
mean density	671.9 ± 520.2	3066.3 ± 1786.9	787.5 ± 624.9	1221.2 ± 976.2	823.8 ± 702.1
mean number of species	11.1 ± 2.9	26.8 ± 7.3	6.3 ± 2.7	14.5 ± 5.1	13.4 ± 5.7
mean diversity	2.46 ± 0.67	3.26 ± 0.45	1.45 ± 0.34	2.63 ± 0.68	2.79 ± 0.67
mean distance	12.3 ± 2.9	9.2 ± 4.4	3.8 ± 0.7	37.2 ± 11.4	28.6 ± 9.9
mean depth	8.8 ± 4.7	14.8 ± 3.2	8.1 ± 2.7	27.9 ± 8.3	22.3 ± 6.9
mean salinity	31.8 ± 0.1	33.5 ± 1.1	31.8 ± 0.6	34.2 ± 0.5	33.9 ± 0.7
mean mud content	1.92 ± 1.49	8.54 ± 8.90	50.87 ± 36.64	1.70 ± 3.90	1.09 ± 0.40
mean median grain size	164 ± 34	172 ± 47	192 ± 296	327 ± 80	279 ± 43
mean sorting grain size	1.42 ± 0.33	2.16 ± 0.80	2.91 ± 0.43	1.91 ± 0.65	1.54 ± 0.23

Table 2: Dominant and Indicator species per group with the species' average density (ind.m^{-2}) in the group and the Indicator value.

GROUP I	Density	GROUP II	Density	GROUP III	Density	GROUP IV	Density	GROUP V	Density
Ensis directus	363 (54%)	*Abra alba*	449 (15%)	*Cirratulidae spp.*	368 (47%)	*Nematoda*	380 (31%)	*Nematoda*	167 (20%)
Nephtys spp.	52 (8%)	*Heteromastus filiformis*	414 (14%)	*Oligochaeta*	298 (38%)	*Polygordius appendiculatus*	212 (18%)	*Oligochaeta*	125 (15%)
Magelona johnstoni	43 (7%)	*Scoloplos armiger*	386 (13%)			*Oligochaeta*	199 (16%)	*Hesionura elongata*	77 (9%)
Nepthys cirrosa	37 (6%)	*Oligochaeta*	345 (11%)			*Hesionura elongata*	99 (8%)	*Urothoe brevicornis*	71 (9%)
Bathyporeia elegans	31 (5%)	*Nematoda*	217 (7%)			*Echinocyamus pussilus*	71 (6%)	*Nephtys spp.*	60 (7%)
		Magelona johnstoni	171 (6%)					*Spiophanes bombyx*	59 (7%)
Indicator species	Ind value	indicator species	Ind value	indicator species	Ind value	indicator species	Ind value	indicator species	Ind value
Ensis directus	46	*Abra alba*	75	*Cirratulidae spp.*	71	*Polygordius appendiculatus*	69	*Urothoe brevicornis*	49
Bathyporeia elegans	38	*Mysella bidendata*	75	*Streblospio benedicti*	51	*Hesionura elongata*	48	*Hesionura elongata*	36
Magelona johnstoni	31	*Heteromastus filiformis*	74	*Macoma baltica*	34	*Echinocyamus pusillus*	39	*Nephtys cirrosa*	23
Nepthys cirrosa	27	*Scoloplos armiger*	66			*Aonides paucibrachiata*	37		
						Glycera spp.	34		
						Nematoda	33		

The coastal zone was further divided into 3 major groups (Table 1). The first division (eigenvalue 0.48) splits off all stations of the *'Vlakte van de Raan'* from the other coastal stations (Group I). The *'Vlakte van de Raan'* is a shallow area at the mouth of the Schelde. The indicator species of this group are *Nephtys cirrosa* and *Ensis directus* (Table 2). The other coastal stations could further be divided in two distinct groups (eigenvalue 0.48). The major indicator species of group II are *Abra alba, Mysella bidendata,* juvenile *Glycera* spp., *Heteromastus filiformis* and *Scoloplos armiger*. These samples are located mainly in the western part of the coastal zone, but occur also in the eastern half of the coastal zone, 10-15 km offshore. Group III is characterised by a higher mud content and the major indicator species are *Cirratulidae* spp. These samples are found mainly < 5km offshore in between the harbour of Oostende and Zeebrugge and the estuary of the Schelde. (Fig 1)

The samples from the offshore area can be further divided into 2 groups, although the separation is not as clear as for the coastal zone (eigenvalue 0.17). The samples from the same group are not spatially clustered but are more or less grouped according to their position on or next to a sandbank (top or gully). The main indicator species for group IV (mainly gully stations) is *Urothoe brevicornis*. Indicator species of group V (mainly top of sandbank) are *Polygordius appendiculatus* and *Hesionura elongata*. The characteristics and indicator species of the different groups are summarized in Tables 1 and 2. Similarity between the samples of the same group was always higher then 45%. The dissimilarity between the different groups ranged between 62% and 88%. The lowest dissimilarity was found between the two offshore groups.

Results of the CCA ordination are presented in figure 3. The offshore groups (IV and V) are located on the left side of the graph, whereas group III on the opposite end of Axis 1, which was mainly correlated with depth, distance offshore and median grain size and mud content. The second axis correlated best with mud content and the third axis with salinity. Species which were mainly observed in the shallow environment with high mud content, low salinity, median grain size and close to shore, were situated at the upper right side of the plot (e.g. *Streblospio benedicti, Macoma baltica, Nephtys hombergi* and *Cirratulidae* species). On the other hand, species characteristic for deeper offshore environments with a coarser grain size were observed at the left side of the graph (e.g. *Streptosyllis websteri, Pisione remota, Brachiostoma lanceolatum* and *Tellina pygmea*).

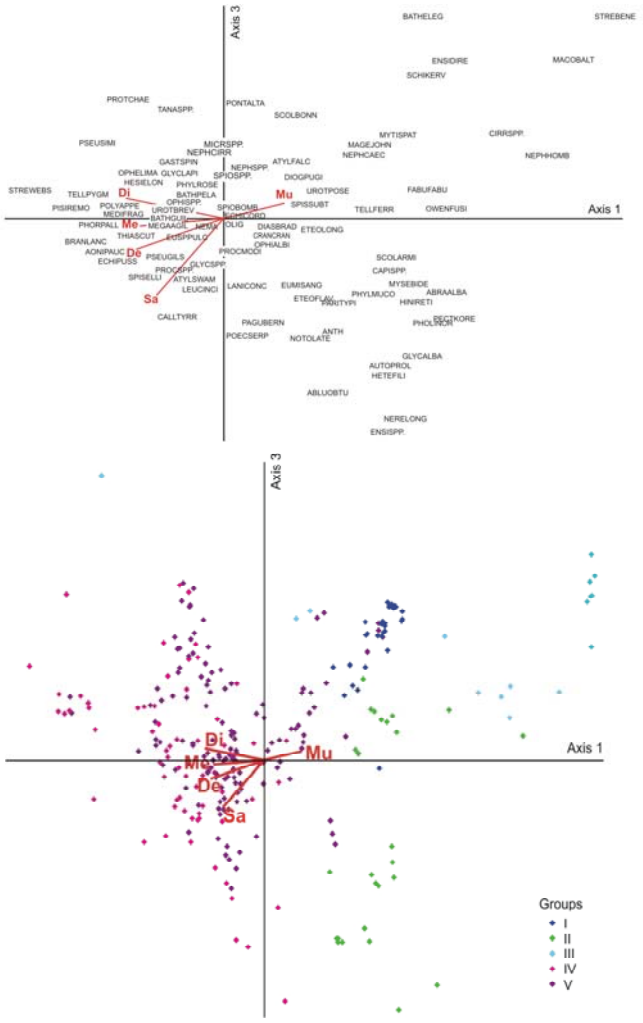


Figure 3: CCA based on the analysis of abundance data. The top figure shows the species distributions in relation to environmental variables. The bottom figure shows the different sample groups.

Table 3: Spearman Rank Correlation between environmental variables and biotic measures (*: p<0.05, **: p<0.00625 (Bonferroni-corrected)). N: number of individuals; S: number of different taxa; H: Shannon-wiener diversity index; Tot: Total; Cru: Crustacea; Ech: Echinodermata; Mol: Mollusca; Pol: Polychaeta.

	Sorting GZ	Median GZ	% Mud	Longitude	Latitude	Distance offshore	Depth	Salinity
Sorting GZ								
Median GZ	0.085							
% Mud	**0.228****	**-0.647****						
Longitude	0.019	**-0.395****	**0.233****					
Latitude	**-0.202****	**0.411****	**-0.247****	-0.114				
Distance offshore	**-0.179****	**0.589****	**-0.427****	**-0.569****	**0.833****			
Depth	0.034	**0.547****	**-0.392****	**-0.438****	**0.588****	**0.783****		
Salinity	-0.009	**0.528****	**-0.443****	**-0.427****	**0.249****	**0.543****	**0.648****	
Tot N	0.148*	-0.081	0.114	-0.041	-0.155*	-0.058	**0.241****	**0.350****
Tot S	0.119*	-0.018	0.038	-0.159*	-0.037	0.071	**0.339****	**0.379****
Tot H	0.023	-0.007	-0.051	**-0.176****	0.029	0.125*	**0.250****	**0.247****
Cru N	0.009	-0.128*	-0.030	0.038	-0.089	-0.022	**0.216****	0.174*
Ech N	**0.262****	0.031	0.197*	0.039	**0.295****	**0.262****	**0.450****	0.027
Mol N	-0.084	**-0.440****	**0.477****	**0.293****	**-0.356****	**-0.499****	**-0.470****	**-0.329****
Pol N	0.125*	-0.009	0.049	-0.151*	-0.150*	-0.011	0.159*	**0.303****
Cru S	-0.137*	-0.142*	-0.036	-0.009	-0.009	0.042	**0.263****	**0.319****
Ech S	0.115	0.146*	-0.064	**-0.261****	0.128*	**0.257****	**0.426****	**0.259****
Mol S	0.130*	**-0.301****	**0.388****	**0.175****	**-0.199****	**-0.306****	**-0.178****	-0.075
Pol S	0.119*	0.035	0.026	**-0.177****	-0.041	0.06	**0.234****	**0.288****

Correlation between the benthos and the a-biotic environment

Correlations between environmental factors and the benthic communities can be seen for sum parameters of the community as well as for the multivariate community composition.

At the scale of the whole BCS, all sum parameters (Density, number of species and diversity) were positively correlated with depth and salinity (Table 3). The highest densities were found when salinity was between 33 and 35 and depth around 15m. The number of species per sample also peaked around a depth of 15m, although the general pattern found was increasing with depth. The highest diversity values were found all over the BCS at all depth ranges, but the lowest values were recorded in the shallow areas, with low salinity. Diversity was also found to be negatively correlated to longitude. No significant correlations were found between the macrobenthic sum parameters and the median grain size or mud content. Density and species number were highest around a median grain size between 150µm and 300µm and mud content between 0 and 10%. Diversity varied at all sediment types, but at low median grain size and high mud content, only low diversity values were found. The sorting of the sediment showed a weak relation (p<0.05) with density and number of species. The density and number of species of the main taxonomic groups (Crustacea, Echinodermata, Mollusca and Polychaeta) were all significantly correlated with either depth, salinity or with both. Interesting is the highly significant correlation of the Mollusca with the distance offshore and the median grain size (both negative correlation) and with mud content and longitude (positive correlation). In contrast, Echinodermata were significantly positively correlated with the distance offshore. The number of Echinodermata was the only biotic parameter that correlated to the sorting of the sediment.

The different assemblage groups are characterised by the occurrence or absence of certain species but are not characterised by a unique density, species richness or diversity as these are highly variable within each group. The different environmental parameters of the samples within each group were also variable (Fig. 4) and these might be responsible for the variance found in density, number of species and diversity.

The density in group I was negatively correlated to sorting, median grain size, distance and depth. (Table 4) In contrast, diversity was positively correlated to distance and depth and also to salinity (+) and longitude (-). The samples from group II did not show significant correlations with the environmental variables. The density and the number of species of group III correlated with the distance offshore (+) and the diversity correlated with longitude (-). For the samples of Groups IV (mainly offshore gullies) and V (mainly offshore sandbanks) a significant correlation was found between density and number of species and depth and salinity. The number of species found in the samples of group V also showed a significant correlation with gravel.

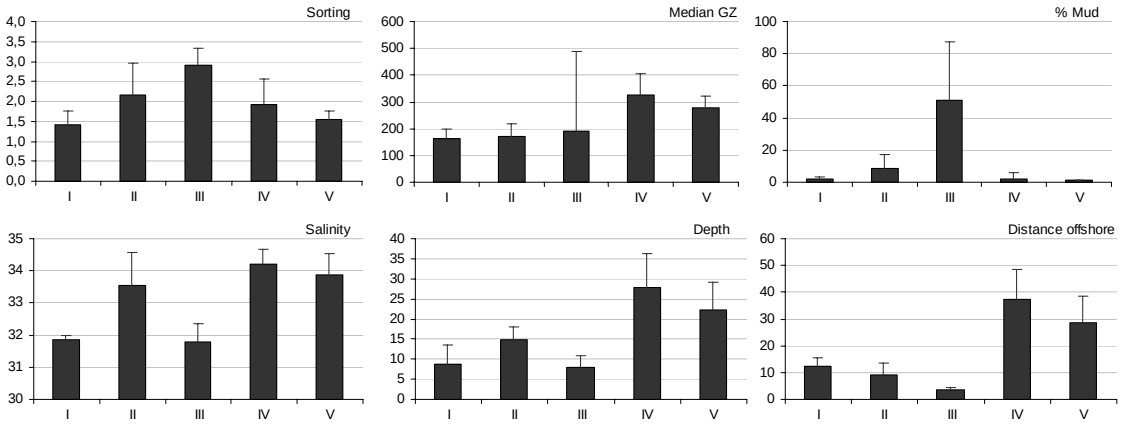


Figure 4: The environmental variables for all samples per groups (average ± standard deviation).

At a different scale, combining only the samples from the Hinderbanken, all macrobenthic parameters (total abundance, number of species and diversity) were significantly correlated to depth (+) and sorting of the sediment (+) but not to median grain size or mud content. (Table 5). Samples of the Thorntonbank area indicated a significant correlation of both density and species number with depth (+). Diversity was correlated with distance offshore and latitude (+). For the samples of the Gootebank area only the density was related to depth (+). Looking at the samples from the near shore area (< 10km) significant correlations were found between all sum parameters and positioning, distance offshore, depth and salinity, but no relation with the sediment characteristics.

The Spearman Rank correlations of single species to the environmental factors indicates a significant correlation between the densities of single species to certain environmental parameters. But because of the high number of zero values in the densities of species, this is not always a reliable analysis. A habitat preference analysis of the top 26 species did result for certain species in a clear delineation (Table 6). Species like *Hesionura elongata, Polygordius appendiculatus, Urothoe brevicornis* and *Echinocyamus pusillus* were not present in samples from locations < 16 km to the coast, a median grain size below 200µm and a depth lower than 12m. Some bivalves like *Abra alba, Ensis directus* and *Mysella bidendata* and some polychaetes like *Heteromastus filiformis* and *Scoloplos armiger* were absent from samples with a median grain size higher than 300µm or a water depth more than 24m. Other species like *Nephtys* species, *Spio* species and *Spiophanes bombyx* occured in a wide range of environments. *Cirratulidae* species were the only species with highest abundance in a muddy environment (mud content > 20%).

Table 4: Spearman Rank Correlation between environmental variables and biotic measures (*: p<0.05, **: p<0.00625 for groups I, II and III and p<0.00556 for groups IV and V (Bonferroni-corrected))

	Sorting GZ	Median GZ	% Gravel	% Mud	Longitude	Latitude	Distance offshore	Depth	Salinity
Group 1 (n=31)									
Density	**-0,545****	**-0,509****		-0,064	0,468*	-0,292	**-0,502****	**-0,696****	-0,409*
Number of species	0,016	-0,009		-0,032	-0,049	0,219	0,422*	0,233	0,424*
Diversity	0,348	0,269		0,060	**-0,563****	0,295	**0,651****	**0,626****	**0,673****
Group 2 (n=27)									
Density	-0.037	0.212		0.021	-0.357	-0.321	-0.042	0.378	0.405*
Number of species	-0.227	0.115		-0.167	-0.353	-0.321	-0.202	0.078	0.289
Diversity	-0.078	0.137		-0.094	-0.040	-0.196	-0.365	-0.353	0.104
Group 3 (n=16)									
Density	0.279	-0.421		0.421	-0.445	-0.088	**0.748****	0.078	0.253
Number of species	0.373	-0.524*		0.524*	-0.614*	-0.271	**0.696****	0.226	0.252
Diversity	0.391	-0.576*		0.576*	**-0.666****	-0.538*	0.439	0.250	0.426
Group 4 (n=66)									
Density	0.081	-0.118	0.029	0.152	0.191	-0.009	-0.032	**0.357****	**0.409****
Number of species	0.115	-0.089	-0.019	0.113	0.043	0.092	0.116	**0.392****	**0.363****
Diversity	0.058	-0.039	-0.033	0.033	-0.083	0.198	0.208	0.224	0.007
Group 5 (n=138)									
Density	0.116	0.001	0.184*	-0.134	0.089	-0.160	-0.039	**0.453****	**0.389****
Number of species	0.217*	-0.056	**0.282****	-0.016	0.069	-0.047	-0.018	**0.435****	**0.241****
Diversity	0.115	-0.048	0.196*	-0.009	0.062	0.026	0.001	**0.244****	0.134

Table 5: Spearman Rank Correlation between environmental variables and biotic measures (*: p<0.05, **: p<0.00625 (Bonferroni-corrected))

	Sorting GS	Median GZ	% Mud	Longitude	Latitude	Distance offshore	Depth	Salinity
Hinderbanken (n=53)								
Density	**0.384****	-0.009	0.063	0.172	0.243	0.199	**0.690****	0.039
Number of Species	**0.468****	-0.052	0.137	0.148	0.188	0.183	**0.734****	0.047
Diversity	0.344*	-0.166	0.228	0.001	0.099	0.144	**0.502****	0.107
Gootebank (n=42)								
Density	0.407*	0.066	0.219	-0.177	0.263	0.361*	**0.557****	0.336*
Number of Species	0.199	0.136	0.088	0.179	0.312*	0.209	0.379*	0.359*
Diversity	-0.135	0.047	-0.144	0.375*	0.008	-0.200	-0.107	-0.051
Thorntonbank (n=35)								
Density	0.227	0.207	0.188	0.001	-0.084	-0.039	**0.656****	0.296
Number of Species	0.065	0.069	0.010	0.022	0.189	0.197	**0.624****	0.253
Diversity	-0.303	0.049	-0.338*	-0.014	**0.455****	**0.471****	-0.055	0.141
Coastal zone (n=42))								
Density	-0.103	0.166	-0.083	**-0.685****	**-0.581****	**0.598****	**0.532****	**0.742****
Number of Species	-0.194	0.193	-0.152	**-0.776****	**-0.657****	**0.545****	**0.587****	**0.788****
Diversity	-0.198	0.278	-0.189	**-0.677****	**-0.596****	0.402*	**0.652****	**0.689****

The rank correlations between single environmental factors and the total square-root-transformed abundance data (BIO-ENV analysis) ranged from 0.106 (latitude) to 0.517 (median grain size) (table 7i). When only taking one variable into account, median grain size showed the highest correlation with the faunal composition (0.517), followed by salinity (0,459) and mud content (0,447). The faunal pattern was best correlated to the subset of mud content, median grain size and salinity (0.605). BIO-ENV analysis for the different sampling groups separately indicated very low correlations between the environmental parameters and the faunal composition of groups IV and V (Table 7ii). The best correlations with a single environmental parameter for groups I, II and III were respectively depth (0.650), salinity (0.585) and distance (0.690). The faunal pattern of samples of group II and III were best correlated to a combination of respectively salinity and longitude (0.623) and distance and median grain size (0.750). For group I, BIOENV found that a subset of depth, sorting, median grain size and mud content (0.764) made the best correlation. The faunal pattern of the different offshore sandbank areas (Table 7iii) was best explained by a combination of depth and median grain size (Hinderbanken), median grain size, distance and depth (Thorntonbank) and sorting, longitude, salinity and depth (Gootebank), although these correlations were relatively weak (respectively 0.329, 0.369 and 0.459). In the coastal area, median grain size (0.516) was best related to the variation in faunal patterns when only taking one variable into account, whereas a combination of 5 variables (median grain size, mud content, longitude, depth and distance offshore) gave the best fit (0.640).

Table 6: Habitat preference of the top 26 species (n.l.: no limitation).

	Distance	Depth	Salinity	Median grain size
Nephtys juv.		n.l.		
Oligochaeta		n.l.		
Nematoda	n.l.	n.l.	+ 33	+ 130 µ
Nephtys cirrosa	n.l.	n.l.	n.l.	+ 130 µ
Spiophanes bombyx		n.l.		
Hesionura elongata	+ 16 km	+ 12 m	+ 33	+ 170 µ
Polygordius appendiculatus	+ 16 km	+ 12 m	+ 33	+ 270 µ
Spio spp.		n.l.		
Bathyporeia guilliamsoniana		n.l.		
Glycera spp.		n.l.		
Urothoe brevicornis	+ 16 km	+ 12 m	+ 33	+ 170 µ
Magelona johnstoni	- 20 km	- 20 m	n.l.	130 - 300 µ
Gastrosaccus spinifer		n.l.		
Scoloplos armiger	- 20 km	- 20 m	n.l.	130 - 300 µ
Eteone longa		n.l.		
Echinocyamus pussilus	+ 16 km	+ 25 m	+ 33	+ 170 µ
Bathyporeia pelagica		n.l.		
Diogenes pugilator	10-30 km	- 30 m	n.l.	n.l.
Ophiura spp.		n.l.		
Ophelia limacina	+ 16 km	n.l.	+ 33	n.l.
Thia scutellata	+ 16 km	+ 12 m	+ 33	n.l.
Tellina pygmea	+ 16 km	+ 16 m	+ 33	n.l.
Aonides paucibrachiata	+ 16 km	+ 12 m	+ 33	n.l.
Notomastus latericeus	- 10 km	n.l.	n.l.	n.l.
Cirratulidae spp.	- 10 km	- 12 m	n.l.	n.l.
Abra alba	- 20 km	10 - 20 m	+ 32	130 - 270 µ
Ensis directus	- 20 km	- 16 m	n.l.	- 170 µ
Microphthalmus species		n.l.		
Phyllodoce mucosa	- 40 km	- 25 m	n.l.	n.l.
Euspira pulchella	n.l.	+ 12 m	n.l.	n.l.
Mysella bidendata	- 20 km	n.l.	n.l.	n.l.
Brachiostoma lanceolatum	+ 25 km	+ 20 m	+ 33	+ 250 µ
Phoronis pallida	+ 16 km	+ 12 m	+ 33	n.l.
Echinocardium cordatum	n.l.	+ 10 m	n.l.	n.l.
Heteromastus filiformis	- 10 km	- 20 m	n.l.	- 270 µ

Discussion

The main objective of this study was to give an indication of the spatial variation of the macrobenthos at species and community level and to look at the relation with the spatial variation of environmental variables at different spatial scales on the Belgian Continental Shelf. The knowledge of the best related environmental parameter at a certain scale will give a good basis for future studies. For this study, data was used from different locations scattered over the Belgian

Continental Shelf, with a special attention for some offshore sandbank areas, for which a more detailed sampling was undertaken. The irregular sampling of the BCS does imply that some areas were not sampled. Nevertheless the present results give a good indication of the general patterns of the macrobenthos of the BCS and the relation to environmental variables.

General characteristics of the Macrobenthos of the Belgian Continental Shelf

The Belgian part of the North Sea is a very diverse area due to the high currents, sandbanks and the mouth of the WesterSchelde. This physically diverse marine area results in a high number of different macrobenthic species assemblages or communities on this relatively small area. A first attempt to document the macrobenthos along the onshore-offshore gradient of the BCS was given by Govaere et al. (1980), who discriminated three zones: (1) a coastal zone with a set of species-poor and density-poor communities; (2) a species-rich and density-rich transition zone; and (3) a species-rich and density poor open sea zone. Because of (1) the increase of the number of samples taken into account and (2) the wider spread distribution of the samples, Van Hoey et al. (2004) managed to give a more detailed view on the onshore/offshore diversity, abundance and community structure patterns. Contrary to Govaere et al. (1980), they concluded that the coastal area of the BCS could not be characterized solely by species- and abundance- poor communities: a wide variety from macrobenthos poor to rich stations was encountered in the coastal zone, including the stations with the highest species richness and densities (*Abra alba-Mysella bidentata* community). This is confirmed by the present study, were the difference in diversity of the coastal samples was high, with even the most diverse samples in the coastal area. The characterization of the open sea zone (15 miles offshore) by Govaere et al. (1980) as a species-rich and density-poor area, was contradicted by Van Hoey et al. (2004) who only found low densities and low species richness in the offshore area. Results from the current study of the BCS indicate that the distribution of the macrobenthic species richness and abundance along the onshore-offshore gradient followed a highly variable pattern, with also species-rich and abundance-rich stations in the offshore zone, although the samples with highest species number and abundance were recorded in the coastal zone. The highest diversity values were recorded along the whole onshore-offshore gradient. The coastal zone (important zone for Water Framework Directive) shows a clear east-west along-shore gradient, with decreasing diversity towards the east. The decrease of molluscs further offshore, agrees with the findings of Van Hoey et al. (2004).

A clear division in faunal pattern was found between the offshore and the coastal stations, which was mainly based on the presence/absence of certain interstitial species (e.g. *Hesionura elongata and Polygordius appendiculatus*). These species did not have such an importance in the study of the different communities described by Van Hoey et al. (2004) as they were not sampled in such high numbers. Due to the fixation of the samples prior to sieving in the present study, these interstitial species were found in significantly greater numbers (Degraer et al. 2007). Despite the difference in the sampling of the benthos and the lack of samples from the eastern coastal zone in the study of Van Hoey et al. (2004), similarities in the grouping of the samples could be found. Sample group II of the current study corresponds to the *Abra alba-Mysella bidendata* community described by Van Hoey et al. (2004). This community was described as the ecological most important. Results from the present study also indicate that this community has the highest densities, the highest number of different species and a high diversity. This community also has the highest percentage of bivalves which are an important food source for higher organisms.

The most important species on the '*Vlakte van de Raan'* is the Razor shell *Ensis directus*. Although this is probably a temporal situation, as in previous years several peaks in the density of this species have been reported in the area (which disappeared again the year after). Because of the presence of this species, the samples of group I were separated from the rest. *Nephtys cirrosa* is the second most important species on the '*Vlakte van de Raan'* but clearly this species can survive in a large range of habitats. It has the highest occurrence and density and lives in both offshore and coastal areas with a median grain size ranging from 50-500μm.

Group III, the community found in the eastern part of the coastal zone, has a low number of species and diversity and a variable density. All samples are located in the vicinity of the harbours of Oostende and Zeebrugge and are all characterised by a higher mud content and lower salinity. This community corresponds with the *Macoma baltica* community found by Degraer et al. (2003). *Cirratulidae* species were the most abundant species in both studies.

Table 7: Summary of results from the BIO-ENV analysis. Combinations of variables, giving the highest rs between biotic and abiotic similarity matrices; (i) best variable combinations for the whole BCS, k at a time. Bold type indicates the highest correlation. (ii) best two single variables and best overall combination for the different sample groups. (iii) best two single variables and best overall combination for the different areas.
Biotic data square root transformed, abiotic data not transformed. Similarity measure: Normalised Euclidean distance. lon: longitude; lat: latitude; mud: fraction of sediment < 0.063 mm (%); mgz: median grain size; sor: sediment sorting coefficiënt; sal: salinity; dis: distance offshore; dep: depth

(i)

k	Best variable combinations			
1	mgz(0.517)	sal (0.459)	mud (0.447)	
2	mgz, sal (0.587)	mgz, mud (0.553)	lon, mgz (0.549)	
3	**mud, mgz, sal (0.605)**	mgz, sal, sor (0.577)	Sal, lon, mgz (0.575)	lon, mud, mgz (0.571)
4	mud, mgz, sal, lon (0.596)	dis, mud, mgz, sal (0.591)	lon, sor, mgz, sal (0.585)	mud, mgz, sal, sor (0.583)

(ii)

	I	II	III	IV	V
Best single	dep (0,650) lon (0,561)	sal (0,585) lon (0,522)	dis (0,690) mgz (0,614)	mgz (0,158) dep (0,148)	sal (0,315) lon (0,307)
Best total	dep, sor, mgz, mud (0,764)	Sal, lon (0,623)	dis, mgz (0.750)	dep, sal, sor, mgz (0,258)	dep, sal, lon, mgz (0,403)

(iii)

	Hinderbanken	Gootebank	Thorntonbank	Coastal area
Best single	dep (0,271) mgz (0,250)	sor (0,354) sal (0,585)	dis (0,203) dep (0,165)	mgz (0,516) sal (0,448)
Best total	dep, mgz (0,329)	sor, lon, sal, dep (0,459)	mgz, dis, dep (0,369)	mgz, mud, lon, dis, dep (0,640)

Model base predictions of communities most likely to occur in a certain area of the BCP, based on sediment data, was developed by Degraer et al. (submitted). The communities used in the model are the ones described by Degraer et al. (2003) and Van Hoey et al. (2004). The predictions of the model correspond well for the *Abra alba* community and the *Macoma baltica* community. In some other areas, e.g. '*Vlakte van de Raan*' (group I), some disagreements were found between the predicted community and the real faunal pattern.

Relation to environmental variables at different spatial scales

A lot of research has been undertaken with the aim of defining the spatial variation of the macrobenthos and finding the driving forces structuring the faunal patterns. Interactions between species and the environment act at different spatial scales and depend on the location. For the North Sea and adjacent areas, many studies on this subject haven been done, at different levels of scale (e.g. Heip et al., 1992; Künitzer et al., 1992; Rees et al., 1999; Sanvicente-Añorve et al., 2002; Ellingsen, 2002; Desroy et al., 2002; Dauvin et al., 2004). On the scale of the whole North Sea, Heip et al. (1992) found that mainly latitude, sediment composition and chlorophyll a were related to biomass and that diversity (Hill's index) was linked with latitude. The factors structuring species distributions and assemblages of the North Sea seemed to be temperature, the influence of different water masses, the type of sediment and the food supply to the benthos (Künitzer et al., 1992). For the Eastern English Channel, Sanvicente-Añorve et al. (1996) found no spatial correlation between diversity (Shannon-wiener) and sediment, but the heterogeneity of the four benthic assemblages in the Eastern English Channel was primarily influenced by the nature of the sediment, and secondly by the velocity of bottom currents (Sanvicente-Añorve et al., 2002). In a study of the North Sea, English Channel and Celtic Sea, Rees et al. (1999) found that both number and density of taxa were related to the sorting coefficient, and the faunal pattern was best explained by a subset of tidal current strength, median grain size, longitude and sorting coefficient. The diversity (sample species richness) of samples taken along the whole Norwegian coast showed no evidence of a relationship to latitude or other environmental variables (Ellingsen en Gray, 2002).

The spatial variation of the macrobenthos of the Belgian part of the North Sea was previously studied by Van Hoey et al. (2004), although they did not analyse the relationship between the variability in the faunal patterns and environmental factors at different spatial scales. Results from the present study clearly indicate that the variability in community structure is related to different driving forces depending on the spatial scale. At the scale of the whole BCS, all sum parameters (Density, number of species and diversity) showed a significant correlation with depth and salinity. Deeper and more saline areas were characterised by higher densities, species number and

diversity. This implicates that the inflow of freshwater from the Schelde and the presence of sandbanks are important factors structuring the large scale pattern of the macrobenthos on the BCS. In contrast to the study of Van Hoey et al. (2004), the present study did not find any significant correlations between the macrobenthic sum parameters and the median grain size and mud content on the scale of the whole BCS. The sorting of the sediment correlated weakly with density and number of species. The same correlation was found by Rees et al. (1999) for the North Sea, English Channel and Celtic Seas. The density and number of species of the main taxonomic groups were correlated with depth and salinity. Molluscs were the only taxa that significantly decreased further offshore and with coarser sediments. Ellingsen (2002) also found that only molluscs were related to depth and median grain size. The faunal pattern, on the scale of the BCS, was best explained by a subset of mud content, median grain size and salinity. Median grain size and mud content together with depth were also found as the major environmental variables influencing the faunal patterns in an area off the Norwegian coast (Ellingsen, 2002). Dauvin et al. (2004) found that mud content and depth explained best the species and assemblage distribution in the Bay of Veys and Desroy et al. (2002) found that sediment and latitude accounted for a significant proportion of the observed variability in assemblage distribution patterns.

Density of the samples of group I decreased with increasing grain size, sorting, distance offshore and depth. The higher densities were mainly caused by the dominance of the invasive species *Ensis directus* (clear increase in the last few years). Therefore diversity is negatively correlated to the density. *E. directus* was clearly more abundant on top of the shallower '*Vlakte van de Raan'*, were median grain size was lower and more stable. In the areas on the slope towards the gullies, the sediment was less stable due to higher currents but also the anthropogenic impacts of the dredge dumping (disposal site S1) and the influence of the estuary of the Schelde, are believed to be responsible for the distribution of *E. directus*. The macrobenthos of the samples from group II did not show a correlation with the environmental variables, except for the relation between density and salinity. Probably other factors are affecting the variability within this community, like biotic factors out of the scope of this study (predation, competition, food supply,…). Van Hoey et al. (2005) also concluded that no correlation existed between the *Abra alba* community structure and granulometry but that the structural and functional community aspects may result from differences in (1) detrital food availability, related to input from rivers and pelagic productivity, along and across the coastline and (2) the amount of suspended matter, impoverishing the community when excessively available. A combination of salinity and longitude best explained the faunal pattern of this group. The increase of salinity and decrease of mud content towards the east resulted in a slight difference in species composition along the east-west gradient. Group III consisted mainly of samples located in anthropogenic disturbed areas (disposal sites of Oostende and Zeebrugge, and other stations in the vicinity of the harbour of Zeebrugge). Most samples that were left out of the databank before analysis, because of the presence of no or only a single species, were located in the same area. The variability found within this community could not be explained within this study, but is thought to be greatly influenced by the different disturbance factors acting on the area. For the offshore area of the BCS (Group IV, mainly offshore gullies, and V, mainly offshore sandbanks) again depth and salinity were the environmental variables best related to density and species number. The faunal pattern could only weakly be explained by the environmental factors, which indicates that other factors, not taken into account in this study, might structure these communities.

In the coastal area (all samples located within 10 km offshore) the variation in density, species richness and diversity was best explained by salinity, but also by the depth and positioning (latitude, longitude and distance offshore). The greater the distance away from the estuary of the Schelde, the higher the density and species number. Median grain size does play a more important role in the structuring of the faunal pattern in the coastal zone. In the offshore areas, the univariate measures of macrobenthos near and on top of the Hinderbanken, Thorntonbank and Gootebank were best related to depth. The faunal composition was only weakly related to the environmental variables. Here other variables are possibly causing the biotic variability (cf. conclusions for groups IV and V, to which the samples of these sandbanks belong).

Although we found some clear habitat preferences for some single species, these were only based on a single sampling period, and thus do not necessarily imply that these species will never occur or have never occurred in other areas. Species like *Hesionura elongata, Polygordius appendiculatus, Urothoe brevicornis* and *Echinocyamus pusillus* were not present in our samples from locations < 16 km to the coast, a median grain size below 200µm and a depth lower than 12m. Degraer et al. (2006) reported on the

most important macrobenthic species of the BCS and they found some of these species in the western coastal area, where areas with coarser sediments are found. These locations were not sampled in our study. Some bivalves like *Abra alba, Ensis directus* and *Mysella bidendata* and some polychaetes like *Heteromastus filiformis* and *Scoloplos armiger* were absent from our samples with a median grain size above 300µm or a water depth more than 24m. Based on long term data records Degraer et al. (2006) found these species in a wider environment. Other species like *Nephtys* species, *Spio* species and *Spiophanes bombyx* occur in a wide range of environments.

Conclusions

The faunal pattern of the BCS was best explained by a subset of mud content, median grain size and salinity, whereas univariate measures were best related to depth and salinity. Depending on the scale and the location of the area analysed, different environmental parameters were of more importance in explaining the spatial variation. Results from the present and other studies indicate that the outcome depends on the location and the scale of the area considered and also on the number of samples and number of environmental factors that were taken into account. It is also important to note that spatial patterns identified are likely to change with time. The statistical analyses indicate a certain correlation with the different parameters but certainly these a-biotic parameters can not explain everything. It is probable that factors other than those measured have an influence on the community structure. Biotic factors such as availability and abundance of benthic larvae/ adults, competition and predation may also be important in determining benthic settlement (Thrush 1991; Wu & Shin 1997).

The understanding of spatial distribution has become important in defining the sampling strategies in benthic ecology (Dauvin et al., 2004). The different relations found between the biological and environmental parameters at different scales and for the different areas, highlight the importance of the knowledge of a specific area prior to setting up a sampling strategy. The present study indicates that a base line study of a sandbank area is best done with a stratified sampling according to the depth contours as well as according to the sediment type. When doing an impact study in the coastal area, the reference area should have a similar distance from the coast, salinity range and median grain size, as these are the most influencing environmental variables in this area.

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