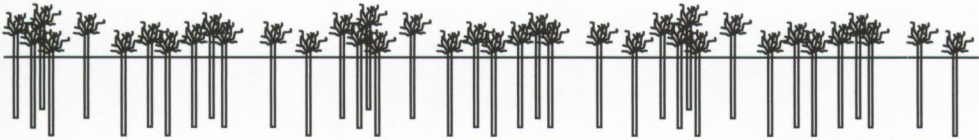

Chapter 2

Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf



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Abstract

Within the frame of different research projects, a large number of sites at the Belgian Continental Shelf (BCS) were sampled for the macrobenthos between 1994 and 2000. These samples cover a diverse range of habitats: from the sandy beaches to the open sea, from the gullies between the sandbanks to the tops of the sandbanks, and from clay to coarse sandy sediments. To investigate the large-scale spatial distribution of the macrobenthos of the Belgian Continental Shelf, the data of all these research projects - 728 samples - were combined and analysed. By means of several multivariate techniques, ten sample groups with similar macrobenthic assemblage structure were distinguished. Each sample group is found in a particular physico-chemical environment and has a specific species composition. Four sample groups are differing drastically, both in habitat and species composition, and are considered to represent four macrobenthic communities: (1) the muddy fine sand *Abra alba* – *Mysella bidentata* community is characterized by high densities and diversity, (2) the *Nephtys cirrosa* community occurs in well-sorted sandy sediments and is characterized by low densities and diversity, (3) very low densities and diversity typify the *Ophelia limacina* – *Glycera lapidum* community, which is found in coarse sandy sediments and (4) the *Eurydice pulchra* – *Scolecopsis squamata* community is typical for the upper intertidal zone of sandy beaches. Of course these macrobenthic communities are not isolated from each other, but are linked through six transitional species assemblages. The transition between the *A. alba* – *M. bidentata* community and the *N. cirrosa* community, is characterized by a reduction in the mud content and is dominated by *Magelona johnstoni*. The transition between the *N. cirrosa* and the *O. limacina* – *G. lapidum* community is distinctive by decreasing densities and coincides with a gradual transition between medium to coarse sandy sediments. From the *N. cirrosa* to the *E. pulchra* – *S. squamata* community, transitional species assemblages related to the transition from the subtidal to the intertidal environment, were found. Each community or transitional species assemblages was found over a specific range along the onshore – offshore gradient, four types can be discerned: (1) almost restricted to the near-shore area, but possible further distribution, (2) distributed over the full onshore – offshore gradient, (3) restricted to the near-shore area and (4) restricted to the sandy beach environment. The diversity pattern on the BCS follows this dividing, with species rich and poor assemblages in the near shore area to only species poor assemblages more offshore. The distribution and diversity patterns are linked to the habitat type, discerned by median grain size and mud content.

Keywords

Macrobenthos, community structure, sandy sediments, Belgian Continental Shelf

Introduction

Different soft-sediment, macrobenthic assemblages were distinguished within the Southern Bight of the North Sea and the English Channel (e.g. Glémarec, 1973; Kingston and Rachor, 1982; Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996; Olivier et al., 1996; Dauvin 1998, Degraer et al., 1999(a); Dauvin, 2000; Ghertsos et al., 2000, 2001; Desroy et al., 2002; Sanvicente-Anorve et al., 2002). The distribution of these macrobenthic communities is highly correlated with the type of sediment, which is related to a wider set of environmental conditions, such as current speed and organic content of the sediment (Gray, 1974; Creutzberg et al., 1984; Buchanan, 1984; Snelgrove and Butman, 1994). At the Belgian Continental Shelf (BCS) characterized by a highly variable and diverse topography, with strongly differing environmental conditions (Degraer et al., 1999a), a wide range of macrobenthic assemblages might thus be expected. Because of the important ecological function of the macrobenthos within the marine ecosystem function, knowledge on the macrobenthic diversity patterns is indispensable to identify priority areas for conservation and for the adjustment of human activities in the marine zone, among other (Costello, 1998).

Early descriptions (1970-1982) of the macrobenthos on the BCS discerned between three zones: a coastal zone with a set of species and abundance poor communities, a species and abundance rich transition zone, and a species rich and abundance poor open sea zone (Govaere et al., 1980; Vanosmael et al., 1982). Although numerous recent data on the macrobenthos of the BCS are available, generalized and updated information on the macrobenthic assemblages and their distribution patterns is lacking. Since 1994, numerous studies focused on the description of the temporal and spatial distribution of the macrobenthos of the BCS (including sandy beaches) are undertaken.

Yet, a clear classification and comparison between the different macrobenthic assemblages described in the different studies is very difficult. To generalize and update the knowledge on the spatial distribution of the macrobenthic assemblages, all macrobenthos data from the Belgian Continental Shelf, collected during the period 1994-2000 (728 samples), were gathered into a database and reanalyzed.

The aims of this paper are (1) to characterize the different macrobenthic communities on the Belgian Continental Shelf on the basis of their species composition, abundance, species richness and their habitat preferences (e.g. sedimentology and bathymetry); (2) to compare the macrobenthic community structure with similar communities in other parts of the North Sea; (3) to understand the relationships between these communities; (4) to investigate the spatial distribution of the communities, with special attention to their diversity patterns along the BCS.

Material and methods

Study area

The study area covers the full Belgian Continental Shelf (BCS) (2600 km²) situated in the southern part of the North Sea and covers less than 0,5 % of the North Sea shelf. The BCS is mainly characterized by the presence of several sandbank systems (Figure 1): (1) Coastal Banks, parallel to the coastline, (2) Flemish Banks, about 10-30 km offshore of the western Belgian coast, (3) Zeeland Banks, some 15-30 km offshore of the eastern Belgian coast, and (4) Hinderbanks, about 35-60 km offshore (Degraer, 1999). Because of the presence of these sandbank systems a high geomorphological and sedimentological diversity is found (Degraer et al., 1999a).

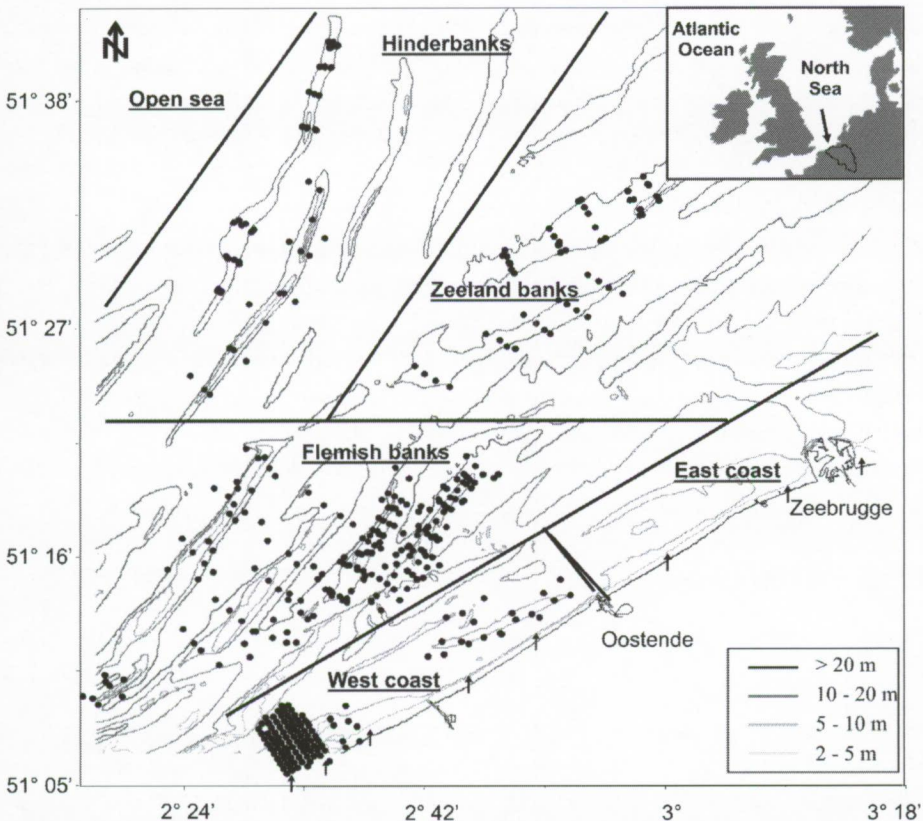


Figure 1. Geographic distribution of the sampling sites investigated for their macrobenthos between 1994 and 2000. Closed circles: subtidal sampling sites; arrows: intertidal sampling transects.

Next to these sandbank systems, the BCS also comprises 65 km of sandy beaches. According to the morphodynamic classification scheme of sandy beaches (Masselink and Short, 1993; Short, 1996), all

beaches are classified as low tide bar/rip or ultra-dissipative beaches: tidal range, 4.5 – 5 m; median grain size: 199 – 352 μm ; modal breaker height and period: 0.5m and 3s, respectively; width intertidal zone, 200 - 400m (Degraer et al., 2003).

Data origin

Within the framework of several studies, a total of 728 macrobenthos samples (443 sampling sites) were collected at the BCS between 1994 and 2000. Most samples were gathered in late Winter (52 %) or early Autumn (42 %). Because the data were gathered within the framework of different research projects, the sampling sites are unevenly distributed throughout the area (Figure 1). The Flemish Banks and, especially, the western part of the Coastal Banks were intensively studied, while no samples from the open sea zone and the eastern part of the Coastal Banks are available. Samples from the Zeeland - and the Hinder banks are concentrated on the sandbanks, while only few samples were situated in the gullies.

Generally, subtidal samples were taken with a Van Veen grab (sampling surface area: 0.1 m²) and sieved alive over a 1 mm mesh-sized sieve. Sandy beach samples were collected by excavating sediment enclosed by a frame (sampling surface area: 0.1026 m²) to a depth of ca. 0.15 m (Elliott et al., 1996) and sieved alive over a 1 mm mesh-sized sieve. All species were identified to species level if possible.

Water depth at each sampling station was recorded in situ and standardized to the mean low water spring level (MLWS). The grain size distribution of a subsample was measured with a LS Coulter particle size analyzer: median grain size and mud content (volume percentage < 64 μm) were used as granulometric parameters.

All species densities and environmental data (water depth, median grain size and mud content) were incorporated in a Microsoft Access database (MACRODAT) and yielded an original set of 254 taxa, of which 192 macrobenthic species. After exclusion of species that were not sampled quantitatively (e.g. hyperbenthic and extremely rare taxa) and lumping taxa, because of inconsistent identification throughout the different studies (e.g. genus level: *Bathyporeia*, *Ensis*, and *Harmothoe*; family level: Cirratulidae and Capitellidae), a set of 156 taxa (140 species) was used for multivariate analyses. These taxa are further referred to as species.

Community analysis

The community structure was investigated by several multivariate techniques: Group-averaging cluster analysis based on the Bray-Curtis similarity (Clifford and Stephenson, 1975), Detrended Correspondence Analyses (DCA) (Hill and Gauch, 1980) and Two-Way Indicator Species Analysis or TWINSpan (Hill, 1979; Gauch and Whittaker, 1981), based on a dataset with 728 samples and 156 taxa. The cutlevels for TWINSpan are chosen in such a way that all the cutlevels contain the same number of values, except the first cutlevel which contains all zero values, and the two last cutlevels which contain an equal number of values that is only the half of that of the other cutlevels (to give a

little extra weight to the abundant taxa). TWINSpan was performed on the non-transformed dataset (cutlevels: 7.9, 9, 17, 39, 100 and 225 ind/m²), while the abundance data were fourth root transformed prior to the cluster analysis and DCA. The results of these techniques were compared to distinguish between groups of biologically similar samples. Indicator species for each of these groups were identified through Indicator Species Analysis (IndVal) and their statistical significance was tested by a Monte Carlo Test (Dufrene and Legendre, 1997).

The sample groups, resulting from the multivariate analyses, were characterized by means of their taxa composition, abundance, species richness and physical habitat (median grain size, mud content and bathymetry). The multivariate analyses and the description of the species assemblages are based on the dataset, which exist of 156 taxa, only species richness is based on a dataset with the presence of the real macrobenthic species (141 species), without different stages for one species.

Results

General characterization of the macrobenthos

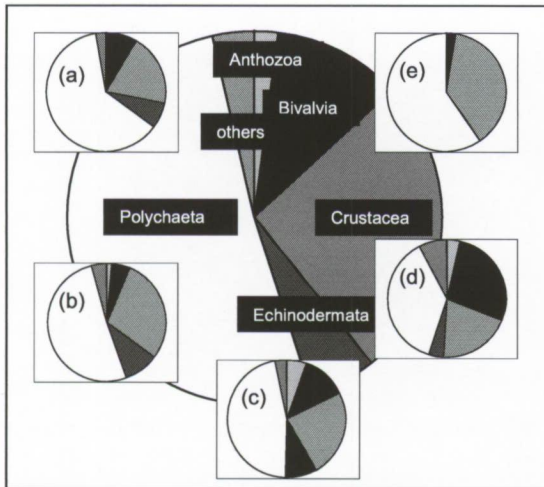


Figure 2. Relative abundance at higher taxonomic levels at the BCS (large pie diagram), (a) the Hinderbanks, (b) Zeeland Banks, (c) Flemish Banks, (d) Coastal Banks and (e) sandy beach (small pie diagrams).

With 83 species (43% of the macrobenthic species), are the polychaetes the most diverse taxon. Crustaceans comprised 65 species (34%), molluscs 32 species (16%), echinoderms 9 species (5%) and 5 species (3%) were anthozoans, nemertineans or pycnogonids. The species with the highest frequency of occurrence were the polychaetes *Nephtys cirrosa* (present in 71% of the samples), *Spiophanes bombyx* (40 %) and *Scoloplos armiger* (40 %).

The total macrobenthic abundance ranged between 8 and 149179 ind/m² (average: 1643 ind/m²). The sites with the highest abundance of macrofauna were situated on the western part of the Coastal Banks. Macrobenthic abundances were dominated by polychaetes, bivalves or crustaceans, depending on the area considered (figure 2). Bivalves (mainly *Spisula subtruncata*, *Abra alba* and *Mysella bidentata*) and polychaetes dominated the fauna of the Coastal Banks, but the dominance of polychaetes increased towards the more offshore bank areas, whereas the relative abundance of the bivalves decreased. Crustaceans and polychaetes were dominant on the sandy beaches. Species richness ranged from 1 to 53 spp./0.1m² (average: 11 spp./0.1m²).

General distribution patterns

The distribution of the macrobenthic species richness and abundance along the onshore-offshore gradient follows a highly variable pattern, with species and abundance poor stations along the full gradient and species and abundance rich stations restricted to the coastal zone (< 15 miles offshore) (Figure 3). However, the trendlines both show a unimodal distribution, with peak values at about 3 nautical miles decreasing both offshore and towards the sandy beaches.

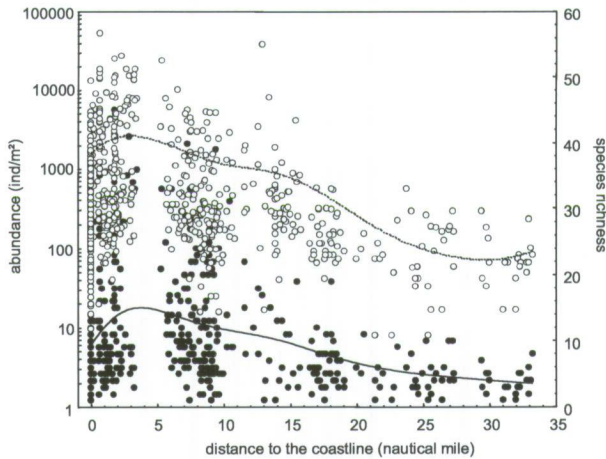


Figure 3. The species richness (species/sample) and abundance (ind/m²) distribution across the onshore – offshore gradient at the BCS. Trend lines set using Least squares methods. Species richness: black points, solid trend line; Abundance: open points, dotted trend line.

The species richness and abundance are highly correlated (Spearman rank: $p < 0.05$) with the sediment's mud content and median grain size. A high species richness (> 15 spp. sample⁻¹) and abundance (> 2000 ind/m²) was mainly found in fine to medium sandy sediments (median grain size: < 300 μm) with a relatively high mud content (> 3 %) (Figure 4). Coarser sediments and/or low mud contents generally yielded species- and abundance-poor samples. Sediments characterized by coarser sediments with a high mud content were not encountered at the BCS. High densities generally corresponded with a high species richness (Spearman rank correlation: $R = 0.756$; $p < 0.05$), explaining the similar distribution patterns of species richness and abundance.

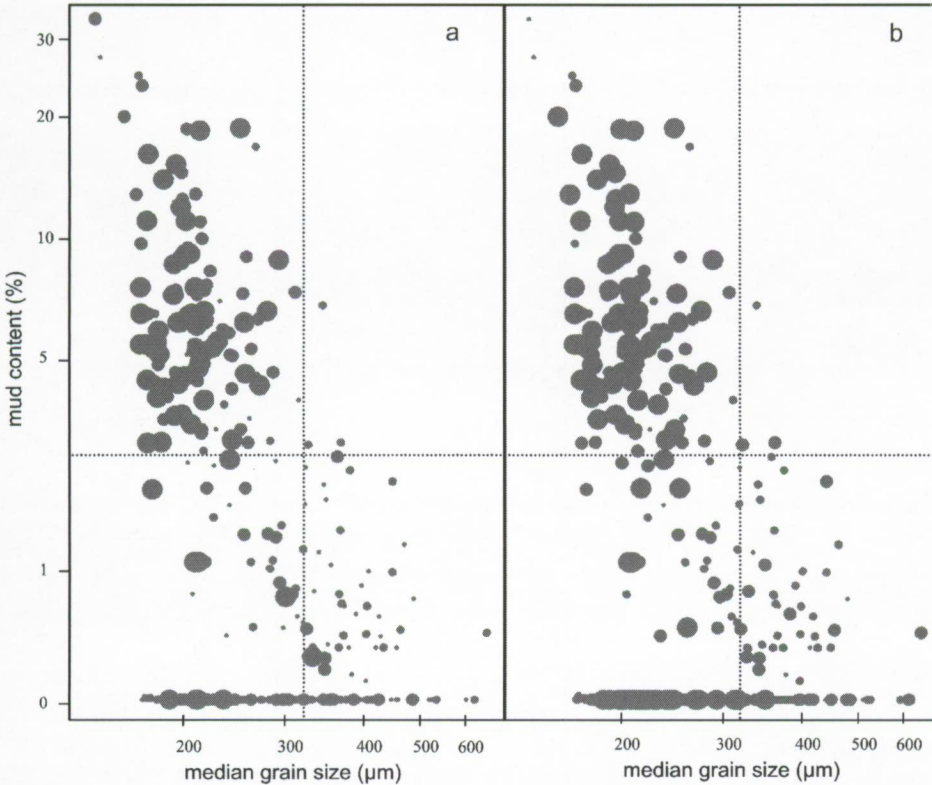


Figure 4. The species richness (N_0) and abundance (ind/m^2) in relation to the sedimentological characteristics (median grain size and mud content). (a) Species richness (species/sample) ● < 10; ● 10-15; ● 15-30; ● 30-55. (b) Abundance (ind/m^2): ● < 150; ● 150-500; ● 500-2000; ● > 2000.

Species assemblages: macrobenthic structure, habitat preferences and distribution

Based on the multivariate analyses, ten sample groups were distinguished (Figure 5). Because each of these groups is composed of samples with a similar species composition, the groups are further referred to as 'species assemblages' (SA). The first DCA axis (Eigenvalue: 0.645) was negatively correlated with the sampled sites' depth and mud content (respectively correlation factors are -0.395 and -0.490); while the second DCA axis (Eigenvalue: 0.215) was positively correlated with the sediment's median grain size (correlation factor is 0.379).

Based on their position in the DCA plot, two types of species assemblages were identified. Type I species assemblages are situated at the edges of the multivariate biological gradients: SA1 and SA10 (ordination axis 1) and SA4 and SA6 (ordination axis 2). Type II species assemblages are positioned in between Type I species assemblages: SA2, SA3, SA5, SA7, SA8, and SA9.

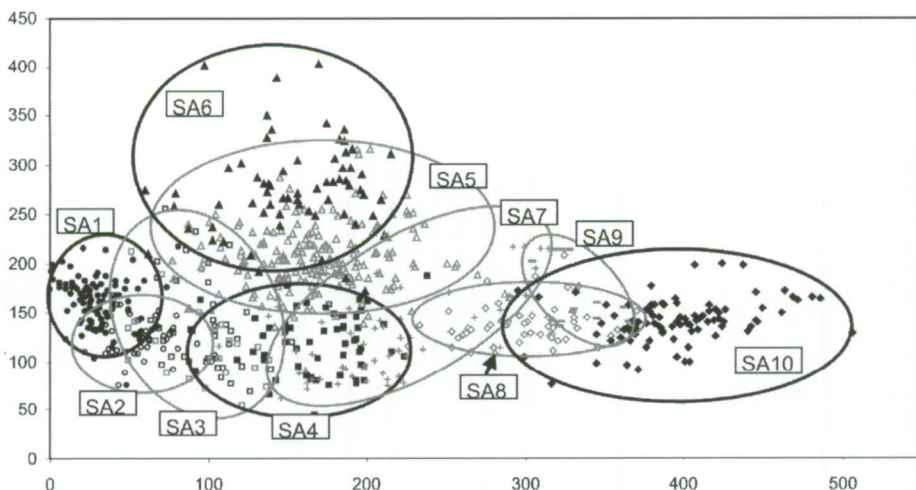


Figure 5. DCA ordination plot along the first two axes. The discrimination between sample groups is based on TWINSpan, Cluster analysis and DCA. Position of the sample groups (species associations) is indicated by the ellipses. ●, SA1; ○, SA2; □, SA3; ■, SA4; △, SA5; ▲, SA6; +, SA7; ◇, SA8; -, SA9; ◆, SA10.

Type I species assemblages (Table 1)

SA1 is characterized by the highest species richness (30 spp./sample) and macrobenthic abundance (6432 ind/m²). Especially the bivalve *Spisula subtruncata* reached very high abundance (2943 ind/m²), followed by several polychaete, bivalve and amphipod species with average abundance of more than 200 ind/m². Eight species were significantly (Monte Carlo permutation test: $p < 0.05$) indicative for SA1, all of which had an indicator value (IV) of at least 50. Three of these indicative species were found in high abundance: the bivalves *Abra alba* (514 ind/m²) and *Mysella bidentata* (419 ind/m²) and the amphipod *Pariambus typicus* (435 ind/m²). Numerous species (e.g. the polychaetes *Sthenelais boa*, *Owenia fusiformis*, and *Pectinaria koreni*, the bivalve *Mya truncata*, and the amphipod *Ampelisca brevicornis*) were exclusively found within this species assemblage. SA1 is found in fine sandy sediments (median grain size: 219 μ m), with a relatively high mud content (6 %), at an average depth of 13 m below MLWS.

SA4 has a rather low species richness (7 spp./sample) and abundance (402 ind/m²). Except for the polychaete *Magelona johnstoni* (105 ind/m²), all species had an abundance less than 100 ind/m². Only two species were significantly indicative for SA4: the polychaetes *Scolecopsis bonnieri* and *Nephtys cirrosa*. Yet, both species had rather low indicator values (IV: 20 and 13, respectively). Only *Nephtys cirrosa* occurred in a relatively high abundance (84 ind/m²). SA4 inhabits well-sorted fine to medium sandy sediments (median grain size: 274 μ m), with low mud contents (< 1%), at an average depth of 12 m below MLWS.

A low species richness (5 spp./sample) and abundance (190 ind./m²) is characteristic for SA6. All species occurred in low densities (maximum 32 ind./m²). Two species are significantly indicative: the polychaetes *Ophelia limacina* (IV: 28) and *Glycera lapidum* (IV: 26), and with a respectively abundance of 17 and 9 ind. m⁻². SA6 is found in medium sandy sediments (median grain size: 409 μ m), with a low mud content (< 1%), at an average depth of 15 m below MLWS.

SA10 is characterized by a very low species richness (5 spp./sample), but relatively high abundance (983 ind/m²). Three species had an abundance of more than 200 ind/m²: the amphipod *Bathyporeia* spp. (357 ind/m²), the polychaete *Scolelepis squamata* (343 ind/m²) and the isopod *Eurydice pulchra* (218 ind/m²). All other species were found in abundances of maximum 21 ind/m². *Eurydice pulchra* (IV: 54) and *Scolelepis squamata* (IV: 44) were significantly indicative. SA10 inhabits pure (mud content: < 1%), fine to medium sandy sediments (median grain size: 248 µm) at the upper intertidal zone of the sandy beaches (4 m above MLWS).

Type II species assemblages (Table 1)

As suggested by the position of the Type II species assemblages in the DCA plot, these species assemblages are representing a gradual biological shift between the different Type I species assemblages.

SA2 and SA3 represent a transition in between the SA1 and SA4: a gradual decrease in macrobenthic abundance (SA2: 2746 ind/m²; SA3: 2017 ind/m²) and species richness (SA2: 18 spp./sample; SA3: 13 spp./sample) is observed. Comparing the list of the ten most abundant species, a gradual shift in taxa composition is found: SA2 has five dominant taxa in common with SA1 and only one with SA4, while SA3 has four dominant taxa in common with SA1 and no less than six taxa with SA4. SA2 and SA3 have four dominant species in common. SA2 and SA3 are characterized each by one species with high densities: post-larval and juvenile *Spisula* (SA2) and *Magelona johstoni* (SA3). SA2 is found in fine sandy sediments (median grain size: 208 µm) similar as SA1, while SA3 occurs in fine to medium sandy sediments (median grain size: 268 µm) similar as SA4. SA2 and SA3 show a gradual decrease in mud content between SA1 and SA4 (4 and 2 %, respectively). The depth range of both species associations falls within the range of 8 and 14 m below MLWS.

SA5 is found in between SA4 and SA6. This species assemblage has a similar species richness as both SA4 and SA6 (NO: 8 spp./sample), while its average macrobenthic abundance (304 ind/m²) was found between that of SA4 and SA6. SA5 had seven abundant taxa in common with SA4 and five with SA6. SA5 is found in medium sandy sediments (median grain size: 333 µm) with a low mud content (< 1%) at a depth of 16 m below MLWS.

In between SA4 and SA10, the gradual transition is represented by a complex of three species assemblages (SA7-SA9). SA7 had five abundant taxa in common with SA4 and only two with SA10, while both SA8 and SA9 had a abundant taxa composition similar to SA10 (7 and 6 spp. in common, respectively) rather than to SA4 (1 and 2 spp. in common, respectively). The species richness and abundance of all three species assemblages ranged between 5 and 8 spp./sample and 101 and 482 ind/m², respectively. The depth ranges from 2 below MLWS (SA7) to 2 m above MLWS (SA8-SA9). The three species assemblages are found in fine sandy sediments (median grain size: 219 – 243 µm) with a low mud content (< 1 %).

Table 1. Characterization of the species assemblage (environment: median grain size (μm), mud content (%), and depth (m); macrobenthos: species richness (N_0 and N_1), abundance (macrobenthic abundance and species-specific abundance of the 10 most abundant species per species assemblage, ind./m²), and indicator species-specific values (*: higher indicator value in another SA)). Species association: typology

	SA 1	SA 2	SA 3	SA 4	SA 5	
Environmental parameters:						
median grain size	219,24	208,28	267,85	274,02	333,07	
mud content	5,79	4,32	1,89	0,37	0,19	
depth	-12,56	-7,9	-13,93	-11,82	-16,07	
Macrobenthic variables:						
Diversity						
N_0	31	19	14	7	8	
N_1	11,008	5,678	6,476	4,754	4,979	
Densities						
mean densities	6432	2746	2017	402	304	
density top 10	<i>Spisula subtruncata</i> 2943 <i>Scoloplos armiger</i> 524 <i>Abra alba</i> 514 <i>Pariambus typicus</i> 435 <i>Myrella bidentata</i> 419 <i>Magelona mirabilis</i> 406 <i>Lanice conchilega</i> 273 <i>Capitellidae</i> spp. 265 <i>Spiophanes bombyx</i> 232 <i>Eumida sanguinea</i> 214	<i>Spisula subtruncata</i> 2943 <i>Magelona mirabilis</i> 524 <i>Spio filicornis</i> 130 <i>Fabulina fabula</i> 76 <i>Lanice conchilega</i> juv 64 <i>Nephtys hombergii</i> 47 <i>Lanice conchilega</i> 32 <i>Spiophanes bombyx</i> 31 <i>Erisis</i> spp. 30 <i>Myrella bidentata</i> 214	<i>Magelona mirabilis</i> 1637 <i>Microphthalmus similis</i> 427 <i>Scoloplos armiger</i> 130 <i>Spiophanes bombyx</i> 76 <i>Nephtys cirrosa</i> 64 <i>Fabulina fabula</i> 47 <i>Bathyporeia</i> spp. 32 <i>Urothoe poseidonis</i> 31 <i>Spisula subtruncata</i> 30 <i>Nephtys</i> spp. juv. 24	<i>Magelona mirabilis</i> 1263 <i>Nephtys cirrosa</i> 116 <i>Bathyporeia</i> spp. 102 <i>Urothoe poseidonis</i> 71 <i>Ophiura</i> spp. juv. 60 <i>Scoloplos armiger</i> 48 <i>Scotelepis bonneri</i> 27 <i>Nephtys</i> spp. juv. 26 <i>Hesionura elongata</i> 21 <i>Urothoe brevicornis</i> 20	<i>Nephtys cirrosa</i> 105 <i>Urothoe brevicornis</i> 84 <i>Bathyporeia</i> spp. 76 <i>Ophiura</i> spp. juv. 22 <i>Spiophanes bombyx</i> 19 <i>Scoloplos armiger</i> 15 <i>Hesionura elongata</i> 10 <i>Ophelia limacina</i> 8 <i>Spio filicornis</i> 8 <i>Nephtys</i> spp. juv. 8	<i>Nephtys cirrosa</i> 60 <i>Urothoe brevicornis</i> 40 <i>Bathyporeia</i> spp. 33 <i>Ophiura</i> spp. juv. 27 <i>Spiophanes bombyx</i> 27 <i>Scoloplos armiger</i> 24 <i>Hesionura elongata</i> 12 <i>Ophelia limacina</i> 9 <i>Spio filicornis</i> 8 <i>Nephtys</i> spp. juv. 5
Indicator species						
<i>Abra alba</i>	64	<i>Spisula subtruncata</i> 46	<i>Magelona mirabilis</i> 16*	<i>Scotelepis bonneri</i> 16*	<i>Urothoe brevicornis</i> 20	
<i>Anatides mucosa</i>	53	<i>Nephtys hombergii</i> 29	<i>Scoloplos armiger</i> 15*	<i>Nephtys cirrosa</i> 13*	<i>Nephtys cirrosa</i> 14*	
<i>Sthenelais boa</i>	53	<i>Sigalion mathildae</i> 21	<i>Spiophanes bombyx</i> 13*		<i>Ophelia limacina</i> 14*	
<i>Cirratulidae</i> spp.	51	<i>Lanice conchilega</i> 21*	<i>Nephtys cirrosa</i> 12*			
<i>Owenia fusiformis</i>	51					
<i>Myrella bidentata</i>	51					
<i>Pariambus typicus</i>	51					
<i>Pectinaria koreni</i>	50					
Species assemblage						
	Type I SA <i>Abra alba</i> - <i>Myrella bidentata</i> community	Type II SA	Type II SA	Type I SA <i>Nephtys cirrosa</i> community	Type II SA	
	SA 6	SA 7	SA 8	SA 9	SA 10	
Environmental parameters:						
median grain size	409,05	218,91	242,64	230,15	248,44	
mud content	0,25	0,04	0,05	0	0,01	
depth	-15,32	-2,12	2,01	2,4	3,8	
Macrobenthic variables:						
Diversity						
N_0	6	5	8	5	5	
N_1	3,968	2,912	4,523	3,395	2,505	
Densities						
mean densities	190	135	482	101	983	
density top 10	<i>Hesionura elongata</i> 32 <i>Nephtys cirrosa</i> 32 <i>Ophelia limacina</i> 17 <i>Ophiura</i> spp. juv. 10 <i>Glycera lapidum</i> 9 <i>Oligochaeta</i> spp. 9 <i>Echinocyamus pusillus</i> 6 <i>Actinaria</i> spp. 6 <i>Ophiura</i> spp. 6 <i>Urothoe brevicornis</i> 5	<i>Nephtys cirrosa</i> 66 <i>Bathyporeia</i> spp. 15 <i>Urothoe poseidonis</i> 11 <i>Magelona mirabilis</i> 5 <i>Spio filicornis</i> 5 <i>Spisula subtruncata</i> 3 <i>Scoloplos armiger</i> 3 <i>Portunus latipes</i> 6 <i>Capitellidae</i> spp. 6 <i>Nephtys hombergii</i> 3	<i>Capitellidae</i> spp. 126 <i>Spio filicornis</i> 61 <i>Pygospio elegans</i> 59 <i>Eteone longa</i> 49 <i>Scotelepis squamata</i> 39 <i>Bathyporeia</i> spp. 37 <i>nt-Calanoida Copepoda</i> 34 <i>Hesionura arenaria</i> 14 <i>Psammodrillus balanoides</i> 14 <i>Cumopsis goodsi</i> 3	<i>Bathyporeia</i> spp. 126 <i>Nephtys cirrosa</i> 61 <i>Scotelepis squamata</i> 59 <i>Spio filicornis</i> 49 <i>Eurydice pulchra</i> 37 <i>Pygospio elegans</i> 37 <i>Eteone longa</i> 34 <i>Hesionura arenaria</i> 14 <i>Polydora</i> spp. 14 <i>Cumopsis goodsi</i> 14	<i>Bathyporeia</i> spp. 48 <i>Scolelepis squamata</i> 19 <i>Eurydice pulchra</i> 15 <i>Psammodrillus balanoides</i> 5 <i>Eteone longa</i> 4 <i>Pygospio elegans</i> 3 <i>Eurydice affinis</i> 2 <i>Capitellidae</i> spp. 2 <i>Hesionura arenaria</i> 2 <i>Ophelia rathkei</i> 1	<i>Bathyporeia</i> spp. 357 <i>Scolelepis squamata</i> 343 <i>Eurydice pulchra</i> 218 <i>Psammodrillus balanoides</i> 21 <i>Eteone longa</i> 10 <i>Eurydice affinis</i> 10 <i>Pygospio elegans</i> 5 <i>Capitellidae</i> spp. 5 <i>Hesionura arenaria</i> 4 <i>Ophelia rathkei</i> 4
Indicator species						
<i>Ophelia limacina</i>	28	<i>Nephtys cirrosa</i> 26	<i>Pygospio elegans</i> 15	<i>Scotelepis squamata</i> 32	26* <i>Eurydice pulchra</i> 54	
<i>Glycera lapidum</i>	26	<i>Portunus latipes</i> 26	<i>Cumopsis goodsi</i> 15	<i>Bathyporeia</i> spp. 32	11 <i>Scolelepis squamata</i> 44	
			<i>Eteone longa</i>	<i>Nephtys cirrosa</i> 27	10*	
Species assemblage						
	Type I SA <i>Ophelia limacina</i> - <i>Glycera lapidum</i> community	Type II SA	Type II SA	Type II SA	Type I SA <i>Eurydice pulchra</i> - <i>Scolelepis squamata</i> community	

Geographical distribution

Each species assemblage was found over a specific range along the onshore – offshore gradient (Figure 6). Four distribution types can be identified. The distribution of a first type (SA1 – SA3) ranged from 0 to 15 nautical miles and showed a nearshore average distribution (4 miles). A second type (S4 – SA6) was found across the full onshore – offshore gradient (range: 34 miles), with a species assemblage dependent average distribution, increasing from SA4 to SA6 (9 – 20 miles). A third type (SA7) showed a strictly nearshore distribution (0 – 3 mile). Finally, SA8 – SA10 were restricted to the coastline (i.e. sandy beaches).

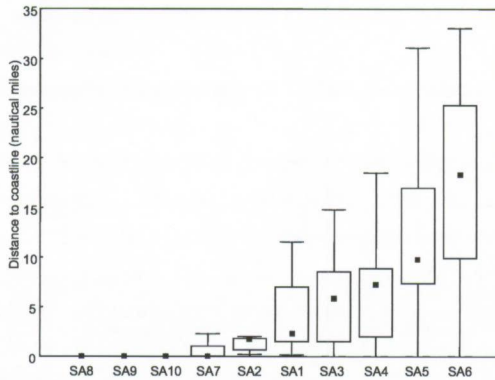


Figure 6. The onshore – offshore distribution of the ten species assemblages. Median distance (•) + Percentiles (25% - 75%) (Boxes) and Non - Outlier range (Min – Max) (Whiskers).

Discussion

Communities and transitions

The term community is widely used and most definitions of communities include the idea of a collection of species found in a particular place (physical habitat); other ecologists found that these species must interact in some significant way to be considered as community members (Morin, 1999). One of the basic studies on the community concept in marine biology is from Mills (1969). He compared several definitions both in plant and animal biology and the discussion resulted in a final definition: “a community is a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment and separable from other groups by means of an ecological survey”. Recently, Morin (1999) gave a good overview of the different approaches to delineate communities: (1) physically, by discrete habitat boundaries, (2) taxonomically, by the identify of a dominant indicator species, (3) interactively, by the existence of strong interactions among species or, (4) statistically, by patterns of assemblages among species.

Based on Morin's (1999) first (habitat boundaries) and fourth (statistical assemblages) approach to distinguish between communities, the four Type I species assemblages (SA1, SA4, SA6 and SA10) can be considered as communities because of (1) their extreme position along the habitat gradients (depth, mud content and median grain size) (figure 7) and, consequently, (2) the absence of overlap between the habitat of each species assemblages, based on the results of the multivariate analyses. The relationship between recurring groups of soft-bottom animals and certain sediment types and depth zones, was first described by Petersen (1914). Jones (1950) put forward an alternative classification of species groupings based on sediment and depth characteristics, followed by several other authors (e.g. Thorson, 1957; Kingston and Rachor, 1982; Duineveld et al., 1991, Heip and Craeymeersch, 1995; Degraer et al., 1999a).

Although these communities are found in a particular habitat (sedimentology and depth) and characterized by typical community parameters (diversity, density and species composition), the physical and biological boundaries of these four macrobenthic communities are not strict. Many ecological studies already demonstrated the unimodal distribution of species along environmental gradients. Following this approach, the discrimination of communities, defined as the collection of organisms occurring in the same environment, is a merely arbitrary abstraction of biological gradients: gradual transitions between different communities exist (Gray, 1981). Gradual biological and physical transitions between the four macrobenthic communities of this study are represented by the Type II species assemblages (further called: transitional species assemblages) (figure 7). These species assemblages are characterized by the occurrence of species of both related communities but in lower densities. Some of the transitional species associations are also characterized by typical species, such as *Magelona johnstoni* in SA3.

The macrobenthic communities of soft-bottom sediments at the BCS

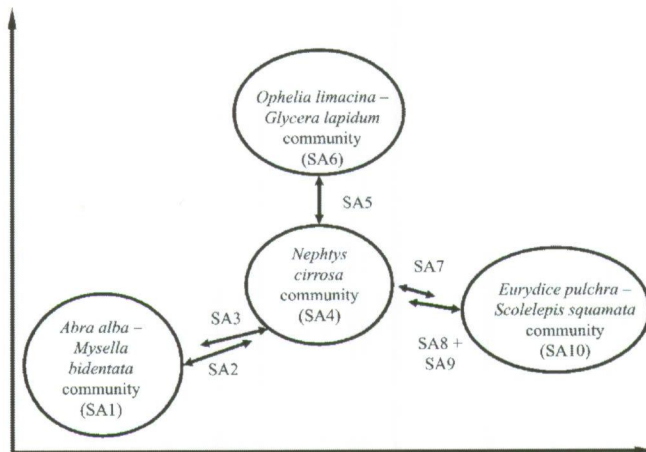


Figure 7. Schematic overview of the relationships between the four macrobenthic communities and the transitional species assemblages.

Four of the ten species associations (Type I species assemblages) thus differ drastically, both in habitat and species composition, and are considered to represent four macrobenthic communities. Based on their discriminating indicator species these communities are further referred to as the subtidal *Abra alba* - *Mysella bidentata* community (SA1), the *Nephtys cirrosa* community (SA4), the *Ophelia limacina* - *Glycera lapidum* community (SA6) and the intertidal *Eurydice pulchra* - *Scolecipis squamata* community (SA10) (Figure 7).

The Abra alba – Mysella bidentata community (SA1)

The *A. alba* – *M. bidentata* community seems to be of exceptional ecological importance: (1) high macrobenthic abundance (6432 ind/m²) and diversity (31 spp./sample), (2) high number of bivalves (e.g. *Spisula subtruncata* and *A. alba*) possibly serving as an important food resource for sea ducks or demersal fishes (Degraer, 1999), (3) numerous unique species for the Belgian Continental Shelf (e.g. *Ampelisca brevicornis*, *Owenia fusiformis*, *Sthenelais boa*, *Pectinaria koreni* and *Mya truncata*), and (4) the occurrence of habitat structuring species, such as *Lanice conchilega* (273 ind./m²) (Buhr and Winter, 1976; Dauvin, 2000; Ropert and Dauvin, 2000; Ropert and Gouletquer, 2000). This community is found in near shore shallow muddy sands (median grain size: 219 µm and mud content: 6%).

Because of its similar habitat preferences, macrobenthic abundance (2500 ind/m²) and diversity (18 spp./0.1m²) and the abundant occurrence of *A. alba* (139 ind/m²) and *L. conchilega* (228 ind/m²), the community should be regarded as a synonym for the *L. conchilega* community, as found and described by Degraer et al. (1999a) at the Belgian Coastal Banks.

A very similar *A. alba* community was described from areas South (French North-Atlantic and English Channel coast: Souplet and Dewarumez, 1980; Prygiel et al., 1988; Olivier et al., 1996; Dauvin 1998, 2000; Ghertsos et al., 2000, 2001; Desroy et al., 2002) and North (Dutch and German coast: Glémarec, 1973; Kingston and Rachor, 1982; Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996) of the BCS and is typically patchy distributed in shallow, nearshore waters (Jones, 1950; Cabioch and Glaçon, 1975). The average densities (5080 ind/m²) diversity (33 spp./0.1m²) and species composition (*L. conchilega*, *A. alba*, *Spiophanes bombyx*) of the *A. alba* community along the Northern French Coast (Calais) are similar to the *A. alba* – *M. bidentata* community of the BCS (Fromantin et al., 1996; Desroy et al., 2002), but the total number of species increased further to the south (from + 150 (Gravelines) to 300 à 400 (Pierre Noire)) (Fromantin et al., 1997). Compared to the BCS, the *A. alba* community along the Dutch coast is characterized by lower densities (average: 2556 ind/m²) and diversity (14 spp./0.1m²) (Holtmann et al., 1996).

Compared with biological classifications provided in literature, the *A. alba* – *M. bidentata* community belongs to the 'boreal offshore muddy sand association', which is equivalent to Petersen's *Echinocardium* - *Amphiura filliformis* communities (Jones, 1950).

The Nephtys cirrosa community (SA4)

The diversity (7 spp./sample) and abundance (402 ind/m²) in the *Nephtys cirrosa* community are low, which is typical for well-sorted mobile sands, and mostly characterized by mobile polychaetes (e.g. *N. cirrosa*) and crustaceans (e.g. *Bathyporeia* spp.).

Because of the large niche width of *N. cirrosa* (eurytopic species) (Rainer, 1991), this polychaete species is found in several transitional species associations (SA3, SA5, and SA7; average abundance: about 60 ind/m²), explaining its low indicator value (IV: 14), as well as the large overlap of the community with several transitional species assemblages. The *N. cirrosa* community takes a central place within the overall macrobenthic community structure of the BCS: all transitions between the communities pass by the *N. cirrosa* community.

At the Belgian Coastal Banks, Degraer et al. (1999a) described a *N. cirrosa* community and a *N. cirrosa* – *Echinocardium cordatum* community, which are characterized by a moderate abundance of *N. cirrosa* (respectively 93 and 70 ind/m²) and a low diversity (respectively 5 and 8 spp./0.1m²). Because of the similar physical habitat both communities were later lumped to the *N. cirrosa* community s.l. (Degraer, 1999).

Within adjacent areas, a species assemblage dominated by *N. cirrosa* (86 ind/m²) and *Bathyporeia* spp. (52 ind/m²) (Holtmann et al., 1996), characteristic for well-sorted sandy sediments with low mud content, is described by many authors (Curras et al., 1991; Duineveld, et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996; Bachelet et al., 1996). Most probably the *N. cirrosa* community of this study should be regarded as part of or as synonym of the species assemblages occurring in well-sorted sandy sediments.

Jones (1950) included this community in the 'Boreal offshore sand association' – equivalent to Petersen's *Venus* communities.

The Ophelia limacina – Glycera lapidum community (SA6)

The *O. limacina* – *G. lapidum* community, with a very low diversity (6 spp./sample) and abundance (190 ind/m²), occurred in medium to coarse sandy sediments. Also the presence of shell fragments in the sediment is an important characteristic (Govaere et al., 1980). *G. lapidum* is typical for coarse sandy sediments, while *O. limacina* can also be found in low abundances in fine to medium sand, with very low mud content (Govaere, 1978; Hartmann-Schröder, 1996).

Interstitial polychaetes, such as *Hesionura elongata* (32 ind/m²), were also found, but most probably the abundance of these species is strongly underestimated in this study: former descriptions of this community revealed high abundances (up to 800 ind/m²) of interstitial polychaetes (Govaere, 1978). This might be explained by differences within the post-sampling treatment used by both authors compared to this study: sieving after fixation (Govaere, 1978) versus sieving alive (this study), allowing the interstitial polychaetes to escape actively through the sieve. Interstitial polychaetes become abundant at a median grain size of more than 300 µm (Willems et al., 1982).

The habitat characteristics (median grain size: 456 µm), diversity (4 spp./sample) and abundance (177 ind/m²) of the '*Mytilus edulis*' community (Degraer et al., 1999a) is similar to the *O. limacina* – *G. lapidum* community. The former community was characterized by the presence of juvenile *M. edulis*

(the '*M. edulis*' community), but this juvenile bivalve may perform strong seasonal fluctuations in density. The juvenile individuals can attach to the coarse sediment particles, but when they grow, the chance of being washed out increases.

The *Venus fasciata* community is typically found in medium to coarse sandy sediments in the English Channel, well subdivided into various facies, and characterized by species such as *Travesia forbesi*, *Lumbrineris latreilli* and *N. cirrosa* (Cabioch, 1968). The facies '*Ophelia borealis* community' (syn. *O. limacina* community) is typically found in medium to coarse sediments mixed with gravel or shell fragments of the coastal sandbanks along the Normandy and Southern North Sea coasts at a depth of more than 10 m (Holtmann et al., 1996, Sanvicente-Anorve et al., 2002). A low number of species (26) (Souplet and Dewarumez, 1980) and abundance is typical for this community (Cabioch, 1968, Cabioch and Glaçon, 1977, Dewarumez et al., 1990). The low values may be explained by the harsh conditions at sandbanks in the Southern North Sea: according to Vanosmael et al. (1982), the top of these sandbanks as well as the ripples are continuously broken down and rebuilt by strong hydrodynamic forces. Hence, sessile tube-building polychaetes only represent a small number of individuals, whereas the dominant species are composed of mobile, burrowing organisms (Whiters and Thorp, 1978).

According to Jones (1950) this community is also included in the 'Boreal offshore sand association' – equivalent to Petersen's *Venus* communities.

The Eurydice pulchra – Scolelepis squamata community (SA10)

The *E. pulchra* – *S. squamata* community is exclusively found at the upper intertidal zone of Belgian sandy beaches and is characterized by a low diversity (5 spp./sample) and moderate abundances (983 ind/m²), mainly of *E. pulchra*, *S. squamata* and *Bathyporeia* spp.

Bathyporeia spp. and *E. pulchra* are found to be abundant on many European beaches (Eleftheriou and McIntyre, 1976, Degraer et al., 1999b), while *S. squamata* is also an abundant species on many Atlantic beaches (Souza and Gianuca, 1995; Eleftheriou and McIntyre, 1976; McDermott, 1987). Parallel communities, in which species might be replaced by (functionally) similar species, can be found within the upper intertidal zone of many sandy beaches worldwide (McLachlan and Jaramillo, 1995).

Special communities

Next to these four macrobenthic communities Degraer et al. (1999a) found an extremely rare (only one station) macrobenthic community in outcropping tertiary clay layers nearby Oostende, which he defined as the *Barnes candida* community. This rather diverse (species richness: 10 spp./sample) community occurs in a muddy (median grain size: 14 µm), shallow (8 m) sediment, containing high numbers of the bivalve *B. candida* (117 ind/m²). Recent sampling surveys confirmed the existence of this community in the gully Kleine Rede nearby Oostende.

Although being present at the BCS, gravel beds were not sampled qualitatively nor quantitatively for their macrobenthos, because of a lack of good sampling gear for this habitat (f.i. Hamon grab). Some accidental samples within this habitat revealed the presence of a very specific fauna (e.g. sponges

and sea spiders) (pers. obs.). The macrobenthos of gravel and boulder beds is characterized by a specific set of species that differs drastically from the surrounding sandy environment, but rather shows similarities with the macrofauna of rocky substrates (Kenny et al., 1996; De Grave, 1999; Newell et al., 2001).

Temporal effects

Macrobenthic communities in temperate regions are subjected to a large year-to-year variability of the community structure (Turner et al., 1995). Temporal variability within the *A. alba* – *M. bidentata*, *N. cirrosa* and *O. limacina* – *G. lapidum* communities at the Western Coastal Banks was studied by Degraer (1999). They concluded that temporal variability in community parameters are prominent, but community shifts were not detected. As long as the main habitat characteristics do not change drastically, the basic composition and the distribution (including natural variability, such as seasonality) of the respective communities will remain stable over long periods of time (Govaere et al., 1980; Turner et al., 1995; Degraer, 1999). Temporal variability should thus be considered as being subordinate to spatial variation and the existence of six relatively stable macrobenthic communities at the BCS can be confirmed.

Only one dramatic temporal event, linked to the recruitment of *Spisula subtruncata*, was discerned in this study. In case of a (very) successful recruitment (e.g. August 1995), a surficial layer of 1 to 2 cm of post-larval *S. subtruncata* possibly caused an increased mortality of several other macrobenthic species and thus altered the general community structure (Degraer, 1999). This phenomenon is probably reflected within the species composition of SA2, which should be considered as a temporally impoverished *A. alba* – *M. bidentata* community.

Geographical distribution

Unlike the relationship between the macrobenthic distribution and the physical habitat (Gray, 1974; Creutzberg et al., 1984; Buchanan, 1984; Snelgrove and Butman, 1994), the macrobenthic geographical distribution across the onshore-offshore gradient is poorly documented. Yet, this geographical distribution is of utmost importance from a national and international legislation perspective, in which distance from the shore (e.g. 3-miles and 12-miles zone) is used to set limits for fisheries (Maes et al., 2000). Detailed knowledge on the macrobenthic geographical distribution will contribute to a well deliberated use of the marine environment.

A first attempt to document the macrobenthos along the onshore-offshore gradient of the BCS is given by Govaere et al. (1980), discriminating between three zones: (1) a coastal zone with a set of species- and density-poor communities, (2) a species- and density-rich transition zone, and (3) a species-rich and density-poor open sea zone. Yet, because this study was based on only 74 sites, of which most were situated in the coastal zone and did not include the different sandbanksystems nor the sandy beaches, it was doubted whether the distinction between three zones provided a detailed and reliable view on the macrobenthic distribution at the BCS. A more complex macrobenthic distribution can be

expected and was indicated through several consequent studies (Vanosmael et al., 1982; Willems et al., 1982; Degraer et al., 1999a, 1999b, 2003).

Because of (1) the increase of the number of samples taken into account and (2) the widespread distribution of these samples, compared to Govaere et al. (1980), a more detailed view on the onshore-offshore diversity, abundance and community structure patterns is attained through this study. This distribution has to be considered as being very scattered: although a weak correlation between the zones of Govaere et al. (1980) and distribution patterns of this study was found, both cannot unambiguously be linked. Contrary to Govaere et al. (1980), the (subtidal) coastal area of the BCS cannot 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 (i.e. *A. alba* – *M. bidentata* community). The high macrobenthic diversity of the coastal zone is further illustrated by the presence of all subtidal species assemblages, distinguished in this study. Analogous to the benthic characterization of the transition zone (Govaere et al., 1980), a set of highly species- and density-rich stations and assemblages (e.g. *A. alba* – *M. bidentata* community) was found in between 5 and 15 miles offshore. Nevertheless, also macrobenthos poor stations and assemblages (e.g. *N. cirrosa* community) were encountered. Finally, the characterization of the open sea zone (> 15 miles offshore) as a species rich and density poor area, is contradicted by this study: a typically low density, but also a low species richness, was found. All assemblages found in this zone (i.e. *N. cirrosa* and *O. limacina* – *G. lapidum* community) have a low species richness and density. This study further demonstrated the existence of a typical intertidal community, with a low species richness but high density, which were not distinguished by Govaere et al. (1980).

The highly complex and diverse geomorphological environment of the subtidal part of the BCS (covered with sandbanks) can explain the rather scattered macrobenthic distribution. Within sandbank areas, even within some tens of meters, completely different types of sediment can be encountered (Gray, 1974; Vlaeminck et al., 1989; Degraer et al., 1999a). Because of the high correlation between the macrobenthos (species richness, density and species assemblages) and the physical environment (sediment mud content and median grain size, this study), this small-scale physical variability thus explains the large benthic variability along the onshore-offshore gradient. Yet, irrespective of the rather scattered benthic distribution an onshore-offshore gradient was detected: the variability at the species richness, macrobenthic density and species assemblage level is decreasing towards the open sea. These macrobenthic distribution patterns on a larger scale are more influenced by ebb-dominated currents (Sanvicente-Anorve et al., 1996). Flood-dominated currents heading towards the northeast along the coast occur onshore, while the offshore area is controlled by ebb-dominated currents pointing towards the southwest (Vlaeminck et al., 1989). The irregular and patchy distribution of sediments in the coastal zone (Ruddick et al., 1998), combined with its diverse topography, creates a wealth in habitats and thus supports a high capacity for various species assemblages, explaining the high benthic variability in the onshore zone. In contrast, sediments in the offshore area are generally coarse, due to strong currents and have a very low mud content (Ruddick et al., 1998). These sediments are inhabited by only relatively few species and density poor assemblages, explaining the

low benthic variability in the offshore area. The local diversity in all these different habitats are strongly influenced by recruitment effects, species interactions or environmental perturbations including those attributable to human activity in the different areas (Dewarumez et al., 1992; Heip et al., 1992).

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