CHAPTER 6

MACROBENTHIC ZONATION PATTERNS ALONG A MORPHODYNAMICAL CONTINUUM OF MACROTIDAL, LOW TIDE BAR/RIP AND ULTRA-DISSIPATIVE BEACHES

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ABSTRACT

The species composition, densities, biomass and zonation patterns of the macrobenthos of sandy beaches is influenced by the morphodynamics and morphology of the beaches to a great extent. To investigate the macrobenthos along a small-scale morphodynamic gradient, from the mean high water spring level (MHWS) to the mean low water spring level (MLWS), eight Belgian beaches have been investigated along a single transect, perpendicular to the water line. At each transect, ten to 14 stations were sampled, each with two replicates. Taking into account the dimensionless fall velocity (Ω) and the relative tidal range (RTR), the beaches were ordered along the gradient from the ultra-dissipative beach type (UD) to the low tide bar/rip beach type (LTBR). The beach state index (BSI) varied between 1.8 and 4.2. Generally, the beach profiles were related with the beaches' morphodynamic state.

At all beaches, the distribution of the macrobenthic characteristics were mainly determined by the height on the beach. In total 35 macrobenthic species, mainly polychaetes and crustaceans, were encountered, varying between 19 and 23 species per beach. The beaches' species composition was quite similar, with *Scolelepis squamata* being abundant at all eight beaches. Still, some remarkable differences, largely explained by the beach morphodynamics and the consequent hydrodynamics, were found. At macrobenthos-rich UD beaches, the highest macrobenthic densities and biomass were found on the upper beach, while at the macrobenthos-poor LTBR beaches, the highest densities and biomass were situated in the middle beach zone. Species, typically occurring on the upper UD beaches, such as *Bathyporeia sarsi*, *S. squamata*, and *Psammodrilus balanoglossoides*, were restricted to the sub-optimal middle beach zone at LTBR beaches. Only *Bathyporeia pilosa* could be found on the upper beach of UD and LTBR beaches, but was clearly more abundant on UD beaches. The robust polychaete *Ophelia rathkei* and the interstitial polychaete *Hesionides arenaria* were exclusively found in the upper beach zone of LTBR beaches. A summarizing zonation scheme, representing the typical species' distributions of the Belgian UD and LTBR beaches, is presented.

INTRODUCTION

The zonation of macrobenthic organisms on sandy beaches is a worldwide, well-known phenomenon: in the intertidal zone, species are occurring in very specific height zones on the beach (McLachlan and Jaramillo, 1995). Attempts to apply universal zonation schemes (Dahl, 1952; Salvat, 1964) often fail, partly due to temporal variations within the zonation patterns (Haynes and Quinn, 1995), but certainly also due to morphodynamic differences between beaches (McLachlan and Jaramillo, 1995).

Originally, the morphodynamic differences were described by differences in waves and sediment characteristics between beaches by means of the dimensionless fall velocity, Ω (Dean, 1973): beaches were classified along the continuum from reflective ($\Omega < 1$), over intermediate ($1 < \Omega < 6$), to dissipative ($\Omega > 6$) beaches (Wright and Short, 1984). Still, the influence of the tidal range on the beach morphodynamics cannot be neglected (Wright *et al.*, 1987). Nowadays, beach morphodynamics can be described by the beach state index (BSI) (McLachlan *et al.*, 1993) and the 2-dimensional beach model of Masselink and Short (1993), both taking into account the wave regime, the sediment characteristics and the tidal range of the beaches under consideration. Short (1996) slightly modified the 2-dimensional beach model and distincted six beach types (Figure 1).

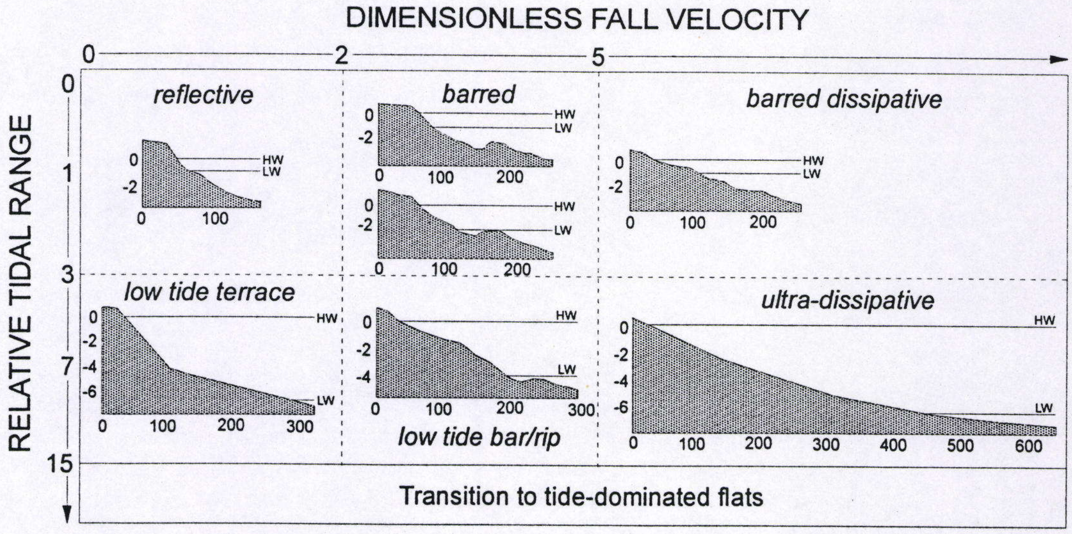

Figure 1. Schematical presentation of beach types, based on the dimensionless fall velocity (Ω) and the relative tidal range (RTR) (modified from Masselink and Short, 1993; Short, 1996). HW, high water level; LW, low water level.

Within the 2-dimensional beach model (Masselink and Short, 1993; Short, 1996), the macrobenthic number of species and density are known to increase with increasing relative tidal range (RTR) and dimensionless fall velocity (Ω): from the reflective to the ultra-dissipative beach type (e.g. McLachlan *et al.*, 1996; Borzone *et al.*, 1996).

So far, the macrobenthos of Belgian beaches is only surveyed at the macrotidal, ultra-dissipative beach of De Panne (Elliott *et al.*, 1997; Degraer *et al.*, in press b). For a detailed description of the macrobenthic community structure and zonation patterns, one is referred to Degraer *et al.* (in press b).

To investigate the influences of Ω and RTR on the macrobenthos within the small-scale morphodynamic gradient along the Belgian coastline, this study investigates the macrobenthos of eight macrotidal Belgian beaches.

MATERIALS AND METHODS

STUDY SITE

The Belgian coastline (65 km) is situated between 2°33'24"E - 51°05'42"N and 3°20'24"E - 51°22'00"N. All beaches have a semi-diurnal, macrotidal regime, with a spring tidal range of 4.5 – 5 m and a neap tidal range of 3.7 – 3.9 m. The tidal range slightly decreases from West to East. The average height and period of the waves just in front of the western Belgian coastline in 1997 were about 0.5 m and 3 s, respectively, while 3.5 m and 7 s were the maximum measured wave height and period (Anonymous, 1998). The beaches are completely composed of fine to medium sands (Degraer, unpublished results). A natural gradient of slightly increasing beach slopes, causing a decrease in beach width, exists from West to East (Depuydt, 1972). This gradient is disturbed by the construction of the harbour walls of Zeebrugge, increasing the sedimentation in their near environment by tempering the tidal currents and, consequently, increasing the width of the beaches. The tidal currents are West – East oriented during flood and East – West during ebb.

Strong tidal currents on the beaches are responsible for beach erosion on several sites along the Belgian coastline. To prevent beach erosion and inundation of the hinterland, a large part of the coastline is subjected to coastal defence works: groins, up to a length of 500 m, are numerous especially Eastwards of Nieuwpoort, while concrete dykes are found along about the whole coastline. Natural beach–dune transitions, with a length of more than 1 km, can only be found in 4 sites (total: about 9 km). A large number of tourists visit Belgian beaches, especially during summer. Most of them are concentrated near the numerous cities. One beach, 'Baai van Heist', situated just East of the harbour of Zeebrugge at Heist, is designated as a nature reserve since October 1997 (Anonymous, 1997).

To study the macrobenthos of Belgian beaches, eight sampling sites, spread over the whole coastline, were selected. From West to East, the sampling sites are: De Panne (DP), Schipgatduinen (SG), St.-Laureins (SL), Raversijde (RA), Vosseslag (VS), Fonteintjes (FO), Heist (HE) and Zwin (ZW) (Figure 2). These sites have little disturbance from recreation compared to other sites. Except for SG and VS, some important anthropogenic influences were found on the beaches (Table 1).

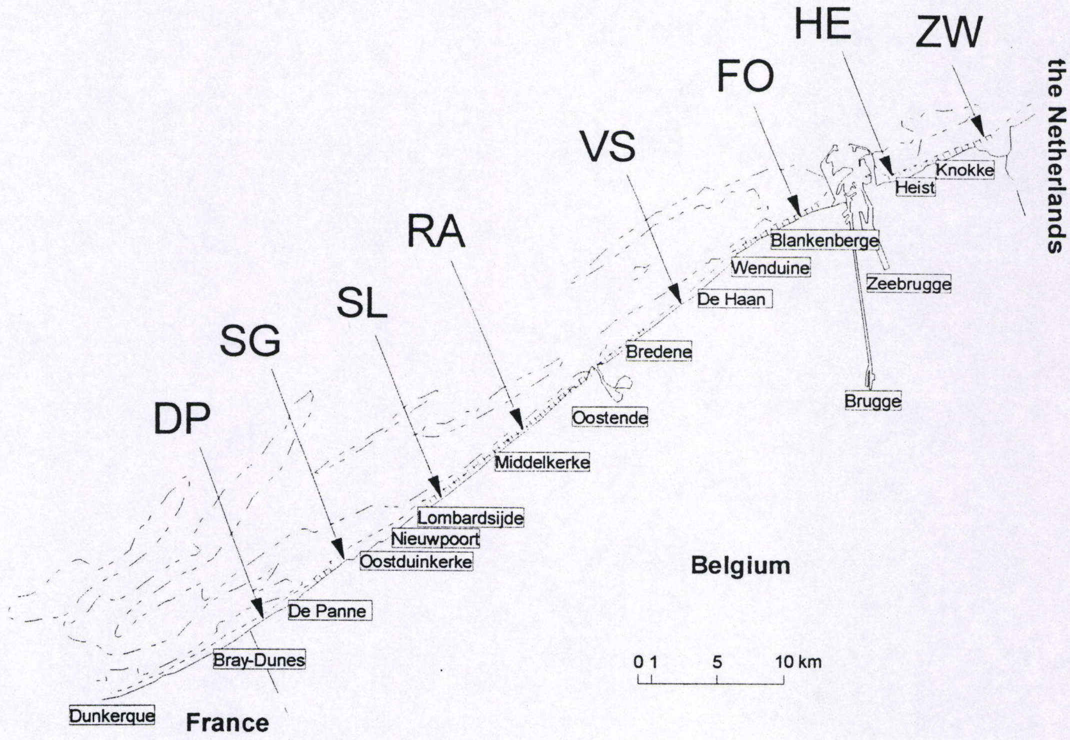

Figure 2. Geographical situation of the eight sampling sites along the Belgian coast. DP, De Panne; SG, Schigatduinen; SL, Sint-Laureins; RA, Raversijde; VS, Vosseslag; FO, Fonteintjes; HE, Heist; ZW, Zwin.

Beach	Dyke	Groins	Remarks
DP	T1	No	Fronting 'De Westhoek' nature reserve (dunes)
SG	---	No	Fronting large dune area
SL	T1	Yes	Fronting small dune area
RA	T2	Yes	
VS	---	No	Fronting small dune area
FO	T1	Yes	Fronting 'Fonteintjes' nature reserve (dunes)
HE	T1	No	'Baai van Heist' nature reserve (beach)
ZW	T1	Yes	Fronting large dune area

Table 1. General characterization of the eight beaches: Presence of a concrete dyke, with ---, dyke absent; T1, dyke above MHWS and T2, concrete dyke below MHWS; Presence/absence of groynes; Special remarks.

SAMPLING

The sampling (one beach per day) took place between 8 and 17 September 1997. At each beach, ten to 14 stations (two replicates) were sampled along a single transect, running from about MHWS to MLWS. A total of 178 samples were collected. Sampling always started at high tide and followed the receding water down the beach, ending at low tide. Samples were taken by excavating a frame (surface area, 0.1026 m²) to a depth of 0.15 m. The samples were immediately sieved through a sieve, with a 1 mm-mesh size and fixed and preserved in an 8% formaldehyde-seawater solution. At each station, one core (diameter, 1.5 cm) for sediment analysis was collected.

LABORATORY WORK

In the laboratory, the sieved samples for faunal analysis were elutriated ten times to collect the macrobenthos. Afterwards, the remaining material was examined to collect the larger macrobenthic organisms that were to heavy to be floated out by elutriation. Macrobenthic organisms were removed using a dissecting microscope, identified to species level, where possible, and counted. Faunal densities were extrapolated to the number of individuals per m² (ind m^{-2}). Biomass (Ash-Free Dry Weight or AFDW) estimates of all polychaetes, except for the Nephtyidae, and crabs were obtained by loss of mass on ignition (500 ± 50°C for 2 h) of oven-dried samples (70°C for 48 h). The biomass of all other macrobenthic organisms was calculated by regression analysis (Govaere, 1978; Mees, 1994; Degraer and Vincx, 1995).

Sediment samples were oven-dried at 105°C for 12 h and ashed at 500 ± 50°C for 2 h to determine the percentage of Total Organic Matter (TOM) by loss on ignition. The percentage of shell fragments was determined by means of the volume of the remaining sediment, consisting of shell fragments for about 100 % (Degraer, unpublished data), versus the total excavated volume of sediment. The grain size distribution of all sediment particles between 2 and 850 µm was determined with a laser COULTER LS.

MATHEMATICAL ANALYSES

The morphodynamic state of the beaches is given by the dimensionless fall velocity ($\Omega = H_b/w_sT$), the relative tidal range ($RTR = MSR/H_b$), and the beach state index ($BSI = \log_{10}\Omega * MSR$), where H_b is the modal breaker height in m, T is the modal wave period in s, MSR is the mean spring range in m, and w_s is the sediment fall velocity in m s^{-1}, obtained from Gibbs *et al.* (1971) (Masselink and Short, 1993; McLachlan *et al.*, 1993).

Macrobenthic abundances are used to calculate the diversity as the number of species per sample (N_0) (Hill, 1973). In order to investigate the mutual similarities and dissimilarities between all stations of the eight beaches, the density data (fourth root transformed) were subjected to a Canonical Correspondence Analysis (CCA) (Ter Braak, 1988). The polynomial functions, showing the general zonation trend of the macrobenthic density and the densities of the most abundant species, were retrieved by means of a distance-weighted least squares smoothing procedure of the data points as calculated by the program STATISTICA 5.1 (StatSoft, 1996). The correlations between the environmental variables were analyzed by means of the non-parametric Spearman rank correlation coefficient (Siegel, 1952; Conover, 1971).

RESULTS

ENVIRONMENT

Based on their profiles, the eight beaches (Figure 3) could be separated into two groups. A first group, including DP, SL, RA, FO, and HE, are showing a straight profile with a slope varying between 0.7° and 1.2°.

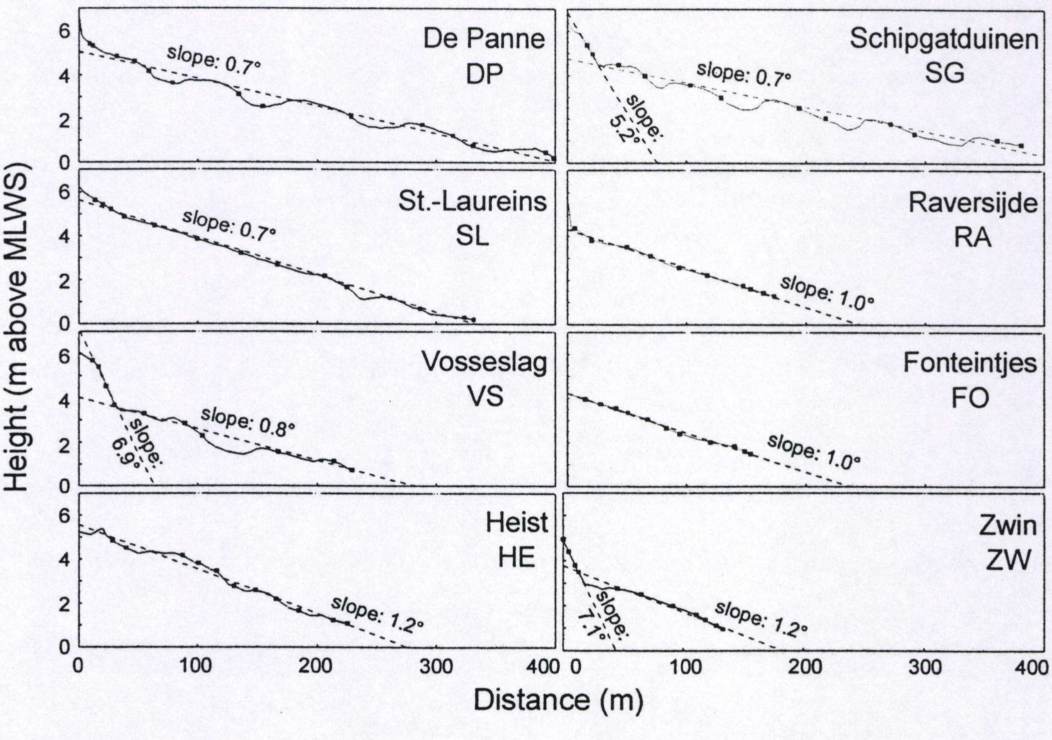

Figure 3. The beach profiles of the eight sampling sites, with indication of (1) the sampling stations (▪) and (2) the overall beach slope (DP, SL, RA, FO, and HE) or the beach slopes of the lower and upper beach (SG, VS, and ZW).

The profiles of the second group (VS and ZW) are having a break in their slope between 3 and 4 m above MLWS, separating the beach into an upper and a lower beach. The slope of the lower beach was situated between 0.7° and 1.2°, while the upper beach slope was found between 6.9° and 7.1°. SG had a large lower beach (slope: 0.7°) and a small upper beach (slope: 5.2°). An alternation of ridges and runnels was present on DP, SG, VS, and HE, while all other beaches had a quite featureless profile.

During the sampling campaign, the salinity of the coastal water was between 35.1 and 31.9 PSU, generally decreasing Eastwards; temperature varied between 15.6 and 18.6°C, generally increasing Eastwards. The average median grain size for each beach varied between 199 and 352 µm (Table 2). A general trend of increasing average median grain sizes from the western towards the eastern beaches, only disturbed by SG and VS, was found. The minimum and maximum median grain sizes were 177 and 525 µm. The percentage TOM varied between 0.4 and 1.9 %, averaging between 0.5 and 0.8 % per beach. Except for VS and ZW, the percentage of shell fragments varied between 1 and 16 %, averaging between 1 and 5 % per beach. VS and ZW had an average of 11 and 15 % of shell fragments and a maximum of 49 and 61 %, respectively. The relative tidal range (RTR) varied only little between 8.5 and 10, while the dimensionless fall velocity (Ω) and the beach state index (BSI) were spread over a larger range: 2.6 – 7.0 and 1.8 – 4.2, respectively.

	Median grain size		TOM		Shell fragments		Ω	RTR	BSI
	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean			
DP	177-235	199	0.5-0.8	0.6	1-10	4	6.8	10	4.2
SG	183-464	247	0.6-1.2	0.7	1-16	3	4.3	9.8	3.1
SL	182-246	209	0.6-1.0	0.8	1-12	5	7.0	9.5	4.0
RA	195-225	211	0.4-0.8	0.6	1-7	3	6.8	9.2	3.8
VS	235-539	352	0.5-1.9	0.7	1-49	11	3.1	9.0	2.2
FO	225-265	241	0.4-0.7	0.5	1-3	1	5.5	8.8	3.3
HE	227-275	255	0.4-1.0	0.6	1-9	2	6.2	8.7	3.4
ZW	249-525	325	0.5-1.2	0.7	1-61	15	2.6	8.5	1.8

Table 2. Median grain size, µm; Total Organic Matter (TOM), mass %; Shell fragments, volume %. Dean's parameter or dimensionless fall velocity: Ω (dimensionless); Relative Tidal Range: RTR (dimensionless); Beach State Index: BSI (dimensionless).

According to the morphodynamical classification scheme of Masselink and Short (1993), DP, SL, RA, FO, and HE are placed within the ultra-dissipative beach type (UD beaches), while SG, VS, and ZW are situated in the low tide bar/rip beach type (LTBR beaches) (Figure 4). The two most extreme beaches, regarding the dimensionless fall velocity, were SL for the UD beaches and ZW for the LTBR beaches.

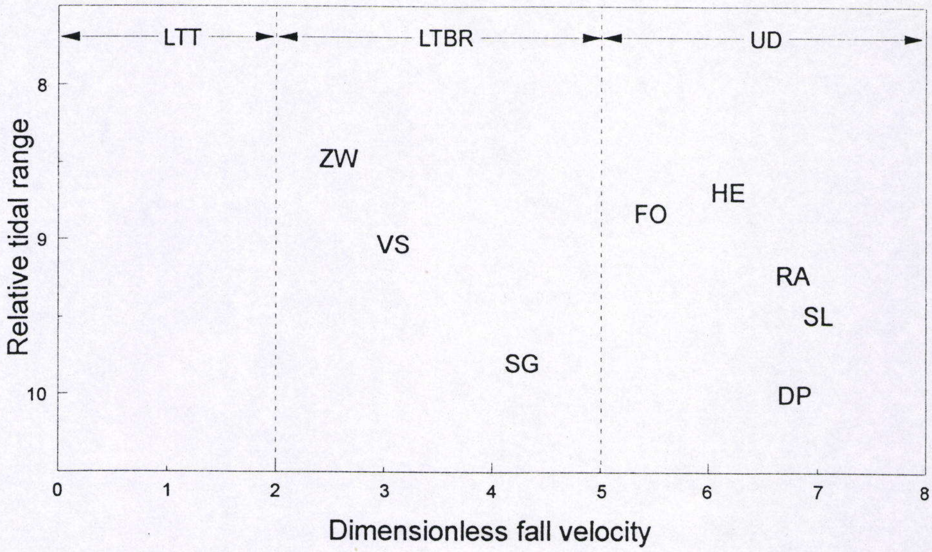

Figure 4. The situation of the eight sampling sites within the morphodynamic classification scheme of Masselink and Short (1993), based on the dimensionless fall velocity (Ω) and the relative tidal range (RTR)

MACROBENTHOS

In total 35 macrobenthic species were encountered: 17 crustaceans, 16 polychaetes and 2 bivalves. The overall average macrobenthic density and biomass were 897 ind m^{-2} and 62 mg AFDW m^{-2}, respectively. The total number of species per beach ranged from 19 to 23 species, evenly divided over the polychaetes and the crustaceans (Table 3). The macrobenthic density (289 – 1841 ind m^{-2}) and the biomass (24 – 122 mg AFDW m^{-2}) were generally dominated by the polychaetes. Combing the five most dominant species of each beach, a total of only 13 species is found. *Scolelepis squamata* was dominant in all beaches, while *Bathyporeia sarsi*, *B. pilosa*, *Eurydice pulchra*, and *Capitella capitata* were abundant in at least five of the eight beaches.

		DP	SG	SL	RA
N° of spp.	All species	19	20	23	19
	Polychaeta	9	8	11	11
	Crustacea	9	12	11	8
Density	All species	1841	289	829	1295
	Polychaeta	177	177	592	674
	Crustacea	1664	112	237	621
Biomass	All species	85	62	68	122
	Polychaeta	61	60	62	107
	Crustacea	19	2	3	15
5 most dominant species		*B. pilosa*	*S. squamata*	*C. capitata*	*B. sarsi*
		E. pulchra	*E. pulchra*	*S. squamata*	*S. squamata*
		S. squamata	*B. pilosa*	*E. longa*	*E. longa*
		C. capitata	*C. capitata*	*E. pulchra*	*P. elegans*
		B. sarsi	*B. sarsi*	*B. pilosa*	*E. pulchra*

		VS	FO	HE	ZW
N° of spp.	All species	19	19	21	19
	Polychaeta	7	7	10	12
	Crustacea	11	11	10	7
Density	All species	377	435	1369	395
	Polychaeta	216	229	972	341
	Crustacea	160	205	390	54
Biomass	All species	27	51	47	24
	Polychaeta	13	40	35	23
	Crustcea	3	4	7	1
5 most dominant species		*S. squamata*	*B. sarsi*	*S. filicornis*	*S. squamata*
		B. pelagica	*S. squamata*	*C. capitata*	*H. arenaria*
		H. arenarius	*P. balanoglossoides*	*B. sarsi*	*P. balanoglossoides*
		B. pilosa	*E. pulchra*	*S. squamata*	*O. rathkei*
		C. capitata	*B. pilosa*	*P. elegans*	*B. sarsi*

Table 3. General macrobenthic characteristics of the eight beaches

The minimum and maximum number of species per station were 0 (SL and ZW) and 15 (HE) species. Generally, an increasing number of species from the mean high water spring level (MHWS) to the mean low water spring level (MLWS) was found (Figure 5). A minimum number of species was found in the highest stations of each beach. In the extreme situation of the UD beaches (SL), the number of species increased from MHWS to 2.2 m above MLWS, then steeply decreased to 1.7 m above MLWS, and finally increased again towards MLWS. Other UD beaches and SG showed the same, though more erratical, trend. The number of species of the LTBR beaches, except SG, slightly increased between MHWS and 3 to 3.5 m above MLWS, then steeply increased to about 1.5 m above MLWS, then steeply decreased to 1 and 1.5 m above MLWS, and finally increased again towards MLWS.

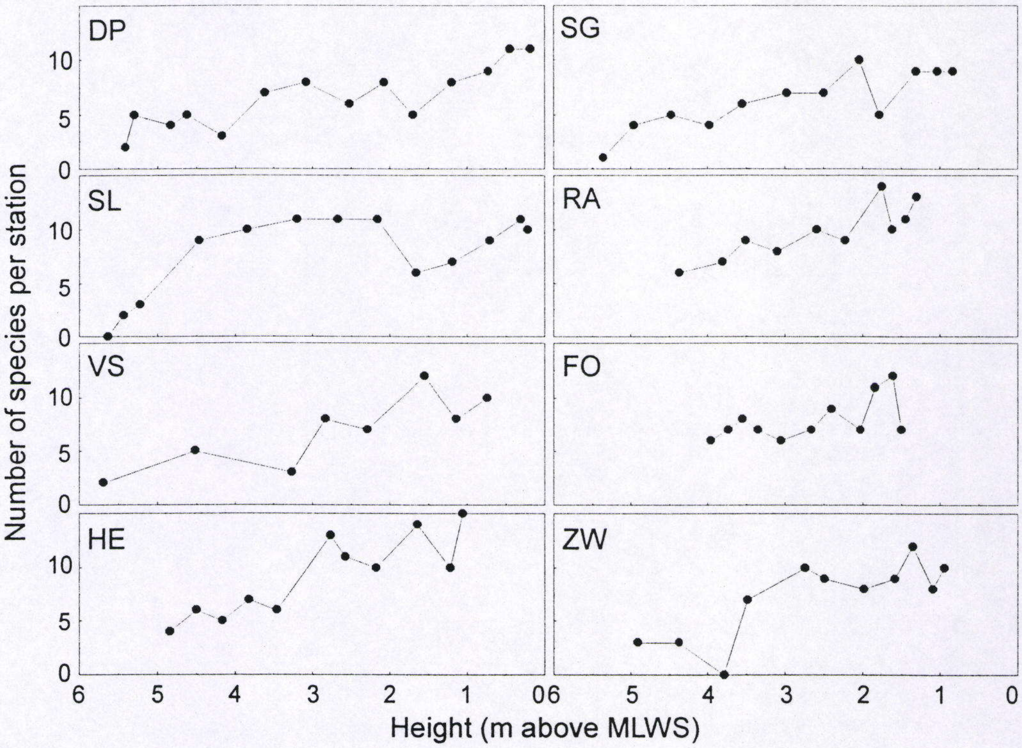

Figure 5. The distribution of the number of species per station over the intertidal zone of the eight sampling sites.

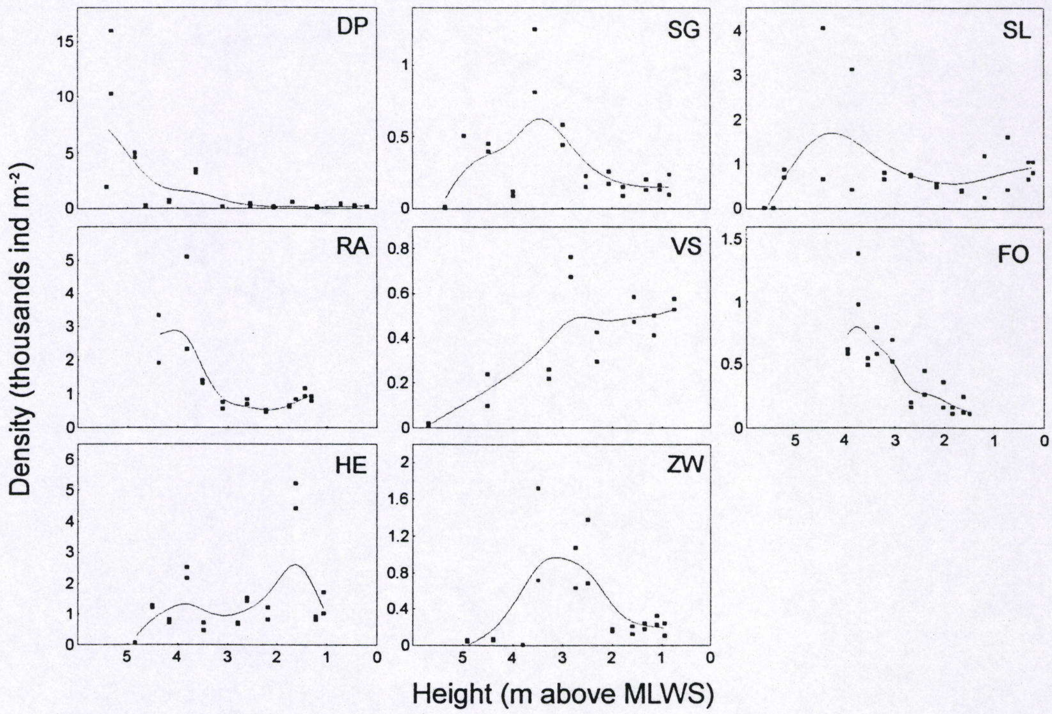

Figure 6. The distribution over the intertidal zone of the macrobenthic density of the eight sampling sites.

The densities of the UD beaches (except HE) and SG were at their maximum (1400 to 16000 ind m^{-2}) between 3.5 and 5 m above MLWS and decreased to a minimum at MHWS and 1.5 and 2.5 m above MLWS (Figure 6). At DP, SL, and RA, the densities slightly increase between 1.5 - 2.5 m above MLWS towards MLWS. Two density peaks, one at 4 m and another at 1.5 m above MLWS (2500 and 5000 ind m^{-2} respectively) were found in HE. The highest densities of the LTBR beaches (800 to 1700 ind m^{-2}), were situated between 2.5 and 3.5 m above MLWS and steeply decreased towards MHWS. At SG and ZW, the density also decreased towards MLWS, while, at VS, the density tended to increase towards MLWS.

The description of the detailed zonation patterns is based on the distributions of the main biological characteristics and the species of the two most extreme UD and LTBR beaches (SL and ZW, respectively) (Table 4). Dividing the intertidal zone into height zones, each of 1 m height, in SL and ZW, respectively, six and five height zones were sampled: in ZW, no samples were taken above 5 m above MLWS.

The average density over all height zones was 995 ind m^{-2} in SL and 443 ind m^{-2} in ZW. The maximum density of SL (2453 ind m^{-2}) was found in zone 4, while in ZW zone 4 had the lowest density (43 ind m^{-2}) and its maximum density was found in zone 2 (933 ind m^{-2}). The average biomass per height zone showed somewhat the same pattern as the average density, with (1) the lowest biomass in zone 4 of ZW (<1 mg AFDW m^{-2}), (2) the highest biomass of ZW in zone 2 (84 mg AFDW m^{-2}), and the highest density of SL in zone 3 and 4 (150 and 173 mg AFDW m^{-2}, respectively). In both beaches the number of species per sample (N_0) increased from the highest zone to zone 2, then decreased in zone 1 to increase again in SL and to further decrease in ZW in zone 0. In contrary to ZW, SL had a relatively high average N_0 over all height zones (5 versus 7 spp.). In SL, a N_0 of 8 species was already found in zone 4, while a N_0 of 8 species in ZW was only found in zone 2. In both beaches the maximum N_0 was found in zone 2. A total of 23 species was found in SL, while only 19 species were encountered in ZW. The lowest total number of species (3 spp.) was found in the highest zone of both beaches, while the highest total number of species (15 spp.) occurred in zone 0 for SL and in zone 1 for ZW. In accordance to N_0, a higher total number of species as found in the zones 4 – 2.

			Typical ultra-dissipative beach: St.-Laureins							Typical low-tide terrace beach: Zwin					
General			5	4	3	2	1	0	0-5	4	3	2	1	0	0-4
Sampled area (m²)			0.6	0.2	0.4	0.4	0.4	0.6	2.6	0.4	0.3	0.4	0.8	0.2	2.1
Average density (ind m^{-2})			263	2453	1252	629	548	925	995	49	806	933	200	175	433
Average biomass (mg AFDW m^{-2})			2	150	173	74	32	59	82	<1	3	84	17	10	23
Average N_0			1.2	8.0	8.3	8.8	5.5	8.3	6.7	2.3	3.3	7.8	7.0	6.5	5.4
Total number of species			3	9	12	14	8	15	23	3	7	11	15	10	19
Species	Taxon	Occurrence	5	4	3	2	1	0	ind.	4	3	2	1	0	Ind.
Eurydice naylori	I	SL	**	***					5						-
Bathyporeia pilosa	A	SL	**	***	*	*			176						-
Eurydice pulchra	I	both	**	***	**				186			***	*		10
Calanoidea	Co	ZW							-	***		*	*		9
Polydora sp.	P	both		***					26	***	**				3
Hesionides arenaria	P	ZW							-		***				171
Ophelia rathkei	P	ZW							-		***	***	*		124
Psammodrilus balanoglossoides	P	both		***	**	*		*	36		*	***	*	*	166
Pygospio elegans	P	both		*	**	**			20			***	**		11
Portumnus latipes	D	SL			***	***			2						-
Gastrosaccus spinifer	M	SL			**	***			4						-
Arenicola marina	P	SL			***	***			7						-
Scolelepis squamata	P	both		***	**	*	*	*	571		*	***	*	*	172
Bathyporeia sarsi	A	both		***	*	**	*	*	91		*	***	**	*	43
Paraonis fulgens	P	ZW							-				***		1
Eteone longa	P	both		*	**	**	**	**	217			**	*	***	23
Capitella capitata	P	both			*	**	**	***	635				***		21
Harpacticoidea	Co	both			*	***	**	**	94	***	*	**	*	*	50
Cumopsis goodsiri	Cu	SL				*	***	**	63						-
Spio filicornis	P	both				*	*	***	52			*	**	***	37
Haustorius arenarius	A	ZW							-			***		***	2
Spiophanes bombyx	P	SL				**		***	4						-
Nephtys cirrosa	P	both					**	***	7				***		2
Pontocrates arenarius	A	ZW							-				***	***	2
Nephtys hombergii	P	both						***	5				*	***	3
Urothoe poseidonis	A	SL						***	8						-
Crangon crangon	D	SL						***	1						-
Pontocrates altamarinus	A	SL						***	1						-
Macoma balthica	B	SL						***	1						-
Bathyporeia pelagica	A	ZW							-					***	1

Table 4. Detailed zonation patterns of the two most extreme beaches considering the dimensionless fall velocity (Ω): SL (= typical UD beach) and ZW (= typical sub-LTT beach). Zones: 5, > 5 m; 4, 4-5 m; 3, 3-4 m; 2, 2-3 m; 1, 1-2 m; 0, 0-1 m above MLWS. Taxon: P, Polychaeta; Co, Copepoda; Cu, Cumacea; I, Isopoda; A, Amphipoda; M, Mysidacea; D, Decapoda; B, Bivalvia. *, 1-20 %; **, 21-40 %; ***, >40 % of the total density over the whole beach. Ind., total number of individuals encounteres on the whole beach.

Thirty species occurred in at least one of the two beaches. These species were divided over the Crustacea (15 spp.), the Polychaeta (14 spp.) and the Bivalvia (1 sp.). 40% of the species (12 spp.) were found in both beaches, 37% is exclusively found in SL, and 23% is only encountered in ZW. Only the polychaete *Scolelepis squamata* was found in large numbers in both beaches (SL, 571 ind; ZW, 172 ind). Other species, encountered with more than 100 individuals, were the polychaetes, *Capitella capitata* and *Eteone longa*, and the isopods, *Eurydice pulchra* and *Bathyporeia pilosa*, in SL and the polychaetes, *Hesionides arenaria*, *Psammodrilus balanoglossoides*, and *Ophelia rathkei*, in ZW.
Clear groupings of species per height zone were not detected: most species were encountered over a specifical range of height zones, each with their own optimal height. A continuum of species' shifts over the full intertidal zone was present on both beaches. Considering the most abundant species of both stations, at SL, the optimal height of *E. pulchra*, *B. pilosa*, *P. balanoglossoides*, and *S. squamata* was found in zone 4, while the optimal height for *E. longa* and *C. capitata* was found in zone 0-3 and 0, respectively. At ZW, a lower optimal height for *E. pulchra*, *P. balanoglossoides*, and *S. squamata* was found (zone 2). *Eteone longa* was also occurred lower on the beach (zone 0), while zone 1 was the optimal height zone of *C. capitata*. Higher on the beach, zone 3 comprized the highest densities of *H. arenaria* and *O. rathkei*. Low densities of Urothoe poseidonis (SL), Crangon crangon (SL), Pontocrates altamarinus (SL), Macoma balthica (SL), and Bathyporeia pelagica (ZW) were exclusively found in zone 0.

GRADIENT ANALYSIS: CCA

The first axis of the CCA (eigenvalue: 0.43), comprizing all samples taken on the eight beaches, is negatively correlated with the height of the stations (Figure 7). This correlation is very clear for the UD beach (SL) and less clear for the LTBR beach (ZW). Within this height gradient no distinct groups of stations could be detected: the stations form a continuum from the upper part of the beaches towards the lower part of the beaches.
The second axis (eigenvalue: 0.15) is faintly correlated with the percentage of very fine sand (125 – 250 µm) and the median grain size. Obviously, a differentiation between the eight beaches shows up along the second axis, with the samples of DP, SG, SL, and RA having the highest values and the samples of VS and ZW having the lowest values. The samples of FO and HE are situated in between (Figure 8).

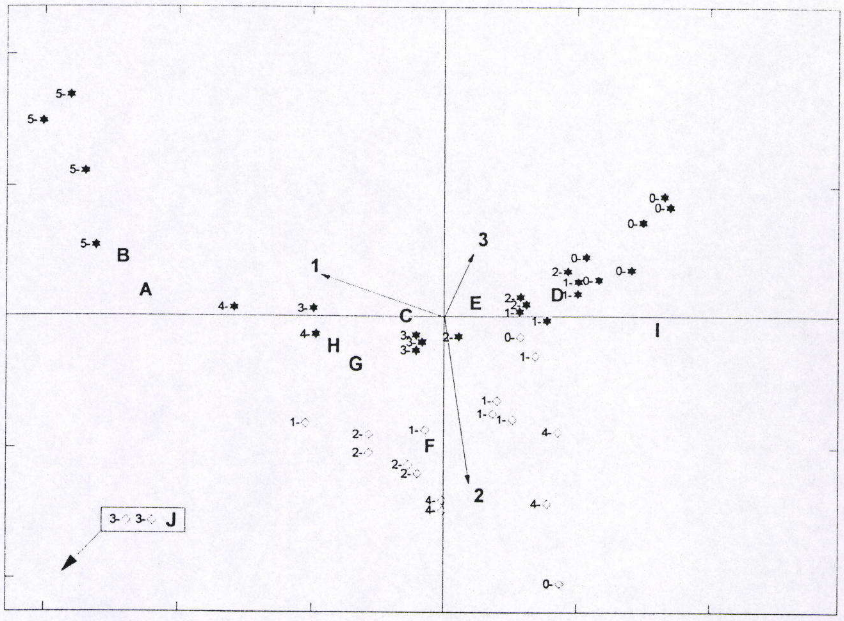

Figure 7. Situation of the samples of the typical UD beach (SL) and the typical LTBR beach (ZW), based on the Canonical Correspondence Analysis (CCA) including the samples of the eight sampling sites. ✱ , SL; ◇ , ZW and 0, 0 – 1 m; 1, 1 – 2 m; 2, 2 – 3 m; 3, 3 – 4 m; 4, 4 – 5 m; 5, 5 – 6 m above MLWS. 1, height; 2, median grain size; 3, very fine sand content. A, *Eurydice pulchra*; B, *Bathyporeia pilosa*; C, *B. sarsi*; D, *Capitella capitata*; E, *Eteone longa*; F, *Ophelia rathkei*; G, *Psammodrilus balanoglossoides*; H, *Scolelepis squamata*; I, *Spio filicornis*; J, *Hesionura augeneri*.

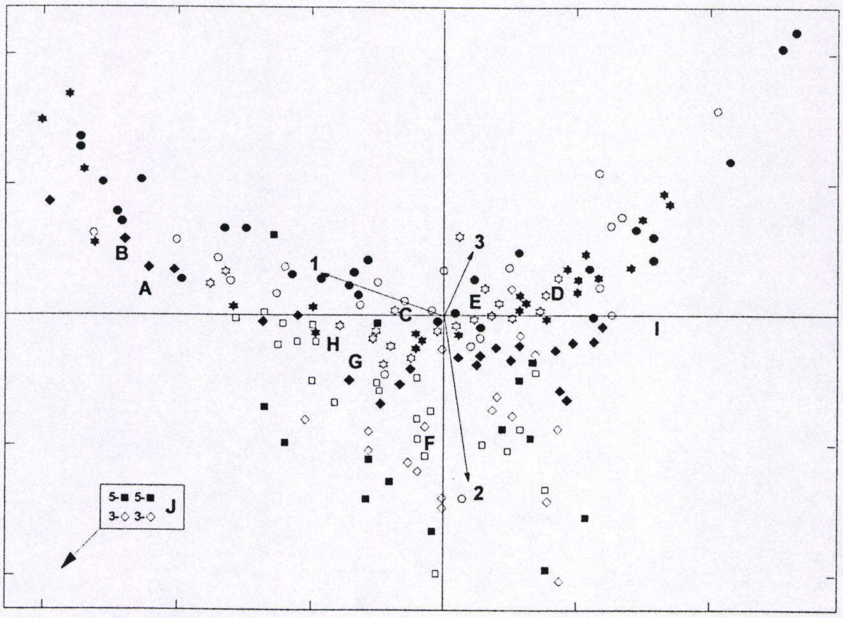

Figure 8. Situation of the samples of all beaches, based on the Canonical Correspondence Analysis (CCA) including the samples of the eight sampling sites. ● , DP; ✱, SL; O, SG; ✩, RA; ■, VS; □, FO; ◆, HE; ◇, ZW and 0, 0 – 1 m; 1, 1 – 2 m; 2, 2 – 3 m; 3, 3 – 4 m; 4, 4 – 5 m; 5, 5 – 6 m above MLWS. 1, height; 2, median grain size; 3, very fine sand content. A, *Eurydice pulchra*; B, *Bathyporeia pilosa*; C, *B. sarsi*; D, *Capitella capitata*; E, *Eteone longa*; F, *Ophelia rathkei*; G, *Psammodrilus balanoglossoides*; H, *Scolelepis squamata*; I, *Spio filicornis*; J, *Hesionura augeneri*.

Their exists a significant relation (Spearman rank correlation, $r > 0.80$; $p < 0.02$) between the average ordination scores of the samples of each beach, along the second axis of the CCA, and the dimensionless fall velocity (Ω), the relative tidal range (RTR) and the beach state index (BSI) (Figure 9). The relation with Ω and BSI is only disturbed by SG, having a lower Ω and BSI than expected form its average CCA-axis 2 score. The relation with the relative tidal range (RTR) is only disturbed by FO and HE, having a lower RTR than expected from their position along the second CCA-axis.

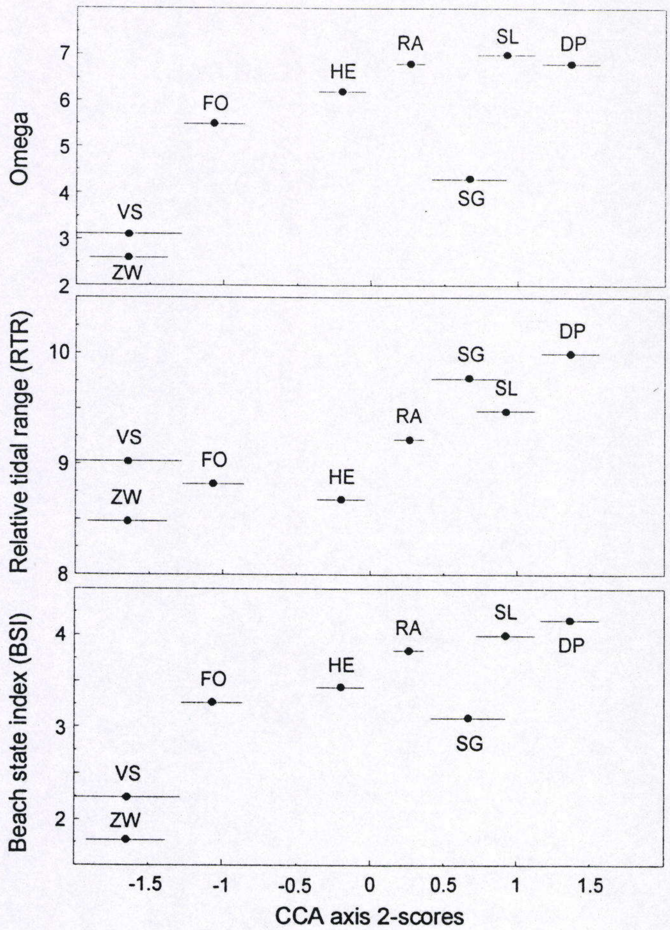

Figure 9. The relation between the average ordination scores of the samples of the eight sampling sites along the second CCA axis and the dimensionless fall velocity (Ω), the relative tidal range (RTR), and the beach state index (BSI) ± standard error.

DISCUSSION

The morphodynamic differences between the sampled beaches along the Belgian coast are small in comparison with other types of beaches (Masselink and Short, 1993). Certainly considering the relative tidal range (RTR), only a slight decrease is observed from West to

East. The major differences in morphodynamics and morphology of the beaches are indicated by the dimensionless fall velocity (Ω) and the beach state index (BSI) and visualized in the profiles of the beaches. Although, two beach types are distincted by means of Ω: the ultra-dissipative or UD beaches (DP, SL, RA, FO, and HE) and the low tide bar/rip or LTBR beaches (SG, VS, and ZW) (Short, 1996), the beaches are ordered gradually between UD and LTBR. The disturbance in the gradual transition (West to East) from UD to LTBR beaches, by FO and HE, can be explained by the presence of the harbour walls of Zeebrugge. These constructions are altering the natural tidal currents and wave regime, possibly influencing the beach morphodynamics and morphology. The beach profiles of FO and HE are also suggesting the unnatural morphology of the beaches, in comparison with the surrounding, relatively undisturbed beaches, VS and ZW.

As expected from the small morphodynamic and morphological differences, the general macrobenthic characteristics of the eight beaches have a lot of similarities (1) a similar number of species, increasing from the mean high water spring level (MHWS) to the mean low water spring level (MLWS), (2) the highest macrobenthic densities between MHWS and 2.5 m above MLWS, (3) the dominance of polychaetes and crustaceans, in terms of number of species, density, and biomass, (4) *Scolelepis squamata* as one of the five most dominant species, (5) the dominance of *Bathyporeia sarsi*, *B. pilosa*, *Eurydice pulchra*, and *Capitella capitata* in most of the beaches.

The total number of species per beach, ranging between 19 and 23 species and generally increasing towards MLWS, is similar to many other studies (e.g. Jaramillo *et al.*, 1993; James and Fairweather, 1996). The lower number of species in comparison with the 39 species, found on the beach of De Panne (39 spp.) (Degraer *et al.*, in press b), can be explained by the presence of samples below MLWS, including typical subtidal species, in the latter study (Degraer *et al.*, in press b). The macrobenthic densities are generally high, but are showing a common zonation pattern, with high densities in the upper intertidal zone. The dominance of polychaetes and crustaceans is common on most of the sandy beaches worldwide (e.g. McLachlan and Jaramillo, 1995) and has already been described for Belgian beaches as well (Elliott *et al.*, 1996; Degraer *et al.*, in press b). *Bathyporeia* spp. and *E. pulchra* are found to be abundant on many European beaches (e.g. Eleftheriou and McIntyre, 1976; Dexter, 1988; Bamber, 1993; Degraer *et al.*, in press b), while *S. squamata* is an abundant species on many Atlantic beaches (e.g. Brasilia: Souza and Gianuca, 1995; Europe: Eleftheriou and McIntyre, 1976; USA: McDermott, 1987; Rakocinski *et al.*, 1993).

Although the morphodynamic differences between the eight beaches are small in comparison with other sandy beaches (Masselink and Short, 1993), the profiles of the beaches show some clear differences. The two most extreme situations are the flat and featureless beach (SL) and the beach type with a distinction between the steeper upper intertidal and the flat lower intertidal zone (ZW). These two extremes are placed within the UD and LTBR beach type (Short, 1996).

The differences within the beach profiles are not only a visualization of the morphodynamic variation, but are directly influencing the hydrodynamical regime during the tidal cycle. On beaches with a flat slope, as the UD beach type (DP, SL, RA, FO, and HE), the swash zone is separated from the breaker zone by means of a wide (> 10 m) surf zone. This situation is also found in the lower part of the LTBR beach type (VS and ZW), where the beaches have a flat slope. On the steeper, upper part of the LTBR beaches, the breaker zone is situated directly in front of the swash zone, in absence of a surf zone. The surf zone creates a hydrodynamically benign situation, by dissipating the wave energy, while in absence of a surf zone the wave energy is directly reflected on the beach face (Masselink and Short, 1993). The high hydrodynamical forces on the upper beach of LTBR beaches, is directly responsible for the high median grain size and percentage of shell fragments, present at SG, VS, and ZW. The presence of a surf zone is thus favouring the more fragile macrobenthic organisms, such as tube-building polychaetes. The profile of SG, with a steep, but small upper beach and a flat, large lower beach, indicates towards a hybrid situation between the UD and the LTBR beach type.

Although the macrobenthos of the eight beaches show a lot of similarities, as described above, some remarkable differences between the two morphodynamically most extreme beaches, (SL for the UD beaches and ZW for the LTBR beaches) are found: (1) a lower average density and biomass in ZW, (2) the lower position of the macrobenthos-rich (density, biomass, number of species) zone in ZW, and (3) the occurrence of beach type-typical species, with *Capitella capitata*, *Eteone longa*, *Eurydice pulchra*, and *Bathyporeia pilosa*, in SL and *Hesionides arenaria*, *Psammodrilus balanoglossoides*, and *Ophelia rathkei*, in ZW. Especially the macrobenthos-rich situation of the UD beach type, SL, also demonstrated by the zonation patterns of the number of species and the density of other UD beaches (DP, RA, FO, and HE), is indicating the more benign environment of the UD beach type, with the richest zone just below MHWS. In contrary to the steeper, upper LTBR beaches (VS and ZW), the flat, lower part of the beaches allows the macrobenthos to reach a relatively high number of species, density and biomass, but still lower than the UD beaches.

The summarizing zonation scheme (Figure 10) is not aiming at the presentation of the detailed zonation patterns of all species, possibly encountered on the Belgian beaches. It rather presents the modal zonation patterns of the abundant species on the two Belgian

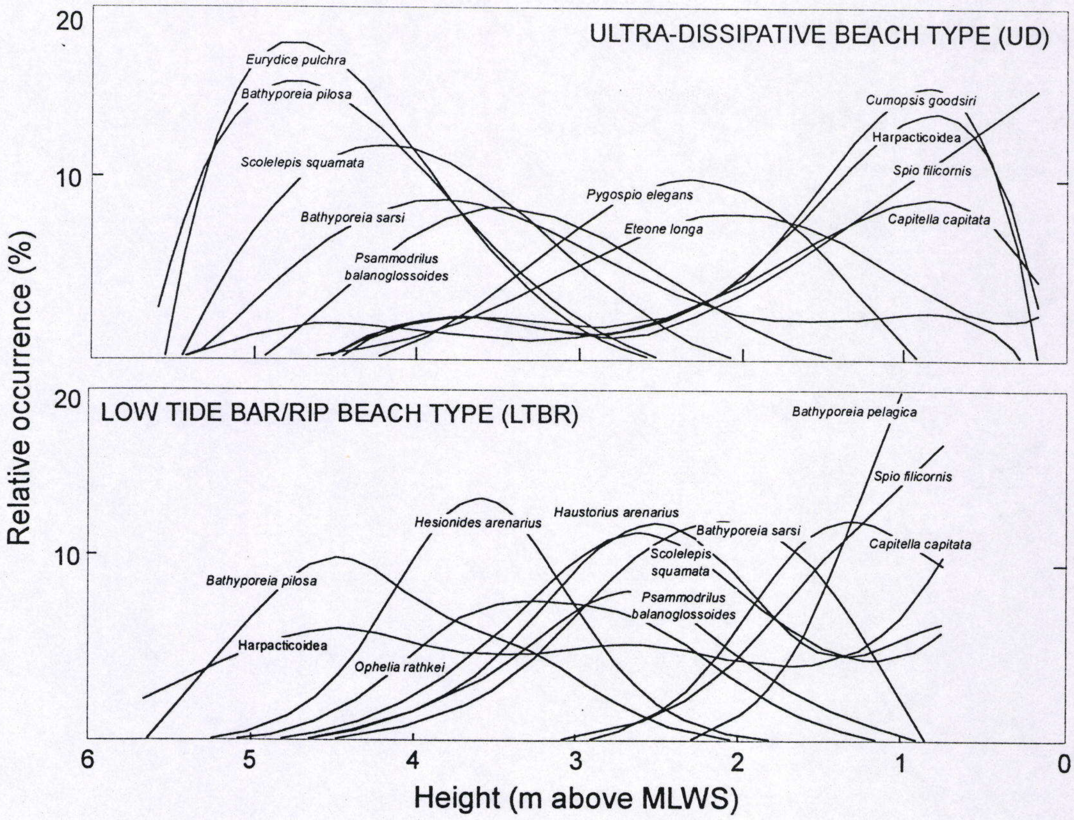

Figure 10. Summarizing zonation scheme of the macrobenthos on the UD and the LTBR beach type in Belgium, with indication of the relative occurrence of the abundant species of each beach type. In order to present the zonation schemes of typical UD and LTBR beaches, the beach SG, situated in the middle of the morphodynamic gradient, is not used to set up the summarizing zonation schemes.

beach types. As the Belgian beaches can be ordered along the morphodynamic gradient from typical UD to typical LTBR beaches, there exists a gradual transition between the two zonation schemes. Both types of beaches have a number of abundant species in common: the amphipods *Bathyporeia pilosa* and *B. sarsi* and the polychaetes *Scolelepis squamata*, *Psammodrilus balanoglossoides*, *Capitella capitata*, and *Spio filicornis*. At the UD beaches, three zones can be distincted: (1) an upper beach zone, with the optima of *Eurydice pulchra*, *B. pilosa*, *S. squamata*, *B. sarsi*, and *P. balanoglossoides* between 3.5 and 5 m above MLWS, (2) a mid beach zone, with the optima of *Pygospio elegans* and *Eteone longa* between 2 and 2.5 m above MLWS, and (3) a lower beach zone, with the optima of *Cumopsis goodsiri*, harpacticoid copepods, *S. filicornis*, and *C. capitata* below 1 m above MLWS. Obviously, a distinction between the upper and middle beach zone on Belgian UD beaches is not always possible. When studying the beach of De Panne, Degraer *et al.* (in press b) only distinguished between two zones: a high intertidal zone, dominated by *S. squamata*, and a low intertidal zone, dominated by *Nephtys cirrosa*. The low intertidal species association corresponds with the lower beach zone in this study, while the high intertidal species association is a combination of the upper and middle beach zone of this study. In this study, *N. cirrosa* is also restricted to the lower beach, but the polychaete is not abundant on any beach studied. Seasonal differences in the species' densities and distributions on sandy beaches, often related with yearly cycles of recruitment, are known to influence the zonation patterns (Haynes and Quinn, 1995). A combination of these seasonal changes and long-term changes within the macrobenthos, possibly caused by dramatic events, such as high summer temperatures or storms (Bamber, 1993), may be responsible for the observed differences of the zonation patterns and the decrease of the density of *N. cirrosa*.

At the LTBR beaches, the zonation pattern is less clear than at the UD beaches: all species are found at a specific place in the intertidal zone, but groupings of species are far less evident. The upper beach of the UD and LTBR beaches only have *B. pilosa* in common, but at the LTBR, some species, uniquely found on these LTBR beaches, as *Hesionides arenaria* and *Ophelia rathkei*, are found at the upper beach. Just like *Ophelia limacina* inhabits dynamical, coarse sediments in the shallow subtidal Belgian coast (Degraer *et al.* in press a), the robust polychaete, *O. rathkei*, is able to survive in an environment with high hydrodynamical forces, as the steep beaches (Hartmann-Schröder, 1971). The interstitial polychaete, *H. arenaria*, is known to inhabit the interstitial spaces of the coarse sediments of beaches (Hartmann-Schröder, 1971). Consequently, both species are found at the steep upper beaches of LTBR beaches, composed of coarse sediments. The optima of typical upper beach species of the UD beaches, as *B. sarsi*, *S. squamata*, and *P. balanoglossoides*, are found much lower on the LTBR beaches, where they are found together with *E. longa*. Obviously, the physical environment of the upper beach does not allow these species to survive in their optimal environment and their specifical occurrence is restricted to the middle beach. Except for *P. balanoglossoides*, they are also encountered in much lower numbers, indicating their occurrence in a sub-optimal environment.

The presence of typical subtidal species in the lower beach is demonstrated by the distribution of *S. filicornis* and *C. capitata* in both beach types, with at least a part of their vertical distribution is located in the subtidal zone (Figure 9) and suggested by the presence of *Nephtys hombergii*, *Urothoe poseidonis*, *Crangon crangon*, *Pontocrates altamarinus*, and *Macoma balthica* at the lowest heights of SL. All seven species are known to be abundant in the shallow subtidal environment of the western Belgian coast (Degraer *et al.,* in press a). The relation between subtidal and low intertidal species association is already demonstrated on several beaches worldwide (McIntyre and Eleftheriou, 1968; Souza and Gianuca, 1995; Borzone, 1996; Degraer *et al.*, in press b)

In conclusion it can be stated that, although a lot of affinities between the macrobenthic characteristics of the different beaches are found, some remarkable differences are detected, as discussed above. Generally, these differences can be explained by the morphodynamic state of the beaches. One of the most obvious differences is the general richer macrobenthos of the UD beaches, with a relatively high number of species, density and biomass on the upper beach. Species, typically found on the upper UD beaches, are restricted to the middle beach zone of the LTBR beaches. Still, the upper LTBR beach zone comprises some unique species, not encountered on UD beaches.