Abstract

Sandy shores or beaches line 70 % of the world's oceans, including the entire Belgian coastline (67 km). They have a multitude of ecosystem functions, constitute an important habitat for a variety of fauna and flora and hold important economic, social and cultural value as prime recreational assets. In order to protect the Belgian coastline against erosion and coastal flooding on a short and long term basis (up to 2050), the Belgian sandy beaches face a multitude of beach nourishment activities over the next years, as stipulated in the Belgian Master Plan for Coastal Safety. Monitoring the ecological characteristics of the Belgian beaches will aid in the detection of possible impact effects of past, current and future beach nourishment activities.

To this end, 686 intertidal and 582 shallow subtidal samples from the period 1997 – 2011 were analysed to describe the macrobenthic communities and corresponding abiotic patterns on 16 Belgian beaches. The 15 intertidal and 9 shallow subtidal locations were treated separately. The partitioning of macrobenthic community structure within the Belgian beach ecosystem showed a large within beach variability, linked to elevation on the beach (intertidal: 44 % and shallow subtidal: 50 %) and median grain size of the sediment (intertidal: 35 % and shallow subtidal: 23 %), in both the intertidal and shallow subtidal zone. Large scale along-shore spatial (intertidal: 14 % and shallow subtidal: 13 %) and long-term temporal (intertidal: 5% and shallow subtidal: 12 %) variability clearly explained less variation. Several spatial and temporal trends in abiotic factors (overall median grain size between 150 and 300 μm) and in macrobenthic species richness (intertidal: 0 – 19 species; shallow subtidal: 0 – 28 species), abundance (intertidal: 0 – 3988.75 individuals.m^{-2}; shallow subtidal: 0 – 1949.32 individuals.m^{-2}) and biomass (intertidal: 0 – 6.95 g AFDW.m^{-2}; shallow subtidal: 0 – 246.14 g AFDW.m^{-2}) were measured. The mean macrobenthic abundance in the intertidal and shallow subtidal zone fluctuates between 0 and 350 individuals.m^{-2} over the years. Furthermore, the realized niches of the dominant macrobenthic species of the Belgian beaches were defined as the area where these species really live during low tide, characterized by elevation on the beach and median grain size of the sediment.

Since all sampling locations were considered to be outside the influence of major impacting activities, these findings improve our knowledge of the natural abiotic and macrobenthic variability of the Belgian beaches. As such, this study can be used as a preconceived basis (t0 situation) of 'natural' macrobenthic variability on the Belgian beaches.

Keywords: natural variation, mesoscale patterns, sandy beaches, macrobenthos

1. Introduction

Sandy shores, also called beaches, cover 70 % of all continental margins (McLachlan & Brown 2006). They have a multitude of ecosystem functions as they are an important habitat for a variety of fauna and flora, and are concurrently of immense economic, social and cultural importance to humans as prime recreational assets. Moreover, natural sandy beaches function as a buffer between land and sea, thus protecting the hinterland from scour, inundation and wave erosion (Young & Bryant 1992; Defeo et al. 2009).
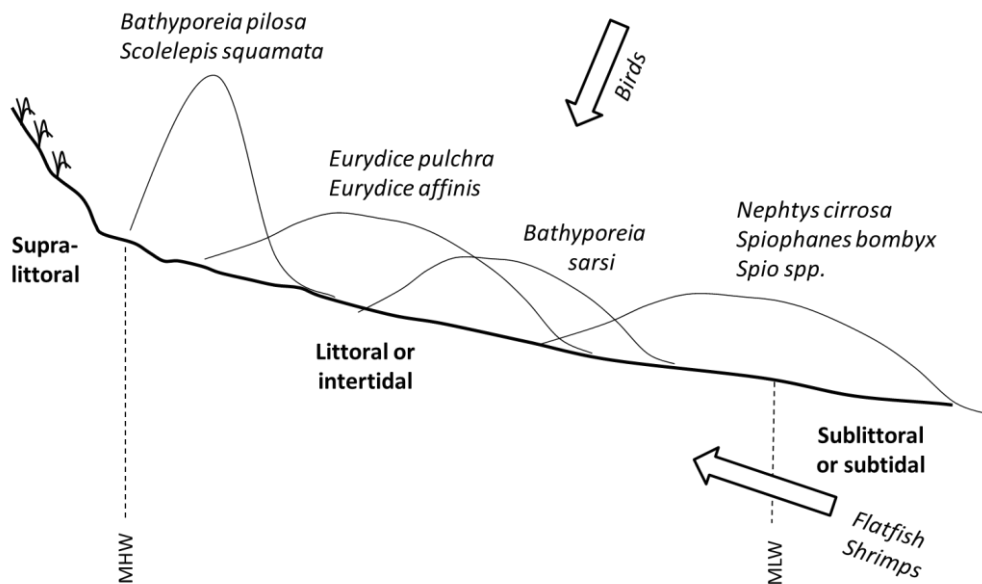
The Belgian coastline is 67 km long and entirely composed of sandy beaches. However, the ecological continuum naturally expected on this type of ecosystem, from the intertidal zone to the foredunes, is disrupted by stone breakwaters and concrete dykes (De Ruyck et al. 2001). These constructions were built as a response to erosion and coastal flood risk (Speybroeck et al. 2006a; Roode et al. 2008). In order to protect the Belgian coast (up to 2050) a multitude of beach nourishment projects are planned over the next years (Mertens et al. 2008). Monitoring the ecological characteristics of the Belgian beaches will aid in the detection of possible impact effects of past, current and future beach nourishment projects.

Belgian beaches are wide and (ultra)dissipative (Speybroeck et al. 2008a), displaying a semi-diurnal macrotidal regime (De Moor 1979, 1986; De Moor & Bloome 1988; De Moor 2006). The sandy sediment has an across-shore average grain size ranging from 160 µm to 380 µm (Speybroeck et al. 2008a). It becomes coarser from west to east and from the subtidal zone up to the supralittoral dry beach. A natural gradient of slightly increasing beach slopes and consequently decreasing beach width also exists from west to east (Depuydt 1972). Sandy beaches have across-shore, defined as perpendicular to the water line, and along-shore, defined as parallel to the water line, dimensions (James & Fairweather 1996), giving rise to small-scale morphodynamic and associated macrobenthic gradients (Degraer et al. 2003b).

Macrobenthos is generally defined as the organisms measuring over 1 mm long and living buried in the seabed. This group of bivalves, polychaetes, crustaceans and echinoderms performs well as an indicator of pollution and stress and plays a key role in the beach ecosystem and foodweb. They feed on detritus, algae and/or other benthic animals (Sundbäck & Persson 1981; Josefson et al. 2002). In turn, they are a major food source for birds and epibenthos (crabs, shrimp, juvenile fish). Owing to the highly dynamic nature of their environment, mainly determined by waves, tides and winds, macrobenthic species have a high tolerance towards several forms of environmental stress. Some key adaptations to their habitat are mobility, burrowing ability, rhythmic (e.g. tidal, circadian, (semi)lunar, seasonal) behavior, orientation mechanisms and flexibility to cope with rapidly changing conditions (McLachlan & Jaramillo 1995; Defeo et al. 2009).

The distribution of macrobenthos on sandy beaches has been well documented in many parts of the world (e.g., (Dexter 1979; Knott et al. 1983; Jaramillo & McLachlan 1993; McLachlan & Jaramillo

1995; Fernandes & Soares-Gomes 2006; Veloso et al. 2006), including the Belgian sandy beaches (Degraer et al. 1999a; Degraer et al. 2003b; Speybroeck et al. 2008a). Along the Belgian across-shore gradient, variability can be detected within the macrobenthic spatial distribution (figure 1), from sparse high intertidal to somewhat diverser shallow subtidal communities (Speybroeck 2007). In general, a very narrow high intertidal zone is the habitat of the amphipod *Bathyporeia pilosa* and the polychaete *Scolelepis squamata*. The isopod *Eurydice pulchra* and the amphipod *Bathyporeia sarsi* live in a wide zone in the middle of the intertidal area. In the lowest parts of the intertidal zone, several polychaetes, e.g. *Nephtys cirrosa*, and bivalves have to share the space. The shallow subtidal zone has never been investigated in detail before, but different subtidal communities can be distinguished from the French to the Dutch border (Degraer et al. 2003b; Van Hoey et al. 2004). The dominant subtidal species are the bivalves *Abra alba*, *Macoma balthica* and *Kurtiella bidentata*, the polychaetes *Cirratulidae* species, *Glycera lapidum*, *Magelona* species, *Nephtys cirrosa*, *Ophelia borealis* and *Spiophanes bombyx*, and the amphipod *Urothoe brevicornis*.

Figure 1: Zonation pattern of different Belgian macrobenthos species (adapted from (Van Tomme 2013)); MHW: mean high water level; MLW: mean low water level

Due to temporal variations within the zonation patterns (Haynes & Quinn 1995) and morphodynamic differences among beaches (McLachlan & Jaramillo 1995), attempts to apply universal zonation schemes in the intertidal and shallow subtidal beach zones (Dahl 1952; Salvat 1964) have often failed. Intertidal sand is a fundamentally unstable habitat for infauna as it is subjected to both regular small-scale disturbance and irregular, often frequent, large-scale disturbance resulting from storms. It also suffers from rapid fluctuations in physical and chemical characteristics. Subtidal sandy deposits are equally unstable but not subjected to the additional stress of twice daily inundation and exposure by the tides (Hayward 1994). In the end, the species composition, richness, abundance (McLachlan & Jaramillo 1995; Veloso & Cardoso 2001) and biomass (Adriaanse & Coosen 1991; McLachlan et al.
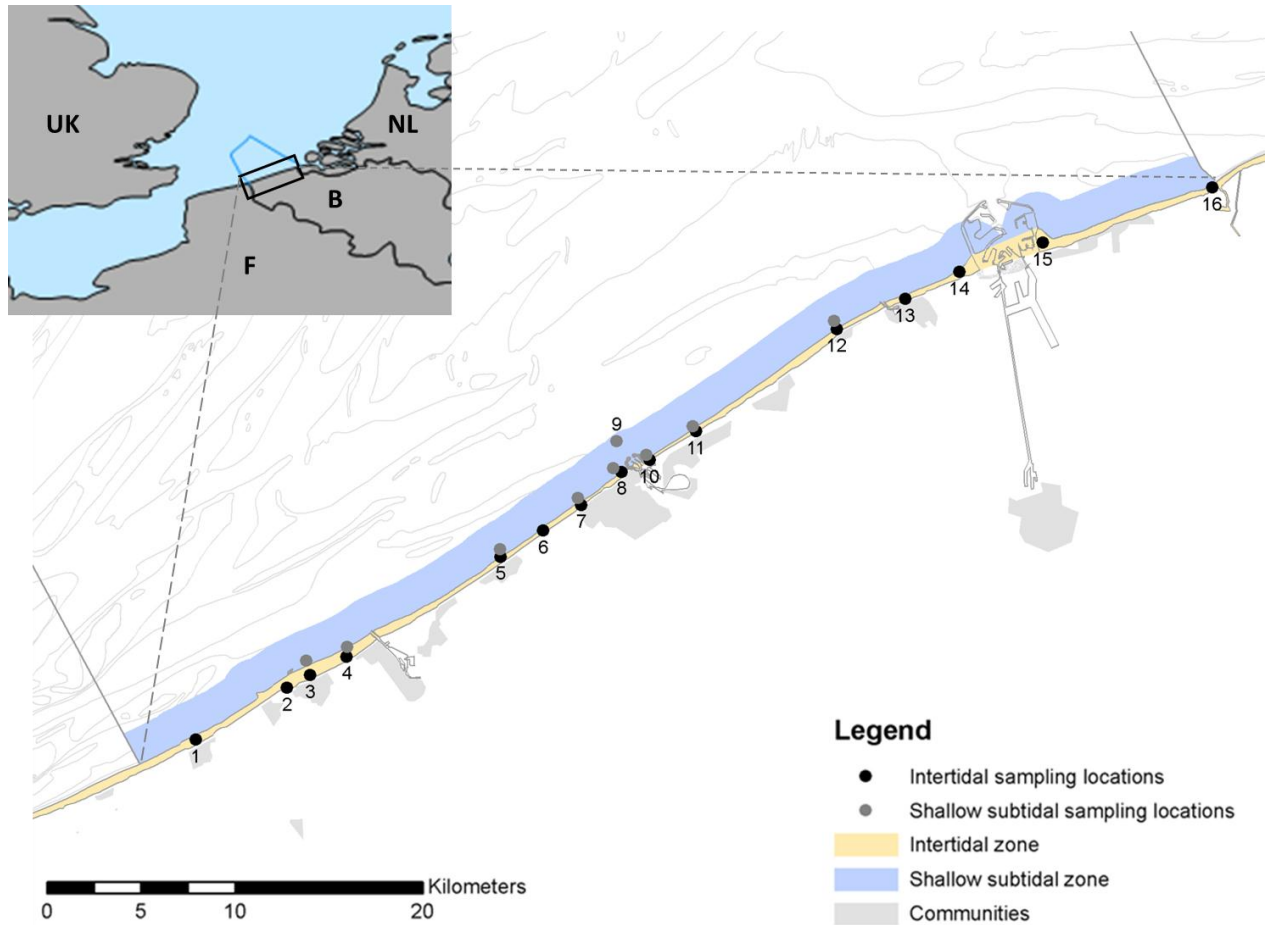
1996a; McLachlan & Dorvlo 2005) always feedback with the abiotic environment. Although currents, salinity and temperature may be basic steering variables (Govaere et al. 1980; Creutzberg et al. 1984), the most important morphodynamic beach characteristics on Belgian beaches are grain size, slope or beach elevation and total organic matter (Degraer et al. 2003b; Speybroeck et al. 2006a). This natural variability and spatial patchiness of macrobenthic organisms complicates the study and quantification of possible impact effects of, for instance, beach nourishment activities.

Previously, the macrobenthos of Belgian beaches has been surveyed in detail at the ultra-dissipative beach of De Panne (Elliott et al. 1997; Degraer et al. 1999a) and on eleven intertidal beaches that were regarded as being pristine (Speybroeck et al. 2005b; Speybroeck et al. 2008a). The general aim of this study is to update our knowledge of the Belgian beach ecosystem in both the intertidal and shallow subtidal zone. An extensive list of longitudinal Belgian macrobenthic data is used to investigate (1) the natural spatial and temporal macrobenthic variability within the Belgian beach ecosystem, (2) the relationship between relevant abiotic factors, such as beach elevation, sediment structure, total organic carbon and total organic matter, and the macrobenthos on Belgian sandy beaches and (3) the observed niche and interpolated occurrence of the dominant macrobenthic species on Belgian sandy beaches.

2.   Material and methods

2.1   Study Area

The subdivision of the shallow Belgian coastal zone follows the ecological zonation, focusing specifically on the intertidal and the shallow subtidal zones (figure 2). It is therefore defined by a landward boundary that follows the high water mark obtained by airborne Light Detection And Ranging (LIDAR) observations of the Belgian coast in 2011 (data provided by the Agency for Maritime and Coastal Services: Coastal division – MDK(Deronde et al. 2008) and a seaward boundary for the shallow subtidal foreshore of 1 nautical mile from the zero depth (0 m) bathymetric line (figure 2).

Figure 2: The Belgian coastal zone, with a distinction between the intertidal (light brown) and shallow subtidal zone (blue), showing the sixteen sampling locations (code specifications in table 1)

2.2   Data

Since 1997, the Marine Biology Research Group of Ghent University coordinated numerous macrobenthic studies along the Belgian coastline. An integrated database comprises all available relevant data gathered during the period 1997 – 2011 in the intertidal and shallow subtidal zones (table 1). Sixteen intertidal locations were investigated, together with 9 nearby shallow subtidal locations. Intertidal and shallow subtidal samples were also taken at the beach of Lombardsijde. As these samples were taken to monitor an actual nourishment (performed in 2009), they will be analysed in the next chapter.

Table 1: Sampling locations used for the integrated macrobenthic database. Only data collected in intertidal and shallow subtidal zones of the Belgian coast (key: S=spring; A=autumn; a (Degraer et al. 2003b); b (Speybroeck et al. 2003); c (Welvaert 2005); d (Van Ginderdeuren et al. 2007); e (Vanden Eede et al. 2008); f (Vanden Eede & Vincx 2010); g (Vanden Eede & Vincx 2011b); h (Vanden Eede et al. 2013))

INTERTIDAL ZONE		1997 A	2002 A	2004	2006 A	2008 S	2009 S	2009 A	2010 S	2010 A	2011 S	2011 A
Study	Codes	a	b	c	d	e	f	f	g	g	h	H
De Panne	1	28										
Schipgatduinen	2	22										
Koksijde-Oostduinkerke	3			15	26							
Nieuwpoort	4					26	26	26	15	15	15	15
Middelkerke	5		18	15	26							
Raversijde	6	20										
Mariakerke	7											15
Oostende-Center	8		33	45	25							
Oostende-East	10			25	25				15	15	15	15
Bredene	11								15	15	15	15
Wenduine	12			15	26							
Blankenberge	13											15
Fonteintjes	14	22										
Heist	15	22										
Zwinduinen en Polders	16	20										
Total amount of samples		**134**	**51**	**115**	**128**	**26**	**26**	**26**	**45**	**45**	**45**	**75**

SHALLOW SUBTIDAL ZONE		1997 A	2002 A	2004	2006 A	2008 S	2009 S	2009 A	2010 S	2010 A	2011 S	2011 A
Study	Codes	a	b	c	d	e	f	f	g	g	h	H
Koksijde-Oostduinkerke	3			15	25							
Nieuwpoort	4					25	25	25	15	15	15	15
Middelkerke	5		18	15	25							
Mariakerke	7											15
Oostende-Center	8		42	45	25							
Oostende-Fairway	9			15	12							
Oostende-East	10			25	25				15	15	15	15
Bredene	11								15	15	15	15
Wenduine	12			15	25							
Total amount of samples		**0**	**60**	**130**	**137**	**25**	**25**	**25**	**45**	**45**	**45**	**60**

2.3   Sampling method

Intertidal sampling always started at high tide and followed the receding water down the beach, as the organisms tend to cluster very close to the water line, ending at low tide. Samples were taken by excavating a quadrat frame (surface area, 0.1026 m²) to a depth of 0.15 m. The samples were immediately sieved (ø 1 mm) and preserved in an 8 % formaldehyde-seawater solution. Next to each biotic sample, one core sample (ø 3.6 cm) for sediment analysis was collected. At every sampling location, a beach profile and the geographic position (geographic wgs84) were noted. As we always sample at the water line, we can deduce the real elevation of the sample locations to the water surface (MLW, mean low water level) using the M2 reduction model (Van Cauwenberghe et al. 1993). The shallow subtidal zone was sampled with a small vessel at high tide. At every sample location, a Van Veen grab was lowered to take a sediment sample (surface area, 0.1026 m²). Simultaneously,

the coordinates (UTMwgs84), time and depth of each sample were determined. The depth was afterwards corrected (compared to MLW) using the M2 reduction model. Before opening the Van Veen grab, a core sample (ø 3.6 cm) for sediment analysis was taken. The samples were immediately sieved (ø 1 mm) and preserved in an 8 % formaldehyde-seawater solution.

2.4   Laboratory procedures

The sieved samples for faunal analysis were stained with Rose Bengal and elutriated ten times to collect the macrobenthos. The remaining material was examined to collect the larger organisms that were too heavy to be floated off by elutriation. All macrobenthic organisms, except for Oligochaeta, Actiniaria and Nematoda, were identified to species level, where possible, and counted. Faunal abundance was extrapolated to the number of individuals per m². Biomass (gram Ash Free Dry Weight or g AFDW) estimates were obtained by loss of mass on ignition (480 °C for 2 h) of oven-dried samples (110 °C for 24 h) (Van Ginderdeuren et al. 2007; Vanden Eede et al. 2008; Vanden Eede & Vincx 2010, 2011b; Vanden Eede et al. 2013). The biomass was calculated on higher taxon level except for the dominant species, being *Bathyporeia pilosa and Bathyporeia sarsi*, *Ensis* juveniles, *Eurydice* species, *Lanice conchilega, Macoma balthica* juveniles, *Nephtys cirrosa*, *Owenia fusiformis, Scolelepis squamata* and *Spisula subtruncata*.

After drying the sediment samples, the grain size distribution was determined with a Malvern Mastersizer 2000G laser with diffraction module (measuring range: 0.02 – 2000 µm). In this paper, sediment was characterized by median grain size (µm) and silt fraction (< 63 µm). The percentage of shell fragments was determined by means of the percent volume of sediment remaining on the 1 mm sieve (carbonate content). The values for Total Organic Carbon (TOC) were calculated with an automatic element analyzer 1500 Carlo Elba. The percentage of Total Organic Matter (TOM) was obtained by loss of mass on ignition, using the biomass analysis strategy.

2.5   Data analysis

In total, 721 intertidal and 582 shallow subtidal samples were gathered between 1997 and 2011. 35 intertidal samples were excluded from the analyses as they contained no macrobenthos. In total, 207 species were identified from which 89 species were taken into account (79 species in the intertidal zone and 86 species in the shallow subtidal zone). The species excluded from these analyses clearly attributed to other benthic groups, e.g. meiobenthos, hyperbenthos or epibenthos, and/or were gathered in a non-representative way, e.g. a frequency of occurrence of less than 0.5 % and a maximum of 5 individuals per sample (Appendices – Chapter 2 – table A). The sampling location maps were created with ESRI ArcMap Version 9.3. Multivariate analyses in Primer v6 were used to detect patterns in the distribution of macrobenthic assemblages, without transforming data. Multidimensional scaling was based on Bray-Curtis similarity, a statistic used to quantify the compositional dissimilarity (abundance data per species) between different sampling locations.

Samples within a cluster are more similar than samples of different clusters. To partition the abiotic and macrobenthic variance on Belgian beaches, the adonis function of the Vegan package in R 2.14.2 was used. It fits permutative linear models (e.g., factors, polynomial regression) to Euclidean (abiotic data) and Bray-Curtis (macrobenthic data) distance matrices and allows for nonparametric analysis of variance using these distance matrices. The Spearman's rank correlation coefficient was calculated in R 2.14.2 to assess the relationship between median grain size (µm) and elevation (m versus MLW). Based on these two abiotic variables, the realized niche of the dominant intertidal and shallow subtidal species of the Belgian beaches could be illustrated by contour plots (R2.14.2, with the akima and lattice packages). All tables and basic graphs were made in Microsoft Excel 2010.
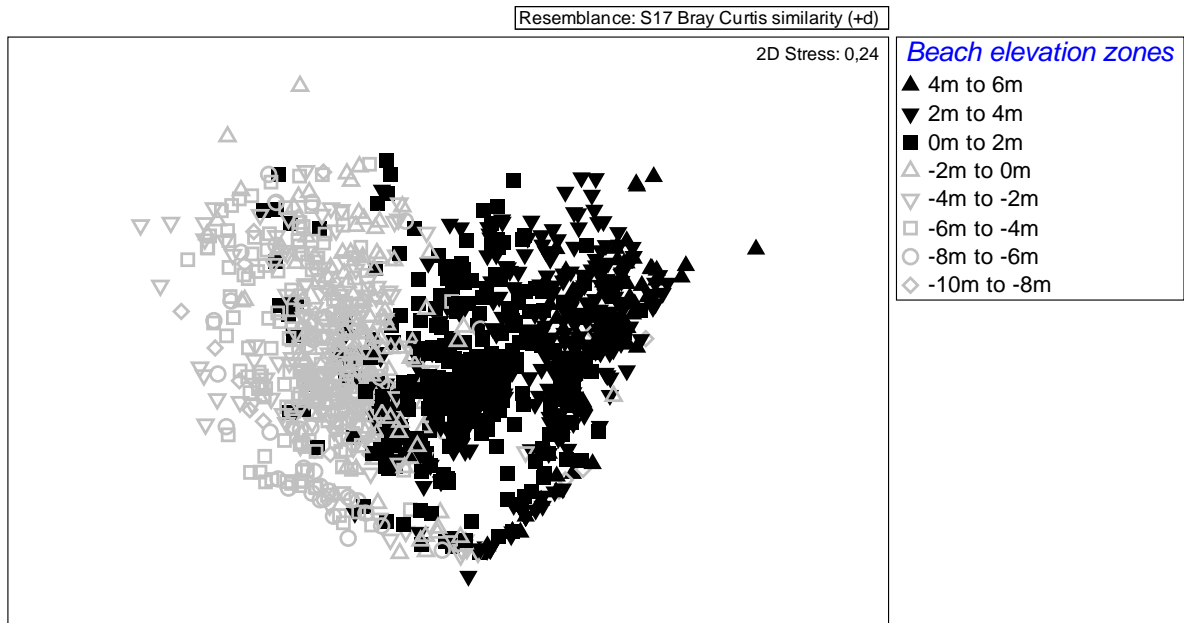
3.   Results

Minimum, maximum and mean intertidal and shallow subtidal values for the measured abiotic and biotic factors are given in table 2. Between these minimum and maximum values the natural variation on Belgian beaches runs its course.

Table 2: Mean, minimum and maximum values for abiotic and biotic factors in the intertidal and shallow subtidal zone (MLW: mean low water level; AFDW: ash-free dry weight)

	Beach elevation (m versus MLW)	Median grain size (µm)	Silt fraction (%)	Total organic matter (%)	Total organic carbon (%)	Carbonate content (%)	Species richness (number of species)	Abundance (number of individuals.m^{-2})	Biomass (g AFDW.m^{-2})
INTERTIDAL									
mean	2.32	241.55	0.02	0.39	0.47	8.71	4.42	104.62	0.34
minimum	0.00	175.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
maximum	5.41	464.00	2.25	1.84	19.00	36.68	19.00	3988.75	6.95
SHALLOW SUBTIDAL									
mean	-3.70	181.44	5.47	0.93	0.63	10.09	8.08	107.57	7.85
minimum	-10.00	17.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00
maximum	-2.67	319.73	89.30	11.75	4.85	36.10	28.00	1949.32	246.14

Multidimensional scaling (MDS) of all sampling data did not indicate a clear separation of the macrobenthic data based on spatial (different beaches) or temporal (different years or seasons) variables. There is an overlap visible between samples from the intertidal and shallow subtidal zone (Figure 3). However, since these two habitats are substantially different to harbor other macrobenthic communities, as described in Chapter 1 and in Van Hoey et al. (2004), the intertidal and shallow subtidal data were treated separately.

Figure 3: MDS plot of all data, showing a partitioning into two groups, being intertidal (black) and shallow subtidal (grey) samples with overlap around mean low water level, and to a lesser extent into beach elevation zones

3.1 Partitioning of abiotic and macrobenthic variance on Belgian beaches

The partitioning of abiotic variance (Appendices – Chapter 2 – tabel B1) is based on six abiotic factors, being beach elevation (m versus MLW), median grain size (µm), silt fraction (%), carbonate content (%), total organic carbon (%) and total organic matter (%). Figure 4 shows an apparent quantitative difference between beaches (intertidal: 57 % and shallow subtidal: 45 %) and between years (intertidal: 22 % and shallow subtidal: 28 %), rather than between seasons (intertidal: 0.5% and shallow subtidal: 1 %).

The partitioning of macrobenthic variance (Appendices – Chapter 2 – tabel B2) is based on the macrobenthic abundance data and all six abiotic factors (figure 4). Large scale spatial (intertidal: 14% and shallow subtidal: 13 %) and temporal (intertidal: 5 % and shallow subtidal: 12 %) variability explains less variation in community structure than within beach elevation (intertidal: 44 % and shallow subtidal: 50 %) and median grain size (intertidal: 35 % and shallow subtidal: 23 %). There appears to be a large within beach variability in macrobenthic abundance, linked to elevation on the beach and median grain size of the sediment.

INTERTIDAL

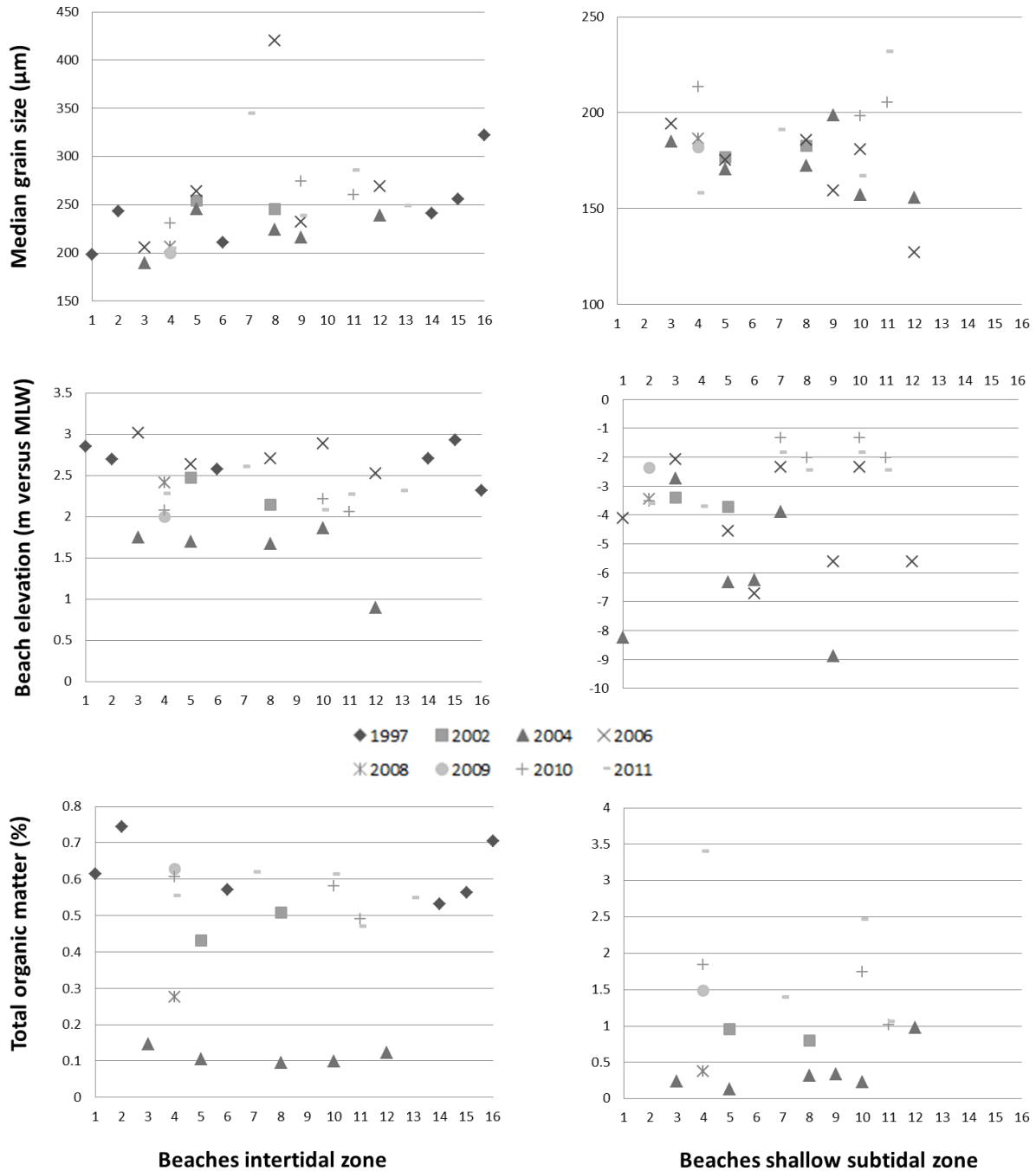**SHALLOW SUBTIDAL**

INTERTIDAL

SHALLOW SUBTIDAL

Figure 4: Partitioning of abiotic (top) and macrobenthic variance (bottom) in the intertidal and shallow subtidal zone along the Belgian coastal area, based on data from 1997 – 2011, representation of the R² values (as percentages) given in Appendices – Chapter 2 – Table B1 and B2
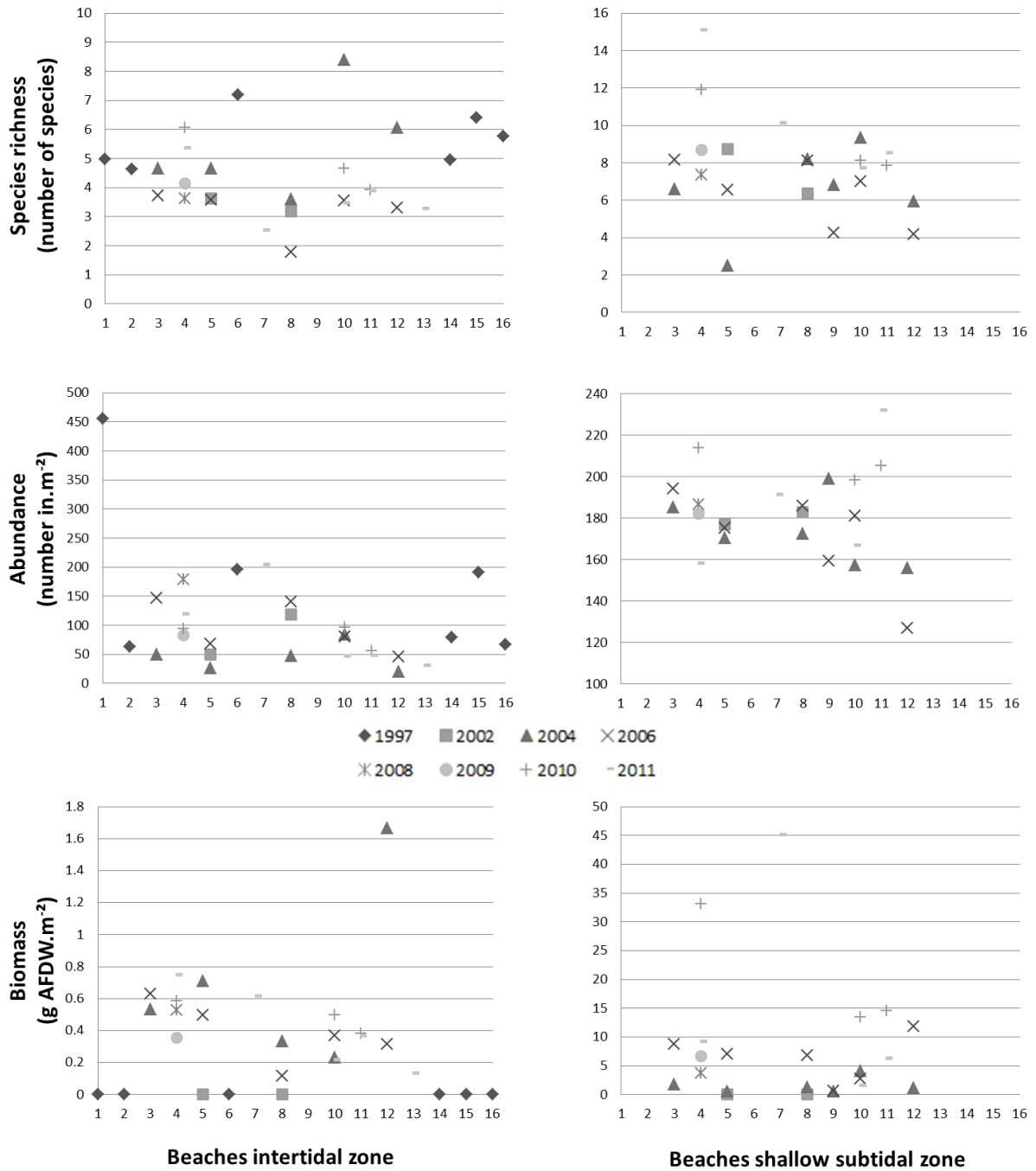
3.2   Spatial and temporal macrobenthos variation

The variation between beaches and the variation between years has been analyzed in great detail and the tables in Appendices – Chapter 2 – table C and D give an overview of the mean abiotic and biotic values, respectively per beach over all the sampled years and per year over all the sampled

beaches. The two most important abiotic characteristics according to figure 4, e.g. grain size (µm)a dn elevation on the beach (m versus MLW), and TOM (%) are analyzed per beach per year (figure 5), next to the three biotic factors, e.g. species richness (number of species), abundance (number of indviduals.m^{-2}) and biomass (g AFDW.m^{-2}) (figure 6). The mean intertidal median grain size coarsens when going from west (200 – 250 µm) to east (250 – 330 µm). A peak mean value of 420.54 µm was only registered once in 2006 on the beach of Oostende-Center. The shallow subtidal zone holds much finer sediment (120 – 230 µm) which appears to become even finer when going from west to east. The intertidal mean beach elevation values vary between 1.5 and 3 m relative to the MLW. The mean depth of the shallow subtidal samples shows greater variation (-1 and -9 m) with the deepest values recorded in 2006. The shallow subtidal zone also holds much higher mean TOM values (0 - 3.5 %) than the intertidal zone (0 – 0.8 %). In 2004, the lowest mean TOM values were recorded in both the intertidal and shallow subtidal zone. Figure 7 shows that the mean species richness is higher in the shallow subtidal (2 – 16 species) than in the intertidal zone (2 – 9 species). The highest mean species richness was recorded in 2011 in the shallow subtidal zone of Nieuwpoort (15 species). The intertidal mean abundance fluctuates between 20 and 200 individuals.m^{-2} with a peak mean abundance value of 456 individuals.m^{-2} recorded in De Panne in 1997. Mean shallow subtidal abundance varies between 120 and 230 individuals.m^{-2}. The mean biomass in the intertidal zone (0 – 0.8 g.m^{-2}) is significantly lower than in the shallow subtidal zone (0 – 45 g.m^{-2}). One mean intertidal peak value can be seen in 2004 in Wenduine (1.7 g.m^{-2}). In the shallow subtidal zone, the mean 2010 biomass value of Nieuwpoort (33.1 g.m^{-2}) and the mean 2011 biomass value of Mariakerke (45.2 g.m^{-2}) are the only outliers.
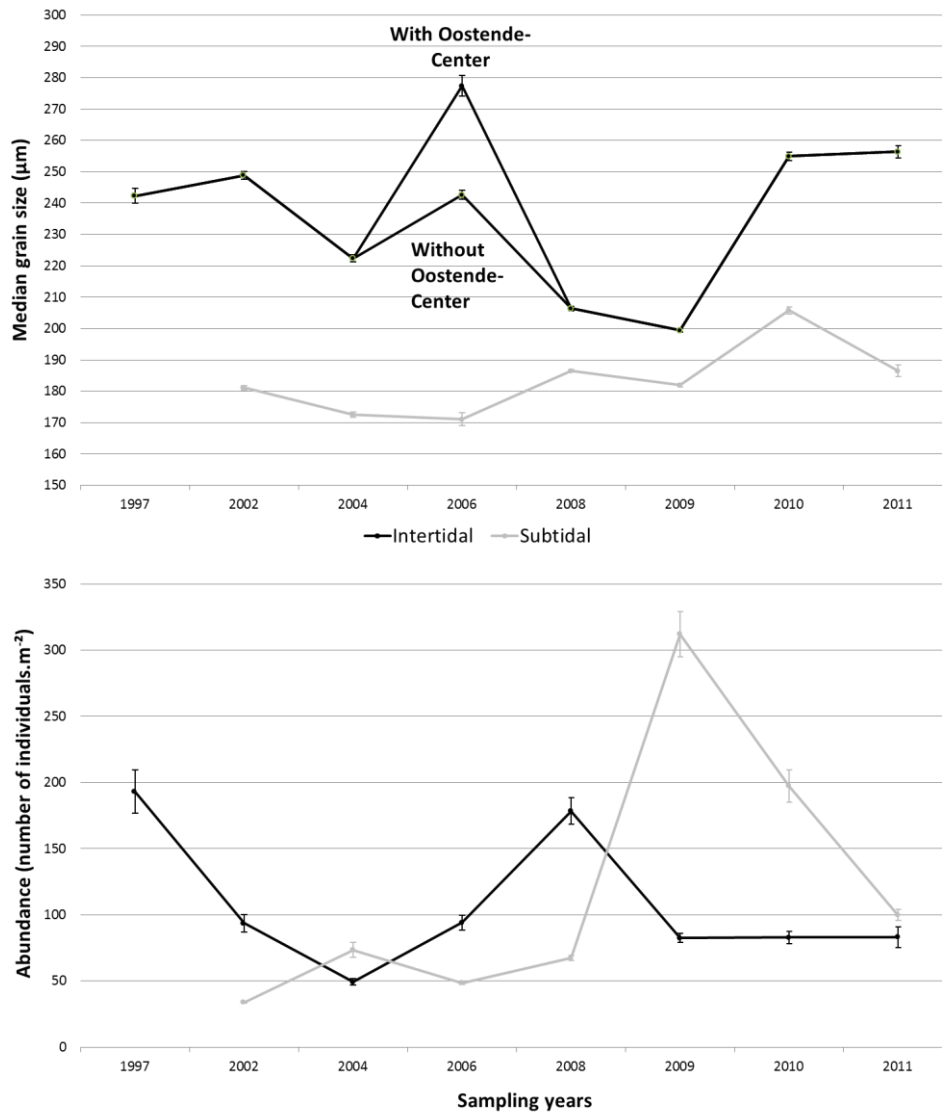
When looking at the evolution of median grain size in time (figure 7), the intertidal values (200 – 280 µm) are always higher than the shallow subtidal values (170 – 210 µm). In 2006, the highest mean median grain size could be detected in the intertidal zone (277.39 ± 3.27 µm; without Oostende-Center: 242.64 ± 1.49 µm). The mean shallow subtidal median grain size peaks in 2010 (205.79 ± 1.31 µm). Figure 8 also shows the temporal evolution of the macrobenthic abundance. Two intertidal peak values (1997: 193.07 ± 16.54 individuals.m^{-2} – 2008: 178.38 ± 10.05 individuals.m^{-2}) and one shallow subtidal peak value (2009: 312.04 ± 17.05 individuals.m^{-2}) can be seen. In 2002, 2006 and 2008, the mean intertidal abundance was higher than the shallow subtidal values.

Figure 5: Mean median grain size (µm), beach elevation (m versus MLW) and total organic matter (%) per beach and per year, for the intertidal (left) and shallow subtidal zone (right) separately; with codes in the X-axis representing the following beaches: (1) De Panne, (2) Schipgatduinen, (3) Koksijde-Oostduinkerke, (4) Nieuwpoort, (5) Middelkerke, (6) Raversijde, (7) Mariakerke, (8) Oostende-Fairway, (9) Oostende-East, (10) Bredene, (12) Wenduine, (13) Blankenberge, (14) Fonteintjes, (15) Heist, (16) Zwinduinen en Polders

Figure 6: Mean species richness (number of species), abundance (number of individuals.m^{-2}) and biomass (g AFDW.m^{-2}) per beach and per year, for the intertidal (left) and shallow subtidal zone (right) separately; with codes in the X-axis representing the following beaches: (1) De Panne, (2) Schipgatduinen, (3) Koksijde-Oostduinkerke, (4) Nieuwpoort, (5) Middelkerke, (6) Raversijde, (7) Mariakerke, (8) Oostende-Fairway, (9) Oostende-East, (10) Bredene, (12) Wenduine, (13) Blankenberge, (14) Fonteintjes, (15) Heist, (16) Zwinduinen en Polders

Figure 7: Mean median grain size (µm; top) and abundance (number of individuals.m⁻²; bottom) of all samples gathered per year with standard error, for the intertidal (black) and shallow subtidal zone (grey) separately
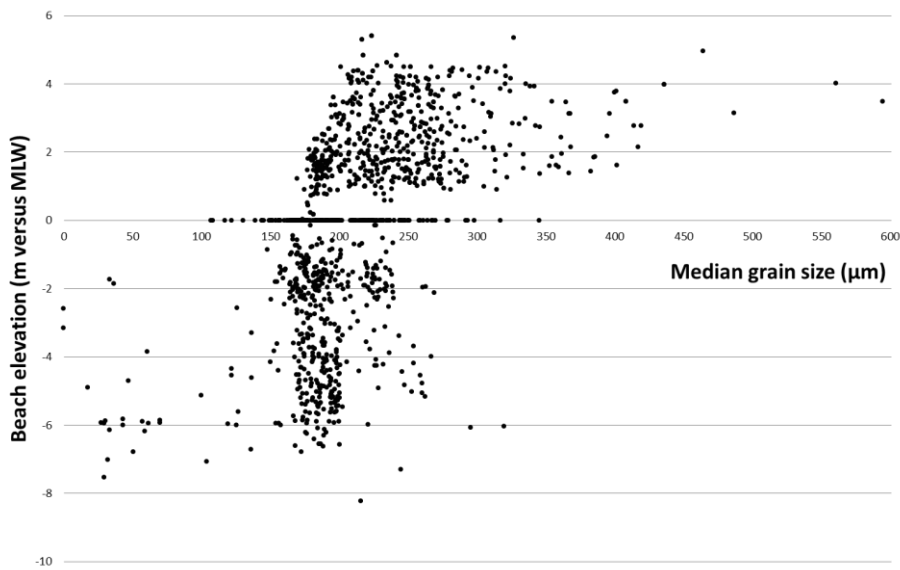

3.3   Variation within beaches

By taking the results of all beaches together and focusing on the different beach elevation zones, it was possible to describe the spatial variation on the beach perpendicular to the water line. High up on the intertidal beach, near MHW, the median grain size is the highest, the silt fraction the lowest, the total organic matter the lowest and the carbonate content the lowest (table 3). The total organic carbon decreases from the MHW to MLW and increases from MLW to -8 m. The species richness increases as the median grain size and beach height decreases, except for the two deepest zones (6.73 and 7.47 species). This trend cannot be detected in the abundance or biomass values, although the biomass values also increase from MLW to -8 m.

45

Table 3: Mean of the abiotic and biotic factors per beach height zone, over all the sampled beaches and years; MHW: mean high water level; MLW: mean low water level

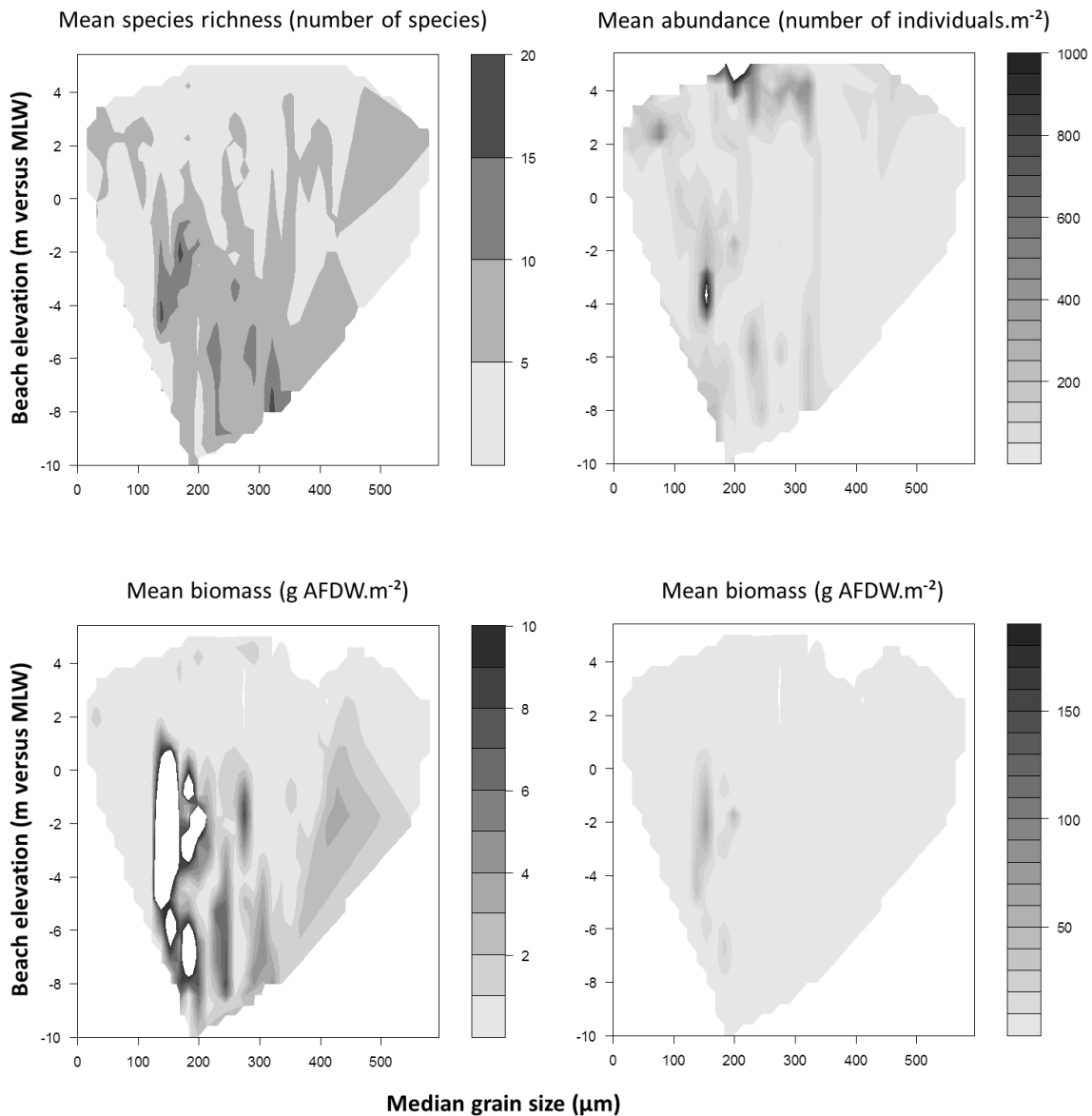| BEACH ELEVATION ZONES		Beach elevation (m versus MLW)	Median grain size (µm)	Silt fraction (%)	Total organic matter (%)	Total organic carbon (%)	Carbonate content (%)	Species richness (number of species)	Abundance (number of individuals.m⁻²)	Biomass (g AFDW.m⁻²)
4m to 6m (MHW)	INTERTIDAL ZONE	4.40	256.01	0.05	0.30	0.61	6.72	3.57	322.12	0.40
2m to 4m		2.90	253.28	0.05	0.41	0.55	8.40	4.24	118.97	0.33
0m (MLW) to 2m		1.44	226.72	0.01	0.44	0.38	9.45	4.73	49.53	0.37
-2m to 0m	SHALLOW SUBDTIAL ZONE	-1.30	191.98	2.05	1.04	0.53	9.39	6.97	89.86	5.97
-4m to -2m		-2.91	183.57	2.48	0.93	0.58	9.68	8.50	118.28	7.75
-6m to -4m		-4.94	178.03	8.63	1.00	0.69	9.47	9.47	135.02	10.04
-8m to -6m		-6.46	168.38	13.84	0.29	0.97	11.39	6.71	78.18	12.04
-10m to -8m		-9.02	170.72	6.29	0.60	0.55	15.29	7.49	64.04	1.73

According to figure 4, median grain size and slope or elevation on the beach account for about 77 % of macrobenthic variance on Belgian beaches. Moreover, the median grain size decreases when the beach height decreases (Spearman rank correlation: r_s = 0.6439136; p<0,01; figure 8). This is clearly visible in the intertidal zone, with only 4 samples showing a median grain size larger than 450 µm: one sample taken in 1997 in Schipgatduinen (464.00 µm) and 3 samples taken in 2006 in Oostende-Center (486.63 µm, 560.34 µm and 594.29 µm). In the shallow subtidal zone, the median grain size generally fluctuates between 150 and 200 µm with some very low values (median grain size smaller than 100 µm) between -1 and -8 m: 2 Oostende-Center samples taken in 2002, 2 Oostende-Fairway samples taken in 2006, 12 Wenduine samples taken in 2006, 2 Oostende-East samples taken in Spring and Autumn 2011 and 4 Nieuwpoort samples taken in Spring 2011. Overall, 96 % of all data points have a median grain size between 150 and 300 µm.

Figure 8: Beach elevation (m versus MLW) versus median grain size (µm)

In figure 9, the highest values of species richness (6 samples: 20 to 28 species), abundance (13 samples: 1000 to 3988 individuals.m^{-2}) and biomass (88 samples: 10 to 246.14 g AFDW.m^{-2}) are not depicted as they were scarce and masked the overall data pattern (1268 samples). However, they are still represented by the white spots in figure 9. Figure 9 shows that the highest species richness could be found in the shallow subtidal zone between -1 and -5 m (150 – 200 µm) and between -7 and -8 m (300 – 350 µm). The abundance is highest between 2 and 5 m when the median grain size varies between 200 and 250 µm. In the shallow subtidal zone, the highest abundance can be found between -2 and -5 m in sediment with a median grain size around 150 µm. The biomass is much higher in the shallow subtidal than in the intertidal zone, reaching its highest values (200 – 250 g AFDW.m^{-2}; white spots in graph) between 1 and -8 m in sediment with a median grain size between 150 and 200 µm.

Figure 9: Contour plots of species richness (number of species), abundance (number of individuals.m^{-2}) and biomass (g AFDW.m^{-2}) over beach elevation (m versus MLW) and median grain size (μm); the highest values of each factor are not depicted but they are still visible in the figure as white spots. The contour plot with the highest biomass values is included to confirm the significance of the white spots.

3.4   Niche properties of the dominant species

The dominant species in the intertidal and shallow subtidal zone were determined by taking the five species that contributed the most to the total abundance (Table 4). The juvenile status of the bivalves *Ensis* species and *Macoma balthica* is clearly stated as they were significantly smaller than the adult individuals. Intertidal and shallow subtidal contour plots were made for each of these
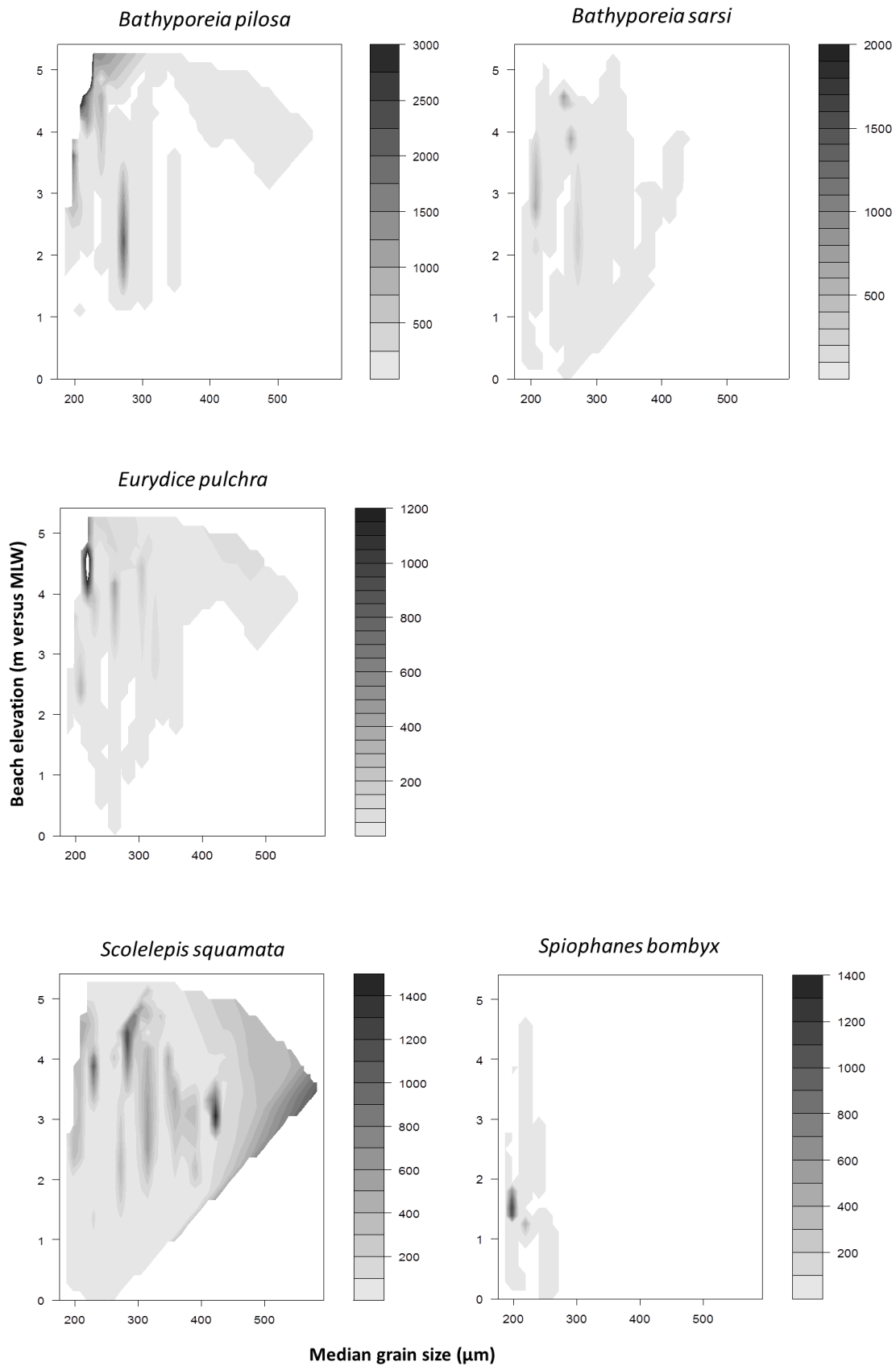
dominant species to unravel their habitat preferences and niche properties, based on beach elevation and median grain size.

Table 4: The dominant species in the intertidal and shallow subtidal zone over all sampled beaches and years
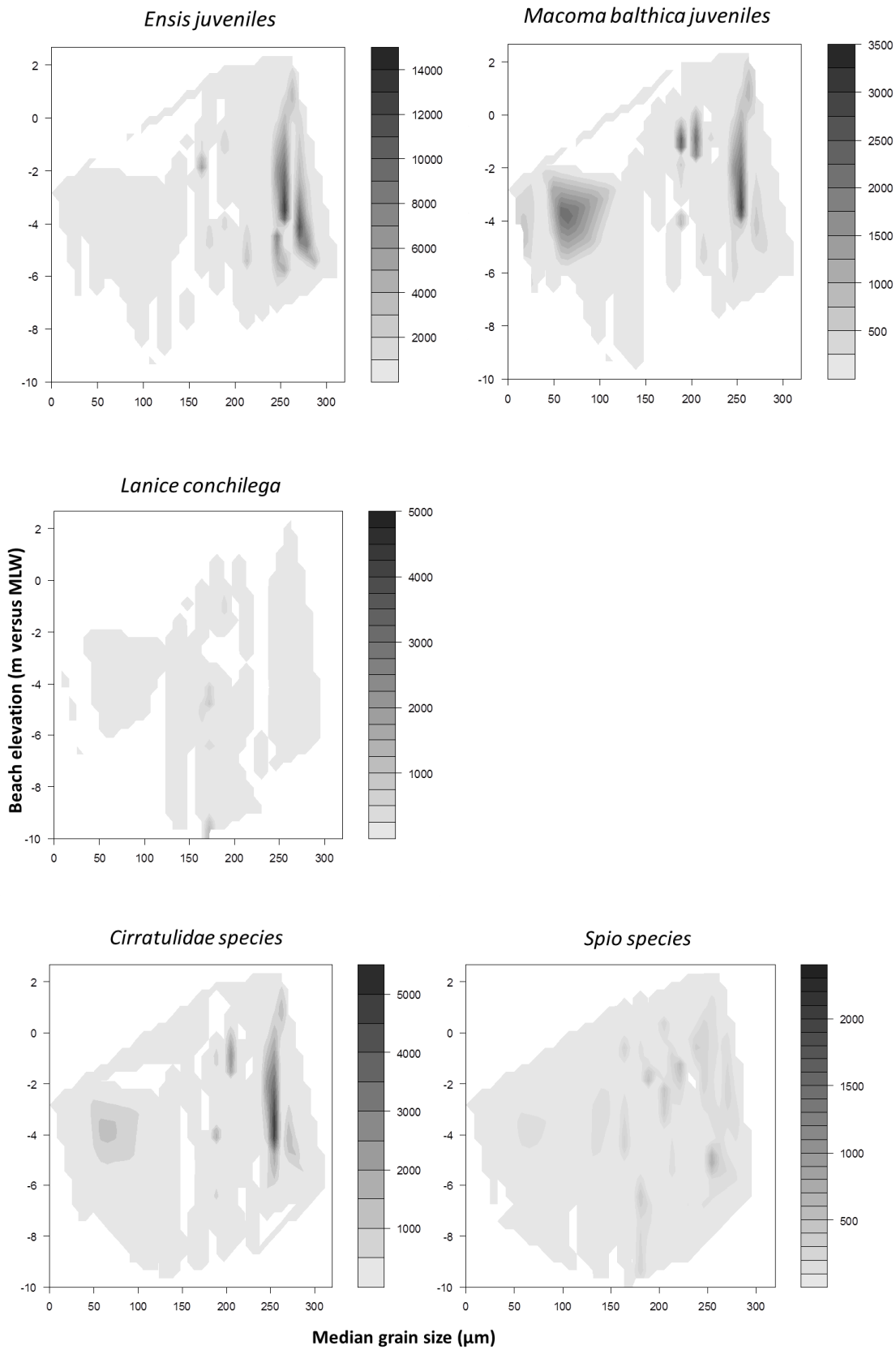
Intertidal zone	% of total abundance	Shallow subtidal zone	% of total abundance
Bathyporeia pilosa	25.04	*Ensis* juveniles	40.70
Scolelepis squamata	21.01	*Lanice conchilega*	7.64
Bathyporeia sarsi	13.36	*Cirratulidae species*	7.57
Eurydice pulchra	7.60	*Spio species*	6.25
Spiophanes bombyx	5.27	*Macoma balthica* juveniles	6.21

In figure 10, the highest values of *Bathyporeia pilosa* (2 samples taken in the high intertidal zone of De Panne in 1997 with 9522 and 15010 individuals.m^{-2}), *Bathyporeia sarsi* (1 sample taken in the middle of the intertidal zone of Nieuwpoort in spring 2009 with 2583 and 1 sample taken in the high intertidal zone of Raversijde in 1997 with 4766 individuals.m^{-2}), *Eurydice pulchra* (2 samples taken in the high intertidal zone of De Panne in 1997 with 1774 and 2554 individuals.m^{-2}; represented by white spot in figure 11), *Scolelepis squamata* (1 sample taken in the high intertidal zone of Mariakerke in autumn 2011 with 1969 individuals.m^{-2} and 1 sample taken in the high intertidal zone of Raversijde in 1997 with 2105 individuals.m^{-2}) and *Spiophanes bombyx* (3 samples taken in the low intertidal zone of Oostende-East in 2004 with 2500, 2558 and 5274 individuals.m^{-2}) are not depicted as they were scarce and masked the overall data pattern (686 samples). *Bathyporeia pilosa* and *Eurydice pulchra* prefer the highest intertidal beach zone (4 m – 5.5 m) and the finest sediment (200 – 250 µm). *Bathyporeia pilosa* also shares the middle of the intertidal zone (2.5 m – 4 m around 200 µm and 1.5 – 3.5 m around 280 µm) with *Bathyporeia sarsi*. On its own, *Bathyporeia sarsi* occupies the zone between 3.5 and 4.5 m (250 – 280 µm). Of the two polychaetes, *Spiophanes bombyx* prefers the lowest beach zone, close to MLW (1 m – 2 m) with sediment around 200 µm. *Scolelepis squamata* on the other hand thrives all over the intertidal beach but prefers the upper and middle area (2 m – 5.5 m). On Belgian sandy beaches, this species occurs in a wide range of sediment grain sizes (200 – 600 µm). Not only do the abundance values peak around 400 µm but they seem to increase again from 500 µm onwards.

In the shallow subtidal zone (figure 11), only the highest values of *Lanice conchilega* (1 sample taken in the shallow subtidal zone of Oostende-Center in 2004 with 9503 individuals.m^{-2}) is not depicted, because it masked the resolution of the classes. The *Ensis* juvenile bivalves prefer the zone between 2 m and -6 m with sediment between 250 and 300 µm. The abundance of *Macoma balthica* juveniles reaches peak levels in three different zones: (1) -2 m to -6 m (50 – 100 µm); (2) 0 m to -2 m (200 µm) and (3) 2 m to -4 m (250 µm). The highest abundance values of *Lanice conchilega* can be found between 0 and -6 m in sediment of 150 – 200 µm. The abundance of *Cirratulidae* species reaches peak values in three different zones: (1) -3 m to -5 m (50 – 100 µm); (2) 0 m to -2 m (200 µm) and (3) 2 m to -6 m (250 – 280 µm). They seem to co-occur with *Macoma balthica* juveniles. *Spio* species prefer two zones: (1) -6 m to -10 m (180 µm) and (2) 1 m to -6 m (150 – 300 µm).

Figure 10: Contourplots showing the abundance of the five dominant macrobenthic species in the intertidal zone versus beach elevation (m versus MLW) on the Y axis and median grain size size (µm) on the X axis

Figure 11: Contourplots showing the abundance of the five dominant macrobenthic species in the shallow subtidal zone versus beach elevation (m versus MLW) on the Y axis and median grain size size (µm) on the X axis

4. Discussion

In this study, we aimed to assess the ecological characteristics of the Belgian beaches prior to the implementation of the Belgian Master Plan for Coastal Safety and the concurrent multitude of beach nourishment projects over the next years. First a quantitative assessment of spatiotemporal variation in abiotic and biotic parameters was performed, followed by a more descriptive synthesis on niche properties of biodiversity metrics and the dominant species. All sampling locations were considered to be outside the influence of major impacting activities, except for Oostende-Center. This beach received a nourishment with very coarse sediment in 2006 and should yield some aberrant values compared to the other beaches. All other data represent the current state of the Belgian beaches. If it is assumed that changes at these locations are the result of natural factors rather than associated with field related disturbances, the abiotic and biotic variance across this group of locations at any one time may be taken to represent the normal limits to naturally induced change (Pearson & Mannvik 1998) in the Belgian coastal zone. As the main aim is to distinguish and allocate natural macrobenthic variation within the Belgian beach ecosystem to possible spatial or temporal trends, focus was placed on the overall trends and not on particular differences between beaches or between samples within beach zones.

4.1 Partitioning of abiotic and macrobenthic variance on Belgian beaches

The irregular and patchy distribution of sediments in the coastal zone (Ruddick et al. 1998), combined with its diverse topography, creates a wealth of habitats between the foredunes and the shallow subtidal zone of a beach. This supports a high capacity for various species assemblages, explaining the high benthic variability along the across-shore gradient. This variability at the macrobenthic species richness, abundance and species assemblage level is decreasing towards the open sea (Van Hoey et al. 2004).

Treatment of the intertidal and (shallow) subtidal zones as distinctly separate habitats is frequently the result of convenience and economy of sampling, with MLW being traditionally regarded as the transition between intertidal and (shallow) subtidal communities (Dexter 1979; Knott et al. 1983). Although multidimensional scaling (MDS) hinted a continuum between the intertidal and shallow subtidal zone (Figure 3), the data from both zones were treated separately to avoid misinterpretation of trends (Van Hoey et al. 2004). Partitioning of macrobenthic variance indicated that larger scale spatial and temporal variability is less important for community differentiation than variability within Belgian sandy beaches, linked to elevation on the beach and median grain size of the sediment, in both the intertidal and shallow subtidal zone. Invertebrate macrobenthos often exhibit patchy along-shore distribution on exposed sandy beaches (Jaramillo & McLachlan 1993; Dugan & McLachlan 1999; Schlacher et al. 2008) resulting in unclear big spatial trends. Large year-to-year temporal variability in macrobenthic community structure is prominent in temperate regions, but community shifts have not been 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). Temporal variability should thus be considered as being subordinate to spatial variation, which seems to be the case on the Belgian beaches. Moreover, exposed marine beaches have been defined as physically stressful environments (McLachlan 1983; McLachlan & Jaramillo 1995) and thus the best way to understand macrobenthic population variability is by documenting response to abiotic factors (Jaramillo & McLachlan 1993). If information is available, the role of biotic intraspecific and interspecific interactions, e.g. competition and predation, will be incorporated as well.

4.2   Spatial and temporal variation

Over all studied beaches and years, minimum and maximum values could be detected between which the natural variation runs its course (table 2). Confirming previous research (Degraer et al. 2003a; Degraer et al. 2003b; De Moor 2006; Speybroeck et al. 2008a), the mean intertidal median grain size coarsens while the finer shallow subtidal sediment becomes even finer when going from west to east. Over the years, the intertidal median grain size is always higher than the shallow subtidal values. On all beaches and in all years, polychaetes, crustaceans and bivalves dominated the macrobenthos, as is the case on most beaches on a world-wide scale (McLachlan & Jaramillo 1995). The distribution limits of beach species can expand and contract over time, displaying considerable fluctuations in abundance coupled with episodic settlement events and/or mass mortalities (Coe 1956; Defeo & McLachlan 2005). Most sandy beach macrobenthic species are short-lived (2 to 8 years), have rapid growth to maturity and high recruitment (McLachlan et al. 1996a). This analysis showed that the mean intertidal species richness, abundance and biomass are generally lower than the shallow subtidal values. Looking at the overall temporal evolution of the abundance however, the mean intertidal values were higher than the shallow subtidal values in 2002, 2006 and 2008. In these years, very high numbers of *Bathyporeia pilosa* (2006 and 2008), *Eurydice pulchra* (2002 and 2006) and *Scolelepis squamata* (2002, 2006 and 2008) were detected in the intertidal zone. These species caused peak abundance values in the intertidal zone, up to 6 times higher than the shallow subtidal values.

4.3   Variation within beaches

Population variations in across-shore distribution may arise from abiotic, e.g. swash activity and tides, and biotic, e.g. interspecific competition and predation, factors acting on different spatio-temporal scales. By jointly analyzing all beaches and focusing on the different beach elevation zones (as depicted in figure 3), it was possible to describe this spatial variation perpendicular to the water line on a Belgian beach. As evidenced in figure 4, median grain size and elevation on the beach account for around 77 % of the variation in macrobenthic abundance on the Belgian sandy beaches. Both abiotic factors are negatively intercorrelated, with the median grain size decreasing when the beach elevation decreases (figure 8). On a typical sandy beach, the coarsest sediment particles do lie

at the top of the beach and grade down to the finest sediments at the waterline, due to wave activity (Short 1991). Three very coarse intertidal outliers were found in Oostende-Center in 2006. Within the time frame of this study, Oostende-Center was nourished with coarse offshore sediment in June 2004 (600 000 m³), spring 2005 (100 000 m³), spring and autumn 2007 (each 75 000 m³), autumn 2008 (75 000 m³), spring 2010 (75 000 m³) and autumn 2011 (75 000 m³). Oostende-Center was monitored in April and May 2004 and in September 2006, so only the 2006 values were influenced by the nourishment projects. The coarse sediment found in Schipgatduinen (464.00 µm) however is unexpected since this area lies in the western part of the Belgian coast, which is characterized by finer sediment (De Moor 2006). Moreover, the beach of Schipgatduinen is part of a nature reserve founded in 1975 so the coarse sediment cannot be attributed to major impacts like beach nourishment. In the shallow subtidal zone, waves are important in distributing and affecting sediments, although the effect decreases exponentially with depth (Gray & Elliott 2009). The median grain size in the shallow subtidal zone was indeed lower than in the intertidal zone with some very low values on different beaches along the Belgian coastline. Overall, 95.85 % of all data points have a median grain size between 150 and 300 µm.

As sand particle size and beach elevation correlate with physical environmental factors affecting the beach, they also influence the distribution of the beach fauna. The Belgian ultra-dissipative beaches are gently sloped with fine to medium sands and they harbour a diverse, abundant macrofauna (Ricciardi & Bourget 1999; Brown & McLachlan 2002; Speybroeck et al. 2008a). Higher up on the beach, near MHW, the median grain size is the highest while the silt fraction, the total organic matter and the carbonate content are the lowest (table 3). The infaunal species richness, abundance and biomass usually increase with decreasing beach elevation and median grain size (Jaramillo & McLachlan 1993; Haynes & Quinn 1995). This trend can be observed for the species richness, except for the two deepest zones (6.73 and 7.47 species) and for the biomass, with peak values between 1 and -8 m in fine sediment (150 – 200 µm). The abundance is highest between 2 and 5 m where the median grain size varies between 200 and 250 µm and between -2 m and -5 m in sediment with a median grain size around 150 µm. Very high intertidal abundance values of species have been recorded before (Degraer et al. 2003b) and were only due to *Scolelepis squamata.* The contour plots however, suggest that these high values can be attributed to *Bathyporeia pilosa*, *Bathyporeai sarsi*, *Eurydice pulchra* and *Scolelepis squamata*. The relatively low abundance of benthic macrofauna near MLW may be related to unfavourable hydrodynamic and environmental conditions like mobile sediments and higher predation pressure of hyperbenthic and epibenthic organisms (Janssen & Mulder 2005). In the shallow subtidal zone, the high abundance values can be attributed to juvenile *Macoma balthica* and *Ensis* bivalves.
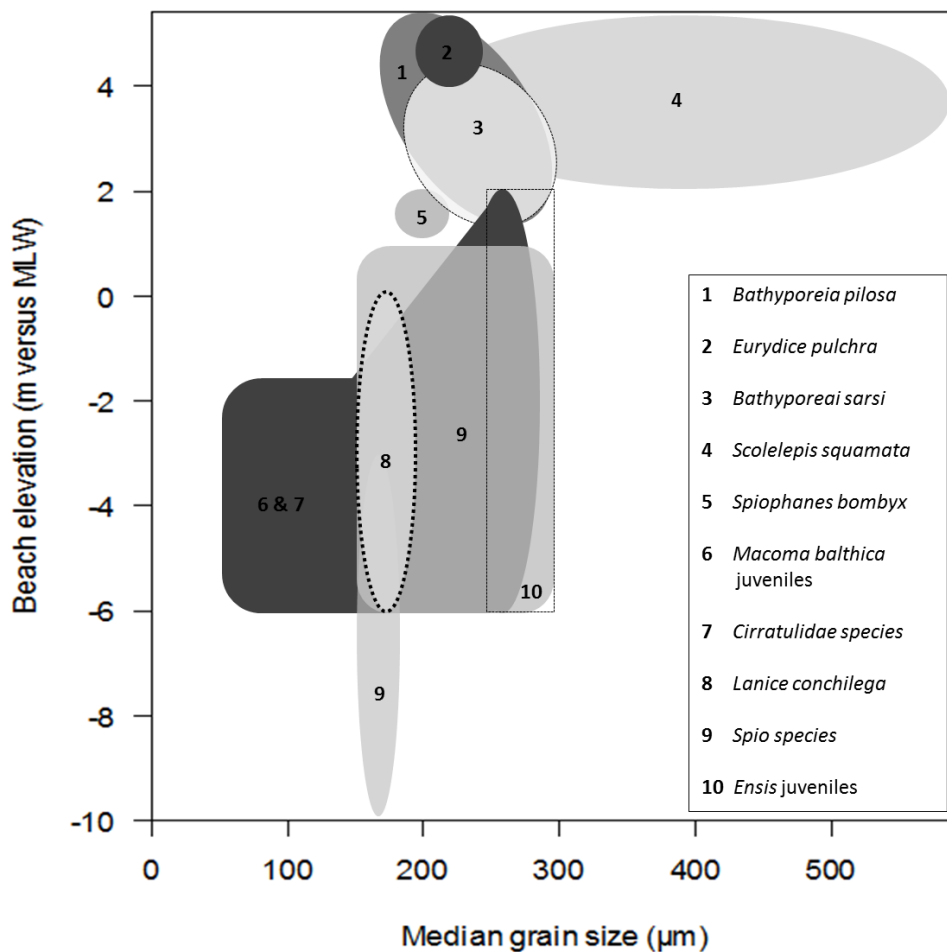
4.4   Niche properties of the dominant species: a synthesis

Zonation as studied by ecologists exists only during the low tide period. As the tide rises, populations move with some entering the water column while zones get compressed. The high mobility of most

species, coupled to the disturbance effects of changing wave energy levels, results in species distributions being quite variable from day to day. Migrations of the fauna shuffle and recreate zones constantly and with each tide (McLachlan & Jaramillo 1995). Hence, faunal zones do not exhibit sharp boundaries, but rather tend to be distinguished by the presence of characteristic taxa. Dominant species typify the macrobenthic community. The five species that contribute the most to the total abundance in either the intertidal or shallow subtidal zone are considered to be dominant species of the Belgian sandy beaches. Knowledge of their observed niche together with their interpolated occurrence greatly improves our understanding of the Belgian sandy beach ecosystem (figure 12).

As stated by Van Hoey (2004), the *Eurydice pulchra – Scolelepis squamata* community is exclusively found at the upper intertidal zone of Belgian sandy beaches and is characterized by a low diversity (5 species per sample) and moderate abundances (983 individuals.m^{-2}), mainly of *Eurydice pulchra*, *Bathyporeia pilosa, Bathyporeai sarsi* and *Scolelepis squamata. Bathyporeia* species, *Eurydice pulchra* (Eleftheriou & McIntyre 1976; Degraer et al. 1999a) and *Scolelepis squamata* (Eleftheriou & McIntyre 1976; McDermott 1987; Souza & Gianuca 1995) are found to be abundant on many European beaches. 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 & Jaramillo 1995). The lower intertidal and shallow subtidal zone cannot be distinguished from one another, based on dominant species, as juvenile *Ensis* and *Macoma balthica* bivalves (indicator species of *Macoma balthica* community, (Van Hoey et al. 2004), *Lanice conchilega* (indicator species of *Abra alba – Kurtiella bidentata* community, (Van Hoey et al. 2004), *Cirratulidae* and *Spio species* occupy both zones. *Spiophanes bombyx* is the only species that lingers in the narrow zone around MLW. None of the dominant species are indicator species of the *Ophelia borealis – Glycera lapidum* and *Nephtys cirrosa* communities (Van Hoey et al. 2004). The juveniles of *Ensis* and *Macoma balthica* bivalves (median grain size > 200 µm) seem to inhabit a different habitat than their adult stages. (median grain size < 200 µm) (Degraer et al. 2006). In the shallow subtidal zone, the polychaete *Lanice conchilega* can be found in fine sediment 150 – 200 µm between 0 and -6 m. This polychaete adds or alters physical, chemical and biological factors and is therefore often referred to as an ecosystem engineer (Rabaut et al. 2007). Reefs of this tube-building and habitat-forming polychaete are known to represent hotspots of biodiversity within intertidal and (shallow) subtidal soft sediments of the North Sea (Degraer et al. 2008a). Whereas individuals can be found in a wide range of fine to medium muddy sands to throughout the North Sea (Degraer et al. 2006; Van Hoey 2006; Willems et al. 2008), dense aggregations or reefs do not (Degraer et al. 2008a). Nonetheless, the habitat created by *Lanice conchilega* seems to be important for higher trophic levels such as juvenile flatfish (Rabaut et al. 2010) and birds (Godet et al. 2008).

Figure 12: Observed niche and interpolated occurrence of the dominant Belgian macrobenthic species along an 'average' Belgian beach transect

5. Conclusion

We assessed the ecological characteristics of the Belgian beaches prior to the implementation of the Belgian Master Plan for Coastal Safety. The results of the present study show (1) a distinct difference in overall community structure between the intertidal and shallow subtidal zone; (2) the higher importance of variability within Belgian sandy beaches, linked to elevation on the beach and median grain size of the sediment, compared to big scale spatial and temporal variability; (3) the confirmation of some generally accepted spatial and temporal trends in abiotic factors, e.g. an overall median grain size between 150 and 300 μm, and in macrobenthic species richness, abundance and biomass; and (4) the realized niches of the dominant macrobenthic species of the Belgian beaches. Since all sampling locations were considered to be outside the influence of major impacting activities, these findings can be used as a preconceived basis (t0 situation) of inherent, natural and normal abiotic and macrobenthic variability on the Belgian beaches. This study will also aid in the detection of possible impact effects of past, current and future beach nourishment projects, as stipulated in the Belgian Master Plan for Coastal Safety.