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Macrobenthic community structure and distribution in the Zwin nature reserve (Belgium and The Netherlands)

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Distribution and structure of intertidal macrobenthic communities in the Zwin nature reserve, a lagoonal inlet consisting of marsh and tidal flat habitats, was investigated using univariate and multivariate analyses. Macrobenthos community structure was related to environmental characteristics and discussed in the framework of the implemented extension of the nature reserve.

Based on explorative multivariate techniques, five different sample groups (SGs) were distinguished, which were, in general, located in different habitats of the Zwin nature reserve. The ecologically most important SGs consisted of the highest macrobenthic density, diversity and highest densities of Nereis diversicolor *and* Scrobicularia plana*; these important prey species for wading birds and fish occurred in the deep tidal inlet channels. This habitat was characterized by fine to medium sand sediment and strong tidal currents, guaranteeing water renewal at each high tide. Other SGs were found in less and erratically submersed and thus stressed areas (i.e. tidal pond, salt pans and shallow flats). These assemblages were characterized by typical r-strategists (i.e.* Capitella capitata *and* Polydora cornuta*) and typical supralittoral, mobile species (i.e.* Orchestia gammarellus *and* Collembola spp.*). Being ecologically most important, the extension of wide, tidal creeks should be a prime target within the future development and management of the nature reserve.*

Keywords: macrobenthic community structure and habitat preferences, Zwin nature reserve, intertidal habitat

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INTRODUCTION

Estuaries and their adjacent intertidal habitats fulfil several important ecosystem functions (e.g. high productivity, nursery and feeding habitats for epibenthic fish, crustaceans and birds) and services (e.g. pollution filter and counteracting coastline erosion) (McLusky & Elliott, 2004). Consequently many of these habitats are incorporated into nature reserves and designated as Special Areas of Conservation (SACs) according to the EU Habitats Directive (Anon, 1992). However, during the last 4 decades, coastal and estuarine ecosystems have been exposed to enhanced anthropogenic nutrient inputs and have been heavily exploited (e.g. dredging for building harbours or aggregate extraction, fishing and tourism) resulting in a general decrease in quality of these ecosystems (Bachelet *et al*., 2000; Diaz, 2001; Wolanksi, 2007). For instance, 2500 hectares of tidal flat and marsh habitats have been lost in the Schelde estuary (The Netherlands) since 1900, mainly due to land reclamation, deepening of the shipping channel and reinforcement of dykes (Eertman *et al*., 2002). To comply with the Water Framework Directive (WFD; Anon, 2000), the Flemish and Dutch governments have proposed to extend the Zwin nature reserve with 120 to 240 hectares of marshes and tidal flats, to be taken from the adjacent, formerly reclaimed polders. The Zwin nature reserve is a lagoonal inlet (i.e. seawater enters inlets on each tide), that has achieved an international reputation because of its function as an important breeding and wintering habitat for birds, especially waders (Struyf & Degraer, 2003).

Since macrofauna is essential for tidal flat ecosystem functioning as food resource (e.g. Cramp & Simmons, 1977: (wading) birds; Hampel *et al*., 2005: fish) and nutrient cycling (McLusky & Elliott, 2004; Wolanski, 2007), knowledge on the structure and distribution of the macrobenthic community in the present Zwin nature reserve is essential as a baseline for the appropriate design and evaluation of the implemented restoration project. However, at present, knowledge on macrobenthic community structure and distribution patterns is lacking. Benthic research in the Zwin nature reserve has formerly focused solely on nekton communities of the tidal creeks (Hampel *et al*., 2004, 2005) and the effects of emersion on macrobenthos in one selected tidal creek (Van Colen *et al*., 2006). The aims of this study were therefore to describe the macrobenthic spatial structure in terms of diversity, abundance, and their relation with the environmental characteristics in the Zwin nature reserve.

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MATERIALS AND METHODS

Study area, sampling and laboratory treatment

The Zwin nature reserve (51°21′N 3°22′E) extends 2.3 km along the North Sea coastline and is situated along the southern shore of the Schelde estuary mouth at the Belgian–Dutch border. It has a total surface area of 158 ha and comprises dunes, salt marshes, salt pans, a constructed tidal pond and two large inlet channels with adjacent tidal flat and creek systems (Figure 1).

In autumn 2003, at low tide, unreplicated macrobenthos samples were collected with a 12.5 cm inner diameter stainless corer to a depth of 40 cm from 104 randomly selected intertidal locations. Samples were sieved over a 500 μm mesh sized sieve and the residual was fixed and preserved with an 8% formaldehyde–seawater solution. All macrofauna was sorted, identified to the species level and counted except for nematodes. Oligochaetes were only partly identified to species level: a set of 730 oligochaetes was randomly selected from the samples for species identification. This set allowed to identify the oligochaete species list of the Zwin nature reserve, but oligochaetes were truncated for all further analyses. Species were classified into functional groups according to their feeding guilds (surface deposit feeders, subsurface deposit feeders, suspension feeders, omnivores and scavengers), based on available literature (Fauchauld & Jumars, 1979; Ysebaert *et al.*, 2003; Volkenborn & Reise, 2007). Species belonging to more than one feeding guild were assigned to their most common feeding mechanism.

At each location, (1) sediment characteristics and (2) intertidal elevation relative to mean high water tide level (MHWS, i.e. marsh border) were measured. The distance below MHWS only gives a relative indication of the tidal position of the sampling location within the Zwin nature reserve (e.g. deep inlet channel, steep versus shallow creeks and flats). Given the highly diverse geomorphology of the Zwin nature reserve, the relative intertidal elevation does not allow to calculate—ecologically more relevant—submersion and emersion times. Samples for grain size distribution of the top 10 cm were collected using a 5 cm inner diameter perspex corer and analysed for median grain size and mud content (volume percentage < 0.63 μm) with a LS Coulter particle size analyser.

Data analysis

Typical hyperbenthic and epibenthic species were excluded from the analysis. Furthermore, samples containing a maximum of one individual were not taken into account for the multivariate analyses (N = 95 samples). Descriptive multivariate techniques on fourth root transformed data were used to analyse the community structure: group-averaging cluster analysis based on Bray–Curtis similarity followed by a similarity profile test (SIMPROF; Clarke & Gorley, 2006) and multidimensional scaling (MDS). The main species contributing to the dissimilarity between the significantly ($P < 0.05$) separated sample groups, resulting from SIMPROF, were identified using the similarity percentage routine (SIMPER; Clarke & Gorley, 2006) and indicator species for each sample group, were identified by indicator species analysis (INDVAL) (Dufrêne & Legendre, 1997). Sample groups were characterized by means of their averaged abundance, species richness, Shannon–Wiener diversity index, taxon composition, feeding group composition and physical habitat characteristics (median grain size, mud content and relative intertidal height). The relationships between community characteristics, community structure and environmental variables were investigated using the BIO-ENV procedure (Clarke & Gorley, 2006) and Spearman rank correlation (Sokal & Rohlf, 1997). Environmental variables and species densities were superimposed on MDS ordination diagrams using correlation vectors in order to allow a better visualization of the relation between sample groups, species and environment. Multivariate analyses were performed using the Plymouth Routines In Multivariate Ecological Research (PRIMER) package, version 6 (Clarke & Gorley, 2006).

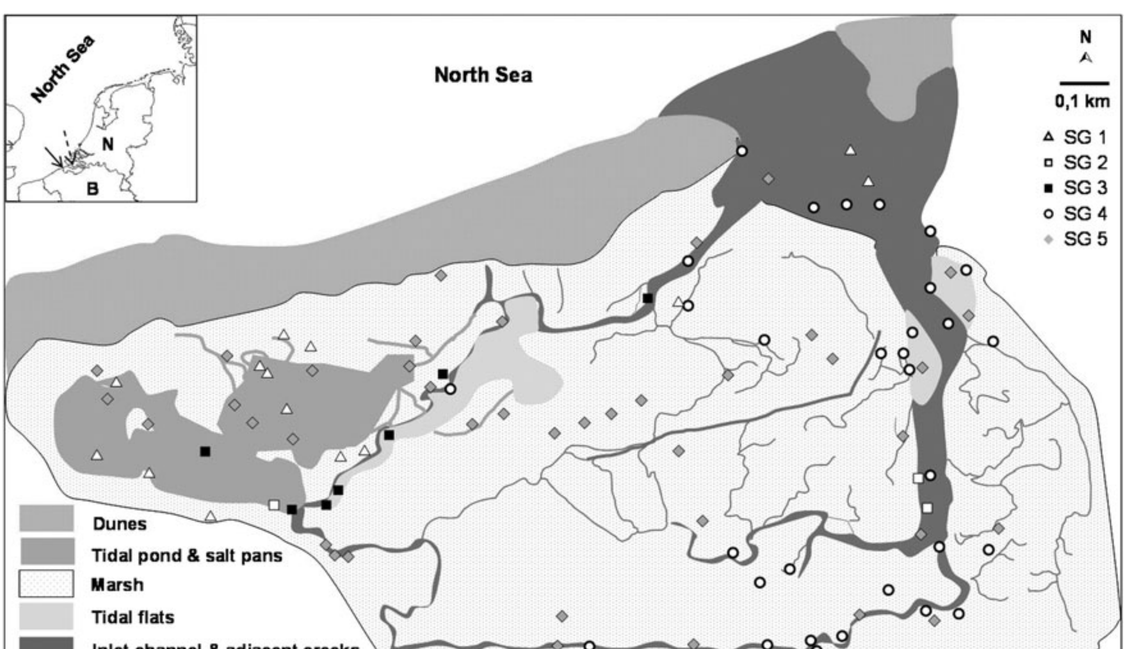

Fig. 1. Location of the Zwin nature reserve (solid arrow), at the mouth of the Schelde estuary (dashed arrow), along the southern shore (Belgian (B)–Dutch (N) border). Sampling stations are indicated by their sample groups (SG 1–5), distinguished by the multivariate analyses.

Table 1. List of macrobenthic species recorded in the Zwin nature reserve during this study. For each species the feeding type is given. SDF, surface deposit feeder; SSDF, subsurface deposit feeder; SF, suspension feeder; O, omnivore; P, predator. Species abbreviations, used in Table 2 and Table 3, are given.

Class	Species	Abbreviation	Feeding guild
Bivalvia	*Cerastoderme edule*	Cer edu	SF
Bivalvia	*Macoma balthica*	Mac bal	SDF
Bivalvia	*Scrobicularia plana*	Scr pla	SDF
Collembola	*Collembola* sp.	Coll sp	SDF
Crustacea	*Orchestia gammarellus*	Orc gam	SDF
Crustacea	*Sphaeroma rugicauda*	Sph rug	SDF
Gastropoda	*Hydrobia ulvae*	Hyd ulv	SDF
Nematoda	*Nematoda* sp.	Nema sp.	O
Oligochaeta	*Enchytraeidae* sp.	Olig sp	SSDF
Oligochaeta	*Tubificidae* sp.	Olig sp	SSDF
Oligochaeta	*Tubificoides benedeni*	Olig sp	SSDF
Oligochaeta	*Tubifex costatus*	Olig sp	SSDF
Polychaeta	*Aphelochaeta marioni*	Aph mar	SDF
Polychaeta	*Capitella capitata*	Cap cap	SSDF
Polychaeta	*Eteone longa*	Ete lon	P
Polychaeta	*Nereis diversicolor*	Ner div	O
Polychaeta	*Heteromastus filiformis*	Het fil	SSDF
Polychaeta	*Malacoceros tetracerus*	Mal tet	SDF
Polychaeta	*Polydora cornuta*	Pol cor	SDF
Polychaeta	*Pygospio elegans*	Pyg ele	SDF
Polychaeta	*Scolelepis squamata*	Sco squ	SDF
Polychaeta	*Streblospio benedicti*	Str ben	SDF

RESULTS

General characterization of the macrobenthos

A total of 23 macrobenthic species were encountered (Table 1). Macrofaunal species richness varied between 0 and 11 spp.sample^{-1}, with an average of 3.4 ± 0.21 SE species. The total macrobenthic density ranged from 0 to 71376 ind m^{-2}, with an average of 7260 ± 1099 SE ind m^{-2}. The most widely distributed species were *Nereis diversicolor* (Müller, 1776) (recorded in 87% of all samples) and Oligochaeta spp. (75%). Other species occurred in less than 20% of the samples.

Total macrobenthic density was dominated by oligochaetes (60%) and polychaetes (38%), while bivalves, arthropods, gastropods and nematodes all contributed to <1% of the total density. Based on a feeding guild approach, subsurface deposit feeders dominated the macrobenthos (71% of the total macrobenthic density), followed by omnivores/scavengers (20%), surface deposit feeders (9%) and suspension feeders (<1%). Five species contributed 96% of the total macrobenthic density: Oligochaeta spp. (60%), *N. diversicolor* (19%), *Heteromastus filiformis* (Claparède, 1864) (9%), *Aphelochaeta marioni* (Saint-Joseph, 1894) (6%) and *Capitella capitata* (Fabricius, 1780) (2%).

Community structure of the macrobenthos

Five sample groups (SGs) were significantly separated based on SIMPROF (Figure 2). Nevertheless, the MDS ordination displayed an overlap between SGs (except for SG 2) and a rather high stress (0.18) which means that not too much reliance should be placed on the details of the plot (Clarke & Warwick, 2001) (Figure 3). Sample groups 2, 3 and 4 were clearly more diverse as compared to SG 1 and 5 (Table 2).

DIVERSE SAMPLE GROUPS (SG 2, 3 AND 4)

Sample group 2 displayed the highest Shannon–Wiener diversity (1.21 ± 0.13 SE), followed by SG 3 and 4

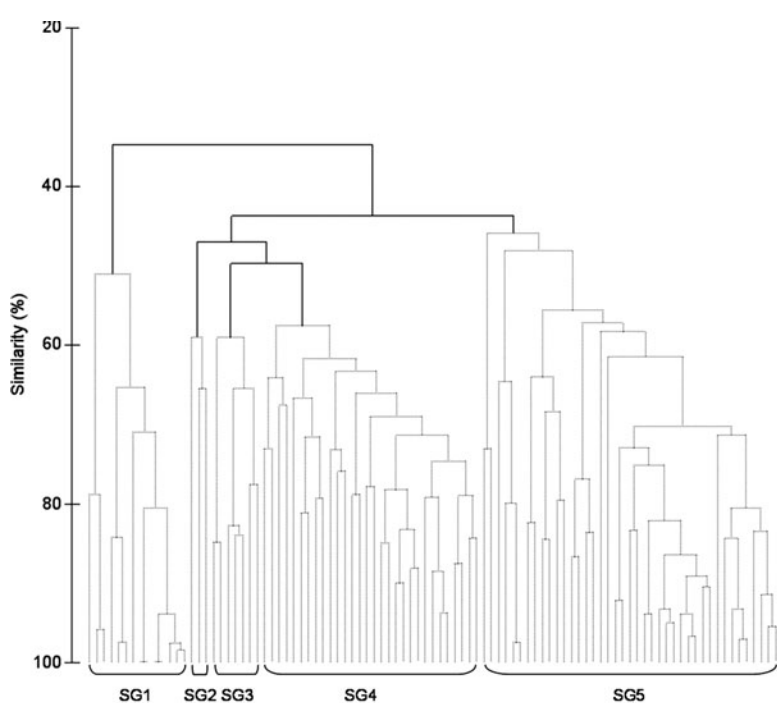

Fig. 2. Dendrogram representing the group average linking cluster analysis based on fourth root transformed macrobenthos density data. The five sample groups (SGs), identified by SIMPROF are indicated by the solid lines and brackets.

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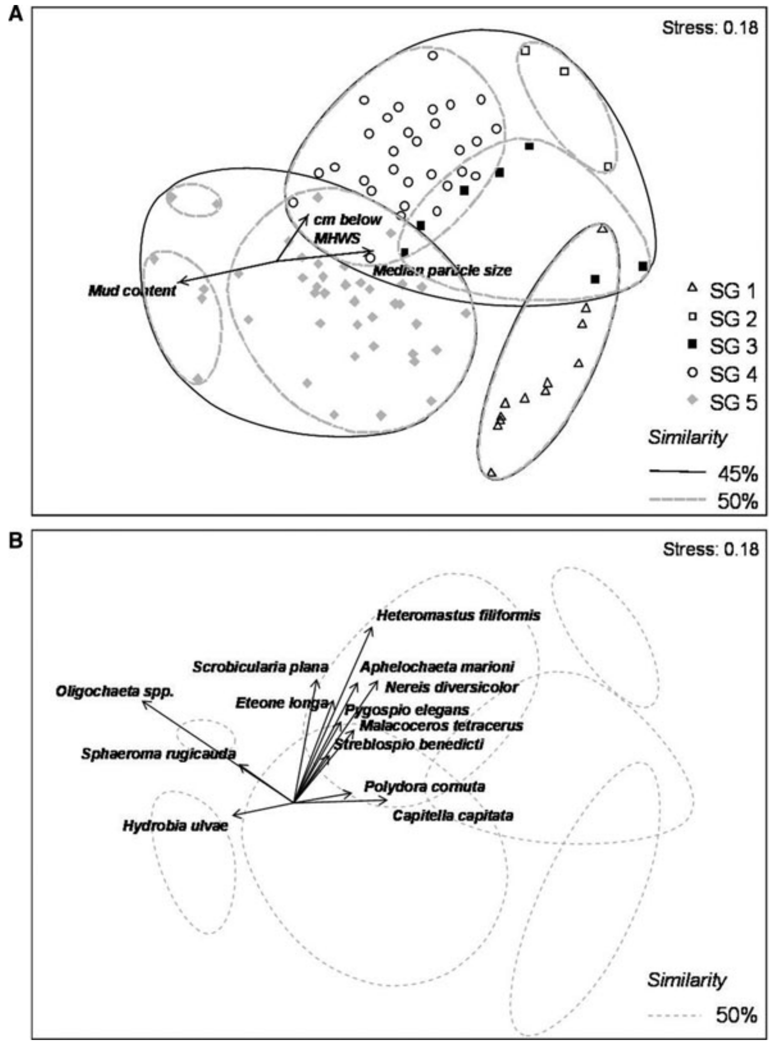

Fig. 3. (A) Multidimensional scaling (MDS) ordination plot of the macrobenthos community structure, based on Bray–Curtis similarity of fourth root transformed species densities. The significantly separated sample groups by SIMPROF are indicated by different symbols. Similarity clusters (45% and 50%) and correlation vectors of the mud content, median particle size and relative intertidal height are superimposed in (A), 50% similarity clusters and species correlations > 0.25 are superimposed in (B).

(respectively, 1.05 ± 0.19 SE and 1.00 ± 0.06 SE). Further, in SG 2, averaged species richness was relatively high (7.6 ± 1.6 SE spp.sample^{-1}) in comparison with other SGs and three species had a significant indicator value (IV) > 40: *Malacoceros tetracerus* (Schmarda, 1861), *Pygospio elegans* (Claparède, 1863) and *A. marioni*. These three surface deposit feeding species reached their highest densities in SG 2 (respectively, 841 ± 476 SE ind m^{-2}, 163 ± 47 SE ind m^{-2} and 5622 ± 4754 SE ind m^{-2}) and can be considered highly indicative for this SG. SG 3 and SG 4 were numerically dominated by Oligochaeta spp., while *A. marioni* was far less abundant in these SGs (Table 2). Consequently, Oligochaeta spp. and *A. marioni* contributed largely to the dissimilarity between SG 3, 4 and 2 (Table 3). The dissimilarity between SG 3 and 4 was mainly determined by the subsurface deposit feeder *C. capitata* (C% = 20.7; see Table 3). This species reached its highest density in SG 3 (1688 ± 877 SE ind m^{-2}, i.e. 21% of the total density), while it was absent in SG 4. INDVAL analysis revealed significant IVs > 40 for *C. capitata* and *Polydora cornuta* (Bosc, 1802) in SG 3, while *Scrobicularia plana* (da Costa, 1778) and Oligochaeta spp., were highly indicative for SG 4 (IV = 44 and 35, respectively).

LESS DIVERSE SAMPLE GROUPS (SG 1 AND 5)

SG 1 and 5 were characterized by a low macrobenthic diversity (species richness = 1.6 ± 0.2 SE spp.sample^{-1} and 2.6 ± 0.2 SE spp.sample^{-1}, respectively for SG 1 and SG 5; Shannon–Wiener diversity = 0.25 ± 0.09 SE and 0.53 ± 0.06 SE, respectively for SG 1 and SG 5). Furthermore, the lowest macrobenthic density (716 ± 108 SE ind m^{-2}) was found in SG 1 (Table 2). Oligochaeta spp. numerically dominated SG 5 (6878 ± 2304 SE ind m^{-2}, i.e. 90% of the total density), while oligochaetes were absent in SG 1. Consequently, Oligochaeta spp. contributed largely (i.e. 53%, SIMPER; Table 3) to the dissimilarity between both SGs. SG 5 was further characterized by the highest densities of the mobile species *Hydrobia ulvae* (Pennant, 1977),

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Table 2. Environmental and macrobenthic characterization of the sample groups. Averaged values of all sampling stations per SG are given for median grain size (μm), mud content (%), and relative intertidal height (cm below MHWS), total species richness (N total), mean species richness (N mean), total density and density of the 10 most abundant species (ind m^{-2}), Shannon–Wiener diversity index *H′(e)*, feeding guild composition (%). Standard errors are given in parentheses. Species with a significant indicator value > 35 for a particular SG are presented as well. °, unique species for this SG. Species abbreviations are listed in Table 1.

	SG 1		SG 2		SG 3		SG 4		SG 5	
Environment										
Median particle size	245 (23)		286 (5)		227 (29)		158 (16)		135 (16)	
Mud content	16 (6)		4 (2)		17 (7)		28 (4)		42 (4)	
Relative intertidal height	32 (9)		50 (29)		7 (7)		53 (10)		20 (4)	
Macrobenthos										
S (total)	6		13		8		15		14	
S (mean)	1.6 (0.2)		7.6 (1.6)		5.1 (0.6)		5.1 (0.2)		2.6 (0.2)	
N	716 (108)		10718 (4894)		8160 (1529)		11275 (1743)		7649 (2285)	
H′(e)	0.25 (0.09)		1.21 (0.13)		1.05 (0.19)		1.00 (0.06)		0.53 (0.06)	
Top 10 density										
	Ner div	646	Aph mar	5622	Oli spp.	2828	Oli spp.	5175	Oli spp.	6878
	Het fil	35	Ner div	2743	Ner div	2386	Ner div	2860	Ner div	556
	Cap cap	17	Het fil	1059	Cap cap	1688	Het fil	1932	Hyd ulv	98
	Aph mar	6	Mal tet	841	Het fil	838	Aph mar	194	Pol cor	29
	Pol cor	6	Cap cap	190	Str ben	210	Scr pla	126	Orc gam°	22
	Pyg ele	6	Pyg ele	162	Pol cor	105	Sph rug	111	Cap cap	16
			Pol cor	135	Aph mar	58	Pyg ele	79	Sph rug	14
			Cer edu	27	Mal tet	47	Nem spp.	63	Nem spp.	10
			Ete lon	27			Ete lon	50	Col spp.°	8
			Hyd ulv	27			Mac bal°	24	Het fil	6
Relative feeding guild density										
Surface deposit feeders	2 (1)		49 (15)		6 (3)		11 (3)		8 (2)	
Subsurface deposit feeders	11 (5)		13 (3)		65 (7)		54 (4)		65 (5)	
Omnivores/scavengers	87 (6)		38 (14)		29 (7)		35 (5)		27 (7)	
Indicator species			Mal tet	88	Cap cap	62	Scr pla	44		
			Pyg ele	72	Pol cor	44	Oligo	35		
			Aph mar	41						

Table 3. Total dissimilarity (D%) and contribution of the three most important taxa (C%) to the dissimilarity between any combination of the five sample groups. Species abbreviations are listed in Table 1.

SG	1		2		3		4	
	Species/D%	C%	Species/D%	C%	Species/D%	C%	Species/D%	C%
2	Mal tet	17.4						
	Aph mar	16.8						
	Het fil	16.2						
	D%	70.0						
3	Cap cap	25.0	Aph mar	15.0				
	Oli spp.	23.6	Oli spp.	14.4				
	Het fil	16.4	Mal tet	13.9				
	D%	63.0	D%	53.6				
4	Oli spp.	30.6	Oli spp.	18.7	Cap cap	20.7		
	Het fil	20.0	Mal tet	14.8	Oli spp.	14.8		
	Ner div	9.6	Aph mar	14.4	Ner div	10.7		
	D%	67.8	D%	52.8	D%	50.2		
5	Oli spp.	53.0	Oli spp.	15.6	Cap cap	24.2	Het fil	23.2
	Ner div	14.8	Het fil	14.1	Oli spp.	18.9	Oli spp.	14.6
	Het fil	6.6	Mal tet	13.6	Het fil	16.1	Ner div	14.3
	D%	63.4	D%	77.5	D%	58.4	D%	53.6

Orchestia gammarellus (Pallas, 1766) and Collembola spp. The latter two species occurred exclusively in SG 5.

Distribution and relations with the abiotic environment

BIO-ENV revealed a weak correlation between the macrobenthic community structure and the environmental variables ($\rho = 0.109$): the combination of median particle size and relative intertidal height best explained the biotic structure in the multivariate space. Nevertheless, in general, distinct distribution patterns, often corresponding with different habitat types (i.e. large tidal inlets, small to medium sized creeks, flats, tidal pond or salt pans) were found for the SGs.

Both SG 3 and 4 occurred in fine sandy sediments but SG 3 was found in the shallow flats along the smaller western inlet channel and the tidal pond and salt pan area while SG 4 was predominantly found along the deeper eastern inlet channel and its adjacent muddier flats and tidal creeks. SG 2 was present in medium sandy sediments (median particle size = 286 $\pm$ 5 SE μm) with a low mud content (4 $\pm$ 2 SE%), at an average depth of 50 $\pm$ 29 SE cm below MHMS (Table 2). From the three samples belonging to SG 2, two were also found along the deep eastern inlet channel. SG 5 was widely distributed over the nature reserve, with no prevailing occurrence to a particular habitat type and SG 1 was predominantly present in and around the tidal ponds and salt pans in the western part of the nature reserve.

Some weak, but significant, relationships were found between the univariate community characteristics, species densities and the environmental variables. Species richness and the total macrobenthos density were positively related to the distance below MHWS and the median particle size ($r = 0.21$ for density and species richness). The species richness was also positively related to the median particle size ($r = 0.29$). Species specific relationships with the environmental variables are presented in Table 4.

DISCUSSION

Macrobenthos community structure, species richness, density and species densities were found to be related to the mud content, median particle size and relative intertidal elevation of the samples. This is consistent with the literature, indicating the importance of sediment characteristics and hydrodynamic conditions (e.g. submersion time and current velocities) in the distribution of macrobenthic communities in estuarine intertidal habitats (e.g. Warwick *et al.*, 1991; Ysebaert *et al.*, 2003). However, correlation coefficients were relatively low. This may partly result from the unreplicated sampling design,

Table 4. Spearman rank correlations between species densities and environmental variables. Significant correlations are presented in bold.

Species	Median particle size	Mud content	Relative intertidal height
Aphelochaeta marioni	0.10	**−0.32**	0.01
Capitella capitata	0.09	**−0.37**	−0.01
Cerastoderma edule	**−0.26**	−0.17	−0.05
Collembola spp.	**−0.26**	−0.02	−0.16
Eteone longa	−0.02	**−0.22**	**0.23**
Hediste diversicolor	0.03	−0.08	0.16
Hydrobia ulvae	**−0.32**	0.05	−0.09
Macoma balthica	**−0.21**	**−0.23**	0.08
Malacoceros tetracerus	0.03	**−0.34**	0.01
Nematoda spp.	**−0.27**	−0.05	0.02
Nereis diversicolor	0.13	**−0.31**	**0.22**
Oligochaeta spp.	**−0.30**	0.23	−0.01
Orchestia gammarellus	**−0.28**	0.01	−0.16
Polydora cornuta	0.05	**−0.31**	0.00
Pygospio elegans	0.00	**−0.31**	**0.31**
Scolelepis squamata	**−0.25**	−0.17	0.05
Scrobicularia plana	−0.13	−0.06	0.14
Sphaeroma rugicauda	**−0.27**	−0.01	0.05
Streblospio benedicti	−0.14	**−0.21**	−0.10

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given the high small-scale patchiness within the macrobenthos in intertidal areas. Further, other variables may explain the distribution of the distinguished species assemblages as well. Based on a review of >50 studies, Snelgrove & Butman (1994) pointed out that although grain size is usually correlated with the benthic distribution patterns, this correlation is not solely due to grain size alone but also to other variables, related to grain size, such as organic matter content. In addition, salinity conditions and ecological interactions (e.g. predation pressure) can explain macrobenthic distribution patterns in tidal flat habitats (Ysebaert *et al.*, 2003; Williams *et al.*, 2004; Beukema & Dekker, 2005).

Sample group 2 and especially SG 4 were here considered ecologically most important because of their high species richness and density of larger macrobenthic species (e.g. 2860 ind *N. diversicolor* m^{-2}, 126 ind *S. plana* m^{-2} and 24 ind *M. balthica* m^{-2}), which may be expected to contribute most to the waders' diet (Cramp & Simmons, 1977). Other typical species for SG 2 and 4 were *A. marioni, M. tetracerus, S. plana* and *P. elegans*. In comparison with the polyhaline tidal flat areas further upstream in the Schelde estuary, species composition, total density and diversity are quite similar (Ysebaert *et al.*, 2003; C. Van Colen, unpublished data) and similar species assemblages have commonly been observed in similar estuarine environments (e.g. Beukema, 1976, 1981; Dörjes *et al.*, 1986). Sample groups 2 and 4 were mainly found within the entrance channel and adjacent wider creeks at the eastern part of the Zwin nature reserve. Contrary to the habitats of the other SGs, this system is characterized by relatively strong tidal currents guaranteeing water renewal at each high tide. This creates a consequent relatively stable highly productive environment in which biomass can accumulate in larger organisms (i.e. k-strategists) (Gamito, 2006), compared to the lesser (shallow flats, i.e. SG 3) and erratically submersed and thus stressed areas (SG 1 and SG 5, i.e. tidal pond and salt pan). Given its high macrobenthic value, the extension of wide, tidal creeks should be a prime target within the future development and management of the nature reserve.

In contrast, SG 3 was characterized by typical r-strategists, such as *C. capitata* and *P. cornuta*. Both are small-sized opportunistic species, typically dominating disturbed environments and early stages of succession after disturbance (Pearson & Rosenberg, 1978; Carvalho *et al.*, 2005; Magni *et al.*, 2005; Van Colen *et al.*, in press). SG 1 was the less diverse sample group, dominated by *N. diversicolor* and predominantly occurred in sediments at the border of the tidal pond in the western part of the lagoon. Given its position in the lagoon, the seawater in this area is only refreshed during spring tides, causing large salinity fluctuations. Ysebaert *et al.* (2003) found that *Nereis diversicolor* dominated the macrobenthic community of the meso/oligohaline transition zone of the Schelde estuary. This zone is subject to large, seasonal salinity fluctuations. Hence, *N. diversicolor* can be considered as a species capable of coping with this variability.

CONCLUSION

The Zwin nature reserve hosts a rich (maximum 71,376 ind m^{-2}) and species diverse (maximum 11 spp.sample^{-1}) macrobenthic life. Based on multivariate analyses, five significantly different sample groups were detected. Macrobenthic density, species richness and species densities were correlated to sediment median grain size, mud content, elevation, as well as larger landscape features. The wide, tidal inlet channel was identified as ecologically most important because it contained the highest species richness and densities of larger macrobenthic species. The extension of wide, tidal creeks will result in added values in terms of both benthos and birds and should therefore be a prime target within the future development and management of the nature reserve.

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