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Macrofaunal communities in the habitats of intertidal marshes along the salinity gradient of the Schelde estuary

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The macrobenthos is important in benthic remineralization processes; it represents a trophic link and is also often used as a bio-indicator in monitoring programs. Variations of the environmental parameters strongly influence the structure of the macrobenthic communities in the marshes and since macrobenthos is the most important food item for marsh-visiting fish species in the Schelde, the variation in food resources can have a strong effect on the higher trophic level. The present study deals with the variation in macrobenthic communities in different habitats of intertidal marshes along the salinity gradient and the differences between the marsh creeks and the intertidal part of the estuary. The study measured density and species richness together with the biomass, and sampled a large intertidal channel and a smaller creek within five marshes along the salinity gradient of the Schelde estuary every six weeks between May and October in 2000.

The small creeks had a smaller grain size and higher organic matter content than those in the large channel although the differences in the environmental parameters did not explain the different communities in the two habitats. Marshes had distinct macrobenthic communities but the abundance of macrofauna fluctuated along the estuary without an identifiable spatial trend. In contrast, the total biomass increased towards the euhaline area due to the domination of *Nereis diversicolor*. Diversity showed a significant positive correlation with the salinity.

Comparison of the macrofaunal communities in the marsh with those on the intertidal flats of the estuary indicated similar trends in density, biomass and diversity along the salinity gradient. The density was similar in both habitats whereas biomass was much higher in the intertidal habitats of the estuary, partly due to the higher biomass of molluscs and annelids. Diversity indices were higher in the marsh, and the freshwater area had more species than in the estuary.

1. Introduction

The macrobenthos of estuarine intertidal areas are exposed to extreme and highly variable environmental conditions. This includes low oxygen concentration in the predominantly fine-grained sediment and fluctuations in salinity, drying and flooding, suspended sediment etc. with which benthic animals with limited mobility have to cope (McLusky et al., 1993). The colonisation by macrofauna and the subsequent development and modification of their communities therefore depends on several factors (Elliott et al., 1998). In estuaries, the macrobenthos is important in benthic remineralization processes, both directly and indirectly through its process of structuring the sediment (Mazik and Elliott, 2000). Macrofauna represent an important trophic link between producers and fish and crustaceans species in the salt marshes (Sarda et al., 1995) and they are also often used as a bio-indicator in monitoring programmes (e.g. Heip et al., 1992).

The macrobenthos of the extensive US salt marshes has been well studied (Rader, 1984; Sheridan, 1992; Sarda et al., 1995; Szalay and Resh, 1996; Angradi et al., 2001) and macrofaunal communities have been compared between mature and created salt marshes to indicate the development of the newly created area (Alphin and Posey, 2000). Characteristics of macrobenthic fauna communities in three salt marsh successional stages of the Yangtze estuary were studied by Yang et al. (2006). In Europe, Jackson et al. (1985) studied macro-invertebrate populations and production in east

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England and Frid and James (1989) investigated the temporal change of macrobenthos of another English salt marsh in North Norfolk. Tagliapietra et al. (2000) sampled macrobenthos in a marsh pond in the Venetian Lagoon, Italy. Other studies have focused on one or two macrobenthic species such as *Nereis diversicolor* (Emmerson, 2000; François et al., 2002), *Nereis oligohalina* (Alves and Lana, 2000) or *Corophium volutator* (Essink et al., 1989; Hughes and Gerdol, 1997).

The present study was conducted in marshes situated along the Schelde estuary (The Netherlands and Belgium). The subtidal and intertidal benthic macrofauna along the salinity gradient of this estuary has been intensively studied by Ysebaert et al. (1993), Ysebaert and Herman (2002) and van der Wal et al. (2008) however macrobenthic communities in the marsh creeks of the Schelde had not been previously investigated. The fish community of this estuary has been extensively studied (Maes et al., 1997, 1998; Hostens, 2000) which shows that the area's marsh creeks are important feeding grounds for several fish species such as the sea bass *Dicentrarchus labrax*, the flounder *Platichthys flesus* and the common goby *Pomatoschistus microps* (Mathieson et al., 2000; Hampel and Cattrijsse, 2004). These species occur in the marsh creeks in high abundance from spring until autumn (Cattrijsse et al., 1994; Hampel et al., 2004) and sea bass and flounder also have feeding maxima during these months (Arntz, 1978; Kelley, 1987). The diet of the three fish species is mainly comprised of macrobenthic species (Elliott et al., 2002; Hampel et al., 2005). For this reason, the investigation on the change of the macrobenthic communities is required to give better understanding of the functioning of these systems, especially in relation to the food availability of the marsh-visiting fish species. The main aim of the present paper is to investigate 1) whether the two marsh habitats (small and large channel) harbour different macrobenhic communities 2) how macrobenthic communities change in marshes along the salinity gradient and 3) whether there is difference in macrobenthos between the marsh and the intertidal part of the estuary.

2. Materials and methods

Five marshes were chosen along the salinity gradient of the Schelde estuary (Fig. 1). In the tidal freshwater part, one of the largest freshwater marshes is the 'Groot Schoor' or the marsh of Grembergen (G). 'Het Verdronken Land van Saeftinghe' (S) lies in

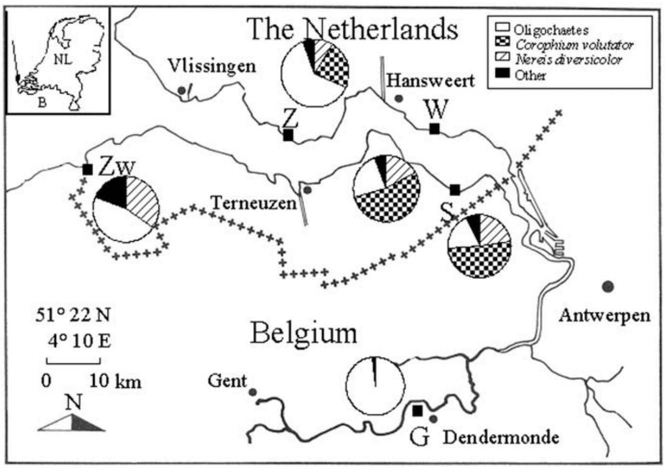

Fig. 1. Location of the five marshes sampled along the Schelde estuary. Marshes labelled by letters: Grembergen (G), Saeftinghe (S), Waarde (W), Zuidgors (Z) and Zwin (Zw). Relative species abundances are indicated next to each marsh.

the oligohaline part of the Schelde estuary. The marsh of Waarde (W) belongs to the mesohaline and the Zuidgors (Z) marsh to the polyhaline zone. Zwin (Zw) is situated at the mouth of the estuary, in the euhaline part. A large intertidal channel and a smaller creek were sampled in each marsh. The small creeks opened from the large channels. The dimensions of the larger creeks varied between 10–20 m wide and 3–4 m deep whereas the smaller creeks were generally 2 m wide and 1–1.8 m deep. Marshes were sampled during the spring tide period when tidal amplitude ranged between 4.5 and 5.5 m NAP (Dutch ground level) in the estuary. The inundation periods in the large channels were 6 h in Saeftinghe, Waarde and Zuidgors, while in Zwin and Grembergen the tide receded within 5 h. In the small creeks the inundation period generally lasted 2 h less compared to the large channels. At low tide the water left the channel and 5 replicate plastic cores (diameter 6.2 cm) were used to sample the macrobenthos to a depth of 15 cm at the centre of the large and small creek channel.

Samples were collected every six weeks between May and October 2000, this period and frequency was considered adequate to indicate the settlement, recruitment, establishment and development of the communities. The five marshes were sampled on consecutive days. In Grembergen, samples could be taken only from the large channel as the small channel became inaccessible after May due to the dense vegetation.

The environmental parameters of water temperature, salinity and dissolved oxygen were measured in the large and small creeks. Measurements were performed in the water column during the ebb period before the macrobenthic samples were taken in order to indicate the conditions experienced by the macrofauna prior to exposure. In each creek, a sediment core of diameter 6.2 cm was taken for the measurement of the medium grain size and organic matter content of the sediment. The values of the environmental parameters in each month were used to calculate the coefficient of variation in each marsh as following: % Coefficient of variation = (standard deviation/mean) × 100 (Jongman et al., 1987).

In the field, samples were preserved in a brackish-water–formalin solution. Samples were washed in the laboratory, sieved using a 1 mm sieve, stained with Rose Bengal and individuals were counted and identified to the lowest possible taxonomic level. The use of a 1 mm sieve after fixing the samples will have collected organisms smaller than the mesh used (pers. obs.). Individuals belonging to the class Oligochaeta were not identified to species level. Density was calculated for each replicate using the surface area of the sampling cores (0.003 m^2) and average densities for each creek. To calculate the biomass the samples (except bivalves) were dried at 60 °C for 4 days and then 2 h at 550 °C. They were placed in a desiccator for 2 h to reach room temperature and ash free dry weight (AFDW) was determined. For bivalves established regressions were used between length and AFDW. To minimise the weighting bias, the 5 replicates from the same creek were measured together.

The Shannon–Wiener function H′ (Pielou, 1966) was used as an indicator of the species diversity and calculated for each replicate and each creek. The non-parametric Mann–Whitney U test was used to test the abundance and diversity differences between the large channels and the small creeks within each site. The non-parametric Wilcox matched pair test was employed to indicate the differences in environmental parameters and sediment characteristics between the small and large creek. Multiple regression models were constructed using forward variable selection, with the software package STATISTICA v6, to identify the environmental variables which best explain the variation in species density, biomass and diversity in the small and large creek. Data from the large creek of Grembergen was excluded from the analyses to make result comparable with the result from the small creek. Temperature, dissolved oxygen concentration, medium grain size and organic matter content were log transformed prior to the analyses.

Spearman-Rank correlation was used to test the relationship between the salinity and the abundance, biomass and diversity of macrobenthic species. One-way ANOVA, using the software package STATISTICA v6, was used to indicate differences of density and diversity in the five marshes. The use of Detrended Correspondence Analysis (DCA) was decided followed Ter Braak (1987). To eliminate the effect of rare species, species which occurred less than 3 times in the samples were omitted. Density and biomass data were fourth root transformed and were used to analyse the differences between the communities in the marshes sampled.

3. Results

The marsh samples yielded 26 taxa or faunal groups of which some were identified to species but others to a higher taxonomic separation (Table 1). Life stages of *Carcinus maenas* were distinguished because of their different ecology. One bivalve, 1 mysid, 3 decapods, 3 amphipods and 3 isopods and 12 polychaete taxa were found in the samples. The taxon Oligochaeta incorporated all the species belonging to this class; it is likely that these included the species *Tubificoides benedii*, *Tubifex costatus*, *Tubifex tubifex* and Enchytraeidae (Barnes, 1994).

3.1. Environmental parameters

Because of the similarity of the environmental variables in the small and large creek (Wilcox matched pair test; $p > 0.05$) only the parameters in the later are presented. The hydroclimagraph (Fig. 2a) indicates that Grembergen is within the freshwater part of the river (0.2–0.4). Salinity varied between 8.0 and 10.8 in Saeftinghe and 14.8 and 16.7 in Waarde. Zuidgors had salinity around 25 while in Zwin the salinity reached the maximum 30.8. Water temperature (Fig. 2a) generally followed the seasonal pattern in all marshes with lower values in the spring and autumn and maximum during the summer. Exceptions were Zuidgors and Zwin where an unattributable and relatively low temperature (16–17 °C) was measured in August. Fig. 2b shows that the dissolved oxygen concentration in the water column is defined more by the position of the marsh in the estuary rather than the temperature increase, which is well known to co-occur with oxygen depletion. Lowest dissolved oxygen (DO) was measured in Grembergen and highest values were detected in Zwin. In Grembergen and Saeftinghe, DO showed similar patterns with low values in the first three months of sampling and increased oxygen concentration in October (7.2 and 7.7 mg l^{-1} respectively). In Waarde and Zuidgors, the water oxygen concentration slightly decreased towards autumn while it remained around 9 mg l^{-1} in Zwin.

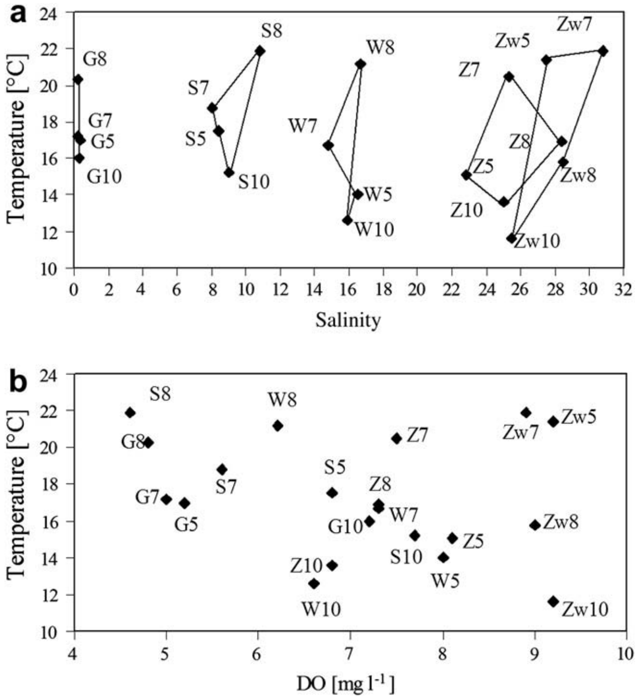

Fig. 2. Measured environmental parameters in the water column of the large marsh creek such as salinity versus temperature (°C) (a) and dissolved oxygen (DO) versus temperature (b). Marshes are labelled as Fig. 1. May (5), July (7), August (8) and October (10) are indicated by numbers.

The average medium grain size of the sediment in the marsh creeks ranged between 9.5 and 36 μm indicating the silt and clay dominance (Table 2a). In each marsh, sediment with smaller grain size was deposited in the small creek in comparison to the larger creek (Wilcox matched pair test; $p < 0.001$). In the oligo-, meso- and polyhaline marshes, the organic matter content was higher in

Table 1
Scientific name of species found in the five sampled marshes: "*j*" indicates the juvenile and "*m*" the megalopa stage of *Carcinus maenas*.

Mysidacea	**Polychaeta**	**Other**
Neomysis integer	*Nereis diversicolor*	*Nematoda* indet.
Caridea	*Heteromastus filiformis*	*Hirundinea* indet.
Crangon crangon	*Spio filicornis*	**Isopoda**
Brachyura	*Eteone longa*	*Cyathura carinata*
Carcinus maenas (*m*)	*Nephtys caeca*	*Isopod* indet.
Carcinus maenas (*j*)	*Streblospio benedicti*	*Sphaeroma rugicauda*
Amphipoda	*Cirratulidae* sp.	**Oligochaeta**
Corophium volutator	*Malacoceros tetraceus*	*Oligochaeta* indet.
Gammarus zaddachi	*Scolelepis squamata*	
Melitta pelludica	*Polydora ciliata*	
Bivalva	*Pygospio elegans*	
Macoma baltica	*Aonides* sp.	

Table 2
The average median grain size (μm) and OM (organic matter) content (%) of the sediment (±standard variation) was measured in the small and large creek. The Coefficient of variation (CV%) is given for each creek type (a). The Coefficient of variation (CV%) of salinity, temperature and dissolved oxygen (DO) during the sampling period in each marsh (b).

a)

	Creek size	Small	Large
	Location		
Median grain size	*Grembergen*		27.22 ± 0.60
	Saeftinghe	13.44 ± 0.41	21.45 ± 0.42
	Waarde	9.53 ± 0.31	16.84 ± 0.21
	Zuidgors	13.18 ± 0.35	22.09 ± 0.17
	Zwin	26.08 ± 0.35	36.09 ± 0.46
CV %		46.51	29.64
OM content	*Grembergen*		7.90 ± 0.51
	Saeftinghe	12.56 ± 0.65	5.76 ± 0.78
	Waarde	14.59 ± 0.57	10.68 ± 0.84
	Zuidgors	13.13 ± 1.07	10.67 ± 0.93
	Zwin	6.33 ± 0.75	6.47 ± 0.98
CV %		31.30	27.81

b)

	Salinity	Temperature	DO
Location	CV%	CV%	CV%
Grembergen	30.2	9.1	17.4
Saeftinghe	11.8	13.2	19.0
Waarde	4.6	20.3	9.8
Zuidgors	7.9	15.6	6.3
Zwin	6.8	24.0	1.4

Table 3
The *p*-values of Mann–Whitney U test comparing the macrobenthic density (a) and diversity (b) in the small and large creeks. Significant differences are labelled by bold numbers and the creek with higher density is indicated (small – s, large – l).

Month	Location			
	Saeftinghe	Waarde	Zuidgors	Zwin
(a)				
05	**0.01 (l)**	0.15	**0.05 (s)**	0.15
07	0.22	**0.01 (s)**	**0.01 (s)**	**0.01 (s)**
08	**0.01 (l)**	**0.01 (l)**	**0.03 (s)**	0.2
10	**0.01 (l)**	**0.02 (l)**	**0.01 (s)**	1.0
(b)				
05	0.42	0.09	**0.01 (l)**	0.69
07	0.84	0.15	**0.01(l)**	**0.03 (l)**
08	0.69	**0.01 (s)**	**0.01(l)**	0.09
10	0.22	1.0	0.15	0.06

the small creeks than in the large channel. In the euhaline area, the organic matter content of the sediment was around 6.4% in both habitats (Table 2a). Wilcox matched pair test indicated significant difference between the organic matter content between the large and small creeks ($p < 0.001$).

The inherent variability within each site and parameter is indicated by the coefficient of variation (%) (Table 2b). The high coefficient of variation for salinity coincided with high oxygen variation in Grembergen (salinity: 30.2%; oxygen: 17.4%) and Saeftinghe (salinity: 11.8%; oxygen: 19.0%). In the three downstream marshes (Waarde, Zuidgors and Zwin), the temperature was the most variable environmental parameter (20.3, 15.6, 24 CV% respectively). The coefficient of variation of the grain size in the small creek was 46.51% and in the large creeks was lower, 29.64% (Table 2b). The variability in OM content was 31.3 in the small and 27.8% in the large creek.

3.2. Qualitative analysis

3.2.1. Relative species abundance

The contribution of macrobenthic species to the total density is shown in Fig. 1. Grembergen was dominated by Oligochaeta composing the 98 percent of the total species density. Other species found in the freshwater marsh were *Cirratulidae* species, *Heteromastus filiformis*, and *Hirundinea* indet. *Nematoda* indet. and insects. *Corophium volutator*, *Nereis diversicolor* and Oligochaeta were the main contributors to the macrobenthic density in Saeftinghe, Waarde and Zuidgors. At Saeftinghe and Waarde, *C. volutator* composed more than 50 percent of the total density. *Cyathura carinata* still comprised approximately 4% of the total density in the oligohaline marsh (S). In the mesohaline (W) and polyhaline (Z) areas, *H. filiformis* (1.2 and 1.4% respectively) and Nematoda (3 and 2.6% respectively) were additionally important. 62 percent of the total density was due to Oligochaeta in Zuidgors. In the euhaline Zwin, 81 percent of the total density is attributed only to *N. diversicolor* and Oligochaete species. *Malacoceros tetraceus*, *Cirratulidae* species, *Streblospio benedicti*, *H. filiformis* and *Macoma balthica* contributed a further 14 percent of the total density in Zwin.

3.3. Small scale difference (small–large creeks)

3.3.1. Density

In Zuidgors, Mann–Whitney U test indicated significantly higher macrofaunal abundance in the small channel in every month while in Saeftinghe, the density was significantly higher in the big creek with the exception of July (Table 3a) (Fig. 3a). In Waarde, higher density was detected in the large channel in the last two months of the sampling and in the small channel in July. In the small channel higher macrobenthic abundance was found only in July. In Zwin, with the exception of July, no difference in macrobenthic density was measured.

Multiple regression analyses indicated that median grain size (beta = −0.38, $p < 0.001$) and temperature (beta = 0.39, $p = 0.003$) were the variables which significantly explain the variation in species densities in the large creek. In the small creek three variables (salinity, beta = 0.85, $p < 0.001$; organic matter content, beta = 0.73, $p < 0.001$; temperature, beta = 0.17, $p = 0.046$) explained the variation in species density.

3.3.2. Biomass

In Saeftinghe, the biomass was higher in the large channel except in the first sampled month (Fig. 3b). In contrast, the smaller

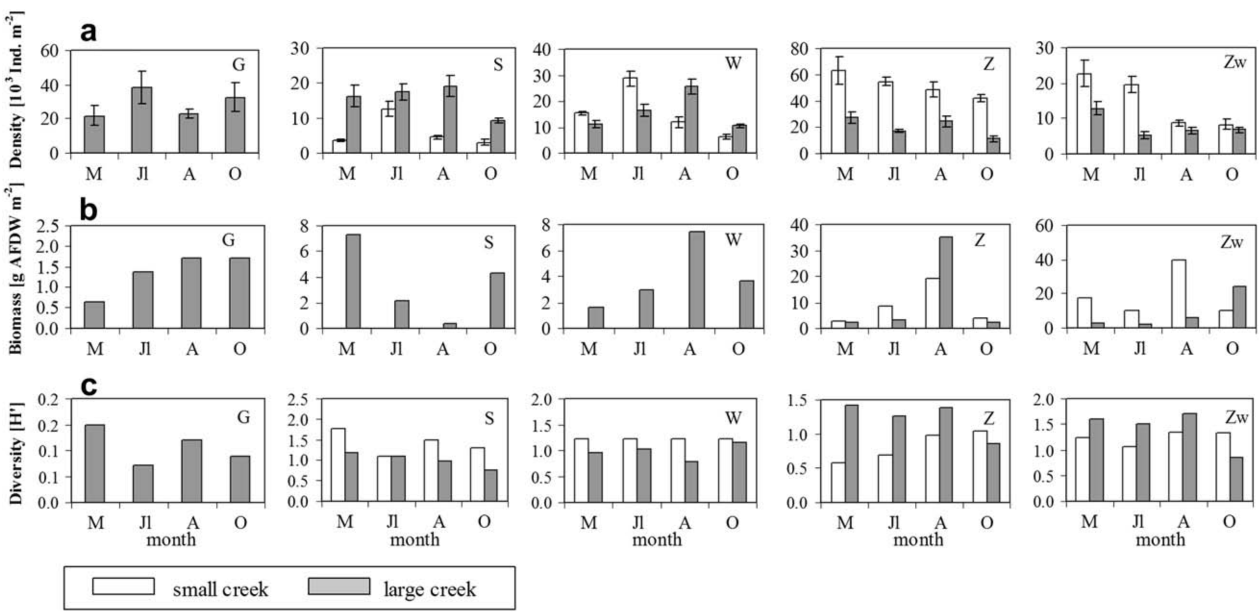

Fig. 3. Macrobenthic density (a), biomass (b) and diversity (c) in the two habitats during the four months (May – M, July – Jl, August – A, October – O) sampled. Small creek is labelled by white bar and large creek with grey colour. Labelling of marshes is used as indicated in Fig. 1.

channels in Waarde (except July), Zuidgors and Zwin generally supported a higher biomass of macrobenthos. Due to the measurement of the ash free dry weight, Mann–Whitney U test was not applicable to test the differences between the two habitats.

Using biomass data there was no environmental variable selected by multiple regression analyses in the large creek. In the small channel, salinity (beta = 0.61, $p = 0.013$) was the only variable which explained the variation of the diversity. However the low number of observation might have weakened the analyses.

3.3.3. Diversity

In Saeftinghe, Mann–Whitney U test did not show significant difference of diversity in the large and small channels (Table 3b) (Fig. 3c). In Waarde, significantly higher diversity was observed in the small creek than in the large one in August ($p = 0.01$). In Zuidgors, the Shannon–Wiener index was higher in the large channel except in the last month, October. The large creek supported more divers fauna in July ($p = 0.03$) in the euhaline Zwin.

Using multiple regression analyses salinity (beta = 1.32, $p < 0.001$), organic matter (beta = −1.07, $p < 0.001$) and median grain size (beta = 1.04, $p < 0.001$) were the main environmental variables influencing the species diversity in the large creek. In the small channel, salinity (beta = 0.43, $p = 0.002$) and organic matter (beta = −0.34, $p = 0.02$) were found to be significant variables.

3.4. Large scale difference (marshes along the salinity gradient)

3.4.1. Density

Locations were separated along the salinity gradient although the Spearman-Rank test did not show a significant correlation ($p > 0.05$) between the salinity and the density of macrofaunal species (Fig. 4a). The highest densities were detected in Zuidgors (avg. max. 63 300 ind. m^{-2}) and in Grembergen (avg. max 38 400 ind. m^{-2}) due to the high number of Oligochaeta. In Saeftinghe and Zwin, the average of the densities was approximately 10 000 ind. m^{-2}. Waarde had intermediate average density.

ANOVA indicated significant density differences between the marshes ($p < 0.001$). Saeftinghe had significantly lower density than Grembergen ($p < 0.001$), Waarde ($p = 0.02$) and Zuidgors ($p < 0.001$). Zuidgors had higher density compared to Waarde ($p < 0.001$) and Zwin ($p < 0.001$). The macrobenthic density was significantly higher in Grembergen than in Zwin ($p < 0.001$).

DCA ordination technique using density data showed the segregation of macrobenthic communities in the 5 different marshes (Fig. 5a). The two first axes explained around 33.7% of the variances. The samples of Zwin grouped together and situated in the right side of the plot while the samples from Saeftinghe grouped at the left side of the plot indicating large community differences between the two stations. The position of the samples of Waarde, Zuidgors and Grembergen on the DCA plot also shows the distinct community structure of these marshes.

3.4.2. Biomass

Marshes were separated along the salinity gradient and the biomass was found to be positively correlated with the salinity (Spearman-Rank correlation, $p = 0.03$) (Fig. 4b). The highest biomass was measured in Zwin (max 39.7 g AFDW m^{-2}) and the lowest value was detected in Grembergen (min 0.65 g AFDW m^{-2}).

DCA ordination technique using biomass data indicated different communities in the freshwater and euhaline marshes (Fig. 5b). The freshwater marsh had very low biomass in every month due to the dominance of Oligochaeta while in Zwin; the macrobenthic biomass reached high values due to *Macoma balthica* and *Nereis diversicolor*. The samples of the other three salt marshes did not segregate from

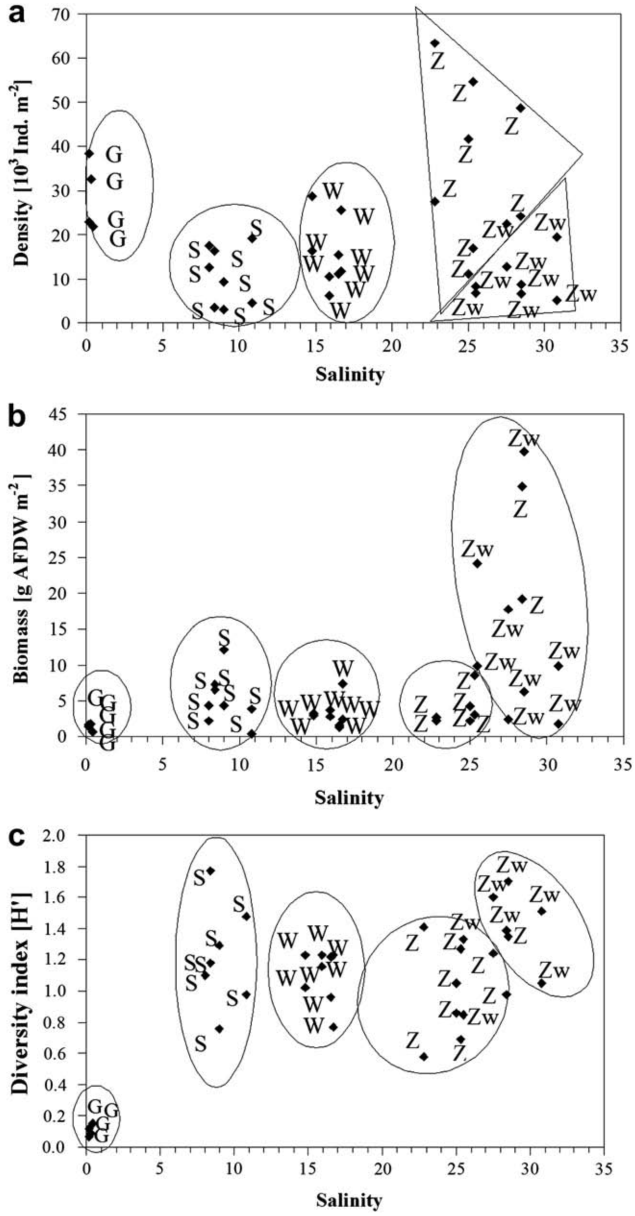

Fig. 4. Average densities (a), biomass (b) and diversity (c) versus salinity. Marshes are labelled as Fig. 1.

each other indicating similar macrobenthic communities. The first and second axes explained about 51% of the variance.

3.4.3. Diversity

The number of taxa found in the replicates of Grembergen ranged between 4 and 6. In Saeftinghe 4–7, Waarde 6–8, Zuidgors 6–14, Zwin 7–15 taxa were sampled. The locations were separated from each other in diversity (H′) (Fig. 4c) and the index values of the different marshes were significantly correlated with the salinity (Spearman-Rank test, $p < 0.001$). The Shannon–Wiener index values were lowest in the freshwater marsh (0.07–0.14). Zwin had the highest Shannon–Wiener indices (0.99–1.63) but the species diversity showed similar values in three marshes: in Zuidgors between 0.58 and 1.41, in Waarde 0.77 and 1.23 and in Saeftinghe 0.76 and 1.77 indices.

ANOVA using diversity indices found significant differences between the marshes ($p = 0.003$). Zwin, which had the highest

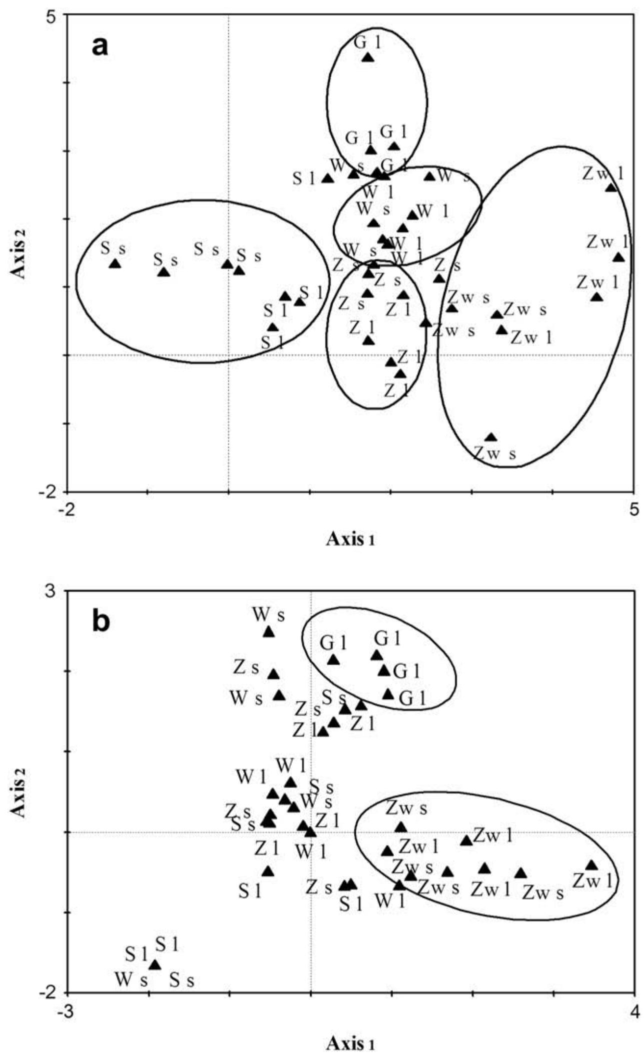

Fig. 5. DCA ordination technique using density (a) and biomass (b) data. Marshes are labelled as indicated in Fig. 1. Small creeks are shown as 's' and large creeks as 'l'.

diversity indices, differed significantly from Waarde ($p = 0.042$) and Zuidgors ($p = 0.001$).

4. Discussion

As indicated by the data from the present study and from elsewhere (e.g. McLusky et al., 1993), along an estuary the source of spatial variability of macrofaunal composition lies within a marsh (e.g. different habitats), between marshes (e.g. situation along the salinity gradient) and between habitats (e.g. mudflats versus salt marsh). Estuarine communities are created according to the combination of physico-variables which produce the fundamental niche for settlement and colonisation (e.g. McLusky, 1981; Costa et al., 2002).

4.1. Small scale differences (small–large creeks)

Ponds on the marsh surface are scare and due to the extreme environmental conditions utilized by very few species. The marsh surface is densely vegetated limiting the utilization of this habitat (Hampel et al., 2003). Hence species entering the marshes cannot progress further into these habitats but are restricted to use the two main habitats which are the small creeks or large channels for refuge or feeding ground. Few studies have focused on the different habitats within one marsh and they have mainly compared the macrobenthic communities on vegetated and bare mudflats (Rader, 1984; LaSalle and Rosas, 1991; Neira et al., 2005). The present study showed a significant community difference between the small and large channels. Macrobenthos in most of the marshes colonised the large and small creeks with different abundance, biomass and diversity however there was no clear pattern observed. Sediment characteristics were important parameters influencing species density and diversity. In the large channels the median grain size while in the small creeks the organic matter (OM) concentration were important environmental variables affecting species densities. Species diversities in both habitats were influenced by the OM concentration. Other studies also have shown the influence of organic matter on the abundance and distribution of macrobenthos, for example Talley and Levin (1999) found a negative relationship between organic matter and densities of macrofaunal taxa in a southern California marsh. In contrast to this observation, a positive association of faunal abundance and composition with organic matter in a *Spartina foliosa* marsh was observed by Levin et al. (1998). Sarda et al. (1995) found that the grain size and organic content defined distinct species assemblages to in a salt marsh in the US. Otani et al. (2008) indicated that distribution of macrobenthos could be explained by the classification of physical characteristics of sediment in tidal flats. An abundance of organic matter and a higher amount of fine particles, which also would influence the organic content, would be expected to favour the predominant deposit and detritus feeding taxa within the marshes.

4.2. Large scale differences (marshes along the salinity gradient)

It may be hypothesised that given that the marshes are covered by water only at the highest tides then they may have a higher salinity exposure than further down the intertidal region and also that they may have a less variable salinity exposure. This study indicates that marshes have distinct macrobenthic communities along the salinity gradient. Although the mean total population density did not show any trend along the salinity gradient due to the high density of *Corophium volutator* in the mesohaline marshes, the biomass and diversity clearly decreased towards the freshwater area. Not only the diversity but also the number of taxa found showed decrease with the declining salinity. This contradicts the general estuarine pattern where the number of species decreases with a progression upstream towards the tidal freshwater area and then increases with a movement into freshwater areas (Remane, 1934; McLusky, 1981). Ysebaert et al. (1998) found that anthropogenic stress affected the macrobenthos in the mudflats of the oligohaline and freshwater part of the Schelde estuary. The average yearly discharge of the upper Schelde estuary increased nearly threefold over the period 1996–2000 (Struyf et al., 2004). This might explain the pattern found in the present study however no measure on the pollution load was carried out. Lerberg et al. (2000) found a different density pattern in the tidal creeks located in Charleston Harbour where the relative abundance and the total number of polychaetes were positively associated with the salinity. In the present study the fluctuations of macrofaunal density are due to the high number of Oligochaeta in the freshwater and polyhaline marshes. The lack of correlation of density with the salinity is also caused by *C. volutator*, which appeared in high densities in the creeks of the three brackish marshes but was almost absent in the euhaline and freshwater marshes. Jackson et al. (1985) also found *C. volutator* as one of the main species contributing to the total density in a *Spartina anglica* marsh in the UK. In contrast to the density fluctuation, the mean total biomass along the salinity gradient showed clear decrease towards the freshwater area. This phenomenon is explained by the decrease of density and biomass of *Macoma balthica* and *Nereis diversicolor*.

4.3. Differences between marsh and estuary

Salt marshes are well known to serve as important feeding ground for several fish species (Minello and Webb, 1997; Craig and Crowder, 2000; Mathieson et al., 2000; Hampel and Cattrijsse, 2004). The macrobenthos comprise a significant part of the diet of some commercially fished species such as the sea bass *Dicentrarchus labrax* and the flounder *Platichthys flesus* (Hampel et al., 2005). Hence a comparison of the macrobenthic community in the marsh creeks with that in the adjacent intertidal area of the estuary will provide further information regarding the potential of marshes as fish feeding grounds. The importance of intertidal areas for water birds along the Schelde estuary was indicated by Ysebaert et al. (2000) who found that the distribution of benthivorous water birds was clearly related to the macrobenthic gradient.

A similar mesh size and method was used for sampling the marsh creeks as the estuary intertidal (Ysebaert et al., 1993) thus the results are comparable. The total density along the salinity gradient did not show any trend, thus agreeing with the observation of Ysebaert et al. (1993) who sampled intertidal areas in the Schelde estuary and found high and low macrofaunal abundance distributed randomly along the estuarine gradient. The average abundance of the macrobenthic species in the marsh creeks was slightly lower than the values reported by Ysebaert et al. (1993) and Ysebaert and Herman (2002) from the intertidal of the Schelde estuary. Among the main macrobenthic species and taxa consumed by the commercially important fish (*Nereis diversicolor*, *Corophium volutator*, Oligochaeta) the measured density of *N. diversicolor* was higher than in the intertidal zone of the Schelde estuary (Ysebaert et al., 1993; Ysebaert and Herman, 2002). Other studies reported a similar value as this study on mudflats of the Danish Wadden Sea (Jensen and Andre, 1993). In contrast, Hughes and Gerdol (1997) found similar densities to those recorded here of *N. diversicolor* in a marsh creek and an adjacent mudflat in eastern England. Ysebaert et al. (1993) indicated a lower density of *N. diversicolor* in the marine zone of the Schelde estuary than in the brackish part. In contrast, our study showed generally a higher density and biomass of *N. diversicolor* in the euhaline than in the brackish marsh creeks. In the euhaline area, the absence of *Platichthys flesus*, which diet is dominated by *N. diversicolor* (Hampel et al., 2005) may allow this species to reach higher abundance and biomass. *C. volutator* represents a very important prey item for *Dicentrarchus labrax* and *Platichthys flesus* (Hampel et al., 2005) in the meso- and polyhaline marshes. Ysebaert et al. (1993) also observed arthropod species mainly in the brackish part of the estuary where *C. volutator* composed the 90% of these species with comparable densities to the marshes. However in the year 2000, density of *C. volutator* reached a high peak comparing to the earlier years and exceeded the densities measured in the marsh creeks (Ysebaert and Herman, 2002). Hughes and Gerdol (1997) reported higher Corophium density from marsh creeks compared to the mudflats in south-east England.

The present study showed a decrease of the mean total biomass in the marshes towards the freshwater area, a feature found similarly in the wider estuarine areas (Schaffner et al., 1987; Meire et al., 1991; Ysebaert et al., 1993, 1998). However, the mean total biomass had lower values in the intertidal marsh creeks than in the estuary (*cf*. Ysebaert et al., 1993; Ysebaert and Herman, 2002). It is notable that the main difference between these studies is the lack of gastropod, *Hydrobia ulvae* and the lower density and biomass of the tellinid bivalves, such as *Macoma balthica* than in the estuarine intertidal. While it is possible that this difference could be the result of a different sampling depth in the sediment (in the estuary, 40 cm of sampling depth was used) this is unlikely. In a study of a marsh of the British east coast, Frid and James (1989) found 10 cm depth to be sufficient to sample macrobenthos and Jackson et al. (1985) used 20 cm depth since less than 2% of animals were recovered below this depth. Hiddink et al. (2002) found that *Nereis diversicolor* has a negative effect on the abundance of *Macoma balthica* in field and laboratory experiments. This observation may contribute to the explanation of the lowered density and biomass of *M. balthica* in the marsh creeks where one of the dominant species was *N. diversicolor.* Despite the lack of a high biomass of molluscs in the marshes compared to the estuary intertidal areas, the biomass of annelids still encountered double in the latter then that found in the marshes (Ysebaert et al., 1993).

The total number of taxa found in the marshes (26) was lower than in the Schelde estuary (35). The number of replicates taken at each sampling site was higher in the estuary and since the number of species correlates with the sampling size (Magurran, 1987), it may result these differences. Diversity (H′) showed a positive and significant correlation with the salinity both in the marshes and in the Schelde (Ysebaert et al., 1993) and other estuaries (Dittmer, 1983; Michaelis, 1983; Mannino and Montagna, 1997). Both in the marshes and the Schelde estuary the correlation coefficients were similarly high although the slope of the correlation was lower in the marshes indicating more exposure for salinity change. Also the coefficient of variation of the salinity in the two more upstream marshes showed exposed environment. Despite of all these facts the marshes along the Schelde had higher Shannon–Wiener index values than in the estuary. This is in contrast to other observations where the sampled marsh creeks tended to have a lower diversity relative to comparable estuarine habitats (Engle et al., 1994). Lerberg et al. (2000) found that tidal creeks were numerically dominated by a few species of stress tolerant oligochaetes and polychaetes. In the Schelde the upper part of the estuary is anoxic during much of the year (Van Eck et al., 1991), this was the main reason suggested by Ysebaert et al. (1993) for the exclusive occurrence of organic-tolerant Oligochaeta in the freshwater part of the estuary. In contrast, Rhode (1982) reported other species (e.g. freshwater gastropods, gammarids, and insect larvae) living in the upper part of the Ems estuary, this may reflect the downstream migration of the freshwater fauna. As indicated by the present study, other species (e.g. insect larvae, freshwater isopods) also inhabited the freshwater marsh of the Schelde. The existence of these species may be supported by the less anoxic/hypoxic conditions in the marsh creeks.

Nowadays several factors threaten the existence of the estuarine marshes. Salt marshes have been filled, diked and impounded for purposes of agricultural or urban land reclamation (Bakker et al., 1993; Mitsch et al., 1994; Airoldi and Beck, 2007). On global level, relative sea-level change influenced by an array of anthropogenic factors affect the coastal wetlands (Kennish, 2001). This study investigated the variation in the macrobenthos in different habitats of intertidal marshes along the salinity gradient. The salinity, medium grain size and organic matter content of the sediment are important environmental variables but did not explain the macrobenthic community differences in the two sampled marsh habitats. Density followed the change of Oligochaeta whereas biomass reflected the pattern of *Nereis diversicolor* and *Macoma balthica*. This study indicated the importance of salinity being the major determining factor for macrobenthic species distribution in the marshes. Density fluctuated along the salinity gradient without any trend but biomass and diversity were positively correlated with the salinity and a comparison of marsh habitat with the intertidal part of the estuary indicated same density, biomass and diversity pattern along the salinity gradient. The remarkably higher biomass of macrobenthos and longer tidal coverage would suggest that estuarine intertidal area is disproportionately a more important habitat for macrobenthic species and might be used better for fish as feeding ground although the similar density values and the higher diversity indices in the marshes seems to contradict to this view.

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