

resource for large crustaceans, fish and birds (Day, Hall, Kemp, & Yanez-Arancibia, 1989). Humans also harvest many species of shellfish and crustaceans.

Estuaries are transitional environments between rivers and the sea, characterized by widely varying and often unpredictable hydrological, morphological and chemical conditions (Day et al., 1989). Estuarine organisms are often restricted to particular sections of environmental gradients, resulting in well-developed distribution patterns (Wolff, 1983). The spatial heterogeneity of macrobenthos along the estuarine gradient is traditionally described in relation to salinity and sediment composition (e.g. Beukema, 1976; Boesch, 1977; Carriker, 1967; Gray, 1974; Holland, Shaughnessy, & Hiegel, 1987; Mannino & Montagna, 1997; McLusky, 1987; Meire, Seys, Buijs, & Coosen, 1994; Michaelis, 1983; Sanders, Mangelsdorf, & Hampson, 1965; Schlacher & Wooldridge, 1996; Wolff, 1973, 1983; Ysebaert, Meire, Coosen, & Essink, 1998; Ysebaert, Meire, Maes, & Buijs, 1993). Warwick and Uncles (1980) and Warwick et al. (1991) pointed out the importance of both dynamic processes (tidal range and wave fetch distance) and static factors (sediment grain size and organic content), in determining the community structure of macrobenthos. Other studies also emphasize the importance of hydrodynamic processes resulting from currents and waves (such as bed shear stress) for the transport and distribution of sediment, food and juvenile macrofauna (e.g. Norkko, Cummings, Thrush, Hewitt, & Hume, 2001; Snelgrove & Butman, 1994; Turner et al., 1997). Recent studies have shown a complex interaction between hydrodynamics, sediment dynamics and benthic biology in structuring distribution patterns of benthos (Hall, 1994; Herman, Middelburg, & Heip, 2001; Paterson & Black, 1999).

Knowledge of the spatial distribution patterns of macrobenthos along estuarine gradients might help to identify the linkages between species distributions and ecological processes and therefore to gain insight into the functioning of estuarine ecosystems (Thrush, Lawrie, Hewitt, & Cummings, 1999), which is essential for implementation of integrated estuarine management. However, in their review Heip et al. (1995) concluded that, because of a biased sampling strategy, few studies dealt with the two major gradients in macrotidal, estuarine benthic habitats, namely the salinity gradient along the estuary and the gradient from high intertidal to deep subtidal sites.

The macrotidal Schelde estuary is one of the longest tidal estuaries in NW Europe. The Schelde estuary is under permanent stress due to a high load of urban, industrial and agricultural waste (Van Eck & De Rooij, 1993). Being an important shipping channel to the harbor of Antwerpen, the estuary is extensively dredged ( $8\text{--}12 \times 10^6 \text{ m}^3$  per year at present). This has resulted in several changes in the morphology of the estuary

(Vroon, Storm, & Coosen, 1997). It is a turbid, nutrient-rich, heterotrophic ecosystem (Heip & Herman, 1995; Soetaert & Herman, 1995a). The Schelde estuary nevertheless has some high ecological values, being internationally important for several bird species (Ysebaert et al., 2000), and with large parts of the estuary being designated under the Ramsar Convention and European Birds and Habitat Directive. Future plans to further deepen the estuary will increase the dredging activities by more than 50%. To evaluate the impacts of the dredging activities, the macrobenthos has been monitored extensively during the last decade, resulting in a very large data set (>3000 samples). In this article, this large macrobenthos data set is used to analyze the spatial distribution patterns of macrobenthic species assemblages on an estuarine meso- and macro-scale, in relation to the estuarine environmental variables salinity, depth (or elevation), current velocity and sediment characteristics. Current velocity was explicitly incorporated in the analyses as a measure of the 'dynamic' condition at our sampling stations, besides the more 'static' variables such as depth and sediment characteristics. Indicator species, trophic structure and community structure were defined along the prevalent estuarine gradients. Variation in macrobenthic community structure, and its relation to changes in the abiotic environment were analyzed using multivariate statistics. The relative importance of the environmental variables in explaining the observed variation in the benthic community at the estuarine scale was further analyzed through direct gradient analyses with variation partitioning.

Species were classified according to trophic groups, and the abundance and biomass of these groups were described as a function of the major gradients in the estuary. Comparison of different estuarine systems showed a relation between average benthic biomass and primary productivity (Herman et al., 1999). It suggested that suspension feeder biomass was the most variable part in this response, whereas deposit feeder biomass is more homogeneously distributed. In this study, spatial patterns of distribution of both groups were studied to check whether a dependence on primary production could also be valid within an estuary.

In a separate contribution, the data set presented here was used to model and predict macrobenthic species responses to environmental conditions in estuarine ecosystems (Ysebaert, Meire, Herman, & Verbeek, 2002).

## 2. Materials and methods

### 2.1. Study area

The Schelde estuary, a macrotidal, nutrient-rich, heterotrophic system, measures 160 km from the mouth near Vlissingen (The Netherlands) to Gent (Belgium)

abundance and biomass per species for such a composite sample. For the subtidal zone, either a Van Veen grab or a Reineck box corer was used. In the intertidal zone, most samples (77%) covered an area of between 0.015 and 0.023 m<sup>2</sup> each, and a further 18% 0.01 m<sup>2</sup> each. In the subtidal zone, most samples (76%) covered an area of 0.015 m<sup>2</sup> each, which is comparable with the samples in the intertidal zone. A minor percentage of the subtidal samples covered a much larger area (0.10–0.12 m<sup>2</sup>). As difference in sample size is rather small between most samples, the effect of sample size on the occurrence of a certain species is expected to be small. All samples were sieved on a mesh size of 1 mm.

In the laboratory all organisms were sorted, identified to species level if possible and counted. Biomass of all species was determined as gram ash free dry weight (g AFDW). Depending on the monitoring program, biomass measurements were made directly, as the difference between the dried (80 °C for minimum 48 h) and ashed (560–80 °C for 2 h), or measurements were based on length–weight relationships and factors converting wet weight into ash free dry weight. For bivalves, regressions were established between length and AFDW, separately for each species, region and season. AFDW of a random sample of animals was determined by drying (80 °C for minimum 48 h) and ashing (560–580 °C for 2 h). Biomass of all other individuals was then calculated using this regression. For the other species, conversion factors between blotted wet weight (determined to the nearest 0.1 mg) and AFDW were established. These factors were again specific for species, region and season. After establishing the conversion factors, AFDW was calculated from the blotted wet weight of all individuals. Occasionally, for rare species, conversion factors for a morphologically similar species were used.

### 2.3. Abiotic variables

For each sample the following abiotic environmental variables were added to the macrobenthos database: depth/elevation (one variable), salinity (two variables), current velocity (two variables) and sediment characteristics (two variables). At subtidal stations depth was recorded at the time of sampling. The elevation of the intertidal stations was measured directly in the field or derived from the RIKZ Geographical Information System, storing all bathymetric data in the area. For 2874 samples depth values were available. Depth is expressed in m NAP (NAP = Dutch Ordnance level, similar to mean sea level).

Salinity was estimated for each sampling location using the 2D-hydrodynamic model SCALDIS400 with a spatial resolution of 400 m. The model calculations are based on values for mean tidal conditions with a yearly averaged discharge, giving an average salinity value. While a high spatial resolution is obtained using the

SCALDIS400 model, the estimates are not seasonally defined. Monthly to fortnightly measurements at nine stations along the Westerschelde were also used to represent the temporal variation in salinity. For each sample temporal salinity was determined as the average salinity of the 3 months previous to the date of sampling. Interpolation between the measurement stations was done along the length axis of the estuary. Tidal excursion in the estuary is in the order of 10 km, which is also the order of distance between measuring points. Estimates obtained from model simulations are called 'model salinities', whereas values derived from field observations are called 'temporal salinities'.

Current velocities (maximum ebb and flood current velocities at the bed in m s<sup>-1</sup>) for each sampling location were estimated with the SCALDIS100 hydrodynamic model for mean tidal conditions, with a spatial resolution of 100 m. For 3037 samples current velocity estimates were available. Current velocities at the bed were estimated from the 2D model, using the vertical current velocity parameterization inherent in the model formulation.

Samples for sediment grain size analysis (by laser diffraction technique) were collected during several campaigns. Sampling methods for grain size differed slightly, but in all cases sediment was collected from 0 to 5 cm deep. Median grain size (1502 samples) and mud content (1386 samples) values were added to the database, respectively. Throughout this article the term mud content is used as a generic name for the fraction <63 µm.

### 2.4. Data analysis

All macrobenthic abundance data were transformed to numbers m<sup>-2</sup> (ind. m<sup>-2</sup>), and biomass data to g Ash Free Dry Weight m<sup>-2</sup> (g AFDW m<sup>-2</sup>). Most species were determined at species level. For some genera the taxonomic resolution of determination differed among studies. As a consequence, species belonging to the genera *Bathyporeia*, *Ensis*, *Microphthalmus*, *Ophelia*, *Polydora*, *Spio*, and *Spisula* were all lumped at the genus level. Each species was classified into feeding groups based on available literature (e.g. Barnes, 1980; Fauchald & Jumars, 1979). Trophic groups included surface deposit feeders (SDF), sub-surface deposit feeders (SSDF), suspension feeders (SF), omnivores and predators. Species feeding by more than one mode was classified by their most common feeding mechanism. Appendix A gives a list of species, together with their feeding type, that are mentioned in the text or figures.

For ease of summarizing the data, the longitudinal gradient of the study area was categorized into four regions: lower estuary (region 1: Vlissingen–Terneuzen); middle estuary (region 2: Terneuzen–Hansweert); inner estuary (region 3: Hansweert–Bath); inner/upper estuary (region 4: Bath–Lillo) (Fig. 1). In regions 1–3 the

Table 1  
Average  $\pm$  standard deviation and minimum–maximum model and temporal salinity of the samples in each region (see text for further explanation;  $n$  = number of samples)

	Regions			
	1	2	3	4
Model salinity				
Average	29.23 $\pm$ 1.36	23.96 $\pm$ 1.52	16.52 $\pm$ 2.04	8.93 $\pm$ 1.41
Minimum–maximum	26.21–31.61	20.33–27.35	10.20–20.33	5.69–13.38
Temporal salinity				
Average	27.56 $\pm$ 2.71	20.36 $\pm$ 4.50	14.22 $\pm$ 5.32	9.78 $\pm$ 3.04
Minimum–maximum	16.96–32.39	8.38–26.87	1.86–21.55	1.15–15.18
$n$	722	959	956	475

polyhaline zone (average salinity  $>18$ ), regions 3 and 4 to the  $\alpha$ - and  $\beta$ -mesohaline zone, respectively (average salinity between 10–18 and 5.5–10, respectively) (Table 1). Based on temporal salinity, region 2 could be considered as a poly-/mesohaline transition zone, whereas region 4 could be considered as a meso-/oligohaline transition zone. Both salinity measures were strongly correlated ( $r = 0.86$ ;  $p < 0.01$ ;  $n = 3112$ ).

A significantly higher median grain size and a significantly lower mud content were observed in the subtidal strata as compared with the intertidal zone (ANOVA,  $F_{3,1498} = 56$ ;  $p < 0.001$  and ANOVA,  $F_{3,1382} = 53$ ;  $p < 0.001$ , respectively) (Table 2). This was also demonstrated by a significant positive correlation between depth and median grain size ( $r = 0.46$ ;  $p < 0.01$ ;  $n = 1436$ ) and a significant negative correlation between depth and mud content ( $r = -0.39$ ;  $p < 0.01$ ;  $n = 1326$ ). This rather weak correlation could be explained by the fact that this trend was not consistent within each region (Fig. 2). In regions 1–3 mud content was significantly higher in the intertidal zone as compared with all subtidal strata, but overall means were relatively low. In comparison, in region 4 much higher mud content was observed in all depth strata, but here differences between depth strata were relatively small, with only a weak trend towards coarser sediments with increasing depth.

There was a significant difference among depth strata for maximum ebb (ANOVA,  $F_{3,3033} = 815$ ;  $p < 0.001$ ) and maximum flood (ANOVA,  $F_{3,3027} = 789$ ;  $p < 0.001$ ) current velocities, with a clear trend of higher current velocities from the intertidal to the (deep) subtidal and

channel (Table 2). This was also demonstrated by the highly significant correlation between depth and maximum ebb ( $r = 0.76$ ;  $p < 0.01$ ;  $n = 2827$ ) and maximum flood ( $r = 0.75$ ;  $p < 0.01$ ;  $n = 2827$ ) current velocities. This pattern was consistent within each region. Current velocities were mutually highly correlated ( $r = 0.83$ ;  $p < 0.01$ ;  $n = 3037$ ).

A significant, but rather weak, correlation was observed between current velocities and median grain size ( $r = 0.45$ ;  $p < 0.01$ ;  $n = 1455$ ) and mud content ( $r = -0.37$ ;  $p < 0.01$ ;  $n = 1340$ ), indicating coarser sediments with lower mud contents with higher current velocities. Finally, a strong negative correlation was observed between median grain size and mud content ( $r = -0.84$ ;  $n = 1386$ ).

### 3.2. General characteristics of macrobenthos

Macrofauna species richness (number of species,  $N_0$ ) in a single sample varied between 0 and 25 species. In 202 samples (6.5%) no macrobenthic animals were found. Most samples (51%) had less than five species and in 28% of the samples between five and ten species were observed. The most common species were *Heteromastus filiformis*, observed in 58% of the samples, *Macoma balthica* (41%), *Pygospio elegans* (36%), *Bathyporeia* spp. (30%), *Nereis diversicolor* (26%) and *Hydrobia ulvae* (25%). Other species occurred in less than 20% of the samples.

Total abundance varied between 0 and 225,568 ind.  $m^{-2}$ . In about half the samples abundance was less than 1000 ind.  $m^{-2}$  and in about one-third abundance

Table 2  
Average  $\pm$  standard deviation for median grain size ( $\mu m$ ), mud content (%  $<63 \mu m$ ), maximum ebb (max. ebb) and flood (max. flood) current velocities ( $m s^{-1}$ ) for each depth stratum ( $n$  = number of samples)

Depth stratum	Median grain size	Mud content	Max. ebb	Max. flood
1 (Intertidal)	139.1 $\pm$ 69.1 $n = 922$	22.9 $\pm$ 23.1 $n = 888$	0.42 $\pm$ 0.19 $n = 1481$	0.39 $\pm$ 0.23 $n = 1481$
2 (Shallow subtidal)	192.9 $\pm$ 84.8 $n = 173$	13.5 $\pm$ 21.6 $n = 150$	0.74 $\pm$ 0.25 $n = 471$	0.79 $\pm$ 0.27 $n = 471$
3 (Deep subtidal)	202.7 $\pm$ 87.2 $n = 143$	14.0 $\pm$ 21.9 $n = 116$	0.83 $\pm$ 0.22 $n = 429$	0.88 $\pm$ 0.26 $n = 429$
4 (Channel)	218.2 $\pm$ 91.9 $n = 264$	10.5 $\pm$ 18.4 $n = 232$	0.97 $\pm$ 0.23 $n = 656$	1.00 $\pm$ 0.27 $n = 656$

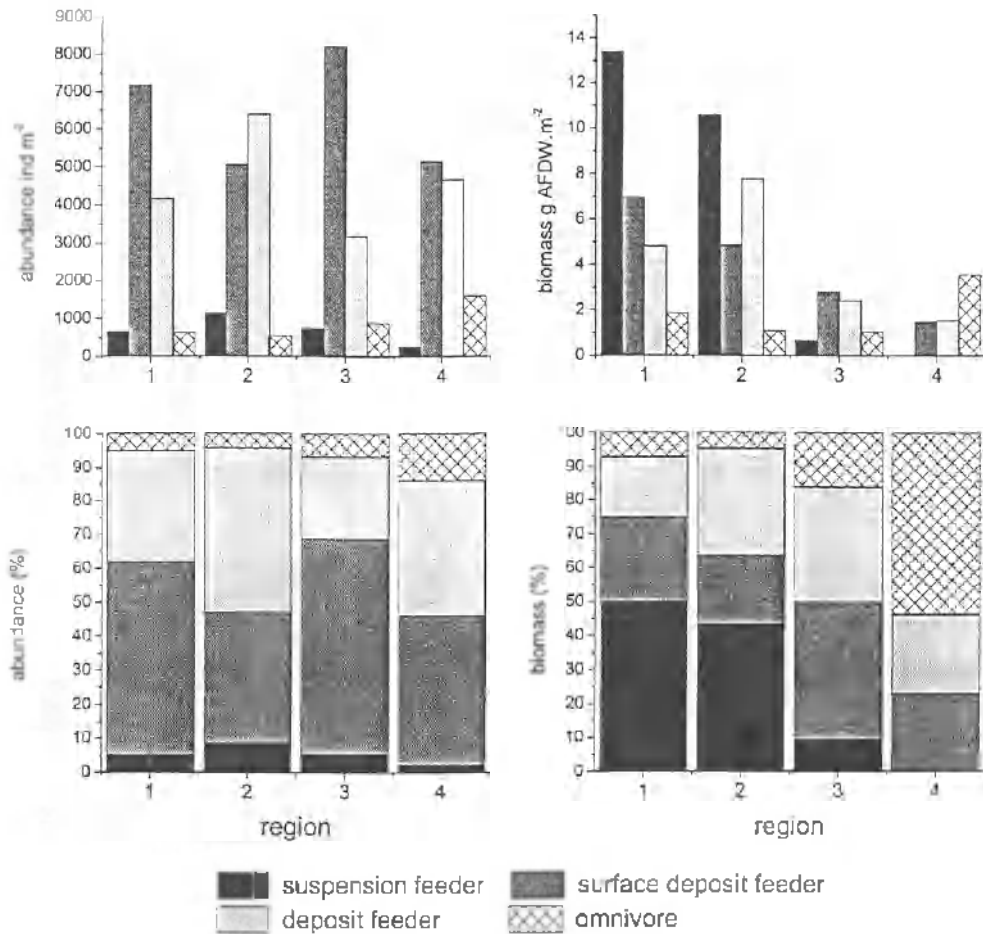


Fig. 4. Absolute and relative dominance (abundance and biomass) of the different feeding guilds in the intertidal (littoral) zone of each region. For the division of regions see text and Fig. 1 (regions 1 and 2: polyhaline zone; regions 3 and 4: mesohaline zone).

2 and 4 (ANOVA  $F_{3,1533} = 26.1$ ;  $p < 0.0001$ ). Abundance of SF was low, with significantly lower numbers in region 4 as compared with the other regions (ANOVA  $F_{3,1533} = 27.0$ ;  $p < 0.0001$ ). Omnivore, predator abundance was low in the regions 1–3, but increased significantly in region 4 (ANOVA  $F_{3,1533} = 37.7$ ;  $p < 0.0001$ ).

Clear gradients in the biomass of the different feeding guilds were observed in the intertidal zone (Fig. 4). SF biomass (mainly *Cerastoderma edule*) dominated in the polyhaline zone and showed a significant decrease in the mesohaline regions 3 and 4 (ANOVA  $F_{3,1533} = 91.0$ ;  $p < 0.0001$ ). The same trend was observed for SDF biomass (ANOVA  $F_{3,1533} = 33.1$ ;  $p < 0.0001$ ) and DF biomass was also significantly higher in the polyhaline zone as compared with the mesohaline zone (ANOVA  $F_{3,1533} = 74.4$ ;  $p < 0.0001$ ). Omnivores (mainly *Nereis diversicolor*) showed an opposite trend, with a significantly higher biomass in region 4 (ANOVA  $F_{3,1533} = 71.7$ ;  $p < 0.0001$ ), where it was the dominant group. Region 3 acted as an intermediate region with SDF and SSDF dominating the biomass.

In the subtidal zone abundance was also dominated by SDF and SSDF (60–85% cumulatively). Only in region 3 was a high proportion of SF observed, due to some samples taken in mussel banks. Biomass was dominated by SF in the subtidal zone. This was due to the presence of high biomass values of SF in only a few samples in all regions. In the polyhaline zone (regions 1 and 2) the SF were mainly *Ensis* and *Spisula*, whereas in region 3 a few samples in *Mytilus* banks were responsible for this dominance. In region 4 a few samples with oysters were responsible for this dominance (Ysebaert, De Neve, & Meire, 2000).

### 3.5. Seasonal variations in the intertidal zone

In the intertidal zone mean number of species per sample, mean total abundance and mean total biomass were significantly higher in autumn as compared with spring in all regions (Table 3). The five most dominant species in each region, both in terms of abundance and biomass, are presented in Fig. 5. In region 1 abundance

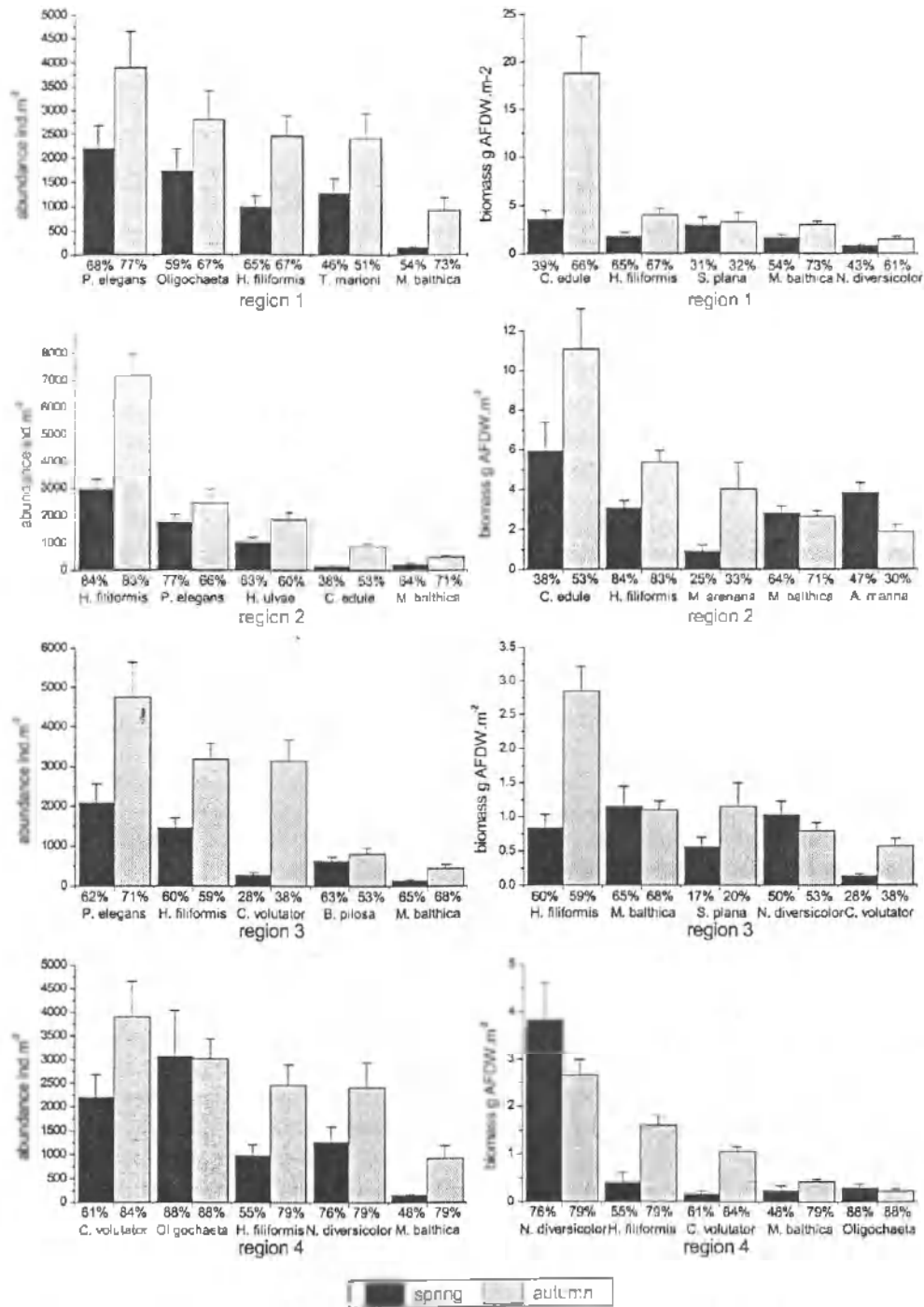


Fig. 5. Abundance (ind. m<sup>-2</sup> ± s.e.) and biomass (g AFDW m<sup>-2</sup> ± s.e.) in spring (March–May) and autumn (August–October) of the five most dominant macrobenthic species in the intertidal (littoral) zone of each region. For the division of regions see text and Fig. 1 (regions 1 and 2: polyhaline zone; regions 3 and 4: mesohaline zone).

zone. Abiotic characterization of this cluster resembled cluster 8; only mean current velocities were somewhat lower. Abundance was relatively low. As for cluster 8, the indicator species was *Bathyporeia* spp., but also a higher occurrence and higher densities of some charac-

teristic species from clusters 3–4 were observed (e.g. *H. filiformis*). Cluster 5 was mainly found in the intertidal zone of both the polyhaline and  $\alpha$ -mesohaline zone, and was characterized by intermediate current velocities and fine/medium sands with low mud content. Biomass

Table 5  
Dendrogram representing the TWINSpan classification based on macrofauna biomass (data set B, n = 1243)

	1	2	3	4	5	6	7	8
Salinity	9.1 ± 5.3	10.6 ± 3.8	21.4 ± 4.8	22.7 ± 1.4	20.6 ± 5.7	19.7 ± 5.0	21.8 ± 5.5	16.4 ± 4.7
Depth	7.9 ± 4.4	-0.7 ± 2.3	0.3 ± 3.3	-0.1 ± 0.7	2.5 ± 5.8	4.0 ± 6.3	9.9 ± 5.6	4.3 ± 4.9
Max. ebb	0.86 ± 0.26	<b>0.39 ± 0.24</b>	0.41 ± 0.14	0.49 ± 0.09	0.54 ± 0.23	0.66 ± 0.23	0.87 ± 0.27	0.77 ± 0.28
Max. flood	0.77 ± 0.27	0.32 ± 0.27	0.31 ± 0.15	0.31 ± 0.14	0.53 ± 0.29	0.60 ± 0.32	0.93 ± 0.28	0.82 ± 0.29
Median	97 ± 91	93 ± 54	182 ± 47	162 ± 58	170 ± 59	213 ± 60	223 ± 63	213 ± 45
Mud content	45 ± 27	41 ± 21	24 ± 19	14 ± 13	11 ± 14	6 ± 9	4 ± 7	3 ± 4
Mean NO	4.4 ± 3.5	5.9 ± 2.1	12.7 ± 3.4	8.7 ± 2.2	7.7 ± 3.6	5.4 ± 3.6	5.7 ± 4.2	2.7 ± 1.6
Mean abundance	1058 ± 2575	11882 ± 10455	32529 ± 26281	12853 ± 9913	6718 ± 7318	1693 ± 2204	560 ± 1330	601 ± 1100
Mean biomass	0.48 ± 1.21	6.6 ± 5.7	50.8 ± 4.0	24.3 ± 16.8	9.1 ± 23.6	3.47 ± 10.34	1.68 ± 14.04	0.21 ± 0.32
<b>Biomass</b>								
<i>Poly lige</i>	<b>0.11/39%</b>	-	-	-	-	-	-	-
<i>Coro volu</i>	0.009/39%	<b>1.12/87%</b>	0.29/40%	0.009/11%	0.065/10%	0.0005/3%	0.00007/1%	0.00001/1%
<i>Oligochacta</i>	0.005/87%	<b>0.23/84%</b>	0.08/30%	0.004/3%	0.008/25%	0.003/5%	0.0004/6%	0.0004/2%
<i>Nere olve</i>	0.001/3%	<b>1.19/87%</b>	2.36/72%	0.53/23%	0.27/30%	0.07/15%	0.00001/1%	-
<i>Cera edul</i>	-	0.0001/1%	<b>14.77/86%</b>	2.25/53%	2.18/33%	0.11/16%	0.0004/14%	0.0001/1%
<i>Mya aren</i>	0.001/4%	0.003/6%	<b>6.35/75%</b>	1.09/48%	0.02/18%	0.0002/2%	0.00002/1%	-
<i>Pygo eleg</i>	0.0003/19%	0.06/36%	<b>0.55/92%</b>	0.06/72%	0.20/71%	0.03/45%	0.0003/4%	0.00004/2%
<i>Sera plan</i>	0.004/1%	0.02/2%	<b>4.26/60%</b>	1.05/15%	0.004/2%	-	0.0001/1%	-
<i>Hydr ulva</i>	-	0.01/22%	<b>0.59/77%</b>	<b>0.32/87%</b>	0.11/59%	0.02/19%	0.0001/6%	0.0002/4%
<i>Maco hali</i>	0.006/7%	0.42/81%	<b>4.80/95%</b>	<b>3.66/86%</b>	1.88/77%	0.36/34%	0.015/17%	0.003/3%
<i>Hete fili</i>	0.05/55%	1.31/71%	<b>9.23/96%</b>	<b>6.34/100%</b>	1.75/84%	0.31/82%	0.03/34%	0.01/14%
<i>Aren mari</i>	-	-	1.26/34%	<b>8.17/75%</b>	0.37/11%	0.50/8%	-	-
<i>Bath spec</i>	0.007/11%	0.02/8%	0.03/17%	0.05/46%	<b>0.14/48%</b>	<b>0.11/60%</b>	0.004/12%	0.07/87%
<i>Spin spec.</i>	-	-	0.002/10%	0.0008/3%	0.006/17%	0.003/14%	<b>0.03/56%</b>	0.0003/2%
<i>Nepht cirr</i>	-	-	-	0.006/2%	0.003/3%	0.012/5%	<b>0.13/48%</b>	0.004/2%
<i>Easis spec.</i>	-	-	0.15/1%	-	-	-	<b>1.13/33%</b>	-
<i>Haus aren</i>	-	-	-	-	-	0.0004/1%	0.001/6%	<b>0.05/31%</b>

The number of samples belonging to each cluster is indicated in the dendrogram. For each cluster mean ± SD of the environmental variables (model salinity, depth (m), maximum ebb (max. ebb) and maximum flood (max. flood) current velocity ( $\text{m s}^{-1}$ ), median grain size (median,  $\mu\text{m}$ ) and mud content (%)) are given. Mean diversity (NO), mean abundance ( $\text{ind. m}^{-2}$ ) and mean biomass ( $\text{g AFDW m}^{-2}$ ) per cluster are given (mean ± SD). For each cluster mean biomass of the dominant macrobenthic species (indicator species) is given, together with its occurrence (% present) in that cluster. Boldfaced numbers represent the main data set structure. For species abbreviations see Appendix A.

presented for the abundance data set B solely (Fig. 6). Adding season as covariable in the CCA explained a negligible percentage of the total inertia (total inertia = equal to the sum of all eigenvalues of a correspondence analysis of the species matrix).

For data set A (abundance and biomass) the first two axes explained about 83% of the total variance which can be explained by the current environmental variables. The third and fourth axes were of minor importance. For data set B the first three axes explained 85–89%. The fourth axis was of minor importance.

The relation between the ordination axes and the environmental variables was similar for all data sets (Table 6). The first axis was most strongly correlated with

depth, with maximum flood and ebb current velocities showing similar gradients (Fig. 6). The second axis mainly correlated with salinity, although often salinity also showed a strong correlation with the first axis. The third axis in data set B mainly correlated with sediment characteristics (mud content), but sediment characteristics also correlated well with the first axis, with mud content showing an opposite gradient (Fig. 6).

Forward selection on the abundance data sets A and B corroborated the correlations observed between ordination axes and environmental variables (Table 7). With each variable considered separately (marginal effects), the highest eigenvalue was observed for depth, but differences with the other environmental variables

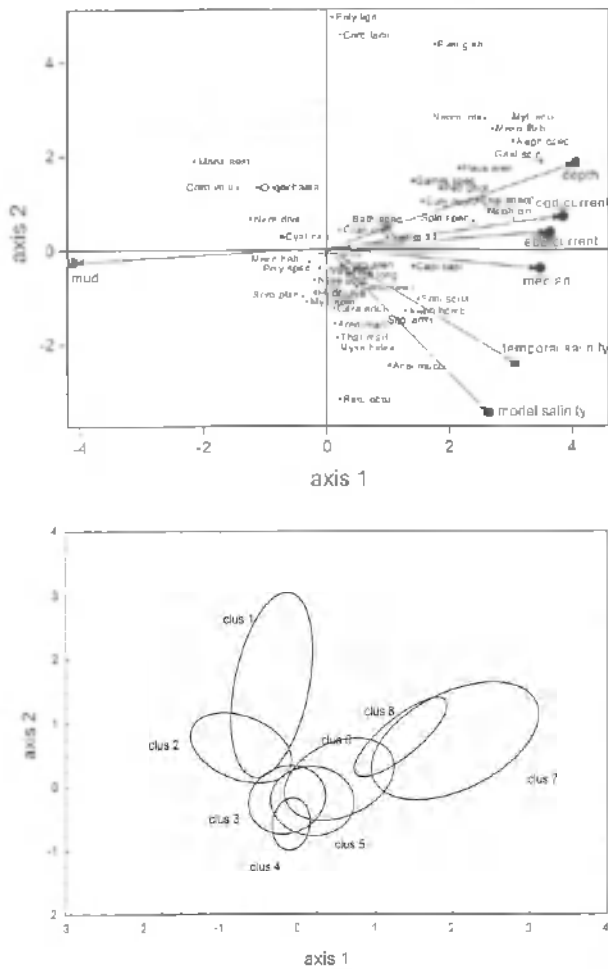


Fig. 6. CCA ordination diagrams based on the analysis of abundance data of dataset B (with sediment variables,  $n = 1243$ ). The top figure shows the species distributions in relation to environmental variables (ebb current and flood current = maximum ebb and flood current velocity; mud = mud content; median = median grain size). The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular environmental gradient. The bottom figure shows the 75% confidence regions of the sample scores for each cluster. For results of the CCA analysis see Table 6. For abbreviation of the macrobenthic species names see Appendix A).

*H. ulvae*) (Fig. 6). Species characteristic for the polyhaline zone were mainly observed in the down right quadrant of the biplot (e.g. *Anaitides mucosa*, *T. marioni*, *Nephtys hombergii*). At the other end, characteristic species for the  $\beta$ -mesohaline zone were e.g. *C. volutator*, *Manayunkia aestuarina* and *P. ligierica*. The position of the different macrobenthos species in the biplot resembled the division in indicator species over the different clusters, as observed by superimposing the different clusters on the biplot (Fig. 6). The superimposed clusters showed to some extent overlap, especially the clusters 3–6, which clustered at a higher

dichotomy. The  $\beta$ -mesohaline clusters 1 and 2 were clearly discriminated, and also the subtidal clusters 7 and 8 were separated from the other clusters.

### 3.8. Variation partitioning

From the forward selection in the CCA analyses it was observed that several variables had very low conditional effects, due to collinearity. To get an idea of the unique effects of the four different groups of environmental variables ((1) depth, (2) salinity (model ebb and maximum flood) and (3) current velocity (maximum ebb and maximum flood) and (4) sediment characteristics (mud content and median grain size)), both constrained and partial CCAs were run for each group of environmental variables. Salinity independent of the other environmental groups accounted for 28% (unique effect) of the total variation explained by the environmental variables in data set B. The unique effect of depth and current velocity was 14.6 and 8.5%, respectively. The relatively low unique contribution of both was attributed to the covariation between both environmental groups (6.3%); as such, combined they explained 29.4%. This was in agreement with the results of the forward selection. The unique effect of the sediment characteristics accounted for 21%. Other covariations accounted for less than 4% each.

## 4. Discussion

### 4.1. Trends along the longitudinal (salinity) and vertical (depth) gradients

In their review Heip et al. (1995) concluded that, because of a biased sampling strategy, few macrobenthic studies dealt with the two major gradients in estuarine benthic habitats: the salinity gradient along the estuary (longitudinal) and the gradients from high intertidal to deep subtidal sites (vertical gradient). The large data set available for the Schelde estuary allowed us to analyze both these gradients, and relate macrobenthic species distributions to the predominant environmental variables.

The univariate and multivariate analyses clearly demonstrated the role of both salinity and depth in relation to diversity, abundance and biomass of the macrobenthos. Many studies have demonstrated that salinity is a major factor affecting macrofauna species distributions and community structure within estuaries. The pattern of species richness and diversity declining with decreasing salinity is a recurring one in most estuaries (Boesch, 1977; Dittmer, 1983; Mannino & Montagna, 1997; Michaëlis, 1983; Remane & Schlieper, 1971; Wolff, 1983) and our data support this. Not only

analyses that sediment characteristics added less to the total fit of the model than depth and salinity. However, mud content explained a significant part not yet explained by the two other main gradients. In a study on macrobenthic responses to natural and contaminant-related gradients in northern Gulf of Mexico estuaries, Rakocinski et al. (1997) showed three primary natural gradients in a CCA analysis: CCA axis 1 represented a predominant salinity gradient, CCA axis 2 a predominant depth gradient and CCA axis 3 a gradient in sediment silt/clay content. Rakocinski et al. (1997) did not include current velocities, and sampling stations were restricted to the subtidal zone, probably explaining why salinity was the most dominant gradient. Warwick et al. (1991), investigating the intertidal macrobenthic community structure of six British estuaries, separated sites mainly along two axes, one determined by static variables (e.g. sediment grain size and organic content), and the other by dynamic variables (i.e. current velocities), but in this study the salinity range was restricted. The scale at which studies are performed (e.g. subtidal vs. intertidal or the inclusion of the freshwater tidal zone into the survey) will influence the perception of their relative importance. Also the type of estuary, e.g. microtidal against macrotidal, might influence the relative importance of the different environmental variables considered.

Collinearity between environmental variables may also differ among estuaries or among zones within an estuary. For instance, in our study mean mud content appeared to be much higher in region 4 (meso/oligohaline) as compared with the higher salinity regions, whereas Schlacher and Wooldridge (1996) observed the opposite for the Gamtoos estuary in South Africa.

Interactions between soft-sediment macroinvertebrates and their environment not only include responses to the physicochemical environment (tolerances), but the effects of species that modify the substratum (biogenic habitat modifiers), as well as biological interactions, such as predation and competition, will also determine the distribution of a certain species (Olafsson, Peterson, & Ambrose, 1994; Wilson, 1991). Although biological interactions are thought to operate within the constraints imposed by large-scale physical factors (Legendre et al., 1997; McArdle, Hewitt, & Thrush, 1997; Thrush et al., 1997, 1999), more information is needed about the interaction of physical and biological factors (Barry & Dayton, 1991).

#### 4.3. Macrobenthic assemblages

The macrobenthic assemblages, distinguished at a broad, estuarine scale, were related to gradients in the environmental conditions observed along the estuary.

Some macrobenthic assemblages were typically related to the subtidal zone, where highest current velocities were observed. A first subtidal assemblage was mainly situated in the polyhaline zone, and occurred in medium sand sediments with a low mud content. This assemblage was characterized by the polychaetes *N. cirrosa* and *Spio* spp. *N. cirrosa* is known as a typical subtidal species, inhabiting sandy sediments (Clark & Haderlie, 1960; Wolff, 1971). In this assemblage, often species were observed which belonged more to the hyperbenthos, such as the mysid *G. spinifer* (Mees, Dewicke, & Hamerlynck, 1993; Mees, Fockedeij, & Hamerlynck, 1995). In a few samples high biomass values were observed of some bivalve species, such as *Ensis* and *Spisula*, but in general diversity, abundance and biomass were low.

A second subtidal assemblage was found mainly in the mesohaline zone, but extending into both the polyhaline and the oligohaline zones. Diversity, abundance and biomass of the macrobenthos were very low. This assemblage was characterized by the very mobile amphipod *Bathyporeia* spp. This species is capable of very fast swimming and digging (Croker, 1967; Nicolaisen & Kannevorff, 1969; Sameoto, 1969) and *Bathyporeia* spp., like most Haustoriidae, are typical, well-adapted inhabitants of unstable, sandy sediments (Bousfield, 1970; Khayrallah & Jones, 1980) and exposed beaches with a lot of wave action (Shackley, 1981). Other characteristic species for this assemblage were the amphipod *H. arenarius* and the isopod *Eurydice pulchra*. This assemblage was not only restricted to the subtidal zone, but extended into the intertidal zone.

A third subtidal community was clearly restricted to the most upstream part of the study area ( $\beta$ -meso/oligohaline zone). Here, this zone being part of the turbidity maximum area of the estuary, high current velocities often coincided with a muddy or very fine sand bottom sediment. This assemblage was characterized by some typical 'genuine brackish water' species (Michaelis, Fock, Grotjahn, & Post, 1992; Wolff, 1973), with indicator species being *P. ligerica* (Ysebaert, De Neve, et al., 2000). In samples, containing hard substrates such as stones and pieces of wood, a relatively species rich community was observed, with several amphipod species like *C. lacustre*, *Corophium insidiosum*, and *P. glaber*. In very muddy sediments, only *Oligochaeta* and *H. filiformis* were observed.

In the intertidal zone assemblages were in the first place related to salinity, and secondly to sediment composition (see also Ysebaert et al., 1993, 1998). The first assemblage was found in the polyhaline zone of the estuary, extending to some extent into region 3. Current velocities are much lower as compared with the subtidal assemblages (low dynamic areas), and sediments consist of very fine sand or mud. Diversity, abundance and



biomass observed. Their distribution, being dependent on pelagic food sources within the polyhaline zone of the estuary, will be mainly determined by the hydrodynamic conditions. In the subtidal zone, current speeds and instability of the sediment will prevent SF from settling down. Where conditions are favorable, such as on hard substrates (peat banks, stones), high biomass of, for instance, mussel spat (up to 455 g AFDW m<sup>-2</sup>) can be observed (personal observations). In the intertidal zone, the distribution of SF will also be determined by the hydrodynamic conditions, but the positive relationship that has been suggested between the SF biomass and current velocities might not be generally valid. Indeed, studies on an intertidal sand flat of the Westerschelde demonstrated that biomass of the SF *C. edule* was highest in the zone with lowest current velocities, probably depending on sinking material (Herman et al., 1999).

A higher primary production in the mesohaline zone of the estuary would probably lead to an increase in SF biomass. Especially *M. arenaria*, a bivalve well adapted to mesohaline salinity conditions, would profit of such a situation. At the meso-/oligohaline transition zone, however, where salinity conditions show large seasonal fluctuations, conditions will become unfavorable.

Deposit feeders are much more evenly distributed over space within an estuary, and their biomass is much less variable from one system to another than the biomass of SF (Herman et al., 1999). The Schelde estuary receives large quantities of allochthonous organic matter and nutrients, and it is supposed that there is no food limitation for deposit feeders, although qualitative aspects should be taken into account as well (e.g. Dauwe, Herman, & Heip, 1998). On a large scale, the distribution of deposit feeders, together with their food, will be determined to a great extent by the hydrodynamic conditions. In the intertidal zone, deposit feeders, especially grazers and SDF, also depend to a large extent on microphytobenthos production and, as this production is relatively constant over a broad range of environments, a relative constancy of the macrofauna groups dependent on this source may be expected (Herman, Middelburg, Widdows, Lucas, & Heip, 2000). In our study, deposit feeders were abundant along the complete salinity gradient, but the biomass of deposit feeders, especially the SDF, was highest in the polyhaline zone (region I) and decreased with decreasing salinities. Several factors could explain this decrease. Firstly, assigning a species to one functional group is difficult as many estuarine macrobenthic species are flexible in their natural history and response to environmental conditions (high generalism). Many species of SDF are known to be facultative SF (e.g. *M. balthica* (Olafsson, 1986; Kamermans, 1994) and 'interface' feeding spionid polychaetes (Dauer, Maybury, & Ewing,

1981; Taghon & Greene, 1992)). Therefore, SDF in the polyhaline zone might profit from the higher phytoplankton primary production (high quality food source) in this part of the estuary, resulting in a higher biomass. Secondly, in estuarine systems with high seasonal variability in river flow rate, disturbance and stress increase towards the lower salinity zones, as a consequence of the highly varying salinity conditions here causing physiological constraints to the benthic macrofauna. Additionally, a maximum turbidity zone is situated near the freshwater-seawater interface (oligohaline zone) and due to a high input of allochthonous organic matter and nutrients, microbial activity is pronounced in this region, resulting in oxygen depletion observed during several months a year, especially in summer (Goosen et al., 1999). This highly variable environment causes numerous, perhaps constant disturbances that might result in communities that seldom progress beyond early benthic-community succession (switch between an oligohaline and mesohaline fauna). The macrobenthic species observed in this zone of the estuary are typically very mobile (e.g. the amphipod *C. volutator*), opportunistic (tubificid *Oligochaeta*, capitellid *H. filiformis*) or omnivorous (the nereid *N. diversicolor*), strategies which resemble the early response to "succession after disturbance series" (Rhoads, McCall, & Yingst, 1978) or "distance to pollution source series" (Pearson & Rosenberg, 1978). In this zone of the estuary probably physical and physiological stress coincides with 'high loading' stress. On top of that, sediment contamination with metals and organic micropollutants is rather high, provoking additional stress (e.g. Rakocinski et al., 1997). Unraveling the contribution and interaction of each of these multiple stressors is necessary in order to determine natural versus human induced disturbances (Ellis, Schneider, & Thrush, 2000).

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