



# Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe

T. Ysebaert<sup>a,b,\*</sup>, P.M.J. Herman<sup>a</sup>, P. Meire<sup>c</sup>, J. Craeymeersch<sup>d</sup>,  
H. Verbeek<sup>e</sup>, C.H.R. Heip<sup>a</sup>

<sup>a</sup>Centre for Estuarine and Coastal Ecology, Netherlands Institute of Ecology (N100-KNAW), P.O. Box 140, 4400 AC Yerseke, The Netherlands

<sup>b</sup>Institute of Nature Conservation, Kliniekstraat 25, 1070 Brussels, Belgium

<sup>c</sup>Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

<sup>d</sup>RIVO-CSO, Postbus 77, 4400 AB Yerseke, The Netherlands

<sup>e</sup>National Institute for Coastal and Marine Management/RIKZ, P.O. Box 8039, 4330 EA Middelburg, The Netherlands

Received 5 February 2002; received in revised form 3 September 2002; accepted 10 September 2002

## Abstract

Few macrobenthic studies have dealt simultaneously 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). In this broad-scale study, a large data set (3112 samples) of the Schelde estuary allowed a thorough analysis of these gradients, and to relate macrobenthic species distributions and community structure to salinity, depth, current velocities and sediment characteristics. Univariate analyses clearly revealed distinct gradients in diversity, abundance, and biomass along the vertical and longitudinal gradients. In general, highest diversity and biomass were observed in the intertidal, polyhaline zone and decreased with decreasing salinity. Abundance did not show clear trends and varied between spring and autumn. In all regions, very low values for all measures were observed in the subtidal depth strata.

Abundance in all regions was dominated by both surface deposit feeders and sub-surface deposit feeders. In contrast, the biomass of the different feeding guilds showed clear gradients in the intertidal zone. Suspension feeders dominated in the polyhaline zone and showed a significant decrease with decreasing salinity. Surface deposit feeders and sub-surface deposit feeders showed significantly higher biomass values in the polyhaline zone as compared with the mesohaline zone. Omnivores showed an opposite trend.

Multivariate analyses showed a strong relationship between the macrobenthic assemblages and the predominant environmental gradients in the Schelde estuary. The most important environmental factor was depth, which reflected also the hydrodynamic conditions (current velocities). A second gradient was related to salinity and confirms the observations from the univariate analyses. Additionally, sediment characteristics (mud content) explained a significant part of the macrobenthic community structure not yet explained by the two other main gradients. The different assemblages are further described in terms of indicator species and abiotic characteristics.

The results showed that at a large, estuarine scale a considerable fraction of the variation in abundance and biomass of the benthic macrofauna correlated very well with environmental factors (depth, salinity, tidal current velocity, sediment composition).

© 2003 Elsevier Science B.V. All rights reserved.

**Keywords:** benthic macrofauna; estuarine habitats; environmental gradients; salinity; depth; canonical correspondence analysis; variation partitioning; suspension and deposit feeders; Schelde estuary

## 1. Introduction

Macrobenthos are an important component of estuarine ecosystems and play an important role in the system dynamics (Herman, Middelburg, Van de Koppel, & Heip, 1999). Macrobenthos are a central element of estuarine food webs, being an important food

\* Corresponding author.

E-mail address: [t.ysebaert@nioo.knaw.nl](mailto:t.ysebaert@nioo.knaw.nl) (T. Ysebaert).

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)

and is one of the longest estuaries in NW Europe with a complete salinity gradient. The study area is limited to the Westerschelde (Dutch part) and a small part of the Zeeschelde (Belgian part) near the Dutch–Belgian border (Fig. 1), comprising the complete polyhaline and mesohaline zone of the estuary. The mean tidal range increases from 3.8 m at Vlissingen to 5.0 m near the border. The river discharge varies from  $20 \text{ m}^3 \text{ s}^{-1}$  during summer to  $400 \text{ m}^3 \text{ s}^{-1}$  during winter, with a mean annual average of  $105 \text{ m}^3 \text{ s}^{-1}$ . The residence time of the water in the estuary ranges from 1 to 3 months, depending on the river discharge (Soetaert & Herman, 1995b). The most seaward region has a residence time of about 10–15 days.

The lower and middle estuary, the Westerschelde (55 km long), is a well-mixed region characterized by a complex morphology with flood and ebb channels surrounding several large intertidal mud and sand flats. The surface area of the Westerschelde is  $310 \text{ km}^2$ , with the intertidal area accounting for 35% of the area. The average channel depth is approximately 15–20 m. Upstream of the Dutch–Belgian border the estuary is characterized by a single channel. The turbidity maximum is situated near Antwerpen but moves over quite a large distance, mainly as a result of tidal action and river run off (Baeyens, van Eck, Lambert, Wollast, & Goeyens, 1998; Wollast & Peters, 1978). Also in this zone of the estuary oxygen concentration decreases rapidly, mainly due to the heavy loading with nutrients and allochthonous organic material, causing high microbial activity (e.g. Goosen, Kromkamp, Peene, van Rijswijk, & van

Breugel, 1999). For more details on the ecological and physical–chemical properties of the estuary see Meire and Vincx (1993), Heip and Herman (1995), Baeyens et al. (1998) and Herman & Heip (1999).

## 2.2. Macrobenthos database

A total of 3112 macrobenthos samples, mainly within the framework of monitoring programs, were collected in the study area by different institutes in the period 1978–1997. By far the most data were collected and analysed by two institutes, namely the Centre for Estuarine and Coastal Ecology NIOO-CEMO and the Institute of Nature Conservation, mainly in co-operation with the National Institute for Marine and Coastal Management (RWS-RIKZ). Most of the samples (90%) were collected from 1990 onwards; 58% were taken in autumn (August–October), 32% in spring (March–May). Most sampling locations (68%) were sampled only once, but several locations were sampled two to five times in the sampling period considered, and a few were sampled more frequently within a long-term program. The sampling effort of the different laboratories is not equally distributed over space (regions of the estuary) and time, but there was frequent methodological exchange between the contributing laboratories to ensure sufficient homogeneity of methods.

In general, multiple sediment cores from a 1 to  $2 \text{ m}^2$  area were used for sampling the intertidal zone. Replicate cores were pooled to produce a single value for

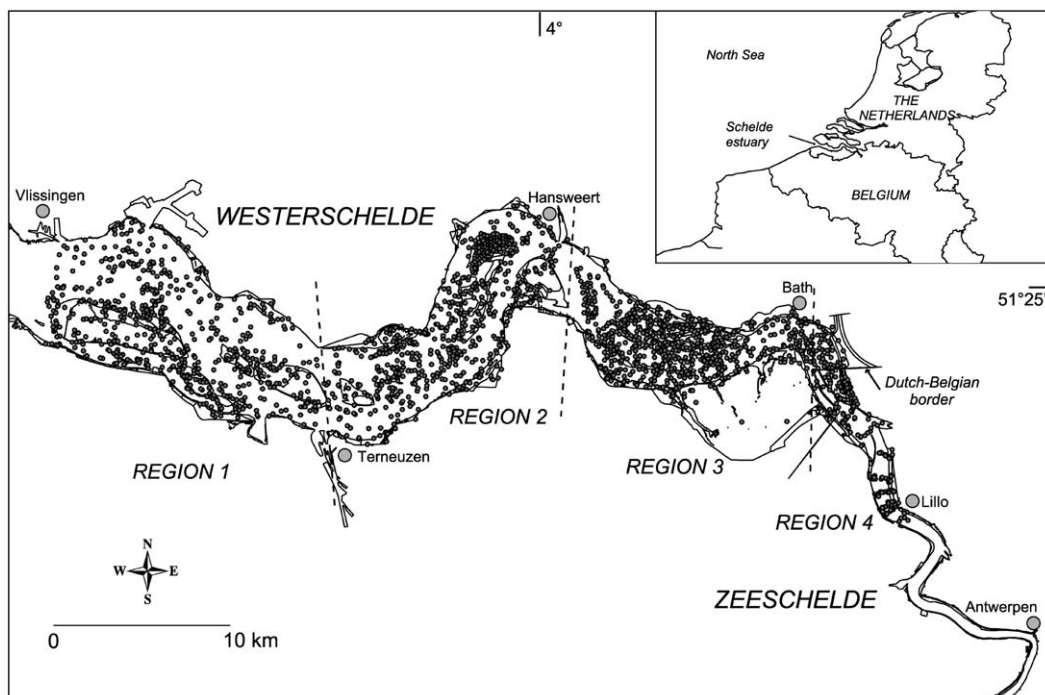


Fig. 1. Map of the Schelde estuary (polyhaline and mesohaline zone only) with indication of the sampling locations and the four regions.

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

proportion of samples collected in spring was similar (36–44%), whereas in region 4 a somewhat smaller proportion of the samples was collected in spring (18%). The vertical (depth) gradient was divided into four depth strata: the intertidal or littoral zone and three strata in the subtidal (shallow 2–5 m beneath NAP; deep 5–8 m beneath NAP; channel >8 m beneath NAP). Comparisons among depth categories and sediment characteristics and current velocities were examined with ANOVA on log-transformed data. The relations between environmental variables were further examined by Spearman rank correlations. The general trends in diversity, total abundance, total biomass and trophic structure of the macrobenthos along the longitudinal and vertical gradients were examined with a two-way ANOVA on log-transformed data. A spring–autumn comparison was made for the intertidal zone. The boundaries used between the regions were a compromise between the aims of spanning an equal fraction of the length of the estuary, spanning an equal salinity range, having an equal number of samples and having sufficient samples in all depth strata. The depth distribution was copied from the main sampling program contributing to the database, which uses stratified random sampling according to these depth categories. In interpreting the ANOVA results, some caution should be exercised because the design is not entirely balanced. However, this will not affect the main conclusions which are readily visible in the results.

Numerical classification and ordination (based on log-transformed data) were used to analyze community structure and its relationship to matching environmental data (Field, Clarke, & Warwick, 1982). Only species observed in more than 15 samples were included in the analyses and all taxa higher than the genus level, except Oligochaeta and Nemertea (always identified at the phylum level only), were excluded. Separate analyses were performed for the data set without sediment data ( $n = 2612$ ) and the data set with sediment data ( $n = 1243$ ), hereafter called data set A and data set B, respectively. The samples were classified into clusters (both for abundance and biomass data) using the classification program Two-Way Indicator Species Analysis—TWINSPAN (Hill, 1979).

Multivariate ordination techniques were used to assess, for data sets A and B separately, the variation in the species data set and the relationship between species composition and distribution and the measured environmental variables. As the gradient length in standard deviation (SD) units, determined in a preliminary detrended correspondence analysis (DCA; with detrending by segments), exceeded 3 SD, all subsequent numerical analyses involved techniques that are based on underlying unimodal species-response model, namely (canonical) correspondence analysis ((C)CA) analyses (Jongman, ter Braak, & Van Tongeren, 1995; ter Braak, 1994; ter Braak & Smilauer, 1998). As the macrobenthos

data were sampled in different seasons, it is likely that there is seasonal variation in the biological assemblage and the environment. This seasonal variation was not the prime research question. Therefore, a partial CCA was applied for all analyses, with season representing covariables (dummy variables) (ter Braak, 1988; ter Braak & Smilauer, 1998; ter Braak & Verdonschot, 1995). Forward selection of environmental variables was used to identify and rank their importance for determining the species composition (ter Braak & Smilauer, 1998; ter Braak & Verdonschot, 1995). In the first step of this method, all environmental variables are ranked on the basis of the fit for each separate variable (marginal effects, using each environmental variable as the sole constraining variable). At the end of the first step of the forward selection the best variable is selected. Hereafter, all remaining environmental variables are ranked on the basis of the fit that each separate variable gives in conjunction with the variable(s) already selected (conditional effects). The statistical significance of the effect of each variable (marginal and conditional) and the significance of the first canonical eigenvalue and of the sum of all eigenvalues was tested with Monte Carlo permutation tests (999 unrestricted permutations) (ter Braak & Smilauer, 1998).

The relative statistical strength of the four different groups of environmental variables [(1) depth, (2) salinity (model and temporal salinity), (3) current velocity (maximum ebb and maximum flood) and (4) sediment (mud content and median grain size)] was further analyzed by running a series of CCAs and partial CCAs for each group of environmental variables (method of variation partitioning, see Borcard, Legendre, & Drapeau, 1992; Liu & Bråkenhielm, 1995; Ökland & Eilertsen, 1994). The unique effects of each group of variables were estimated by using the group of variables as the sole predictor variables and all other groups of variables as covariables in partial CCA. Also, the effect of overlapping prediction between two different groups (e.g. joint prediction (covariance component) between depth and current velocity) was estimated. Absolute estimates of variation explained by constrained ordination are not strictly comparable among different data sets (Ökland, 1999). The effect of the different groups was expressed as a value relative to the total variation explained by the explanatory variables instead (Ökland, 1999). All ordinations were performed using the program CANOCO v4 (ter Braak & Smilauer, 1998).

### 3. Results

#### 3.1. Characterization of the abiotic environment

Average model salinity varied between 5.7 and 31.6 for the study area. Regions 1 and 2 belonged to 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,  $F_{3,3033} = 789$ ;  $p < 0.001$ ) 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)

	Median grain size	Mud content	Max. ebb	Max. flood
Depth stratum				
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 $n = 656$

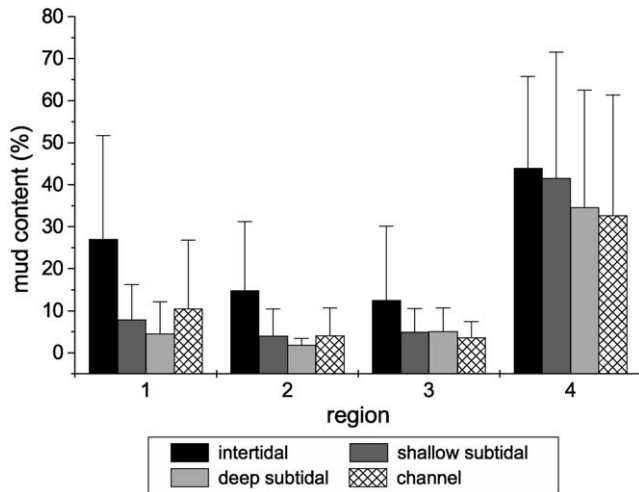


Fig. 2. Mean mud content ( $\pm$ SD) observed in each depth stratum per region. For the division of regions see text and Fig. 1. (regions 1 and 2: polyhaline zone; regions 3 and 4: mesohaline zone).

varied between 1000 and 10,000 ind.  $m^{-2}$ . The three most abundant macrofauna taxa were Polychaeta, Mollusca and Crustacea.

Total biomass varied between 0 and 466.5 g AFDW  $m^{-2}$ . In about half of the samples, biomass was less than 1 g AFDW  $m^{-2}$  and in about one-third biomass varied between 1 and 10 g AFDW  $m^{-2}$ .

### 3.3. General trends along longitudinal (salinity) and vertical (depth) gradients

As the ratio spring/autumn samples was more or less similar within each region, except for region 4, trends were based on all available data. The mean number of species per sample was significantly different among regions (two-way ANOVA,  $F_{3,3095} = 15.5$ ;  $p < 0.0001$ ) and depth strata (two-way ANOVA,  $F_{3,3095} = 499$ ;  $p < 0.0001$ ), with also a significant interaction term salinity  $\times$  depth (two-way ANOVA,  $F_{9,3095} = 14$ ;  $p < 0.001$ ). In the intertidal zone, a clear decrease in  $N_0$  from the polyhaline zone towards the mesohaline zone was observed (Fig. 3). In each region a significantly higher number of species (per sample) was observed in the intertidal zone as compared with the subtidal zone. In the subtidal zone, the average number of species observed per sample did not show a clear trend and was similar within each region and within each depth stratum.

Macrofauna total abundance was significantly different among regions (two-way ANOVA,  $F_{3,3095} = 8.7$ ;  $p < 0.0001$ ), although differences were small, and was highly significant with depth (two-way ANOVA,  $F_{3,3095} = 762$ ;  $p < 0.0001$ ), showing a significantly higher abundance for the intertidal zone as compared with the subtidal strata (Fig. 3). Within the subtidal strata, no

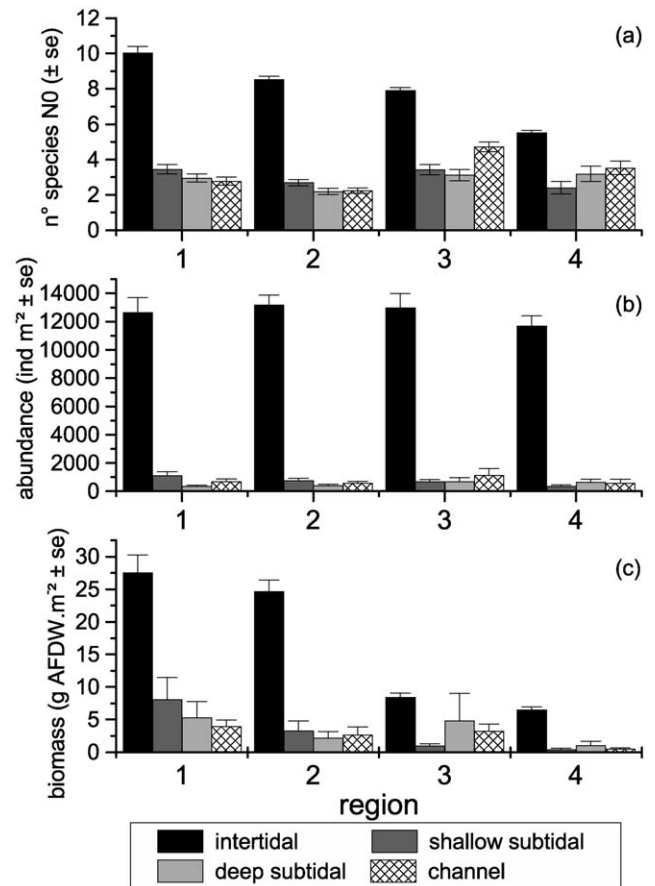


Fig. 3. Mean number of species, mean abundance (ind.  $m^{-2}$ ) and mean biomass (g AFDW  $m^{-2}$ ) observed along the longitudinal (regions) and vertical gradients (depth strata) in the Schelde estuary. For the division of regions see text and Fig. 1 (regions 1 and 2: polyhaline zone; regions 3 and 4: mesohaline zone).

significant difference was observed, which explains the significance of the interaction term (two-way ANOVA,  $F_{9,3095} = 5.9$ ;  $p < 0.0001$ ).

Macrofauna total biomass showed both a strong significant difference among regions (two-way ANOVA,  $F_{3,3095} = 21$ ;  $p < 0.0001$ ) and depth strata (two-way ANOVA,  $F_{3,3095} = 439$ ;  $p < 0.0001$ ), with also a significant interaction term salinity  $\times$  depth (two-way ANOVA,  $F_{9,3095} = 7$ ;  $p < 0.001$ ). Highest biomass values were observed in the highest salinity regions (polyhaline zone) and the intertidal zone (Fig. 3). Within the subtidal strata, no significant difference was observed.

### 3.4. Trophic structure of the macrobenthos

In the intertidal zone of all regions, abundance was dominated by SDF and sub-surface deposit feeders (SSDF), showing (cumulatively) no clear trends with region (Fig. 4). SDF abundance did not significantly change among regions, SSDF abundance was significantly lower in regions 1 and 3 as compared with regions

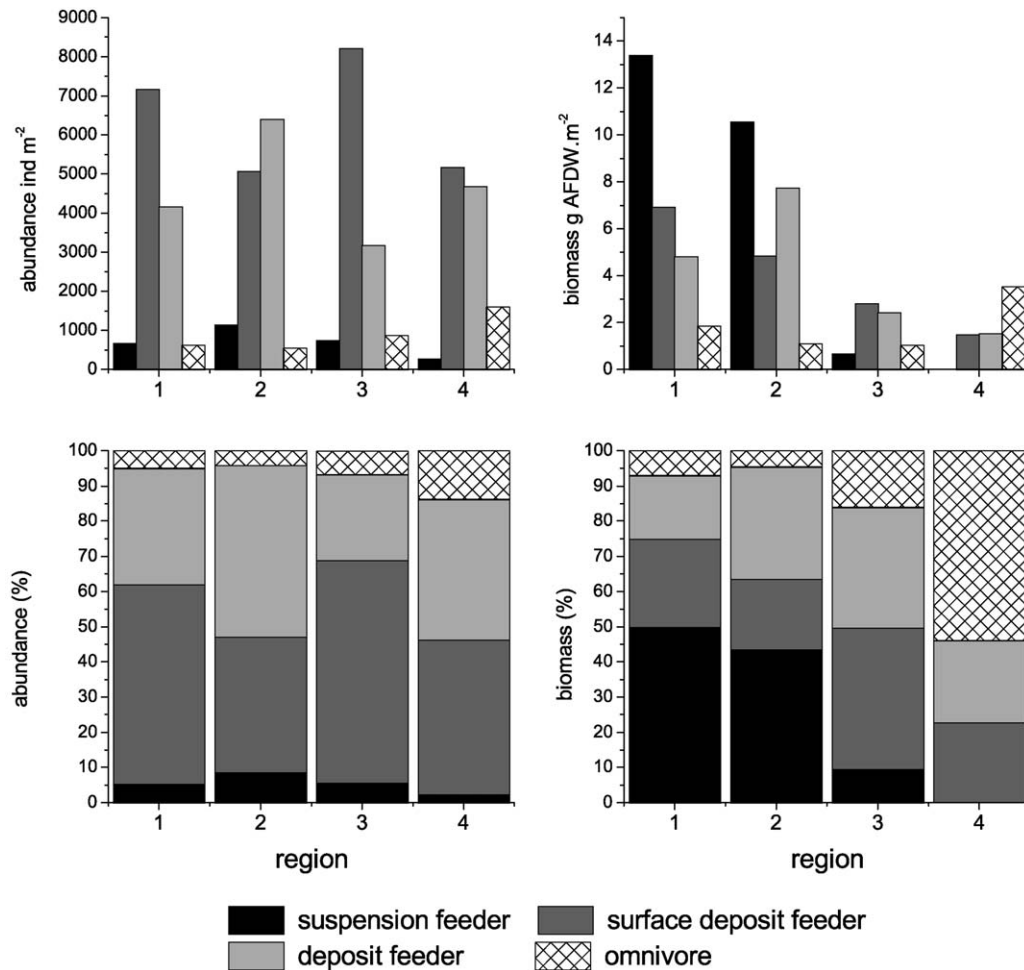


Fig. 4. Absolute and relative dominance (abundance and biomass) of the different feeding guilds in the intertidal (littoral) zone of each region. For the division of regions see text and Fig. 1 (regions 1 and 2: polyhaline zone; regions 3 and 4: mesohaline zone).

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



Table 3

Mean number of species per sample (species richness), mean total abundance (ind. m<sup>-2</sup>) and mean total biomass (g AFDW m<sup>-2</sup>) in spring (March–May) and autumn (August–October) per region in the intertidal zone of the Schelde estuary (means ± standard error; *n* = number of samples)

	Regions							
	1		2		3		4	
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn
Species richness	8.57 ± 0.55	10.90 ± 0.48	8.12 ± 0.62	8.95 ± 0.31	6.59 ± 0.28	8.36 ± 0.27	4.18 ± 0.35	5.78 ± 0.14
Abundance	7833 ± 1171	16 139 ± 1658	8205 ± 642	16 682 ± 1340	6378 ± 764	15 766 ± 1559	5325 ± 997	12 614 ± 838
Biomass	14.50 ± 1.88	34.48 ± 4.68	20.39 ± 2.07	31.32 ± 3.60	4.99 ± 0.73	8.90 ± 0.92	4.97 ± 0.79	6.06 ± 0.44
<i>n</i>	97	135	169	218	147	249	33	214

For regions see Table 1 and Fig. 1.

was dominated in both seasons by the SDF *P. elegans* and *Tharyx marioni* and the DF *H. filiformis*. Biomass in spring was more evenly distributed among several species, whereas in autumn the SF *C. edule* dominated. In region 2 abundance was dominated by *H. filiformis* and *P. elegans*, and to a lesser extent by the grazer *H. ulvae*. For biomass, most dominant species in both seasons was *C. edule*, but also *H. filiformis*, the SDF *M. balthica*, the SF *Mya arenaria* (autumn) and the SSDF *Arenicola marina* (spring) contributed substantially to the biomass. In region 3 abundance was dominated by *P. elegans* and *H. filiformis*, with the SDF *Corophium volutator* also predominantly present in autumn. In spring, biomass was dominated by *M. balthica*, the omnivore *N. diversicolor* and *H. filiformis*, whereas in autumn the dominance of *H. filiformis* was more pronounced. In region 4 abundance was dominated by *C. volutator*, *H. filiformis* and *N. diversicolor* in both seasons. Biomass was dominated by *N. diversicolor*, with *H. filiformis* and *C. volutator* also predominantly present in autumn.

The relatively large differences in abundance and biomass between spring and autumn for most macrobenthic species could only partially be attributed to a difference in occurrence (presence), since the proportion of samples where a species was present was similar in both seasons. Largest differences in presence between both seasons were observed for *C. edule* and for most species of region 4.

### 3.6. Classification and indicator species

The clusters distinguished were only used to detect the large-scale estuarine patterns. Up to five levels of the TWINSpan classification are summarized in Tables 4 and 5 for data set B on abundance and biomass data, respectively. Further divisions were not considered. The classification based on abundance and biomass data resulted in similar divisions. Clusters 2, 7 and 8 were very similar, with 77–94% of the samples mutually observed. The division of clusters 3–6 was slightly different for abundance and biomass, with

several samples interchanged among clusters in the two classifications. Abiotic characterization and indicator species of all biomass clusters were similar to the abundance clusters, but the relative contributions of the individual species differed.

In a first division two clusters (7–8) were separated, both characterized by high current velocities, a high median grain size and low mud content. Samples of cluster 7 were mainly situated in the subtidal (95% of the samples), polyhaline zone, but this community occurred up to the mesohaline zone. Abundance and biomass were low, with indicator species *Spio* spp. and *Nephtys cirrosa*. Cluster 8 was situated more in the mesohaline zone, with 60% of the samples observed subtidally. Cluster 8 had the lowest diversity, abundance and biomass of all clusters. The indicator species was *Bathyporeia* spp.

The remaining samples were then further separated into two clusters (clusters 1–2), representing mainly the β-mesohaline zone (region 4), and four clusters (clusters 3–6) representing mainly the polyhaline and α-mesohaline zone (regions 1–3). Clusters 1 and 2 (with approximately 95 and 85% of the samples from region 4) were separated into a characteristic subtidal cluster with high current velocities (cluster 1) and an intertidal cluster with low current velocities (cluster 2). Both clusters had high mud content. Cluster 1 had more samples in the biomass classification, with also 35 samples of abundance cluster 2 included, which were all separated from the other samples in the next division. The indicator species of cluster 1 was *Polydora ligierica*. Other characteristic species for this cluster were several amphipods such as *Corophium lacustre* and *Pleusymtes glaber*, and Oligochaeta. Mean biomass was low. Cluster 2 had a relatively high abundance and indicator species were *C. volutator*, Oligochaeta and *N. diversicolor*, the latter contributing the highest to the biomass.

The communities revealed from clusters 5 and 6 could be considered as transitional between the low diversity clusters 7–8 and the high diversity clusters 3–4. In both clusters a relatively high proportion of winter and spring samples was observed. Samples of cluster 6 were found in all regions, in the subtidal as well as in the intertidal

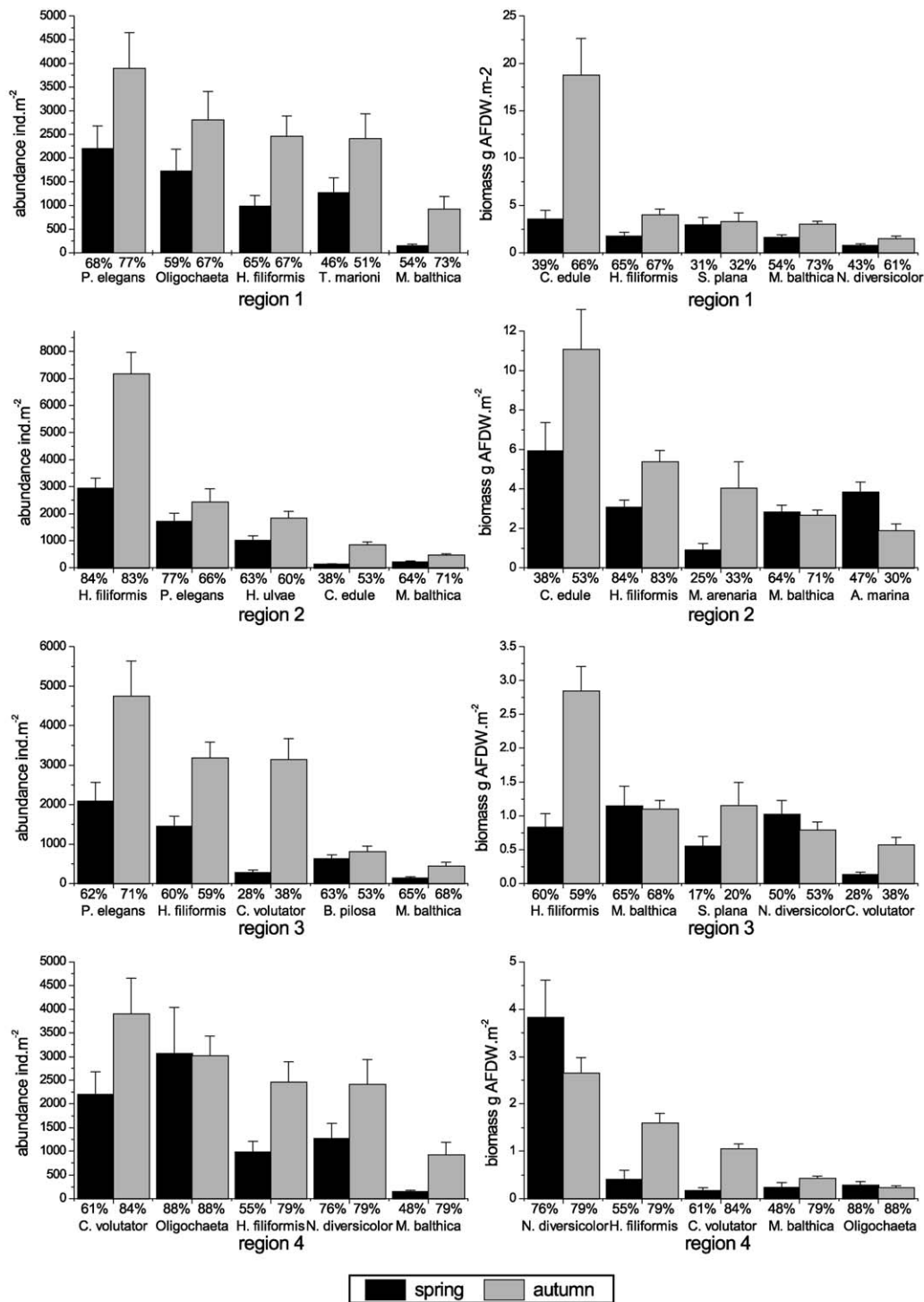


Fig. 5. Abundance (ind.m<sup>-2</sup> ± s.e.) and biomass (g AFDW m<sup>-2</sup> ± s.e.) in spring (March–May) and autumn (August–October) of the five most dominant macrobenthic species in the intertidal (littoral) zone of each region. For the division of regions see text and Fig. 1 (regions 1 and 2: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

Dendrogram representing the TWINSpan classification based on macrofauna abundance (data set B,  $n = 1243$ )

	1	2	3	4	5	6	7	8
Salinity	7.8 ± 3.8	11.0 ± 4.4	20.1 ± 5.1	21.9 ± 3.4	21.3 ± 4.4	18.8 ± 5.7	22.6 ± 5.2	16.4 ± 4.3
Depth	8.4 ± 4.4	0.7 ± 4.9	0.7 ± 4.7	0.4 ± 2.6	1.2 ± 4.1	5.0 ± 6.2	9.7 ± 5.6	5.1 ± 5.5
Max. ebb	0.90 ± 0.22	0.44 ± 0.28	0.39 ± 0.18	0.47 ± 0.10	0.51 ± 0.20	0.71 ± 0.24	0.86 ± 0.26	0.81 ± 0.29
Max. flood	0.81 ± 0.23	0.38 ± 0.30	0.37 ± 0.22	0.30 ± 0.14	0.45 ± 0.26	0.69 ± 0.32	0.93 ± 0.26	0.87 ± 0.30
Median	83 ± 85	95 ± 61	112 ± 48	134 ± 59	179 ± 51	222 ± 59	227 ± 75	213 ± 45
Mud content	52 ± 24	40 ± 23	3 ± 19	21 ± 17	7 ± 7	6 ± 8	4 ± 7	3 ± 4
Mean N0	6.7 ± 3.9	5.7 ± 2.6	13.4 ± 3.5	9.4 ± 2.5	7.8 ± 3.5	4.2 ± 2.7	5.8 ± 4.3	3.0 ± 2.0
Mean abundance	2114 ± 3582	9899 ± 10398	29609 ± 29065	21680 ± 17530	5682 ± 6233	1012 ± 1765	768 ± 2535	597 ± 1197
Mean biomass	0.98 ± 1.67	6.6 ± 9.9	41.5 ± 55.8	37.3 ± 38.9	10.7 ± 22.9	1.76 ± 5.76	1.05 ± 3.32	0.20 ± 0.35
Density								
<i>Poly lige</i>	<b>1333/80%</b>	–	–	–	–	–	–	–
<i>Oligochaeta</i>	215/83%	<b>1834/96%</b>	1101/48%	23/7%	132/22%	11/4%	3/6%	0.2/2%
<i>Nere dive</i>	0.3/3%	<b>1299/72%</b>	<b>868/84%</b>	87/34%	80/34%	4/10%	0.01/1%	0.01/1%
<i>Coro volu</i>	77/60%	<b>3669/78%</b>	<b>3712/61%</b>	60/12%	100/14%	0.4/2%	2.6/2%	0.2/1%
<i>Pygo eleg</i>	9/33%	573/35%	<b>10240/96%</b>	1650/77%	1486/78%	45/23%	1/4%	0.5/3%
<i>Eteo long</i>	0.3/3%	8/10%	<b>489/74%</b>	48/34%	54/41%	13/14%	3/17%	0.1/2%
<i>Maco balt</i>	0.3/3%	337/74%	<b>1029/95%</b>	444/87%	233/75%	22/23%	3/17%	0.6/4%
<i>Nere succ</i>	63/70%	9/9%	171/44%	<b>685/84%</b>	17/15%	2/3%	1/3%	0.3/3%
<i>Hete fili</i>	209/63%	1652/71%	6318/96%	<b>13673/98%</b>	1740/86%	146/83%	20/35%	3/6%
<i>Hydr ulva</i>	–	18/22%	925/77%	<b>1777/87%</b>	523/59%	44/19%	0.3/6%	2/4%
<i>Bath spec.</i>	5/7%	92/11%	119/18%	170/25%	<b>634/65%</b>	<b>526/60%</b>	21/25%	<b>453/87%</b>
<i>Spio spec.</i>	–	–	4/13%	15/4%	30/15%	4/8%	<b>245/60%</b>	3/6%
<i>Neph cirr</i>	–	–	0.7/1%	0.15/1%	1.3/3%	5/8%	<b>30/51%</b>	0.5/1%
Other species	<i>Coro lacu</i> <i>Coro insi</i>	<i>Mana aest</i>	<i>Cera edul</i> <i>Thar mari</i> <i>Poly spec</i> <i>Scro plan</i>	<i>Cera edul</i> <i>Thar mari</i> <i>Maya aren</i>	<i>Scol armi</i>	<i>Gast spin</i> <i>Ensi spec</i>	<i>Haus aren</i> <i>Eury pulc</i>	

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 (N0), mean abundance ( $\text{ind. m}^{-2}$ ) and mean biomass ( $\text{g AFDW m}^{-2}$ ) per cluster are given (mean ± SD). For each cluster mean abundance 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. Other species are species that are common in a certain cluster, but do not contribute substantially to the overall abundance of that cluster. For species abbreviations see Appendix A.

cluster 5 had many fewer samples than abundance cluster 5. Abundance and biomass were much lower than in cluster 4, but the occurrence of several species was similar (e.g. *P. elegans*, *M. balthica*, *H. filiformis*). As for cluster 6, the indicator species of cluster 5 was *Bathyporeia* spp., but it only marginally contributed to the total biomass.

Clusters 3 and 4 were intertidal clusters (>92%), characterized by low current velocities, and by fine sand sediments with a relatively high mud content. Biomass cluster 3 contained a lot of samples of abundance cluster 4. The clusters represented the macrobenthic communities with the highest mean diversity, abundance and biomass. Cluster 3 had the highest mean diversity, with indicator species for abundance being *P. elegans*,

whereas bivalves contributed most to the biomass, with the SF *C. edule* having the largest contribution. Indicator species for cluster 4 differed, with *H. filiformis* contributing most to abundance. Biomass in this cluster was mainly dominated by the sub-surface deposit feeders *A. marina* and *H. filiformis*. This cluster was also characterized by a higher proportion of spring and winter samples as compared with cluster 3.

### 3.7. Ordination and relation with the abiotic environmental variables

The results of the different CCA ordinations are summarized in Table 6. Ordination diagrams are

Table 5

Dendrogram representing the TWINSPLAN 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	0.39 ± 0.24	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	112 ± 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 N0	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>Oligochaeta</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 dive</i>	0.001/3%	<b>3.39/87%</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>Scro 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 balt</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>	0.007/18%	0.02/8%	0.03/17%	0.05/46%	<b>0.14/48%</b>	<b>0.11/60%</b>	0.004/12%	<b>0.07/87%</b>
<i>Spio spec.</i>	–	–	0.002/10%	0.0008/3%	0.006/17%	0.003/14%	<b>0.03/56%</b>	0.0003/2%
<i>Neph cirr</i>	–	–	–	0.006/2%	0.003/3%	0.012/5%	<b>0.13/48%</b>	0.004/2%
<i>Ensis 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 ( $m\ s^{-1}$ ), median grain size (median,  $\mu m$ ) and mud content (%) are given. Mean diversity (N0), mean abundance (ind.  $m^{-2}$ ) and mean biomass ( $g\ AFDW\ m^{-2}$ ) 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

Table 6

Results of CCA (partial CCA with season as covariable) for macrobenthic assemblages from data set A ( $n = 2612$ ) and data set B ( $n = 1243$ ), for abundance and biomass data, respectively

	Abundance data (data set A)		Abundance data (data set B)		
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 3
Eigenvalue CCA	0.32	0.18	0.39	0.22	0.13
Species-environment correlation	0.81	0.71	0.86	0.78	0.63
Percent variance of species data	3.4	5.3	7.1	11.0	13.5
Percent variance of species-environment	52.9	83.0	47.1	73.2	89.3
Inter-set correlation of environmental variables with axes					
Model salinity	0.50	−0.56	0.41	−0.66	0.10
Temporal salinity	0.55	−0.43	0.50	−0.48	0.19
Depth	0.61	0.38	0.63	0.34	0.30
Maximum ebb current velocity	0.55	0.29	0.56	0.07	0.02
Maximum flood current velocity	0.61	0.27	0.60	0.13	0.04
Median grain size			0.54	−0.07	−0.32
Mud content			−0.63	−0.05	0.38
	Biomass data (data set A)		Biomass data (data set B)		
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 3
Eigenvalue CCA	0.50	0.30	0.53	0.35	0.17
Species-environment correlation	0.83	0.75	0.85	0.81	0.59
Percent variance of species data	3.0	4.8	5.1	8.5	10.1
Percent variance of species-environment	51.9	82.9	43.2	71.8	85.4
Inter-set correlation of environmental variables with axes					
Model salinity	0.31	−0.64	0.17	−0.51	−0.12
Temporal salinity	0.37	−0.50	0.22	−0.38	−0.10
Depth	0.78	0.23	0.71	0.11	−0.05
Maximum ebb current velocity	0.56	0.09	0.41	−0.23	0.03
Maximum flood current velocity	0.59	−0.16	0.42	−0.21	0.04
Median grain size			0.21	−0.12	0.26
Mud content			−0.27	0.18	−0.32

Given are the eigenvalues of the first, second and third (data set B only) canonical axes. The species-environment correlation, and the cumulative percentage variance of the species data and the cumulative percentage variance of the species-environment relation explained by the axes are given. Inter-set correlation of each environmental variable with the ordination axes is presented. Both the first canonical eigenvalue as the sum of all canonical eigenvalues were statistically significant by Monte Carlo permutation test with 999 unrestricted permutations ( $p = 0.001$ ).

were relatively small. When included (data set B), mud content also showed a relatively high eigenvalue. Forward selection (conditional effects) showed that depth and model salinity added most to the total fit. When included (data set B), mud content also added considerably to the total fit. As temporal salinity was strongly co-varying with model salinity, the extra fit of this variable was very small, because a large part of the effect was already explained by model salinity. The same holds for the two current velocity estimates and for median grain size (co-varying with mud content). The smaller conditional effect of current velocity as

compared with its marginal effect was also explained by a co-variation of current velocities with depth.

The position of the different macrobenthic species along the two axes was similar for the CCA analyses on abundance data of data set A and data set B, respectively. Species which were mainly observed in the subtidal zone, at high current velocities, were situated at the right side of the biplot (e.g. *Gastrosaccus spinifer*, *Haustorius arenarius*, *N. cirrosa*, *P. ligerica*), whereas species characteristic for the intertidal zone, observed at low current velocities, were observed at the left side of the biplot (e.g. *C. volutator*, *N. diversicolor*, *M. balthica*,



Table 7

Ranking environmental variables in importance by their marginal (left) and conditional (right) effects of the macrobenthos in data set A (sediment data excluded,  $n = 2612$ ) and data set B ( $n = 1243$ ), as obtained by forward selection on the CCA

Marginal effects (forward: step 1)				Conditional effects (forward: continued)			
$j$	Variable	$\lambda_1$	$p$	$j$	Variable	$\lambda_a$	$p$
<i>Abundance data (set A, <math>n = 2612</math>, 58 species)</i>							
1	Depth	0.24	0.001	1	Depth	0.24	0.001
2	Model salinity	0.23	0.001	2	Model salinity	0.23 (0.47)	0.001
3	Max. flood current velocity	0.23	0.001	3	Max. flood current velocity	0.08 (0.55)	0.001
4	Temporal salinity	0.22	0.001	4	Temporal salinity	0.03 (0.58)	0.001
5	Max. ebb current velocity	0.19	0.001	5	Max. ebb current velocity	0.03 (0.61)	0.001
<i>Abundance data (set B, <math>n = 1243</math>, 44 species)</i>							
1	Depth	0.28	0.001	1	Depth	0.28	0.001
2	Mud content	0.26	0.001	2	Model salinity	0.24 (0.52)	0.001
3	Model salinity	0.25	0.001	3	Mud content	0.18 (0.70)	0.001
4	Temporal salinity	0.23	0.001	4	Max. ebb current velocity	0.05 (0.75)	0.001
5	Max. flood current velocity	0.20	0.001	5	Temporal salinity	0.04 (0.79)	0.001
6	Max. ebb current velocity	0.19	0.001	6	Max. flood current velocity	0.02 (0.81)	0.001
7	Median grain size	0.19	0.001	7	Median grain size	0.01 (0.82)	0.002

( $\lambda_1 = \text{fit} = \text{eigenvalue}$  with variable  $j$  only;  $\lambda_a = \text{additional fit} = \text{increase in eigenvalue}$ ;  $p = \text{significance level}$  of the effect, as obtained with a Monte Carlo permutation test under the null model with 999 unrestricted permutations). For results on the CCA analyses see Table 6.

the mean number of species per sample but also the total number of species decreased with decreasing salinity (see also Ysebaert, et al., 1993, 1998; Ysebaert, De Neve, et al., 2000). In several estuaries also a trend from lower biomass in the upper estuarine regions to higher biomass in the more downstream regions was observed, e.g. Ems, Schelde and Elbe estuary (Meire, Seys, Ysebaert, & Coosen, 1991; Ysebaert et al., 1998), James River Estuary (Schaffner, Diaz, Olsen, & Larsen, 1987), Lavaca Bay, Texas (Kalke & Montagna, 1991) and Chesapeake Bay (Dauer, 1993). In the present study, the same trend was observed, although it was most pronounced in the intertidal zone, and less clear in the subtidal zone. In contrast to diversity and biomass, no clear trend in abundance was observed, similar to observations in 50 intertidal locations along the salinity gradient of the Schelde estuary (Ysebaert et al., 1993). Other studies on the intertidal macrobenthos of the Schelde estuary, based on a much smaller sampling effort, revealed remarkably similar values for density and biomass (Meire et al., 1991; Ysebaert et al., 1993, 1998).

Only a few studies have dealt with the zonation of macrobenthos from high intertidal to deep subtidal sites (e.g. Elliot & Taylor, 1989). The present study showed much higher values of diversity, abundance and biomass in the intertidal zone as compared with the subtidal zone. Especially in the subtidal channels of the Schelde estuary tidal current speeds and instability of the sediment clearly become the limiting factors, leading to very poor communities. In more shallow estuaries, such as James River Estuary (Schaffner et al., 1987), subtidal macrobenthic biomass might reach high values.

Heip et al. (1995) showed that on a system-wide scale, biomass values for complete benthic assemblages among estuaries are not very different, but that variability within an estuary is usually high. The mean biomass values found in this study were within the range described by Heip et al. (1995).

#### 4.2. The role of the abiotic environment

The different multivariate analyses, based on macrofauna abundance or biomass, and data sets with or without sediment characteristics included, confirmed the strong relationships between the macrobenthic assemblages and the predominant forces (gradients) in the Schelde estuary.

The overview provided by the CCA and the variance partitioning showed how three natural gradients primarily driven by depth, salinity and sediment mud content influenced macrobenthic community structure on a broad scale, but these environmental variables were not fully orthogonal.

The first gradient was related to depth, which reflected also the hydrodynamic conditions (current velocities). This was clear from the ordinations, in which depth and current velocities were closely correlated with the first ordination axis. Therefore, it appeared that the vertical gradient, reflecting mainly the hydrodynamic regime was dominant upon the salinity gradient. A second gradient (second axis in the ordination) was clearly related to salinity and confirms the observations from the univariate analysis.

A third gradient was formed by the sediment characteristics, but it was apparent from the ordination

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, Fockedeey, & 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 (Crocker, 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 of the macrobenthos were much higher than in the other assemblages. Abundance of this assemblage is mainly determined by spionid (*P. elegans*) and capitellid polychaetes (*H. filiformis*). Biomass was mainly determined by bivalves, of which the SF *C. edule* was the most important. In the more sandy sediments of the polyhaline zone a second intertidal assemblage was observed, which was characterized by a high biomass of the sub-surface deposit feeder *A. marina*. This assemblage was only obvious from the biomass classification, as *A. marina* was observed only in very low densities. Diversity, abundance and biomass were lower, with another sub-surface deposit feeder, *H. filiformis*, dominating this assemblage numerically. Both polyhaline assemblages are also commonly observed in other estuaries and shallow coastal zones, such as the Wadden Sea (e.g. Beukema, 1976, 1981; Dörjes, Michaelis, & Rhode, 1986).

A third intertidal assemblage was found in the mesohaline zone of the estuary, especially in region 4. As for the first intertidal assemblage, this assemblage occurred in the low dynamic areas, characterized by sediments with a high mud content, but with a lower macrobenthos species diversity and biomass. Indicator species was *C. volutator*, this species being almost absent in the polyhaline zone of the estuary. *N. diversicolor* was the main species determining biomass in this assemblage. In this part of the estuary Oligochaeta also became a predominant part of the benthic community, a dominance which increased towards the oligohaline and freshwater tidal zone of the estuary (Seys, Vincx, & Meire, 1999; Ysebaert et al., 1993), and which was also more pronounced in spring as compared with autumn (this study; Ysebaert, personal communication). The near absence of *C. volutator* from the polyhaline zone could be due to a negative effect of *C. edule* and especially *A. marina* (e.g. Flach, 1992, 1996), both very common in the polyhaline zone of the Schelde estuary. In the Wadden Sea, a zonation pattern was observed with a *Corophium* zone in the muddy upper tidal flats and a zone dominated by *A. marina* and *C. edule* at the lower edges. In the Schelde estuary it rather appeared that this pattern was observed along the longitudinal salinity gradient.

A fourth assemblage could be considered as the intertidal extension of the second subtidal assemblage, characterized by the amphipod *Bathyporeia* spp. This assemblage is observed at intermediate current velocities in fine/medium sand sediments with a low mud content. Several species from the other assemblages were also observed in this assemblage, but at much lower densities. A characteristic polychaete of these sandy sediments in the polyhaline zone was *Scoloplos armiger*. In the most dynamic areas, sand flats characterized by pronounced megaripples, only a few mobile crustaceans were observed. This assemblage resembles the benthic

communities that are found on exposed sand beaches with a pronounced wave action (Degraer, Mouton, De Neve, & Vincx, 1999; Shackley, 1981).

It should be emphasized that the previously described assemblages should not be considered as static, nor is the transition from one assemblage to another abrupt. This was noticed from the large overlap in the clusters superimposed on the ordination diagrams. Therefore, seriation is a more appropriate term to describe the benthic community structure than the more common term zonation (Clarke, Warwick, & Brown, 1993). The exact extent and position of estuarine zones will differ between assemblages, seasons and years, but their persistent occurrence points to a real underlying structure in the distribution of biota of the estuarine ecosystem at large (Bulger, Hayden, Monaco, Nelson, & McCormick-Ray, 1993).

#### 4.4. Trophic and functional structure

The search for a meaningful measure of community response (e.g. to disturbance) led investigators to consider trophic ecology (feeding ecology) of macrobenthos (Boesch & Rosenberg, 1981; Gaston, Rakocinski, Brown, & Cleveland, 1998; Pearson & Rosenberg, 1978). Trophic ecology provides a functional approach to help clarify the complex community changes that occur along estuarine gradients.

Based on field evidence, a relation between system-averaged macrobenthic biomass and pelagic primary productivity of shallow well-mixed estuarine systems was presented by Herman et al. (1999). Between 5 and 25% of the annual primary production is consumed by macrobenthos respiration. On a system-average basis, SF are often the dominant component (with respect to biomass) of estuarine benthic assemblages (Heip et al., 1995). Also in the Schelde estuary, SF, mainly *C. edule*, dominated the macrobenthic biomass in the polyhaline zone. However, in the turbid Schelde estuary and other estuaries at the low productive end of this spectrum, SF are, both in absolute and relative terms, less dominant compared with estuaries with higher productivities (Herman et al., 1999). In the Schelde estuary light, rather than nutrients, is limiting primary production. The underwater light climate is better in the most seaward part (polyhaline zone) of the estuary, and one can conclude that the benthic (SF) biomass is, in general, following the trend of primary productivity in the system (Heip et al., 1995).

Herman et al. (1999) showed that in the comparison of macrofauna biomass in different systems, particularly the SF seem to constitute the most variable part. Indeed, SF appeared very patchy in the Schelde estuary, with 68 samples containing a SF biomass  $>50 \text{ g AFDW m}^{-2}$ , which was 66% of the total SF

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 1) 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).

## Acknowledgements

We express special thanks to Dr Herman Hummel and his colleagues of the benthos monitoring laboratory for providing most of the benthos data. Simon Thrush and Donald Boesch are thanked for many valuable comments on an earlier version of the manuscript. The study is part of the ECOFLAT project, a research project funded by the European Commission in the framework of the Environment and Climate Programme (contract number ENV4-CT96-0216), being part of ELOISE (European Land Ocean Interactions Studies). This study was also partly supported by the FWO project G.0104.99. This is contribution no. 357/23 to the EU programme ELOISE and contribution no. 3133 of the Netherlands Institute of Ecology (NIOO-KNAW).

## Appendix A

A list of macrobenthic species is given in Table A1.

Table A1  
List of macrobenthic species mentioned in the text and figures, together with the abbreviations used

Abbreviation	Species name	Feeding type
Anai muco	Anaitides mucosa	P
Abra tenu	Abra tenuis	SF
Aren mari	Arenicola marina	SSDF
Bath spp.	Bathyporeia spp.	SDF
Capi capi	Capitella capitata	SSDF
Carc maen	Carcinus maenas	O
Cera edul	Cerastoderma edule	SF
Coro aren	Corophium arenarium	SDF
Coro insi	Corophium insidiosum	SDF
Coro lacu	Corophium lacustre	SDF
Coro volu	Corophium volutator	SDF
Cran cran	Crangon crangon	P
Cyat cari	Cyathura carinata	P
Ensi spp.	Ensis spp.	SF
Eteo long	Eteone longa	P
Eury pulc	Eurydice pulchra	P
Gamm sali	Gammarus salinus	O
Gast spin	Gastrosaccus spinifer	O
Haus aren	Haustorium arenarium	SF
Hete fili	Heteromastus filiformis	SSDF
Hydr ulva	Hydrobia ulvae	SDF
Maco balt	Macoma balthica	SDF
Mana aest	Manayunkia aestuarina	SF
Meso slab	Mesopodopsis slabberi	SDF
Mya aren	Mya arenaria	SF
Myse bide	Mysella bidentata	SDF
Myti edul	Mytilus edulis	SF
Nemertinae	Nemertinae	P
Neom inte	Neomysis integer	O
Neph cirr	Nephtys cirrosa	O
Neph homb	Nephtys hombergii	O
Nere dive	Nereis diversicolor	O
Nere succ	Nereis succinea	O
Oligo	Oligochaeta	SSDF
Ophe spp.	Ophelia spp.	SDF
Petr phol	Petricola pholadiformis	SF
Pleu glab	Pleusymtes glaber	O
Pygo eleg	Pygospio elegans	SDF
Poly lige	Polydora ligérica	SDF
Poly spp.	Polydora spp.	SF
Retu obtu	Retusa obtusata	P
Scol armi	Scoloplos armiger	SSDF
Scro plan	Scrobicularia plana	SDF
Spio bomb	Spiophanes bombyx	SDF
Spio spp.	Spio spp.	SDF
Spis spp.	Spisula spp.	SF
Thar mari	Tharyx marioni	SDF

For each species the feeding type is given. SF, suspension feeder; SDF, surface deposit feeder; SSDF, sub-surface deposit feeder; O, omnivore; P, predator.

## References

- Barnes, R. D. (1980). *Invertebrate zoology* (4th ed., pp. 1089). Philadelphia: Holt-Saunders.
- Barry, J. P., & Dayton, P. K. (1991). Physical heterogeneity and the organization of marine communities. In K. Kolasa, & S. T. A.

- Pickett (Eds.), *Ecological heterogeneity* (pp. 270–320). New York: Springer.
- Baeyens, W., van Eck, B., Lambert, C., Wollast, R., & Goeyens, L. (1998). General description of the Scheldt estuary. *Hydrobiologia* 366, 1–14.
- Beukema, J. J. (1976). Biomass and species richness of the macrobenthic animals living on tidal flats of the Dutch Wadden-sea. *Netherlands Journal of Sea Research* 10, 236–261.
- Beukema, J. J. (1981). Quantitative data on the benthos in the Wadden Sea proper. In N. Dankers, H. Köhl, & W. J. Wolff (Eds.), *Invertebrates of the Wadden Sea* (pp. 132–142). Rotterdam: Balkema.
- Boesch, D. F. (1977). A new look at the zonation of benthos along the estuarine gradient. In B. C. Coull (Ed.), *Ecology of marine benthos, The Belle W. Baruch Library in Marine Science*, 6 (pp. 245–266). Columbia, SC: University of South Carolina Press.
- Boesch, D. F., & Rosenberg, R. (1981). Response to stress in marine benthic communities. In G. W. Barrett, & R. Rosenberg (Eds.), *Stress effects on natural ecosystems* (pp. 179–200). New York: Wiley.
- Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Bousfield, E. L. (1970). Adaptive radiation in sand burrowing amphipod crustaceans. *Chesapeake Science* 11, 143–154.
- ter Braak, C. J. F. (1988). Partial canonical correspondence analysis. In H. H. Bock (Ed.), *Classification and related methods of data analysis* (pp. 551–558). North-Holland, Amsterdam: Elsevier.
- ter Braak, C. J. F. (1994). Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* 1, 127–140.
- ter Braak, C. J. F., & Smilauer, P. (1998). CANOCO Reference Manual and user's guide to Canoco for windows: software for Canonical Community Ordination (version 4) (pp. 352). Ithaca, NY: Microcomputer Power.
- ter Braak, C. J. F., & Verdonschot, P. F. M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57, 255–289.
- Bulger, A. J., Hayden, B. P., Monaco, M. E., Nelson, D. M., & McCormick-Ray, M. G. (1993). Biologically-based estuarine salinity zones derived from a multivariate analysis. *Estuaries* 16, 311–322.
- Carriker, M. R. (1967). Ecology of estuarine benthic invertebrates, a perspective. In G. H. Lauff (Ed.), *Estuaries* (pp. 442–487). Washington DC: American Society for the Advancement of Science, Washington.
- Clark, R. B., & Haderlie, E. C. (1960). The distribution of *Nephtys cirrosa* and *Nephtys hombergii* on the south-western coasts of England and Wales. *Journal of Animal Ecology* 29, 117–147.
- Clarke, K. R., Warwick, R. M., & Brown, B. E. (1993). An index showing breakdown of seriation, relation to disturbance, in a coral-reef assemblage. *Marine Ecology Progress Series* 102, 153–160.
- Crocker, R. A. (1967). Niche diversity in five sympatric species of intertidal amphipods (Crustacea: Haustoriidae). *Ecological Monographs* 37, 173–200.
- Dauer, D. M. (1993). Biological criteria, environmental health and estuarine macrobenthic community structure. *Marine Pollution Bulletin* 26, 249–257.
- Dauer, D. M., Maybury, C. A., & Ewing, R. M. (1981). Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 54, 21–38.
- Dauwe, B., Herman, P. M. J., & Heip, C. H. R. (1998). Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology Progress Series* 173, 67–83.
- Day, J. W., Hall, A. S., Kemp, W. M., & Yanez-Arancibia, A. (1989). *Estuarine ecology* (558 pp.). New York: Wiley.

- Degraer, S., Mouton, I., De Neve, L., & Vincx, M. (1999). Community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative sandy beach: summer–winter comparison. *Estuaries* 22, 742–752.
- Dittmer, J.-D. (1983). The distribution of subtidal macrobenthos in the estuaries of the rivers Ems and Weser. In W. Wolff (Ed.), *Ecology of the Wadden Sea Vol. 1* (pp. 4/188–4/206). Rotterdam: Balkema.
- Dörjes, J., Michaelis, H., & Rhode, B. (1986). Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian Coast, Germany). *Hydrobiologia* 142, 217–232.
- Elliot, M., & Taylor, C. J. M. (1989). The production ecology of the subtidal benthos of the Forth Estuary, Scotland. *Scientia Marina* 53, 531–541.
- Ellis, J. I., Schneider, D. C., & Thrush, S. F. (2000). Detecting anthropogenic disturbance in an environment with multiple gradients of physical disturbance, Manukau Harbour, New Zealand. *Hydrobiologia* 440, 379–391.
- Fauchald, K., & Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology—An Annual Review* 17, 193–284.
- Field, J. G., Clarke, K. R., & Warwick, R. M. (1982). A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8, 37–52.
- Flach, E. C. (1992). The influence of four macrozoobenthic species on the abundance of the amphipod *Corophium volutator* on tidal flats of the Wadden Sea. *Netherlands Journal of Sea Research* 29, 379–394.
- Flach, E. C. (1996). The influence of the cockle *Cerastoderma edule* on the macrozoobenthic community of tidal flats in the Wadden Sea. *Marine Ecology—Pubblicazioni della stazione zoologica di Napoli* 17, 87–98.
- Gaston, G. R., Rakocinski, C. F., Brown, S. S., & Cleveland, C. M. (1998). Trophic function in estuaries: response of macrobenthos to natural and contaminant gradients. *Marine Freshwater Research* 49, 833–846.
- Goosen, N. K., Kromkamp, J., Peene, J., van Rijswijk, P., & van Breugel, P. (1999). Bacterial and phytoplankton production in the maximum turbidity zone of three European estuaries: the Elbe, Westerschelde and Gironde. *Journal of Marine Systems* 22, 151–171.
- Gray, J. S. (1974). Animal–sediment relationships. *Oceanography and Marine Biology—An Annual Review* 12, 223–261.
- Hall, S. J. (1994). Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology—An Annual Review* 32, 179–239.
- Heip, C. H. R., Goosen, N. K., Herman, P. M. J., Kromkamp, J., Middelburg, J. J., & Soetaert, K. (1995). Production and consumption of biological particles in temperate tidal estuaries. *Oceanography and Marine Biology—An Annual Review* 33, 1–149.
- Heip, C. H. R., & Herman, P. M. J. (1995). Major biological processes in European tidal estuaries. *Hydrobiologia* 311 (266 pp.).
- Herman, P. M. J., & Heip, C. H. R. (1999). Biogeochemistry of the Maximum Turbidity Zone of Estuaries (MATURE). *Journal of Marine Systems* 22, 89–228.
- Herman, P. M. J., Middelburg, J. J., & Heip, C. H. R. (2001). Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. *Continental Shelf Research* 21, 2055–2071.
- Herman, P. M. J., Middelburg, J. J., Van de Koppel, J., & Heip, C. H. R. (1999). Ecology of estuarine macrobenthos. *Advances in Ecological Research* 29, 195–240.
- Herman, P. M. J., Middelburg, J. J., Widdows, J., Lucas, C. H., & Heip, C. H. R. (2000). Stable isotope labelling experiments confirm the importance of microphytobenthos as food for macrofauna. *Marine Ecology Progress Series* 204, 79–92.
- Hill, M. O. (1979). TWINSpan: a Fortran program of arranging multivariate data in an ordered two-way table by classification of the individuals and attributes (48 pp.). New York: Section of Ecology and Systematics, Cornell University Ithaca.
- Holland, A. F., Shaughnessy, A. T., & Hiegel, M. H. (1987). Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. *Estuaries* 10, 227–245.
- Jongman, R. H. G., ter Braak, C. J. F., & Van Tongeren, O. F. R. (1995). *Data analysis in community and landscape ecology* (299 pp.). Cambridge: Cambridge University Press.
- Kalke, R. D., & Montagna, P. A. (1991). The effect of freshwater inflow on macrobenthos in the Lavaca River Delta and upper Lavaca Bay, Texas. *Contributions in Marine Science* 32, 49–71.
- Kamermans, P. (1994). Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves. *Marine Ecology Progress Series* 104, 63–75.
- Khayrallah, N. H., & Jones, A. M. (1980). The ecology of *Bathyporeia pilosa* (Amphipoda: Haustoriidae) in the Tay estuary. II. Factors affecting the microdistribution. *Proceedings of the Royal Society of Edinburgh B* 78, 121–130.
- Legendre, P., Thrush, S. F., Cummings, V. J., Dayton, P. K., Grant, J., Hewitt, J. E., Hines, A. H., McArdle, B. H., Pridmore, D., Schneider, D. C., Turner, S. J., Whitlatch, R. B., & Wilkinson, M. R. (1997). Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* 216, 99–128.
- Liu, Q. H., & Brakenhielm, S. (1995). A statistical approach to decompose ecological variation. *Water, Air and Soil Pollution* 85, 1587–1592.
- Mannino, A., & Montagna, P. A. (1997). Small-scale spatial variation in macrobenthic community structure. *Estuaries* 20, 159–173.
- McArdle, B. H., Hewitt, J. E., & Thrush, S. F. (1997). Pattern and process: it is not as easy as it looks. *Journal of Experimental Marine Biology and Ecology* 216, 229–242.
- McLusky, D. S. (1987). Intertidal habitats and benthic macrofauna of the Forth estuary, Scotland. *Proceedings of the Royal Society of Edinburgh B* 93, 389–400.
- Mees, J., Dewicke, A., & Hamerlynck, O. (1993). Seasonal composition and spatial distribution of the hyperbenthic communities along the estuarine gradients in the Westerschelde. *Netherlands Journal of Aquatic Ecology* 27, 359–376.
- Mees, J., Fockedeij, N., & Hamerlynck, O. (1995). Comparative study of the hyperbenthos of three European estuaries. *Hydrobiologia* 311, 153–174.
- Meire, P. M., Seys, J., Buijs, J., & Coosen, J. (1994). Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm-surge barrier? *Hydrobiologia* 282/283, 157–182.
- Meire, P. M., Seys, J. J., Ysebaert, T. J., & Coosen, J. (1991). A comparison of the macrobenthic distribution and community structure between two estuaries in SW Netherlands. In M. Elliott, & J.-P. Ducrest (Eds.), *Estuaries and Coasts: Spatial and temporal intercomparisons* (pp. 221–230). Fredensborg: Olsen and Olsen.
- Meire, P., & Vincx, X. (1993). Marine and estuarine gradients. Proceedings of the 21th Symposium of the Estuarine and Coastal Science Association. *Netherlands Journal of Aquatic Ecology* 27 (496 pp.).
- Michaelis, H. (1983). Intertidal benthic animal communities of the estuaries of the rivers Ems and Weser. In W. J. Wolff (Ed.), *Ecology of the Wadden Sea Vol. 1* (pp. 4/158–4/188). Rotterdam: Balkema.
- Michaelis, H., Fock, H., Grotjahn, M., & Post, D. (1992). The status of intertidal zoobenthic brackish-water species in estuaries of the German Bight. *Netherlands Journal of Sea Research* 20, 201–207.
- Nicolaisen, W., & Kannevorff, E. (1969). On the burrowing and feeding habits of the amphipods *Bathyporeia pilosa* Lindström and *Bathyporeia sarsi* Watkin. *Ophelia* 6, 231–250.

- Norkko, A., Cummings, V. J., Thrush, S. F., Hewitt, J. E., & Hume, T. (2001). Local dispersal of juvenile bivalves: implications for sandflat ecology. *Marine Ecology Progress Series* 212, 131–144.
- Olafsson, E. B. (1986). Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal Ecology* 55, 517–526.
- Olafsson, E. B., Peterson, C. H., & Ambrose, W. B. (1994). Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediment: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology—An Annual Review* 32, 65–109.
- Ökland, R. H. (1999). On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science* 10, 131–136.
- Ökland, R. H., & Eilertsen, O. (1994). Canonical correspondence analysis with variation partitioning: some comment and an application. *Journal of Vegetation Science* 5, 117–126.
- Paterson, D. M., & Black, K. S. (1999). Water flow, sediment dynamics and benthic biology. *Advances in Ecological Research* 29, 155–193.
- Pearson, T. H., & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology—An Annual Review* 16, 229–311.
- Rakocinski, C. F., Brown, S. S., Gaston, G. R., Heard, R. W., Walker, W. W., & Summers, J. K. (1997). Macrobenthic responses to natural and contaminant-related gradients in Northern Gulf of Mexico estuaries. *Ecological Applications* 7, 1278–1298.
- Remane, A., & Schlieper, C. (1971). *Biology of brackish water* (372 pp.). New York: Wiley.
- Rhoads, D. C., McCall, P. L., & Yingst, J. Y. (1978). Disturbance and production on the estuarine seafloor. *American Scientist* 66, 577–586.
- Sameoto, D. D. (1969). Comparative ecology, life histories, and behavior of intertidal sand-burrowing amphipods (Crustacea: Haustoriidae) at Cape Cod. *Journal of Fisheries Research Bd. Canada* 26, 361–388.
- Sanders, H. L., Mangelsdorf, P. C. J., & Hampson, G. R. (1965). Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limnology and Oceanography* 10(Suppl.), 216–229.
- Seys, J., Vincx, M., & Meire, P. (1999). Spatial distribution of Oligochaeta (Clitellata) in the tidal freshwater and brackish parts of the Schelde estuary (Belgium). *Hydrobiologia* 406, 119–132.
- Schaffner, L. C., Diaz, R. J., Olsen, C. R., & Larsen, I. L. (1987). Faunal characteristics and sediment accumulation processes in the James River Estuary, Virginia. *Estuarine, Coastal and Shelf Science* 25, 211–226.
- Schlacher, T. A., & Wooldridge, T. H. (1996). Axial zonation patterns of subtidal macrozoobenthos in the Gantoois Estuary, South Africa. *Estuaries* 19, 680–696.
- Shackley, S. E. (1981). The intertidal soft sediments and their macrofauna in the Greater Swansea Bay Area (Worm's Head to Nash Point), South Wales. *Estuarine, Coastal and Shelf Science* 12, 535–548.
- Snelgrove, P. V. R., & Butman, C. A. (1994). Animal–sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology—An Annual Review* 32, 111–177.
- Soetaert, K., & Herman, P. M. J. (1995). Carbon flows in the Westerschelde estuary (The Netherlands) evaluated by means of an ecosystem model (MOSES). *Hydrobiologia* 311, 247–266.
- Soetaert, K., & Herman, P. M. J. (1995). Estimating estuarine residence times in the Westerschelde (The Netherlands) using a box model with fixed dispersion coefficients. *Hydrobiologia* 311, 215–224.
- Taghon, G. L., & Greene, R. R. (1992). Utilization of deposited and suspended particulate matter by benthic interface feeders. *Limnology and Oceanography* 37, 1370–1391.
- Thrush, S. F., Cummings, V. J., Dayton, P. K., Ford, R., Grant, J., Hewitt, J. E., Hines, A. H., Lawrie, S. M., Pridmore, R. D., Legendre, P., McArdle, B. H., Schneider, D. C., Turner, S. J., Whitlatch, R. B., & Wilkinson, M. R. (1997). Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult/juvenile interactions. *Journal of Experimental Marine Biology and Ecology* 216, 153–169.
- Thrush, S. F., Lawrie, S. M., Hewitt, J. E., & Cummings, V. J. (1999). The problem of scale: uncertainties and implications for soft-bottom marine communities and the assessment of human impacts. In J. S. Gray, W., Jr., Ambrose, & A. Szaniawska (Eds.), *Biogeochemical cycling and sediment ecology* (pp. 195–210). The Netherlands: Kluwer Academic.
- Turner, S. J., Grant, J., Pridmore, R. D., Hewitt, J. E., Wilkinson, M. R., Hume, T. M., & Morrisey, D. J. (1997). Bedload and water-column transport and colonisation processes by post-settlement benthic macrofauna: does infaunal density matter? *Journal of Experimental Marine Biology and Ecology* 216, 51–75.
- Van Eck, G. T. M., & De Rooij, N. M. (1993). Potential chemical time bombs in the Schelde estuary. *Land Degradation and Rehabilitation* 4, 317–332.
- Vroon, G., Storm, C., & Coosen, J. (1997). *Westerschelde, stram of struis? Eindrapport van het project OOSTWEST, een studie naar de beïnvloeding van fysische en verwante biologische patronen in een estuarium* (106 pp.). Rapport RIKZ-97.023 (in Dutch), Rijks-waterstaat, Rijksinstituut voor Kust en Zee, Middelburg.
- Warwick, R. M., Goss-Custard, J. D., Kirby, R., George, C. L., Pope, N. D., & Rowden, A. A. (1991). Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn estuary different? *Journal of Applied Ecology* 28, 1004–1026.
- Warwick, R. M., & Uncles, R. J. (1980). Distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. *Marine Ecology Progress Series* 3, 97–103.
- Wilson, W. H. (1991). Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics* 21, 221–241.
- Wolff, W. J. (1971). Distribution of four species of *Nephtys* (Polychaeta) in the estuarine area of the rivers Rhine, Meuse and Scheldt. Troisième Symposium Européen de Biologie Marine. *Vie et Milieu, supplément* 22, 677–699.
- Wolff, W. J. (1973). The estuary as a habitat. *Zoologische Verhandlungen Leiden* 126 (242 pp.).
- Wolff, W. F. (1983). Estuarine benthos. In B. H. Ketchum (Ed.), *Ecosystems of the World, Estuaries and Enclosed Seas Vol. 26* (pp. 337–374). Amsterdam: Elsevier.
- Wollast, R., & Peters, J. J. (1978). Biogeochemical properties of an estuarine ecosystem: the river Scheldt. In E. Goldberg (Ed.), *Biogeochemistry of estuarine sediments* (pp. 279–293). Paris: UNESCO.
- Ysebaert, T., De Neve, L., & Meire, P. (2000). The subtidal macrobenthos in the mesohaline part of the Schelde estuary (Belgium): influenced by man? *Journal of the Marine Biological Association of the United Kingdom* 80, 587–597.
- Ysebaert, T., Meininger, P. L., Meire, P., Devos, K., Berrevoets, C. M., Strucker, R. C. W., & Kuijken, E. (2000). Waterbird communities along the estuarine salinity gradient of the Schelde estuary, NW-Europe. *Biodiversity and Conservation* 9, 1275–1296.
- Ysebaert, T., Meire, P., Coosen, J., & Essink, K. (1998). Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. *Aquatic Ecology* 32, 53–71.
- Ysebaert, T., Meire, P., Maes, D., & Buijs, J. (1993). The benthic macrofauna along the estuarine gradient of the Schelde estuary. *Netherlands Journal of Aquatic Ecology* 27, 327–341.
- Ysebaert, T., Meire, P., Herman, P. M. J., & Verbeek, H. (2002). Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Marine Ecology Progress Series* 225, 79–95.