J. Mar. Biol. Ass. U.K. (2000), **80**, 587–597
Printed in the United Kingdom

The subtidal macrobenthos in the mesohaline part of the Schelde Estuary (Belgium): influenced by man?

Tom Ysebaert*[†], Liesbeth De Neve* and Patrick Meire*[‡]

*Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussel, Belgium. [†]E-mail: tom.ysebaert@instnat.be
[‡]Present address: University of Antwerp, Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium

The macrobenthos of the subtidal, mesohaline zone of the Schelde Estuary (Belgium) was sampled in October 1996 and 1997 at 54 and 73 sampling locations respectively. Sediments ranged from silty to very coarse, with the dominant sediment type being silt (33% of all locations). Of the 35 macrobenthic species observed, only seven species occurred in more than 20% of the samples. The polychaete *Heteromastus filiformis* and Oligochaeta were most common. Multivariate techniques revealed three distinct communities, linked mainly with sedimentological factors: (1) a species-poor (nine species) community with a dominance of the amphipod *Bathyporeia pilosa*, a low mean abundance and biomass (86 ind m^{-2}, 0.0189 g ash-free dry weight (AFDW) m^{-2}), and a mean median grain size of 215 ±19 μm (fine sand); (2) a species-rich (22) community, with the small polychaete *Polydora ligerica* as indicator species, a relatively high mean abundance and biomass (2298 ind m^{-2}, 1.395 g AFDW m^{-2}, oysters excluded), a mean median grain size of 133 ±41 μm, and also the occurrence of sediments with hard substrates being characteristic for this community; (3) a community with an intermediate species richness (12), abundance and biomass (248 ind m^{-2}, 0.249 g AFDW m^{-2}), with *H. filiformis* and Oligochaeta as indicator species, and a median grain size of 76 ±9 μm. In the study area several typical brackish water species were observed (e.g. *Polydora ligerica*, *Corophium lacustre*, *Gammarus salinus*).

Mean total abundance and biomass were very low, and the benthic communities appeared to be under stress, with a dominance of mainly small, subsurface deposit and surface deposit feeding opportunistic species. This is probably a combined effect of both natural physical and human-induced disturbance. Only sediments with hard substrates (e.g. rocks) seems to favour species richness, providing a shelter against physical disturbance.

INTRODUCTION

The inner and upper parts of estuaries are often severely impacted by man. Land reclamation results in a high degree of estuarine habitat loss. Drainage of waste water, dredging for shipping, safety constructions (e.g. dykes, storm surge barriers), fixation of banks, etc. change the chemical and physical properties of these estuarine habitats (Costanza et al., 1993; Gray, 1997).

The Schelde Estuary is one of the larger north-west European estuaries with a complete salinity gradient, including a large freshwater tidal area. Especially the part between the Dutch–Belgian border and the Rupel is severely impacted and heavily polluted by domestic, industrial and agricultural waste loads and the concentrations of micropollutants are high (Van Eck & De Rooij, 1993; Soetaert & Herman, 1995a,b; Zwolsman, 1999). From the 1980s on water quality has started to improve slowly, and this improvement continues in the 1990s (Van Damme et al., 1995; Van Eck et al., 1998). Near the Dutch–Belgian border, the large industrialized area of Antwerpen Harbour is situated. Being a major sedimentation area, this zone is dredged intensively in order to keep it accessible for navigation (Claessens et al., 1991). During the last decade several harbour infrastructures (e.g. container terminals) have been constructed in the area, and the shipping channel has been deepened.

Although the intertidal macrobenthic communities along the Schelde Estuary are well known (e.g. Ysebaert et al., 1993, 1998), recent data about the spatial distribution of macrobenthos in the mesohaline subtidal part of the Zeeschelde were so far almost completely lacking. However, knowledge about the present status of the macrobenthos in this part of the estuary could give an indication of the present ecosystem health, since benthos is recognized as a suitable ecological group for monitoring and detecting effects of stress and pollution (e.g. Pearson & Rosenberg, 1978; Boesch & Rosenberg, 1981; Warwick & Clark, 1993; Diaz & Rosenberg, 1995; Gaston et al., 1998).

In this study the spatial distribution of macrobenthic communities in the mesohaline subtidal part of the Zeeschelde is described based on data collected in 1996 and 1997. The results are compared with the species diversity along the complete Schelde salinity gradient and with data from 1952 (Leloup & Konietzko, 1956). Possible effects on benthic communities of dredging operations and other anthropogenic influences, like the occurrence of hard substrates within the sediment are discussed.

MATERIALS AND METHODS

Study area

The Schelde Estuary, a macrotidal coastal plain estuary, is situated near the border between The Netherlands and Belgium. It measures 160 km with a surface

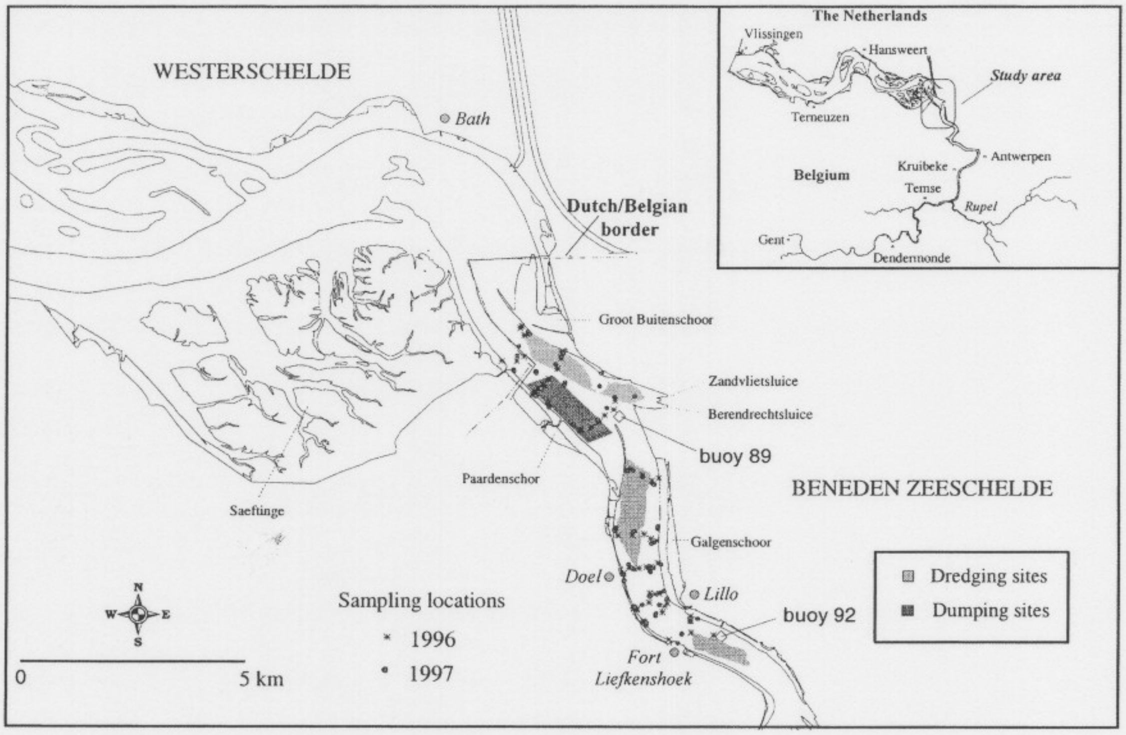

Figure 1. Geographical view of the Beneden Zeeschelde area with indication of the 54 and 73 sampling locations in 1996 and 1997, and with the main dredging and dumping sites in this part of the estuary.

area of approximately 350 km^2. The Westerschelde (55 km) represents the downstream Dutch part with the poly-/mesohaline zone of the estuary; the Zeeschelde (105 km), the Belgian part of the Schelde Estuary, represents the meso-/oligohaline and freshwater tidal zones (Figure 1). The mean tidal range is 3.8 m in Vlissingen, 5.2 m in Antwerpen and 2.0 m in Gent.

The study area is situated in the maximum turbidity and mesohaline zone of the Zeeschelde (Baeyens et al., 1998; Fettweis et al., 1998), between the Dutch–Belgian border and Fort Liefkenshoek (Figure 1). In this part of the estuary mean tidal range is about 4.94 m.

Sampling and laboratory analysis

Temperature, salinity and oxygen concentrations were measured monthly at two buoys in the study area (Figure 1). The macrobenthos was sampled in October 1996 and October 1997 in 9 and 10 transects respectively (Figure 1). In every transect about 6–7 locations were sampled, divided over three depth strata (<2.95 m; 2.95–7.95 m; >7.95 m below mean low low water spring). In total 54 and 73 locations were sampled in 1996 and 1997. On each location one Van Veen grab (0.105 m^2) was taken, from which one small core (ϕ 2 cm) for sediment analysis was taken. The benthic samples were sieved through a 1 mm mesh in the field and preserved in neutralized formaline. Position and water depth of the grab sample were noted.

In the laboratory samples were sorted after staining with 0.02% rose bengal. All organisms were identified to species level, except for the genus Ostrea, the Oligochaeta and one spionid specimen, and counted. The ash-free dry weight (AFDW) biomass was obtained by drying all specimens at 105°C for 12 h and ashing them at 550°C.

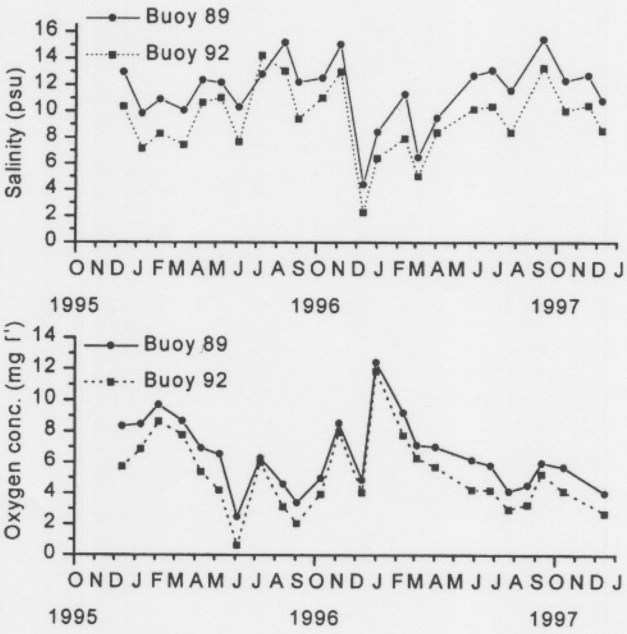

Figure 2. Monthly measurements of salinity and oxygen concentrations at buoy 89 and 92 within the study area (for geographic positions of the buoys, see Figure 1).

Sediment characteristics (median grain size, mud content (percentage volume $<63\,\mu$m)) were determined by laser diffraction with a Malvern Mastersizer S. Six sediment types were distinguished, according to Kramer et al. (1994). Sediment samples containing hard substrates (e.g. stones) were all classified as type 7. Maximum ebb and flood current velocities were estimated for an average tide with the hydrodynamical model SCALDIS (van der

Table 1. *Sediment types, based on median grain size, of the subtidal sampling locations in 1996 (N=54) and 1997 (N=73) respectively.*

	Sediment type	Range (μm)	1996		1997	
			No. of samples	%	No. of samples	%
Type 1	clay	<2	0	0.0	0	0.0
Type 2	silt	2–63	18	33.3	24	32.9
Type 3	very fine sand	63–125	9	16.7	9	12.3
Type 4	fine sand	125–250	17	31.5	16	21.9
Type 5	medium sand	250–500	3	5.5	7	9.6
Type 6	coarse sand	500–1000	0	0.0	2	2.7
Type 7	hard substrate	–	7	13.0	15	20.5

Table 2. *Number of observations (%), mean density (ind m^{-2}) and mean biomass (g AFDW m^{-2}) of all macrobenthic species observed in the subtidal, mesohaline zone of the Zeeschelde Estuary in 1996 (N=54) and 1997 (N=73) respectively.*

	1996			1997		
	No. of observations (%)	Density (ind m^{-2})	Biomass (g AFDW m^{-2})	No. of observations (%)	Density (ind m^{-2})	Biomass (g AFDW m^{-2})
Annelida						
Eteone longa (P)	5.5	0.9	0.0004	*	*	*
Harmothoe impar (P)	3.6	0.4	0.0004	1.4	0.1	0.0001
Heteromastus filiformis (DF)	65.5	143.4	0.0575	32.9	74.4	0.0642
Marenzelleria spp. (P)	1.8	0.4	–	1.4	0.3	*
Nereis diversicolor (O)	*	*	*	1.4	0.1	0.0001
Nereis succinea (DF)	25.5	23.0	0.0492	26.0	22.2	0.0403
Oligochaeta (DF)	61.5	58.2	0.0015	50.7	72.3	0.0014
Polydora ligerica (SDF–SF)	34.5	479.6	0.0908	27.4	232.0	0.0501
Polydora ligni (SDF–SF)	23.6	47.0	0.0085	27.4	55.3	0.0077
Pygospio elegans (SDF–SF)	16.4	4.2	0.0002	15.0	6.0	0.0016
Spionidae spp. (SDF–SF)	1.8	0.2	–	*	*	*
Mollusca						
Barnea candida (SF)	1.8	0.4	0.0040	*	*	*
Cerastoderma edule (SF)	1.8	0.2	0.0004	*	*	*
Crassostrea angulata (SF)	5.5	2.4	0.8432	*	*	*
Hydrobia ulvae (SDF)	3.6	0.4	0.0001	*	*	*
Macoma balthica (SDF–SF)	16.4	2.9	0.0267	16.4	3.3	0.0206
Mya arenaria (SF)	9.1	2.1	0.0037	4.1	1.2	0.0004
Mytilus edulis (SF)	7.3	1.0	0.0002	2.7	0.4	0.0006
Ostrea spp. (SF)	*	*	*	2.7	0.4	0.1337
Petricola pholadiformis. (SF)	*	*	0.0004	1.4	0.4	–
Arthropoda						
Bathyporeia elegans (SDF)	7.3	0.9	0.0002	1.4	0.1	0.0000
Bathyporeia pilosa (SDF)	31.0	23.4	0.0023	22.0	5.9	0.0004
Corophium insidiosum (SDF)	11.0	8.3	0.0005	13.7	5.7	0.0002
Corophium lacustre (SDF)	14.5	15.2	0.0019	13.7	16.2	0.0016
Corophium volutator (SDF)	23.6	23.7	0.0049	32.9	38.4	0.0055
Crangon crangon (P)	14.5	1.4	0.0517	15.1	1.8	0.1755
Eurydice pulchra (P)	9.1	1.9	0.0015	9.6	1.0	0.0022
Gammarus salinus (O)	1.8	0.2	0.0003	4.1	1.3	0.0011
Melita palmata (SDF)	1.8	0.2	0.0004	1.4	0.3	0.0006
Mesopodopsis slabberii (O)	3.6	0.4	0.0001	5.5	0.7	0.0000
Neomysis integer (O)	1.8	0.2		*	*	*
Palaemon longirostris (P)	3.6	0.5	0.0845	9.6	1.0	0.1241
Pleusymtes glaber (SDF)	12.7	4.8	0.0008	15.1	8.7	0.0011
Rhithropanopeus harrisii (P)	3.6	0.5	0.0186	9.6	1.3	0.0481
Balanus spp. (SF)	Present			present		

*, not found; –, not determined.

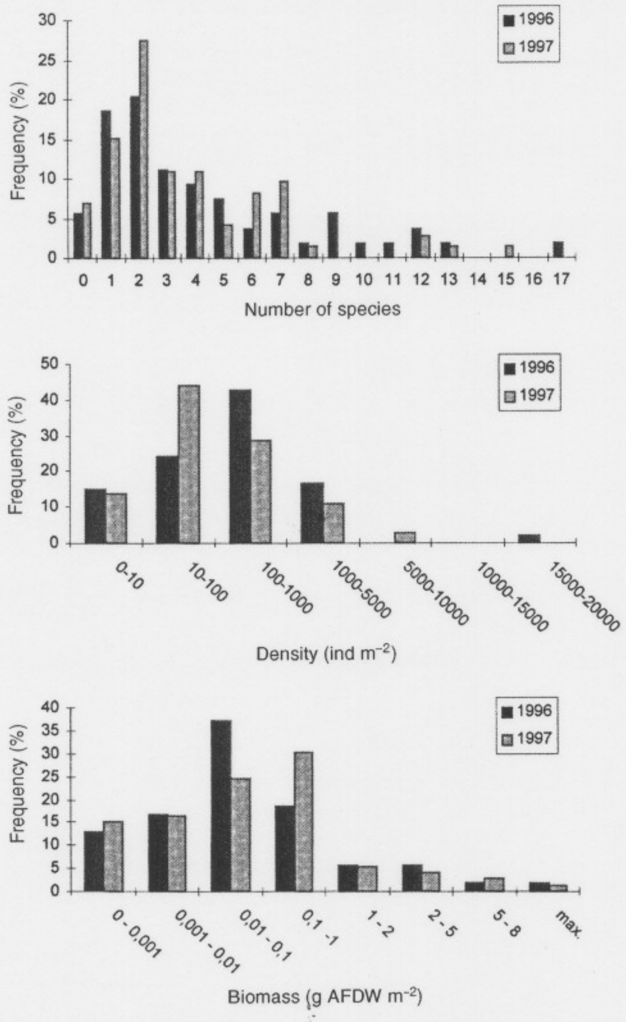

Figure 3. Species distribution (%), density distribution (%) and biomass distribution (%) of the 54 and 73 sampling locations in 1996 and 1997 respectively.

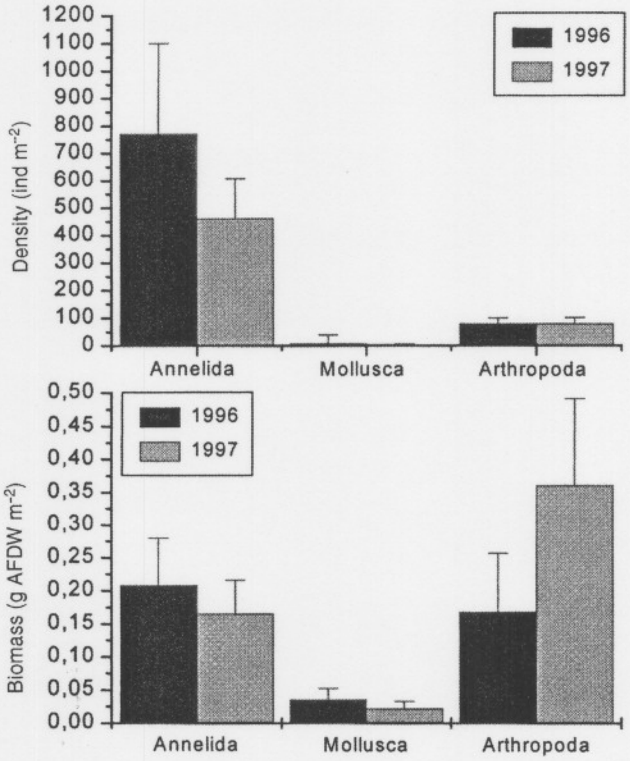

Figure 4. Mean density (ind m^{-2}) and mean biomass (g AFDW m^{-2}) of Annelida, Mollusca and Arthropoda in 1996 and 1997. The biomass of oysters is not included in the mean total biomass of the Mollusca.

Meulen & Sileon, 1997), having a spatial resolution of 100 m.

Data analysis

Macrobenthic species were classified into trophic groups based on the food source: subsurface deposit-feeders (SSDF), surface deposit-feeders (SDF), suspension-feeders (SF), omnivores (O) and predators (P). Spionid species and *Macoma balthica* (Linnaeus) were classified as SDF–SF, as these species may switch between both feeding types.

The abundance/biomass comparison method (ABC) (*k*-dominance curves for species abundance and biomass (Lambshead et al., 1983)) was used to detect environmental stress (Warwick, 1986; Meire & Dereu, 1990).

To identify groups of similar locations the following analyses were performed on the density datasets of 1996, 1997 and 1996–1997 together (fourth root transformed): a classification (clustering based on the Bray–Curtis similarity index and group average sorting (GAS)) (Clifford & Stephenson, 1975), an ordination (multidimensional scaling (MDS)) (Kruskal & Wish, 1978), and a hybrid technique (two-way Indicator Species Analysis (TWINSPAN)) (Hill, 1979). Cut-levels used were 0, 2.0, 2.3, 2.7, 3.5, 4.5. Rare species (single observation), the epibenthic shrimps *Crangon crangon* (Linnaeus) and *Palaemon longirostris* (Milne-Edwards), empty samples (three in 1996, five in 1997) and samples with only one individual were excluded from the analyses. The relationship between the spatial distribution of the locations in the MDS ordination and the environmental variables was indicated by a Spearman rank order correlation between the axes from the ordination and the environmental variables. The clusters, resulting from the multivariate analyses, were characterized by their typical species composition, diversity (Shannon–Wiener diversity index H′) and environmental variables. Statistical differences for biotic and abiotic variables among groups were analysed by Kruskal–Wallis test. Mean values are given with standard error (SE).

RESULTS

Abiotic characterization of the sampling locations

Water quality measurements at the two buoys in the study area (Figure 1) showed a strong seasonal pattern in water temperature and smaller seasonal fluctuations in salinity and oxygen concentrations, which were related to the river run-off, being higher in winter (Figure 2). The area was mesohaline (yearly average 1996: 10.5 psu; 1997: 10.1 psu) throughout the year (one exception in December 1996). Oxygen concentrations were often less than 5 mg $O_2\ l^{-1}$, especially in summer.

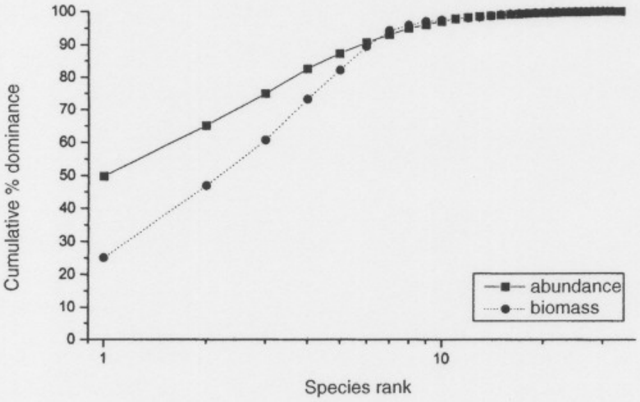

Figure 5. Combined *k*-dominance curves for species abundance and biomass (ABC-curve), based on all sampling locations (1996 and 1997 together).

Mean median grain size and mean mud content were 141 ±19 μm and 38 ±4% respectively, both showing a large variation. In both years the dominant sediment type was silt (Table 1); 5.5% in 1996 and 12% in 1997 belonged to the sediment types medium sand (250–500 μm) and coarse sand (500–1000 μm), hereafter considered together as the sediment type medium-coarse sand. Thirteen per cent in 1996 and 20.5% in 1997 of the samples were of sediments with hard substrates. Mud fraction slightly decreased and median grain size slightly increased with depth, but there was no significant correlation with depth (median grain size: Spearman $r=0.18$; $P=0.06$ and mud fraction: $r=0.17$; $P=0.08$; N=86).

Based on model calculations, mean maximum ebb and flood current velocities were 0.886 ±0.06 m s^{-1} and 0.786 ±0.020 m s^{-1} (N=127) respectively. The model calculated current velocities lower then 0.20 m s^{-1} at only three locations. Highest current velocities observed were 1.23 and 1.16 m s^{-1} under ebb and flood conditions respectively. No correlation was found between current velocities and depth (N=127; $r=0.13$; $P=0.16$), nor between current velocities and median grain size (N=106; $r=0.13$; $P=0.20$) or mud content (N=106; $r=-0.12$; $P=0.22$).

General characteristics of the macrobenthic fauna

Of the 35 species observed (28 in 1996; 24 in 1997), 31% were annelids, 26% molluscs and 43% arthropods (Table 2). Only seven species occurred in more than 20% of the samples. The polychaete *Heteromastus filiformis* (Claparède) (65% of the samples in 1996, 33% in 1997) and Oligochaeta (61.5% in 1996, 50.7% in 1997) were

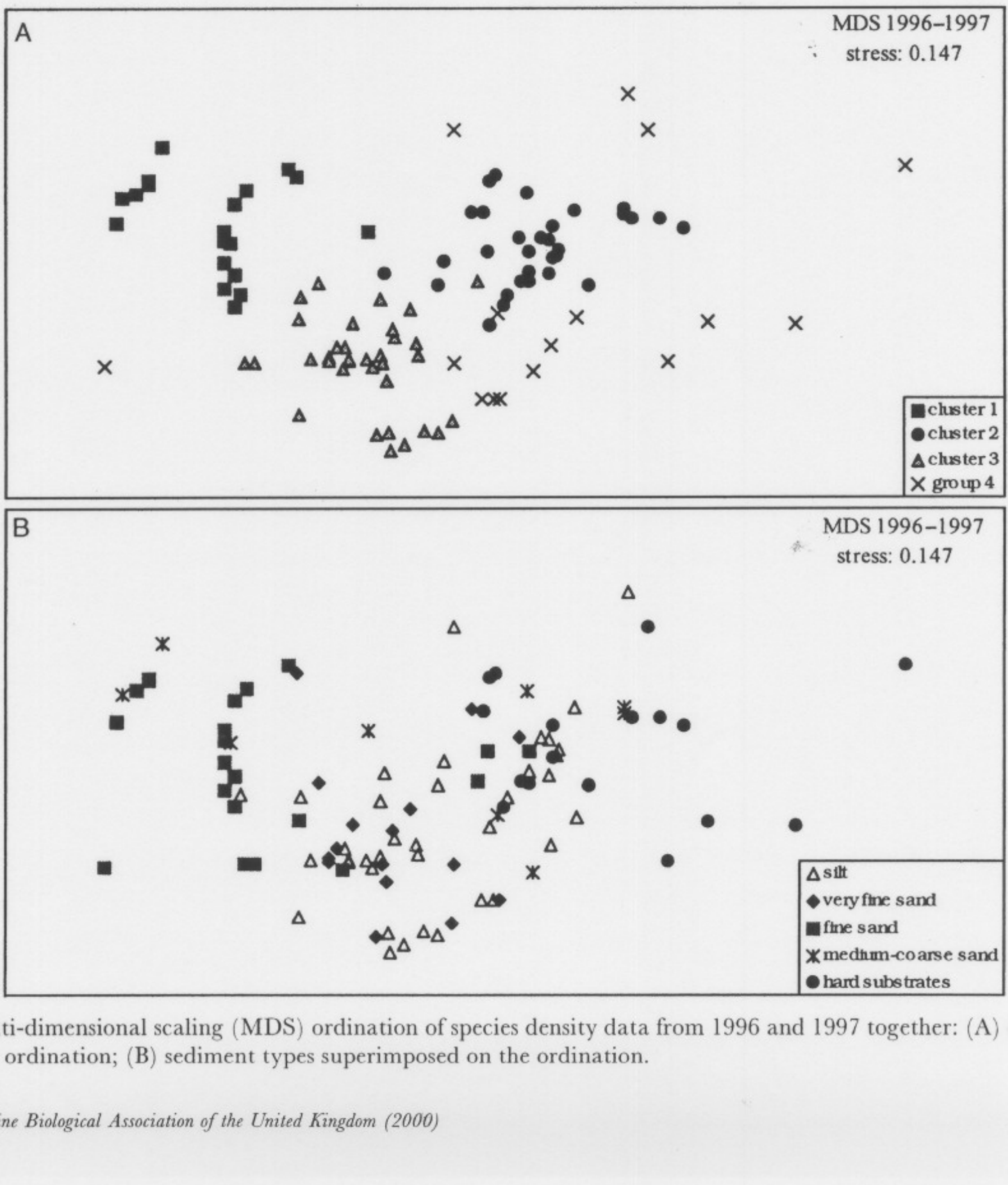

Figure 6. Multi-dimensional scaling (MDS) ordination of species density data from 1996 and 1997 together: (A) clusters superimposed on the ordination; (B) sediment types superimposed on the ordination.

Table 3. *Spearman rank order correlations between environmental factors (depth, mud content, median grain size) and the number of species, biomass, density, and MDS X- and Y- coordinates. The Spearman* r *and the* P*-value are given. Significant correlations at the level* $P<0.05$ *are in bold.*

	Depth (N=105)		Mud fraction (N=86)		Median grain size (N=86)	
	r	*P*	*r*	*P*	*r*	*P*
Number of species	−0.052	0.60	0.24	**0.03**	−0.14	0.20
Biomass	−0.108	0.27	0.05	0.63	0.001	0.99
Density	0.04	0.67	0.30	**0.005**	−0.20	**0.05**
MDS X coordinates	0.15	0.12	0.57	**<0.0001**	−0.41	**<0.0001**
MDS Y coordinates	0.10	0.31	−0.42	**<0.0001**	0.39	**0.0002**

MDS, multi-dimensional scaling.

Table 4. *Biotic and abiotic characterization of the three clusters (mean ±SE), with indication of the test statistic (H) of the Kruskal–Wallis test together with the* P*-level for differences among the three clusters.*

	Cluster 1 (N=23)	Cluster 2 (N=35)	Cluster 3 (N=31)	H	*P*-level
Total number of species	9	22	12		
Mean number of species	2.3 ±0.25	8.8 ±0.56	2.9 ±0.22	71.245	<0.0001
Shannon–Wiener diversity H′	0.53 ±0.079	1.20 ±0.097	0.69 ±0.069	16.037	0.0003
Mean density (ind m^{-2})	86 ±18	2298 ±613	248 ±76	40.513	<0.0001
Mean biomass (g AFDW m^{-2})	0.02 ±0.004	3.07 ±1.343	0.25 ±0.087	44.397	<0.0001
Indicator species					
Bathyporeia pilosa	65 ±13	0.6 ±0.43	2.7 ±1.81	68.873	<0.0001
Polydora ligerica	5.2 ±4.36	1379 ±571	0	58.779	<0.0001
Heteromastus filiformis	2.4 ±0.86	234 ±143	170 ±70	20.876	<0.0001
Oligochaeta	6.3 ±4.75	168 ±56	54 ±11	22.275	<0.0001
Mud content (%)	7.5 ±3.38	48 ±5.9	48 ±4.1	22.509	<0.0001
Median grain size (*m)	215 ±19	133 ±41	76 ±9	22.776	<0.0001
Depth	6.2 ±1.1	6.3 ±0.8	5.1 ±0.8	0.827	0.661

Mean biomass of cluster 2 with oysters included, without oysters mean biomass amounted to 1.40 ±0.372 g AFDW m^{-2}.

most common. Six species were observed only once. The number of species per location was low (Figure 3); locations with one or two species were most common (44%).

The mean total density of all locations was 681 ±171 ind m^{-2}, the mean density in 1996 (861 ±341 ind m^{-2}) was noticeably higher than in 1997 (549 ±158 ind m^{-2}), although not significantly (Mann–Whitney *U*-test: N(1996)=54; N(1997)=73; *U*=1720; *P*=0.2227). Densities were dominated by annelids (87% of the total density; 89% in 1996; 84% in 1997) (Table 2). Arthropods occurred to a lesser extent and molluscs occurred only in very low densities (Figure 4). Most locations had a total density between 100–1000 ind m^{-2} in 1996 (42%) and between 10 and 100 ind m^{-2} in 1997 (44%) (Figure 3). Highest densities observed were 17352 and 9286 ind m^{-2} in 1996 and 1997 respectively.

The mean total biomass of all locations was 0.94 ±0.35 g AFDW m^{-2}. In 1996 mean biomass (1.26 ±0.75 g AFDW m^{-2}) was higher than in 1997 (0.68 ±0.24 g AFDW m^{-2}), although not significantly (Mann–Whitney *U*-test: N(1996)=54; N(1997)=73; *U*=1911.5; *P*=0.77). The difference in biomass was caused by the high biomass of a few oysters (*Crassostrea angulata* (Lamarck) and *Ostrea* spp.) found at three and two sampling locations in 1996 and 1997 respectively, making 67% of total biomass in 1996 and only 20% of total biomass in 1997. If oysters were removed from the dataset, mean biomass of both years was more comparable (1996: 0.41 ±0.13 g AFDW m^{-2}, 1997: 0.55 ±0.16 g AFDW m^{-2}). Contrary to density, biomass was not only dominated by annelids (1996: 50%; 1997: 30%), but also by arthropods (1996: 42%; 1997: 66%) (Figure 4). The dominant annelids were *Polydora ligerica* (Ferronière) and *H. filiformis*; the dominant arthropods were *Crangon crangon* and *Palaemon longirostris* (Table 2). It should be emphasized that these arthropods were all epibenthic species, and therefore do not belong to the sedentary infauna. Most locations (55%) had a total biomass between 0.01 and 1 g AFDW m^{-2} (Figure 3), with a maximum of 40 g AFDW m^{-2} (a location with 12 oysters) in 1996 and 15 g AFDW m^{-2} in 1997.

The macrobenthic community was numerically dominated by SDF–SF species (59%), which were mainly the spionids *Polydora ligerica* and *Polydora ligni* (Webster). The

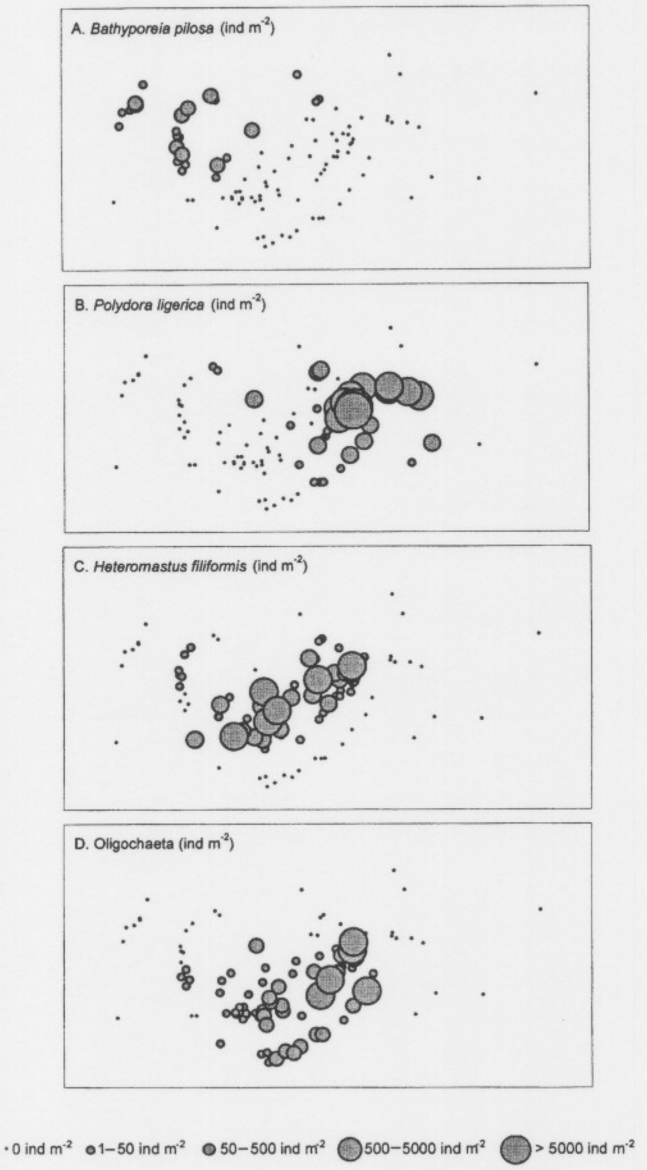

Figure 7. Multi-dimensional scaling (MDS) configuration from Figure 6 with circles scaled in size to represent individual species density of: (A) *Bathyporeia pilosa*; (B) *Polydora ligerica*; (C) *Heteromastus filiformis*; and (D) Oligochaeta.

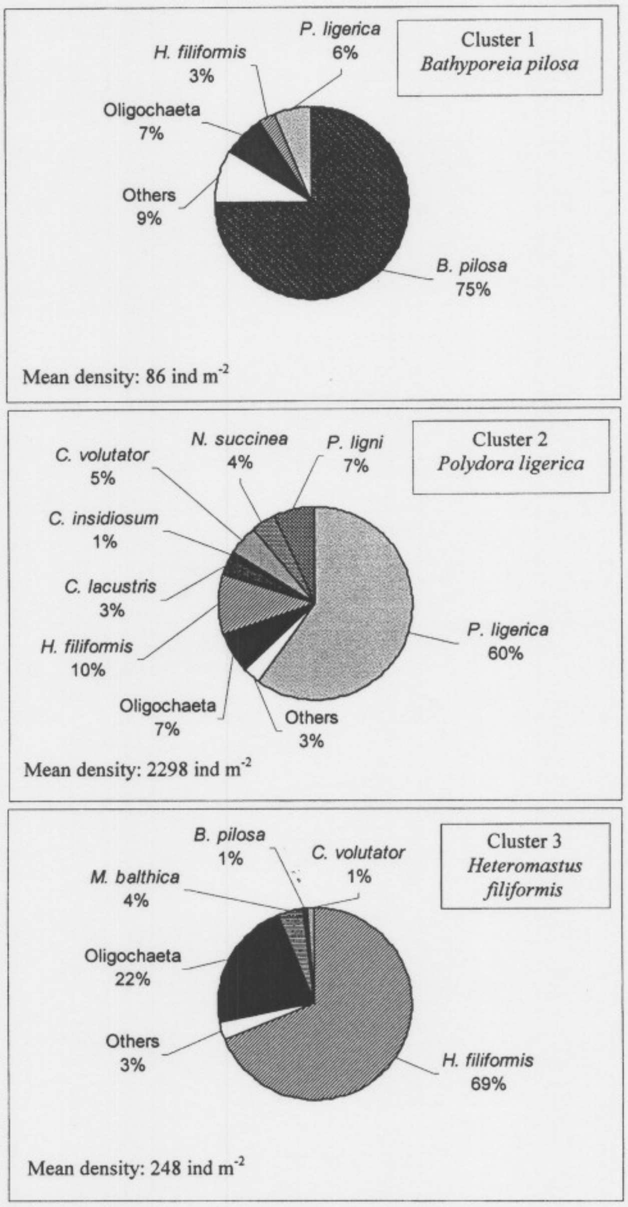

Figure 8. Mean species density per cluster based on density data 1996 and 1997 together. For full species names see Table 2.

other important group were SSDF with 29%, being represented by *H. filiformis* and Oligochaeta. Suspension-feeders (oysters) dominated the biomass (47%), but when these few oysters were excluded predators dominated (55%), followed by SDF–SF (spionids) with 20%. The predators were mainly the epibenthic shrimps *C. crangon* and *Palaemon longirostris*, not being a permanent part of the benthic infauna.

The *k*-dominance curves for species abundance and biomass (besides oysters) (ABC-curves) showed a stressed pattern, as indicated by the abundance curve falling above the biomass curve (Figure 5). This means that the benthic community was dominated by one or a few very small species and only a few larger species were present.

Community structure and environmental variables

The multivariate analyses did not produce a distinction between the datasets of 1996 and 1997. Therefore the further analysis and discussion of community structure is based on the data of both years together. Both TWINSPAN and cluster analyses produced three clusters, which also returned in the MDS ordination (Figure 6A). In the GAS-classification the first cluster (cluster 1) was separated at a 15% similarity, the two remaining at a 35% similarity. Sixteen locations mutually showed very little similarity and did not form a cluster. These locations were considered as group 4 (rest group).

Neither macrobenthos species richness, density, biomass, nor one of the MDS-axes were significantly correlated with depth (Table 3). On the other hand, mud content was significantly correlated with macrobenthos species richness and density, being highest for the silt type sediment. Both axes of the MDS ordination were significantly correlated with mud content and median grain size, indicating that the distribution of the samples in the MDS ordination was mainly determined by the sediment parameters. The superimposed sediment types on the ordination (Figure 6B) showed a clear tendency of grouping. Cluster 1 mostly occurred on fine sand sediment (70%), cluster 2 on silt (34%) and hard substrate (34%) sediments, and cluster 3 mainly on silt (58%)—very fine sand (39%) sediments.

The ABC-curves for each cluster seperately showed a similar stressed pattern as observed for all sampling locations together (see Figure 5).

The abiotic and biotic characteristics of the three clusters and the statistical difference among the clusters are summarized in Table 4. Cluster 1 was characterized by a species-poor benthic fauna with a typical dominance of the amphipod *Bathyporeia pilosa* (Lindström) (Figures 7A & 8A). Cluster 2 consisted of locations with a relatively species-rich benthic fauna with a high mean density and biomass. The small polychaete *Polydora ligerica* was the indicator species (Figures 7B & 8B). Oysters occurred exclusively in this cluster, explaining the relatively high biomass. Cluster 3 was characterized by intermediate species richness, density and biomass. The indicator species of this cluster were *Heteromastus filiformis* and Oligochaeta (Figures 7C,D & 8C). *Macoma balthica,* only present in low densities, appeared almost exclusively in cluster 3. Sediment characteristics were significantly different among the three clusters, depth was not significantly different.

Of group 4, 37% of the locations were situated in the silt sediment type, 30% on hard substrates, and the remaining locations in the other sediment types. Generally the samples contained few species in low densities. Characteristically 57% of the locations of group 4 were found in the depth stratum >7.5 m, with a mean depth of 9.5 ±1.4 m, which was noticeably deeper than the mean depth of the three clusters.

DISCUSSION

Species diversity along the salinity gradient in the Schelde Estuary

The most important variables controlling the occurrence of benthic organisms on an estuarine scale are salinity and sediment characteristics (e.g. Wolff, 1973; Boesch, 1977; Holland et al., 1987; Rakocinski et al., 1997; Ysebaert et al., 1998), which are in turn determined largely by hydrodynamic conditions (e.g. Wildish & Kristmanson, 1979; Warwick & Uncles, 1980; Warwick et al., 1991; Hall, 1994). It is assumed that the environmental stress, due to salinity and hydrodynamic conditions, is greatest in the subtidal part of the middle and upper regions of estuaries, resulting in a lower diversity of benthic invertebrates predicted in these areas. The aim of this study was to investigate the macrobenthic community of the subtidal mesohaline part of the Zeeschelde Estuary.

Seys et al. (1999) recently investigated the benthos of the Zeeschelde, but this study concentrated on Oligochaeta, and therefore was based on only one small sediment core per sampling location (diameter 3.5 cm). Only a few locations were situated within the subtidal mesohaline part of the Zeeschelde Estuary. Apart from two Oligochaeta species found (*Heterochaeta costata* (Claparède) and *Tubificoides heterochaetus* (Michaelsen)), only four macrobenthic species were determined in these locations: *Polydora ligerica*, *Heteromastus filiformis*, *Nereis succinea* (Frey & Leuckart) and *Macoma balthica*. The different sampling method and the small amount of locations may explain the large difference in species number as compared to this study.

The subtidal part of the Westerschelde was recently studied as part of a monitoring programme (e.g. Brummelhuis et al., 1997; Craeymeersch, 1999). For the same period (autumn 1996–1997), 55 macrobenthic species were observed. Species diversity decreased from the polyhaline zone (40 species, 30 sampling locations each year), over the poly-/mesohaline transition zone (31 species, idem) to the α-mesohaline zone (27 species, idem). In this study no further decrease in the number of species was observed in the β-mesohaline part of the estuary. Instead, species diversity slightly increased (35 species). The presence of sediments with hard substrates, often having a high macrobenthic species richness, may account for this. Also, the sampling effort in this study was larger as compared to the sampling effort in the monitoring programme of the Westerschelde. When considering the available data from this study for all sampling years (1990–1997), to increase the sampling effort, about 100 taxa were found in the subtidal part of the Westerschelde. The number of species also decreased from the polyhaline (70 species) towards the mesohaline zone (50 species). Therefore, the observed species diversity was also a function of sampling effort. Many species were reported to occur irregularly and rather accidentally, with in general very few species per sampling location, and this was also observed in this study. On the other hand, species diversity 'hot spots' were sometimes observed. In this study one sampling location represented 17 macrobenthic species, half of the total number of species observed.

Species diversity was reported to be much lower in the oligohaline zone of the Zeeschelde, characterized by an impoverished benthic fauna, with a few Oligochaeta species and very few macrobenthic species, such as *P. ligerica* and *Corophium volutator* (Pallas) (Ysebaert et al., 1993; Seys et al., 1999). In the subtidal freshwater tidal zone the community was almost completely composed of a few Oligochaeta species (Seys et al., 1999). This very low species diversity was explained by the heavy pollution in the oligohaline and freshwater tidal zones of the Zeeschelde.

The subtidal mesohaline part of the Zeeschelde was characterized by some typical 'genuine brackish-water' species, species which according to Remane (1969) showed a distribution strictly limited to the mixohaline zones without expansion into the marine or freshwater regions (Wolff, 1973 ; Michaelis et al., 1992). In our study the observed 'brackish-water' species are the polychaete *Polydora ligerica,* the amphipods *Gammarus salinus* (Spooner), *Corophium insidiosum* (Crawford) and *C. lacustre* (Vanhöffen), the shrimp *Palaemon longirostris* and the crab *Rhitropanopeus harrisii* (Gould). The remaining species were euryhaline and also occurred in the whole Westerschelde. The observation of *Marenzelleria* spp., an immigrant from North American shores (Bastrop et al., 1997; Essink & Schöttler, 1997), and for the first time reported to occur in Europe in 1982 (McLusky et al., 1993), is the most southern observation of *Marenzelleria* to date (Ysebaert et al., 1996; Essink, 1999).

Subtidal vs intertidal macrobenthos

The observed species richness of the subtidal zone of the Zeeschelde was higher than that of the intertidal zone, the densities and biomass however were lower. In a study from 1990–1996 on 24 intertidal locations within the study area, 24 species were found, five of which (*C. volutator, Heteromastus filiformis, Nereis diversicolor* (Müller), *Macoma balthica* and Oligochaeta) contributed to 96% of mean densities and 99.3% of mean biomass (personal observations). The same five species were also found subtidally, but generally at much lower densities. *Polydora ligerica*, the most abundant species of the subtidal zone of the Zeeschelde, was not found intertidally. Total mean intertidal densities were 7000 $\pm 1060 \text{ ind m}^{-2}$, being dominated by *C. volutator* (37%) and total intertidal mean biomass was 4.79 ± 0.34 g AFDW m^{-2}, being dominated by *N. diversicolor* (40%).

Historical comparison with Leloup & Konietzko (1956)

The macrobenthos of the β-mesohaline part of the Zeeschelde has been studied in 1952 on 21 subtidal locations in the same area of the Zeeschelde (Leloup & Konietzko, 1956). At that time anthropogenic pressure was lower but water quality was already bad. The number of species in 1952 (15 species) was lower as compared to this study (35 species), but sampling effort was also lower. Eleven of the taxa were found in both studies. Some recently very abundant species, like *P. ligerica* and *H. filiformis*, were totally absent in 1952. The subtidal macrobenthic community in 1952 resembled cluster 1 of this study, being dominated by *Bathyporeia pilosa*, and showing low mean densities ($85 \pm 24 \text{ ind m}^{-2}$). Communities of cluster 2 and 3 were nearly absent. As shown in this study, the occurrence of the community of cluster 1 is related to the presence of relatively coarse, sandy sediments. In 1952, the sediment was indeed coarser as compared with this study, as 70% of the sampling locations contained less than 5% of mud (fraction $< 50\,\mu$m, determined by sieving).

Human impacts

The mesohaline subtidal zone of the Zeeschelde is by nature characterized by a high degree of 'unstability', caused by large fluctuations in salinity, high current velocities and high turbidity, making an assessment of human impacts on the benthic communities difficult. Human activities, such as the discharge of waste and dredging of sludge, are superimposed on these natural processes and, moreover, interfere with them. The combination of favourable hydrodynamic conditions, several fine suspended matter sources (including a large anthropogenic part), and the flocculation process, leads in salinity zone 2–10 psu to bottom sediments that locally contain high percentages of fine material (Baeyens et al., 1998). Being a major sedimentary environment, the shipping channel is extensively dredged. The processes of sedimentation and resuspension, at least locally, are probably enhanced by these dredging operations, that increased from 11 million m^3 dredged and 4 million m^3 dumped in the period 1951–1960 to 20 million m^3 dredged and 11 million m^3 dumped in 1981–1990 (J. Claessens, personal commmunication).

The fact that the subtidal zone of the Zeeschelde is a highly stressed environment was in this study confirmed by the very low density and biomass of the macrobenthos, and the most common occurrence of *H. filiformis* and tubificid Oligochaeta, small, subsurface deposit-feeding, opportunistic species. It was also clear from the ABC-curves that the communities considered were under stress. This provides strong evidence that the communities remain in early succession, and indicates stress or disturbance (e.g. Warwick, 1986; Gaston et al., 1998). The occurrence of three different macrobenthic communities in 1996–1997, two of which are typical for muddy sediments (clusters 2 and 3), might be explained by a difference in origin and magnitude of disturbance. A less common, typically low-diversity community (cluster 1) was found on more sandy sediments, being dominated by the amphipod *Bathyporeia pilosa*, a well-adapted inhabitant of unstable, sandy sediments (Khayrallah & Jones, 1980). This community is characteristic for the mesohaline, subtidal part of the Schelde Estuary, at places where by nature tidal current speeds and instability of the (sandy) sediment become the limiting factors (Craeymeersh et al., 1999). It was also the only dominant community in 1952.

The dredging and dumping activities might have direct effects (being washed out, being buried) on the occurrence of macrobenthos. Seventy per cent of the samples taken at locations where intensive dredging took place (Figure 1) belonged to cluster 3, dominated by the capitellid *H. filiformis* and tubificid Oligochaeta, which are known to be very tolerant to both physical and chemical (organic enrichment, anoxia) disturbance factors (Rakocinski et al., 1997; Gaston et al., 1998). Although most of the locations from cluster 2 and 3 occurred in silty sediments, species characteristic for cluster 2 (e.g. *Polydora ligerica*) were almost completely absent at dredging and dumping sites.

In the study area also several 'hard substrates' were constructed (e.g. dams, dykes, rubbles) to suppress erosion, to conduct the streamflow and for safety reasons. In many places these constructions subsided, causing the occurrence of stones and other similar hard substrates in the river, next to natural substrates like peat and shells. Most of the sediments with hard substrates were characterized by a high number of species and a relatively high density (cluster 2), although a lot of the samples taken were incomplete. Hard substrates can form a suitable habitat for several soft bottom species, as these substrates might provide shelter and prohibit species being washed out from the sediment. *Balanus* spp., often found in several layers on these hard substrates, might provide shelter for other animals, or create a multitude of habitats for other species, even for soft bottom ones, when silt is deposited in between (Dittmer, 1983). The hard substrates also allowed the settlement of bivalves, like oysters. These suspension-feeders could be considered an indication of improving water quality.

We are grateful for the financial assistance provided by the Ministry of the Flemish Community (AWZ) and for the logistical support by Ir. Taverniers, Ir. Wouters and the crews of the 'Veereman'. Data on the model calculations for current velocities were provided by Ir. Harm Verbeek (RWS-RIKZ) and Ir. Claessens provided data on the dredging and dumping activities in the Zeeschelde. We thank Nico De Regge and Jan Soors for their support in the field and in the laboratory.

REFERENCES

Baeyens W., Van Eck, B., Lambert, C., Wollast, R. & Goeyens, L., 1998. General description of the Scheldt Estuary. *Hydrobiologia*, **366**, 1–14.

Bastrop, R., Röhner, M., Sturmbauer, C. & Jürss, K., 1997. Where did *Marenzelleria* spp. (Polychaeta: Spionidae) in Europe come from? *Aquatic Ecology*, **31**, 119–136.

Boesch, D.F., 1977. A new look at the zonation of benthos along the estuarine gradient. In *Ecology of marine benthos* (ed. B.C. Coull), pp. 245–266. Columbia, South Carolina: University of South Carolina Press, Columbia, South Carolina. [The Belle W. Baruch Library in Marine Science, no. 6.]

Boesch, D.F. & Rosenberg, R., 1981. Response to stress in marine benthic communities. In *Stress effects on natural ecosystems* (ed. G.W. Barrett and R. Rosenberg), pp. 179–200. New York: John Wiley & Sons.

Brummelhuis, E., Craeymeersch, J., Markusse, R. & Sistermans, W., 1997. Het macrobenthos van de Westerschelde, de Oosterschelde, het Veerse meer en het Grevelingenmeer in het najaar 1996. *Rapport in het kader van het Biologisch Monitoring Programma, NIOO-CEMO Yerseke*, 43 pp.

Claessens, J., Van Hoof, J. & De Ruig, J.H.M., 1991. Interactie morfologie en baggerwerken. *Water*, **60**, 182–189.

Clifford, H.T. & Stephenson, W., 1975. *An introduction to numerical classification.* New York: Academic Press.

Costanza, R., Kemp, W.M. & Boynton, W.R., 1993. Predictability, scale, and biodiversity in coastal and estuarine ecosysems: implications for management. *Ambio*, **22**, 88–96.

Craeymeersch, J.A., 1999. *The use of macrobenthic communities in the evaluation of environmental change.* PhD thesis, University of Gent, Belgium.

Diaz, R.J. & Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology. Annual Review*, **33**, 245–303.

Dittmer, J.-D., 1983. The distribution of subtidal macrobenthos in the estuaries of the rivers Ems and Weser. In *Ecology of the Wadden Sea*, vol. I (ed. W. Wolff), pp. 4/188–4/206. Rotterdam: A.A. Balkema.

Essink, K., 1999. Dispersal and development of *Marenzelleria* spp. (Polychaeta, Spionidae) in NW Europe and The Netherlands. *Helgoländer Meeresuntersuchungen*, **52**, 367–372.

Essink, K. & Schöttler, U., 1997. Studies on *Marenzelleria* spp. (Polychaeta: Spionidae). *Aquatic Ecology*, **31**, 117–258.

Fettweis, M., Sas, M. & Monbaliu, J., 1998. Seasonal, neap-spring and tidal variation of cohesive sediment concentration in the Scheldt Estuary, Belgium. *Estuarine, Coastal and Shelf Science*, **47**, 21–36.

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 and Freshwater Research*, **49**, 833–846.

Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, **6**, 153–175.

Hall, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology. Annual Review*, **32**, 179–239.

Hill, M.O., 1979. *TWINSPAN: a Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* New York: Section of Ecology and Systematics, Cornell University.

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.

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.

Kramer, K.J.M., Brockmann, U.H. & Warwick, R.M., 1994. *Tidal estuaries. Manual of sampling and analytical procedures.* Rotterdam: A.A. Balkema.

Kruskal, J.B. & Wish, M., 1978. *Multidimensional scaling.* Beverly Hills: Sage Publications.

Lambshead, P.J.D., Platt H.M. & Shaw, K.M., 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History*, **17**, 859–874.

Leloup, E. & Konietzko, B., 1956. Recherches biomogiques sur les eaux saumâtres dus Bas-Escaut. *Verhandelingen van het Koninklijk Belgisch Instituut voor Natuurwetenschappen*, no. 132, 100 pp.

McLusky, D.S., Hull, S.C., Elliot, M., 1993. Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper Forth Estuary. *Netherlands Journal of Aquatic Ecology*, **27**, 101–109.

Meire, P.M. & Dereu, J., 1990. Use of the Abundance/Biomass Comparison method for detecting environmental stress: some considerations based on intertidal macrozoobenthos and bird communities. *Journal of Applied Ecology*, **27**, 210–223.

Meulen, A. van der, & Sileon, M., 1997. Overzicht van modellen in gebruik bij het RIKZ en het RIZA. *Rijkswaterstaat, Rapport RIKZ-97.008*, 109 pp.

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.

Pearson, T.H. & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology. 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., 1969. Wie erkennt man eine genuine Brackwasserart? *Limnologica*, **7**, 9–21.

Seys, J., Vincx, M. & Meire, P., 1999. Spatial distribution of Oligochaeta in the tidal freshwater and brackish parts of the Schelde Estuary (Belgium). *Hydrobiologia*, **406**, 119–132.

Soetaert, K. & Herman, P.M.J., 1995a. 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., 1995b. Estimating estuarine residence times in the Westerschelde (The Netherlands) using a box model with fixed dispersion coefficients. *Hydrobiologia*, **311**, 215–224.

Van Damme, S., Meire, P., Maeckelberghe, H., Verdievel, M., Bourgoing, L., Taverniers, E., Ysebaert, T. & Wattel, G., 1995. De waterkwaliteit van de Zeeschelde: evolutie in de voorbije dertig jaar. *Water*, **85**, 244–256.

Van Eck, G.T.M., De Bruijckere, F.L.G., De Meyer, E. & Maeckelberghe, H., 1998. Naar een Schone Schelde. *Water*, **102**, 293–303.

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.

Warwick, R.M., 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology*, **92**, 557–562.

Warwick, R.M. & Clark, K.R., 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Marine Ecology Progress Series*, **92**, 221–231.

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**, 329–345.

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.

Wildish, D.J. & Kristmanson, D.D., 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. *Journal of the Fisheries Research Board of Canada*, **6**, 1197–1206.

Wolff, W.J., 1973. The estuary as a habitat. *Zoologische Verhandelingen Leiden*, no. 126, 242 pp.

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., De Block, M., De Regge, N. & Soors, J., 1996. First record of *Marenzelleria viridis* (Verril, 1873) (Polychaeta, Spionidae) in the Schelde Estuary (Belgium). *Biologisch Jaarboek Dodonea*, **64**, 176–181.

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.

Zwolsman, J.J.G., 1999. Geochemistry of trace metals in the Scheldt Estuary. *Geologica Ultraiectina, Mededelingen van de Faculteit Aardwetenschappen, Universiteit Utrecht*, no. 171, 183 pp.

Submitted 1 November 1999. Accepted 30 March 2000.