A comparison of the macrobenthic distribution and community structure between two estuaries in SW Netherlands

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Abstract

The Wester- and Oosterschelde are the only two remaining estuaries in the Delta area of SW Netherlands. In the Westerschelde the normal estuarine gradient from a brackish to a marine tidal system is found, whereas in the Oosterschelde major coastal engineering works have profoundly changed the character of the area. There is now no salinity gradient, and turbidity and pollution are very low.

The intertidal macrofauna of both estuaries was studied intensively in 1987 and found to be similar in species composition. However, more species occurred in the Oosterschelde mainly because of the presence of extensive mussel beds. The average density was greater in the Westerschelde, but biomass was much greater in the Oosterschelde.

Multivariate statistical analyses (TWINSPAN and DECORANA) were used to determine similarities between stations and almost no overlap occurred between stations from the Ooster- and Westerschelde. Water parameters (salinity, turbidity etc.) correlated with the first ordination axis and sediment parameters (median grain size, mud content) were correlated with the second axis. The data indicate that between the Wester- and the Oosterschelde, a clear gradient from a filter-feeder to a deposit-feeder dominated community was found. These correspond to coastal and detritus food chains. It is concluded that the absence of filter feeders in the brackish part of the Westerschelde is caused by the highly dynamic character of the estuary rather than by pollution or lack of food. Increased dredging activities could further impoverish the fauna.

Keywords: estuaries, intertidal macrobenthos, community structure, Oosterschelde, Westerschelde.

Introduction

The benthic macrofauna of the whole Delta area in the south-western part of the Netherlands was studied intensively by Wolff (1973). However, since then the area has been changed profoundly by major coastal engineering projects. Several estuaries have been dammed and in the Oosterschelde a storm-surge barrier has been built. This has strongly influenced the hydrodynamic properties of the estuary and stimulated much research (see also Smaal *et al.* 1991). The Westerschelde has remained the only natural estuary in the whole Delta area, showing a clear gradient in salinity, turbidity, nutrient load etc., although it is severely polluted. Surprisingly little is known about the ecological value of the Westerschelde.

In the present study, the distribution of the macrobenthos in both estuaries is described and compared in relation to the prevailing environmental factors.

Methods

Study area

The Westerschelde is the estuarine part of the River Schelde, bordered at the east by the Dutch-Belgian border and at the west by the line Breskens-Vlissingen (Figure 1). The freshwater input, mainly through the River Schelde, is small (on average 105 $m^3 \cdot s^{-1}$, Claessens 1988) compared to a tidal volume of 10^9 m^3. The mean tidal range is 3.85 m at the mouth and 4.58 m at the Belgian border. Typical estuarine gradients in the abiotic factors are present from the mouth to the river, such as a decrease of chlorinity and oxygen content and an increase in turbidity, particulate organic matter and

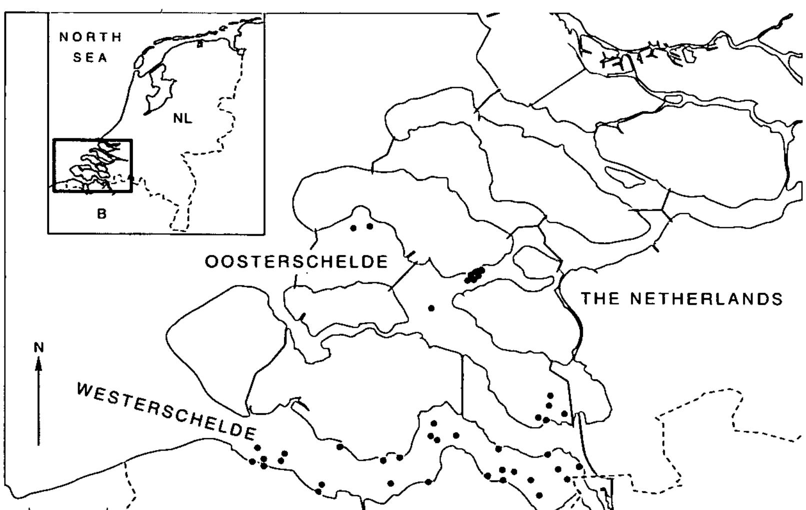

Figure 1.
Location of the sampling stations in the Oosterschelde and the Westerschelde.

nutrients (Table 1). There is a high anthropogenic stress due to dredging activities and from large amounts of inorganic and organic contaminants from various effluents, especially in the brackish part and the River Schelde (Moerland 1987, Duursma *et al.* 1988).

Table 1.
Abiotic characteristics of the Oosterschelde (OS) and the Westerschelde (between Dutch-Belgian border and the mouth) (WS) Estuary (data from Rijkswaterstaat).

	Tidal range, m	Chloride content, $g\ Cl \cdot l^{-1}$	Sus-pended matter, $mg \cdot l^{-1}$	Secchi disc trans-parency, m	Mean N content, $mg \cdot l^{-1}$	Mean P content, $mg\ P \cdot l^{-1}$	Mean mud content, bottom, %	Mean Cd content, dissolved, $\mu g \cdot l^{-1}$
OS	2.8-3.8	14-18	4- 9	2.1-2.3	0.9-1.2	0.09-0.14	2.6	0.03-0.05
WS	3.8-4.5	4-17	27-66	0.2-0.8	1.6-8.1	0.18-0.86	3.3	0.13-0.22

Since the closure of the Volkerak Dam in 1969, the freshwater input in the Oosterschelde (through Volkerak sluices, a few small rivers, and some polderwater discharge) has been strongly reduced and regulated at about 50 $m^3 \cdot s^{-1}$ (Smaal *et al.* 1991). This has resulted in a stable high chlorinity in the whole area and small nutrient and pollutant loads with very low concentrations of suspended matter (Table 1). The exchange with water from the North Sea was reduced after the construction of the storm-surge barrier in 1987. The mean tidal amplitude is lower than in the Westerschelde (3.5 m near Yerseke). The creek flow-rates are low and vary between 0.5 $m^3 \cdot s^{-1}$ and 1.2 $m^3 \cdot s^{-1}$ (see also Smaal *et al.* 1991).

The sampling programme

The survey was carried out in September-October 1987. In the Westerschelde (Figure 1), 28 sampling stations were placed in different habitat types along the whole gradient. Within each station 2-4 sites were chosen, and at each site 10 cores, 4.5 cm diameter (15.9 cm^2), and 3 cores, 15 cm diameter (176.6 cm^2), were taken to a depth of 30 cm. The larger cores were washed in the field through a 3-mm-mesh sieve, whereas the smaller ones were fixed in the field with 35 % neutral formalin, brought to the laboratory and washed through a 1-mm-mesh sieve. The data from the Oosterschelde are from two different sampling programmes. The first programme was carried out at the Slikken van Vianen, an intertidal area in the central part of the estuary, where the interaction between waders and macrozoobenthos has been investigated since 1979 (Meire 1987, Meire & Kuyken 1984, Meire & Coosen 1985, Meire & Ervynck 1986). In each of the six permanent study plots situated in the different habitat types (defined according to inundation time and sediment type), 30 cores, 4.5 cm in diameter (15.9 cm^2), and 5 cores, 15 cm in diameter (176.6 cm^2), were taken to a depth of 30 cm. The treatment of these samples was as described for the Westerschelde.

The second programme was started in 1983 to investigate the effects of the construction of the storm-surge barrier on the macrozoobenthos. Eight permanent stations were chosen in the intertidal area, taking account of the west-east gradient, and sampled twice a year (March-April, August-September). At each station, three sets of 5 core samples, 10.3 cm in diameter (83 cm^2), were taken to a depth of 30 cm. They were sieved in the field on a 1-mm-mesh sieve and fixed with 7 % neutral formalin. The water parameters (chlorinity, suspended matter, particulate organic carbon, oxygen saturation, total-N, total-P, dissolved Si, chlorophyll-*a*, dissolved Cd) are mean values of monthly measurements for 1987 (Rijkswaterstaat, unpubl. data). Data were used from areas close to the sampling station. Samples for sediment analysis were collected simultaneously with the macrofaunal samples.

Laboratory methods

The small samples were washed through a 1-mm-mesh sieve and all organisms were extracted, after staining with Rose Bengal, identified to species level – except Oligochaeta and Nemertini – and counted. Bivalves were measured to the nearest mm. Density and biomass of all but two species are based on the small samples. From the large samples only *Mya arenaria* L. and *Arenicola marina* L. were extracted. The density and biomass of these two species is entirely based on the large samples. Ash-free dry weight (AFDW) biomass was obtained by weighing (±0.0001 g) all individuals per species per sample after drying for 12 hours (110 °C), and weighing again after incinerating for 2 hours (550 °C). All bivalves were weighed without the shell and length-weight regressions were calculated. The resulting station/species/abundance matrix data were analysed using the multivariate techniques TWINSPAN and DECORANA (Gauch 1982). For the analysis the following congeneric species pairs were combined because of identification problems: *Coro-*

phium arenarium Crawford/*C. volutator* Pallas, *Anaitides mucosa* Ørsted/*A. maculata* L., *Eteone longa* Fabricius/*E. flava* Fabricius, *Bathyporeia pilosa* Lindstrøm/*B. sarsi* Watkin and *Gammarus* sp. The cut-levels used in the TWINSPAN analysis were: 0, 1, 4, 16, 64, 256, 1024, 4096, 9999. No data transformation nor down-weighting of rare species was used.

Results

The total number of species was lower in the Westerschelde (36) than in the Oosterschelde (43) (Table 2) although the species composition was comparable and there were 29 species in common. The latter are all typical estuarine organisms such as *Cerastoderma edule, Hydrobia ulvae, Macoma balthica, Nereis diversicolor, Nephtys hombergii* and *Arenicola marina*. Fourteen species were found only in the Oosterschelde, although some of them (*Mytilus edulis, Scrobicularia plana*) are known to be present in limited numbers in the Westerschelde (pers. obs.). Seven species were restricted to the Westerschelde samples.

The mean total density was higher in the Westerschelde than the Oosterschelde, respectively 24042 (SE: 4244) and 16501 (SE: 3343) individuals $\cdot m^{-2}$. However, mean total biomass was much higher in the Oosterschelde (111.5 g AFDW$\cdot m^{-2}$; SE: 36.3 g) than in the Westerschelde (14.6 g AFDW$\cdot m^{-2}$; SE: 3.3 g).

	Oosterschelde	Westerschelde
Mean total density, N $\cdot m^{-2}$	16501	24042
Mean total biomass, g AFDW$\cdot m^{-2}$	111.5	14.6
Species richness	43	36

Species composition:

Species found in both estuaries
- *Cerastoderma edule* (Linnaeus)
- *Hydrobia ulvae* (Pennant)
- *Macoma balthica* (Linnaeus)
- *Mya arenaria* (Linnaeus)
- *Mysella bidentata* (Montagu)
- *Retusa obtusa* (Montagu)
- *Anthozoa* sp.
- *Bathyporeia* sp.
- *Carcinus maenas* (Linnaeus)
- *Corophium* sp.
- *Crangon crangon* (Linnaeus)
- *Gammarus* sp.
- *Anaitides* sp.
- *Antinoella sarsi* (Kinberg)
- *Arenicola marina* (Linnaeus)
- *Capitella capitata* (Fabricius)
- *Eteone* sp.
- *Heteromastus filiformis* (Claparède)
- *Magelona papillicornis* (Müller)
- *Nemertea* indet.
- *Nephtys hombergii* (Savigny)
- *Nereis diversicolor* (Müller)
- *Nereis succinea* (Leuckart)
- Oligochaeta indet.
- *Polydora* sp.
- *Pygospio elegans* (Claparède)
- *Scoloplos armiger* (Müller)
- *Spio filicornis* (Müller)
- *Tharyx marioni* (Saint Joseph)

Species in Westerschelde only
- *Manayunkia aestuarina* (Bourne)
- *Ophelia rathkei* (McIntosh)
- *Scolelepis squamata* (Müller)
- *Spiophanes bombyx* (Claparède)

Species in Oosterschelde only
- *Crassostrea angulata* (Lamarck)
- *Crepidula fornicata* (Philibert)
- *Lepidochitona cinerea* (Linnaeus)
- *Littorina littorea* (Linnaeus)
- *Mytilus edulis* (Linnaeus)
- *Scrobicularia plana* (da Costa)
- *Jaera albifrons* (Leach)
- *Melita palmata* (Montagu)
- *Pagurus bernhardi* (Linnaeus)
- *Urothoe poseidonis* (Reibisch)
- *Lanice conchilega* (Pallas)
- *Microphthalmus aberrans* (Webster & Benedict)
- *Pholoe minuta* (Fabricius)
- *Scolelepis foliosa* (Audouin & Milne Edwards)

Table 2.
Mean density, biomass and species composition of the locations sampled in the Oosterschelde and the Westerschelde.

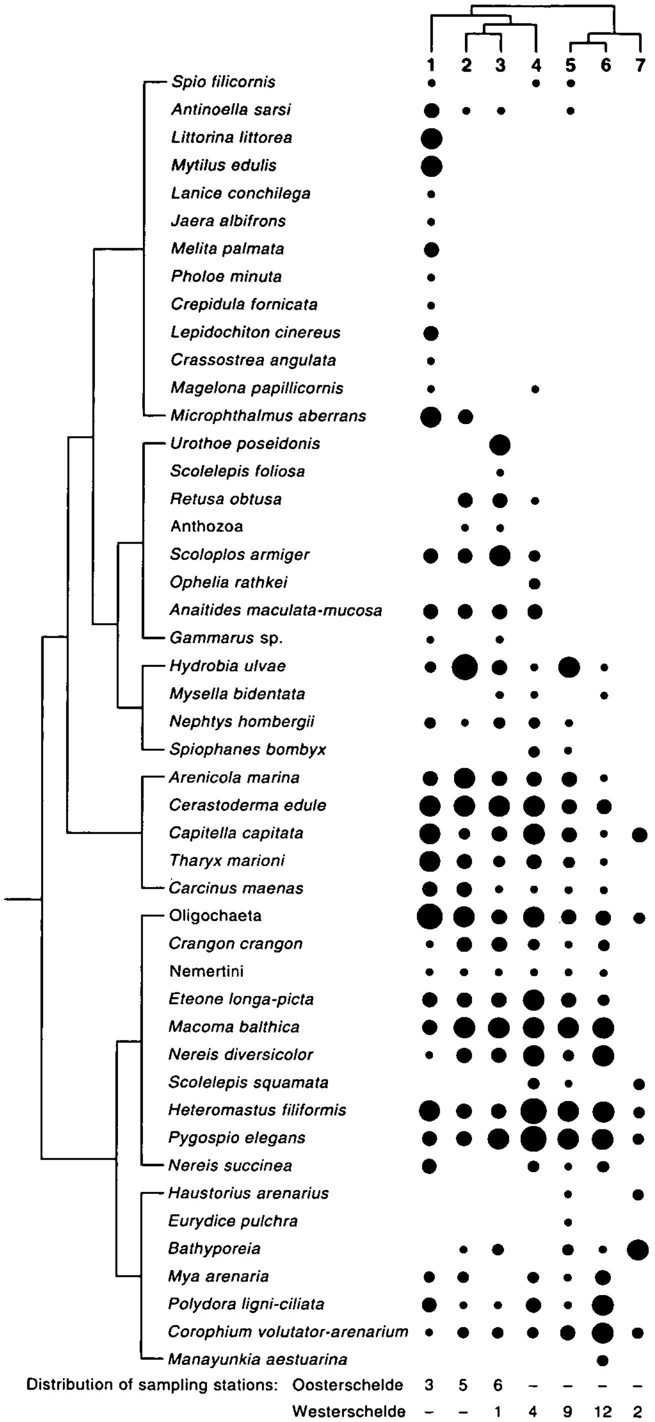

Figure 2.
TWINSPAN based on the densities of macrobenthic organisms in Oosterschelde and Westerschelde in 1987. Seven groups were separated and within each group the mean densities of the species are represented with dots.

Key: • 0-4·m^{-2}
● 4-64·m^{-2}
● 64-1024·m^{-2}
● 1024-4096·m^{-2}
● > 4096·m^{-2}

Based on the densities of each species per station, seven station groupings can be separated using TWINSPAN (Figure 2). Group 1 stations are in the Oosterschelde and are characterised by the presence of *M. edulis* and a series of species such as *Crepidula fornicata* and *Littorina littorea* which are associated with the mussel beds. Group 7 consists of two stations with an impoverished benthic fauna whereas the remaining five groups have a rather similar species composition although the relative abundance of species differs between groups. After the second division in the analysis, all samples from the Oosterschelde are separated from those in the Westerschelde. When performing TWINSPAN on the biomass data all samples from both estuaries were separated after the first division (unpubl. data). However, groups identified were very similar, therefore further analysis here is restricted to the analysis based on the density of the macrofauna.

In order to characterise the seven TWINSPAN-groups (Figure 2), average values of some important abiotic factors are given in Figure 3A-E. With the exception of group 7 – which consists of two impoverished stations – a clear gradient in salinity between the groups is observed. Groups 1-3 (all stations from the Oosterschelde) and group 4 (stations from the marine part of the Westerschelde) have high mean chlorinities (14.9-16.6 g $Cl^{-}\cdot l^{-1}$). Group 6 consists of stations in the brackish part of the Westerschelde, group 5 (11.2 g $Cl^{-}\cdot l^{-1}$) and group 7 (10.3 g $Cl^{-}\cdot l^{-1}$) are intermediate. Oxygen saturation follows a similar gradient, with more than 100% saturation on a yearly base in the Oosterschelde, only 84% in the marine part of the Westerschelde decreasing to 63% in the brackish part. Suspended matter, nutrients etc, follow an opposite gradient with low values in the Oosterschelde and increasing values towards the brackish part of the Westerschelde. Sediment parameters also differ between groups: groups 1-3 consist of fine sand (median grain size: 134-154 µm) with a low mud content (1.0-4.6%), whereas the Westerschelde groups (4-7) consist of fine to medium sand (125-233 µm) and higher mud contents (0.8-12.0%).

A Detrended Correspondance Analysis (DECORANA) based on the species/abundance matrix reveals the same gradients (Figure 4). Stations from the Oosterschelde and Westerschelde are clearly separated along the first axis (eigenvalue: 0.696) which is related to the water chlorinity, suspended matter, nutrient content and pollution stress (Cd content) (Table 3). The second axis (eigenvalue: 0.290) is correlated with sediment characteristics (median grain size, mud content) (Table 3). Axes 3 and 4 (eigenvalues: 0.156 and 0.063, respectively) are unimportant and not considered further. The biomass data gave similar results.

The abiotic gradients are reflected in the faunal parameters. Total biomass and species richness were highest in the mussel beds (group 1) and in the Oosterschelde as a whole in comparison to the Westerschelde (Table 4). Within the Westerschelde, the lowest values were found in the brackish part (group 6). Species were not distributed uniformly over the different groups. Some species (*Heteromastus filiformis*, *Polydora ligni-ciliata* and *Pygospio elegans*) were much more abundant in the Westerschelde. Other species (*Hydrobia ulvae* and *Scoloplos armi-*

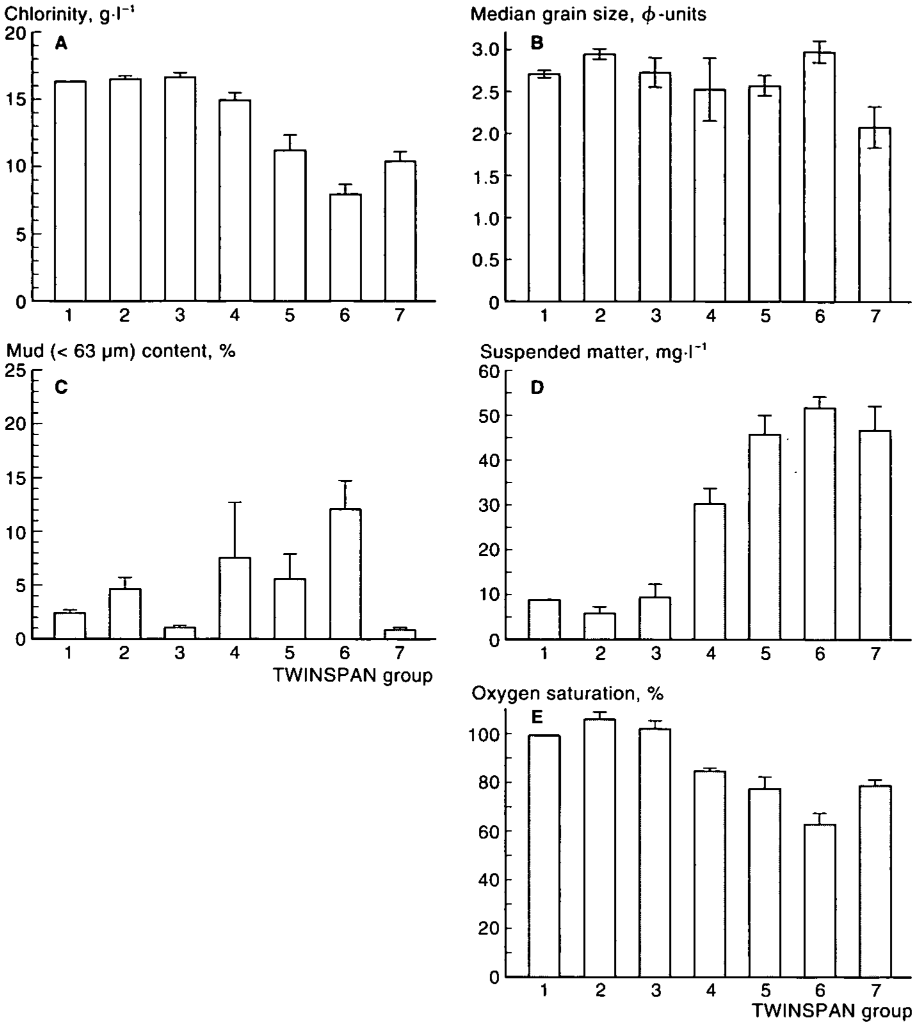

Figure 3.
Abiotic factors (mean values ± SE) per TWINSPAN-group: chlorinity, median grain size , mud content, suspended matter, oxygen saturation.

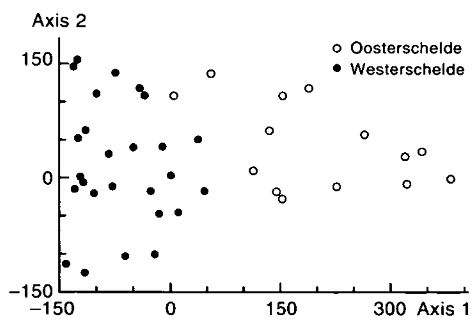

Figure 4.
Detrended Correspondance Analysis based on the densities of macrozoobenthos in Oosterschelde and Westerschelde: position of the sampling stations along the first two DCA-axes.

Factor	Axis 1 r_s	Axis 1 Significance	Axis 2 r_s	Axis 2 Significance
Chlorinity	0.70839	***	0.42963	**
O_2-saturation	0.75881	***	0.39758	*
Particulate organic carbon	−0.76803	***	−0.26775	n.s.
Suspended matter	−0.81476	***	−0.32976	*
Total-P content	−0.63559	***	−0.45601	**
Total-N content	−0.69314	***	−0.47044	**
Dissolved Si	−0.70235	***	−0.45474	**
Dissolved Cd	−0.81719	***	−0.07609	n.s.
Median grain size	0.19376	n.s.	−0.51253	***
Mud content	−0.22151	n.s.	−0.61466	***
Inundation time	−0.11953	n.s.	−0.24170	n.s.

* $p \leq 0.05$; ** $p \leq 0.005$; *** $p \leq 0.001$; n = 40.

Table 3.
Correlation coefficients (Spearman's rank) between the scores on the two first DCA-axes and some environmental factors.

Table 4.
Mean biomass (g AFDW · m^{-2}), number of species and density (N · m^{-2}) and biomass (g AFDW · m^{-2}) of some species in the different TWINSPAN-groups.

TWINSPAN-group	1	2	3	4	5	6	7
Mean biomass	300.7	64.6	48.8	36.5	6.9	16.2	0.5
Number of species	25.3	17.4	17.3	17.8	12.2	11.3	6.5
Density							
Heteromastus filiformis	2704	405	67	1004	2745	5342	32
Polydora ligni/ciliata	294	4	2	334	118	3615	0
Pygospio elegans	112	129	996	7228	6026	9872	24
Hydrobia ulvae	42	10675	1849	8	65	17	0
Scoloplos armiger	196	439	1166	51	0	0	0
Macoma balthica	363	617	446	2846	851	1625	0
Cerastoderma edule	3207	2417	520	4249	333	461	0
Biomass							
Macoma balthica	3.4	3.3	1.7	4.4	1.8	1.4	0
Cerastoderma edule	179.6	49.4	34.3	17.1	1.0	1.0	0

ger) had higher densities in the Oosterschelde. The density of *Macoma balthica* and *Cerastoderma edule* was highest in group 4 stations but their biomass was higher in the Oosterschelde (Table 4). This can be attributed to the differences in length-frequency distributions, since larger individuals were almost absent in the Westerschelde (Figures 5 & 6), particularly in the brackish part. This feature also applies to *Mya arenaria* whose largest individuals measured only between 6 and 7 mm, although densities varied between a few and 4350 · m^{-2}.

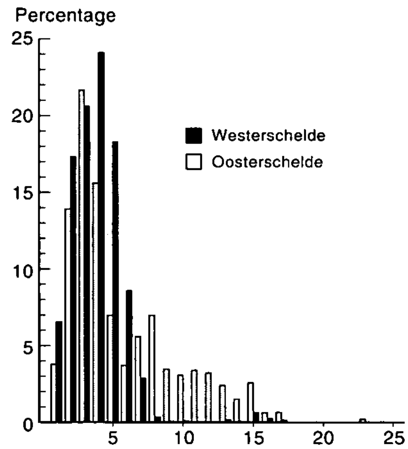

Figure 5. (left)
Length-frequency distributions of *Macoma balthica*, as found in the Oosterschelde (n = 514) and Westerschelde (n = 2249) in 1987.

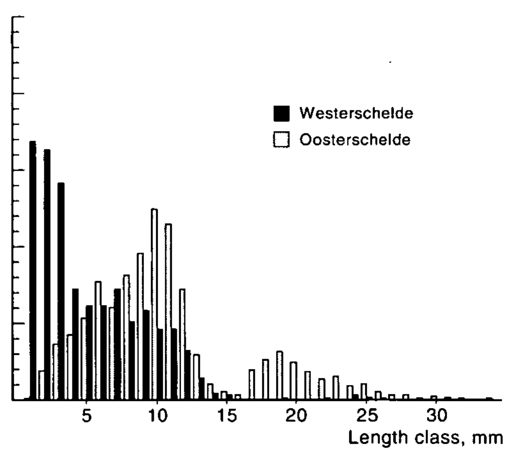

Figure 6. (right)
Length-frequency distributions of *Cerastoderma edule*, as found in the Oosterschelde (n = 1745) and Westerschelde (n = 1481) in 1987.

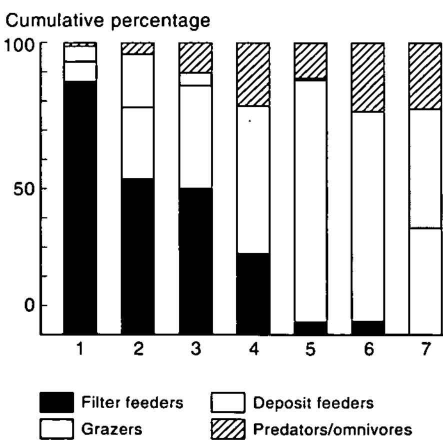

Figure 7. (left)
Relative biomass proportions of the different trophic groups over the seven TWINSPAN-groups.

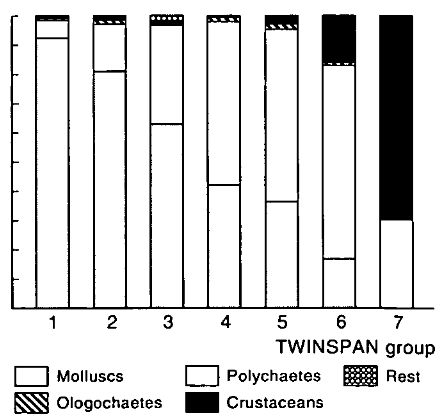

Figure 8. (right)
Relative biomass proportions of the different systematic groups over the seven TWINSPAN-groups.

The difference between the TWINSPAN-groups is not only reflected in the species composition but also in the distribution of trophic and major taxonomic groups (Figures 7 & 8). A gradual decrease in the proportion of the biomass of filter feeders and a gradual increase in that of deposit feeders occurred from the Oosterschelde to the brackish part of the Westerschelde (Figure 7). A similar gradient can be found for taxonomic groups where it seem that polychaetes replaced molluscs in the brackish, more turbid zone of the Westerschelde (Figure 8).

Discussion

The species composition was similar between both estuaries and is typical for Northwest European estuaries (Wolff 1973). Although the area sampled in the Oosterschelde is about 20% less than in the Westerschelde, seven more species were found, indicating the higher diversity. However, most species found in only one estuary are known also to occur in the other (unpubl. data), although in low numbers or in small patches. Some differences exist however. *Manayunkia aestuarina* is a typical brackish water species and is only found in the Westerschelde at chlorinities of 5-8 g $Cl^{-} \cdot l^{-1}$. *Crassostrea angulata* on the other hand occurs only in the Oosterschelde. This species has been cultivated for some years by oyster farms and is now spreading gradually throughout the estuary.

	Ems	Weser	Westerschelde
Zone 1:			
Chlorinity, g $Cl \cdot l^{-1}$	2.5-6.5	3.5-5	4.5-6.5
Total number of species	8	17	13
Mean biomass (g AFDW $\cdot m^{-2}$)	2.5		9
Numerical dominant species in common:	Oligochaeta/*Nereis diversicolor*/*Corophium volutator*		
Zone 2:			
Chlorinity, g $Cl \cdot l^{-1}$	6.5-9	5-8	6.5-9
Total number of species	35	20	17
Mean biomass (g AFDW $\cdot m^{-2}$)	8.8		15
Numerical dominant species in common:	*Nereis diversicolor*/*Corophiumvolutator*/Oligochaeta/ *Macoma balthica*/*Heteromastus filiformis*		
Zone 3:			
Chlorinity, g $Cl \cdot l^{-1}$	9-13	8-13	9-13
Total number of species	34	28	28
Mean biomass (g AFDW $\cdot m^{-2}$)	13.6		8.4
Numerical dominant species in common:	*Macoma balthica*/*Heteromastus filiformis*/*Arenicola marina*		
Zone 4:			
Chlorinity, g $Cl \cdot l^{-1}$	13-17	13-17	13-17
Total number of species	80-140*	120*	34
Mean biomass (g AFDW $\cdot m^{-2}$)	22		33
Numerical dominant species in common:	*Heteromastus filiformis*/*Pygospio elegans*		

*Based on more surveys than has been used for the Westerschelde.

Table 5.
Comparison of the macrobenthic fauna in the Ems, Weser and Westerschelde. The data for Ems and Weser are extracted from Michaelis (1983).

The gradient in the fauna of the Westerschelde is similar to that found by Vermeulen & Govaere (1983) and can also be compared with those of the Ems and the Weser (Michaelis 1983). In the upper and middle parts of these estuaries, the same species are dominant (zones 1, 2 and 3 in Table 5) although some differences exist. Species such as *Macoma balthica, Heteromastus filiformis* and *Pygospio elegans* are much more abundant in the Westerschelde-mouth compared to the other estuaries. For *H. filiformis*, mean biomass values of 7.1 g AFDW $\cdot m^{-2}$ were found compared to less than 1 g AFDW $\cdot m^{-2}$ in Ems- and Weser-mouth. In contrast, a typical brackish water species such as *Streblospio shrubsolii* is common in the brackish part of the Weser, much rarer in the Ems and lacking in the Westerschelde. The polychaete *Manayunkia aestuarina* follows the opposite trend. Compared to the Loire (Robineau 1987), more species have been found in the Westerschelde.

The biomasses found on the mussel beds in the Oosterschelde were lower than those recorded by Asmus (1987) for the Danish Wadden Sea. However, the overall

	Mean flood volume, $10^6 m^3$	Mean tidal amplitude, cm
Eider	40	273
Elbe	650	297
Ems	780	311
Weser	155	364
Westerschelde	1100	382-490
Oosterschelde	850*	308

*This is the value predicted for the period after the construction of the storm surge barrier. In the pre-barrier period a value of 1220 $10^6 m^3$ was measured.

Table 6.
Comparison of some general characteristics of the Ems, Weser, Elbe, Eider, Westerschelde and Oosterschelde. Data from Kühl & Mann (1983), Claessens (1988) and Anon. (1986).

biomass of macrobenthos in the Oosterschelde is high in comparison to the Westerschelde and other estuarine areas such as the Dutch Wadden Sea, which has an average value of 27 g AFDW· m^{-2} (Beukema 1983). However, the average value of over 110 g AFDW· m^{-2} for the Oosterschelde is too large because mussel beds were overrepresented in the samples compared with their actual distribution. Van der Meer *et al.* (1989) estimated the average biomass for the whole Oosterschelde at nearly 50 g AFDW· m^{-2}. In the Westerschelde a gradient from lower biomass values in the brackish (9 g AFDW· m^{-2}) to higher biomass in the marine zone (33 g AFDW· m^{-2}) was found, a trend which is found in other estuaries such as the Ems (Table 5). The biomass in the Westerschelde on average was higher than in the Ems.

In the present study, the water parameters (salinity, turbidity etc.) and sediment characteristics (median grain size and mud content) were found to be the most important factors influencing the estuaries' macrozoobenthos. This agrees with Vermeulen & Govaere (1983) who analysed the benthic fauna along four transects in the Westerschelde. The importance of these factors is very well documented (e.g. Gray 1974, Michaelis 1983). Compared to the Oosterschelde, Ems, Weser, Elbe and Eider, the Westerschelde had the largest tidal amplitude and flood volume (Table 6), both indicating the highly dynamic character of the system. However, this factor is difficult to measure but is considered here to have a very important influence on the fauna. The greater dynamics of the Westerschelde compared to the Oosterschelde is partly reflected in the greater variability of the sediment types (median grain size varied between 123 and 176 µm in the Oosterschelde and between 71 and 292 µm in the Westerschelde; mud content varied between 0.4 and 7.7 % in the Oosterschelde and between 0.7 and 36.3 % in the Westerschelde).

The trophic structure of the benthic communities differed strongly between the Ooster- and Westerschelde and also within the Westerschelde a clear gradient was found. This corresponds with different types of food chains within the estuaries as suggested by Hummel *et al.* (1988). The brackish part of the Westerschelde is characterised by a detritus-based food chain, the mouth of the estuary by a coastal phytoplankton-based food chain. The large input of organic matter from the river and the flocculation of organic material in the brackish zone results in high concentrations of organic matter. The corresponding low transparency inhibits primary production although concentrations of nutrients are high. Organic detritus is an important link between primary and secondary production, bacteria being essential for the transfer of energy through this food chain. In the marine tidal zone, the importance of suspended organic matter is less and the primary production is higher. Therefore the energy flow from nutrients through phytoplankton to zooplankton and zoobenthos is more important than the flow from detritus to zooplankton and zoobenthos. The high proportion of filter feeders in the Oosterschelde and in the marine part of the Westerschelde and the predominance of deposit feeders in the brackish part are consistent with these food chains. Some problems exist however. First of all, although the proportion of deposit feeders in the brackish part was much higher, their actual biomass was not. Highest values were found on the mussel beds (24 g AFDW· m^{-2}) where the input of pseudofaeces probably is a very important food source for the deposit feeders, but in groups 2 and 3 their biomass was at least similar to the values found in the Westerschelde (13, 17, 20, 7 and 12 g AFDW· m^{-2} in TWINSPAN-groups 2-6, respectively). This is despite the much lower values of suspended matter or detritus in the Oosterschelde. The absence of filter feeders in the brackish part of the Westerschelde, and hence the predominance of deposit feeders warrants further consideration. A poor food supply for filter feeders should explain their absence. Indeed, primary production is lower in the Westerschelde (100 g C· m^{-2} in the brackish part and 200 g C· m^{-2}· y^{-1} in the marine part) compared to the Oosterschelde (300 g C· m^{-2}· y^{-1}, unpubl. results Rijkswaterstaat). The differences in primary production are however much smaller than the differences in the biomass of filter feeders (255, 31 and 25 g AFDW· m^{-2} in TWINSPAN-groups 1-3 compared with 11, 0.5 and 0.75 g AFDW in TWINSPAN-groups 4-6, respectively). Therefore it is likely that several other factors, such as turbidity, salinity, exposure time, pollution, oxygen saturation, sediment dynamics etc., contribute to the difference in trophic structure. Analysis of the distribution of individual bivalve species, such as *Mya arenaria*, suggests that the master-factor causing the absence of this and other filter feeders from the Westerschelde, is its highly dynamic nature, corresponding to the 'Umlagerung' (mobility of the sediment) as described by Jepsen (1965).

The differences in basal food sources (detritus versus phytoplankton) between the brackish and marine part of the Westerschelde and the Oosterschelde have certainly an impact on the composition of the macrobenthic populations. However,

it also seems probable that hydrodynamic factors to a large extent determine the benthos. The dynamic nature of the Westerschelde is presently influenced by dredging. About 15 million cubic metres are removed yearly from the channels, of which a large part is dumped again in the river in the flood channels (Belmans 1988). The deepening of the channels causes a greater volume of water entering the estuary and hence an increase of current velocities. This has also caused an increase in tidal amplitude during the last decades (Doekes 1986). These processes may strongly influence macrobenthic populations in the Westerschelde in future years.

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Résumé

Le Westerschelde et l'Oosterschelde seuls subsistent en tant qu'estuaires dans la région du Delta au Sud-Ouest des Pays-Bas. Dans le Westerschelde, on trouve toujours le gradient estuarien normal, d'une eau dessalée jusqu'à l'eau marine soumise aux marées. Dans l'Oosterschelde, des aménagements importants ont transformé profondément les caractéristiques de la zone. Le gradient de salinité a disparu et la turbidité et la pollution ont diminué.

La macrofaune intertidale des deux estuaires a été étudiée de façon intensive en 1987. La composition spécifique en est comparable. Cependant, un plus grand nombre d'espèces est trouvé dans d'Oosterschelde à cause, essentiellement, de la présence de bancs de moules. La densité moyenne est plus forte dans le Westerschelde mais la biomasse est bien plus importante dans l'Oosterschelde.

L'analyse multivariée (TWINSPAN, DECORANA) a permis de mettre en évidence des similarités entre stations et il n'y a pratiquement pas de chevauchement entre stations de l'Oosterschelde et du Westerschelde. Les paramètres de l'eau (salinité, turbidité etc.) sont corrélés avec le premier axe de l'ordination alors que ceux concernant le sédiment (médiane, teneur en fines) sont corrélés avec le second. Les données montrent un gradient bien marqué depuis un peuplement à dominance d'organismes filtreurs jusqu'aux déposivores entre le Westerschelde et l'Oosterschelde et à l'intérieur même du Westerschelde. Ces peuplements correspondent à des chaînes alimentaires côtières et dépendent des détritus. On conclut que l'absence de filtreurs dans les eaux dessalées du Westerschelde est dûe aux caractéristiques hydrodynamiques de l'estuaire plutôt qu'à un manque de nourriture dû à la pollution. La faune pourrait souffrir d'un accroissement des activités de dragage.