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THE BENTHIC MACROFAUNA ALONG THE ESTUARINE GRADIENT OF THE SCHELDE ESTUARY

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KEY WORDS: intertidal macrofauna; estuarine gradient; freshwater tidal area; Schelde estuary

ABSTRACT

The intertidal benthic macrofauna of the Schelde estuary (The Netherlands and Belgium) was sampled in late autumn of 1990 at 50 stations along the whole salinity gradient (between Vlissingen and Dendermonde), including the freshwater tidal part. All stations were situated in sheltered areas with a relatively muddy sediment.

Species richness, diversity and total biomass of the benthic macrofauna decreased along the salinity gradient from Vlissingen to Dendermonde, while total density showed no clear trend. Especially the oligohaline and freshwater tidal part of the Schelde estuary was characterized by a very impoverished benthic community, composed only of Oligochaeta. No other species (freshwater, marine or brackish) was observed in this part of the estuary. The marine part had a more diverse macrozoobenthos structure than that of the brackish part. Species found only in the marine zone are *Cerastoderma edule*, *Tharyx marioni*, *Eteone longa*, *Nephtys hombergii* and *Capitella capitata*. In the brackish part of the estuary, *Corophium volutator* was a typical, dominant species. However, a lot of the dominant species were common in both the marine and brackish part of the Schelde estuary (*e.g. Heteromastus filiformis*, *Pygospio elegans*, *Nereis diversicolor*, *Macoma balthica*).

The observed gradient in species composition and dominance is compared with some other European estuaries. The marine and brackish part of the Schelde estuary is quite similar to other european estuaries. The freshwater tidal part, however, was more impoverished.

INTRODUCTION

Estuaries and the nearby coastal zones are characterized by steep gradients in chemical, physical and biological features. However, many studies have been restricted to small parts of these gradients and are mainly focussed on the marine or brackish part of the estuary. In most ecological studies on estuarine ecosystems, research on the tidal freshwater environments, which are essential parts of an estuary, has been neglected. ODUM (1988) attributed this phenomenon to the fact that limnologists ignored tidal freshwater environments because of the presence of oceanic tidal influence, and marine ecologists neglected these areas because they contain freshwater and are inhabited primarily by freshwater organisms.

This study deals with the occurrence of macrozoobenthos along the whole estuarine gradient in the Schelde estuary, including the freshwater tidal part. The tidal part of the river Schelde represents one of the few remaining European estuaries that are characterized by a natural salinity gradient from salt water, over brackish water to freshwater. As such, the Schelde estuary has an unique ecological value. Unfortunately, this estuary is also one of the most polluted estuaries, due to large industrial, agricultural and domestic waste effluents (WOLLAST, 1988; LUDIKHUIZE, 1989; HUPKES, 1990; VAN ECK *et al.*, 1991). Also extensive dredging activities and

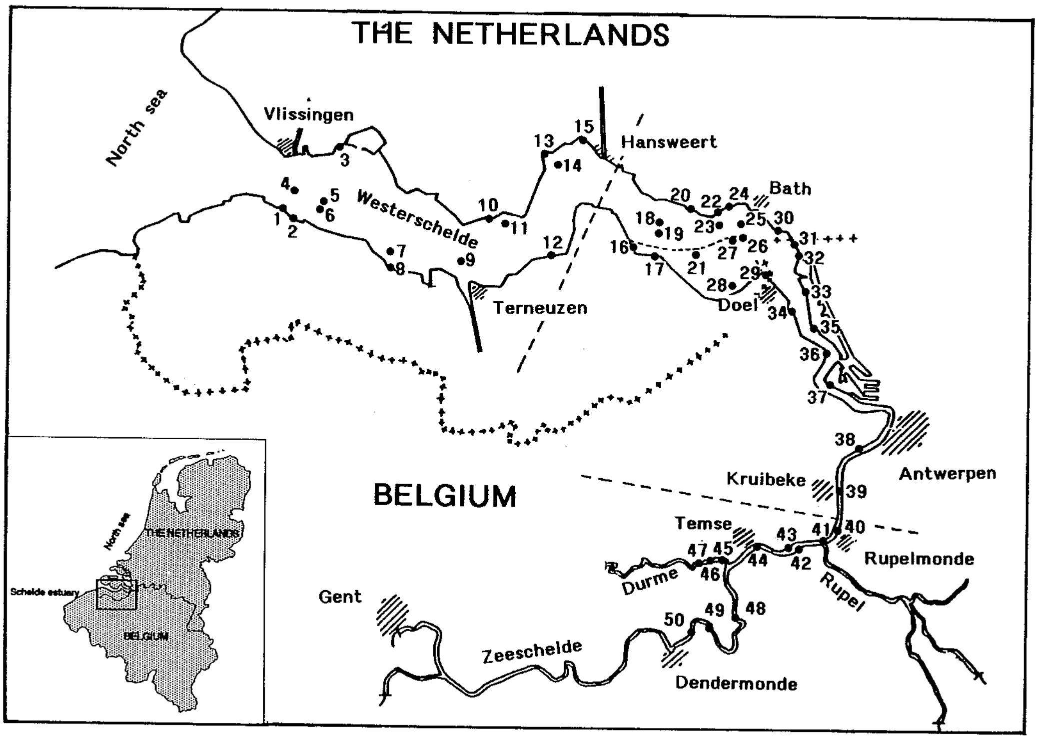


Fig. 1. The Schelde estuary with the locations of the sampling stations (1-50).

expanding harbour activities have a large morphological impact on the Schelde ecosystem (CLAESSENS *et al.*, 1991; PIETERS *et al.*, 1991).

Freshwater and marine benthic macrofauna have been identified as a suitable ecological group for monitoring and detecting the effects of stress and pollution (PEARSON and ROSENBERG, 1978; BAYNE *et al.*, 1988; GRAY, 1989) and community structure of estuarine macrobenthos has been used as an indication of water and sediment quality (WARWICK, 1986; WARWICK *et al.*, 1987; AUSTEN *et al.*, 1989; HARREL and HALL, 1991). A survey of the benthic community along the Schelde estuary may therefore not only give valuable information on the ecological diversity along the whole estuarine gradient, but also on the present pollution status of the estuary. The objectives of this study were to characterize the intertidal benthic communities along the whole estuarine gradient of the Schelde estuary.

MATERIALS AND METHODS

Study area

The river Schelde has its source in Saint-Quentin (France) and it flows into the North Sea after 350 km. The influence of the tide is perceptible up to Gent (Belgium), where it is stemmed by a weir. The total length of the Schelde estuary between Gent and Vlissingen is 160 km (Fig. 1). The width is about 50 m at Dendermonde, 250 m at Temse, 500 m at Antwerpen and 4.5 km at Vlissingen. The maximal width is 7.8 km. The mean tidal range increases from 3.8 m at Vlissingen, 4.5 m at Hansweert and 4.9 m at Antwerpen, to a maximum of 5.2 m at Kruibeke; it diminishes more upstream to about 2 m near Gent.

Upstream the Dutch/Belgian border, the upper estuary (called Zeeschelde) is characterized by a more or less single tideway. Brackish water and freshwater tidal marshes and mudflats are situated along the dikes. However, the width of the intertidal area is generally less than a few tens of meters. Only at a few locations there are larger mudflats and marshes. Downstream the Dutch/Belgian border, the more or less single tideway changes into a wide bed, characterized by large intertidal sand flats with meandering channels and gullies, the so-called Westerschelde (Fig. 1). Brackish water and saltwater marshes and mudflats are situated at the

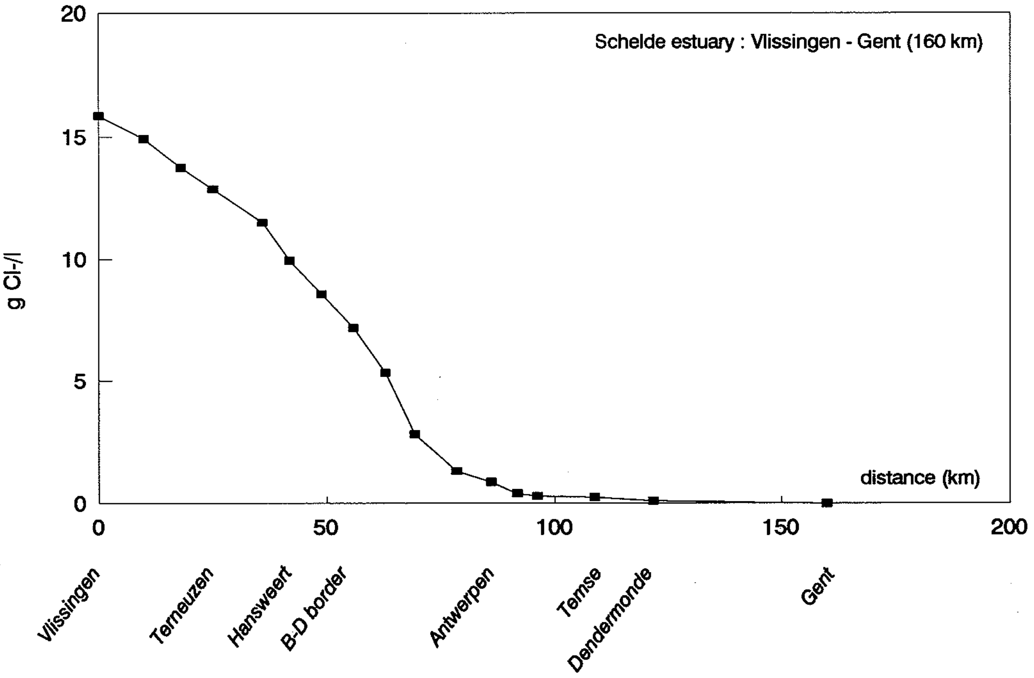


Fig. 2. Mean annual chlorinity gradient in the Schelde estuary.

outer edges, often several hundreds of meters wide.

The sediment of the Schelde estuary ranges from sandy to clayish, depending on hydrodynamic forces and sediment discharges (OENEMA *et al.*, 1988). In the channels and gullies as well as on the sand flats, the sediment is mainly sandy. In the more sheltered areas the sediment is muddy. Sandy sediment is found far upstream in the estuary. Mud characterizes the sediment of the freshwater intertidal area.

The freshwater input of the Schelde amounts on average 100 m^3 s^{-1}. Seasonal fluctuations in drainage range from high values during winter (average 180 m^3 s^{-1}, maximum 500-600 m^3 s^{-1}) to low values during summer (average 50 m^3 s^{-1}, minimum 10 m^3 s^{-1} or less). Quantitatively, the river discharge of $5*10^6$ m^3 per tide is negligible compared to the mean tidal flood volume of $1100*10^6$ m^3 per tide near Vlissingen. This results in a very well mixed estuary with a relatively large transition zone from salt to freshwater, as reflected in the chlorinity gradient (Fig. 2). The chlorinity decreases from *c.* 16.6 g Cl^- l^{-1} near Vlissingen to *c.* 4.5 g Cl^- l^{-1} at the Belgian-Dutch border; near the tributary Rupel the water becomes fresh (< 0.3 g Cl^- l^{-1}). Generally spoken, the whole estuary can be divided into three main zones: a marine (polyhaline) zone between Vlissingen and Hansweert, a brackish (mesohaline and oligohaline) zone between Hansweert and the tributary Rupel, and a freshwater zone (limnetic zone) more upstream. Seasonal and annual fluctuations in chlorinity may be large, especially in the brackish zone (variations up to 10 g Cl^- l^{-1} occur on a single location). The water column is well-mixed because of the tidal movement; the vertical chlorinity gradient is less than 0.2 %.

The Schelde estuary is heavily contaminated with heavy metals and organic micropollutants and experiences a huge organic matter input. The concentrations of PCBs, PAHs and cadmium are high in the freshwater and brackish part of the estuary. Most of the pollutants behave conservatively and concentrations generally decrease when salinity increases, as a result of the mixing of riverine and marine particulates (VAN ZOEST and VAN ECK, 1990; VAN ECK *et al.*, 1991). The large organic matter load causes oxygen depletion in the Schelde river and in the upper estuary. The upper estuary is often anoxic, especially in the summer period (ANONYMOUS, 1990; VAN ECK *et al.*, 1991). These (near-)anoxic conditions may prevail as far as the Dutch-Belgian border. Table 1 gives some physical and chemical characteristics of the water column along the whole estuarine gradient.

Table 1. Physical characteristics and water quality parameters (annual average of 1990 with standard errors) along the whole estuarine gradient at Vlissingen (1), Terneuzen (2), Hansweert (3), Dutch-Belgian border (4), Kruibeke (5), Temse (6), Dendermonde (7) and Melle (8). Data from 'Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterzuivering' (station 1 – 4: *c.* 12 observations per year), and 'Ministerie van Volksgezondheid en Leefmilieu, Instituut voor Hygiëne en Epidemiologie' (station 5 – 8: *c.* 5 observ. per year)

Location	1	2	3	4
Distance (km)	160	137	124	111
Tidal range (m)	3.8	4.2	4.5	4.9
Width (m)	5000	5500	4300	2500
Chlorinity (g Cl^{-} $^{-1}$)	17.8 ± 0.1	14.9 ± 0.3	11.3 ± 0.4	6.0 ± 0.5
O_2 Water (mg^{-1})	8.9 ± 0.3	8.5 ± 0.3	8.1 ± 0.3	3.9 ± 0.5
BOD_5 Water (mg^{-1})	0.7 ± 0.2	0.9 ± 0.3	0.6 ± 0.2	2.6 ± 0.3
$NH4^+$ (mg N^{-1})	0.09 ± 0.01	0.14 ± 0.02	0.14 ± 0.05	0.83 ± 0.20
$NO2^-$ (mg N^{-1})	0.03 ± 0.01	0.05 ± 0.01	0.07 ± 0.01	0.15 ± 0.02
$NO3^-$ (mg N^{-1})	0.88 ± 0.15	1.58 ± 0.21	2.89 ± 0.31	4.56 ± 0.35
o-PO4 (mg P^{-1})	0.11 ± 0.02	0.19 ± 0.01	0.26 ± 0.01	0.35 ± 0.02
Location	5	6	7	8
Distance (km)	78	63	40	6
Tidal range (m)	5.2	5.1	3.7	2.0
Width (m)	350	250	100	50
Chlorinity (g Cl^{-} $^{-1}$)	0.8 ± 0.4	0.4 ± 0.2	0.2 ± 0.1	0.1 ± 0.01
O_2 Water (mg^{-1})	1.2 ± 0.7	1.3 ± 0.8	1.3 ± 1.1	1.4 ± 0.7
BOD_5 Water (mg^{-1})	3.7 ± 0.5	6.8 ± 1.5	8.0 ± 1.8	6.4 ± 0.6
$NH4^+$ (mg N^{-1})	5.97 ± 1.66	7.66 ± 2.13	9.84 ± 2.99	11.3 ± 3.56
$NO2^-$ (mg N^{-1})	0.1 ± 0.05	0.1 ± 0.06	0.14 ± 0.10	0.21 ± 0.13
$NO3^-$ (mg N^{-1})	1.70 ± 1.05	1.34 ± 1.08	3.51 ± 1.42	2.23 ± 1.26
o-PO4 (mg P^{-1})	0.85 ± 0.16	1.23 ± 0.35	1.54 ± 0.37	1.95 ± 0.49

Sampling and laboratory analysis

The macrozoobenthos was sampled in the autumn of 1990 (September/October) at 50 sampling stations situated between Vlissingen and Dendermonde (Fig. 1). All stations were situated in the intertidal zone, especially in sedimentation areas, at approx. 1.5 m above mean low water. On each station 15 small cores (diameter 4.5 cm) were taken to a mean depth of 25 cm and 5 large cores (diameter 15 cm) to a mean depth of 40 cm. The large cores were sieved in the field through a 3 mm mesh. All benthic samples were preserved in 4% neutralized formalin. Samples for sediment analysis were taken using a PVC core of 6.7 cm diameter to a depth of 10 cm. 6-8 cores taken per station, were mixed and preserved in a refrigerator at 4°C.

In the laboratory the samples of the small cores were sieved through a 1 mm mesh and sorted after staining with 0.02% Rose Bengal. The organisms were identified to species level, except in the genera *Spio* and *Polydora,* in *Nemertini* and in *Oligochaeta,* and counted. The large cores were only used for estimation of density and biomass of large and deep living species (*e.g. Arenicola marina, Mya arenaria*). The ash-free dry weight (AFDW) biomass was measured by drying all specimens at 105°C for 12 h and ashing at 550°C. Surface sediment characteristics (median particle size, mud content (fraction <63µm), organic matter and pH) at all stations were determined by standard methods.

Water quality characteristics were obtained from fixed locations near the sampling stations (data from 'Rijkswaterstaat' (Dutch part) and IHE (Belgian part) (see Table 1).

Data analysis

Data were first organized into a samples by species matrix. Species diversity was measured using the Shannon-Wiener function H' (PIELOU, 1966). All statistics were performed with the statistical package SYSTAT (WILKINSON, 1990). Abiotic and biotic characteristics along the longitudinal gradient were fitted with a smoothing line, using the option LOWESS of the SYSTAT package. It smoothes by running along the X values and finding predicted values from a weighted average of nearby Y values.

Sorenson's index (SORENSON, 1948) of similarity was calculated to compare overlap of species between each pair of subareas using the formula

$$S = \frac{2C}{A + B}$$

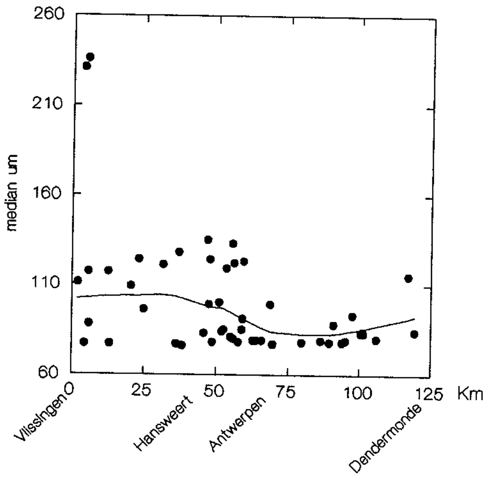


Fig. 3. Median particle size of sediment (μm) at the sampling stations.

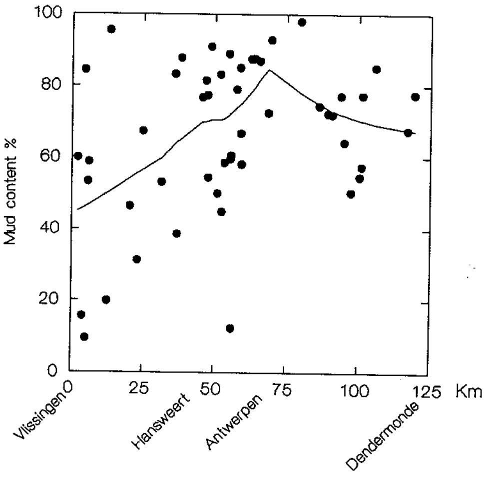


Fig. 4. Mud content (fraction < 65 μm) of sediment at the sampling stations.

where C is the number of species common to both subareas, and A and B are the number of species occurring in each subarea.

The between-subarea similarity matrix was then projected as a series of curves plotted for subareas ordered along an environmental (*i.e.* salinity) gradient, the so-called coenocline similarity projection (CSP, *see* BOESCH, 1977). The subareas were defined by the longitudinal salinity gradient and consists of 4 to 6 stations.

Numerical classification (TWINSPAN, *see* HILL, 1979), based on species abundance, was used to assess multispecies patterns. Only species which were observed in five or more stations were used for the analysis. Two stations (3 and 36) were not used in the analysis. All absolute abundances were transformed by $x = \log(x+1)$. Cut levels used in the TWINSPAN analysis were: 1.00, 2.00, 3.00, 4.00, 5.00, and 6.00.

RESULTS

Sediment characteristics

The dominant sediment type throughout the intertidal zone of the Schelde estuary, sampled in this study, was muddy sand (median grain size between 75-125 μm). The variation in median grain size of the stations was more pronounced in the marine part (Fig. 3). Two stations (3 and 4) in the mouth of the estuary had a much coarser sediment with a median grain size of approx. 235 μm. The mud content of the sediment was highly variable, especially in the marine part (Fig. 4). Highest values occurred in the brackish part and remained relatively high in the freshwater tidal part.

The organic matter content showed also large variation, but a clear increasing trend towards the freshwater tidal part was observed (Fig. 5). It is stressed again that especially sedimentation areas were chosen for this study (see Material and Methods).

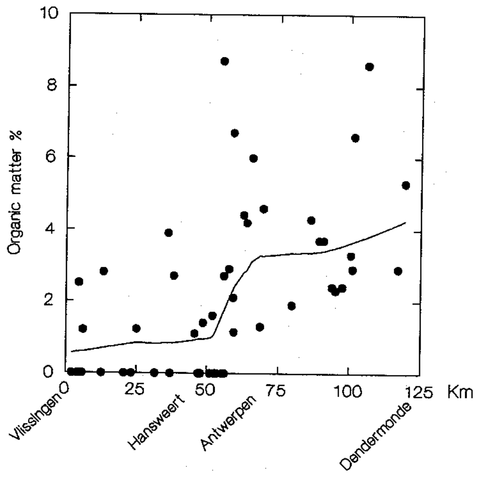


Fig. 5. Organic matter content (%) of sediment at the sampling stations.

Table 2. List of observed macrobenthic species and their frequency of occurrence (%) in the sampling locations. Trophic position: DF = Deposit Feeders; FF = Filter feeders; O = Omnivors; P = predators

Species name	Code	Occurrence
Annelida		
Anaitides mucosa (P)	ANAI MUCO	2
Arenicola marina (DF)	AREN MARI	14
Capitella capitata (DF)	CAPI CAPI	20
Eteone longa (P)	ETEO LONG	38
Heteromastus filiformis (DF)	HETE FILI	58
Nephtys caeca (P/O)	NEPH CAEC	2
Nephtys hombergii (P/O)	NEPH HOMB	22
Nereis diversicolor (O)	NERE DIVE	62
Nereis succinea (O)	NERE SUCC	10
Oligochaeta (DF)	OLIG	84
Polydora spec. (DF)	POLY SPEC	32
Pygospio elegans (DF)	PYGO ELEG	58
Scolelepis squamata (U)	SCOL SQUA	2
Scoloplos armiger (DF)	SCOL ARMI	6
Spio spec. (DF)	SPIO SPEC	18
Tharyx marioni (DF)	THAR MARI	24
Mollusca		
Cerastoderma edule (FF)	CERA EDUL	34
Ensis minor (FF)	ENSI MINO	12
Hydrobia ulvae (DF)	HYDR ULVA	26
Macoma balthica (DF)	MACO BALT	62
Mya arenaria (FF)	MYA AREN	12
Mysella bidentata (FF)	MYSE BIDE	6
Mytilus edulis (FF)	MYTI EDUL	2
Retusa obtusa (P)	RETU OBTU	2
Scrobicularia plana (DF)	SCRO PLAN	32
Tellina fabula (DF)	TELL FABU	4
Arthropoda		
Bathyporeia pilosa (DF)	BATH PILO	10
Carcinus maenas (O)	CARC MAEN	4
Corophium arenarium (DF)	CORO AREN	10
Corophium volutator (DF)	CORO VOLU	30
Crangon crangon (P)	CRAN CRAN	18
Cyathura carinatha (U)	CYAT CARI	10
Gastrosaccus spinifer P)	GAST SPIN	2
Sphaeroma rugicauda (DF)	SPHA RUGI	2
Nemertini		
Nemertini spec. (P)	NEME SPEC	6

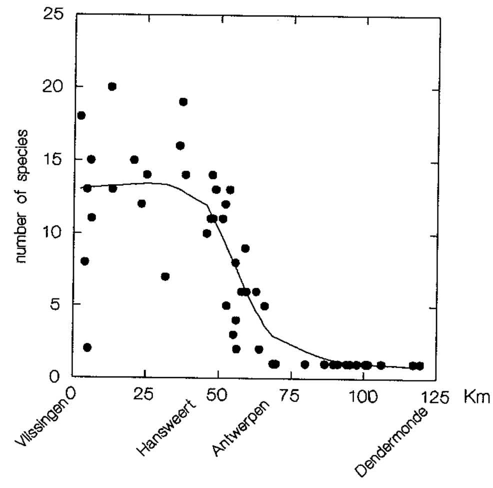


Fig. 6. Number of species per sampling station.

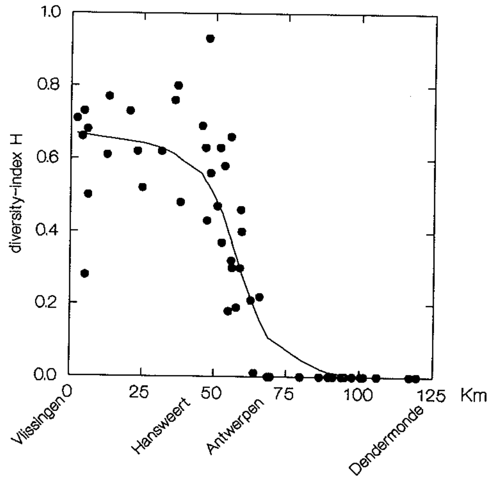


Fig. 7. Species diversity (Shannon-Wiener function H') per sampling station.

Benthic fauna

Diversity

Of the 35 species observed, almost 50% were annelids, 28% molluscs and 23% arthropods (Table 2). Taking the throphic structure into account, 23% of the observed number of species were predators, 14% filter feeders, and 6% omnivores; the remaining and dominant part (57%) were deposit feeders. Oligochaeta were present at almost every station. The annelids *Nereis diversicolor*, *Heteromastus filiformis* and *Pygospio elegans* and the mollusc *Macoma balthica* were also very common (>50%). Seven species are observed only once.

The number of species and the diversity H' showed a significant positive correlation with chlorinity and oxygen content, and a significant negative correlation with BOD. To a less extent the number of species also showed a correlation with organic matter (Table 3). The number of species at each station along the longitudinal gradient between Vlissingen and Dendermonde is shown in Fig. 6.

Table 3. Correlation coefficients (Spearman's rank) between some environmental variables and biotic characteristics (N= 50). * = p < 0.01; ** = p < 0.005; NS = not significant

Environmental variable	Species		Density		Biomass		H'	
Water chlorinity	.85	**	.19	NS	.58	**	.66	**
Water oxygen content	.86	**	.21	NS	.61	**	.69	**
Water BOD	-.86	**	-.18	NS	-.60	**	-.62	**
Median grain size	.25	NS	-.18	NS	-.08	NS	.22	NS
Organic matter	-.54	**	.01	NS	-.21	NS	-.43	*
Fraction <63 μm	-.14	NS	.01	NS	.04	NS	-.18	NS

The mean number of species per sampling station remained relatively constant up to Hansweert, but clearly declined in the brackish zone. Upstream of Antwerpen, only *Oligochaeta* occurred. The same pattern was shown by the diversity index H' (Fig. 7). At one station (36) no benthic invertebrates were observed.

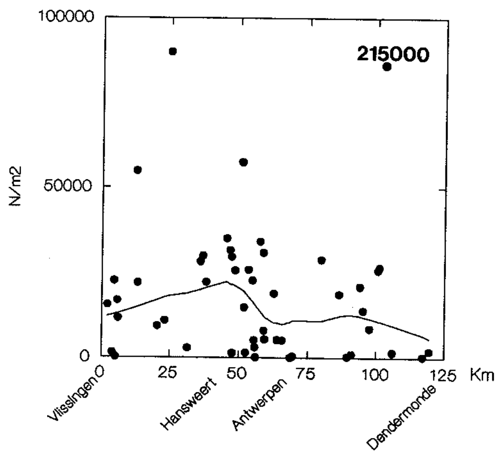


Fig. 8. Mean total population density (Nm^{-2}) per sampling station.

Population density

The mean total population density (± SE) of all sampling stations was 21000 ± 4600 ind m^{-2}, ranging from 0 ind m^{-2} (station 36) to a maximum density of $2.16*10^5$ ind m^{-2} (station 47). Six stations had densities less than 1000 ind m^{-2}. Densities were mainly determined by annelids (84% of the total density), especially Oligochaeta (56% of the annelids), *Pygospio elegans* (22%) and *Heteromastus filiformis* (12%). To a less extent arthropods, notably *Corophium volutator* (90% of the arthropods) and molluscs, notably *Cerastoderma edule* (48% of the molluscs), *Hydrobia ulvae* (21%) and *Macoma balthica* (16%) also contributed to the total densities. Deposit feeders were dominant in all sampling stations and represented 95% of the total density.

The total density along the longitudinal gradient between Vlissingen and Dendermonde is summarized in Fig. 8. A large variation was observed with no clear trend along the estuarine gradient; high and low density values were randomly dis-

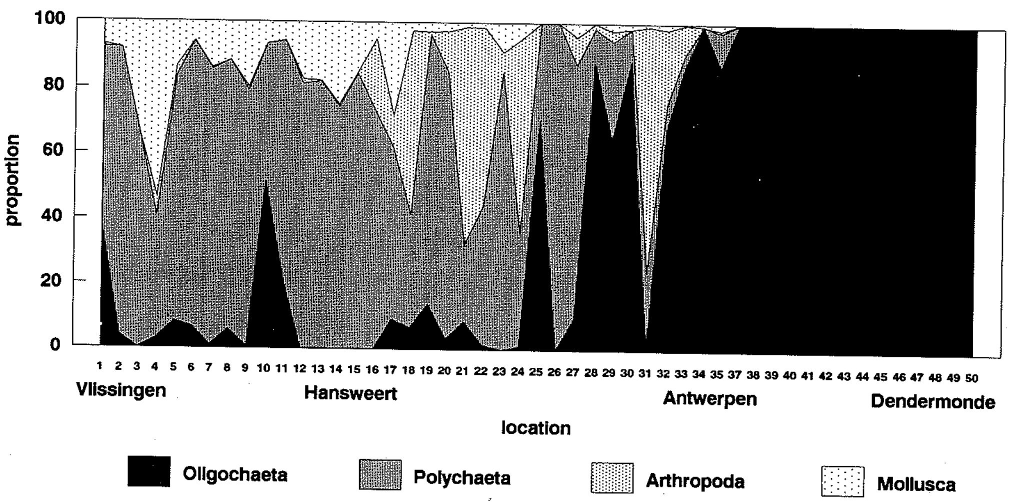


Fig. 9. Contribution (%) of the different taxa to the total density at each sampling station.

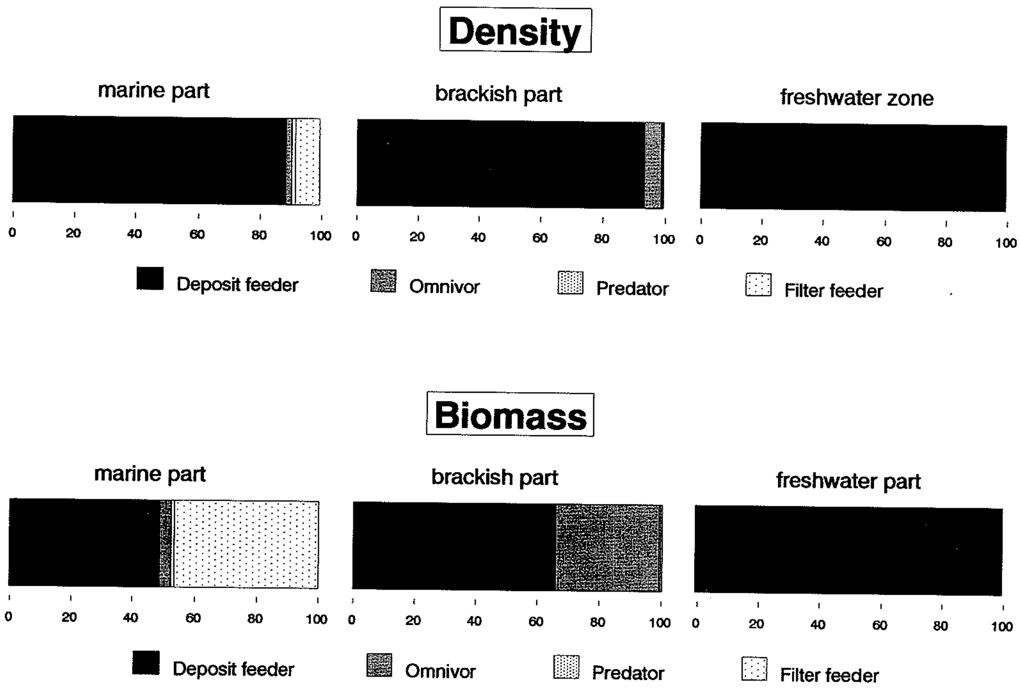


Fig. 10. Contribution (%) of the different trophic groups to total population density and biomass in the marine, brackish and freshwater part of the Schelde estuary.

tributed. Density did not significantly correlate with the measured abiotic characteristics (Table 3). At station 47 a very high density of Oligochaeta was found ($2.16*10^5$ ind m^{-2}). However, the relative contribution to the density of the different taxa changed markedly from the marine zone, over the brackish zone to the oligohaline-freshwater zone (Fig. 9). Between Vlissingen and Hansweert, *i.e.* in the marine zone, the macrobenthic densities were mainly determined by dense populations of Polychaeta and to less extent by Mollusca. Between Hansweert and Antwerpen (brackish zone) both Polychaeta and Arthropoda contributed to the macrobenthic densities; at some sampling stations Oligochaeta tended to predominate. Upstream of Antwerpen (oligohaline-freshwater zone) only Oligochaeta were present. Deposit feeders contributed mostly to the density in all three zones along the gradient, although the filter feeder *Cerastoderma edule* in the marine zone and the omnivore *Nereis diversicolor* in the brackish zone were also relatively important (Fig.10).

Biomass

The mean total biomass (± SE) of all sampling stations was 21 ± 4.5 g AFDW m^{-2}, ranging between 0.0031 and 153.1 g AFDW m^{-2}. Contrary to the population density, biomass was not only determined by annelids (54% of the total biomass), but also by molluscs (44%), due to their high individual biomass. Dominant annelids were *Heteromastus filiformis* (52% of the annelids), *Oligochaeta* (18%) and *Nereis diversicolor* (18%), whereas *Cerastoderma edule* was the dominant mollusc (75% of the molluscs). The latter contributed by far the most to the mean total biomass of the whole study area. The dominant arthropod is *Corophium volutator* (73% of the arthropods).

The total biomass along the longitudinal gradient between Vlissingen and Dendermonde is summarized in Fig. 11. On the average, there was a gradient from high biomass in the marine and brackish zone to low biomass in the oligohaline-freshwater zone, with a sharp decline at the Dutch-Belgian border. Biomass was significantly correlated with all water quality characteristics. No correlations were found with the sediment characteristics. Only at station 47 a relatively high biomass was found (*c.* 50 g AFDW m^{-2}), due to the very high density of Oligochaeta. As with the density, the relative contribution to the biomass of the different taxa changed markedly from the

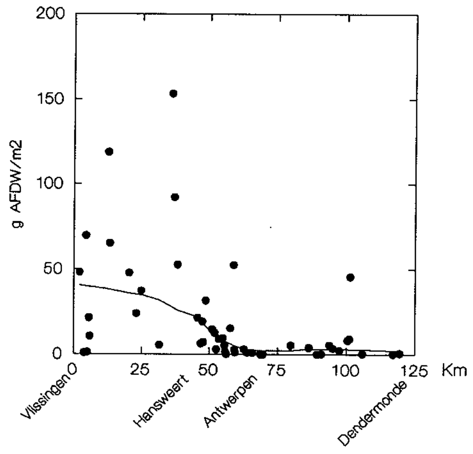


Fig. 11. Mean total biomass (g AFDW/m²) per sampling station.

marine zone, over the brackish zone to the oligohaline-freshwater zone (Fig. 12). Between Vlissingen and Hansweert (marine zone) Mollusca and Polychaeta contributed mostly to the biomass. Between Hansweert and Antwerpen (brackish zone) Polychaeta tended to predominate; Oligochaeta already dominated at some sampling stations (Fig. 12). Upstream of Antwerpen, Oligochaeta were dominated. Contrary to the density, there was a clear gradient in the trophic position of the organisms contributing most to the biomass (Fig. 10). Filter feeders, notably *Cerastoderma edule*, and deposit feeders dominated in the marine zone. The brackish zone was dominated by omnivores, especially *Nereis diversicolor,* and deposit feeders, whereas in the freshwater part only deposit feeders occurred.

Change along the estuarine gradient

The coenocline similarity projections show a more or less gradual and continual change in assemblage along the estuarine gradient (Fig. 13). The rate of change in the benthic coenocline of the Schelde estuary was by far the greatest between subarea 7 and 8. Between other subareas, this change was much less pronounced. From this figure it is clear that especially towards the oligohaline zone, the benthic community abruptly changed.

Community structure

Cluster analysis of all stations produced three station groups (Fig. 14). The first group (group 3) includes the stations 37-50, together with stations 28 and 34, and represents the whole freshwater tidal part and the most upstream situated brackish part (oligohaline zone). This community was characterized by a very impoverished benthic fauna with only one taxon dominating, namely Oligochaeta. Oligochaeta were very abundant, resulting in a mean density which was comparable to that of the other two groups, but with a significantly lower mean biomass. In a further division, the remaining stations were separated into group 1, with the marine stations 1-17 and 19, and group 2 with the brackish water stations 18, 20-27, 29-33 and 35.

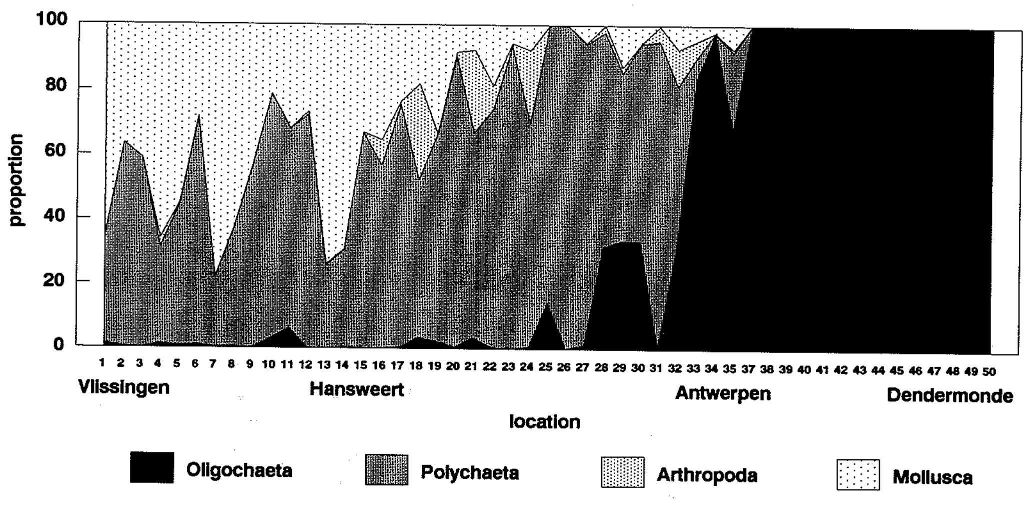


Fig. 12. Contribution (%) of the different taxa to the total biomass at each sampling station.

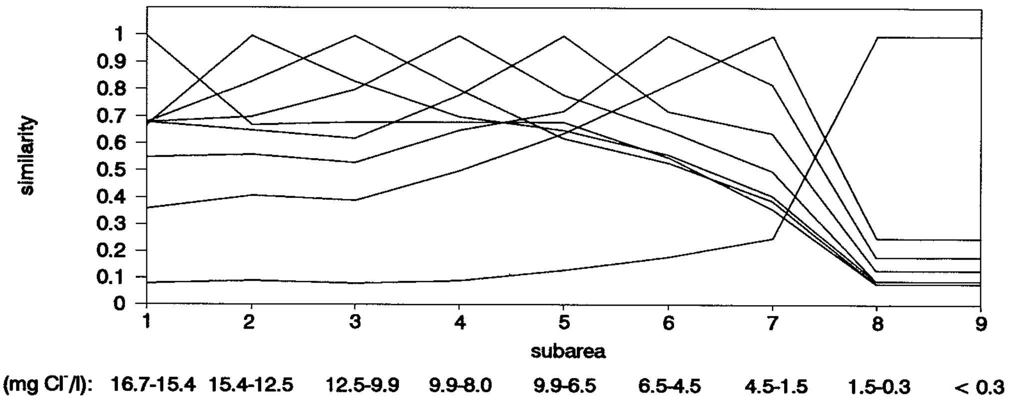
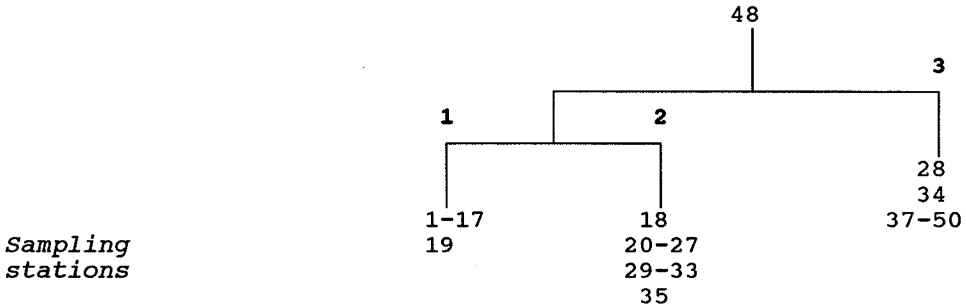


Fig. 13. Coenocline similarity projections of qualitative similarity (Sorensen's index) along the estuarine gradient. Nine subareas of 4 to 6 sampling stations each are distinguished. Chlorinity range of sub areas is indicated.



Number of taxa	33	22	3
Mean total density N/m2	22384 ± 5801	18527 ± 4002	23093 ± 1235
min./max.	126 - 89883	93 - 57343	31 - 216387
Mean total biomass g AFDW/m2	45.4 ± 19.2	11.1 ± 3.5	5.5 ± 2.6
min./max.	0.8 - 153.1	0.1 - 52.4	0 - 45.5

Fig. 14. Characterization of the different station groups, distinguished by a TWINSPAN analysis.

The total number of observed species as well as the mean number of species per sampling station was clearly higher in group 1 as compared to group 2. The mean biomass was significantly higher in group 1 as compared to group 2.

Group 1 (the marine group) consisted of sampling stations with a relatively species rich benthic fauna. Molluscs as well as the dominance of the filter feeders characterized this community (see above). Characteristic species of this group were *C. edule*, *Tharyx marioni*, *Eteone longa*, *Nephtys hombergii* and *Capitella capitata* (Fig. 15). *Cerastoderma edule* was very common with a mean density of $1.34 \pm 0.39*10^3$ ind m^{-2} (max: $5.2*10^3$ ind m^{-2}). *C. edule* contributed most to the total biomass of the marine part with a mean biomass of 20.3 ± 7.3 g AFDW m^{-2} (max: 96 g AFDW m^{-2}). *C. edule* penetrated the estuary up to the brackish part, but here only young brood occurred. *Tharyx marioni* was also a very common species of the marine part and did not occur upstream from Hansweert. The mean density in the marine zone was $1.37 \pm 0.57*10^3$ ind

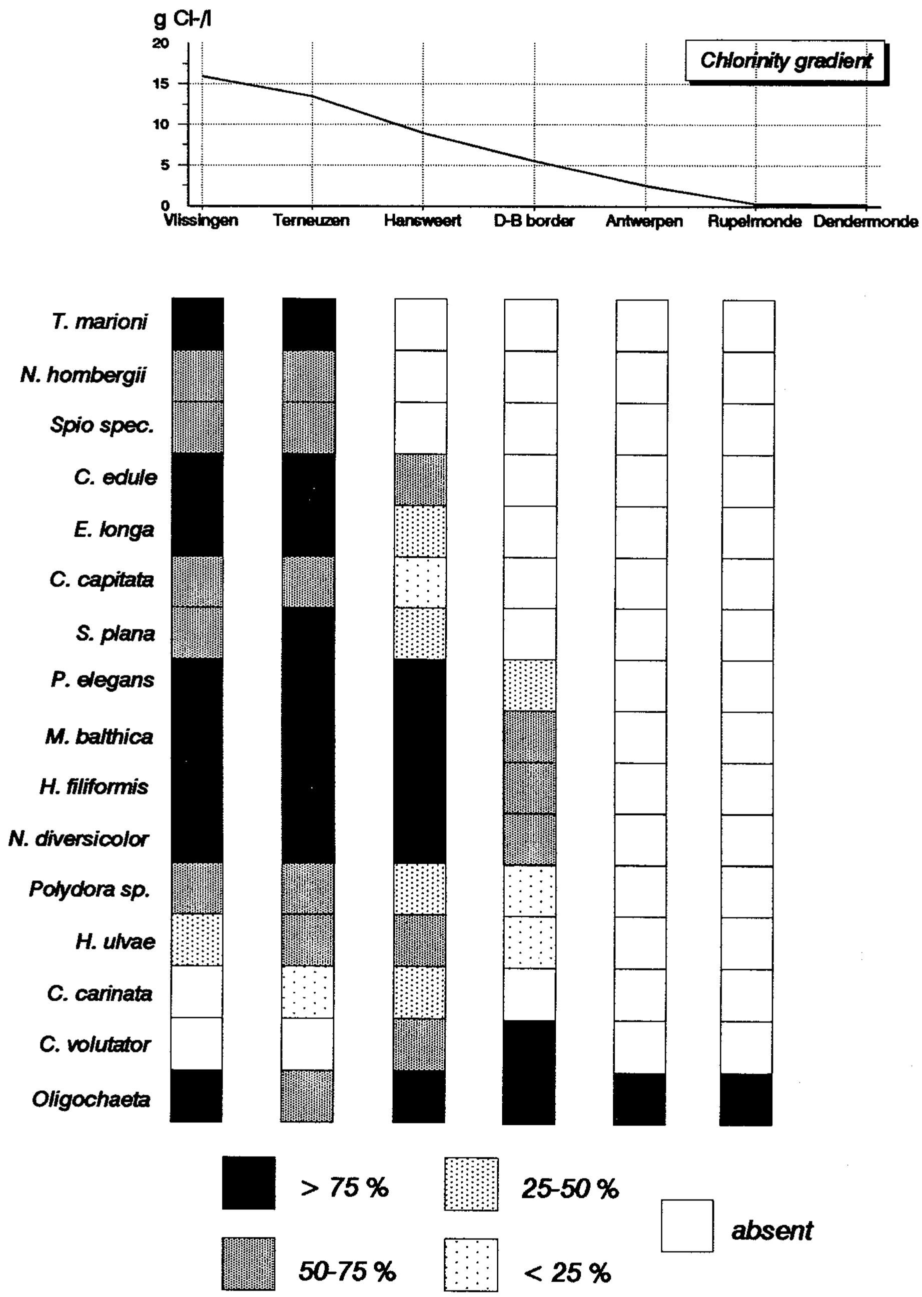


Fig. 15. Distribution and average constancy of the most dominant species in six subareas along the salinity gradient.

m^{-2} (max: $8.0 \cdot 10^3$ ind m^{-2}). *Eteone longa* was another very common species, but also penetrated into the brackish part. The densities were always lower than 300 ind m^{-2}. *Capitella capitata* was a common species in the marine part. In the brackish part this species was only observed twice. The densities did not exceed more than 550 ind m^{-2} and biomass was low. *Nephtys hombergii* was typical for the marine part but the observed densities were low, not exceeding 250 ind m^{-2}.

Group 2 (brackish group) sampling stations had a less species-rich benthic fauna with a typical dominance of *Corophium volutator*. It is the only important species which was found in the brackish part of the estuary, and not in the marine part (Fig. 15). *C. volutator* contributed substantially to the total density having a mean density of 7.0 ± 2.9*10^3 ind m^{-2} (max: 40*10^3 ind m^{-2}). The biomass on some stations was relatively high, with a maximum of 3.7 g AFDW m^{-2}.

Several species are common to both group 1 and group 2, and were very abundant, notably *Heteromastus filiformis*, *Nereis diversicolor*, *Pygospio elegans* and *Macoma balthica* (Fig. 15). *Heteromastus filiformis* was one of the most common species in this study, penetrating the estuary up to Antwerpen. Mean (*c.* 4.0*10^3 ind m^{-2}) and maximum (*c.* 15.5*10^3 ind m^{-2}) densities in the marine and brackish zone were comparable.

H. filiformis contributed considerably to the total biomass. On some locations the biomass was >30 g AFDW m^{-2}. *N. diversicolor* was the most important omnivore in the Schelde estuary, and was found up to Antwerpen. Especially in the brackish zone, high densities (mean 1096 ± 455 ind m^{-2}; max: 7.0*10^3 ind m^{-2}) are reached. In this zone, the contribution of *N. diversicolor* to the total biomass was quite important, with a maximum biomass of 50 g AFDW m^{-2}. In the marine zone, densities were much lower (mean: 482 ± 126 ind m^{-2}; max: 1718 ind m^{-2}).

Pygospio elegans was a very common species of both the marine and the brackish zone, penetrating the estuary up to Antwerpen. It contributed substantially to the total density with a mean density in the marine zone of 9.5 ± 3.7 *10^3 ind m^{-2} (max: 56.6*10^3 ind m^{-2}) and in the brackish zone of 2.2 ± 0.9*10^3 ind m^{-2} (max: 21.5*10^3 ind m^{-2}). The maximum biomass was 5 g AFDW m^{-2}, but on most stations the biomass did not exceed 1 g AFDW m^{-2}.

Macoma balthica was the most common mollusc in the Schelde estuary. This species occurred upstream to Antwerpen. The mean density amounts 285 ± 61 ind m^{-2} (max: 1048 ind m^{-2}) in the marine zone and 199 ± 45 ind m^{-2} (max: 545 ind m^{-2}) in the brackish zone. *M. balthica* contributed substantially to the total biomass and the maximum biomass was 11.2 g AFDW m^{-2}.

Some species like *Polydora* spec. and *Hydrobia ulvae* were also common in both the marine and brackish part, but are less abundant than the species mentioned above. *Polydora* spec. was a relatively common species, penetrating the estuary up to the Dutch-Belgian border. It was most abundant in the marine zone (mean 1.84 ± 0.75*10^3 ind m^{-2}; max: 9.2*10^3 ind m^{-2}). In the brackish zone, densities did not exceed 1000 ind m^{-2}. The observed biomass was very low. *H. ulvae* was a common species in the marine and brackish zone, although less common near the mouth of the estuary. Mean density was much higher in the marine zone (535 ± 221 ind m^{-2}; max: 3311 ind m^{-2}), as compared to the brackish zone (63 ± 32 ind m^{-2}; max.: 461 ind m^{-2}). The biomass was relatively low.

As illustrated already by the direct gradient analysis, it can be concluded from the cluster analysis that the stations are separated in groups closely linked with the salinity gradient of the Schelde estuary. However, since many dominant species (*Heteromastus filiformis*, *Pygospio elegans*, *Nereis diversicolor*, *Macoma balthica*) were common in both the marine and brackish part, the distinguished groups are likely to be variants of one community type, rather than that a clear distinction into two totally different benthic communities can be made.

The macrozoobenthos of the marine part had a more complex structure than that of the brackish part, which was a more impoverished form. However, due to the presence of the filter feeder *Cerastoderma edule* in the marine part, the trophic structure differed clearly between the marine and brackish part of the Schelde estuary.

DISCUSSION

This study is the first on the Schelde estuary investigating the macrozoobenthos along the whole estuarine gradient, including the freshwater tidal part. Previous studies on the macrozoobenthos of the Schelde estuary dealt only with the marine and brackish part of the estuary, but found the same gradient, as presented here (VERMEULEN and GOVAERE, 1983; MEIRE *et al.*, 1991; YSEBAERT and MEIRE, 1991). However, in these studies other benthic communities, besides the one described here, were distinguished. The difference is due to sampling exclusively in the intertidal zone in this study, particularly in the most sheltered areas of the estuary with relatively muddy sediment with a low dynamic nature. The sampling stations in VERMEULEN and GOVAERE (1983) and YSEBAERT and MEIRE (1991) covered a wide range of habitats, including the sublittoral zone. These studies clearly demonstrated the important role of sediment characteristics in determining the environmental conditions of the benthic habitat (see also GRAY, 1974; RHOADS, 1974). The community types described in this study are by far the most common in the intertidal zone of the Schelde estuary. Another important intertidal community, dominated by very mobile species like *Bathyporeia* spec., *Haustorius arenarius* and *Eurydice pulchra*, was observed on places with a highly dynamic nature, and therefore with a much coarser sediment ('megaripples', see YSEBAERT and MEIRE, 1991). This community was not observed in this study but is found on some parts of the sand banks and mudflats, mainly in the brackish part of the estuary.

Distribution of the intertidal macrozoobenthic species in the Schelde estuary seems to be mainly controlled by salinity. The observed species distribution follows the classical concepts of species response to salinity gradients (REMANE and SCHLIEPER, 1958; REMANE, 1971), except that the reduction of species was more acute and that a lag occurred in the increase in number of species from the oligohaline to the freshwater tidal zone of the Schelde estuary.

The observed gradient in species composition and dominance in the marine and brackish part of the Schelde estuary is comparable with other European estuaries like the Ems, Weser, Elbe, Loire and Forth (WOLFF, 1973; MICHAELIS, 1983; ROBINEAU and MARCHAND, 1984; ROBINEAU, 1987; McLUSKY, 1987). Many similarities, especially in the marine part, can be demonstrated, but on the other hand every estuary has its own physical and therefore ecological characteristics (see also MEIRE *et al.*, 1991; WARWICK *et al.*, 1991). For instance, how far a marine species is able to penetrate into an estuary largely depends on the amount and variability of the freshwater discharge, relative to the tidal inflow of sea water.

The macrozoobenthos of the oligohaline and freshwater tidal part of the Schelde estuary, characterized by the presence of only Oligochaeta, is at present quite different from some other European estuaries. However, as compared to the marine and brackish parts of estuaries, less data on the occurrence of benthic invertebrates in the freshwater tidal parts of estuaries is available. The oligohaline zone, which is both a physical and a biological buffer, is in estuaries like Weser, Elbe and Loire also characterized by the lowest species richness. Contrary to the Schelde estuary, however, in these estuaries also other species, both real freshwater species (*e.g.* insect larvae) and marine/brackish water species (*e.g. Corophium lacustre*), occur (MICHAELIS, 1983; ROBINEAU, 1987; HAESLOOP, 1990).

In the real freshwater tidal parts of the Ems, Weser and Elbe estuaries an increase in freshwater species richness has been found. Besides various Oligochaeta species, also molluscs (*e.g. Potamopyrgus jenkinsi*, *Pisidium* spp.), insect larvae (*e.g.* chironomids) and crustaceans (*e.g. Gammarus* spp.) are observed (DÖRJES and REINECK, 1981; RHODE, 1982; HAESLOOP, 1990). However, compared to the marine part of these estuaries, species richness is still very low. In the Weser estuary a special situation occurs since the freshwater tidal part is suffering from an anthropogenic increase in salinity, coming from industries more upstream. Therefore, no real distinction can be made between the brackish and freshwater part of the Weser estuary since also a lot of brackish water species are observed in the freshwater part, besides the normal fresh water species (HAESLOOP, 1990). However, the above mentioned studies did not find the same species richness as described for the former freshwater tidal area Biesbosch (WOLFF, 1973) and for the Elbe estuary (CASPERS, 1948). In the latter, CASPERS observed more than 30 species, of which 8 Oligochaeta (*e.g. Limnodrilus hoffmeisteri* and *Tubifex tubifex*), larvae of 10 chironomids, 8 molluscs (*e.g. Pisidium* and *Sphaerium*), 3 gastropods and 4 crustaceans (*e.g. Gammarus zaddachi* and *Neomysis integer*). This is however still much lower as compared to the marine part of estuaries. In the North-American estuaries the oligohaline and freshwater tidal parts are also characterized by a relatively low species richness, with Oligochaeta and chironomids, and to a less extent amphipods and molluscs, as the dominating species (SIMPSON *et al.*, 1986; ODUM *et al.*, 1988; DIAZ, 1989).

The impact of pollution on estuarine ecosystems is particularly difficult to assess because of a high degree of natural biological variability (in time and space), due to the highly dynamic nature of the estuarine physical environment (see also MEIRE *et al.*, 1991). Therefore, it is very difficult to separate pollution effects from natural variation in these benthic communities or to determine the impact of pollution on benthic communities.

Especially in the Schelde estuary it is very difficult to relate the distribution patterns of the macrozoobenthos to anthropogenic stress, since concentrations of most pollutants are following the same gradient as the salinity. There is, however, evidence that the benthic fauna in the freshwater tidal zone and the upstream part of the brackish zone (the oligohaline zone) is suffering from the pollutants entering the estuary. In the Schelde estuary the reduction of species is extremely acute and more severe than predicted by Remane's model. Over a very large stretch only a very uniform benthic comunity, existing of Oligochaeta, was found. Unfortunately, no historical data exists on the benthic fauna of the freshwater tidal part of the Schelde estuary before the heavy industrialization and urbanization. Other evidence for impact of pollution on the structure of the benthic community is the observation that some euryhaline (*e.g. Nereis diversicolor*) or brackish water (*e.g. Corophium volutator*) species don't enter the Schelde as far as in other estuaries. Also the lack of some typically brackish water species (*e.g. Streblospio shrubsolii*) can probably be attributed to pollution.

Based on these observations it seems that the Schelde estuary is suffering more severe from pollution than many other European estuaries. The way how pollution is responsible for this impoverishment, is at this moment not yet unraveled. The lack of oxygen in both water and sediment, which appears very often in the freshwater tidal zone of the estuary as a consequence of the very high inputs of organic matter and nutrients, is probably a main cause. Interaction between sediment contaminants (organic and inorganic micropollutants) and benthic organisms is not yet well understood, but sublethal effects on the benthic fauna are expected.

Finally, not only pollution is threatening freshwater tidal parts of European and North-American estuaries. Some authors mention impacts of canalization and dredging on the freshwater tidal ecosystem in general, and more particularly on the benthic fauna (ROBINEAU and MARCHAND, 1984; HAESLOOP, 1990).

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