Spatial distribution of oligochaetes (Clitellata) in the tidal freshwater and brackish parts of the Schelde estuary (Belgium)

J. Seys[1,2], M. Vincx[1] & P. Meire[2,3]

[1]*University of Gent, Department of Morphology, Systematics and Ecology, Marine Biology Section, K.L. Ledeganckstraat 35, B9000 Gent, Belgium*
[2]*Ministry of the Flemish Community, Institute of Nature Conservation, Kliniekstraat 25, B1070 Brussel, Belgium*
[3]*University of Antwerp, Department of Biology, Universiteitsplein 1, B2610 Wilrijk, Belgium.*

Key words: macrozoobenthos, oligochaetes, tidal fresh- and brackish water, spatial patterns

Abstract

The benthic fauna of the Belgian part of the polluted Schelde estuary, called the Zeeschelde, was studied in September–October 1996 at 143 stations along 35 transects. This study is part of the OMES research program, funded by the Flemish Government, to build an ecosystem model of the Zeeschelde in order to help policy makers to decide upon the future of this unique estuarine system. Of all organisms retained on a 250 μm mesh-size, oligochaetes were co-dominant in the mesohaline part and the only dominant group in the tidal freshwater zone. The oligochaete fauna of the ß-mesohaline zone consisted of two brackish water tubificids, *Heterochaeta costata* and *Tubificoides heterochaetus*, and the euryhaline naidid *Paranais litoralis*. The freshwater species *Limnodrilus hoffmeisteri* penetrated as far as Boerenschans. Abundance in this zone is rather low with numbers increasing with exposure. The part of the oligohaline zone that coincides with the maximum turbidity zone is extremely poor in benthos, due to high physical, chemical and biological stress, with very low numbers of *L. hoffmeisteri*, *Tubifex tubifex* and *P. litoralis*. In the tidal freshwater section, mass populations of the tubificids *L. hoffmeisteri* and *T. tubifex* occur (peak densities of almost 3.10^6 ind m^{-2}, maximum biomass: 25.7 g ADW m^{-2}) with lower numbers of *Limnodrilus claparedeianus*, *Limnodrilus udekemianus* and *Limnodrilus profundicola* mainly in the part of the Zeeschelde close to Gent where better oxygen conditions are found. Oligochaetes are more abundant in finer sediments, resulting in a clear vertical gradient with low mean values in the deeper subtidal coarse sediments and highest numbers in the upper intertidal where fluid muds consolidate. In comparison with *L. hoffmeisteri*, *T. tubifex* was more abundant in the finest sediments. Vorticellidae are more common on tails of oligochaetes in the oxygen-enriched part (4–9%) than in the oxygen-deficient zone (< 0.5%). Regeneration rates, being considered as a suitable measure of predation pressure, increase with salinity and size of the worms and are highly specific. In comparison with other temperate estuarine systems, the Zeeschelde has impoverished communities with oligochaetes as the dominant taxa. Though a future improvement of the water quality will definitely result in a less productive but more varied benthic community in the freshwater tidal zone, oligochaetes will probably continue to play an important role due to sustained harsh conditions.

Introduction

In recent years, the Schelde estuary has become one of the best studied estuarine ecosystems in the world (several papers in: Meire & Vincx, 1993; Heip & Herman, 1995). However, most research was done in the Dutch part of the estuary, the Westerschelde, which stretches out over about 55 km from the α-mesohaline zone to the mouth of the estuary. The Belgian part which extends about 105 km, the Zeeschelde, received little scientific attention, and moreover, most studies were limited to the mesohaline reach near the Belgian-Dutch border. In the early 1990s, renewed scientific interest in the Zeeschelde coincided with a slight improvement in the water quality (Meire et al., 1992; Van Damme et al., 1995). The OMES (Onderzoek Milieu Effecten Sigmaplan = Study Environmental Impact Sigma plan) research program, initiated by the Flemish Government, should result in an ecosystem model that will help policy makers to decide upon the future of this unique estuarine system (Meire et al.,1997). Within this research program, data on the distribution and the role of the benthic component are being collected.

From earlier studies on distribution patterns of macrobenthic invertebrates in the Zeeschelde, it appeared that a typical mesohaline estuarine community occurred which is dominated by polychaetes (e.g. *Nereis diversicolor* O. F. Müller, *Heteromastus filiformis* Claparède), bivalves (e.g. *Macoma balthica* L), crustaceans (e.g. *Corophium volutator* Pallas) and oligochaetes. This community is similar to those of other NW-European estuaries (Ysebaert et al., 1993). From the freshwater tidal part of the Zeeschelde, only scattered data are available. They indicate the occurrence of mass populations of oligochaetes. In general, little is known about the ecology and the response to disturbance of communities in tidal freshwater systems around the world (Odum et al., 1984).

On the other hand, the role of oligochaetes within food chains and their impact on the physics and biochemistry of the sediment-water interface are well-studied and known to be considerable. Their mass populations result in substantial reworking of the sediments they inhabit. Appleby & Brinkhurst (1970) showed that oligochaetes in Toronto harbour reworked the top 4–6 cm, 12 times a year, displacing quantities of mud eight times their own body weight within 24 h. The oligochaetes control the geochemical cycle within the top 4 cm and have a profound effect on Eh-discontinuities (Diaz, 1980). In a detailed study on the effects of tubificids on physical and chemical properties of Lake Erie sediments, McCall & Fisher (1980) demonstrated the huge impact tubificids have on grain size distribution, erosion, water content, diffusion, permeability and oxygen demand of the sediments, mainly by creating a pelletized layer of sediment at the sediment–water interface. Chatarpaul et al. (1978) describe the impact of tubificids on the denitrification process and several studies indicate the role they can play in depleting pollutants from sediments by their bioturbating activity (Giere & Pfannkuche, 1982).

This study aims to provide data on the distribution and role of oligochaetes in the brackish and freshwater tidal part of the Zeeschelde and its tidal tributaries. The spatial distribution of oligochaete assemblages over gradients in salinity, depth, oxygen saturation and sediment composition is discussed.

Study area

The Zeeschelde is part of the well-mixed Schelde estuary, and is characterised by strong currents, a large tidal amplitude and an extensive freshwater tidal zone (Table 1). This zone extends from Gent – where the tidal influence is levelled by a weir – to the mouth of the Rupel tributary (Figure 1). The main freshwater input comes from the upper Schelde (25%), Antwerp harbour and backwaters (25%), and the Rupel-Zenne tributaries (50%) (Lefèvre & Stronkhorst, 1988). The latter causes the major input of organic pollution, including all the untreated sewage water of the city of Brussels. Bacterial production rates in the Zeeschelde are among the highest values reported (Goosen et al., 1995).

Oxygen conditions are poor throughout the system with a significant dissolved oxygen ‘sag curve’ in the maximum turbidity zone between Antwerp and the mouth of the Rupel (Van Eck & de Rooij, 1990). Compared to the conditions in the 1970s, a slight improvement in oxygen concentrations and a shift of the oxygen deficient zone from Antwerpen upstream towards the Rupel has taken place (Van Damme et al., 1995). The Schelde estuary is highly contaminated with heavy metals and organic micropollutants. The concentrations of PCBs, PAHs and cadmium are high in the freshwater and brackish part of the estuary (Van Zoest & Van Eck, 1993; Zwolsman & Van Eck, 1993).

In order to preserve the shipping lanes to the port of Antwerp, a large amount of sediment is removed from the channels and relocated (Belmans, 1988). Tidal flats consist mainly of very fine sands or silts. Subtidal areas on average have coarser sediments and display a wider spectrum of substrate types including peat-, clay- and stony-bottoms.

Material and methods

Oligochaetes

Benthic fauna was sampled from September 2nd to October 8th 1996 at 143 sampling stations distributed over 35 transects, in 10 sections numbered 9 through 19, along the whole reach of the Zeeschelde (Figure 1). Intertidal stations were sampled with a PVC-corer (ø 3.5 cm) to a depth of 10 cm; subtidal samples were collected using Van Veen grab samplers, a Reineck box corer or an aluminium extendable corer, from which samples were taken with the PVC-corer. In

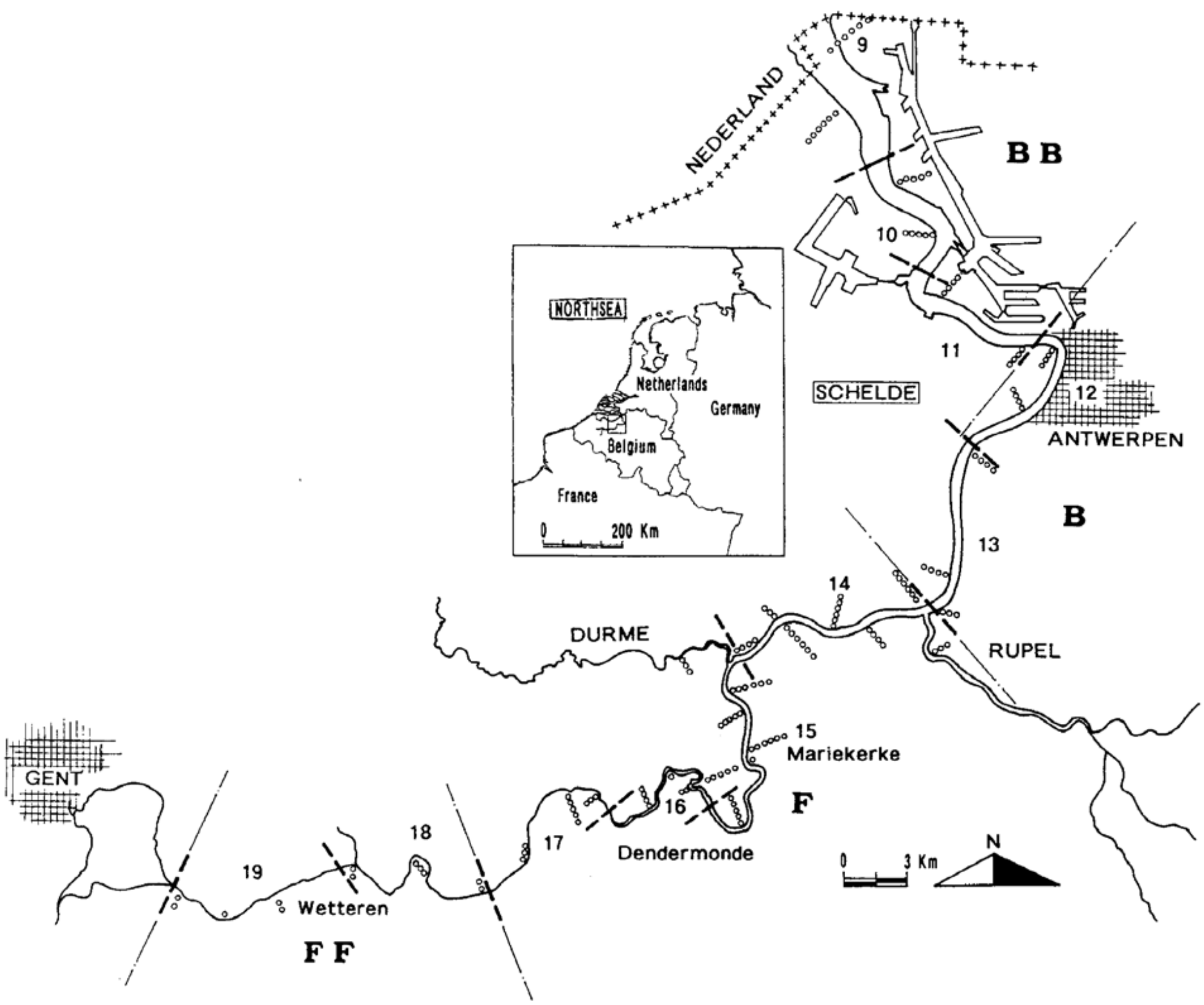

Figure 1. The Zeeschelde study area showing the ten sections (9–19), the sampling transects (oooooo) and the four main zones FF, F, B, BB.

the laboratory, the samples were preserved with a 4% formaldehyde solution after sieving over a 1mm and a 250 μm mesh-size sieve. Both fractions were sorted under a dissecting microscope and the animals were counted.

A maximum of 100 and 50 oligochaetes out of the 1 mm and the 250 μm fractions, respectively, were mounted on slides according to a standard method that was adapted for our purposes. The animals were transferred from formalin to 70% ethanol, stained with a paracarmine solution and washed with hydrochloric acid. To avoid shrinkage a gradual transfer to glycerine was carried out through a 95 parts 96% ethanol/ 5 parts glycerine medium (Seinhorst, 1959). Oligochaetes in pure glycerine were cleared by storing them overnight at 70 °C. Semi-permanent, reversible slides are obtained by sealing with paraffin rings. This method is suitable for macrobenthic as well as meiobenthic oligochaetes and provides stained and cleared material that can be stored for long periods. All oligochaetes – including immature specimens – were identified to species level, measured (width at V), and classified as one of the four age/reproductive groups:

1. juvenile= newly hatched,
2. immature,
3. adult= + penis sheath, or
4. reproductive= + eggs or spermatozeugmata in spermatheca.

They were also checked for the presence of epizoic Vorticellidae and regenerated tails. For this purpose,

Table 1. Characteristics of the Zeeschelde study area as sampled over ten sections in September/October 1996 (section 9 at the Belgian-Dutch border, section 19 near Gent). Data on salinity, O_2 saturation and BOD are derived from monthly monitoring campaigns on the Zeeschelde during the period December 1995 – November 1996 (data Institute Nature Conservation, pers.comm. Van Damme). Maxima and minima are highest and lowest measured monthly values over the one year period. For general characteristics of the Zeeschelde, references are added. (* TAW = Belgian ordnance level = MLLWS – 0.47 m)

Section	Salinity (psu)	O_2 saturation (%)	BOD (mg l^{-1})	Sampling depth (m TAW	Mean tidal range (m)	Median grain size (μm)		Silt fraction <38μm (%)	
	min–max	min–max	min–max	min–maxmin–max	min–max				
9	9.8 – 15.2	27 – 89	3 – 14	−21.0 + 4.5	4.8	19	250	2	65
10	7.2 – 14.3	7 – 82	2 – 13	−15.0 + 3.8	4.9	38	342	2	50
11	2.5 – 11.9	5 – 63	3 – 17	−12.2 + 3.2	5.0	1	289	4	73
12	0.7 – 10.3	4 – 48	4 – 24	−15.0 + 2.4	5.0	10	750	0	81
13	0.2 – 6.1	2 – 22	5 – 25	−10.2 + 2.4	5.1	9	550	0	85
14	0.2 – 2.0	1 – 38	6 – 30	−7.1 + 4.5	5.1	9	550	0	79
15	0.2 – 0.5	5 – 51	9 – 24	−10.1 + 4.3	4.9	10	800	0	81
16	≤ 0.2	3 – 54	13 – 32	−6.8 + 2.3	4.3	18	800	0	71
17	≤ 0.2	2 – 55	8 – 37	−4.5 + 4.7	3.4	13	274	3	67
18	≤ 0.2	5 – 54	11 – 36	−3.8 + 2.5	2.7	18	487	4	70
19	≤ 0.2	6 – 54	9 – 35	−2.6 – 0.8	2.3	1	260	2	80

Zeeschelde	length (km):		105	Meire et al., 1995
	width (m):		50 – 1350	–
	tidal flats (ha):		655	–
	intertidal marshes (ha):		507	–
		mesohaline &oligohaline	180	–
		freshwater tidal	322	–
	river water discharge (m^3 s^{-1})	mean	100	Lefèvre &Stronkhorst, 1988
		winter	180 (avg)	–
			500 – 600 (max)	–
		summer	50 (avg)	–
			<10 (min)	–
	maximal depth (m TAW*)		−5 à − 25	own observations

only ‘complete’ specimens were considered, excluding all oligochaetes with recently broken tails. The proportion of the total population identified as 3. adult plus 4. reproductive, was used as a measure of the reproductive state of the population.

Biomass was calculated based on a regression between the width of V and the ash-free dry weight of specimens of *Tubifex tubifex* and *Limnodrilus* sp. For this purpose, about 150 specimens of *Limnodrilus* sp. and 20 specimens of *T. tubifex* were measured. Eight width classes were distinguished and separately weighed on a microbalance. The ash-free dry weight (ADW) biomass was obtained by drying at 60 °C to constant weight and ashing at 550°C. Since we found no significant difference between *T. tubifex* and *Limnodrilus* sp. in the relationship width-ADW, data of both species were lumped.

The regression equation is:

$$\text{ADW=antiln((10.84256*width)-7.62636)} \quad (R^2 = 0.96;\ N=10;\ p < 0.01). \qquad (1)$$

Species diversity was expressed as the total number of species per sample, i.e. Hill number N_0 (Hill, 1973).

Environmental variables

Data on salinity, O_2 -saturation and BOD per section (see Figure 1) were obtained from monthly monitoring within the framework of the OMES project (data Institute for Nature Conservation, S. Van Damme, pers. com.).

Tidal levels of the sampling stations were either calculated by comparing data on tidal heights with reference points and/or depth measurements on board the research vessels, or directly measured with a theodolite. For further analysis six depth classes were established:

Depth class	1:	subtidally	< -6 m TAW
	2:	subtidally	-6 to -3 m TAW
	3:	subtidally	> -3 m to 0 m TAW
	4:	intertidally	on average < 33% of time exposed
	5:	intertidally	33–67% exposed
	6:	intertidally	> 67% exposed

At each sampling station, one additional sediment sample was taken to obtain data on median grain size, silt% (< 38 μm) and total organic content. The top 2 cm of the sediment was used for standard granulometry measurements. Most of the samples were processed with laser-diffraction devices, 40 samples (mostly deep subtidal stations) were analyzed with a wet-sieving technique, supplemented with an X-ray diffraction method on the fine sediment fraction. Total organic content was determined as the ADW (ash free dry weight) of a fixed amount of sediment, expressed as the weight percentage of the ADW to the DW (dry weight). Each station was fitted into one of eight sediment classes partly based on the Wentworth scale:

Sediment class	1	Clay	< 4 μm
	2:	Silt	4–62 μm
	3:	Very fine sand	62–125 μm
	4:	Fine sand	125–250 μm
	5:	Medium sand	250–500 μm
	6:	Coarse sand	500–1000 μm
	7:	Peat	
	8:	Stones and /or shells	

Data processing

The study area was divided into four zones based on salinity and oxygen conditions:

Zone	FF:	freshwater sections 19 & 18	improved oxygen conditions
	F:	freshwater sections 17 to 14	low oxygen levels
	B:	oligohaline sections 13 & 12	very low oxygen levels
	BB:	mesohaline sections 9 to 11	improved oxygen conditions

Density and biomass data for oligochaetes are expressed as units.m^{-2} and include both the 250 μm and 1 mm fraction. All statistical analyses were done with the STATISTICA-package (StatSoft, 1995). A multiple regression on the density data was carried out after carefully selecting a set of environmental variables that were not closely interrelated ($R^2{}_{\text{adj}}$ <0.250).

Results

Benthos

Oligochaetes constitute more than 95% of the total density in the freshwater part of the Zeeschelde. Other taxa are rare (Nematoda: up to 50 000 ind m^{-2}), very rare (only single specimens of larval Chironomidae & Ceratopogonidae) and/or basically not benthic (Copepoda, Acari) (Table 2). The same holds for the oligohaline zone where low numbers of oligochaetes are accompanied by single specimens of the polychaete *Boccardia redeki* Horst and a few copepods.

The β-mesohaline zone is much more diverse in terms of species composition with several species of polychaetes (*B. redeki*, *Heteromastus filiformis*, *Polydora ligni* Webster, *Pygospio elegans* Claparède, *Nereis diversicolor*, *N. succinea* Leuckart, *Manayunkia aestuarina* Bourne and *Eteone longa* Fabricius), amphipods (*Corophium volutator*, *Bathyporeia* sp.), molluscs (*Macoma balthica*, *Mysella bidentata* Montagu, *Littorina littorea* L. and *Hydrobia ulvae* Pennant) and unidentified ostracods, plathelminths and barnacles. In the β-mesohaline subtidal parts, mean densities are much lower (16 000 ind m^{-2}) than in the intertidal zone (85 000 ind m^{-2}) and dominated by *B. redeki* (12 000 ind m^{-2}). The most abundant taxa intertidally are oligochaetes (52 000 ind m^{-2}), nematodes (14 000 ind m^{-2}), the polychaetes *H. filiformis* (6500 ind m^{-2}) and *M. aestuarina* (2770 ind m^{-2}), and the amphipod *C. volutator* (3850 ind m^{-2}). Benthic invertebrates were found in 80% of all the samples (143) with more samples without benthos in the brackish zone (45%) compared to the freshwater area (only 8%).

Oligochaetes

Two distinct oligochaete assemblages exist in the Zeeschelde with a β-mesohaline association of *Tubificoides heterochaetus* Michaelsen/*Heterochaeta costata* Claparède and a freshwater group of the four *Limnodrilus* species (*L. hoffmeisteri* Claparède, *L. claparedeianus* Ratzel, *L. udekemianus* Claparède and *L. profundicola* Verrill) and *Tubifex tubifex* Müller (Tables 2, 3). The naidid *Paranais litoralis* Müller is found in the freshwater section as well as in the brackish part of the Zeeschelde, with peak numbers

Table 2. Total density of benthic invertebrates, the relative abundance of different taxa and the composition of the oligochaete fauna in four sections and six depth zones in the Zeeschelde during a sampling survey in September/October 1996. For explanation of sections FF/F/B/BB and depth zones 1–6 see 'Materials and methods'

Zone	FF			F						B					BB					
depth class	2	3	4	1	2	3	4	5	6	1	2	3	4	5	1	2	3	4	5	6
BENTHOS density (N.10 cm^{-2})	1	216	27	81	12	162	224	526	669	0	0	12	7	2	17	1	22	35	53	143
Gastropoda (%)	0	0	0	0	0	0	0	0	0			0	0	0	0	0	0	5.7	0	0.2
Bivalvia (%)	0	0	0	0	0	0	0	0	0			0	0	0	0	0	0	1.9	0.5	0.7
Amphipoda (%)	0	0	0	0	0	0	0	0	0			0	0	0	0	25.0	0	0	0	5.8
Acari (%)	0	0.1	0	0	0	0	0	0	0.1			0	0	0	0	0	0	0	0	0
Copepoda (%)	100	0.7	0	0.2	3.8	0.2	2.2	0.4	0.7			0	28.6	0	0	0	0	0.9	1.0	3.8
Nematoda (%)	0	0.3	7.4	0.5	1.6	0.3	0.2	0.2	1.9			0	0	0	2.9	25.0	0	5.7	0	21.1
Diptera larvae (%)	0	0	0	0	0	0	0	0	0.1			0	0	0	0	0	0	0	0	0
Polychaeta (%)	0	0	0	0	0	0	0	0	0			0	0	11.1	57.3	0	94.8	52.8	5.2	8.4
Oligochaeta (%)	0	98.9	92.6	99.4	94.6	99.5	97.6	99.4	97.1			100	71.4	88.9	23.3	25.0	5 .2	33.0	93.3	59.8
rest (%)	0	0	0	0	0	0	0	0	0.2			0	0	0	16.5	25.0	0	0	0	0.1
OLIGOCHAETA																				
density (N. 10 cm^{-2})	0	213	25	81	11	161	219	522	650	0	0	12	5	2	4	0	1	12	49	86
biomass (gADW m^{-2})	0	3.18	0.16	2.51	0.23	1.82	2.08	4.85	7.08	0	0	0.33	0.04	0.04	0.02	0.00	0.05	0.06	0.37	1.11
density species																				
T. heterochaetus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	10	37	16
H. costata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	64
P. litoralis	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	0	0	0	1	6
T. tubifex	0	106	15	23	2	22	47	147	241	0	0	0	1	0	0	0	0	0	0	
L. hoffmeisteri	0	44	7	51	8	79	158	319	361	0	0	12	4	1	0	0	1	0	6	0
L. claparedeianus	0	44	1	3	1	17	10	38	26	0	0	0	0	0	0	0	0	0	0	0
L. udekemianus	0	12	0	3	0	2	2	7	8	0	0	0	0	0	0	0	0	0	0	0
L. profundicola	0	6	1	1	0	3	2	5	7	0	0	0	0	0	0	0	0	0	0	0
rest	0	2	1	0	0	0	1	6	3	0	0	0	0	0	0	0	0	0	0	0

Table 3. Species composition, mean total density and total biomass of oligochaetes per station in the different Zeeschelde sections in Sept/Oct 1996. Species: Lh=*L. hoffmeisteri*, Lc=*L. claparedeianus*; Lu=*L. udekemianus*; Lp=*L. profundicola*; Tt=*T. tubifex*; Hc=*H. costata*; Th=*T. heterochaetus*; Pl=*P. litoralis*; Dd=*D. digitata*; En=Enchytraeidae sp.; Pb=*P. bavaricus*; Sf=*S. ferox*

Section	N stations	Density Oligochaetes (ind m^{-2})	Biomass Oligochaetes (g AFDW m^{-2})	Oligochaete species present	Nr of species per station
9	12	38 833	0.46	Th Hc	1.0
10	10	9300	0.18	Th Hc	0.5
11	9	24 444	0.17	Lh Pl Th Hc	1.0
12	8	3875	0.10	Lh Pl	0.4
13	8	3750	0.09	Lh Tt	0.6
14	31	216 032	2.63	Lh Lc Lu Lp Tt Pl	2.6
15	30	243 400	2.51	Lh Lc Lu Lp Tt Pl En	3.2
16	12	271 417	2.68	Lh Lc Lu Lp Tt	2.8
17	11	103 182	1.06	Lh Lc Lu Lp Tt Dd	3.1
18	7	55 000	0.67	Lh Lc Lu Lp Tt Sf	3.0
19	5	354 800	5.45	Lh Lc Lu Lp Tt Pb	4.6

of 33 000 ind m^{-2} in section 11. Four other species were found in the freshwater zone in very low numbers: *Dero digitata* Müller, *Potamothrix bavaricus* Oschmann, *Spirosperma ferox* Eisen and one unidentified Enchytraeidae. The freshwater species *L. hoffmeisteri* penetrates the brackish area as far as Boerenschans (= section 11), other freshwater species do not occur far downstream of the mouth of the Rupel. Oligochaetes were found in 85% of the freshwater stations, with most frequently observed species: *L. hoffmeisteri* (87%), *T. tubifex* (65%), *L. claparedeianus* (62%), *L. udekemianus* (45%) and *L. profundicola* (37%). Frequency of occurrence of oligochaetes in the brackish part is much lower (43%) with dominant species present in less than one third of the samples: *T. heterochaetus* (28%), *H. costata* (19%), *L. hoffmeisteri* (15%) and *P. litoralis* (6%).

Total density and biomass show a pattern of moderate values in the mesohaline zone, low values in the oligohaline oxygen-deprived part and high values all over the freshwater section. The high mean values in section 19 (Table 3) are partly due to one very rich station at a depth of -0.8 m TAW near the bridge of Melle, with a biomass of 25.7 g ADW m^{-2}. At six freshwater stations, densities exceeded 1.10^6 ind m^{-2} and at Mariekerke (section 15) mass populations amounting to almost 3.10^6 ind m^{-2} were present in very soft muds.

Throughout the salinity gradient total density increases with increasing exposure time (Table 2), i.e. toward the higher intertidal. The most exposed intertidal reaches are richest in terms of total density and densities of the dominant species. The shallow subtidal zone, however, has densities of oligochaetes comparable to the low intertidal area, with higher numbers of *T. tubifex*, *L. claparedeianus*, *L. udekemianus* and *L. profundicola*.

The relationship between total density and exposure time is caused by the close interaction between depth and sediment structure, with sediment characteristics responsible for the structuring of oligochaete communities.

Total density and total biomass are significantly correlated with sediment and silt fraction ($p < 0.05$), but not with depth as such. A multiple regression confirms the impact of salinity on density, biomass and species diversity, and reveals the relationship between mass populations of mainly *L. hoffmeisteri* and *T. tubifex* and the more exposed fine sediments (Table 4). One deep, subtidal station near the mouth of the Durme tributary, with a very fine sandy sediment at the time of sampling, contained high densities (548 000 ind m^{-2}) and biomasses (17.73 g ADW m^{-2}) of oligochaetes indicating at least the potential of deep gullies for colonisation by oligochaetes if optimal sediments are found. This also shows that oxygen limitation in the subtidal areas – where oligochaetes cannot supplement their oxygen demands by direct uptake – is not the (only) reason for lower subtidal worm densities here. The total amount of organic carbon, as measured in the top 2 cm of the sediment, was not a good predictor of oligochaete distribution.

The patterns in total density and biomass reflect the relationships between the abiotic environment and the most abundant species in the freshwater part, *L. hoffmeisteri* and *T. tubifex*. Other abundant species are less clearly determined in their distribution by sediment and/or depth properties (Table 4). The densities of the two dominant brackish water species, *H. costata* and *T. heterochaetus*, are significantly correlated with depth and not with sediment characteristics.

Reproductive specimens of *P. bavaricus* were identified from the shallow subtidal station near Melle only. Both *S. ferox* and *D. digitata* were found in very low numbers on one and two, respectively, muddy intertidal stations between Wetteren and Dendermonde.

The four *Limnodrilus* species and *T. tubifex* form an association throughout the freshwater section of the Zeeschelde, in proportions that average 59:25:10:4:2% for *L. hoffmeisteri*:*T. tubifex*:*L. claparedeianus*:*L. udekemianus*:*L. profundicola*, respectively. *Limnodrilus claparedeianus* is most abundant between Gent and Dendermonde, where it can represent up to 35% of the total density. *Limnodrilus udekemianus* and *L. profundicola* show the same trend with relatively higher proportions from Gent to Mariekerke. Downstream Mariekerke, *Limnodrilus hoffmeisteri* and *T. tubifex*, become dominant and together comprise more than 85% of the total oligochaete population.

Although *L. hoffmeisteri* and *T. tubifex* are found together in most freshwater stations and appear to prefer fine sediments, they do show differences in their habitat preference. *Tubifex tubifex* becomes relatively more abundant in sediments with high silt percentages irrespective of depth, as shown by the results of a multiple regression of the ratio *T. tubifex*/*Limnodrilus* sp. against a set of environmental variables (Table 4). Sediments with median grain sizes ≥ 125 μm on average contain not more than 10–15% *T. tubifex*; clays and silts have much higher values (38%). The very fine sands have values around 30%, except for the

Table 4. Summary results of a multiple regression on density data, total biomass, total number of species N_0 and relative abundance of adults against a selection of environmental variables; only significant standardised regression coefficients are presented; for overall coefficient of determination (R^2_{adj}): *p <0.05; **p <0.01;***p <0.001

	Salinity max	Silt%	OC	Depth	Nr. of observations	R^2_{adj}
Biomass total	−0.190	0.235			132	0.115***
Density total	−0.190	0.212		0.224	132	0.150***
L.hoffmeisteri	−0.200			0.215	132	0.141***
L.claparedeianus	−0.180				132	0.037
L.udekemianus					132	0.038
L.profundicola	−0.200				132	0.044*
T.tubifex	−0.190	0.235		0.176	132	0.133***
T.heterochaetus	0.272				132	0.078**
H.costata	0.367			0.267	132	0.193***
P.litoralis		0.208		0.198	132	0.083**
%*T.tubifex*/Limnodrilus	−0.270	0.490			77	0.267***
Number of species	−0.460			0.416	132	0.435***
% Adults	−0.260			−0.300	65	0.180**

two depth zones near the low water line where *T. tubifex* has a lower representation in comparison to those found in coarser sediments.

The structure of the oligochaete communities as sampled in September–October 1996, depends on species composition and hence on salinity. Neither *T. heterochaetus* nor *H. costata* reproduce in late summer, resulting in an immature oligochaete population at the time of sampling. The same holds for the spring-reproducing *T. tubifex* in the freshwater part in contrast with species of the genus *Limnodrilus*. Populations of *Limnodrilus* sp. were found to constitute on average of 85% immatures, 5% newly hatched juveniles, 5% adults and 5% reproducing individuals. Cocoons of *Limnodrilus* were abundant in many freshwater stations with densities of 100 000–200 000 m^{-2} in several intertidal locations. The relative abundance of adult individuals of oligochaetes in the Zeeschelde was found to be inversely related with depth and salinity (Table 4). In the oligohaline zone, where only small numbers of *L. hoffmeisteri* live, adults become more important as a result of a high maturation rate characteristic for such impoverished habitats.

Epizoic Vorticellidae were found on tails of oligochaetes in small numbers throughout the freshwater range. Large animals (1 mm fraction) were more affected than small ones (250 μm fraction), and incidence of vorticellids tends to increase in the Zeeschelde sections near Gent up to values of 4% (250 μm) to 9% (1 mm) in the FF-zone. The oxygen-deficient freshwater section (F) had only very few worms with Vorticellidae (< 0.5%).

Regeneration rates of oligochaetes appear to increase with salinity and size (Figure 2). This is mainly due to differences in species composition: high % of regenerated animals are found in *T. tubifex* (5–10%) and *H. costata* (10%), low values in freshwater *Limnodrilus* (1–5%) and no regenerated specimens were detected in *T. heterochaetus* and *P. litoralis*. However, the very few specimens of *L. hoffmeisteri* in the brackish part that could be checked showed remarkable results: none of the 20 specimens in the oxygen-deficient oligohaline section (B) showed any sign of regeneration, contrasting with eight out of eleven specimens in the mesohaline section.

Discussion

Benthic fauna: species composition

How do the findings of this study, in terms of the species composition and distribution of benthic invertebrates, relate to results found in other estuaries ? Is the benthic fauna of the Zeeschelde impoverished due to pollution and do we find effects in mesohaline, oligohaline, and freshwater tidal reaches ?

The benthic fauna of the mesohaline part of the Zeeschelde appears similar in species composition and abundance to benthic communities in other estuar-

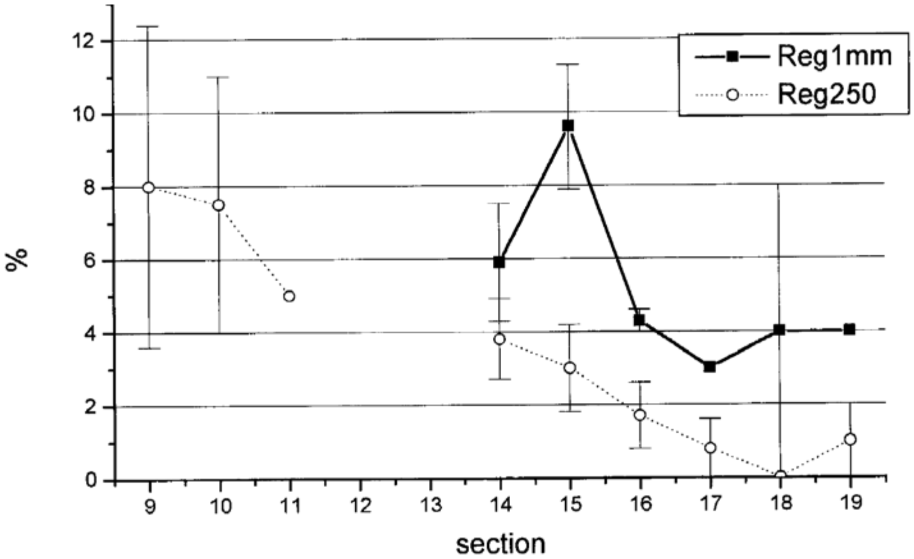

Figure 2. Regeneration rates of oligochaetes in the ten sections of the Zeeschelde for the 250 μm and the 1 mm fractions.

ies, as already observed by Ysebaert et al. (1993). We found that oligochaete populations, not identified to species level in the study of Ysebaert, are dominated by *H. costata*, *T. heterochaetus* and *P. litoralis* in the ß-mesohaline. These three species are also common inhabitants of many estuaries and brackish basins (Giere & Pfannkuche, 1982). *Heterochaeta costata* is a widespread European brackish water species, whereas *T. heterochaetus* is amphi-North Atlantic in its distribution and considered endemic to brackish water. It is reported from the oligohaline reaches of estuaries in New England (Diaz, 1980) and from Elbe (Giere & Pfannkuche, 1982) and Weser (Schuchardt et al., 1993). *Paranais litoralis* is found in many marine and brackish habitats (e.g. Schlei-Förde, Elbe, Weser, Tees, Forth estuary: Giere & Pfannkuche, 1982) but can extend into limnetic waters (e.g. Elbe). The tubificid *Monopylephorus rubroniveus*, frequently encountered in the ß-mesohaline, has not been found in the Zeeschelde. The absence of naidid species other than *P. litoralis* in the Zeeschelde is almost certainly a consequence of the sampling period. Many naidids peak in abundance in spring and become much less abundant in late summer/winter (Giere & Pfannkuche, 1982). Although oligochaetes of the α-mesohaline and polyhaline reaches of the Schelde estuary have never been studied in detail, records of *Tubificoides benedii* Udekem and *Tubificoides pseudogaster* Dahl in the Westerschelde (Verdonschot, 1981) indicate a similarity in species composition to other estuaries.The three dominant ß-mesohaline species in the Zeeschelde, *H. costatus*, *T. heterochaetus* and *P. litoralis*, reach maximum densities in the Zeeschelde comparable with peak abundances in other areas. Giere & Pfannkuche (1982) report *P. litoralis* and *T. costatus* as inhabitants of heavily polluted waters, still abundant where most animals are eliminated (also Muus, 1967; Gray, 1976), and Leppäkoski (in Giere & Pfannkuche, 1982) found *T. heterochaetus* in very polluted, oligohaline, Finnish coastal waters, increasing with the degree of pollution.

The oligohaline zone of the Zeeschelde is extremely poor in terms of species diversity and abundance of benthos in general. Only *L. hoffmeisteri* was found in densities of ca. 20 000 ind m^{-2} restricted to two shallow subtidal stations. This freshwater species is highly tolerant to salinity and thus penetrates far into brackish water (Chapman et al., 1982; Diaz, 1989). We found *L. hoffmeisteri* as far as Boerenschans (10 km downstream from Antwerp, at salinities of 4.7 psu, in September 1996), while *T. tubifex* and the other *Limnodrilus* species were absent downstream of the Rupel tributary. Since sampling took place within one month of a major freshet in the area and salinities remained reduced into September, there is a question why other freshwater species did not take advantage of the high freshwater flows. Possible explanations are:

1. High freshwater flows at the end of August did not have profound effects on interstitial salinities (Chapman & Brinkhurst, 1981);
2. *L. hoffmeisteri* is more sensitive to erosion of the bottom sediment; and

3. *L. hoffmeisteri* enters the water column sooner in an (semi-) active way under such circumstances.

An abrupt change from the brackish part towards the freshwater tidal range, with a very poor oligohaline zone, was also observed in the James River estuary (Diaz, 1980). Oligohaline zones are very often physical, chemical and biological buffers, where large fluctuations in salinity, a high turbidity and low oxygen levels prevents most species from settling. The physiography of the oligohaline part of the Zeeschelde (with a deep, clay-bottomed straight shipping lane and very few tidal flats), the oxygen-deficiency throughout the year and major concentrations of heavy industry along its course are considered the main causes for the diminished biota in this part of the estuary.

The freshwater tidal range of the Zeeschelde is very poor in species and characterised by mass populations of the eurytopic species assemblage *T. tubifex*, *L. hoffmeisteri*, *L. claparedeianus*, *L. udekemianus* and *L. profundicola.* Single specimens of *S. ferox*, *P. bavaricus*, *D. digitata* and Enchytraeidae were found upstream. Other taxa are very poorly represented in the soft sediments with only nematodes and copepods in moderately high numbers. Single specimens of Ceratopogonidae and Chironomidae larvae are the only other biota recorded in this study. Data on invertebrates from hard substrates in the Zeeschelde (De Pauw et al., 1992; own observations) confirm the general picture and reveal only very few taxa not known from the Zeeschelde soft sediments (*Erpobdella* sp., chironomids, *Gammarus* sp., *Asellus* sp., *Corixa* sp.). Intertidal vegetation has not been investigated so far for epibenthic invertebrates but is known to be populated with several small semi-terrestrial gastropods and other animals.

We can conclude that the very low species diversity reflects the heavy pollution in the Zeeschelde. Oligochaetes and particularly tubificids are being widely used as good indicators of environmental conditions in lakes and rivers, in terms of organic pollution and oxygen levels (Chapman et al., 1982; Brinkhurst & Gelder, 1991). With respect to organic pollution, *T. tubifex* and species of the genus *Limnodrilus* are considered as the most tolerant (Brinkhurst , 1980; Milbrink, 1980; Lang, 1984). Basically, tidal freshwater is dominated by pelophilic species which are opportunists and rather resistant and resilient to perturbations (Diaz, 1994), and therefore compares quite well with eutrophic large lakes, the profundal of smaller lakes or polluted harbours. High silt loads create low habitat diversity and severely restrict the composition of the biota, since suitable substrates are not available for epifaunal or crevice-dwelling organisms frequently found in fast flowing freshwater (Diaz, 1989).

Which environmental variables determine the abundance of Oligochaetes in the freshwater tidal zone of the Zeeschelde ?

The results of this study emphasised the importance of the sediment composition, in close correlation with depth, as the key factor for abundance of benthic invertebrates in the Zeeschelde. Intertidal flats are sedimentation areas for fluid mud and are inhabited by large populations of tubificids, larger than those found in the subtidal coarser sediments which are subject to strong currents. The very dense population of tubificids in at least one deep subtidal freshwater station, suggests that the oxygen conditions, as found in this part of the Zeeschelde, are not limiting the abundance of the opportunistic species *T. tubifex* and *L. hoffmeisteri*. Indications for elimination and reduced reproductive abilities due to oxygen deficiency in certain periods, as found in the Thames (Hunter, 1981), were not found.

Poor correlation of tubificid abundance with total organic carbon, as found in this study, is reported in many studies because it includes not only valuable food sources such as bacteria or recent algal remains but also substances resistant to decomposition and presumably unavailable as a food source (Pasteris et al., 1994). Wagner (1968), on the basis of experiments with freshwater tubificids, stressed the importance of finer sediment fractions (< 63 μm) for oligochaete abundance and Birtwell & Arthur (1980) link large populations of *L. hoffmeisteri* in the Thames to substantial deposition of fine sediment (< 63 μm). Several studies also indicate increases in populations due to an increase in sedimentation of fine particles (Pfannkuche, 1977; Lang, 1989; Sloreid, 1994) and McLusky et al. (1993) found reductions in oligochaete populations due to a reduction in the organic inflow to the Forth estuary. Juget (in Giere & Pfannkuche, 1982) discussed the relation between particle size and gut diameter of freshwater oligochaetes and formulated an index for sediment consumability. In the tidal freshwater part of the Zeeschelde, the correlation of tubificid abundance with sediment type, with highest numbers in the fluid muds, reflects the close relationship between mass populations and easily accessible organic food with associated microflora.

The impact of wave action and water currents on the abundance of tubificids is poorly studied (Birtwell & Arthur, 1980) and insufficiently understood. Sediments with particles of 180–200 μm are especially exposed to agitation by currents and waves, which could explain the avoidance reactions of both macro- and meiobenthic oligochaetes in studies on the Isle of Sylt (Giere & Pfannkuche, 1982), 200 μm also seems to be a critical level for other mechanical reasons (Wieser in Giere & Pfannkuche, 1982). This is in accordance with the sudden drop in abundance of tubificids in the Zeeschelde when one moves from the shallow subtidal freshwater part, with median grain size of 159 μm to the deeper stations which have a mean median grain size of 218 μm.

Mass populations and trophic role

Great plasticity and dependence of the life cycle of *L. hoffmeisteri* and *T. tubifex* upon local conditions, enable them to form mass populations as found in the freshwater part of the Zeeschelde. Peak densities of 3.10^6 ind m^{-2}, of which 700 000 were macrobenthic (retained on a 1 mm mesh-size), and a corresponding biomass of 25.7 g ADW m^{-2} can compete with some of the highest values ever described. Caspers (1948) reports mass populations in well-aerated, polysaprobe silts of Hamburg harbour up to 800 000 macrobenthic tubificids m^{-2} and Palmer (1968) found densities up to $5.7.10^6$ ind m^{-2} of *T. tubifex* and *L. hoffmeisteri* close to a heated effluent discharge from an electrical generating plant in the river Thames. The combination of excess of organic material with low but sufficient oxygen supply is the key for mass populations, conditions apparently also met in large parts of the Zeeschelde these days. In these populations, physical space is believed to be limiting further increase of abundance (Caspers, 1948).

It is clear that such mass populations constitute a very attractive food source for higher trophic levels. Rofritz (1977) demonstrated the dominant role of tubificids (*T. tubifex* and *L. hoffmeisteri*) in polluted, limnetic bottoms as food for ducks. Gray (1976) concluded that oligochaetes and small polychaetes form an important part of the diet of estuarine birds particularly in polluted estuaries such as the Forth. Warnes (1981) showed that *T. benedii* is a significant part of the diet of the Shelduck *Tadorna tadorna* in the same area. A study on the foraging behaviour of the Teal *Anas crecca* in the Zeeschelde (Dethier, 1997) and in the former freshwater tidal Ventjager flats in the Netherlands (Zwarts, 1976), strongly suggests that mass populations of tubificids can be exploited by the ducks. If one considers the high caloric value of freshwater tubificids (5575 cal g^{-1} DW, compared to 3503 cal g^{-1} DW for polychaetes: Cummins & Wuycheck, 1971) and the unusually high biomasses in these areas – highest biomasses in the Zeeschelde reach up to more than 1 kg wet weight m^{-2} – this is hardly a surprise. The question of whether this direct transfer of bacterial energy to top carnivores such as birds takes place is an important issue to be adressed in the near future.

Oligochaete predation by young fish has been widely documented in brackish-marine (Giere & Pfannkuche, 1982) as well as in fresh water areas (Yaroskhenko et al., 1980). Tail-cropping followed by regeneration can give an insight on predation pressure by fish on certain species of oligochaetes. Wisniewski (in Drewes & Zoran, 1989), in a study of tubificids in Polish lakes, concludes that predation on tubificids is easier to detect in terms of increasing regeneration proportions than in decreasing numbers of worms. Diaz (1980) found 1–2% of the tidal freshwater James river *Limnodrilus* sp. with cropped tails, a figure similar to the values in this study of the Zeeschelde. However, Diaz never observed any tail-cropping in brackish water oligochaetes and ascribes this to the smaller size of the species that results in their being swallowed whole, and to a different behaviour of the worms. In the Zeeschelde, higher proportions of cropped tails are found in larger specimens and when one goes from the freshwater to the brackish area. Further research will be needed to investigate whether this is due to higher predation pressure by fish, knowing that the abundance of several species of fish in the Zeeschelde increases towards the Belgian-Dutch border, with only scattered observations in the oxygen-deficient tidal freshwater part (Maes, 1997).

The Zeeschelde: in the future ?

There are no quantitative data on oligochaete distribution in the Zeeschelde from the past. The study of Konietzko (1953) in the ß-mesohaline confirms the occurrence of a similar species composition as found today (with *T. heterochaetus*, *P. litoralis*, *H. costatus*, *T. tubifex*, *Nais elinguis* and Enchytraeidae), but no quantitative information is given. Thus, it is not clear whether mass populations of tubificids existed in the tidal freshwater Zeeschelde in the past (i.e. before 1990). The situation now found is characteristic for hypertrophic water bodies with a minimal oxygen supply. With improved oxygen conditions and lower organic input we might expect to see an evolution towards higher species diversity. Pfannkuche (1977) describes 16 naidid, 1 *Aeolosoma* sp., 1 enchytraeid and 10 tubificid species from the Fährmannsand, a freshwater tidal flat in the hypertrophic Elbe with higher oxygen saturation values than in the Zeeschelde, with *Aulodrilus pluriseta*, *Psammoryctides barbatus* and *Potamothrix moldaviensis* restricted to the more sandy habitats. Mass populations of *T. tubifex* and *L. hoffmeisteri* (and *L. claparedeianus*) were found at other locations in the Elbe with higher organic pollution and hence lower oxygen levels. Hunter (1981) mentions *P. barbatus* from the freshwater part of the Thames becoming extinct where oxygen levels drop below a certain level.

Besides the possible colonisation by a limited number of oligochaete species, a substantial reduction in the organic input into the Zeeschelde will definitely affect the abundance of the worms. However, much will depend on the balance between natural organic input and sewage water discharge. Since the natural production and sedimentation of organic material will probably remain very substantial even in the case of reduction of sewage water input, we expect a rather slow and limited reduction in tubificid populations.

In the former and the small vestiges of an extensive tidal freshwater ecosystem in the lower Rhine-Meuse Delta (Amer, Biesbosch, etc.) of the Netherlands, typical assemblages included several molluscs (*Pisidium* sp., *Unio* sp., *Dreissena polymorpha*, *Sphaerium* sp., *Potamopyrgus antipodarum*), chironomids, a few amphipods and rich populations of oligochaetes (Wolff, 1973). However, in areas of the Hollandsch Diep with high sedimentation rates and soft muds, the subtidal fauna is poor and dominated by tubificids (four *Limnodrilus* species, *Quistadrilus multisetosus* and *D. digitata*), with small numbers of *Gammarus* sp., *Pisidium* sp., *Valvata* sp. and *Potamopyrgus* sp. and only two chironomid species. Tubificids were found here in populations of 320 000 ind m^{-2}, the cumulative abundance of the other species was ten times smaller (36 000 ind m^{-2}) (Smit et al., 1995). In the tidal freshwater section of the James River estuary, where good oxygen conditions prevail, tubificids are dominant (75% of density) and a rather limited number of other taxa is found (14 chironomids, 5 bivalves) (Diaz, 1989).

The tidal freshwater section of the Zeeschelde with its high tidal ranges and substantial sediment transport is a typical example of the kind of tidal freshwater system described by Diaz (1994). Interactions between physical disturbance regimes and species result in low species richness. Probably the physiography of the Zeeschelde and the high physical stress caused by the constant movement of vast amounts of fluid mud and strong water currents prevent it from becoming a system rich in benthic organisms, even though oxygen conditions improve and pollution decreases. However, at locations infrequently covered with fine muds, opportunities for the development of a richer fauna than found today certainly exist.

Acknowledgements

We are grateful for the financial assistance provided by the Ministry of the Flemish Community and for the logistical support by Ir.Taverniers, Ir.Wouters and the crews of the ‘Scaldis’ and the ‘Veereman’. Part of the sediment samples were processed by Dr Wartel and his colleagues (KBIN). N. Deregge and T. Ysebaert (Institute Nature Conservation) analyzed more sediment samples and were very helpful during the sampling campaign. The authors thank their many colleagues at the University of Gent and at the Institute of Nature Conservation for their generous assistance with sample collection and analysis, in particular Danielle, Guy, Johan, Ranan, Annick, Koen and Ludwig. Data from the monitoring campaigns on the Zeeschelde were generously provided by S.Van Damme.

References

Appleby, A. G. & R. O. Brinkhurst, 1970. Defecation rate of three tubificid oligochaetes found in the sediments of Toronto Harbour, Ontario. J. Fish. Res. Bd Can. 27: 1971–1982.

Belmans, H., 1988. Verdiepings- en onderhoudsbaggerwerken in Wester- en Zeeschelde. Water 43: 184–194.

Birtwell, I. K. & D. R. Arthur, 1980. The ecology of tubificids in the Thames estuary with particular reference to *T. costatus* (Claparède). In R. O. Brinkhurst & D. G. Cook (eds), Aquatic Oligochaete Biology, Plenum Press, New York, London: 175–184.

Brinkhurst, R. O., 1980. Pollution biology – the North American experience. In R. O. Brinkhurst & D. G. Cook (eds), Aquatic Oligochaete Biology. Plenum Press, New York: 205–209.

Brinkhurst, R. O. & S. Gelder, 1991. Annelida: Oligochaeta and Branchiobdellida. In U. H. Thorp & A. P. Covich (eds), Ecology and Classification of North American Freshwater Invertebrates. Academic Press, San Diego: 401–435.

Caspers, H., 1948. Ökologische Untersuchungen über die Wattentierwelt im Elb-Ästuar. Verh. Dt. Zoologen Kiel 1948: 350–359.

Chapman, P. M. & R. O. Brinkhurst, 1981. Seasonal changes in interstitial salinities and seasonal movements of subtidal benthic invertebrates in the Fraser River estuary, B.C. Estuar. coast. shelf Sci. 12: 49–66.

Chapman, P. M., M. A. Farrell & R. O. Brinkhurst, 1982. Relative tolerances of selected aquatic oligochaetes to individual pollutants and environmental factors. Aquat. Tox. 2: 47–67.

Chatarpaul, L., J. B. Robinson & N. K. Kaushik, 1978. Role of oligochaete worms in nitrogen transformation in stream sediments, Abstracts, 26th Annual Meeting, N. Am. Benthological Society. Winnipeg, Manitoba.

Cummins, K. W. & J. C. Wuycheck, 1971. Caloric equivalents for investigations in ecological energetics. Mitt. int. Ver. theor. angew.Limnol. 18: 1–158.

De Pauw, N., V. Lambert & A. Van Kenhove, 1992. Kunstmatige substraten voor biologische monitoring van grote rivieren en kanalen in Vlaanderen en Nederland. Studie in opdracht van de Vlaamse Milieumaatschappij; Report University Gent: 57pp. (in Dutch).

Dethier, K., 1997. Feeding ecology of the Teal (*Anas crecca* L) on two tidal flats in the Zeeschelde: exploratory study on the foraging behaviour and food availability. MSc thesis University Gent. 79 pp. (in Dutch).

Diaz, R. J., 1980. Ecology of tidal freshwater and estuarine Tubificidae (Oligochaeta). In: R. O. Brinkhurst & D. G. Cook (eds), Aquatic Oligochaete Biology. Plenum Press, New York: 319–330.

Diaz, R. J., 1989. Pollution and tidal benthic communities of the James River Estuary, Virginia. Hydrobiologia 180: 195–211.

Diaz, R. J., 1994. Response of tidal freshwater macrobenthos to sediment disturbance. Hydrobiologia 278: 201–212.

Drewes, C. D. & M. J. Zoran, 1989. Neurobehavioral specializations for respiratory movements and rapid-escape from predators in posterior segments of the tubificid *Branchiura sowerbyi*. Hydrobiologia 180: 65–71.

Giere, O. & O. Pfannkuche, 1982. Biology and ecology of marine Oligochaeta: a review. Oceanogr. mar. Biol. Ann. Rev. 20: 173–308.

Goosen, N. K., P. van Rijswijk & U. Brockmann, 1995. Comparison of heterotrophic bacterial production rates in early spring in the turbid estuaries of the Scheldt and the Elbe. Hydrobiologia 311: 31–42.

Gray, J. S., 1976. The fauna of the polluted Tees estuary. Estuar. coast. mar. Sci 4: 652–676.

Heip, C. & P. M. J. Herman, 1995. Major biological processes in European tidal estuaries: a synthesis of the JEEP-92 Project. Hydrobiologia 311: 1–7.

Hill, M. O., 1973. Diversity and eveness: a unifying notation and its consequences. Ecology 54: 427–432.

Hunter, J., 1981. Survival strategies of tubificids in the Thames and other estuaries. In N. V. Jones & W. J. Wolff (eds), Feeding and Survival Strategies of Estuarine Organisms. Plenum Press, New York: 53–63.

Kaster, J. L., 1989. Observations of predator-prey interaction on dispersal of an oligochaete prey, *Limnodrilus hoffmeisteri*. Hydrobiologia 180: 191–193.

Konietzko, B., 1953. Notes sur les Oligochètes de Belgique. I. Eaux saumâtres du Bas-Escaut. Med. Kon. Belg. Inst. Natuurwet. 29: 1–14 (in French).

Lang, C., 1984. Eutrophication of Lakes Léman and Neuchâtel (Switzerland) indicated by oligochaete communities. Hydrobiologia 115: 131–138.

Lang, C., 1989. Effects of small-scale sedimentary patchiness on the distribution of tubificid and lumbriculid worms in Lake Geneva. Freshwat. Biol. 21: 477–481.

Lefèvre, F. & J. Stronkhorst, 1988. Chloridegehalte in de Westerschelde, zoetwaterbelasting en biotische aspekten. Rijkswaterstaat GWWS-88.514.11 pp.

Maes, J., 1997. Vis in de Zeeschelde: terug van weggeweest Schelde nieuwsbrief 12: 1–3.

McCall, P. L. & J. B. Fisher, 1980. Effects of tubificid oligochaetes on physical and chemical properties of Lake Erie sediments. In R. O. Brinkhurst & D. G. Cook (eds), Aquatic Oligochaete Biology. Plenum Press, New York: 253–317.

McLusky, D. S., S. C. Hull & M. Elliott, 1993. Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper Forth estuary. Neth. J. aquat. Ecol. 27: 101–110.

Meire, P., G. Rossaert, N. De Regge, T. Ysebaert & E. Kuijken, 1992. Het Schelde-estuarium: ecologische beschrijving en een visie op de toekomst. Gent, RUG, Rapport RUG-WWE 28/IN A 92.57 en Instituut voor Natuurbehoud: 150 pp.

Meire, P. M. & M. Vincx (eds), 1993. Marine and Estuarine Gradients. Proceedings 21st Symposium ECSA, Gent, 9–14 Sept 1991, Neth. J. aquat. Ecol. 27: 1–496.

Meire, P., M. Hoffmann & T. Ysebaert (eds), 1995. De Schelde: een stroom natuurtalent. Instituut voor Natuurbehoud, Hasselt, rapport 95.10. 32 pp.

Meire, P. M., M. Starink & M. Hoffmann, 1997. Integratie van ecologie en waterbouwkunde in de Zeeschelde: aanleiding tot en situering van het Onderzoek Milieu Effecten Sigmaplan (OMES). Water 95: 147–165.

Milbrink, G., 1980. Oligochaete communities in pollution biology: the European situation with special reference to lakes in Scandinavia. In R. O. Brinkhurst & D. G. Cook (eds), Aquatic Oligochaete Biology. Plenum Press, New York:. 433–455.

Muus, B. J., 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Meddr. Danm. Fisk. -og Havunders 5: 1–316.

Odum, W. E., T. J. Smith, J. K. Hoover & C. C. McIvor, 1984. The ecology of tidal freshwater marshes of the United States east coast: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-83/17: 177 pp.

Palmer, M. F., 1968. Aspects of the respiratory physiology of *Tubifex tubifex* in relation to its ecology. Proc. zool. Soc. Lond. 154: 463–473.

Pasteris, A., C. Bonacina & G. Bonomi, 1994. Observations on cohorts of *Tubifex tubifex* cultured at different food levels, using cellulose substrate. Hydrobiologia 278: 315–320.

Pfannkuche, O., 1977. Okologische und systematische Untersuchungen an naidomorphen Oligochaeten brackiger und limnischer Biotope. PhD thesis University Hamburg. 138 pp (in German).

Rofritz, D. J.,1977. Oligochaetes as a winter food source for the Old Squaw. J. Wildl. mgmt 41: 590–591.

Schuchardt, B., U. Haesloop & M. Schirmer, 1993. The tidal freshwater reach of the Weser estuary: riverine or estuarine? Neth. J. aquat. Ecol. 27: 215–226.

Seinhorst, J. W., 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. Nematologica 4: 67–69.

Sloreid, S., 1994. Oligochaete response to changes in water flow in the Dokka Delta, Lake Randsfjorden (Norway), caused by hydroelectric power development. Hydrobiologia 278: 243–249.

Smit, H., H. C. Reinhold-Dudok van Heel & S. M. Wiersma, 1995. Sublittoral macrozoobenthic assemblages in the enclosed sediment polluted Rhine-Meuse Delta; their relationship to environmental conditions. Neth. J. aquat. Ecol. 29: 31–49.

StatSoft, Inc., 1995. STATISTICA for Windows , Statistics II, 2nd edn. 5405 pp.

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

Van Eck, G. Th. M. & N. M. de Rooij, 1990. Development of a water quality and bio-accumulation model for the Scheldt estuary. In W. Michaelis (ed.), Coastal and Estuarine Studies Springer-Verlag, Berlin: 95–104.

Van Zoest, R. & G. Th. M. Van Eck, 1993. Behaviour of selected PCBs, PAHs and ϒ-HCH in the Scheldt estuary, S. W. Netherlands. Neth. J. aquat. Ecol. 27: 288–300.

Verdonschot, P., 1981. Some notes on the ecology of aquatic oligochaetes in the Delta Region of the Netherlands. Arch. Hydrobiol. 92: 53–70.

Wagner, G., 1968. Zur Beziehung zwischen der Besiedlungsdichte von Tubificiden und dem Nahrungsangebot im Sediment. Int. Rev. ges. Hydrobiol. 53: 715–721.

Warnes, J. M., 1981. The impact of overwintering birds on the production ecology of estuarine benthic invertebrates. University of Stirling PhD thesis. 177 pp.

Wolff, W. J., 1973. The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Rijksmuseum van Natuurlijke Historie, Leiden, Zoologische Verhandelingen 126: 3–242.

Yaroskhenko, M. F., OI. Val'kovskaya & V. Kh. Chokyrian, 1980. Fresh-water Oligochaeta and their importance as food for fish. In G. M. Belyaev (ed.), Aquatic Oligochaete Worms: Taxonomy, Ecology & Faunistic studies in the USSR. Amerind Publishing Co.Pvt Ltd, New Delhi: 191–196.

Ysebaert, T., P. Meire, D. Maes & J. Buijs, 1993. The benthic macrofauna along the estuarine gradient of the Schelde estuary. Neth. J. aquat. Ecol. 27: 327–341.

Zwarts, L., 1976. Density-related processes in feeding dispersion and feeding activity of Teal (*Anas crecca*). Ardea 64: 192–209.

Zwolsman, J. J. G. & G. T. M. Van Eck, 1993. Dissolved and particulate trace metal geochemistry in the Scheldt estuary, S. W. Netherlands (water column and sediments). Neth. J. aquat. Ecol. 27: 280–287.