Macrozoobenthic assemblages in littoral sediments in the enclosed Rhine-Meuse Delta

Abstract

Littoral macrozoobenthos in the enclosed Rhine-Meuse Delta was investigated by taking 95 sediment samples from 17 sites between 1984 and 1990. In addition, a set of environmental parameters was determined. The aim was to identify the main assemblages and the environmental conditions under which they occur. By the use of TWINSPAN, three main littoral zoobenthic assemblages were distinguished, which were related to geographical zones and differences in sediment grain size distribution.

1) The 'littoral river sand' assemblage was found in the most upstream part; it mainly consisted of 'interstitial' invertebrates, including the indicator species *Vejdovskyella comata*, *Propappus* sp. and *Kloosia pusilla*.
2) The 'littoral sedimentation area silt' assemblage was dominated by *Gammarus tigrinus*, *Einfeldia dissidens* and *Pisidium* sp. It was found in several river sections and contained the indicator species *Einfeldia dissidens, Potamopyrgus antipodarum* and *Valvata piscinalis*.
3) The 'littoral sandy basin' assemblage was concentrated in the littoral fine sands of the Haringvliet and contained the indicator species *Pisidium henslowanum*, *P. moitessierianum*, *Cladotanytarsus* sp. and *Lipiniella arenicola*.

The three assemblages are the reflection of an interaction between habitat, food and disturbance.

Palaeoecological analysis of insect remains revealed that 14 out of the 24 insect taxa, that were formerly common in the river sand habitat, are now extinct from the Rhine. The river silt habitat seems less impoverished: two out of the 19 insect taxa found in palaeoecological analysis are now extinct from the Rhine and seven are rare. Exotic species (*Corbicula fluminea, C. fluminalis* and *Corophium curvispinum*) have recently colonized the Rhine-Meuse Delta, but their impact on the macrozoobenthos seems limited. *Corbicula* spp. have become abundant in the 'littoral river sand' assemblage only.

Introduction

During the last decades, environmental characteristics of the Rhine-Meuse Delta changed drastically (Ferguson & Wolff, 1983; Van Nes & Smit, 1993). The closure of the main outlet of the Rhine-Meuse river system, the Haringvliet, in 1970 caused a complete alteration of the hydromorphology and current and sedimentation patterns completely changed. Today, the Delta shows characteristics of a river, of a lake and some freshwater tidal characteristics. During the 20th century, water quality of the Rivers Rhine and Meuse deteriorated (Table 1). After 1970, water quality of the Rhine improved due to management measures. In the Rhine-Meuse Delta, similar trends could be observed, but differences were less pronounced. Before the enclosure of the Haringvliet (1970), water quality conditions in the Delta were generally better than in upstream sections, due to dilution with sea water and self-purification. Afterwards, the water quality of the Rhine-Meuse Delta became totally dependent on that of these rivers. Due to the lower current velocities, large amounts of polluted sediments were deposited in the Delta and caused a serious environmental problem (Van Otterloo *et al.*, 1987; Van Urk & Smit, 1989).

The former littoral macrozoobenthos was characterized by high densities of a few characteristic brackish water species (Wolff, 1973). It was a vital component of the estuarine ecosystem, being an important food source for fish and waterfowl. Recent studies show that macrozoobenthos, particularly Chironomidae, occur in high densities and biomass on freshwater tidal sandy flats in the Haringvliet (Smit *et al.*, 1991) forming an important food source for waders (Dirksen *et al.*, 1992). These studies provide no general insight into the present littoral macrozoobenthos in soft sediments in the enclosed Rhine-Meuse Delta. This insight is highly desirable, both to have baseline knowledge and to provide a framework for possible future management measures.

Recently, the Rhine is being (re)colonized by both indigenous and immigrant macroinvertebrate species, partly as a result of improving water quality conditions (Van den Brink *et al.*, 1989; Bij de Vaate *et al.*, 1992; Den Hartog *et al.*, 1992). This might also influence the littoral macrozoobenthos composition in the Rhine-Meuse Delta.

The present study addresses the following questions:

1) what are the main littoral macrozoobenthic assemblages in the Rhine-Meuse Delta 15-20 years after closure and under improved river water quality conditions?
2) under which environmental conditions do these assemblages exist?
3) to what extent are the habitats of the main assemblages subject to recent colonization by immigrant species?
4) what can be concluded about the present species richness of the insect fauna of the main littoral habitats, when compared with palaeoecological data from the River Rhine?

Table 1. The water quality of the River Rhine at the German-Dutch border (Lobith), of the River Meuse at the Belgian-Dutch border (Eijsden) and of the Haringvliet near the Haringvliet dam. Values are annual averages.

		Rhine at Lobith				Meuse at Eijsden			Haringvliet		
		±1900[1]	1972	1982	1992	1972	1982	1992	1972	1982	1992
Temperature	(°C)	10.9	13.0	13.4	13.7	12.4	14.3	14.8	10.6	12.4	12.4
BOD5	($mg\ l^{-1}$)	2	9	3	2	4	3	4	-	-	-
Suspended solids	($mg\ l^{-1}$)	-	48	32	29	38	29	19	11.3	7.3	7.5
Secchi depth	(dm)	-	4.8	4.6	4.9	9.6	9.6	-	14.2	11.6	13.9
Nutrients											
(NO3 + NO2)-N	($mg\ l^{-1}$)	0.34	2.64	3.56	3.71	2.26	2.59	3.21	3.1	3.3	3.6
NH4-N	($mg\ l^{-1}$)	0.15	3.22	0.55	0.30	1.23	0.59	0.46	2.2	0.4	<0.2
PO4-P	($mg\ l^{-1}$)	0.05	0.36	0.35	0.10	0.43	0.32	0.24	0.19	0.26	0.11
total P	($mg\ l^{-1}$)	0.15	0.90	0.56	0.24	0.63	0.51	0.42	0.27	0.34	0.18
Macro-ions											
Cl	($mg\ l^{-1}$)	13	236	151	163	40	45	43	262	143	144
SO4	($mg\ l^{-1}$)	35	92	68	-	57	48	40	-	65	65
Micro-pollutants											
total Cd	($\mu g\ l^{-1}$)	-	3.7	0.9	0.07	6.1	0.86	0.33	-	0.42[2]	0.083[2]
Cd dissolved	($\mu g\ l^{-1}$)	-	1.8	0.3	<0.02	2.3	0.15	<0.05	-	-	-
total Hg	($\mu g\ l^{-1}$)	-	2.3	0.12	0.05	0.3	0.09	0.06	-	0.087[2]	0.028[2]
Hg dissolved	($\mu g\ l^{-1}$)	-	0.4	0.02	<0.02	0.1	0.02	<0.02	-	-	-
PAH silt bound	($mg\ kg^{-1}$)	0	-	-	4.04	-	-	9.22	-	-	-

1) data 1900 from DEN HARTOG et al. (1992); all other data from Rijkswaterstaat DONAR database.
2) silt bound

Study area

The present state of the Rhine-Meuse Delta is strongly influenced by man. Large scale river canalization started in the second half of the 19th century, when the Nieuwe Waterweg and Nieuwe Merwede were dug. The 'Delta project' (1953-1987) drastically changed the ecological properties of the Delta by closing off the Haringvliet in 1970 (Ferguson & Wolff, 1983).

Today, the Rhine-Meuse Delta (Fig. 1) consists of two main longitudinal gradients. The first gradient runs from the River Waal (the main Rhine branch) along the Boven Merwede, with the sedimentation area of sand in the upper Nieuwe Merwede and silt in the lower Nieuwe Merwede and eastern Hollandsch Diep, to the freshwater basin of the Haringvliet with low current velocities and higher transparencies (Secchi depth 1-2 m). The second gradient runs from the River Waal to the North Sea along the Boven Merwede, the Beneden Merwede, the tidal River Oude Maas with sedimentation of sand and transport of silt, and the brackish Nieuwe Waterweg. In the Oude Maas where the vertical tidal range is still 0.8-1.4 m, freshwater tidal characteristics have remained (Admiraal *et al.*, 1993). Similar characteristics are present in the downstream part of the River Lek, an impounded Rhine branch.

The present littoral habitats are the result of historical and recent erosion and sedimentation processes. In the littoral zone, erosion now prevails over sedimentation. This is due to the reduction of the tidal influence and the increased erosive power of waves generated by ships. At the study sites in the Rivers Waal, Boven Merwede and Beneden Merwede, sedimentation of silt was negligible. The top layers only consisted of a few centimetres of coarse river sand. In these river parts, intensive shipping greatly contributes to the littoral sediment texture. Ship induced waves cause a high turbulence washing out all fine particles. In areas with net sedimentation, sediment structure is highly variable, due to local differences in sedimentation processes occurring at different river discharges. Local variations in wind exposure may further generate these differences. In the Haringvliet, the most important former silt flats like the Slijkplaat (Dutch for 'mud flat') have now become sand flats: wind induced waves have washed out the fine sediment fractions. Yet the Haringvliet still has some silt flats like the Beninger Slikken (site BS), where breakwaters have been constructed to prevent ongoing erosion.

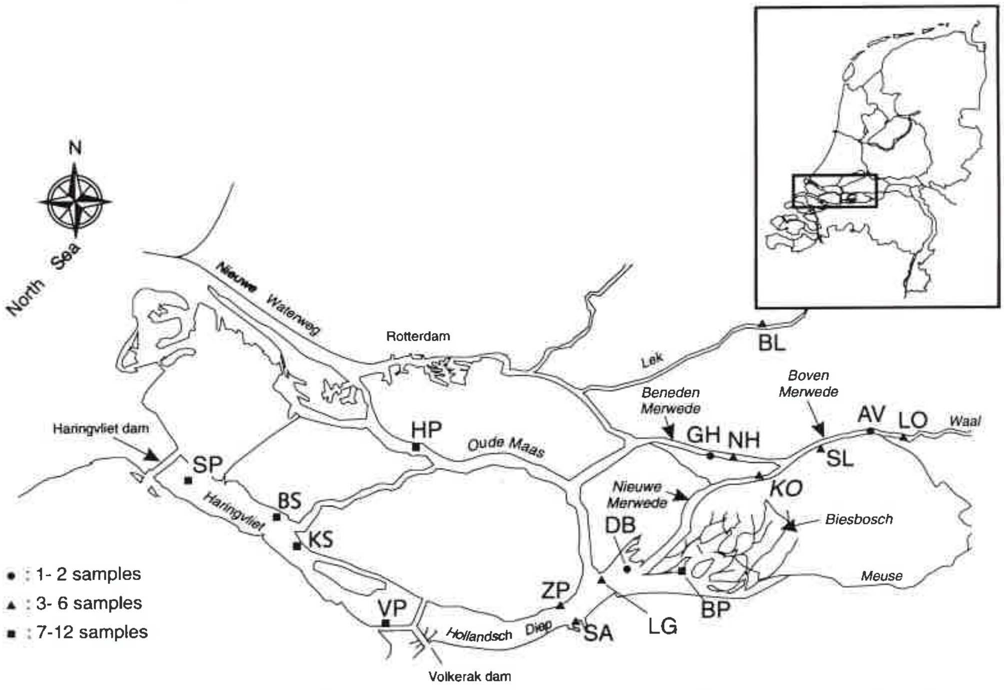

Figure 1. An overview of the study area including the most important river branches, water bodies and all sampling stations. The sampling stations are shown by a two-letter code, indicating the locality. AV: Avelinge Diep, BL: Buitenlanden, BP: Boerenplaat, BS: Beninger Slikken, DB: Dordtse Biesbosch at the Dam van Engeland, GH: Gat van de Hengst (Sliedrechtse Biesbosch), HP: Hooiplaat, KO: Kop van 't Oude Wiel, KS: Korendijkse Slikken, LG: Lepelaarsgat, LO: Loevestein, NH: off Neder-Hardinxveld, SA: Sasseplaat, SL: Sleewijk, SP: Slijkplaat, VP: Ventjagers platen, ZP: Zeehondenplaat.

Materials and methods

From 1984 to 1990, macrozoobenthos was sampled by taking 95 sediment samples (Table 2) from 17 sites (Fig. 1) in the littoral zone (mean depth 0-1.2 m). The benthos was collected by taking sediment samples of the upper 10 cm using a hand corer with an inner diameter of 11.0 cm (one sample; 1984, 1986) or 5.9 cm (three samples; 1987, 1989, 1990) with surface areas of 95 or 82 cm^2 respectively. All samples were sieved using a mesh size of 250 µm, sorted under a stereo-microscope (magnification 7.5x) and preserved in 70% ethanol until identification. In addition, one or more core samples were collected for physico-chemical analysis of the sediment. Besides grain size distribution, dry matter, calcite, particulate organic carbon and pH, a standard series of heavy metals (As, Hg, Cd, Cr, Cu, Ni, Pb and Zn) and organic micropollutants, including 7 PCB's, the most common benzene compounds, pesticides and polycyclic aromatic hydrocarbons were analyzed (Smit *et al.*, 1994).

Table 2. Periods of sampling and sample numbers at the 17 sites (see Fig. 1).

Site	Period(s) of sampling (month/year)	total number of samples
AV	3/90	1
BL	9/89, 11/90	6
BP	8/86, 9/87	9
BS	7/84, 9/86	10
DB	9/89	2
GH	11/86	2
HP	9/89, 9/90	6
KO	9/89	4
KS	7/84, 8/84, 8/86	12
LG	9/86	3
LO	3/90	4
NH	9/89, 3/90	5
SA	10/86	3
SL	11/90	3
SP	9/86, 9/87	10
VP	8/86, 9/87	12
ZP	9/89	3

Chemical analyses were not carried out at all sites and values of many parameters were below the detection limit. Principal Component Analysis showed collinearity between most contaminants and the grain size fraction < 63 µm. Therefore, contaminants were not included in the ordination (see below).

In 1992, an additional macrozoobenthic survey was undertaken at all sites to assess new immigrant species. Five cores (diameter 5.9 cm) per site were taken and mixed to one sample, sieved using a mesh size of 500 µm and sorted in a bottom-lighted tray.

Palaeoecological samples were taken between 1983 and 1988 in two different ways. Floodplain deposits in the Rhine (Schenkenschans: near German-Dutch border), Waal (Ochten), and Boven Merwede (Woudrichem: between sites LO and SL) were sampled using hand auger equipment for soil research. This was drilled into the sediment up to a coarse sand layer, indicating the former river bed. Samples were taken from the silt layer directly on the top of the sand. The river bed was sampled in the Nieuwe Merwede near site DB and in the IJssel near Kampen (the sedimentation area of another Rhine branch), using a mud corer. In total, 7 cores were taken from which 50 samples were derived. Chitinous parts formed the most important remains of macroinvertebrates in the deposits. The following selected parts of insect groups were considered and identified: mandibles (Ephemeroptera), frontoclypeus (Trichoptera) and head capsule (Chironomidae). Taxa assumed to have lived in former sand and silt habitats were selected and classified. The frequency of occurrence was calculated per river branch. For more details see Klink (1989).

Clustering and ordination of the sediment samples were performed using the computer programmes TWINSPAN (Hill, 1979) and CANOCO 3.1 (Ter Braak, 1991) respectively. In TWINSPAN, default options were used, whereas species densities were divided into five cut levels (0, 150, 2000, 5000 and 10000 m^{-2}). Animals were included in the input file, when found in at least three samples and identified to the species level or aggregate level for chironomids, or to the genus level when further identification was not possible. This was done to reduce the influence of differences in taxonomic levels and rare species. Samples only containing taxa that could not be identified to that level were omitted. In total, 46 out of 98 identified taxa and 89 samples were included. Site SP (Sasseplaat) was left out, since it was a man made habitat.

Default (standard) options were used in the Canonical Correspondence Analysis (CCA), except that densities were logarithmically (Ln) transformed.

Results

Multivariate analysis

The classification of the 89 samples with the aid of TWINSPAN (Fig. 2) resulted in three assemblages. A group of 13 samples separated (eigenvalue 0.729) at level 1 with *Kloosia pusilla, Propappus* sp. and *Vejdovskyella comata* as indicators. Since this assemblage was found in the upstream river parts, it is referred to as the 'littoral river sand' assemblage.
Division two (eigenvalue 0.379) separated a group of 22 samples with the indicators *Einfeldia dissidens, Potamopyrgus antipodarum* and *Valvata piscinalis*. It included sites in the sedimentation area. The fauna was characterized as the 'littoral sedimentation area silt' assemblage .
Division three (eigenvalue 0.355) divided the 54 samples of the positive group further into a negative group of 49 samples, mainly from the Haringvliet sites. It included the indicators *Cladotanytarsus* sp., *Lipiniella arenicola, Pisidium henslowanum* and *Pisidium moitessierianum*. The fauna was characterized as the 'littoral sandy basin' assemblage.
The group of five remaining samples contained the positive indicators *Corbicula* spp. and *Polypedilum scalaenum*. The samples originated from river sections, where silt is present. This group is, however, not presented here as a fourth assemblage, since only five samples are included.

CANOCO showed a clear relation between grain size distribution and the indicator species of the three assemblages. The grain size >210 µm vector pointed in the direction of the indicator taxa of the 'littoral river sand' assemblage; the grain size <63 µm vector pointed in the direction of the indicator species of the 'littoral sedimentation area silt' assemblage; the grain size 63-210 µm vector pointed in the direction of the indicator species of the 'littoral sandy basin' assemblage.

Assemblages

TWINSPAN indicator taxa, accompanying taxa and dominant taxa of the three assemblages are summarized in Table 3. Associated river stretches and sites and values of some environmental parameters are given as well. Accompanying taxa have a lower presence (fraction of samples) than indicator taxa. They were absent from or occurred in very low densities ($n < 20$ m^{-2}) in other assemblages. The three taxa with the highest relative abundance, each amounting to at least 10%, were indicated as dominant.

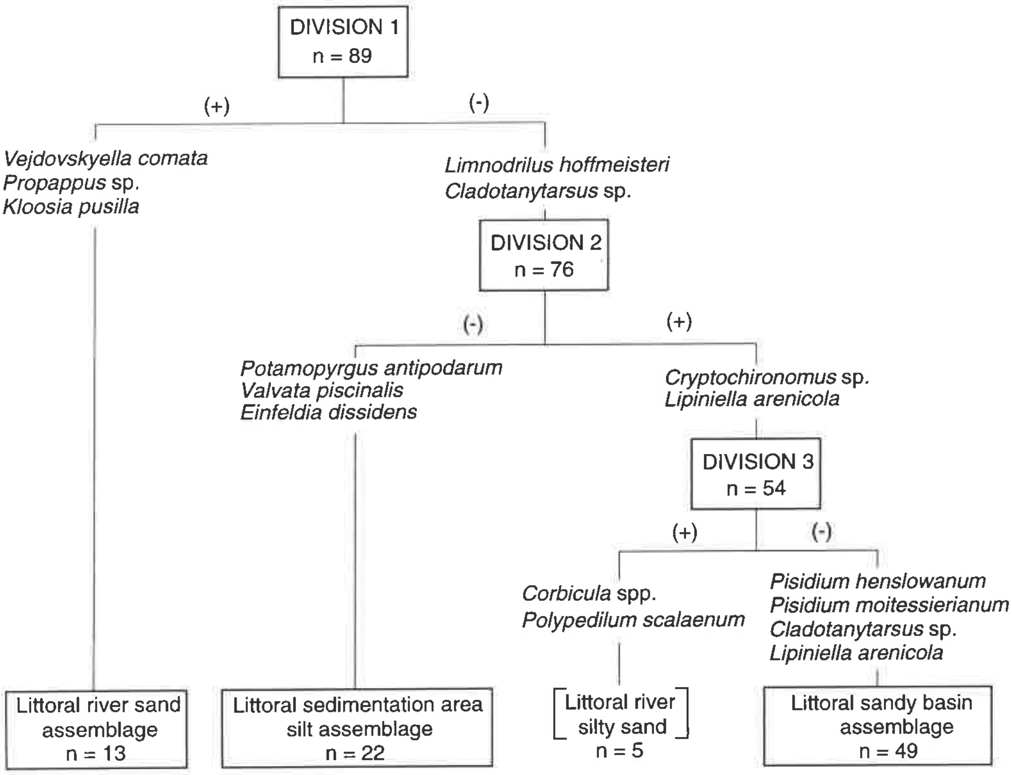

Figure 2. Classification of 89 samples from 17 sites with the aid of TWINSPAN to level 3. Positive and negative indicators are given for all divisions.

Densities

An overview of the presence and average density (± S.E.) of the various taxa in these assemblages is given in Table 4. The highest macroinvertebrate densities were observed in the 'littoral river sand' assemblage, where the small Naididae and Enchytraeidae dominated. In the 'littoral sedimentation area silt' and 'littoral sandy basin' assemblages, tubificids were numerically dominant. In the latter assemblage they did not have the main share in the biomass, since the individual weight of chironomids was higher (Smit & Snoek, 1989). Most of the tubificids were juvenile and could therefore not be identified to the species level. High densities of *Pisidium* sp. and *Einfeldia dissidens* were characteristic of the 'littoral sedimentation area silt' assemblage. The 'tidal sandy flat' assemblage showed high densities of chironomids (*Cladotanytarsus* sp. and *Lipiniella arenicola*).

Table 3. The main characteristics of the three main littoral macrozoobenthic assemblages in the enclosed Rhine-Meuse Delta. The terms 'accompanying' and 'dominant' are defined in the text.

name of assemblage	'littoral river sand'	'littoral sed. area silt'	'littoral sandy basin'
TWINSPAN indicator taxa	*Vejdovskyella comata* *Propappus* sp *Kloosia pusilla*	*Potamopyrgus antipodarum* *Valvata piscinalis* *Einfeldia dissidens*	*Pisidium henslowanum* *Pisidium moitessierianum* *Cladotanytarsus* sp. *Lipiniella arenicola*
accompanying species	*Vejdovskyella intermedia* *Amphichaeta leydigi* *Paranais frici* *Polypedilum scalaenum*	*Pisidium supinum* *Microchironomus tener* *Paracladius conversus*	*Limnodrilus profundicola* *Chironomus nudiventris* *Stictochironomus histrio*
dominant taxa (max. numbers m^{-2})	*Propappus* sp. (23%, 39000) *Vejdovskyella comata* (22%, 23000) *Vejdovskyella* intermedia (15%, 20000)	Tubificidae (44%, 7200) *Einfeldia dissidens* (15%, 6000) *Pisidium* sp. (12%, 3500)	Tubificidae (52%, 72000) *Cladotanytarsus* sp. (22%, 27000)
recent colonizers	*Corbicula fluminea* *Corbicula fluminalis*	*Corbicula fluminea* *Corbicula fluminalis* *Corophium curvispinum*	*Corbicula fluminea*
associated sites	LO AV NH	BL HP DB LG ZP	VP KS BS SP
associated river stretches	Waal Beneden Merwede	Lek Oude Maas Nieuwe Merwede Hollandsch Diep	Haringvliet
physic-chemical parameters	mean ± S.D. (n); range	mean ± S.D. (n); range	mean ± S.D. (n); range
grain size distribution			
% > 210 µm	55 ± 17 (8); 33-79	20 ± 29 (22); 1-91	5 ± 10 (48); 0-67
% 63-210 µm	34 ± 19 (8); 10-64	23 ± 27 (22); 1-85	72 ± 17 (48); 30-97
% < 63 µm	10 ± 16 (8); 0-76	57 ± 30 (22); 8-98	23 ± 16 (48); 2-63
Cadmium (mg kg^{-1})	-	3.5 ± 4.0 (12); 0-14	0.9 ± 0.4 (15); 0- 2
Mercury (mg kg^{-1})	-	1.4 ± 2.2 (12); 0- 8	0.3 ± 0.2 (15); 0- 1
total PAH (mg kg^{-1})	-	8 ± 14 (5); 1-37	2 ± 5 (15); 0-23

Table 4. Frequencies of occurrence and average density (±S.E.) of macrozoobenthos in three assemblages. *: taxon found in 1-25% of the samples; **: 26-50% of samples; ***: 51-100% of samples; +: taxon present in assemblage but frequency not calculated; -: density < 0.5 m^{-2}; n.d.: not determined.

	PRESENCE littoral river sand	littoral sed. area silt	littoral sandy basin	DENSITY littoral river sand	littoral sed. area silt	littoral sandy basin
OLIGOCHAETA						
Lumbriculidae	*			-	-	-
Tubificidae	***	***	***	-	5417 ± 3414	4066 ± 1249
Tubificidae with setae				461 ± 306	104 ± 33	6629 ± 2569
Tubificidae without setae				1315 ± 1061	1525 ± 522	46 ± 28
Aulodrilus sp.		*		-	-	-
Aulodrilus limnobius Bretscher		*		-	-	-
Limnodrilus claparedeanus Ratzel	*	*	**	-	94 ± 94	125 ± 35
Limnodrilus hoffmeisteri Claparède		**	***	-	266 ± 178	789 ± 263
Limnodrilus profundicola (Verrill)			*	-	-	34 ± 17
Limnodrilus udekemianus Claparède		*	*	-	-	18 ± 9
Potamothrix moldaviensis (Vejdovsky & Mrázek)		*	*	-	17 ± 12	53 ± 20
Quistadrilus multisetosus (Keilty)		*		-	-	-
Tubifex tubifex (Müller)		*	*	-	369 ± 341	66 ± 30
Amphichaeta leydigi Tauber	***	*	*	4053 ± 2393	9 ± 9	12 ± 12
Chaetogaster limnaei Von Baer	*			-	-	-
Nais barbata Müller		*		-	94 ± 62	-
Nais communis Piguet		*		-	9 ± 9	-
Nais elinguis Müller	**	*	***	786 ± 465	69 ± 45	1185 ± 906

Table 4. continued	PRESENCE			DENSITY		
	littoral river sand	littoral sed. area silt	littoral sandy basin	littoral river sand	littoral sed. area silt	littoral sandy basin
Nais pardalis Piguet		*	*	-	43 ± 24	356 ± 215
Nais simplex Piguet		*		-	9 ± 9	-
Ophidonais serpentina (Müller)		*		-	17 ± 17	-
Paranais frici Hrabe	*		*	2386 ± 1583	-	4 ± 4
Paranais litoralis (Müller)	*	*	*	-	-	470 ± 319
Stylaria lacustris (L.)			*	-	-	2 ± 2
Vejdovskyella comata (Vejdovsky)	***			7293 ± 3231	-	-
Vejdovskyella intermedia Bretscher	***	*		5043 ± 2711	17 ± 12	-
Enchytraeidae	***	*	*	2020 ± 872	35 ± 27	46 ± 36
Propappus sp.	***			7835 ± 4185	-	-
MOLLUSCA						
Anodonta anatina (L.)		*		-	-	-
Unio pictorum (L.)		*	*	-	9 ± 9	1 ± 1
Corbicula fluminalis (Müller)	+	+		n.d.	n.d.	-
Corbicula fluminea (Müller)	+	+	+	n.d.	n.d.	n.d.
Dreissena polymorpha (Pallas)	*	*		-	-	-
Pisidium sp. indet.		**	**	-	1282 ± 397	39 ± 32
Pisidium casertanum Malm			*	-	-	12 ± 9
Pisidium henslowanum (Sheppard)	*	*	**	-	651 ± 429	156 ± 42
Pisidium moitessierianum Paladilhe		*	**	-	120 ± 96	160 ± 47
Pisidium supinum Schmidt		*	*	-	26 ± 14	3 ± 3
Pisidium subtruncatum Malm			*	-	-	4 ± 4
Sphaerium corneum (L.)	*	*		-	17 ± 17	-
Sphaerium solidum Normand	*			-	-	-
Valvata piscinalis (Müller)		**	*	-	614 ± 293	3 ± 3
Potamopyrgus antipodarum (Gray)		**	*	-	764 ± 240	4 ± 4
CRUSTACEA						
Neomysis integer (Leach)		*		-	-	-
Corophium sp.				-	279 ± 244	-
Corophium curvispinum Sars	+	+		n.d.	n.d.	-
Corophium multisetosum Stock		*		-	n.d.	-
Gammarus tigrinus Sexton	**	***	*	68 ± 30	1908 ± 1274	33 ± 19
DIPTERA						
Ceratopogonidae	*	**		-	305 ± 142	-
Chironomidae indet.				-	214 ± 214	523 ± 221
Chironomus sp.				-	34 ± 20	465 ± 129
Chironomus acutiventris Wülker, Ryser & Scholl		*	*	-	51 ± 51	109 ± 49
Chironomus bernensis Wülker & Klötzli		*		-	9 ± 9	-
Chironomus muratensis Ryser, Scholl & Wülker		*	*	-	9 ± 9	131 ± 76
Chironomus nudiventris Ryser, Scholl & Wülker		*	**	-	17 ± 17	245 ± 83
Chironomus plumosus (L.)		*		-	-	-
Cladotanytarsus sp.	*	***	***	14 ± 14	545 ± 305	5069 ± 1394
Cricotopus sp.		*	*	-	9 ± 9	4 ± 4
Cricotopus gr. *sylvestris*			*	-	-	22 ± 18
Cryptochironomus sp.	*	*	**	41 ± 41	52 ± 30	186 ± 62
Dicrotendipes nervosus (Staeger)	*	*		-	9 ± 9	3 ± 2
Einfeldia dissidens (Walker)		**	*	-	2617 ± 1251	8 ± 5
Harnischia sp.	*	*	*	-	9 ± 9	12 ± 9
Kloosia pusilla (L.)	***			1613 ± 405	-	-
Lipiniella arenicola Shilova			***	-	-	1451 ± 298
Microchironomus tener (Kieffer)		*	*	-	148 ± 139	5 ± 4
Paracladius conversus (Walker)		*		-	17 ±+ 12	-
Parachironomus arcuatus agg.		*		-	-	-
Paratendipes albimanus agg.	*	*		27 ± 27	17 ± 12	-
Polypedilum scalaenum Schrank	**	*	*	474 ± 262	9 ± 9	4 ± 4
Polypedilum nubeculosum agg.		*	*	70 ± 54	55 ± 35	-
Procladius sp.	*	**	**	14 ± 14	112 ± 46	98 ± 34
Prodiamesa olivacea Meigen		*		-	9 ± 9	-
Psectrocladius sp.		*	*	-	9 ± 9	11 ± 6
Stictochironomus histrio (Fabricius)			**	-	-	138 ± 42
Tanytarsus sp.	*			-	-	-
Tanypus kraatzi (Kieffer)		*		-	9 ± 9	-
Tanypus punctipennis Meigen		*		-	9 ± 9	-
Tanypus vilipennis (Kieffer)		*		-	9 ± 9	-

Table 5. Frequencies (%) of occurrence in palaeoecological samples from several river branches of the Rhine and comparison with results of this study and present abundance in the Rhine and study area. R/W: Rhine and Waal; BM: Boven Merwede; NM: Nieuwe Merwede; IJ: River IJssel near Kampen. Habitat types: R= river sand, S= silt, E= eurytope.

	river stretch				Habitat	Characteristic	Present
	R/W	BM	NM	IJ	type	for assemblage	abundance
Number of cores	2	1	2	2			
Total number of samples	4	4	20	22			
Ephemeroptera							
Ephemera sp.	50	25	10	5	R	-	extinct
Ephoron virgo (Olivier)	75	-	10	-	R	-	recovering
Palingenia longicauda Olivier.	-	50	-	18	S	-	extinct
Trichoptera							
Psychomyia pusilla (Fabricius)	100	50	44	60	R	-	extinct
Sericostomatidae	25	-	20	5	R	-	extinct
Molanna sp.	-	-	-	5	R	-	extinct
Mystacides longicornis (L.)	25	25	-	10	R	-	rare
Chironomidae							
Beckidia zabolotzkyi (Goetghebuer)	-	25	-	18	R	-	extinct
Chernovskiia macrocera (Tshernovskij)	-	25	5	-	R	-	extinct
Demicryptochironomus vulneratus (Zetterstedt)	-	25	5	-	R	-	extinct
Heterotrissocladius marcidus (Walker)	-	-	5	-	R	-	extinct
Kloosia pusilla (L.)	-	-	-	5	R	river sand	common
Monodiamesa bathyphila Kieffer	25	-	-	-	R	-	extinct
Paracladopelma sp.	-	-	10	-	R	-	extinct
Parametrocnemius stylatus (Kieffer)	-	25	45	-	R	-	extinct
Paratendipes connectens 3 Lipina	-	25	5	-	R	-	extinct
Paratendipes albimanus agg.	25	100	65	23	R	river sand	rare
Paratendipes intermedius Tshernovskij	-	25	5	-	R	-	extinct
Polypedilum scalaenum Schrank	100	50	75	82	R	river sand	abundant
Potthastia gaedii (Meigen)	-	25	30	14	R	-	extinct
Pseudochironomus sp.	-	-	-	5			
Pseudochironomus prasinatus (Staeger)	-	-	5	-			
Stempellina sp.	-	-	30	9	R	-	rare
Tanytarsus brundini agg.	25	50	55	23	R	-	rare
Cladotanytarsus mancus agg.	-	-	35	86	R	sandy basin	abundant
Lipiniella arenicola Shilova	50	50	15	41	R	sandy basin	common
Stictochironomus sp.	75	50	25	59	R	sandy basin	common
Chironomus plumosus agg.	100	100	85	100	S	-	common
Chironomus uliginosus agg.	-	-	100	59	S	-	common
Cladopelma laccophila (Kieffer)	50	-	45	55	S	-	rare
Cryptotendipes holsatus agg.	-	-	20	5	S	-	very rare
Einfeldia dissidens (Walker)	-	-	-	9	S	sed. area silt	locally abundant
Endochironomus albipennis (Meigen)	50	50	10	73	S	-	common
Endochironomus tendens Fabricius	25	-	10	5	S	-	rare
Glyptotendipes pallens agg.	75	75	85	100	S	-	common
Harnischia sp.	50	25	40	64	S	-	common
Microchironomus tener (Kieffer)	50	25	30	41	S	sed. area silt	common
Microtendipes chloris agg.	100	50	100	64	S	-	very rare
Paracladius conversus agg.	50	25	-	9	S	sed. area silt	locally common
Phaenopsectra sp.	25	25	65	36	S	-	very rare
Polypedilum nubeculosum (Meigen)	100	50	45	95	S	-	common
Prodiamesa olivacea Meigen	75	75	40	36	S	-	rare
Robackia demeijerei (Kruseman)	-	-	30	14	S	-	extinct
Tanypus sp.	-	-	-	9	S	-	rare
Zavrelia pentatoma Kieffer	-	-	15	-	S	-	flood plain
Cryptochironomus sp.	100	50	65	95	E	-	common
Nanocladius sp.	-	50	70	14	E	-	abundant
Procladius sp.	100	100	50	100	E	-	common

Recent colonizers

During the period of investigation, several invertebrate species (re)colonized the Dutch part of the River Rhine (Den Hartog *et al.*, 1992): *Corbicula fluminalis* and *C. fluminea* (Bij de Vaate & Greijdanus-Klaas, 1990), *Corophium curvispinum* (Van den Brink *et al.*, 1989) and *Ephoron virgo* (Bij de Vaate *et al.*, 1992).
The survey in 1992 showed that both *Corbicula* species occur in the larger part of the area investigated. *C. fluminalis* was only absent from the Haringvliet and River Lek, while *C. fluminea* was absent from the Nieuwe Merwede. *C. fluminalis* was most abundant in the littoral river sand habitat, with a density ranging from 800 to 3070 m^{-2} (n=4). The highest density was found in the River Waal within a *Potamogeton pectinatus* L. stand. Low densities of this species were found in the lower Nieuwe Merwede, the Beneden Merwede and the Oude Maas. *C. fluminea* was most abundant in the Lek and occurred in low densities in the Boven Merwede, Beneden Merwede, Oude Maas, Hollandsch Diep and Haringvliet near the mouth of the Spui. *Corbicula* species were not found at the other sites in the Haringvliet. Both *Corbicula* species occurred together between the sites LO and HP, a stretch of 46 km (Fig. 1).
Corophium curvispinum, which can occur in very high densities on stones in the River Rhine (Van den Brink *et al.*, 1991), was found in low densities ($n < 250$ m^{-2}) at sampling sites in the Waal, Nieuwe Merwede and Hollandsch Diep. One specimen of the mayfly *Ephoron virgo* was found in the Boven Merwede. Several emerging specimens of *Caenis luctuosa* were found in the Oude Maas, suggesting that their larvae had lived in the sediments of this river section. Both indigenous species have recently recolonized this section of the River Rhine (Bij de Vaate *et al.*, 1992).

Palaeoecological analysis

Twenty-four taxa were assigned to former littoral sand habitats of the Lower Rhine (Table 5). One of these (*Kloosia pusilla*) is nowadays an indicator species and one (*Polypedilum scalaenum* agg.) is an accompanying taxon of the 'littoral river sand' assemblage. The other taxa of the former river sand have become rare (three taxa) or extinct (fourteen taxa) from the Dutch part of the Rhine and Meuse.
Nineteen taxa were assigned to the former silt habitat. One of these (*Einfeldia dissidens*) is an indicator species and two (*Microchironomus tener* and *Paracladius conversus* agg.) are accompanying species of the 'littoral sedimentation area silt' assemblage. From the other taxa, seven are still common, seven have become rare or very rare and two (*Palingenia longicauda* and *Robackia demeijerei)* have become extinct.

Discussion

Present state of littoral zoobenthos

The present macrozoobentic species composition of the enclosed Rhine-Meuse Delta area has little in common with the former brackish communities of the Haringvliet (Wolff, 1973), and those of other estuaries, such as the Scheldt (Ysebaert *et al.*, 1993) and those present in the German Bight (Michaelis *et al.*, 1992). No brackish fauna was found, while the most abundant taxa found are absent from or scarce under estuarine conditions. The differences are attributable to the completely different hydrodynamical, salinity and morphological conditions created by enclosing the Rhine-Meuse estuary.

Only the former freshwater sections showed some similarity with the present macrozoobenthos. For example, most Oligochaeta (Verdonschot, 1981) and Pisidiidae (Kuiper & Wolff, 1970) of the former freshwater section were found in this study as well.

Most species found occur in large rivers and/or lakes. *Propappus* sp., an indicator of the 'littoral river sand' assemblage, was abundant in medium grained sands (mean diameter 355-500 µm) in the main stream of the lower Meuse (Peeters, 1988).

Propappus sp., was also very abundant in the River Dnieper (Ukrain), where very high densities were found in pure sands in the middle of the main channel. In this basin, *Vejdovskyella intermedia* and *Amphichaeta leydigi* were found in slightly or moderately muddy sands (Fomenko, 1980). The indicator species of the 'littoral river sand' assemblage were also found in the profundal muddy sediments of the eastern Hollandsch Diep, (Klink & Dudok van Heel, 1993). These animals, however, probably originated from upstream parts of the River Rhine, since densities were especially high in periods of high Rhine discharges. *Amphichaeta leydigi* and *Vejdovskyella comata*, the indicator species of the 'littoral river sand' assemblage may have been overlooked in many studies because of their small size. Perhaps the high densities of these oligochaetes are characteristic for sandy habitats in (large) rivers. *Kloosia pusilla*, another indicator of the 'littoral river sand' assemblage, lives in shifting sands (Pagast, 1936) and is known from several large rivers, *e.g.* the Volga, the Danube and the Po (Reiss, 1988).

The recent colonization by *C. fluminea* and *C. fluminalis*, both preferring lotic water systems (Belanger *et al.*, 1985), may have caused a change in the ecological state of the littoral river sand, since these species now have a great share in the total invertebrate biomass.

Einfeldia dissidens, an indicator of the 'littoral sediment area silt' assemblage, is known to prefer shallow silty habitats with a low rate of disturbance (unpublished data A.G. Klink). *P. supinum*, an accompanying species of this assemblage, prefers slight water movement (Kuiper & Wolff, 1970). Before 1970, this species was also common in the River Meuse and its branches. The low average density (26 m^{-2}) is normal; Kuiper & Wolff (1970) never found more than 13 individuals m^{-2}.

Of course, the indicators of the 'littoral sandy basin' assemblage are new in this former brackish area. Before 1970, the pisidiid indicators of this assemblage (*P. henslowanum* and *P. moitessierianum*) occurred in the freshwater tidal parts of the Delta. They lived in mud or fine sands and preferred the quiet parts of rivers (Kuiper & Wolff, 1970). The chironomid indicators of this assemblage are common in several Dutch water bodies: *Lipiniella arenicola* is common in sands of alkaline lakes (Smit *et al.*, 1993); the indicators *Cladotanytarsus* sp. and *Stictochironomus* sp. coexist in several water bodies, such as eutrophic Lake Maarsseveen (Heinis, 1993), well oxygenated clear, vegetated standing or slowly flowing waters in the province of Overijssel (Verdonschot, 1992) and poorly buffered lentic waters (Leuven *et al.*, 1987).

Relation with environmental processes

'River sand' assemblage. In the littoral zone of the river, the high turbulence almost continuously washes out the fine particles. Therefore, the interstitial spaces in the coarse sediment are not silted. Since algal food is amply present in the water column (Admiraal *et al.*, 1993), the interstitial spaces are an excellent habitat for zoobenthos: both shelter and food are present. The 'littoral river sand' assemblage consists mainly of 'interstitial' zoobenthos. The small size of the Naididae (*Amphichaeta leydigi, Vejdovskyella comata, V. intermedia* and *Paranais frici*) and Enchytraeidae (*e.g. Propappus* sp.) leaves no doubt about this. *Kloosia pusilla*, the most abundant chironomid, also inhabits the interstitial spaces: only third instar larvae were found, with a head capsule width of 68-84 µm (mean 77 µm, n=8). They seem small enough to live between the coarse sand grains with mean diameters exceeding 500 µm (pers. obs. H. Smit). *Corbicula* spp. are the only abundant species in this habitat which do not belong to the interstitial fauna. Their thick and heavy shells and their capability to burrow partly into the sediment obviously enable these molluscs to survive in this physically stressed habitat.

'Littoral sedimentation area silt' assemblage. When turbulence diminishes, sedimentation of finer particles becomes more apparent. These particles are a suitable food source for deposit-feeders. On quiet shallow sediments microphytobenthos may develop. The 'littoral sedimentation area silt' assemblage is characterized by invertebrates inhabiting both silty sand and silt. The key species of this assemblage are collectors-gatherers, grazers or filterfeeders. Bijkerk (1993) showed that the larvae of the chironomid *E. dissidens* feed by grazing and Haynes & Taylor (1984) showed that the gastropod *P. antipodarum* feeds both by collecting and grazing. The lower sediment disturbance allows the light-weight *Pisidium* species, which can easily be swept away by waves, to survive in the sedimentation area. This is in contrast with the littoral river sand habitat, where they were found only occasionally.

'Littoral sandy basin' assemblage. The higher transparency in the Haringvliet enables a high autotrophic microphytobenthos production (mainly diatoms and green algae) in the littoral zone (Bijkerk, 1993). Fine sand prevails over silty sediments. Wind exposure and to a lesser extent geomorphological history determine local differences in the area. The chironomid indicators live in fine sand and silty sand sediments and feed by grazing the sediment surface. *Lipiniella arenicola* is restricted to sands with low silt contents (Smit *et al.*, 1993), whereas *Cladotanytarsus* sp. is also abundant at sites with a higher silt content. In sheltered places rich in silt (like site BS), the assemblage shows some overlap with that in the sedimentation area. In very exposed areas, the sand is mobile throughout the year. In those habitats *L. arenicola* thrives, partly because of its capability to construct strong tubes and to burrow deep in the sediment (Smit *et al.*, 1991).

There are obvious differences with the littoral river sand. First, the littoral river sand is very tightly packed, whereas the exposed Haringvliet sand is not. Secondly, the mean grain size of the sand in the Haringvliet is smaller. This may be a reason why the indicators of the 'littoral river sand' assemblage are scarce or lacking in the Haringvliet.

Interstitial fauna

In this study, we found an interstitial invertebrate assemblage, occurring in high densities between the sand grains in the littoral zone of the river bed. This was possible, since we used sieves with a small mesh size (250 µm). So far, the river sand community has been regarded as extremely poor (Van Urk & Smit, 1989). It is beyond doubt that the interstitial fauna has simply been overlooked. This is attributable to the larger mesh size of the sieves used by earlier investigators (Wolff, 1973: 1 mm; Van Urk & Smit, 1989: 0.5 mm). In this study, a high number of larvae of the chironomid *Kloosia pusilla* was found. Adults of this species have been recorded in the 1930's several times from the Nieuwe Merwede and Beneden Merwede (Kruseman, 1933). Outside the River Rhine, however, this species has not been observed. It is possible that *K. pusilla* has recently recolonized the Netherlands part of the Rhine. In May 1993, larvae of this species were observed for the first time and in high numbers in the littoral sands of the Nederrijn (a River Rhine branch) near Opheusden, a site which had been sampled during 20 consecutive years (pers. comm. J.J.P. Gardeniers).

Species richness compared with palaeoecological data

Palaeoecological analysis has shown that the littoral river sand habitat has become strongly impoverished in the last century. The impoverishment in this habitat was much greater, than in the silt habitat, from where only two taxa have become extinct. Apparently, environmental conditions changed more drastically in the littoral river sand habitat: three formerly common taxa (*Lipiniella arenicola, Stictochironomus. histrio* and *Cladotanytarsus* sp.) are now absent from the littoral river sand, but are indicator or accompanying taxa of the 'littoral sandy basin' assemblage. Since these three species mainly feed on microphytobenthos, this food source was probably vital in the former littoral river sand habitat. Lauterborn (1918) observed a microbenthic algae cover of the shallow bottom of the Lower Rhine. Water transparency must have been higher, and the mean depth much lower than today. A few centuries ago the Waal was a 500-800 m wide braiding river. The present width of the regulated Waal is only about 260 m and the depths have increased to several metres. Today, light can no longer penetrate to the bottom, the light extinction coefficient being about 2 m^{-1} (Van Urk & Smit, 1989). Moreover, the present river banks -the last remaining shallow

zones- experience too much turbulence due to the wave action caused by passing ships, to be a suitable substrate for microphytobenthos production.
Changes in the silt-inhabiting fauna were less dramatic than those in the littoral river sand habitat. Both habitat conditions and sediment contamination have contributed to these changes. *Microtendipes* gr. *chloris*, the most common chironomid in the palaeoecological samples, is still common in flood plain waters connected to the Rhine (Van den Brink & Van der Velde, 1991). It is, however, rare in the main channel and was not found in the areas investigated. The scarcity of the genus *Chironomus*, however, is probably related to the high contamination levels in sediments. This relation was shown by Van Urk *et al.* (1992) for *Ch.* cf. *plumosus*, in the outlet of the River IJssel, another Rhine branch. *Ch. plumosus* lives in habitats similar to that of the 'littoral sedimentation area silt' assemblage.

Influence of sampling strategy
The samples in this study were taken over a period of 6 years and in different seasons. One could argue whether assemblages can be derived from such a dataset. Of course, macrozoobenthic species composition and densities are generally variable in space and time and no doubt this is also the case in this study. In spite of this, three assemblages could be distinguished, which were mainly related to large scale differences in hydraulics and geomorphology. Since geomorphological processes proceed only slowly, a maximum difference in sampling date of six years is unlikely to have seriously affected the composition of the three assemblages. Moreover, no sudden morphological changes have occurred in this period.

The influence of the season of sampling on the composition of the assemblages is probably restricted, since sampling occurred in different months and the chironomid and pisidiid indicator species are known to occur in all seasons in the area (Smit, Van der Velde & Dirksen, this thesis; Klink & Dudok van Heel, 1993). Seasonality may, however, have influenced the oligochaete indicator and accompanying taxa of the 'littoral river sand' assemblage. Most samples from the littoral river sand were taken in spring, when the Naididae are most numerous.

Conclusions

1. Three main assemblages were distinguished: 1) a 'littoral river sand' assemblage, 2) a 'littoral sedimentation area silt' assemblage and 3) a 'littoral sandy basin' assemblage.
2. From the River Waal to the Haringvliet dam, the fauna gradually changed under the influence of a series of factors. These included decreasing current velocities, decreasing erosive power of ship-generated waves, a sedimentation peak and higher water transparencies in the Haringvliet.
3. The littoral river sand, generally considered a very poor habitat, contained high densities of interstitially living worms (Naididae and Enchytraeidae) and of the chironomid *Kloosia pusilla*.
4. Immigrant species contributed little to the macrozoobenthic densities. Only in the 'littoral river sand' assemblage, *Corbicula* sp. sometimes reached high densities.
5. The river sand insect fauna is strongly impoverished compared with palaeoecological samples from Rhine deposits. The river silt fauna is less impoverished, in spite of the high contamination levels.

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