Degradation and recovery
of the freshwater fauna
in the lower sections
of the rivers Rhine and Meuse

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Abraham bij de Vaate

CONTENT

CHAPTER 1

GENERAL INTRODUCTION AND OUTLINE OF THE THESIS

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INTRODUCTION

The valleys of the rivers Rhine and Meuse, including the Rhine delta, have been densely populated for many centuries. From the point of view of water management these rivers have different functions, varying from discharge of water to transport route (Anonymous 2001) (Fig. 1). Anthropogenic influence evolved in the 12th century with the construction of levees along the main channel for the purpose of protecting inhabitants against flooding (Middelkoop 1997).
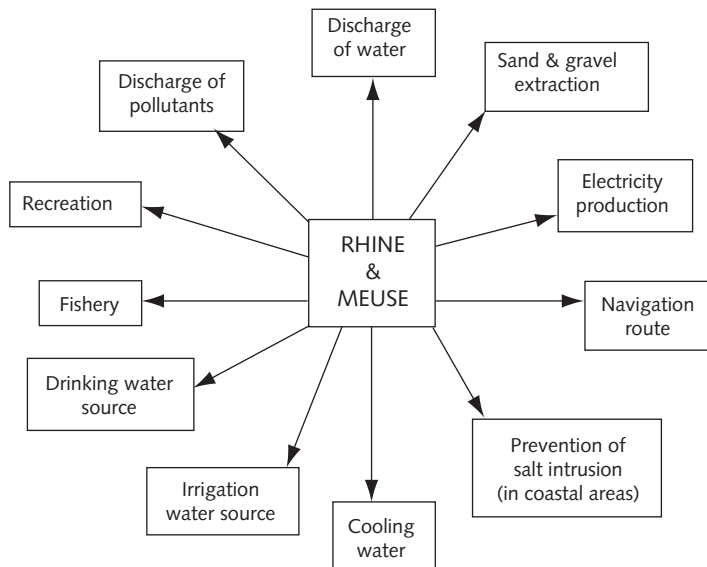
Figure 1. *Functions of the rivers Rhine and Meuse.*

Later on, shipping asked for the adjustment of the main channel to allow larger freighters sailing on both rivers. These activities led to irreversible changes, not only in riverine habitats caused by the disruption of the natural evolution of backwaters, but also in the disappearance of aquatic-terrestrial transition zones (e.g., Gore & Shields 1995, Sparks 1995, Galat *et al.* 1998, Nienhuis & Leuven 2001). In the delta area (in The Netherlands) the smaller distributaries were dammed, and the remaining larger ones (called IJssel, Nederrijn and Waal, Fig. 2) changed from meandering streams, with extensive floodplains, into shipping canals surrounded by relatively low so-called summer dikes on the banks and major dikes at a greater distance (Fig. 3) (Middelkoop, 1997, Van Urk & Smit 1989). Moreover, from the 19th century the summer beds in the distributaries were fixed with groynes to promote river bed erosion (Van Urk 1984, Kalweit 1993), a measure to deepen the channel in a 'natural' way for shipping.

Effects of domestic and industrial waste water discharges into the whole catchment area surfaced in the second part of the 19th and first part of the 20th century and resulted in a strong reduction of population sizes and large scale extinction of many riverine organisms (Klink 1989, Lelek 1989, Van den Brink *et al.* 1990). However, from the 1960s measures have been taken to improve the water quality (Cals *et al.* 1996). The first signs of water quality improvement became visible in macroinvertebrate and fish communities from the second half of the 1970s (Lelek 1989, Van Urk & Bij de Vaate 1990, Admiraal *et al.* 1993).

An international ecological rehabilitation programme for the River Rhine was initiated in 1987 after the so-called 'Sandoz-accident' in November 1986; an environmental disaster caused by a fire control in the Sandoz chemical concern in the vicinity of the Swiss town of Basel. Heavy polluted extinguishing water was running then into the river (Van Dijk *et al.* 1995). In addition to further water quality improvement, ecological rehabilitation of the River Rhine in The Netherlands has been focused from that time on the longitudinal connectivity of the main channel and on the river forelands, the remaining part of the floodplain between the summer and major dikes on both sides of the river channel (Fig. 3) (Schropp & Bakker 1998). The reason for exclusion of the main channel in other aspects of river rehabilitation is its function as a transport route and the need for unhampered discharge of water, ice and suspended matter.

Floodplain rehabilitation and nature development in the Dutch part of the River Rhine has been based on insights formulated by De Bruin *et al.* (1987) and WWF (1992). The aim is to restore, as much as possible, the natural dynamics in the forelands with regard to its imposed functions (Fig. 1) (Cals *et al.* 1996). Helmer *et al.* (1991) developed a plan to combine nature development in the Grensmaas stretch of the River Meuse with the demand for gravel. Excavation of the floodplain offers the gravel-miners a valuable resource, while simultaneously enhancing the natural potentials of the river. It also contributes to flood protection by facilitating the water flow in the river during extreme high discharges (Van Leussen *et al.* 2000).

Effects of biotope alterations on the fauna in the Rhine delta and in the lower sections of the River Meuse are the topic of this thesis. Results of investigations performed from the 1980s must lead to a better insight into the functioning of the river ecosystem when influenced by

Figure 2. *The rivers Rhine and Meuse in the Netherlands.*

severe anthropogenic stress. In discussing ecological rehabilitation or river restoration, one should consider that most of the alterations in both rivers are irreversible in practice, due to unacceptable social and economical impacts.

RIVER ENGINEERING

River regulation and damming are considered to have an important destructive impact on biota due to terrestrialisation and fragmentation of the river floodplain system (Schiemer 1999). Alterations in the catchment area changed runoff patterns. Its originally large water storage capacity had reduced strongly with the result that the relatively slow release of water during wet periods had disappeared. This led to increased water level fluctuations, which in turn resulted in alterations in sediment transport. The forelands between the summer and winter dikes (Fig. 3) became a trap for fine-grained sediment and in the course of time the natural relief was levelled down by the deposition of clay and by activities of farmers and river managers (Nienhuis & Leuven 2001). Natural geomorphological processes changed drastically, and were captured in straight jackets by dikes, groynes and weirs. During and after the process of river normalisation, the lateral connectivity between the main channel and the water bodies in the forelands gradually decreased due to increasing incision of the river bed in the remaining single channel. This resulted in a severe loss of shallow lotic habitats.
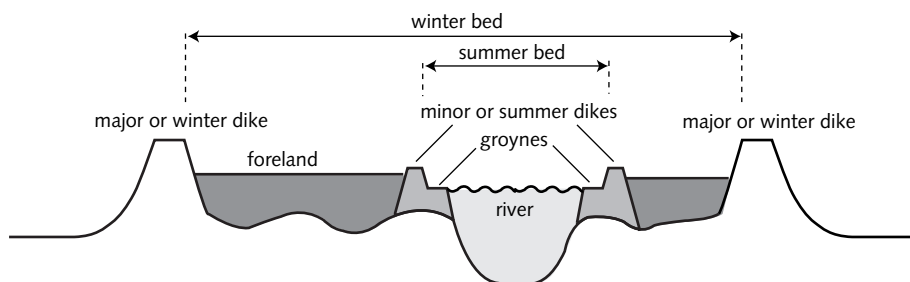
Figure 3. *Cross section of the large rivers in The Netherlands.*

River Rhine

After embankments in the 12th-14th century, of both the distributaries in the Rhine delta and the River Meuse, the former flood plain was regularly exposed to flooding as the result of dike bursts, particularly in the 18th and in the first part of the 19th century. These bursts were the result of a combination of the poor discharge capacity of the river channels and the relatively poor condition of the river dikes (Middelkoop 1997). Ice jams in spring were an important cause of the bursts (Driessen 1994).

River engineering activities in the main channel of the Rhine distributaries initially focused on the improvement of the discharge of water and ice, and thereafter on the improvement of navigation. Adjustments of the discharge distribution at the bifurcations in the Rhine delta contributed to those improvements. The first adjustment occurred in the 17th century. Main

interventions in the past three centuries are listed in table 1 (Van der Ven 1993, Middelkoop 1997, 1998).

Table 1. *Main interventions in the Rhine delta in the past three centuries.*

Period/year	Intervention
1707	Opening of the Pannerdensch Kanaal, constructed for the improvement of the northern distributary at the first bifurcation in the Rhine delta. Later on this bifurcation was adjusted several times.
1727-1734	Damming of the connections between the rivers Meuse and Waal at Heerewaarden and Voorn. Both connections served as an overflow for the River Waal in periods with high Rhine discharge
1775	Reconstruction of the second bifurcation where the Pannerdensch Kanaal splits into the rivers Nederrijn and IJssel.
1850-1870	Digging of the Nieuwe Merwede.
1850-1885	Normalisation of the river IJssel.
1868	Opening of the Nieuwe Waterweg. Construction of this canal was needed to improve the entrance to the harbours of Rotterdam for sea-going vessels. It forms an artificial outlet in the Rhine delta.
1875-1916	Normalisation of the river Waal
1932	Completion of the Zuiderzee damming, creating Lake IJsselmeer.
1954-1967	Construction of three weirs in the Nederrijn/Lek.
1970	Completion of damming the Haringvliet, the joint estuary of the rivers Rhine and Meuse.
1989-present	Lowering of forelands and construction of secondary channels along the distributaries.

River Meuse

As with the Rhine delta, river engineering in the river Meuse focused on improvement of the discharge of water and ice. Later on, improvement of navigation possibilities became an important issue. Being a rain river, with relatively low discharge during summer and autumn, weirs were needed to maintain a desired water level for navigation. Main activities performed in the past two centuries are summarised in table 2 (Berger 1992, Van der Ven 1993, Middelkoop 1997, 1998, Bosch & Van der Ham 1998).

Table 2.   *Main interventions in the River Meuse in the past two centuries.*

Period/year	Intervention
1856	Damming of the connection with the River Waal near the fortification of St. Andries.
1875	Start of the normalisation.
1885-1904	Damming of the outlet of the River Meuse into the River Waal at Gorinchem. For this intervention a new outlet for the river Meuse was constructed. Main features of this activity were: (a) construction of the first part of the outlet, the Bergse Maas (1887-1894), and (b) normalisation of the Amer, the second part, followed by (c) damming of the Meuse stretch called Andelse Maas. Main problems at that the former outlet were the floodings occurring when discharge peaks of both rivers coincided.
1918-1926	First canalisation. During this period, five complexes of weirs and ship locks were constructed at the places of Grave, Sambeek, Belfeld, Roermond and Linne, including the construction of the Meuse-Waal canal, a regulated shipping canal between both rivers in the vicinity of Nijmegen. All these complexes were equipped with a fish ladder (Denil type). However, the weirs became barriers in the longitudinal connectivity of the river due to the malfunctioning of the fish ladders (Muyres, Organisatie ter Verbetering van de Binnenvisserij, Nieuwegein, pers. mededeling). During this period and afterwards, the banks of the main channel were reinforced with riprap, an artificial substrate in the downstream part of the river where coarse bed load (pebbles and gravel) is absent. Inhabitants of such a habitat were able to colonise that part of the river at that time.
1930-1940	Meander cut-offs. The result was shortening of the river channel. The 42 km long section between Grave and Heerewaarde, for example, reduced with 23 km (Van der Ven 1993).
1926-1934	Second canalisation. This activity started after the flood of January 1, 1926, when discharge of the river reached its highest discharge ever measured (3,000 m^2 s^{-1} measured at Borgharen) till 1993. During the second canalisation period two complexes of weirs and ship locks were constructed at the villages of Borgharen (completed in 1935) and Lith (completed in 1936), the up- and downstream most weirs respectively in the Dutch part of the river.
1926-1935	Construction of the Juliana canal. This lateral navigation canal, connects the towns of Maasbracht and Maastricht. Adjustment for navigation of the river stretch between both towns (called Grensmaas, of which the thalweg forms the border between Belgium and The Netherlands) was no longer necessary. Problems between both countries on river management were solved in this way and the positive effect was that this river stretch has been least disturbed by river engineering.
1950-present	Sand and gravel extraction in the main channel and in the forelands.
1970	Completion of the Haringvliet damming, the joint estuary of the rivers Rhine and Meuse.
1989-1990	Construction of hydro-electric power station in the weirs at Linne (1989, 11.5 MWatt) and Lith (1990, 14 MWatt).
1989-present	Construction of pool type fish ladders at the weirs. By the end of 2002, such a ladder was still absent at the Borgharen and Grave weirs.
1995-present	Studies on widening and deepening the main channel, followed by realisation. This measure was considered to be needed for two reasons: (a) for improvement of navigation (larger barges), and (b) to improve discharge, especially to lower water level during discharge peaks. With regard to the latter reason, immediate causes were the extreme discharges in 1993 and 1995 when maximum discharges were 3,050 and 2,820 m^2 s^{-1} respectively.

WATER QUALITY DEVELOPMENT

Klink (1989) distinguished four stages of river pollution covering more or less successive phases in pollution history. Pollution started with the discharge of organic substances in domestic waste waters, causing an increase of the chemical and biological oxygen demand (COD and BOD), and resulting in a decrease of the dissolved oxygen concentration. This was followed by the pollution from heavy metals, being the combined result of mining and industrial activity. The third stage is formed by pollution with chlorinated organic compounds (e.g., PCB's, PAH's), and the lasting the contamination by pesticides. Pollution in both the later mentioned stages are caused by organic micro-pollutants, which have been produced by the chemical industry in the river valleys (point sources of pollution), are everywhere used, causing diffuse pollution.

Discharge of industrial waste water became a serious problem during the process of industrialisation of the river valleys in the 19th century. However, water quality data from the rivers Rhine and Meuse are very scarce from the period before 1965. Analysis of dated sediment layers in the forelands have shown to be a helpful tool in reconstructing pollution history with heavy metals and organic micropollutants (Klink, 1989, Rang & Schouten 1989, Beurskens *et al.* 1993).

The implementation of national laws against pollution and protection of the environment, and the establishment (in 1950) of the International Commission for Protection of the River Rhine, which got its internationally recognised juridical basis after signing the Treaty of Bern in 1963, were important impulses for the development and realisation of chemical monitoring programs (Dieperink 1997). Permanent monitoring stations were erected at several places. Those in the vicinity of the places Lobith and Eijsden, in the rivers Rhine at the German-Dutch border and Meuse at the Belgian-Dutch border respectively, became the primary Dutch reference stations for water quality developments in both rivers.

The Rhine and Meuse Action Programmes, launched in 1987 and 1997 respectively, initially focused on water quality improvement. The countries in the Rhine basin, united in the International Commission for Protection of the River Rhine against Pollution (ICPR), agreed upon a target reduction of at least 50% of the pollution caused by priority compounds by the year 1995 (compared with the situation in 1985). Furthermore, water quality targets for the river Rhine were set for about 50 priority compounds, not only based on requirements for drinking water production and the protection of aquatic life, but also on human tolerance levels for fish consumption (Van Dijk *et al.* 1995). The International Commission on Protection of the River Meuse (ICPM), in which the countries in the Meuse basin have been united from 1994, did not set specific targets for pollution reduction and improvement of the ecological quality (ICPM 1997).

Although calamities in the River Rhine caused a political reveille needed for the rehabilitation of both the rivers Rhine and Meuse (Dieperink 1997, *viz.* the endosulphan and the so-called Sandoz calamity in 1969 and 1986 respectively), calamitous pollution accidents still occur including dissolved oxygen deficits in the river Meuse upstream from the Grensmaas stretch

(Breukel 2001). Long and short term impacts on the river fauna of these short lasting accidents are unknown due to the lack of suitable monitoring programs for short term impacts. Furthermore, it is difficult to assign effects of specific pollutants on colonisation, growth and reproduction of autochthonous aquatic fauna in an environment of continuous changing water quality variables in the case of long term effects (e.g., Hellawell 1989).

River Rhine

Around the turn of the 19th and 20th centuries, the river was already seriously polluted with domestic and industrial waste water (Tittizer & Krebs 1996). Phenols in the river made the commercially interesting fish species, such as Atlantic salmon (*Salmo salar*) and eel (*Anguilla anguilla*), unfit for consumption (Lobrecht & Van Os 1977, Van Drimmelen 1987). Rock bottom of the river pollution was reached in the first part of the 1970s. At that time the river water was acute toxic for water fleas and trout embryos, and caused malformation and other effects in fish and insect larvae (Alink *et al.* 1980, Poels *et al.* 1980, Slooff 1982[A], 1982[B], 1983, Slooff *et al.*, 1983, Van Urk & Kerkum 1986, 1987, Van der Gaag 1987).

From the second half of the 1970s water quality improved considerably because of:
a. the implementation of environmental protection laws;
b. the construction of waste water treatment plants;
c. international agreements;
d. policy foundation with monitoring results;
e. improvement of production techniques;
f. reduction of spills (e.g., caused by calamities);
g. increased public awareness.

Firstly, focussing on priority substances, the organic load and the amount of polluting substances such as heavy metals and organic micro-pollutants in discharges of domestic and industrial waste water decreased dramatically within a period of approximately 10 years (De Kruijf, 1982, Van der Weijden & Middelburg 1989, Heymen & Van der Weijden 1991, Van der Klei *et al.* 1991). A significant decrease of the organic load resulted in improved oxygen conditions for the river fauna (Table 3, Fig. 4). Between 1952 and 1972 the oxygen concentrations, measured at the German-Dutch border, had significantly decreased. However, from 1973 onwards, a significant improvement was observed (Table 3). Of relevance here is the fact that the yearly observed minimum concentration in the latter period increased from 2 to 8 mg l^{-1}.

Table 3. *One-way ANOVA of trends in water quality parameters measured in the River Rhine at the German-Dutch border.*

Parameter	Unit	Period	N [a]	Slope [b]	R^2	F	P
O_2	mg l^{-1}	1952-1972	21	-0.019	0.560	26	<0.001
O_2	mg l^{-1}	1973-2000	28	0.021	0.831	134	<0.001
COD	mg l^{-1}	1968-1996	23	-0.043	0.846	122	<0.001
Chlorophyll a	µg l^{-1}	1977-2000	23	-0.070	0.610	33	<0.001
Cl^-	mg l^{-1}	1971-2000	30	-0.021	0.600	42	<0.001
Cl^-	mg l^{-1}	1990-2000	11	-0.070	0.778	31	<0.001
Cd_{total}	µg l^{-1}	1975-2000	26	-0.179	0.834	127	<0.001
Cu_{total}	µg l^{-1}	1970-2000	31	-0.076	0.870	202	<0.001
Hg_{total}	µg l^{-1}	1971-2000	30	-0.033	0.900	263	<0.001
Pb_{total}	µg l^{-1}	1971-2000	30	-0.144	0.867	191	<0.001
Zn_{total}	µg l^{-1}	1971-2000	30	-0.043	0.922	344	<0.001
Mineral oil	µg kg^{-1}	1972-1987	16	-0.270	0.888	111	<0.001
PCB_{sum} [c]	µg l^{-1}	1988-2000	13	-0.054	0.463	11	<0.01
PAH's [d]	µg l^{-1}	1979-1988	10	-0.239	0.891	66	<0.001
γ-HCH [e]	µg l^{-1}	1973-2000	27	-0.134	0.874	181	<0.001
ACEI [f]	µg l^{-1}	1973-2000	28	-0.123	0.735	76	<0.001

[a] number of yearly averages (number of observations ≥6 per year)
[b] based on ln transformed averages
[c] sum of the 28, 52, 101, 118, 138, 153 and 180 PCB congeners
[d] six of Borneff
[e] lindan
[f] acetyl-choline esterase inhibitors
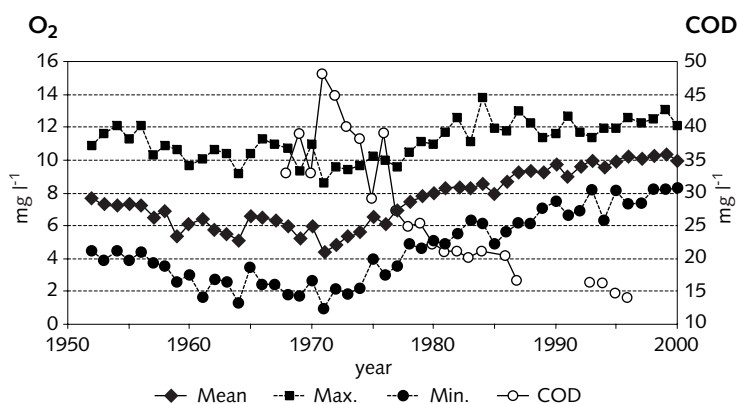
Figure 4. *Yearly average, minimum and maximum observed dissolved oxygen concentrations, and yearly average of the COD in the River Rhine measured at the German-Dutch border.*

Concentrations of toxic substances in the river water such as heavy metals organic micro-pollutants (e.g., PAH's, γ-HCH), as well as and mineral oil, significantly reduced with at least a factor 10 in the period 1970-1990 (Fig. 5 and 6, Table 3) (Heymen & Van der Weijden 1991, Van der Velde *et al.* 1991, Admiraal *et al.* 1993, Van Urk *et al.* 1993). As a result of this decrease, the differences, in general, between the yearly average and the maximum observed concentrations were also strongly reduced (Fig. 5 and 6).
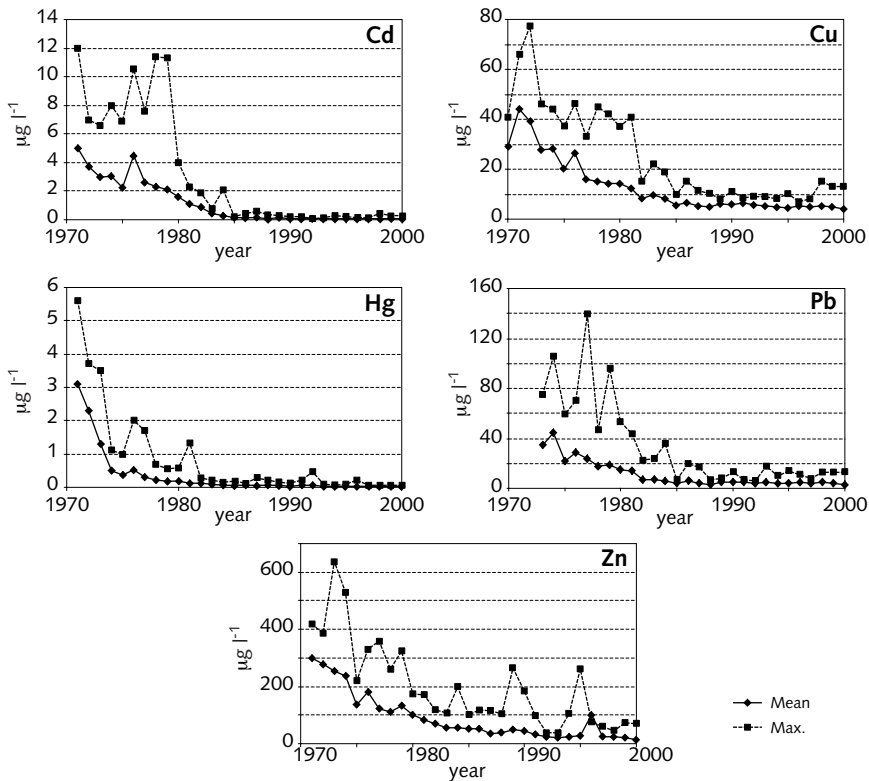
Figure 5. *Yearly average and maximum observed total concentrations of Cd, Cu, Hg, Pb and Zn in the River Rhine measured at the German-Dutch border.*
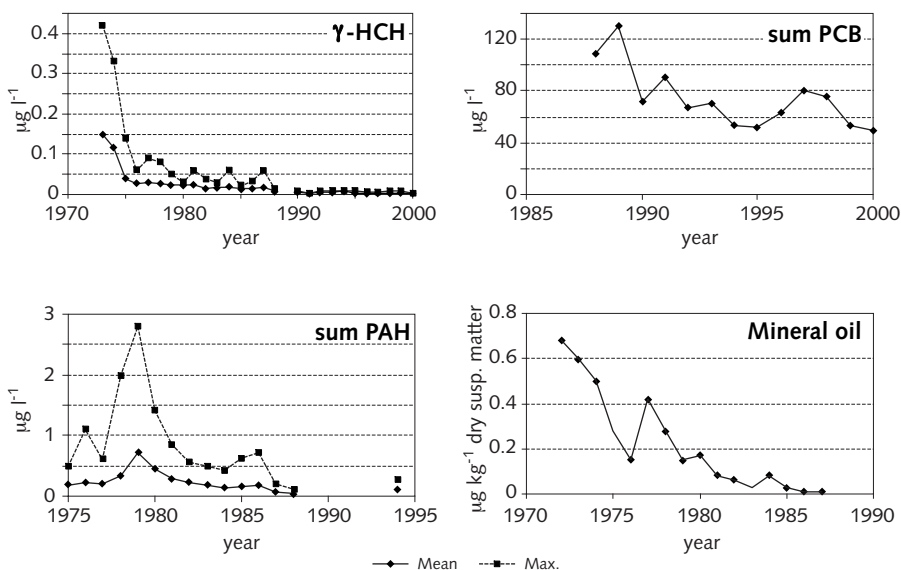
Figure 6. *Yearly average concentrations of PCB's, PAH's, γ-HCH and mineral oil in the River Rhine measured at the German-Dutch border, including maximum observed concentrations of γ-HCH and sum PAH.*

Although water quality improvement of the River Rhine became a success story, toxicity of the Rhine water did not disappear completely because of the sum-toxicity of thousands of chemical compounds present in the water, most of them in concentrations below the chemical detection level (Hendriks *et al.* 1994). In 1993, for example, Nolan *et al.* (1997, 2000) observed toxic effects on the skin and in the immune system of sea trout smolts (*Salmo trutta*). Other important water quality related habitat components for the indigenous river fauna, such as chloride concentration and water temperature, did not improve to the same extent (chloride, Fig. 7) or, quite the contrary, even became worser (water temperature, Fig. 8). Main sources of chloride enrichment are the potassium mines in the Alsace (France) and the brown coal mines in Germany. In the period 1960-2000 the yearly average chloride concentration varied between 90 and 240 mg l^{-1} (Fig. 7) with minimum and maximum concentrations measuring 35 and 420 mg l^{-1} respectively (this maximum value was reported in the annual reports of the Combined Rhine and Meuse Waterworks, RIWA, Amsterdam).
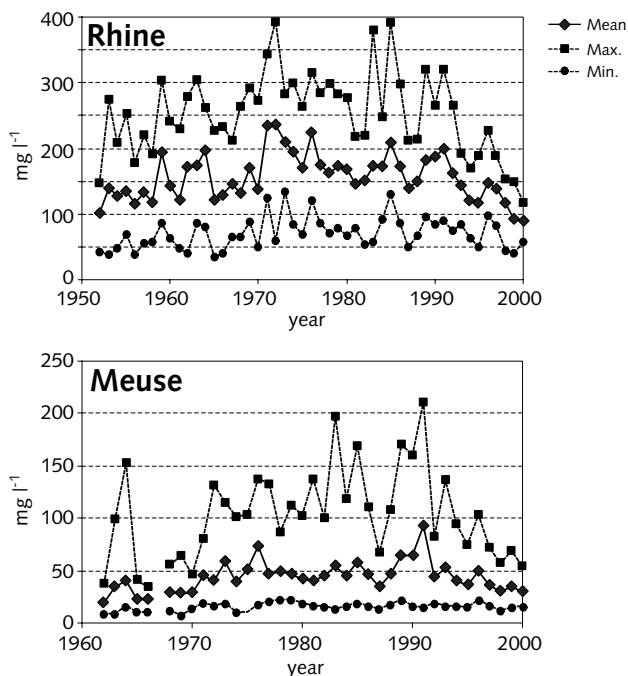
Figure 7. *Yearly average, minimum and maximum observed chloride concentrations in the rivers Rhine and Meuse measured at the German-Dutch and Belgian-Dutch border respectively.*

The natural chloride concentration was assessed at 12 mg l^{-1} on average (Molt 1961). Reduction of the chloride discharge of the potassium mines was an important issue in international discussions on water quality improvement in the period 1960-1990. A final agreement with France was reached in 1991 consisting of a salt discharge reduction of 60 kg s^{-1} and salt storage during periods with low Rhine discharge (Dieperink 1997). Results of all negotiations were visible in a significant decline of the average chloride concentration from 1971, noticeably after 1990 (Table 3).

Thermal pollution has been mainly caused by the discharge of cooling water from electric power plants and industries. Recently part of the water temperature increase could also be attributed to global warming. Compared with the situation around the start of the 20th century, the average water temperature had increased by 3°C till around 1980 (Wessels 1984), and has increased with 0.5°C per 10 years from 1952 (Fig. 8).
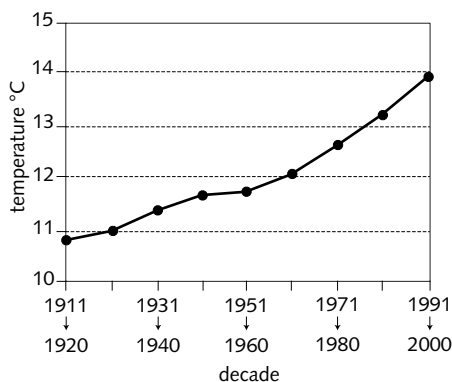
Figure 8. *Decade averages of the water temperature of the River Rhine.*

River Meuse

As a reference for the water quality development, Zuurdeeg (1980) made an estimation of the natural composition of the water in the River Meuse (Table 4). For the macro-elements, this corresponds with the natural composition of River Rhine water, except for Na^+ and Cl^-. Natural concentrations in that river were estimated at 5 and 12 mg l^{-1} respectively (Molt 1961). In an overview of the water quality of the River Meuse in the period 1953-1980, Dijkzeul (1981) mentioned that previous to 1970, concentrations of chloride, phosphates and nitrogen compounds, including the BOD_5, increased. Reductions after 1970 were considered to be the result of a decrease in industrial activity in the upstream river valley, an increase of public awareness and improvement of legislation. More extensive water quality monitoring programs for this river started in 1971 (Volz *et al.* 2002).

Table 4. *The natural average composition of the River Meuse water. Data for Eijsden at the Belgian-Dutch border and Kerksloot just before entering the estuary (Zuurdeeg 1980).*

Parameter	Unit	Eijsden	Kerksloot
Na^+	mg l^{-1}	7.3	9.1
K^+	mg l^{-1}	3.7	4.2
Ca^{2+}	mg l^{-1}	59	55
Mg^{2+}	mg l^{-1}	5.7	5.6
Fe_{total}	µg l^{-1}	120	300
Mn_{total}	µg l^{-1}	54	71
Cu_{total}	µg l^{-1}	4	4
Zn_{total}	µg l^{-1}	24	62
Cl^-	mg l^{-1}	14.9	18.5
HCO_3^-	mg l^{-1}	172	150
SO_4^{2-}	mg l^{-1}	28	35
PO_4^{3-}	mg l^{-1}	0.22	0.21

These programs include measurements of heavy metals and organic micro-pollutants. Lack of knowledge about concentrations of these toxicants were probably the main reason for some drinking water companies to decide, at that time, to switch from the River Rhine to the River Meuse for drinking water extraction, due to its assumed relatively better water quality (Table 5). As was with the River Rhine, water quality in the River Meuse also reached rock bottom in the first half of the 1970s (Volz *et al.* 2002). The peak of heavy metal pollution was already reached about one century earlier, coinciding with the zenith of ore mining in the Belgian part of the catchment area (Rang & Schouten 1989). From 1972 onwards, decrease of heavy metal concentrations continued (Fig. 9 and Table 6) including the yearly observed maximum concentrations. In general, the maximum concentrations coincided with relatively high discharges causing increased concentrations of suspended matter.

Table 5. *Comparison of heavy metal concentrations in the rivers Rhine and Meuse, at Lobith and Eijsden respectively, in 1972.*

Parameter	Unit	Rhine			Meuse		
		N	Mean	Maximum	N	Mean	Maximum
Cd_{total}	µg l^{-1}	9	3.7	7.0	22	6.1	15.5
Cu_{total}	µg l^{-1}	9	39	77	22	14.4	28
Hg_{total}	µg l^{-1}	11	2.3	3.7	22	0.3	0.8
Pb_{total}[a]	µg l^{-1}	42	35	75	17	80	500
Zn_{total}	µg l^{-1}	9	280	386	22	330	815

[a] 1973

Of the organic micro-pollutants, only the concentration of the sum of the main PCB's congeners did not reduce from the initial measurements in 1988 (Fig. 10). However, the observed increase of the yearly average concentration was not statistically significant (Table 6). Consistent with the River Rhine, the yearly average concentration of PAH's reached a maximum in 1979. From that year onwards, this value significantly decreased (Table 6). From the start of the monitoring program, the yearly average concentrations of mineral oil and γ-HCH significantly decreased as well (Fig. 10, Table 6). Chloride concentration in the River Meuse slightly increased until 1991 (Fig. 7, Table 6), but the 95-percentile of the yearly observed maximum concentrations did not exceed 175 mg l^{-1} which is two times less than in the River Rhine. From 1991 onwards, the yearly observed average concentration significantly decreased (Table 6). Reduction of mining and industrial activities in the catchment area is considered to be the main cause.

Table 6. *One-way ANOVA of trends in water quality parameters measured in the River Meuse at the Belgian-Dutch border (for foot notes see table 3).*

Parameter	Unit	Period	N [a]	Slope [b]	R^2	F	P
O_2	mg l^{-1}	1961-2000	39	-0.040	0.288	16	<0,001
COD	mg l^{-1}	1976-2000	19	-0.019	0.438	15	0.001
Cl$^-$	mg l^{-1}	1962-1991	30	0.030	0.517	29	<0.001
Cl$^-$	mg l^{-1}	1991-2000	10	-0.088	0.622	13	<0.01
Cd$_{total}$	µg l^{-1}	1972-2000	29	-0.123	0.821	129	<0.001
Cu$_{total}$	µg l^{-1}	1972-2000	29	-0.049	0.647	52	<0.001
Hg$_{total}$	µg l^{-1}	1972-2000	29	-0.125	0.902	260	<0.001
Pb$_{total}$	µg l^{-1}	1972-2000	29	-0.088	0.736	79	<0.001
Zn$_{total}$	µg l^{-1}	1972-2000	29	-0.087	0.804	116	<0.001
Mineral oil	µg kg^{-1}	1972-1988	17	-0.153	0.737	42	<0.001
PCB$_{sum}$ [c]	µg l^{-1}	1988-2000	13	0.072	0.048	1.6	0.23
PAH's [d]	µg l^{-1}	1979-1988	14	-0.188	0.885	61	<0.001
γ-HCH [e]	µg l^{-1}	1972-2000	25	-0.050	0.365	15	0.001
ACEI [f]	µg l^{-1}	1972-2000	29	-0.016	-0.006	0.8	0.37
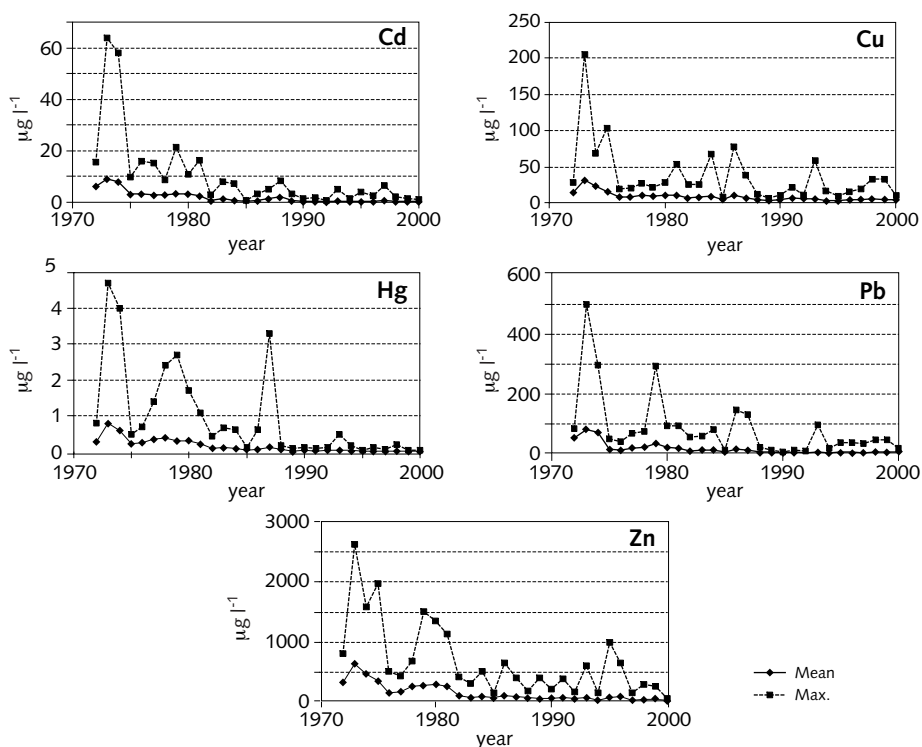
Figure 9. *Yearly average and maximum observed total concentrations of Cd, Cu, Hg, Pb and Zn in the River Meuse measured at the Belgian-Dutch border.*
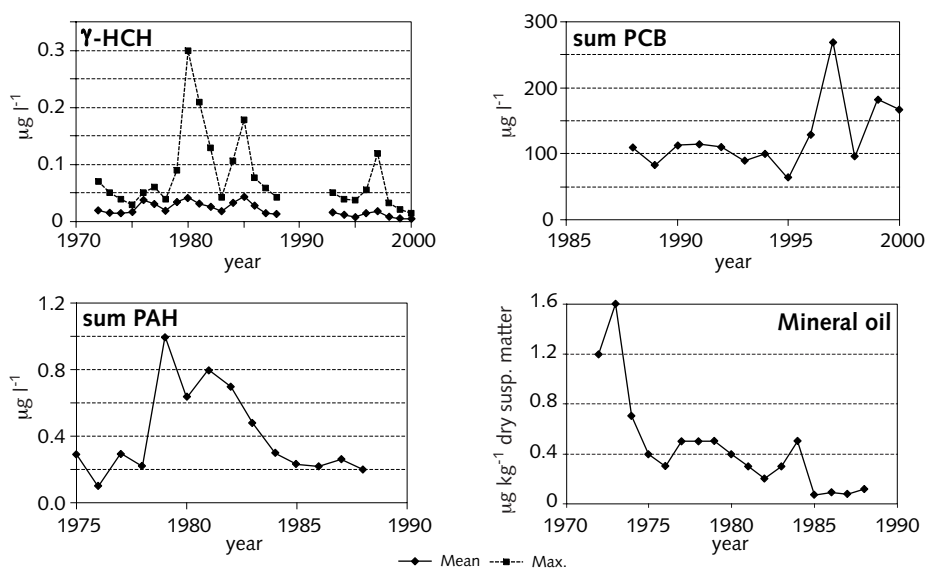
Figure 10. *Yearly average concentrations of PCB's PAH's, γ-HCH and mineral oil in the River Meuse measured at the Belgian-Dutch border, including the maximum observed concentrations of γ-HCH.*

Water quality in the lower Meuse still has an acute effect on the survival of macroinvertebrates. Stuijfzand (1999) observed significantly higher mortality of *Hydropsyche angustipennis, H. exocellata* and *H. siltalai* when subjected to water from the River Meuse collected at the Belgian-Dutch border in April (*H. angustipennis* and *H. siltalai*), May-June (*H. siltalai*), and August 1996 (*H. angustipennis* and *H. exocellata*), as compared with animals subjected to water from the lower Rhine. In April 1996 the experiment coincided with elevated concentrations of diazinon, di-isopropylether and ammonium, and with reduced oxygen concentrations; in May-June with elevated concentrations of diuron and tri-chlorethane; in August with elevated concentrations of di-isopropylether, diuron and ammonium. During a field study in the period August - October 2002, effects of elevated concentrations of diazinon, dimethoate and chlorpyrifos (max. concentrations: 0.14, 0.78 and 0.40 µg l^{-1} respectively, measured at the Belgian-Dutch border) were visible in the macroinvertebrate community that colonised a standardised artificial substrate (De Pauw *et al.* 1994, Pashkevich *et al.* 1996) suspended into the main channel at Grave (Fig. 2). The substrates were retrieved after a four week colonisation period on September 7, October 5 and 17, before and after passage of the toxicants on September 14. The short term effect was that density and species richness of the community on the artificial substrate had strongly reduced (M. Greijdanus-Klaas, RIZA, unpubl. results).

EFFECTS ON THE FAUNA

Before the initiation of the National Biological Monitoring Program in the rivers Rhine and Meuse in 1992, data on macroinvertebrates and fish were not collected systematically with a long-term horizon, but only in relatively short-term research projects. In 1973 Van Urk (1981, 1984) started to study changes in the epilithic littoral macroinvertebrate fauna in the River IJssel, one of the three main distributaries of the River Rhine. This study has been continued until today and has resulted in the longest macroinvertebrate time series from larger rivers in The Netherlands. Macroinvertebrates in the River Meuse, sampled by means of an artificial substrate, were monitored from 1983 (Frantzen 1991). Before fish monitoring became part of the National Biological Monitoring Program in 1992, it was mainly focussed, from the 1960s, on stock assessment of commercially interesting species (Klinge *et al.* 1998).

River Rhine

Macroinvertebrates
As mentioned above, the macroinvertebrate community on riprap in the littoral zone of the River IJssel has been monitored from 1973 on a yearly basis (Van Urk 1984, Van Urk & Bij de Vaate 1990, Bij de Vaate 1994). Apart from an incidental survey made by Lauterborn in the beginning of the 20th century (Lauterborn 1918), the IJssel data are the only source for data older than 15 years. To fill the gap between the survey of Lauterborn and the start of the monitoring, results of palaeolimnological investigations are used (Klink 1989) to reconstruct macroinvertebrate communities, e.g. for the description of targets and references. Especially the remains of insects can be recognised in sediment layers which are representative for the main part of the species richness in a healthy river. Van den Brink *et al.* (1990) combined different sources to reconstruct macroinvertebrate development in the Rhine delta from the start of the 20th century. They concluded that in the period 1900 - 1985 the number of rheophilic species had declined, while the number of euryoecious species had increased. As a result of the increased chloride concentration (Fig. 7) a number of brackish water crustaceans were found approximately 100 km upstream from their original limits of distribution (Den Hartog *et al.* 1989).

From recolonisation patterns of autochthonous species in the Rhine delta, two phases in water quality recovery could be distinguished. Between 1975 and 1980 some stress tolerant insects (in this initial period mainly chironomid and a few caddis fly species) and molluscs began to recolonise the river. Density increase of these macroinvertebrates in the years after that period correlated well with a decrease of chemical pollutants in the river water (Van Urk 1981, Van Urk & Bij de Vaate 1990, Van Urk *et al.* 1993).
Recolonisation of the Lower Rhine by the burrowing larvae of the mayfly *Ephoron virgo* in 1991 (Bij de Vaate *et al.* 1992) and its mass development in the following years marked the start of a new phase in water quality rehabilitation of the river. Concentrations of toxicants had strongly decreased in the past two decades, and oxygen concentration had reached a level that no longer seemed to be the limiting factor for the colonisation of many

macroinvertebrate species with a higher demand for oxygen. Another example is the dragonfly *Gomphus flavipes* that recolonised the Rhine delta from 1996 (Habraken & Crombaghs 1997, Goudsmits 1998). Although potentially several other sensitive autochthonous macroinvertebrate species could also extend their territory in the Rhine distributaries due to water quality improvement, other factors such as the absence of a physical habitat and the increased water temperature most probably prevent successful colonisation of these species.

Table 7. *Dominant (••) and subdominant (•) macroinvertebrate species in two habitats in the free flowing distributaries in the Rhine delta in the period 1985-2000 (R = riprap in the littoral zone; B = river bed). Species were considered to be dominant or subdominant if their density contributed to >20% of the total macroinvertebrate density or >20% of the macroinvertebrate density minus the dominant species respectively. If no dominant species were present, those species contributing to 10-20% of the total macroinvertebrate density were considered to be subdominant. Nonindigenous species underlined.*

Taxon	1975		1980		1990		1995		2000	
	R	B	R	B	R	B	R	B	R	B
River Waal										
Corbicula fluminalis							•			
Corbicula fluminea						•	••			••
Dreissena polymorpha							•			
Potamopyrgus antipodarum						•				
Propappus volki								••		
Chelicorophium curvispinum					••	••	••		••	
Jaera istri									••	
Dikerogammarus villosus									••	
Gammarus tigrinus					•			••		•
Cricotopus bicinctus									•	
Kloosia pusilla								•		
Neozavriella sp.									•	
River IJssel										
Corbicula fluminea										•
Dreissena polymorpha	•				•					
Ancylus fluviatilis									•	
Potamopyrgus antipodarum								•		
Hypania invalida										••
Asellus aquaticus	••									
Jaera istri									••	
Chelicorophium curvispinum					••		••	••	••	••
Dikerogammarus villosus									•	••
Gammarus tigrinus					•		•	••		
Hydropsyche contubernalis			•							
Dicrotendipes nervosus			•							
Cricotopus intersectus							•			
Cricotopus sp.			••							

Macroinvertebrate communities are currently (since 1985) dominated by nonindigenous species (Table 7), mainly species from the Ponto-Caspian area, that were supported to colonise the River Rhine by the opening of the Main-Danube Canal in September 1992 (Bij de Vaate *et al.* 2002, Van der Velde *et al.* 2002). Some of these Ponto-Caspian species (e.g., *Chelicorophium curvispinum* and *Dikerogammarus villosus*) have had a relatively strong negative impact on other macroinvertebrate densities (Van den Brink *et al.* 1991, 1993, Van der Velde *et al.* 1994, Rajagopal *et al.* 1999, Dick & Platvoet 2000).

Fishes

Van den Brink *et al.* (1990) gave a brief overview of developments in the fish fauna in the Rhine delta from the start of the 20th century till 1985. In general, densities of most species were relatively low in the period 1960-1980. The groups of the rheophilic and anadromous species suffered the most from the combination of water quality deterioration, river engineering, damming, and the closure of river outlets (e.g., Lelek 1989). The fish fauna took most advantage of the ecological rehabilitation programs that were introduced after the Sandoz-accident in 1986, especially Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) which have been reintroduced on a large scale in the main tributaries. In 2000, species richness was higher than in the second part of the previous century (Fig. 11), being the result of colonisation of the Rhine delta by introduced species. Nature development in the river forelands has been important for fish as well. The construction of secondary channels positively contributed to fish stocks in the main channel of the distributaries (Grift, 2001).
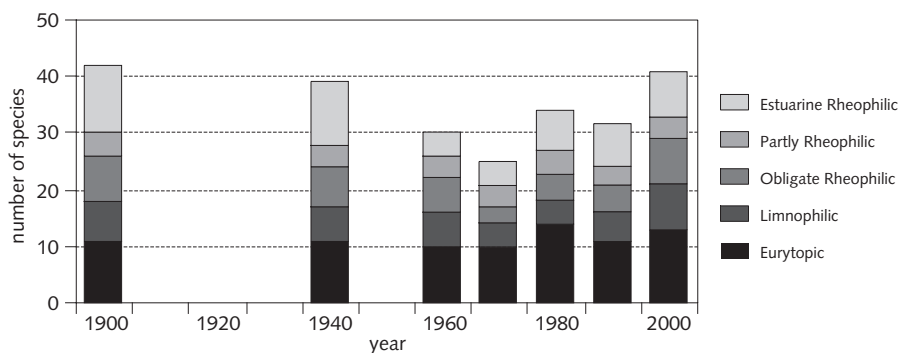
Figure 11. *Number of fish species per guild in the Rhine distributaries (1900-2000). Sources: Lelek (1989), Oosterbroek (1990), Van den Brink et al. (1990), De Nie (1997), and unpublished results of the National Biological Monitoring Program 1992-2000.*

River Meuse

Macroinvertebrates

Before 1992, macroinvertebrates in the River Meuse were for various reasons studied at irregular intervals (Bij de Vaate 1995). Hardly any information on macroinvertebrate communities is known before the period in which human impacts, such as canalisation and water pollution, became obvious. Redeke (1948) mentioned some macroinvertebrates as dominant or typical for the downstream reaches of the River Meuse. Species of the genus *Simulium* (black flies) and chironomid larvae belonging to the genera *Chironomus* and *Tanytarsus* were considered to be dominant; the mayflies *Cloeon dipterum* and *Heptagenia sulphurea*, the caddish fly *Hydropsyche angustipennis*, the water bug *Aphelocheirus aestivalis* and the water beetle *Helophorus arvernicus* were considered to be typical. Klink & Bij de Vaate (1994) concluded that originally 219 species at least lived in the Grensmaas stretch (Fig. 2). By the 1980s, this number had reduced to 51 (Bij de Vaate 1995). All species identified by Redeke (1948) as typical for the River Meuse were not observed, included species of Plecoptera, Odonata, Hemiptera and Coleoptera; while the number of Ephemeroptera and Trichoptera species was strongly reduced. Also obvious was the low diversity and density of Crustacea, Hirudinea and Tricladida. Main causes were (Klink 1985, 1986, Klink & Bij de Vaate 1994):

a. pollution of the river with heavy metals and mineral oil;
b. eutrophication;
c. canalisation of the lower stretches;
d. in the Grensmaas stretch, artificial discharge fluctuations caused by the hydro-electric power station in the Lixhe weir (Belgium).

Recent developments show an increased importance of nonindigenous species, especially in the dammed and tidal sections (Table 8). These species are expected to migrate mainly through the Maas-Waal Canal, a connection between the Rivers Waal and Meuse in the vicinity of Nijmegen. In the Grensmaas stretch (autochthonous) chironomids were the most relevant until 1996. However, in 2000, nonindigenous species mainly dominated the river bottom and riprap communities.

Table 8. *Dominant (••) and subdominant (•) macroinvertebrate species in two habitats in the Dutch stretches of the River Meuse in the period 1985-2000 (R = riprap in the littoral zone; B = river bed). For a definition of dominante species see table 7; nonindigenous species underlined).*

Taxon	1985	1986	1982		1996		2000	
	R[1]	R[1]	R	B	R	B	R	B
Grensmaas								
Ancylus fluviatilis							•	
Dreissena polymorpha			••					
Naididae	•							
Propappus volki								••
Stylaria lacustris					•			
Asellus aquaticus	••	•	•		•			
Chelicorophium curvispinum							••	
Dikerogammarus villosus							•	
Ecnomus tenellus				•				•
Hydropsyche contubernalis						•		
Chironomidae	••							
Cricotopus bicinctus					••			
Dicrotendipes nervosus		••	••		•			
Parachironomus arcuatus		•						
Dammed Meuse								
Corbicula fluminea				•		•		•
Dreissena polymorpha			••		••		••	
Valvata piscinalis				•				
Limnodrilus claparedeianus				•				
Hypania invalida								•
Chelicorophium curvispinum							••	•
Dikerogammarus villosus					••		••	
Gammarus tigrinus								•
Ecnomus tenellus			•					
Procladius sp.				•				
Tidal Meuse								
Ancylus fluviatilis					•			
Corbicula fluminea					•		•	
Dreissena polymorpha	••	••	••		•	•	•	•
Pisidium casertanum				•				
Pisidium henslowanum				••				
Hypania invalida								••
Naididae	•							
Chelicorophium curvispinum					••		••	••
Dikerogammarus villosus							••	
Gammarus tigrinus		•	•		•			
Ecnomus tenellus			•					
Cricotopus bicinctus							•	
Cricotopus intersectus gr.							•	

[1] Data from artificial substrate sampling (Frantzen 1991). The substrate consisted of coarse mesh steel wire boxes filled with small pieces of grauwacke (Grauwacke is generally used for bank protection).

Fishes

Main causes that negatively influenced macroinvertebrates communities in the River Meuse also affected fish stocks strongly (Prignon *et al.* 1999). However, with respect to species richness rest populations in tributaries and refuges, introductions and stocking of game species did not lead to a drastic diversity decrease in the 1960s and 1970s when anthropogenic stress was at a maximum (Fig. 12). Damming of the lower Meuse in the 1920s (Table 2) primarily affected migration of anadromous species such as Atlantic salmon (*Salmo salar*), sea trout (*Salmo trutta*), sturgeon (*Acipenser sturio*), houting (*Coregonus oxyrhynchus*), twaite and allis shad (*Alosa fallax* and *A. alosa* respectively), and sea and river lamprey (*Petromyzon marinus* and *Lampetra fluviatilis* respectively) to upstream situated spawning areas (Prignon *et al.* 1999). In addition, construction of weirs in the tributaries contributed to the decrease of rheophilic species. Fish kills were common for an extended period, lasting until 1990, in the river section upstream of Borgharen, due to a combination of extremely low oxygen content in the water and/or relatively high concentrations of pollutants (e.g., Van Hoof 1984). Public concern for fish, and specially the Atlantic salmon, in the River Meuse was triggered by the end of the 1990s in Walloon by the program "Saumon Meuse 2000" (Philippart & Gillet 1990, Philippart *et al.* 1994). The aim of the program was to reintroduce juvenile stages of the Atlantic salmon in Walloon tributaries and to define constructive proposals for the improvement of smolt migration at hydropower stations and for upstream migration of adults. The program was facilitated by water quality improvement and the construction of fish passes at weirs in the Dutch part of the main channel.
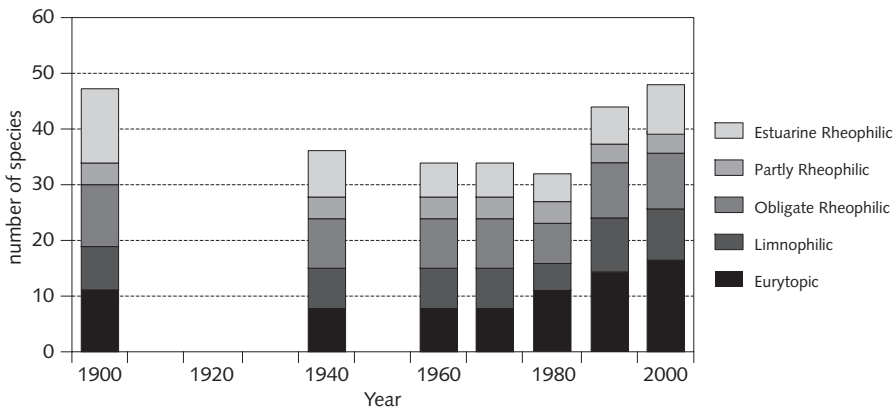
Figure 12. *Number of fish species per guild in the Dutch part of the River Meuse (1900-2000). Sources: Redeke (1941), Steenvoorden (1970), Van Esch (1981), Raat (1996), De Nie (1997), Crombaghs et al. (2000), and unpublished results of the National Biological Monitoring Program 1992-2000.*

OUTLINE OF THE THESIS

The thesis consists of a palette of results obtained from different studies on macroinvertebrates and fish migration in the lowers sections of the rivers Rhine and Meuse. The reported work has been done over a period of many years and is not the result of a designed research plan. Nonetheless, all the studies have been devoted to the question how we may restore the structure and functioning of the original ecosystems that were once present in the lower sections of the rivers Rhine (including the lake IJsselmeer area as a part of its catchment area) and Meuse, and how success in such attempts can be measured. This is the theme which links all studies, and on which I reflect in a in a broader sense in the the final chapter of the thesis.

Chapter 2 deals with long-term changes in the macroinvertebrate fauna of the littoral riprap in the River IJssel. Changes were thought to be caused by water quality changes in the period 1975-1991.

In chapter 3, macroinvertebrate communities of several biotopes in the Grensmaas stretch of the River Meuse were described based on information available in unpublished reports (the so-called "grey" literature) as a base-line reference to assess effects of nature development on these communities. At the time of publication of this chapter, ideas were published to combine gravel extraction on the river banks with nature development. Previous to possible interventions in the future, an environmental risk assessment on effects of possible ways of such a project realization recently (in 2002) started.

In chapter 4, the practicability of the Index of Trophic Completeness (ITC) was tested for running waters. The index was developed in a previous study and is an indicator for the functionality of the macroinvertebrate community.

Range expansion and migration patterns of nonindigenous macroinvertebrate species from the Ponto-Caspian region are discussed in chapter 5. Nonindigenous macroinvertebrates from this region are the dominant species now on solid substrates in the lower sections of the rivers Rhine and Meuse.

In chapter 6, results are described of a study on population dynamics of one of the Ponto-Caspian species, the zebra mussel *(Dreissena polymorpha)* in the Lake IJsselmeer area, mainly receiving Rhine water

Chapter 7 deals with sea trout (*Salmo trutta*) migration in the Rhine delta and in the lower Meuse. This species was selected as a representative species to study potential migration routes in both areas of the Atlantic salmon (*Salmo salar*) of which the typical Rhine breed became extinct in the first part of the 20th century. The sea trout was tagged and released in the Dutch coastal area and telemetrically detected during their upstream migration.

Finally, chapter 8 focusses on the possibilities of river restoration for rivers having different functions now, which are all, from the point of view of decision makers, considered to be important. It was concluded that the endpoint of river restoration in The Netherlands should not beformulated as target communities or target species (in desired densities), but, as a functional integrity, represented by trophic guilds.

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CHAPTER 2

LONG-TERM CHANGES IN THE MACROINVERTEBRATE

FAUNA OF THE RIVER IJSSEL, THE NETHERLANDS

LONG-TERM CHANGES IN THE MACROINVERTEBRATE FAUNA OF THE RIVER IJSSEL,

THE NETHERLANDS

ABSTRACT

Macroinvertebrates on stones in the littoral zone of the River IJssel, one of the three distributaries in the Rhine delta, were monitored in the period 1975-1991. Due to water quality improvement during that period, their density increased considerably in the period 1975-1982. In 1990 and 1991 a further increase of the total macroinvertebrate density was the result of a mass development of the non-indigenous amphipod *Chelicorophium curvispinum* which colonised the Rhine delta in 1987.

INTRODUCTION

Macroinvertebrates in rivers are not only important in food webs but also as indicators for morphological changes and water quality (Hellawell 1986). With respect to the indicator function, the lithophilous macroinvertebrate fauna of the River IJssel, one of the distributaries in the downstream area of the River Rhine (Fig. 1), was analysed from 1975 to 1991. During this period, water quality in the Rhine improved considerably. This improvement started by the end of the 1960s when water quality had reached rock bottom, being the result of severe pollution with domestic and industrial waste water (Van der Klei *et al.* 1991). Measures to reduce waste water discharge into the Rhine started to be fruitful then. Now more rigid measures were executed within agreements for an international program for ecological rehabilitation of this river. An important goal of this program is to create chances for the recolonisation of the river by riverine plant and animal species by means of extension or recovery of suitable natural habitats.

STUDY AREA

The River IJssel is one of the three distributaries of the River Rhine in The Netherlands (Fig. 1). Its total length is about 120 km. Discharge of the IJssel is strongly regulated by the weirs in the River Nederrijn, one of the two other distributaries. This means for the River IJssel a discharge maintenance at 285 m^3.s $^{-1}$ for as long as possible during low discharge in the River Rhine. Average current velocities in the IJssel at minimum and maximum discharges are 0.3 and 1.1 m.s $^{-1}$ respectively. In general the main canal in the Lower Rhine and its distributaries was fixed by groynes. Where groynes are absent, the river bank was mostly protected against erosion with stones. Detailed information about the distributaries of the River Rhine is given by Van Urk (1984), Van Urk & Smit (1989) and Anonymous (undated).
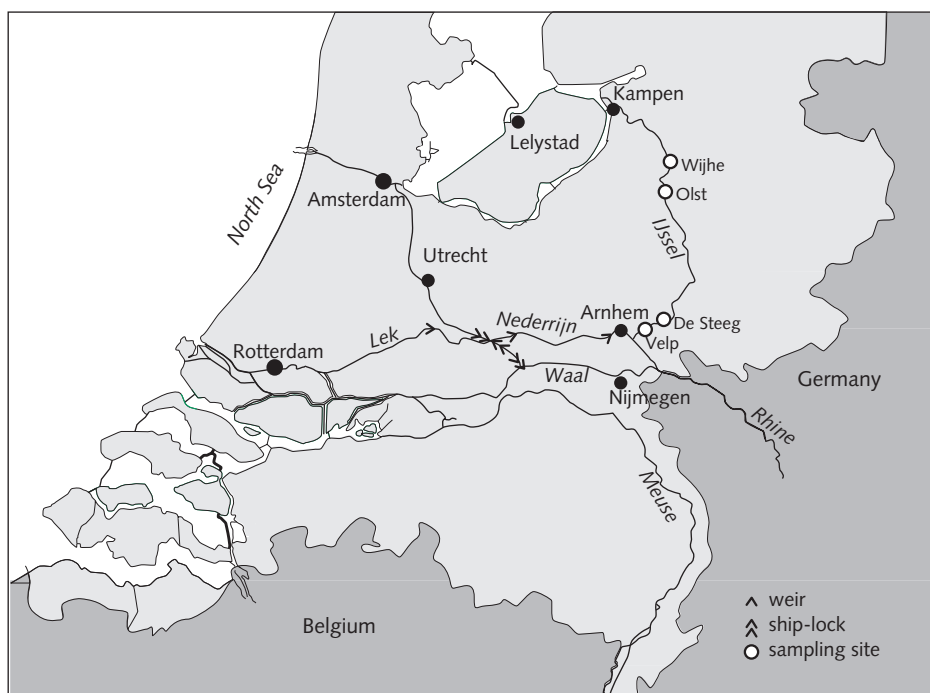
Figure 1. *Sampling locations in the River Rhine and its distributaries.*

The amount of polluting substances in discharges of domestic and industrial waste water into the Rhine decreased considerably during the past two decades (Heymen & Van der Weijden 1991), resulting as well in better oxygen conditions in the river water. However, the amount of discharged chloride including thermal pollution did not reduce. Main sources of chloride are the potassium mines in the Alsace (France) and the brown coal mines in Germany.

Between 1970 and 1991 the yearly average chloride concentration varied between 140 and 240 mg 1^{-1} with minimum and maximum concentrations of 45 and 420 mg 1^{-1} respectively (Heymen & Van der Weijden 1991). In contrast to these values, average natural chloride concentration was estimated to be 12 mg 1^{-1} (Molt 1961). Thermal pollution has been mainly caused by industrial activity and electric power plants. Compared with the situation around the start of this century, average chloride concentration increased by a factor 15, and average water temperature by 3°C (Wessels 1984).

MATERIAL AND METHODS

In the period 1975-1991, with exception of the years 1984-1986, stones in the littoral zone were sampled yearly in September and/or October. This yearly sampling period was chosen because minimum water levels normally occur in these months. Five well colonised stones were collected by hand from a depth of about 30 cm. Each stone was put into a plastic tray and brushed carefully to remove the macroinvertebrates. Zebra mussels were cut from the stones. The macroinvertebrates were cleaned by washing them on a 0.5 mm mesh sieve before preservation in 96% ethanol. After brushing, the surface area of the stones was measured. Samples were taken at four study locations (Fig. 1, Table 1).

Table 1.   *Study locations in the River IJssel.*

Location	River km[1]
Velp	885
De Steeg	896
Olst	957
Wijhe	966

[1] Internationally accepted distance indication (km) in the Rhine

RESULTS AND DISCUSSION

Changes in densities of the most important taxa of macroinvertebrates on the stones in the IJssel are illustrated in figure 2. Surface area of each circle in this figure represents the total number of macroinvertebrates found on all stones (five stones on four locations) in the successive years. Due to the improvement of water quality (Van Urk & Bij de Vaate 1990, Van der Velde *et al*. 1991), notable in oxygen content of the river water and in the concentrations of heavy metals and some organic micropollutants (Van Broekhoven 1987), density increased considerably in the period 1975-1982.

Relatively low densities found in 1987 and 1988 can probably be attributed to effects of natural river discharge fluctuations in the period before sampling in those years. The further increase of the total number of macroinvertebrates in 1990 and 1991 is the result of the colonisation of the Rhine and its branches by the amphipod *C. curvispinum* (Van den Brink *et al.* 1989, 1991).
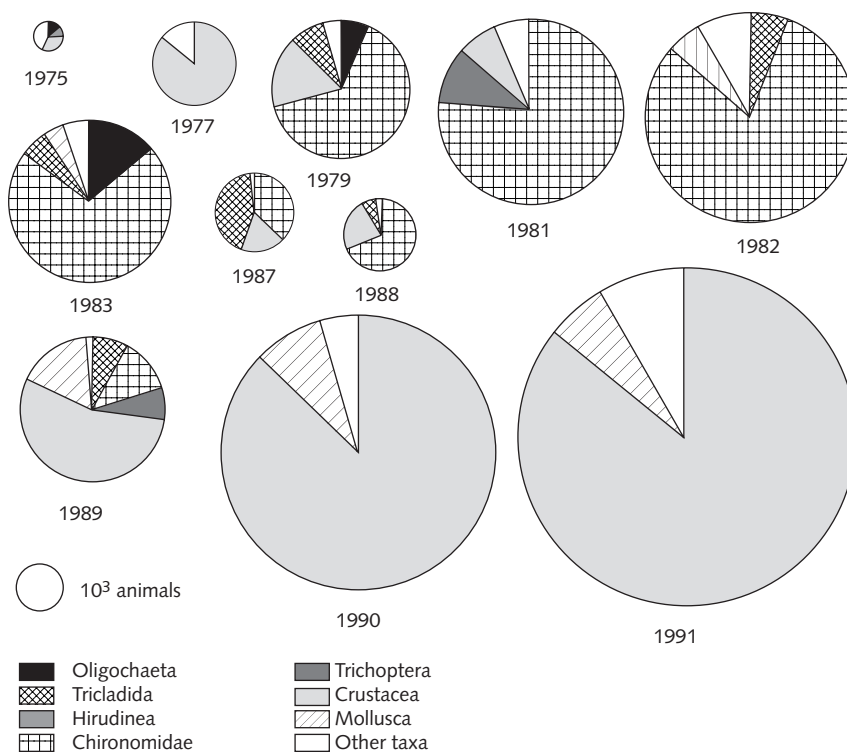
Figure 2. *Changes in densities (expressed in numbers per 20 stones) of the most important taxa of macroinvertebrates on stones in the River IJssel in de period 1975-1991.*

A survey of dominant and subdominant taxa in the period 1975-1991 is given in Table 2. When the contribution of a taxon was >25% or 10-25% to the average density, it was considered to be dominant or subdominant respectively. In the period 1975-1978, at still relatively low densities, the isopod *Asellus aquaticus* was the dominant species. *A. aquaticus* is, in general, an abundant species in littoral and sublittoral zones of European freshwater systems, and can be found in various habitats, e.g. bottoms, macrophytes, stones, litter and

detritus (Williams 1962, Økland 1980, Murphy & Learner 1982). Organic pollution increases its density (Aston & Milner 1980). At the locations in the IJssel, yearly average concentration of total organic carbon decreased from 10.5 mg l^{-1} in 1975 to 8.7 and 5.8 mg l^{-1} in 1980 and 1990 respectively (Heymen & Van der Weijden 1991, interpolated values).
Besides *A. aquaticus*, Chironomidae were also a dominant group of organisms in 1978 and the only dominant taxon in the period 1979-1983. Up to 1979 and in 1983 chironomids were not identified to species level. In the periods 1979-1982 and 1987-1991, 9-17 taxa were identified each year (Fig. 3). Between 1984 and 1986 no results were available.

In 1987 the amphipod *Gammarus tigrinus* became subdominant. This nonindigenous species, originating from North America, was found for the first time in the IJssel in 1981 (Van Urk & Bij de Vaate 1990). First records in The Netherlands date from 1964 (Pinkster 1975). *G. tigrinus is* relatively tolerant to polluted water and has a much greater reproductive capacity in oligohaline waters than any of the indigenous gammarid species (Pinkster 1975, Pinkster *et al.* 1977).

Table 2. *Dominant (**) and subdominant (*) taxa of macroinvertebrates in the River IJssel in the periode 1975-1991.*

Taxon	75	76	77	78	79	80	81	82	83	87	88	89	90	91
Hirudinea	*	*												
Gammarus tigrinus										*	*	**	*	*
Asellus aquaticus	**	**	**	**	*									
Chelicorophium curvispinum													*	**
Dreissena polymorpha	*									**		*		
Chironomidae		*		**	**	**	**	**	**	**	**	*		

In 1991 the amphipod *Corophium curvispinum* was the only dominant species. Colonisation of the IJssel by this nonindigenous species, originating from the Ponto-Caspian area, started in 1989 (Table 3). The first record of *C. curvispinum* in the Rhine, and in The Netherlands, was made in 1987 (Van den Brink *et al.* 1989). Colonisation success of this amphipod can be attributed to its tolerance of relatieve high salinity (2.5-7.0 mMol Na$^+$) in the Rhine, its breeding behaviour (three generations per year), and to the fact that the animals live in muddy tubes, which provide shelter from predators (Van den Brink *et al.* 1991).

Development in species richness of the macroinvertebrates in the period 1975-1991 is summarized in figure 3. In the first (1975-1977) and last three years (1989-1991) of this long term survey, 11-12 and 21-23 macroinvertebrate taxa respectively were found each year (Chironomidae and Oligochaeta excluded). Numbers of taxa within different groups observed in both periods are summarized in Table 4. The number of taxa in all groups had increased considerably in the second period. Part of this increase was caused by nonindigenous species (11 species observed during the whole period) due to higher chloride concentrations and the increase of the water temperature (Bij de Vaate 1993).
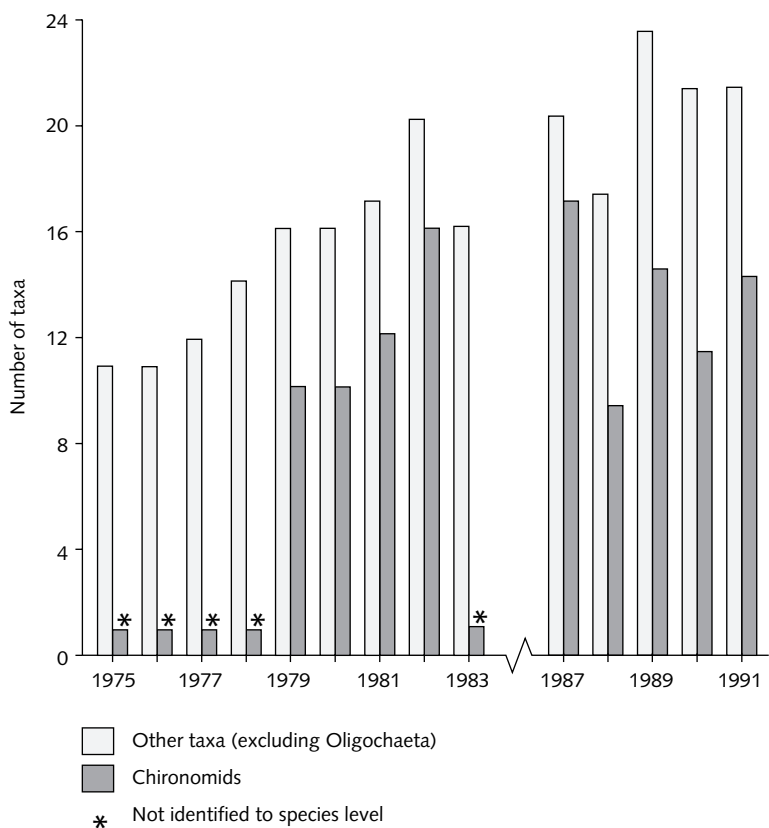
Figure 3. *Development of the number of macroinvertebrate taxa, excluding Oligochaeta, found on stones in the River IJssel in the period 1975-1991.*

Table 3. *Average density of the amphipod Chelicorophium curvispinum at four study locations in the River IJssel in the period September/October 1989, 1990 and 1991. Results based on numbers found on five stones per location (between brackets standard deviation; n.f. = not found).*

Location	^{10}log density per m^2		
	1989	**1990**	**1991**
Velp	2.7 (1.0)	4.5 (4.6)	5.0 (4.6)
De Steeg	<1.3	3.7 (3.7)	5.3 (4.9)
Olst	n.f.	<1.3	3.8 (3.6)
Wijhe	n.f.	1.5 (1.0)	2.4 (2.3)

Table 4. *Number of taxa observed on stones in the littoral zone of the River IJssel in the periods 1975-1977 (A), and 1989-1991 (B).*

Taxon	Period	
	A	**B**
Tricladida	1	4
Hirudinea	3	5
Oligochaeta	n.i.[1]	n.i.
Gastropoda	5	7
Lamellibranchia	1	5
Amphipoda	-	3
Isopoda	1	3
Chironomidae	n.i.	29
Trichoptera	-	4
Zygoptera	1	-
Arachnida	-	1
Total[2]	12	32

[1] Not identified
[2] Without Oligochaeta and Chironomidae

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CHAPTER 3

MACROINVERTEBRATE COMMUNITIES IN THE GRENSMAAS STRETCH

OF THE RIVER MEUSE 1981-1990

MACROINVERTEBRATE COMMUNITIES IN THE GRENSMAAS STRETCH

OF THE RIVER MEUSE: 1981-1990

ABSTRACT

Macroinvertebrate communities in the Grensmaas stretch of the River Meuse (The Netherlands) were described for the period 1981-1990, largely based on unpublished data. Three biotopes were distinguished: (a) stones in the littoral zone, (b) the river bottom in the littoral zone, and (c) the deeper river bottom in the navigable section. Fifty-one taxa were found in the communities described for these biotopes: 31 on the stones in the littoral zone, 38 in/on the river bottom in the littoral zone and 20 in/on the deeper river bottom in the navigable section of the Grensmaas. The majority (58%) of the taxa were Chironomidae. Mollusca were represented by only eight taxa; gammarids were absent as well as several pollution intolerant groups (Ephemeroptera, Trichoptera, Coleoptera, Odonata and Plecoptera).

INTRODUCTION

The River Meuse, rising in France, is a canalized river in Belgium and in The Netherlands, with the exception of a stretch forming the border between both countries. This river stretch is called "Grensmaas". Instead of canalization, the up- and downstream section of the Grensmaas were connected by a parallel canal (Juliana Canal, Fig. 1). Upstream of Maaseik the Grensmaas is unnavigable. Plans have been made to recover gravel from the Grensmaas in the near future by widening the river channel and deepening the floodplain, enabling the river to assume a more natural course (Helmer *et al.* 1991). Another objective is to reduce unnatural discharge fluctuations caused by an upstream hydro-electric power station in the Lixhe weir. Finally, water quality improvement of the River Meuse is expected in the near future as result of European Union obligations.

In order to establish baseline information on macroinvertebrate communities in the period before the proposed environmental alterations, a description was made of the

macroinvertebrate communities in three natural biotopes: (a) stones in the littoral zone, (b) the river bottom in the littoral zone, and (c) the deeper river bottom in the navigable section of the Grensmaas. Results of investigations from the period 1981-1990 were used to describe these communities. Except a study of Smit & Gardeniers (1986) the information used was obtained from the so-called "grey literature".

METHODS

Literature sources used formed a mixture of quantitative and/or qualitative data due to the use of different sampling techniques. In some studies stones were gathered *ad random* by hand in the littoral zone at depths of approx. 30 cm. Macroinvertebrates were brushed off and subsequently collected during a cleaning procedure of the samples on a 500 µm mesh sieve. The deeper parts of the river bottom were sampled with a tow box (Smit 1982, Klink 1985, 1991) according to Bovens (1984), and the macroinvertebrates in the samples were also collected according to the procedure described above (Smit 1982). At locations with sufficient stream velocity the "kick method" (Frost *et al.* 1970) was applied (Neven 1985[A,B], Peeters 1988, Janssen 1989). Exuviae were sampled by skimming the water surface with a 250 µm mesh hand net (Klink, 1991). Drift nets (0.5 or 2 mm mesh) were also used in this type of sampling (Klink 1985, 1991, Van Urk 1985). Artificial substrates were used by Klink (1991) and Neven (1985[A,B]).

Next criteria were accepted to determine whether an aquatic invertebrate species was part of a described community:
a. A taxon was included if it was found in at least 50% of all samples from a specific biotope, irrespective of the numbers found.
b. A taxon found in less than 50% of such samples was included if the number of specimens was at least 1% of the total number of animals found. An exception to this criterion was item d.
c. Taxa of which only the exuviae were found were classified in biotopes on the basis of their aquatic habitat requirements.
d. A taxon was not considered to be part of a community if it was found only once (i.e. in one single sample), irrespective its quantity.

The level to which the various researchers made their identifications was not always equal. Taxa identified at genus level were only included in a species list if no species within this genus were distinguished by any researcher. The actual number of species in a community would therefore be greater than the number of taxa distinguished. Oligochaeta were mostly not or inadequately identified, therefore this group was left out of consideration. Within the Chironomidae, it was not always possible to identify the larvae to species level. Further identification was made in a few cases on the basis of group characteristics.
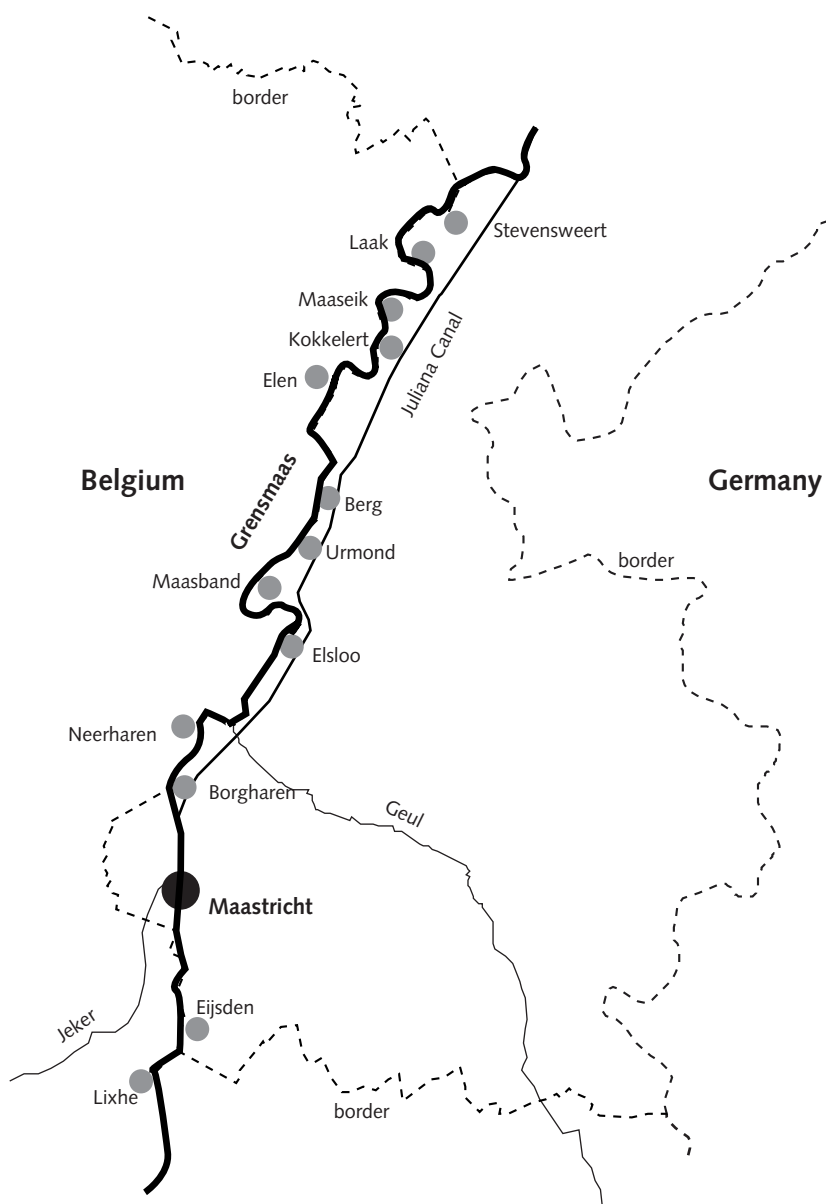
Figure 1. *The sampling locations in the Grensmaas stretch of the River Meuse.*

The sampling locations are summarized in table 1 and indicated in figure 1. Table 1 also gives additional information on the biotopes studied by the individual researchers in the different stretches distinguished in the Grensmaas.

Table 1. *List of the sampling locations and biotopes sampled per researcher in the periode 1981 - 1990.*

Location		Biotopes[1] sampled					
Place	River kilometer	Smit (1982)	Van Urk (1985)	Neven (1985 a,b)	Klink (1985, 1991)	Peeters (1988)	Janssen (1989)
Borgharen	17-20			b	s,b	s,b	
Neerharen	21-22			b,a			
Elsloo	27-29				s,b,e	s,b	
Maasband	33-36			b,a	s,e		b
Urmond	36-38	b			e		b
Berg	38-40						b
Elen	43-48			b,a			
Kokkelert	50-52	s,b					
Maaseik	52-53	s,b		b	s,b,e,a	s,b	
Laak	57-60	d			s,b,d	d	
Stevensweert	61-62		e				

[1] a = artificial substrate, b = bottom littoral zone, d = deeper river bed, e = exuviae, and s = stones in the littoral zone

RESULTS & DISCUSSION

Studies on macroinvertebrates in the Grensmaas were made very fragmentarily in the period 1981-1990. Consistent series of measurements, collected at fixed locations in defined biotopes and samplings according to standardised methods, do not exist. Consequently the results of these studies are not entirely complementary to each other. That was the reason to sketch only communities, of the biotopes defined, on the basis of the arbitrary chosen pre-conditions.

Based on the information available, three natural biotopes were distinguished: (a) stones in the littoral zone, (b) the river bottom in the littoral zone, and (c) the deeper river bottom in the navigable section of the Grensmaas. However, lack of data on stream velocity, in particular, made it impossible to use this important variable in the distinction of biotopes. The macroinvertebrate community found on artificial substrates is described as well. Strictly taken, this biotope does not form a full alternative to a natural biotope. Each artificial substrate possesses a certain selectivity for invertebrates. However, for the monitoring of invertebrates in a river, artificial substrates are an excellent aid (Rosenberg & Resh 1982, De

Pauw *et al.* 1986). By considering habitat requirements of the occurring taxa, supplementary information was gained on the profusion of species in communities in the natural biotopes examined.

In Table 2 the macroinvertebrate communities are described for the three natural biotopes and for the artificial substrate. Excluding the oligochaetes, at least 52 taxa of invertebrates were found. Compared with other rivers, this number of taxa is relatively low. In a sampling of comparable natural biotopes and an artificial substrate in the River Rhine branches in The Netherlands, a total of 68 taxa was found (Bij de Vaate & Greijdanus-Klaas 1991). Taxonomic criteria were similar and so this provides at least a numerical reference for taxa abundance in geographically similar rivers. However, both the rivers Rhine and Meuse differ in many aspects (e.g. degree of pollution, discharge regime).

Taxa found on the artificial substrates in the Grensmaas are expected to occur in at least one of the three natural biotopes. This was actually the case with six exceptions: four of chironomids *(Cardocladius fuscus, Eukiefferiella discoloripes, Glyptotendipes* gr. *pallens, Rheotanytarsus photophilus)*, a flatworm *(Dugesia tigrina)*, and the American crayfish *(Orconectes limosus)*. However, from autoecological information it can be concluded that these six taxa were likely to be part of at least one of the natural communities. They simply were not found in the natural biotopes probably because of insufficient sampling. According to Cranston *et al.* (1983), the larvae of the chironomid genus *Cardocladius* mainly live on stones in large rivers in parts with very fast flowing water. Moller Pillot and Buskens (1990) mention the weirs as their domiciles, with their locally "torrent-like" stream conditions. They may be quite numerous in such places. *E. discoloripes* is an inhabitant of solid substrates (Moller Pillot & Buskens 1990). The larvae are not sensitive to organic pollution. Species of the genus *Glyptotendipes* generally live in the littoral zone in detrital sediments or between sessile algae (Pinder & Reiss 1983). *G.* gr. *pallens*, however, is lithophilous (Klink & Moller Pillot 1982). The flatworm *D. tigrina* also prefers solid substrates, while the crayfish *O. limosus* freely moves between obstacles of any kind.

Three species from the deeper river bottom biotope did not occur in the communities of the two littoral biotopes: two chironomids *(Procladius* spec. and *Chironomus nudiventris*) and one leech species *(Glossiphonia heteroclita)*. The two chironomid larvae are mud inhabitants (Moller Pillot & Buskens 1990, Fittkau & Roback 1983): *G. heteroclita* is found in slow-flowing rivers (Elliott & Mann 1979). The autoecology of these species explains their presence in the deepened part of the Grensmaas. Water velocity in this downstream part of the Grensmaas is considerably lower than in the upstream part, which leads to increased sedimentation.

Table 2. *List of macroinvertebrates (excluding (Oligochaeta) present in the different communities of the biotopes distinguished in the Grensmaas and of the artificial substrate in the period 1980-1990.*

Taxon	Stones littoral zone	Bottom littoral zone	Deeper river bottom	Artificial substate
TRICLADIDA				
Dendrocoelum lacteum				+
Dugesia lugubris/polychroa	+	+		+
Dugesia tigrina				+
HIRUDINEA				
Erpobdella octoculata	+	+	+	+
Erpobdella testacea	+	+		
Glossiphonia complanata	+	+	+	+
Glossiphonia heteroclita			+	+
MOLLUSCA				
Gastropoda				
Acroloxus lacustris		+	+	+
Ancylus fluviatilis	+	+		+
Bithynia tentaculata	+	+	+	+
Physa fontinalis				+
Radix peregra	+			+
Bivalvia				
Dreissena polymorpha	+	+		
Pisidium spec.		+		
Sphaerium corneum		+		+
CRUSTACEA				
Asellidae				
Asellus aquaticus	+	+	+	+
Proasellus meridianus	+	+	+	+
Astacidae				
Orconectes limosus				+
EPHEMEROPTERA				
Baetis spec.	+	+		
Caenis macrura		+		+
TRICHOPTERA				
Hydropsyche contubernalis	+	+	+	+
CHIRONOMIDAE				
Tanypodinae				
cf. *Conchapelopia* spec.		+		
Rheopelopia ornata	+	+		+
Procladius spec.			+	
Orthocladiinae				
Brillia longifurca	+	+		
Cardiocladius fuscus				+
Cricotopus bicinctus	+	+	+	+
Cricotopus intersectus	+			
Cricotopus gr. *sylvestris*	+	+		
Cricotopus triannulatus	+	+		+

Table 2, continued

Taxon	Stones littoral zone	Bottom littoral zone	Deeper river bottom	Artificial substate
Eukiefferiella calvescens	+	+		+
Eukiefferiella claripennis	+	+		
Eukiefferiella discoloripes				+
Nanocladius bicolor	+	+	+	
Orthocladius spec.	+	+		
Paratrichocladius rufiventris	+	+		
Rheocricotopus chalybeatus	+	+		+
Synorthocladius semivirens	+	+		
Prodiamesinae				
Prodiamesa olivacea		+		
Chironomini				
Chironomus nudiventris			+	+
Cryptochironomus spec.		+	+	
Dicrotendipes gr. *nervosus*	+	+	+	+
Glyptotendipes gr. *pallens*				+
Harnischia spec.	+	+		
Parachironomus gr. *arcuatus*	+	+	+	+
Parachironomus gr. *longiforceps*	+	+	+	+
Polypedilum gr. *breviantennatum*		+	+	
Polypedilum scalaenum		+	+	
Tanytarsini				
Micropsectra atrofasciata	+	+	+	+
Rheotanytarsus photophilus				+
Rheotanytarsus rhenanus	+	+	+	+

The number of taxa in the two littoral biotopes and on the artificial substrate was approximately the same (31, 38 and 32, respectively; the Oligochaeta excluded). Only 20 taxa occurred in the deeper river bottom biotopes. Major causes for the low variety of macroinvertebrates in the Grensmaas in the period 1981-1990 are: the poor water quality (Klink 1985, 1986), the seasonally unnatural discharge fluctuations (Klink 1986), and the lack of habitats. With respect to this last point, the Grensmaas can be roughly described as a deeply carved river with steep banks. There are relatively few gravel banks and no sand banks. There is no floodplain forest, and therefore no snag in the main and secondary channels; aquatic and littoral vegetation is notably absent as well.

The small number of molluscs taxa present in the Grensmaas is striking. In the same period, at least 22 species were found in the Dutch part of the River Rhine (Bij de Vaate, unpublished data). Fruget (1991) found 18 species in the deeper and shallow river bottom biotopes in the dammed part of the River Rhône in 1985. The gastropod *Bithynia tentaculata* occurred in relatively large numbers on the stones in the littoral zone. This may reflect the fact that this snail is nog only a grazer but also an opportunistic filter feeder (Schäfer 1951, Starmühlner 1952).

The majority (58%) of the Grensmaas taxa were chironomids. In general, this is true for all three river biotopes. Most of the chironomids were inhabitants of solid substrates (stones, aquatic plants). *Cryptochironomus* spec. and *Polypedilum* gr. *breviantennatum* are inhabitants of sandy river bottoms. Four taxa were definitely mud inhabitants *(C. nudiventris, Micropsectra atrofasciata, Procladius* spec. and *Prodiamesa olivacea)*, while *Parachironomus* gr. *longiforceps* inhabits colonies of Bryozoa. The species belonging to the genus *Eukiefferiella* are well represented in brooks (Moller Pillot & Buskens 199), particularly in the tributaries of the Grensmaas (Lambrechts, pers. com.). The most abundant taxon in the Grensmaas biotopes was the chironomid *Dicrotendipes* gr. *nervosus*. Smit & Gardeniers (1986) established that this taxon hardly occurred in the vicinity of Hermalle, in the adjoining upstream river section, where the River Meuse has been seriously polluted. However, the population rapidly increased in downstream reaches. *D.* gr. *nervosus* is also dominant in the Rhine branches (Bij de Vaate & Greijdanus-Klaas 1991, 1993).

Aquatic invertebrates which are relatively sensitive to water pollution and/or distortion of their habitats were noticeably absent or rare. These included mayflies (Ephemeroptera), caddisflies (Trichoptera), water beetles (Coleoptera), dragonflies (Odonata) and stoneflies (Plecoptera). *Caenis macrura*, one of the mayfly species that was present, is hardly sensitive to poor water quality (Malzacher, 1984). This also applies to the caddisfly *Hydropsyche contubernalis* (Van Urk & Bij de Vaate 1990). Gammarids were strikingly absent, but this is not due to the absence of suitable habitats. Heavy metals and/or organic pollutants are expected to be implicated. Cadmium is one of the problem-substances in the River Meuse, and gammarids are sensitive to this heavy metal (e.g., Wright & Frain 1981, Brown & Pascoe 1988). However, in the course of the 1980s, the cadmium concentration dropped considerably (Boonk & Van der Weijden 1991), but the gammarids did not return, in spite of the possibility of colonisation from upstream habitats. Because the actual cadmium concentration in the Grensmaas was observed not to be a problem for the leech *Glossiphonia complanata*, a species equally sensitive to cadmium (Brown & Pascoe 1988), the continuous loading of the River Meuse with toxic organic substances (Boonk & Van der Weijden, 1991) is considered to be a more important factor for the absence of gammarids.

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CHAPTER 4

PRACTICABILITY OF THE INDEX OF TROPHIC COMPLETENESS

FOR RUNNING WATERS

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PRACTICABILITY OF THE INDEX OF TROPHIC COMPLETENESS

FOR RUNNING WATERS

ABSTRACT

Effects of stress caused by anthropogenic activities in rivers negatively act on the intricate system of trophic links within invertebrate communities and other components of the aquatic ecosystem. These effects can be made visible with the Index of Trophic Completeness (ITC), which was developed as an indicator for the functioning of the river ecosystem, based on the trophic classification of benthic macroinvertebrates. We tested the index using data collected from rivers exposed to different degree of anthropogenic pressure. In undisturbed rivers, all trophic guilds distinguished are present irrespective the part of the river studied and its geographical region. No significant seasonal effect on the outcomes was observed. Disturbances cause the extinction of specific trophic guilds, however due to overlap of effects, the result of an ITC outcome does not indicate the type of anthropogenic pressure. The ITC can be applied to the results of each combination of biotopes sampled, although one has to consider a varying biotope-density relation for species in the trophic guilds. Although the outcomes are projections of trophic guilds present, they can be arranged into quality classes.

INTRODUCTION

Effective river management takes into account ecological information, specifically geared to the water manager and decision maker (Van der Velde & Leuven, 1999). Compression of this information is facilitated by use of relatively simple indices. In rivers, the community structure of benthic macroinvertebrates has become an important quality element in many of the water quality assessment procedures (Rosenburg & Resh, 1993; Canfield *et al.*, 1994; Chapman, 1994). Advantages of the use of macroinvertebrate assemblages in biological assessments include their abundance, sedentary nature, suitable life span, biodiversity and trophic levels, sensitivity and swift response to various stress types (Metcalfe-Smith, 1994).

They play an important role in aquatic ecosystems by the primarily mechanical breakdown of coarse particulate organic material (CPOM), the consumption of fine organic matter (FPOM), including microbes and algae, and their preying and parasitizing on other invertebrates. Benthic macroinvertebrates also constitute a major food source for other invertebrates, fish and waterfowl, making them an important link between microbes and vertebrates (Cummins, 1992), and thus important for the transfer of energy and the transformation of substances.
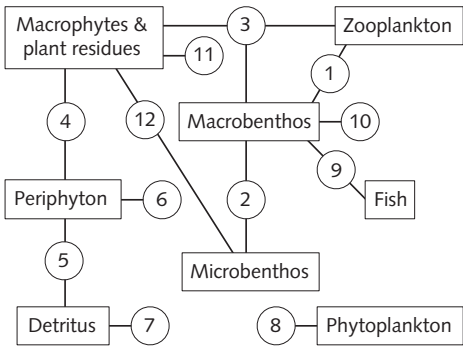
Figure 1. *Food web relations of the twelve trophic guilds (Table 1) of macroinvertebrates distinguished in the ITC.*

Disturbance caused by anthropogenic activities (e.g., water pollution, river engineering) has an impact on substance and energy flows, because any significant stress to the ecosystem has a negative effect on macroinvertebrate communities. This results in the disappearance of food web links if lost species with the same trophic function are not replaced by others belonging to the same guild. To make this visible the Index of Trophic Completeness (ITC) was developed (Pavluk *et al.*, 2000), based on their trophic classification (Fig. 1) (e.g., Konstantinov, 1967; Cummins, 1973; Miroshnichenko, 1983). The ITC indicates the presence of twelve trophic guilds. These guilds were distinguished after data examination from geographically diverse rivers (Pavluk *et al.*, 2000). Trophic characteristics of the animals in these guilds are listed in table 1.

Our objective was to study the practicability of the ITC. Effects of variables like (a) biotope structure, (b) sampling period, (c) river section, (d) climate, and (e) pollution type were made visible.

Table 1. *Characteristics of the macroinvertebrate guilds distinguished in the ITC (Pavluk et al., 2000), including the relative number of taxa per guild present in the database.*

Guild no.	Diet	Feeding behavior	Food size (mm)	Relative number (%)
1	Carnivory	Active shredder/chewer	>1	9.8
2	Carnivory	Passive shredder/chewer	>1	3.6
3	Omnivory	Shredder/chewer/collector	>1	5.9
4	Herbivory	Shredder/chewer	>1	7.8
5	Herbivory	Shredder/chewer	<1	2.6
6	Herbivory	Scraper	<1	26.3
7	Herbivory	Collector	<1	22.7
8	Herbivory	Filter-feeder	<1	8.7
9	Carnivory	Sucker (incomplete food ingestion)	>1	6.6
10	Carnivory	Sucker (total food ingestion)	>1	2.4
11	Herbivory	Sucker	>1	1.9
12	Omnivory	Shredder/chewer	<1	1.7

MATERIAL AND METHODS

Trophic characteristics of the macroinvertebrate species were put together into a taxa database which is part of the index calculation program MaTros (http//www.riza.nl/itc/) The database is still growing and contains already information on 920 species (situation on January 1, 2002). However, the number of taxa per trophic guild differs considerably due to unequal food supply in trophic niches.

The practicability of the ITC was tested with data sets from selected rivers (Fig. 2): (a) rivers subjected to different types of anthropogenic activity (Rhine and Meuse Rivers, The Netherlands; Chusovaya, Salda and Iset Rivers, Russia), (b) a pristine river (Sylva River, Russia), and (c) bottom substrates with a different pollution degree (Rhine distributary called Waal River, The Netherlands). Those data sets were accompanied by data on pollutants. The t-test for independent variables was applied to conclude statistically differences between data sets (Fowler *et al.*, 1998). Conclusions were checked for statistical significance at a 95% level.
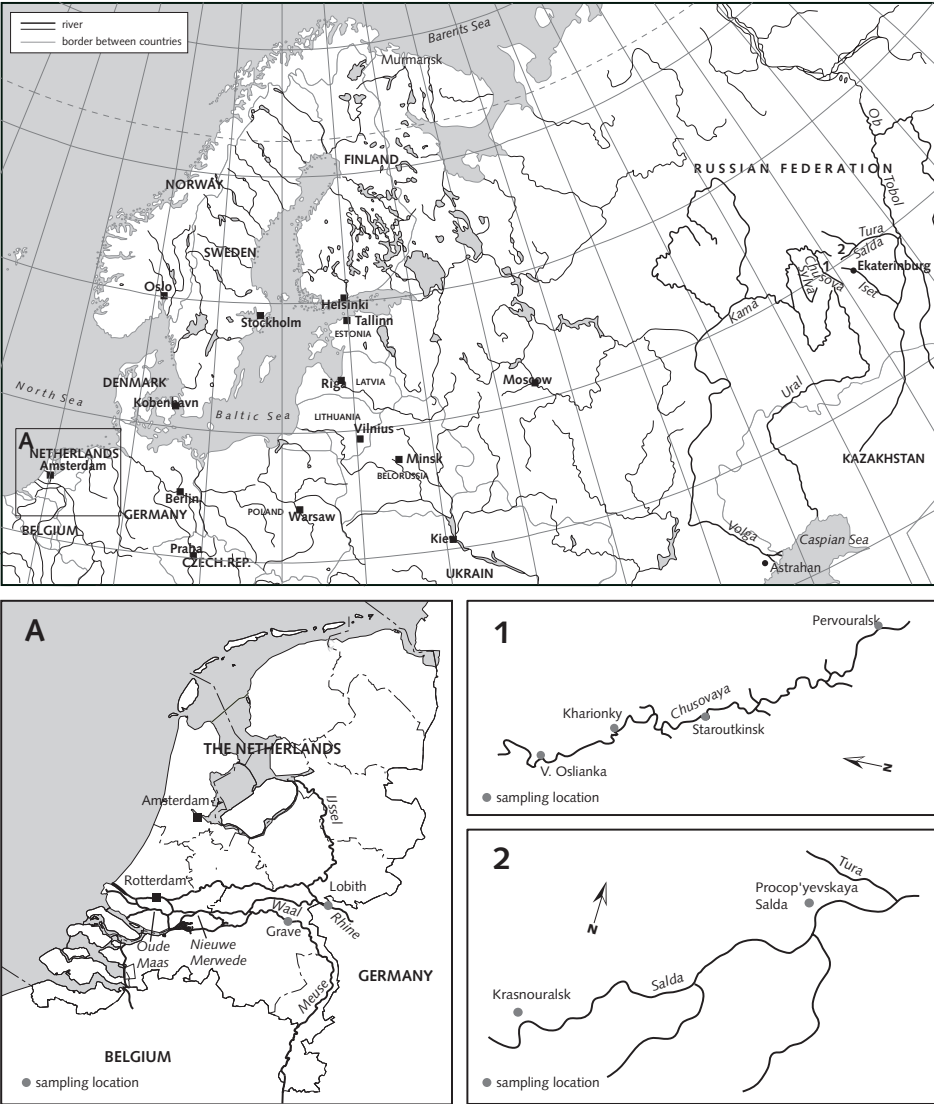
Figure 2. *Sampling stations in the investigated rivers. Top: overview; A: sampling stations in the Rhine and Meuse Rivers, The Netherlands; 1: sampling stations along the Chusovaya River, Russia; 2: sampling stations along the Salda River, Russia.*

Common practice is to group results of index outcomes into quality classes, indicating the status of the surface water monitored. No linear relation is present between the number of trophic guilds and quality classes since the guilds represent different trophic levels. Therefore an indication value (or weight factor) was introduced for each guild for compensation, being $\frac{100}{A}$,

in which A is the relative number of species in each trophic guild (Table 2). The quotient of the sum of the Ln transformations of these values (Table 3) and the number of classes gives the class width. In the case of five classes, width is 7 (34.4/5=6.9 ($\approx$7)). Quality class score is calculated with the formula: $C_{tot} = \sum_{i=1}^{n} C_i$

in which: C_{tot} is the total score, n is number of trophic guilds present in the data-set, and C_i is the ln transformed indication value of trophic guild i. The relation between C_{tot} and the quality classes is given in table 3 for an assessment system with five quality classes.

Table 2. *Indication value (C) of the trophic guilds.*

Trophic guild	C	Ln C
1	10.2	2.3
2	27.6	3.3
3	16.9	2.8
4	12.8	2.6
5	39.2	3.7
6	3.8	1.3
7	4.4	1.5
8	11.5	2.4
9	15.2	2.7
10	41.4	3.7
11	53.2	4.0
12	57.3	4.1
Total		34.4

Table 3. *Quality class score for an assessment system with five quality classes.*

Quality class	C_{tot}	Quality description
I	≥28	high
II	21-28	good
III	14-21	moderate
IV	7-14	poor
V	0-7	bad

RESULTS

A reliable survey of the aquatic ecosystem status, e.g. in the process of improving its ecological values, directly depends on the design of an appropriate monitoring program in which sampling methods and sampling period are very important. Ecological assessment, in general, is based on species richness which strongly depends on the number of microhabitats sampled, the time of the year, and the water type. For testing the applicability of the ITC, different aspects were studied that could influence the outcome of an ITC-calculation: (a) sampling strategy, (b) season, and (c) river stretch (e.g., up-, downstream section).

Influence of the sampling strateg

Data of the Chusovaya (1994 and 1995), Rhine (1995) and Meuse (1996) Rivers were used to study the contribution of the sampled biotopes on the outcome of an ITC-calculation. For the Chusovaya River, a tributary of the Kama River in the Volga basin that is undisturbed by river engineering (Fig. 2), macrozoobenthos data sets were taken into account from two natural biotopes (sandy bottom and pebbles), sampled with a handnet (Pashkevich *et al.*, 1996), including data sets from a standardised artificial substrate sampling (glass marbles) (De Pauw *et al.*, 1994; Pashkevich *et al.*, 1996). The benthic macroinvertebrate community was collected in the vicinity of Stauroutkinsk and Kharionky, in a decreasing gradient caused by an upstream chromium pollution source (Leslie *et al.* 1999). The most complete trophic structure was observed on pebbles and on the artificial substrate (Fig. 3).
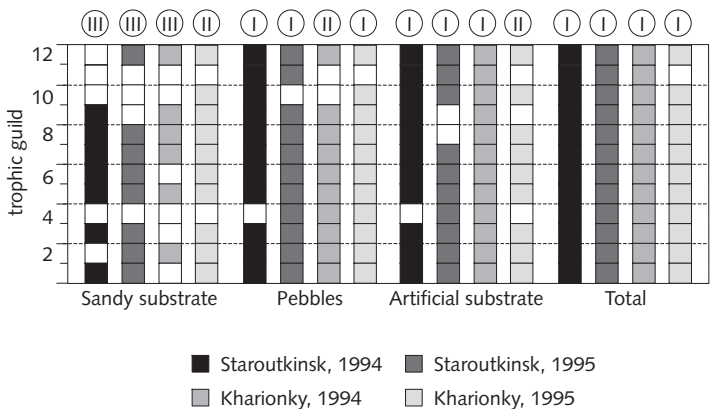
Figure 3. *Number of trophic guilds in different biotopes sampled in the Chusovaya River in the vicinity of Stauroutkinsk and Kharionky in 1994 and 1995. For the ITC calculations the total number of species found in August each year (three samplings) was used; white squares indicate absent guilds. Numbers in the circles represent the calculated quality class (Table 3).*

Statistical analysis (t-test) of the data showed that the number of trophic guilds found in the sandy biotope and on pebbles differed significantly ($p<0.05$). Such was not shown between the sandy biotope and the artificial substrate and between the pebbles and the artificial substrate ($p<0.05$). In the sandy biotope the trophic guilds 4 and 11 (herbivorous shredder/chewers and suckers respectively) were absent in both years, while guild 10 (carnivorous suckers) was only present at Kharionky in 1995. All twelve guilds were met in the samples from the pebbles as well as from the artificial substrate, although guild 11 was absent in all samples taken at Kharionky in 1995. If the results of the sampled biotopes are put together, the results from the sandy substrate samplings do not contribute to the ITC outcomes. No significant differences were observed between the results of the pebbles and artificial substrate samplings. The combined results of all samplings per location and per year indicate a high ecosystem quality.

In the Dutch part of the Meuse River in the vicinity of Grave (Fig. 2), comparable biotopes were sampled in 1992, 1996 and 2000. However, instead of pebbles, stones in the littoral zone were sampled. These stones in this normalised and dammed stretch in the downstream section of the Meuse River are in fact an artificial substrate for the macrozoobenthos community because they were introduced for bank protection. The results (Fig. 4) show that either with the stone or the artificial substrate sampling the maximum number of trophic guilds was found. Also no differences were observed in the quality classes calculated from the ITC outcomes of each sampling method. Results from sandy substrate samplings did not contribute to the ITC outcomes. Herbivorous small and large size particle shredder/chewers, and omnivorous shredder/chewers (guilds 4, 5, and 12 respectively) were absent in all three years; passive carnivorous and omnivorous shredders/chewers, and herbivorous suckers (guilds 2, 3 and 11 respectively) were only present with one species in relatively low densities.
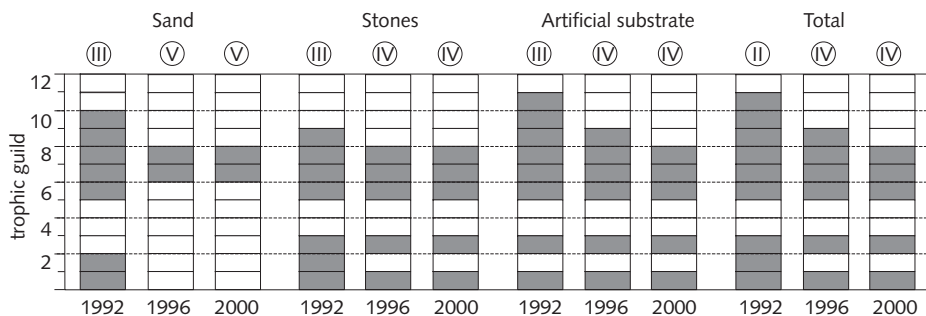
Figure 4. *Trophic guilds present (white rectangles indicate absent guilds) in different biotopes sampled in the Meuse River in the vicinity of Grave in September/October 1992, 1996 and 2000 (only one sampling in the given years). Numbers in the circles represent the calculated quality class (Table 3).*

Using the results of the Netherlands biological monitoring program in the Rhine delta, five biotopes sampled in 1995 and 1999 were compared. The Rhine River is an example of a heavily modified river due to long term (>1000 years) anthropogenic activity in its densely populated floodplain (Kalweit, 1993; Van de Ven, 1993). In 1995 and 1999 three free flowing distributaries in the Rhine delta were sampled in the same period each year. The results of the ITC-calculations are given in figure 5. It is evident that the number of trophic guilds varied between the biotopes sampled, but the differences were not statistically significant (p<0.05). In all biotopes sampled the herbivorous shredder/chewers (trophic guilds 4 and 5), the herbivorous suckers (trophic guild 11) and the omnivorous shredder/chewers (trophic guild 12) were absent in 1995. In 1999 trophic guild 5 was the only absent guild, the other guilds absent in 1995 were present with two species at maximum. In both years the monitoring results of the profundal sand bottom did not contribute to the total number of trophic guilds observed in all distributaries.
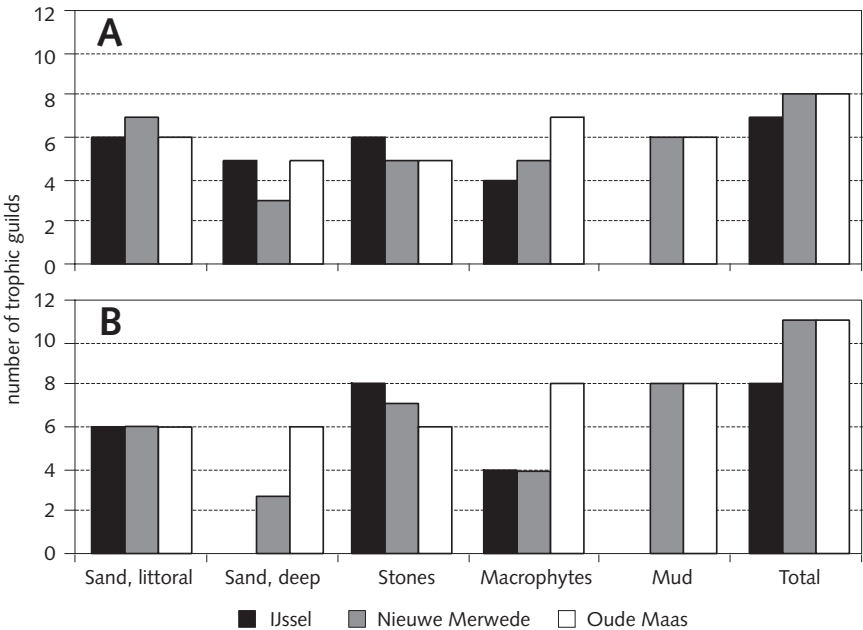
Figure 5. *Number of trophic guilds found in the most important biotopes in three free flowing distributaries in the Rhine delta in 1995 (A) and 1999 (B).*

Seasonal influence

Species composition and the density of macroinvertebrates varies in the course of the year depending on their life cycles. In an ideal situation, season dynamics should not have any influence on the assessment outcomes. Influence of sampling date on species composition and subsequently on the ITC outcomes was examined with time series gathered with artificial substrate sampling only in the 1992, 1996 and 2000 monitoring programs from the Rhine (sampling location Lobith) and Meuse Rivers (sampling location Grave). In general, the ITC outcomes seem to be inversely proportional, that is, more stable with the number of trophic guilds presented in the samples (Fig. 6). This can be explained by the low number of trophic guilds present containing >2 species (n= 4 and 6 for the Rhine and Meuse Rivers respectively). In addition, when trophic guilds were present with <2 species, the density of these species in the samples was relatively low.
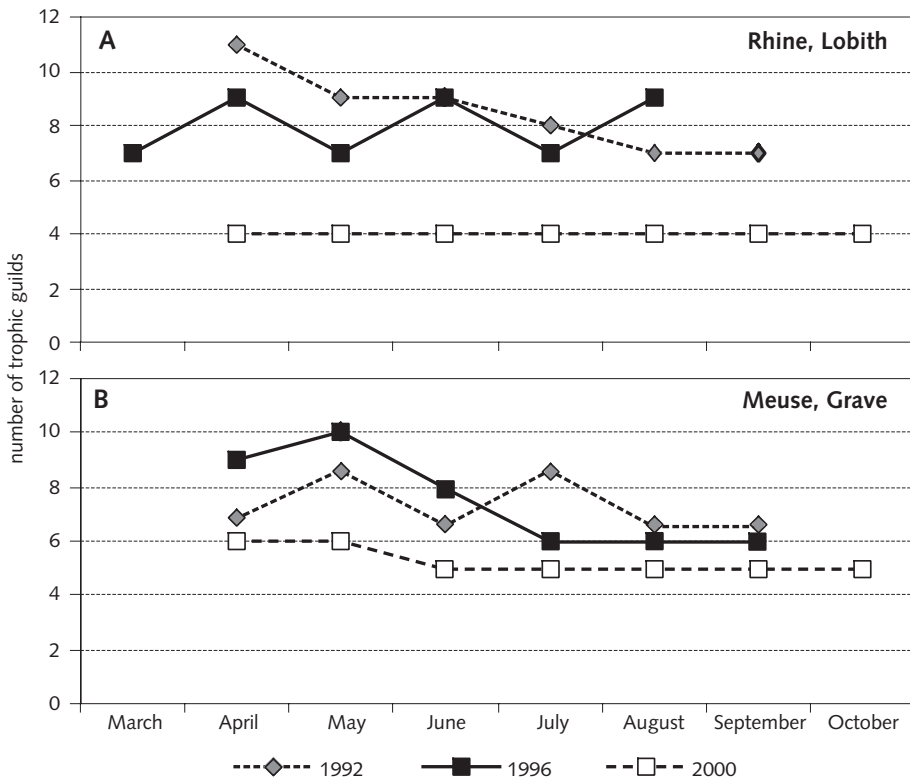

Figure 6. *ITC outcomes for the Rhine (A) and Meuse (B) Rivers based on artificial substrate samples taken in 1992, 1996 and 2000 in the vicinity of Lobith and Grave respectively.*

No statistically significant difference (p<0,05) was found between the number of trophic guilds present in spring and summer at both locations. The relatively low number of guilds present in 2000 coincide with the colonisation of both rivers by the Ponto-Caspian gammarid *Dikerogammarus villosus* which is dominantly predaceous in these new areas (Van der Velde *et al.*, 2000; Dick and Platvoet, 2002).

River section

As summarized in the River Continuum Concept, a gradual change of many stream parameters (e.g., depth, current velocity, bottom substrates, chemical composition of the river water) takes place from the river's source to its mouth (Vannote *et al.*, 1980). This change of environmental conditions results in a shift of the benthic macroinvertebrate community. However, changes in species composition does not necessarily result in loss of trophic guilds (Cummins, 1977). Only the number of taxa in each trophic guild will change as illustrated (Fig. 7) with results obtained from the Sylva River (Middle Urals), a 493 km long pristine tributary of the Kama River in the Volga River basin (Fig. 2). In the River Sylva stony biotopes were sampled in July and August 1996. All trophic guilds were present in the three river sections sampled. With respect to species richness, scrapers and collectors (*guilds 6 and 7*) were the dominant guilds in all river sections, filter-feeders (*guild 8*) in the lower section as well.
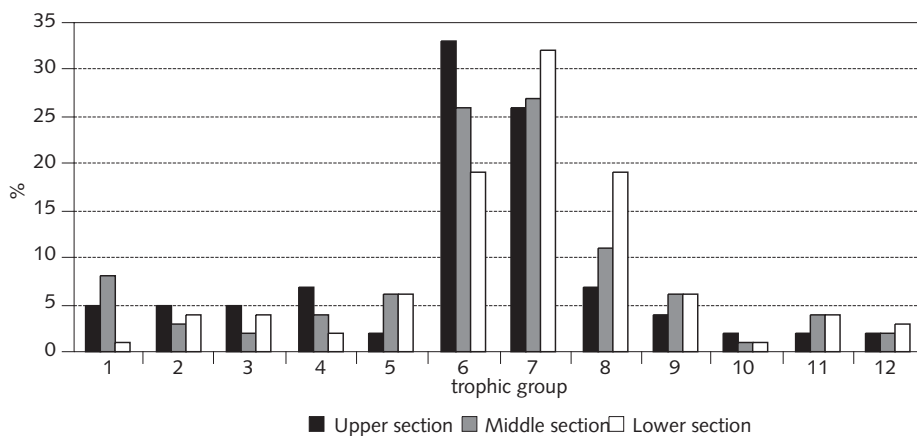
**Figure 7.** *Relative abundance of macroinvertebrate species in stony biotopes in three sections of the Sylva River arranged by their trophic status.*

In the Rhine River, macroinvertebrates were monitored in 1995 and 2000 as part of an extensive international monitoring program organised by the International Commission for Protection of the Rhine River against Pollution (ICPR, Koblenz, unpublished data).

Downstream of Lake Constance, the influence of anthropogenic stress is clearly reflected by the absence of trophic guilds in the lower sections (Fig. 8). Based on the relative number of taxa per trophic guild, the diversity of scrapers and collectors (guilds 6 and 7) was relatively high in all river sections. In the lower sections this was also the case for the filter-feeders guild (guild 8). In the two most upstream sections all trophic guilds were present, despite the presence of a series of dams. In downstream direction, a gradual decrease in the relative abundance of shredders/chewers species (trophic guilds 1 and 4) was observed. Small particle shredders/chewers (trophic guilds 5 and 12) and plant suckers (trophic guild 11) were absent in the downstream sections, the later guild most likely due to the absence of vegetation in the river channel.
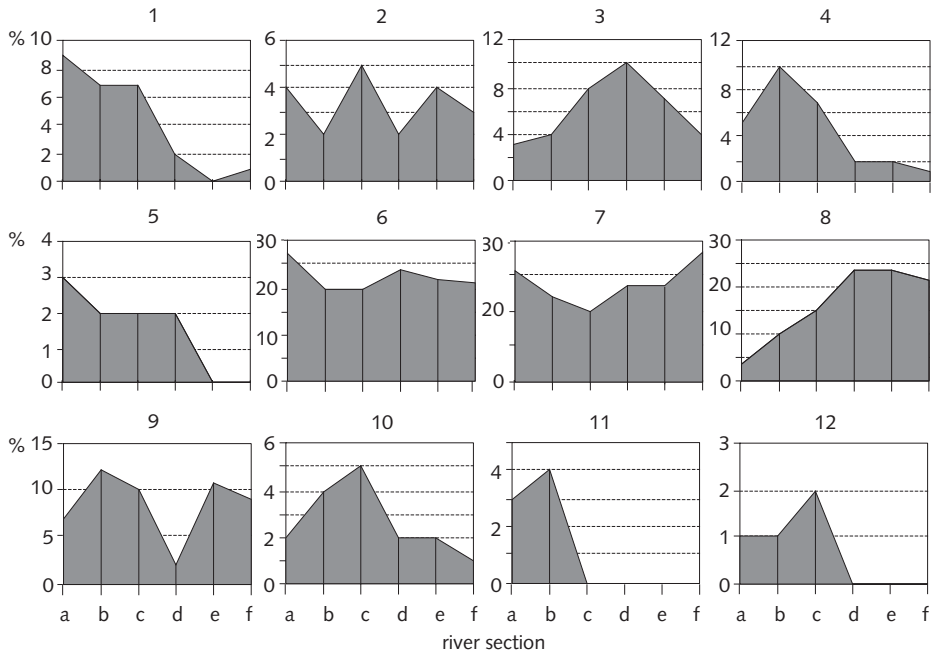
Figure 8. *Relative species number, arranged per trophic guild (1-12), present in successive sections of the Rhine River in 1995. Numbers on the X-axis refer to the river section indicated with river km's (starting at the outlet in Lake Constance and running up in downstream direction): a: 28-64; b: 127-168; c: 220-316; d: 496-696;e: 860-951 and f: 990-1002.*

Climate

According to the theoretical postulates of the ITC (Pavluk *et al.* 2000), the trophic structure of an aquatic ecosystem tends towards the greatest possible diversity of trophic niches

present. In rivers exposed to a continental or a sea climate (respectively the Sylva and Rhine Rivers) all trophic guilds were observed. A crosscheck with another climate zone was made, using data from the Greek rivers Aliakmon, Strymon and Axios (data kindly made available by Dr. Konstantinos Gritzalis, National Centre for Marine Research, Athens, Greece), all situated in a subtropical climate zone. Samples were taken with a standard handnet in June and September 1997 (Gritzalis *et al.*, 1998). The results of all samplings in each river were joined for the ITC-calculation. Not all trophic guilds were present in each river due to significant differences in water pollution (Skoulikidis *et al.*, 1998), however, no guild was absent when taking the three rivers into account (Fig. 9).
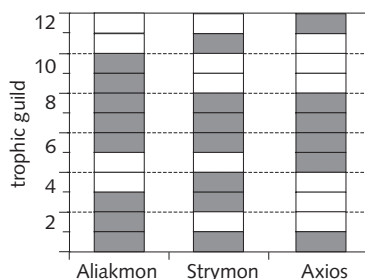
Figure 9. *Trophic structure in three Greece rivers as shown by ITC-calculations (white rectangles indicate absent guilds).*

Types of water pollution

In the Sverdlovsk Oblast, rivers have been subjected to water pollution with specific substances like heavy metals and oil as mono-dominant pollutants. The main pollutant in the Chusovaya River is chromium, in the Salda River copper while the Iset River is subjected to oil pollution. Macroinvertebrate communities in these rivers were studied in the period 1995-1998 by means of handnet sampling and a standard artificial substrate (Pashkevich *et al.*, 1996).

In the Chusovaya River, samples were taken in July, August and September 1995 and 1997 at a location in the vicinity of Pervouralsk downstream of an ore enrichment plant, which is the source of a diffuse and permanent chromium contamination. Total chromium concentrations in the river water measured were mostly above 0.5 mg l^{-1} (Fig. 10). Although species density was relatively low compared with downstream locations, at least eight trophic guilds were present in the combined results of handnet and artificial substrate samplings, resulting in a good quality score most of the time (Fig. 10). Sucking animals (guilds 10 and 11) and small particle shredders/chewers (guild 12) appeared to be the most chromium sensitive.
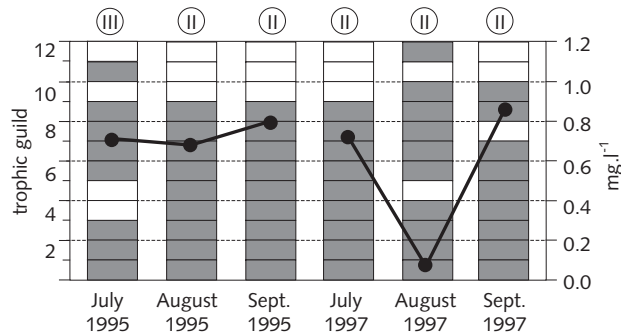
Figure 10. *Trophic structure (white squares indicate absent guilds) in the chromium polluted Chusovaya River near Pervouralsk in the summer seasons of 1995 and 1997, including total chromium concentrations measured (right Y-axis). Numbers in the circles represent the calculated quality class (Table 3).*

Copper pollution in the Salda River has been caused by a melting plant in the vicinity of Krasnouralsk (Fig. 2). At the sampling site, copper concentration ranged between 200 and 230 mg l^{-1} in the summer of 1997 and 1998, except on the last sampling date when the concentration had dropped to 50 mg l^{-1} (Fig. 11). From the combined results of handnet and artificial substrate samplings it can be concluded that, despite low densities compared to locations further downstream, at least seven trophic guilds were present during each sampling, except in September 1997 when extremely few animals were sampled. In general the same guilds were absent as in the Chusovaya River including small particle herbivorous shredders/chewers (guild 5) and sucking animals with total food ingestion (guild 9). Quality score ranged between moderate and poor.
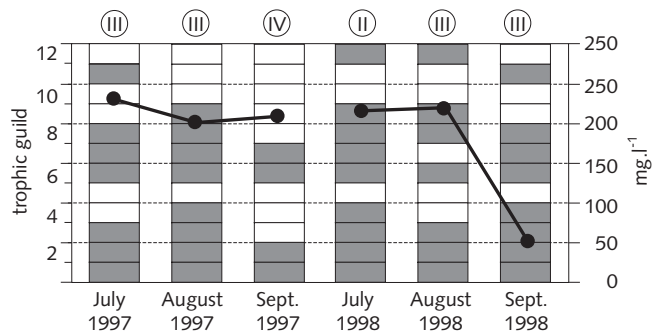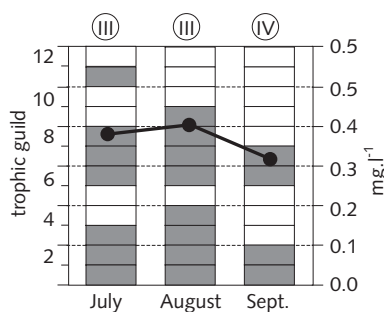

Figure 11. *Trophic structure (white squares indicate absent guilds) in the copper polluted Salda River near Krasnouralsk in the summer seasons of 1997 and 1998, including copper concentrations measured (right Y-axis). Numbers in the circles represent the calculated quality class (Table 3).*

The effect of oil substances on macroinvertebrate communities was studied in the summer of 1997 in a free flowing section of the Iset River in the vicinity of Ekaterinburg (Fig. 2). Relatively high oil concentrations in the range of 0.3-0.4 mg l^{-1} have been the main reason for the degradation of the benthic community. The ITC, calculated from the results of all samples taken on each sampling date (Fig. 12), showed a permanent absence of three trophic guilds (guilds 5, 10 and 12), resulting in a quality score being moderate or poor.

Figure 12. *Trophic structure (white rectangles indicate absent guilds) in the oil polluted Iset River near Ekaterinburg in the summer season of 1997, including oil concentrations measured (right Y-axis).*

Polluted sediments

Chemical sediment quality is an important component of the pelephilic macroinvertebrate's habitat and may thus influence trophic structure of the community when they feed on sedimented particles. Effects of polluted sediments on the results of the ITC outcomes were studied in 1995 in a man-made side channel of the Waal River, the most important distributary in the Rhine delta (Fig. 2). Three identical bottom biotopes were sampled with different degrees of pollution (De Jonge *et al.*, 1999). The bottom consisted of a mixture of sand and mud and was mainly polluted with a mixture of cadmium, chromium, lead, mercury, PCB-153 and ∑-DDT. At three locations examined, situated in a gradient, an enhanced bio-availability was observed of cadmium and chromium (Fig. 13, location A); cadmium, chromium and mercury (Fig. 13, location B); and cadmium, lead, mercury, PCB-153 and ∑-DDT (Fig. 13, location C) respectively. The impact of these combinations of pollutants on the benthic macroinvertebrates is reflected by a gradual disappearance of trophic guilds from location A to C. At location C only herbivorous scrapers and collectors (guilds 6 and 7 respectively) were found (Fig. 13).
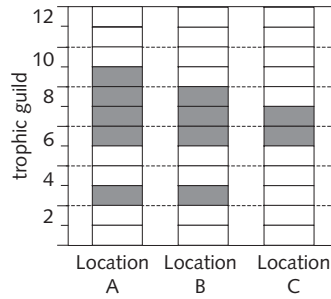
Figure 13. *Trophic structure (white rectangles indicate absent guilds) of the sediment preferring macroinvertebrate community in side channels along the Waal River.*

DISCUSSION

The ITC belongs to the group of indices based on functional trophic relations, taking into account the presence of trophic guilds in the benthic macroinvertebrate community (Pavluk *et al.*, 2000). Outcomes of the index are not given in concrete numbers, but by a projection of trophic relations within a biocenosis. The index indicates the functionality of the community and is based on the functional redundancy hypothesis. If input and transfer of energy and organic matter in the ecosystem change, the composition of the macroinvertebrate community changes as well. Species will disappear and subsequently specific trophic guilds if it was the last remaining species in a functional group (Aarts & Nienhuis, 1999). The index is based on the assumption that in a healthy environment all trophic guilds will be present, irrespective the number of species per guild. The correctness of this assumption was proved in this study. From the investigations we concluded that the trophic structure is a relatively stable mark of the aquatic ecosystem condition. Planas *et al.* (2000) concluded that functional biodiversity of phytoplankton seems a better predictor of stability than species biodiversity. Ecosystems normally exist in a dynamic equilibrium in which structural parameters (e.g., biomass, species density, diversity) may change in different periods of the year and functional properties only will vary through anthropogenic activities (Odum, 1971). Natural fluctuations (e.g., floods, drought, ice covering) may influence the community structure, but their long term effects do not result in the extinction of trophic guilds, which was also demonstrated in our study. Results from the Sylva River with relatively long periods of ice cover, and from the Greek Aliakmon, Strymon and Axios Rivers, exposed to drought during summer and autumn, show the presence of species from all twelve trophic guilds in these rivers (Fig. 7 and 9). No significant seasonal changes were observed in the course of a year in the Meuse and Rhine Rivers (Fig. 6).

In contrast to natural disturbances, anthropogenic induced stress factors have a very short history on the evolutionary scale. Aquatic organisms have not yet developed an adequate response to the heterogeneous and sometimes highly toxic stressors. Specific impact of chemical or physical stress factors on the trophic structure of macroinvertebrate communities is still difficult to indicate due to lack of information. It seemed that the application of the ITC on monitoring results of many rivers was impossible because the assessment methods prescribed in many monitoring programs do not require identification of the macroinvertebrates to species level, which is a necessity. On the other hand, effects of some physical factors on the trophic structure are clear. An excess of suspended matter, for example, affects filter-feeders negatively by blocking their filtering apparatus (Rusanov *et al.*, 1990) and reduces growth of primary producers and thus the occurrence of their consumers (herbivorous animals). In the case of thermal pollution the decomposition rate of organic substances increases, leading to the reduction of dissolved oxygen in the water column and an accumulation of FPOM in the sediments. Under such conditions oxyphilic and thermophobic taxa are under threat, on the other hand, the number of generations per year of other taxa can increase (Allan, 2000).

Chemical stressors can act in different ways in the trophic structure. Chromium pollution in the Chusovaya River leads to the disappearance of the trophic guilds 10, 11 and 12, but did not result in their extinction due to the recolonisation of some representatives of these guilds from the unpolluted river section upstream of the sampling location and the chromium discharge point in the vicinity of Pervouralsk (Fig. 10). Although the other trophic guilds were present nearly all the time, diversity and abundance of the macroinvertebrate fauna was strongly reduced. Copper pollution in the Salda River resulted in the extinction of the trophic guilds 5 and 10, whereas the guilds 11 and 12 balanced on the edge of extinction (Fig. 11). From the latter two guilds, only one species each was present in the given months in relatively low numbers (*Ithytrichia lamellaris* and *Cheumatopsyche lepida* respectively). Oil pollution in the Iset River has a disastrous effect on the occurrence of most trophic guilds except the numbers 1, 2, 6, and 7 (Fig. 12) consisting of carnivorous shredders/chewers (guilds 1 and 2) and herbivorous scrappers (guild 6) and collectors (guild 7) (Table 1). Although oil was the monodominant pollutant, frequently occurring oil contaminants like PCB's also could play an important role in the disappearance of trophic guilds (Swindoll *et al.*, 1987; Le Blanc *et al.*, 1988). Effects of these organo-micropollutants were visible in the macroinvertebrate community of polluted sediments in the Waal River (Fig. 13). In these sediments as well as in the Iset River the guilds of predatory animals were absent, possibly due to effects of bioaccumulation in the food web.

When outcomes of the ITC-calculations are arranged into quality classes the Meuse River at Grave scores well in 1992 and poor in 1996 and 2000 (Fig. 4); all three Rhine distributaries (IJssel, Nieuwe Merwede and Oude Maas Rivers) score moderate and good in 1995 and 1999 respectively (Fig. 5). In both the Rhine and Meuse Rivers anthropogenic pressure is relatively high mainly due to river engineering and industrial pollution (Admiraal *et al.*, 1993). Although macrozoobenthos density was relatively low in the Chusovaya River near Pervouralsk, chromium pollution did result in a much lower quality qualification compared to

downstream reaches. At Pervouralsk the score ranged between moderate and good (Fig. 10), downstream at Stauroutkinsk and Kharionky between good and high (Fig. 3). Copper pollution in the Salda River resulted in quality scores ranging from poor to good (Fig. 11), while oil pollution in the Iset River near Ekaterinburg resulted in scores between poor and moderate (Fig. 12). Also in the Salda and Iset Rivers macrozoobenthos density was relatively low at the sampling locations. However, in all three Russian rivers, the macrozoobenthos community at the polluted sampling locations was positively influenced by a permanent colonisation pressure from the unpolluted upstream river stretch, resulting in elevated quality scores.

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CHAPTER 5

GEOGRAPHICAL PATTERNS IN RANGE EXTENSION OF

PONTO-CASPIAN MACROINVERTEBRATE

SPECIES IN EUROPE

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SPECIES IN EUROPE

ABSTRACT

Range extensions of aquatic Ponto-Caspian macroinvertebrate species in Europe has mainly been facilitated by the interconnection of river basins through man-made canals and intentional introductions. Three inland migration corridors can be distinguished: (a) a northern corridor: Volga → Lake Beloye → Lake Onega → Lake Ladoga → Neva → Baltic Sea, (b) a central corridor connecting the rivers Dnieper → Vistula → Oder → Elbe → Rhine, and (c) a southern corridor connecting the Danube and Rhine rivers. Important trade harbours in Europe were connected via these corridors allowing further range extensions of macroinvertebrate species attached to a vessel's hull or in ballast water. The central corridor was the main migration route before 1992, after which the southern corridor became the most important migration route for the range expansions to the west because of the reopening of the Main-Danube Canal, connecting the Rhine and Danube basins. Especially the water level maintenance in the upper part of the canal, with water supply from the Danube basin, facilitated migration of mobile animals (e.g., crustaceans) from the Danube basin towards the Rhine basin, however, contribution of other transport mechanisms (e.g., shipping) is expected in the near future.

RÉSUMÉ

L'éxtension vers l'Europe des aires de répartition des espèces pontocaspiennes de macroinvertébrés aquatiques a été facilitée principalement par l'interconnection des bassins hydrographiques par la construction de canaux, ainsi que par de introductions délibérées.

On peut reconnaître trois corridors de migration à l'intérieur du continent : (a) un corridor boréal: Volga → lac Blanc → lac Onega → lac Ladoga → Néva → mer Baltique, (b) un corridor central reliant les fleuves Dnieper → Vistule → Oder → Elbe → Rhin et (c) un corridor austral joignant le Danube et le Rhin. D'importants ports commerciaux européens sont reliés par ces corridors, ce qui permet des extensions d'aires supplémentaires d'espèces de macroinvertébrés attachées aux coques des navires ou contenues dans l'eau de ballastage. Le corridor central constituait la voie principale de migration avant 1992, après quoi la voie australe est devenue la route privilégiée d'extension des aires vers l'Occident à cause de la réouverture du canal Main-Danube, reliant les bassins du Rhin et du Danube. En particulier, le maintien des niveaux d'eau dans la partie supérieure du canal par apport d'eau provenant du bassin du Danube favorise la migration d'animaux mobiles (e.g., les crustacés) du bassin du Danube vers celui du Rhin. Néanmoins, l'importance d'autres mécanismes de transport (e.g., le commerce maritime) augmentera, sans doute, dans un avenir rapproché.

INTRODUCTION

The introduction of aquatic organisms outside their native ranges has occurred intentionally and unintentionally for centuries, intentionally because of their economic importance (e.g., Decksbach 1952; Welcome 1988), and unintentionally via ballast water of vessels, through canals connecting river basins, or as non-target species associated with intentionally introduced ones (Jazdzewski 1980). Important reasons for the intentional introduction of aquatic species include (a) aquaculture, (b) the improvement of wild stocks, and (c) the control of unwanted organisms (Welcome 1988; Williamson 1996).

The transport of large quantities of water in ballast tanks from one biogeographical region to another is considered to be one of the most important sources of unintentional intercontinental introductions (Carlton 1985; Gollasch 1996). Recently, it was estimated that the world's major cargo vessels transfer 8-10 billion tons of ballast water per year (Carlton and Geller 1993), and that on average 3000 to 4000 species are transported by ships each day (Carlton and Geller 1993; Gollasch 1996). However, not only transport of macroinvertebrates by sea-going vessels is important for their spread, but also the construction of canals, connecting previously separated biogeographic regions. The interconnection of river basins has facilitated the range expansions of many species in Europe (e.g., Jazdzewski 1980). Numerous canals have been constructed during the last two centuries in Europe as a result of industrial and economic activities. In Germany for example, approximately 1770 km of all inland water ways are man-made (Tittizer 1996). Also, intentionally released or escaped specimens have taken advantage of interconnected river basins.

In this paper, range expansion to the west of 22 Ponto-Caspian macroinvertebrate species is reviewed to make clear their expansion routes. Knowledge of these routes and their mechanisms of spread are important to assess the expansion potential of these animals in and

outside Europe. In addition, biological attributes to make them successful invaders are discussed.

INVASION SUCCESS

The introduction of a species will be successful if all abiotic and biotic factors in its new environment are tolerable. That means it has to arrive in sufficient numbers at the right time. Successful invasions usually proceed through a number of successive stages. After its initial introduction, an invasive species must be able to adapt to its new habitat. Subsequently, the species must be able to reproduce and complete its life cycle. Finally, it will disperse within the new range, usually by gradual local dispersal, but also by jumps often aided by human transport (secondary introductions). It will exhibit exponential population growth, sometimes to densities higher than those in its native range, followed by somewhat lower steady-state numbers.

In spite of the increased opportunities for the immigration of non-indigenous species, not all of these species are successful invaders. To explain this phenomenon, the rule of ten was formulated. This rule states that only ten percent (in practice between 5 and 20%) of the established immigrant species are able to develop populations dense enough for them to be regarded as pests (Williamson 1996). Examples of species considered to be pests are the Ponto-Caspian bivalve *Dreissena polymorpha*, which already spread across Western Europe in the 19th century (Kinzelbach 1992), and the Ponto-Caspian amphipod *Chelicorophium curvispinum*, which spread via river basin connecting canals draining westward (Jazdzewski 1980), and into brackish areas of the Baltic Sea (Gollasch and Leppäkoski 1999). Both species were also transported in ballast water (e.g., to Great Britain).

Immigrant species appear to be especially successful in regions with a climate comparable to where they originated from, in combination with biological attributes to make invasions successful (Table 1). Species dispersing or transferred from the Ponto-Caspian area into the Baltic Sea drainage system arrive in an area with many similar habitats. Both seas belong to the east Atlantic boreal climate zone, and salinity gradients are also comparable (Gollasch and Leppäkoski 1999).

Range extensions by non-indigenous species can be aided by anthropogenic modification of habitats as well (Den Hartog *et al.* 1992). As a result, new species can be pre-adapted because of the similarity of their ancestral habitat resulting in relatively quick colonisation, whereas indigenous species are simultaneously weakened by the modifications. Sometimes new niches are exploited because equivalent indigenous species are not present. Pollution calamities in rivers, for example, can create empty niches, giving invasive species an opportunity to colonise. Persistent pollution can create such empty niches as well (Den Hartog *et al.* 1992). Water quality improvement subsequently gives newcomers the opportunity to settle.

Table 1. *Biological attributes associated with successful Ponto-Caspian invaders into Europe*

Attribute	*Cordylophora caspia*	*Dendrocoelum romanodanubiale*	*Hypania invalida*	*Caspiobdella fadejewi*	*Lithoglyphus naticoides*	*Dreissena polymorpha*	*Caspihalacarus hyrcanus*	*Astacus leptodactylus*	*Hemimysis anomala*	*Limnomysis benedeni*	*Chelicorophium curvispinum*	*C. sowinskyi*	*Dikerogammarus bispinosus*	*D. haemobaphes*	*D. villosus*	*Echinogammarus ischnus*	*E. trichiatus*	*E. warpachowskyi*	*Obesogammarus crassus*	*Obesogammarus obesus*	*Pontogammarus robustoides*	*Jaera istri*
1 Relatively short life span and generation time		+	+						+	+	+	+	+	+	+	+	+	+	+	+	+	+
2 Rapid growth with early sexual maturity						+																
3 High fecundity						+						+										
4 Dispersal by larvae	+					+																
5 Protection of juveniles								+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6 Larger than closely related species or much smaller													+	+	+							
7 Euryoecious								+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
8 Euryhaline	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
9 Non-specific food preference		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
10 Suspension feeding						+			+	+	+	+					+	+				
11 Special adaptations	+			+		+								+	+							
12 Gregarious behaviour	+					+	+		+	+	+	+										

INVASION ROUTES

Range extensions of aquatic Ponto-Caspian species in Europe has been mainly facilitated by the interconnection of river basins, beginning in the 17th century. An important phase was the construction of canals that connected the Bug (Vistula basin) and Pripyat (Dnieper basin) rivers, the Vistula and Oder rivers, and the Elbe and Oder rivers in the 18th century. The Volga-Don Canal connecting the Volga and Don rivers, which opened for shipping in 1952, provided a connection between the Caspian and Black seas. Although attempts were already made in the 19th century to connect the rivers Danube and Main (Rhine basin), the canal constructed at that time (Ludwig Canal) only functioned briefly for a relatively small number of cargo vessels. During the second world war the link between both rivers was interrupted and afterwards not restored. However, a new shipping canal (Main-Danube Canal), which

officially opened in September 1992, is an important new route for Ponto-Caspian species to migrate from the Danube River to the west (Tittizer 1997).

Intentionally introduced species could also take advantage of the river basin connections. In the former Soviet Union large quantities of crustaceans were used as live food for commercial fish species (Decksbach 1952). The Ponto-Caspian region has been the preferred source for the so-called "acclimatisation" of new species to different types of water bodies, especially impoundments on large rivers for the purpose of enriching the fauna and as fish food (Mordukhai-Boltovskoi 1979). The most frequently used Ponto-Caspian invertebrates were mysids of the genera *Paramysis*, *Limnomysis* and *Hemimysis* and the amphipods *Dikerogammarus haemobaphes*, *Pontogammarus robustoides*, *Obesogammarus crassus*, *Echinogammarus ischnus*, *E. warpachowskyi*, and *Chelicorophium curvispinum* (Karpevich 1975; Jazdzewski 1980). All together, nine species of Mysidacea, seven species of Cumacea and 17 species of Amphipoda were used in the period 1940-1970 (Karpevich 1975).

In general, the interconnection of river basins in Europe resulted in corridors for aquatic animals to migrate actively or passively (e.g., by vessels in humid places or attached to the ship's hull) from one geographical region to another. Three important canal corridors for the range extension of Ponto-Caspian species can be identified (Fig. 1).
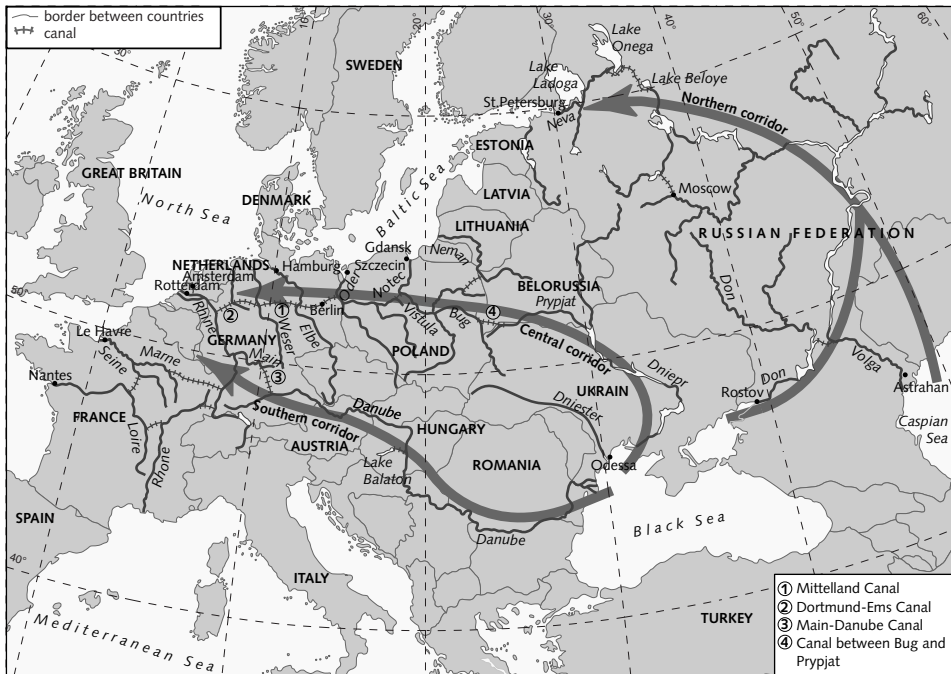

Figure 1. *The migration corridors of Ponto-Caspian species in Europe.*

Northern corridor

The northern corridor covers the route Volga River → Lake Beloye → Lake Onega → Lake Ladoga → Neva River → Baltic Sea. In the past there was another northern corridor from the Dnieper River to the Kuronian Lagoon in the Baltic Sea (via the Oginskiy Canal and the Neman River), but this corridor does not exist anymore (S. Olenin, Klaipeda University, Manto, Lithuania, personal communication). The bivalve *D. polymorpha* likely used this corridor, which opened by the end of the 18th century, for its range extension (Decksbach 1935).

Central corridor

The central corridor covers the route Dnieper River → Vistula River → Oder River → Elbe River → Rhine River. Invasive species were able to reach the Baltic Sea and Western Europe via this corridor. The amphipod *Chelicorophium curvispinum* was probably the first Ponto-Caspian crustacean that successfully used the corridor for range extension (Jazdzewski 1980; Jazdzewski and Konopacka 2000).

Both the northern and central corridors have been important routes for Ponto-Caspian macroinvertebrates to immigrate to the Baltic Sea. Which one has been the most important could not be determined. Species that reached relatively high densities in the Baltic Sea lagoons, especially in the Kuronian Lagoon, are: *D. polymorpha, Paramysis lacustris, Limnomysis benedeni, Pontogammarus robustoides, Obesogammarus crassus, Echinogammarus ischnus* and *Echinogammarus warpachowskyi* (Olenin and Leppäkoski 1999).

Southern corridor

The southern corridor covers the route Danube River → Rhine River. As indicated above the Main-Danube Canal forms the link between these river basins. The water level maintenance in the upper part of the canal, with water supply from the Danube basin, especially facilitates migration of mobile animals (e.g., crustaceans) from the Danube basin towards the Rhine basin. Tittizer (1997) estimated that 150 million m^3 of water from the Danube basin flows into the Rhine River each year. The corridor to the Rhine delta has already been successfully traversed by some amphipod species such as *Dikerogammarus haemobaphes* (Schleuter *et al*. 1994), *D. villosus* (Bij de Vaate and Klink 1995) and *Echinogammarus trichiatus* (Podraza *et al*. 2001), the isopod *Jaera istri* (Schleuter and Schleuter 1995) and the mysid *Limnomysis benedeni* (Reinhold and Tittizer 1998), the polychaete *Hypania invalida* (Klink and Bij de Vaate 1996), as well as the planarian *Dendrocoelum romanodanubiale* (Schöll and Behring 1998).

Using one of the three corridors, Ponto-Caspian species have been able to reach important trade harbours outside their native ranges (Fig. 1). Subsequently, transport in ballast water has been an important vector for their further dispersal (secondary introduction). *D. polymorpha* and *C. curvispinum* are two clear examples of species which have made use of this dispersal mechanism.

INVASIVE PONTO-CASPIAN SPECIES

Ricciardi and Rasmussen (1998) identified some Ponto-Caspian euryhaline macro-invertebrate species with recent invasion histories, that have likely been transported in ballast water. As a result, these species have been classified as high invasion risk species: the amphipods *Chelicorophium curvispinum, C. sowinskyi, Dikerogammarus haemobaphes, D. villosus, Obesogammarus obesus, O. crassus,* and *Pontogammarus robustoides,* the mysids *Hemimysis anomala, Limnomysis benedeni, Paramysis intermedia, P. lacustris* and *P. ullskyi,* the freshwater polychaete *Hypania invalida,* and the bivalve *Monodacna colorata.* Most of these species have already been found either in the brackish areas of the Baltic Sea (Table 2) or in the Rhine basin (Table 3).

Table 2. *Ponto-Caspian macroinvertebrate species found in coastal waters of the Baltic Sea.*

	Species	**References**
Cnidaria	*Cordylophora caspia*	Olenin and Leppäkoski 1999
Oligochaeta	*Paranais frici*	Panov *et al.* 1997
	Potamothrix heuscheri	Panov *et al.* 1997
	P. vejdovskyi	Panov *et al.* 1997
Mollusca	*Lithoglyphus naticoides*	Piechocki 1979
	Theodoxus pallasi	Mordukhai-Boltovskoi 1979
	Dreissena polymorpha	Panov *et al.* 1997
Crustacea	*Hemimysis anomala*	Salemaa and Hietalahti 1993
	Limnomysis benedeni	Olenin and Leppäkoski 1999
	Paramysis lacustris	Gollasch and Leppäkoski 1999
	Chelicorophium curvispinum	Gollasch and Leppäkoski 1999
	Dikerogammarus haemobaphes	K. Jazdzewski and A. Konopacka, unpublished data
	Echinogammarus ischnus	Jazdzewski 1975
	E. warpachowskyi	Olenin and Leppäkoski 1999
	Obesogammarus crassus	Gollasch and Leppäkoski 1999
	Pontogammarus robustoides	Gruszka 1999

Table 3. *Ponto-Caspian macroinvertebrate species found in the Rhine basin.*

	Species	**References**
Cnidaria	*Cordylophora caspia*	Tittizer 1996
Tricladida	*Dendrocoelum romanodanubiale*	Schleuter and Schleuter 1998
Polychaeta	*Hypania invalida*	Klink and Bij de Vaate 1996
Hirudinea	*Caspiobdella fadejewi*	Geissen and Schöll 1998
Mollusca	*Lithoglyphus naticoides*	Gittenberger *et al.* 1998
	Dreissena polymorpha	Bij de Vaate *et al.* 1992
Acarina	*Caspihalacarus hyrcanus*	A. Bij de Vaate, unpublished data
Crustacea	*Astacus leptodactylus*	Holthuis and Heerebout 1986
	Chelicorophium curvispinum	Van den Brink *et al.* 1989
	Hemimysis anomala	Schleuter *et al.* 1998
	Limnomysis benedeni	Kelleher *et al.* 1999
	Dikerogammarus haemobaphes	Schleuter *et al.* 1994
	D. villosus	Bij de Vaate and Klink 1995
	Echinogammarus ischnus	Schöll 1990
	E. trichiatus	Podraza *et al.* 2001
	Jaera istri	Schleuter and Schleuter 1995

Cordylophora caspia

The hydroid *Cordylophora caspia* originates from the Black and Caspian seas where it lives in brackish as well as fresh water. In general it commonly occurs in estuaries, lagoons and coastal lakes (Arndt 1989), rarely in oligohaline freshwater. Colonies of *C. caspia* develop well at 2-12‰ salinity with relatively constant environmental conditions, and at 2-6‰ with considerable tidal influence (Arndt 1989). The occurrence of *C. caspia* has also been reported from upper reaches of rivers at favourable conditions such as fast flow, high oxygen availibility and positive ion anomalies (Ca^{2+}, Mg^{2+}, Na^+) (Arndt 1989).

C. caspia has been dispersed via canals and rivers attached to ship's hulls, floating reed, water lily stems and other macrophytes (Roos 1979) and in ballast water for overseas transportation. Most likely the northern but certainly the southern corridor (Fig. 1) (Kinzelbach 1995) was used for range expansion. According to Tittizer (1996) the species occurs in all rivers and canals in the Rhine, Weser, Oder and Danube basins. *C. caspia* was recorded in 1874 in The Netherlands (Vervoort 1946). In 1924 the species already had a world wide distribution, from the cold boreal and antiboreal to the subtropical regions (Roch 1924, Arndt 1989). However, its distribution was discontinuous owing to its dispersal via ballast water into estuaries, from where it then dispersed upstream.

Cordylophora colonies are very plastic and numerous growth forms are described relative to the environmental conditions (e.g., salinity, light, temperature). The species has no medusal stage, its sexual stage is at the polyp and planula larvae released settle after a short planktonic life. Asexual dispersal mechanisms, e.g. body fragments (hydrorhiza) and

menonts, which survive in winter time, contribute to its colonisation success. In its menont stage *C. caspia* can easily be transported over large distances because in this stage the species is temperature and drought resistant. Menonts survive in sea water and even can develop into polyps at maximum salinity of 40‰ (minimum: 0.08‰) (Vervoort 1946). The polyp prefers solid substrates (stones, wooden piles, bivalve shells like *Dreissena*), crabs, macrophytes). It is carnivorous (eating small crustaceans, worms, insect larvae, watermites) and profits from eutrophication.

Dendrocoelum romanodanubiale

According to Weinzierl and Seitz (1994) the Ponto-Caspian triclad *Dendrocoelum romanodanubiale* was first recorded in the upper Danube (Germany) in 1994, indicating that the southern corridor (Figs. 1) was used for western range expansion. In August 1997 and July 1998 the species was observed in the Rhine River (Schöll and Behring 1998) and first recorded in the Rhine delta in September 1999 (Bij de Vaate and Swarte 2001).

Hypania invalida

Migration pattern of the polychaete *Hypania invalida* has been similar to that of the isopod *Jaera istri*. Its range expansion to the west was only observed through the southern corridor (Fig. 1). In 1967, the species was first observed in the upper section of the Danube River (Germany) (Kothé 1968). Although the colonisation of the Main River was reported in 1996, *H. invalida* was already observed in the lower Rhine River in 1995 (Klink and Bij de Vaate 1996).

Caspiobdella fadejewi

Outside its native distribution area, mainly in rivers emptying into the Black Sea (Geissen and Schöll 1998), the Ponto-Caspian leech *Caspiobdella fadejewi* is known from two Vistula River affluents, the San and Biebrza rivers, in Poland (Bielecki 1990) and from the Rhine River. In the Biebrza River it was observed in 1989 on the heads and gill opercula of several common fish species (Bielecki 1990), in 1998 in the lower Rhine River on solid substrates (Geissen and Schöll 1998), and in 2000 in bottom samples from a river restoration area in the forelands along the Waal River, the main distributary in the Rhine delta (A. bij de Vaate, unpublished data). *C. fadejewi* is the dominant species of the Piscicolidae in the Austrian part of the Daunbe River and was recently observed upstream in the German part of that river (Geissen and Schöll 1998). To reach the Rhine delta, it is thought that the southern corridor (Fig. 1) must be traversed; however, unintentional introductions caused by living fish trade remains a possible vector for the spread of this fish parasite.

Lithoglyphus naticoides

The gastropod *Lithoglyphus naticoides* originates from the western Black Sea, and it is considered to be a species of slowly flowing waters like those in the downstream parts of rivers, canals and lakes (Gittenberger *et al.* 1998). In the second part of the 19th century it was discovered in The Netherlands (Schepman 1874). The dispersal of this species was thought to be a consequence of canal construction in the previous centuries. The northern and the central corridor (Fig. 1) could have been the main route for western migration. Records of the species in Poland (Piechocki 1979) and in the vicinity of Berlin (Sukopp and Brande 1984) support this hypothesis. However, Gittenberger *et al.* (1998) considered the southern corridor (Fig. 1) to be the most probable migration route to The Netherlands. *L. naticoides* was suspected to have dispersed via the Ludwig Canal, which was the first connection between the Rhine and Danube basins. In Poland, the species generally shows a similar distribution pattern to *D. polymorpha*, occurring in large and medium-sized lowland rivers, in the Szczecin and Vistula Lagoons, and in lakes of the Mazurian Lake district (Piechocki 1979). In The Netherlands *L. naticoides* has been found in the Rhine delta and in Lake IJsselmeer (Gittenberger *et al.* 1998).

Dreissena polymorpha

Distribution of the zebra mussel in Europe was reviewed by Strayer and Smith (1993). It represents the first mass invasion of a Ponto-Caspian species in the area and therefore provides a good example of how and in which directions a Ponto-Caspian invader is able to extend its range. The construction of canals in the 18th century, connecting the Dnieper, Neman and Vistula rivers was the beginning of its westward expansion (Decksbach 1935; Kinzelbach 1992). In general, expansion took place through the northern and central corridor (Fig. 1), *(i)* attached to rafts by which timber was transported through canals and rivers to harbours along the Baltic Sea, and from there overseas by ships, *(ii)* attached to ship's hulls, and *(iii)* by planktonic larvae using canals that connect rivers and lakes (Sukopp and Brande 1984). In the case of expansion by timber transport aboard ships, *D. polymorpha* was able to reach Great Britain in 1824 and The Netherlands in 1826 (Kinzelbach 1992). Its recent invasion of Ireland, in 1997, is most likely a result of the transportation of yachts, aboard ships, from Great Britain or The Netherlands (Minchin and Moriarty 1998). The species can also be transported across land while attached to boats on trailers because it is able to withstand exposure to air for several weeks (Ricciardi *et al.* 1995). In Western Europe, the zebra mussel crossed the Alps between 1960 and 1970, and established in Italy (Giusti and Oppi 1972). Transportation of yachts from one lake to another was considered to be the vector for their spread (Kinzelbach 1992). Recently the Pyrenees mountains were probably crossed in the same way, first observation of the species was made in Spain in the lower part of the Ebro River in 2001 (Araujo and Álvarez Halcón 2001). Its range extension futher north seems to be limited by climatic conditions, largely because it requires a water temperature above approx. 12°C for spawning (Borcherding 1991).

Dreissena bugensis, which is sympatric with *D. polymorpha* in the Ponto-Caspian area, did not disperse into Western Europe despite its further range of expansion in Russia (Pligin 1979) and its successful immigration to the North American Great Lakes between 1985 and 1989 (Mackie 1999).

Caspihalacarus hyrcanus

According to Bartsch (1998) the distribution area of the freshwater mite *Caspihalacarus hyrcanus* covers the Caspian and Black seas, including the rivers emptying into these basins. In the Danube River it was found upstream as far as Bratislava (Slovakia). It has been recorded in fresh and brackish waters up to a salinity of 12.5‰. In 2000 the species was found in the same area in the Rhine delta where *Caspiobdella fadejewi* was found. *C. hyrcanus* had colonised woody debris in a newly constructed secondary channel (A. bij de Vaate, unpublished data). Lack of data from other regions in Western Europe hampers the reconstruction of their spreading history to the Rhine delta. However, the southern corridor (Fig. 1) forms the shortest connection between the Rhine delta and the nearest by known population in the Danube River. It should be noticed that *C. hyrcanus* easily can be overlooked during sampling because of its size (± 500 µm) if unsuitable (>500 µm mesh) handnets are used for sampling and if coarse-meshed sieves are used for rinsing the samples.

Astacus leptodactylus

According to Ingle (1997) the crayfish *Astacus leptodactylus* is endemic to rivers discharging into the Black and Caspian seas. Intentional introductions and subsequent escapes from aquaculture facilities appear to have been the major vector for its range extension in Western Europe during the 19th century. Today *A. leptodactylus* has been dispersed all over Western Europe and can be found in different water types such as rivers, canals and lakes.

Hemimysis anomala

The euryhaline mysid *Hemimysis anomala* occurs in a wide range of salinities in the Ponto-Caspian area, from freshwater to 19‰ salinity (Bacescu 1954; Mordukhai-Boltovskoi 1979; Komarova 1991). Preferring lentic conditions, it has been observed in the coastal regions of the Caspian, Black and Azov seas, in adjacent lagoons and up to 50 km upstream in the Don, Dniestr, Dnieper, Pruth and Danube rivers (Bacescu 1954, 1966; Komarova 1991). In the 1950's and 1960's, *H. anomala* was intentionally introduced into several impoundments in the Dnieper River, water reservoirs near Chernorechensk and Simferopol on the Crimean peninsula, and the Dubossary reservoir in Moldavia (Komarova 1991). In the 1960's, *H. anomala* was successfully transferred from the Dnieper hydropower reservoir into reservoirs in Lithuania, for example, the Kaunas reservoir in the Neman River (Gasjunas 1968b; Mordukhai-Boltovskoi 1979). From there it dispersed into the Baltic Sea, where it was first recorded in 1992 in the Gulf of Finland (Salemaa and Hietalahti 1993). The first observation in the Rhine basin (Neckar River) is from 1997 (Schleuter *et al.* 1998). In July

1998 *H. anomala* was recorded in the Main River, another tributary of the Rhine River (Schleuter and Schleuter 1998). Kelleher *et al.* (1999) found *H. anomala* in stomachs of young percids caught in the Rhine delta near Nijmegen in September 1997, being its first record in The Netherlands. All of these obervations including that in the upper Danube (Wittmann *et al.* 1999) indicate that the southern corridor (Fig. 1) was used for range extension. However, *H. anomala* has been observed in the same period at several locations in the western part of The Netherlands: *(i)* in June 1997 and November 1998 in the littoral zone of the brackish Lake Noorder-IJ close to, but isolated from the North Sea Canal and the port of Amsterdam, The Netherlands, *(ii)* in 1998 in the Andijk reservoir, and *(iii)* from 1997 onwards in the Biesbosch reservoirs (Ketelaars *et al.* 1999). In 1999 the species was also found in Belgium in the Broechem reservoir, close to the port of Antwerp (H.A.M. Ketelaars, unpublished data). Since all these observations were made in the vicinity of the international ports, *H. anomala* was likely introduced as a result of ballast water transfer as well. Its recent observation in the Salzgitter Canal in northern Germany (Eggers *et al.* 1999) is an indication that the central corridor also has been used for range expansion.

From the above mentioned observations it can be concluded that the present distribution of *H. anomala* in Western Europe is very scattered, and raises suspicions that it might not have been found in monitoring studies because of its nocturnal activity. Emphasis should therefore be placed on more appropriate sampling in monitoring programs (e.g., Ketelaars *et al.* 1999).

Limnomysis benedeni

The mysid *Limnomysis benedeni* is an euryhaline species; 6.5‰ salinity is tolerated (Wittmann 1995). Lentic environments with aquatic vegetation are its preferred habitats. It is endemic to the coastal waters of the Black and Caspian seas and can be found several hundred kilometres upstream in rivers discharging into both seas (Bacescu 1954). The species was intentionally introduced into several habitats along the Baltic coast of the former Soviet Union (Leppäkoski 1984) and in Lake Balaton (Hungary) for the enhancement of fish production (Woynarovich 1955).

In 1947, *L. benedeni* was found in the Danube River in the vicinity of Budapest (Dudich 1947). Further range extension upstream has been well documented from 1973 to present. The upper Danube (in Germany) was reached in 1993 (Wittmann 1995), and in 1998 the species was found in the Main-Danube Canal (Reinhold and Tittizer 1998). However by 1998, the species had already reached the middle Rhine River, and the Rhine delta (Kelleher *et al.* 1999; Ketelaars *et al.* 1999). The successive records of *L. benedeni* in the Danube River, the Main-Danube Canal, and the Rhine basin clearly indicate that the southern corridor was the migration route for westward range extension (Figs. 1 and 2).

Figure 2. *Migration patterns of Limnomysis benedeni and Jaera istri.*

Chelicorophium curvispinum

The amphipod *Chelicorophium curvispinum* originates from large rivers discharging into the Black Sea and the Caspian Sea (Volga, Dnieper, Dniester, Danube and many other rivers). It was dispersed via canals and rivers attached to the hulls of ships, and in ballast water for overseas transportation. The earliest report of *C. curvispinum* outside the Ponto-Caspian drainage was in the Spree-Havel system near Berlin in Germany. The species was described then as new to science (as *Corophium devium*) and later synonimised with *C. curvispinum* (Jazdzewski and Konopacka 1996). *C. curvispinum* clearly dispersed into the Baltic Sea and North Sea drainage systems through the central corridor (Figs. 1 and 3). The species was the first Ponto-Caspian crustacean to immigrate to Polish waters and was probably already present in the middle Vistula and Notec basins before its discovery in Poland in the 1920's (Leppäkoski 1984). Today *C. curvispinum* is common and abundant in the Vistula and Oder basins, as well as in waters connecting these two systems (Jazdzewski and Konopacka 2000). It also inhabits rivers in Northern Germany (Herbst and Bäthe 1993) and was found in the Mittelland Canal and Dortmund-Ems Canal in 1956 and 1977 respectively (Van den Brink *et al.* 1989). The most western locality of *C. curvispinum* is in Great Britain where it was recorded in the early 1930's by Crawford (1935). The ancestors of the British populations were likely dispersed by ships sailing from Northern Germany ports after its appearance in the Elbe River in 1920 (Harris 1991). Soon after being recorded in the middle and lower Rhine in

1987 (Van den Brink *et al.* 1989) *C. curvispinum* developed such dense populations that it became the most numerous macroinvertebrate on solid substrates in this river. Monitoring data from artificial substrate samplings and other field observations have shown that the macroinvertebrate species richness was reduced with high densities of *C. curvispinum* (Van den Brink *et al.* 1991; Van der Velde *et al.* 1998). The animals collect suspended particles from the water column for the construction of tubes on solid substrates in which they live. In such densities as found in the Rhine River, the species was able to cover large parts of the substrates with these tubes, altering the environment for lithophilic communities. According to Kinzelbach (1997), *C. curvispinum* also outcompeted the freshwater isopod *Asellus aquaticus* and several species of chironomid larvae. The high densities of *C. curvispinum* observed in the Rhine River strongly impacted another Ponto-Caspian invader negatively, the zebra mussel *(D. polymorpha)* (Van der Velde *et al.* 1998), which was a dominant species in the Rhine delta around 1990 (Bij de Vaate *et al.* 1992). In contrast in Lake Balaton (Hungary), both *D. polymorpha* and *C. curvispinum* arrived at about the same time after their expansion from the Ponto-Caspian region (1932 and 1935, respectively), but seemed to be associated with each other (Sebestyen 1938). Similar observations were made in the lower Vistula, where *D. polymorpha* was always accompanied by *C. curvispinum*.

Chelicorophium sowinskyi

Migration patterns of *Chelicorophium sowinskyi* are unclear because of the difficulty distinguishing it from *C. curvispinum* (Jazdzewski 1980; Jazdzewski and Konopacka 1996). The species originates from the Danube, Dnieper, Volga, Don and Dniester rivers (Mordukhai-Boltovskoi 1979; Jazdzewski and Konopacka 1996). Records of this species in the Danube River in the Czech Republic indicate that the southern corridor (Fig. 1) could become the most obvious route for its range extension.

Dikerogammarus bispinosus

Although *Dikerogammarus villosus* and *D. bispinosus* are clearly different species (Müller and Schramm 2001), *D. bispinosus* is often considered and mentioned as a subspecies of *D. villosus*. In the Dniester River, the relative abundance of *D. bispinosus* decreased in the downstream direction. *D. bispinosus* penetrates farthest upstream in Ponto-Caspian rivers (Jazdzewski and Konopacka 1988). *D. bispinosus* and *D. haemobaphes* invaded Lake Balaton in Hungary in the early 1950's, where they outcompeted *Gammarus roeselii*. It is interesting that the latter species had replaced the indigenous *Gammarus pulex* between 1930-1950 (Muskó 1994). Recent observations of *D. bispinosus* in Austria and Germany make clear that the southern corridor (Fig. 1) is traversed for westward range extension (Müller and Schramm 2001).

Figure 3. *Migration patterns of Chelicorophium curvispinum.*

Dikerogammarus haemobaphes

The gammarid *Dikerogammarus haemobaphes* is an euryoecious species preferring solid substrates, macrophytes and filamentous algae in large rivers and lakes (Kititsyna 1980; Muskó 1994). It tolerates salinities from freshwater up to 8‰ (Ponomareva 1976), and is able to tolerate a wide temperature range (6-30°C) (Kititsyna 1980). It generally reproduces from April to October, but year round in thermal polluted waters, like cooling water discharges of electric power plants (Kititsyna 1980). In Lake Balaton, this species reproduces from May to the end of August on submerged macrophytes (Muskó 1994).

In the 1960's Mordukhai-Boltovskoi (1964) predicted that *D. haemobaphes* soon would penetrate into another sea basin beyond the Ponto-Caspian system. It migrated up the Danube River using the southern corridor (Figs. 1 and 4) (Nesemann *et al.* 1995). The first record of the species in the upper Danube (the German section of the river) is from 1976 (Tittizer 1996) followed by observations in the Main-Danube Canal in 1993 (Schleuter *et al.* 1994) through which the North Sea basin was reached via the Rhine River (Schöll *et al.* 1995). In 1997, Konopacka (1998) found that *D. haemobaphes* had immigrated to Poland. Studies along the lower and middle Vistula in 1998 and 1999 revealed that the species was already a dominant gammarid in this river. In the lower sections, it co-occurred with two other Ponto-Caspian immigrants: the less numerous *Pontogammarus robustoides* and the scarce *Echinogammarus ischnus*. In the middle section (at least as far as upstream to

Sandomierz) it was the only gammarid species present. *D. haemobaphes* was also found in the Notec and Bug rivers, tributaries of the Oder and Vistula rivers respectively, clearly indicating that the central corridor (to the Baltic Sea basin) has been used for range extension as well. In the Notec River *D. haemobaphes* co-occurs with *Gammarus roeselii* and *G. varsoviensis* (Jazdzewski and Konopacka 2000). Recent observations of *D. haemobaphes* in the central and southern corridors as well as in the upper Volga basin (L'vova *et al.* 1996) clearly indicate that the species is still dispersing.

Figure 4. *Migration patterns of Dikerogammarus haemobaphes and Dikerogammarus villosus.*

Dikerogammarus villosus

The gammarid *Dikerogammarus villosus* evidently used the southern corridor (Figs. 1 and 4) for range extension. After invading the lower and middle reaches of the Danube River the species was found for the first time in the upper reaches of that river in 1992 (Nesemann *et al.* 1995), where it had outcompeted *D. haemobaphes* (Weinzierl *et al.* 1996). Two years later *D. villosus* was discovered in the lower reaches of the Rhine River (Bij de Vaate and Klink 1995) and is currently developing relatively dense populations in that river (A. bij de Vaate, unpublished data).

The species is suspected to be more predatory than the other gammarids. Isotope analyses (δ^{15}N) indicated that they are active at the same trophic level as fish species (Marguillier

1998). Dick (1996) mentioned that differences in predatory and survival abilities of gammarid species are influenced by body size. Larger specimens prey upon the smaller ones. Therefore *D. villosus* may have considerable impact on populations of the North American invader *Gammarus tigrinus*, the dominant gammarid in the Rhine River before the introduction of *D. villosus*. Recently, *D. villosus* started to dominate the rheolithophilic gammarid communities in that river while *G. tigrinus* dominates the gammarids in lentic psammophilic communities (Kelleher *et al.* 2000a). In The Netherlands, *D. villosus* also immigrated into canals and lakes (e.g., Lake IJsselmeer) reducing populations of the indigenous *Gammarus duebeni* and the nonindigenous *G. tigrinus* (Dick and Platvoet 2000).

Echinogammarus ischnus

The earliest record of *Echinogammarus ischnus* outside the drainage systems of the Black and Caspian seas is from 1928 (Jarocki and Demianowicz 1931). In that year, the species was found in the middle and lower sections of the Vistula River below Warsaw (Jarocki and Demianowicz 1931). The presence of this species in the Vistula estuary was confirmed by Jazdzewski (1975). Samples taken in the summer of 1998 in the middle and lower Vistula and in its tributary the Bug River, showed that *E. ischnus* still occurs in these rivers but not as abundantly as *D. haemobaphes*. Nevertheless, *E. ischnus* is evidently an invasive species, exploiting the central corridor (Figs. 1 and 5). In the late 1970's it was recorded in the North Sea drainage basin, in the canals joining the Elbe, Weser and Ems rivers, and at the end of the 1980's in the Rhine-Herne Canal and Weser-Dattel Canal (Schöll 1990). At about the same time, *E. ischnus* was also found in some Mecklenburgian and Pommeranian lakes (Jazdzewski and Konopacka 1990; Köhn and Waterstraat 1990) being an indication that in Western Europe habitats are being colonised that are comparable to its natural Ponto-Caspian distribution area, where it occurs in several inshore Black Sea lakes (Jazdzewski 1980). The species arrived in the lower Rhine in 1989 (Schöll 1990) and in 1991 in the Rhine delta (Van den Brink *et al.* 1993). However, *E. ischnus* did not develop dense populations in that river. It may have been hindered by *G. tigrinus* as well as by the mass abundance of *C. curvispinum*. The latter species probably reduced the colonisation success of *E. ischnus*, being a lithophilic dweller, by covering the solid substrates in the river with mud tubes. When densities of *C. curvispinum* decreased, the subsequent invasion of *D. villosus* may have prevented *E. ischnus* from increasing its density.

Köhn and Waterstraat (1990) suggested that *E. ischnus* is closely associated with *Dreissena* clumps in Lake Kummerow (Germany). In the Great Lakes in North America it forms relatively high densities in *Dreissena* dominated habitats, despite its somewhat lower fecundity and shorter life span in comparison to the indigenous *Gammarus fasciatus*. The physical structure of *Dreissena* clumps favours *E. ischnus*. However, in dense submerged vegetation or turbid water, *E. ischnus* shows lower densities than *G. fasciatus* which is well equipped to cling to vegetation. *Cladophora* growing on rocks supports *G. fasciatus* as well (Dermott *et al.* 1998). The association between *Dreissena* and *E. ischnus* provides a good example of a habitat being conditioned for *E. ischnus* by an earlier Ponto-Caspian invader, *D. polymorpha*.

Figure 5. *Migration patterns of Echinogammarus ischnus and Pontogammarus robustoides.*

Echinogammarus trichiatus

First observations of *Echinogammarus trichiatus* in Western Europe were made by Weinzierl *et al.* (1997) in the German part of the Danube River in 1996. Podraza *et al.* (2001) found the species in the middle and lower Rhine River in 2000 and 2001 respectively. It was also found in the Rhine delta in 2001 (A. bij de Vaate, unpublished data). Although the number of observations is relatively low, they clearly demonstrate that the southern corridor (Fig. 1) was traversed to the west, if the absence of information from potential migration routes is taken into account.

Echinogammarus warpachowskyi

Echinogammarus warpachowskyi originates from the brackish parts of the Caspian Sea and the deltas and estuaries of many large Ponto-Caspian rivers. The species has been used in the former Soviet Union for intentional introductions. It was introduced into reservoirs and lakes in the Ukraine, and in Lithuania in the Neman River drainage area. *E. warpachowskyi* penetrated into artificial reservoirs in the Dnieper River (Jazdzewski 1980) and into the Kuronian Lagoon (Olenin and Leppäkoski 1999).

Obesogammarus crassus

This species was intentionally introduced in the 1960's into the Kaunas reservoir (Lithuania) in the Neman River, and in several aquatic habitats along the Baltic coast of the former Soviet Union (Jazdzewski 1980; Leppäkoski 1984). From the Neman river the species colonised the Kuronian Lagoon. Recently *O. crassus* was observed in the Vistula Lagoon (A. Konopacka and K. Jazdzewski, unpublished data). Westward dispersal has been the result of offshore transportation (in ballast water) via the Baltic Sea, however, part of the central corridor (Fig. 1) is considered to be a potential second dispersal route.

Obesogammarus obesus

Although Nesemann *et al.* (1995) concluded that this species belongs to macroinvertebrate communities in the middle and lower parts of the Danube River, Weinzierl *et al.* (1996) found *Obesogammarus obesus* for the first time in the upper part of that river in 1995. Like other Ponto-Caspian gammarids, it is unclear why the species began to move upstream. Because of its mobility, *O. obesus* is expected to invade the Main-Danube Canal in the near future using the southern corridor (Fig. 1) for further dispersion into Western Europe.

Pontogammarus robustoides

Pontogammarus robustoides originates from the lower sections of large Ponto-Caspian rivers (Volga, Don, Dnieper, Dniester and Danube rivers) as well as from some inland brackish and freshwater lakes around the Black Sea (Jazdzewski 1980). In the 1960's, this species was successfully introduced into many Ukrainian, Caucasian, and Lithuanian artificial lakes. In Lithuania the species 'naturalised' in the Neman drainage system, including the Kuronian Lagoon of the Baltic Sea (Gasjunas 1968a; Jazdzewski 1980). *P. robustoides* was recently found in Poland in the Vistula River (including the Vistula Lagoon) (Konopacka 1998; Jazdzewski and Konopacka 2000) and in the mouth of the Oder River (including the Szczecin Lagoon) (Gruszka 1999), whereas in Germany records exist from Mecklenburgian waters and the Mittelland Canal (Martens *et al.* 1999). There are two possible routes for the range extension of this species from the Dnieper basin: (a) westward through the Neman River and the Kuronian Lagoon, and (or) (b) via the central corridor (Figs. 1 and 5).

Jaera istri

The lithophilous isopod *Jaera istri* inhabits the littoral zones of the lower reaches and estuaries of large rivers discharging into the Black and Caspian seas (Tittizer 1997). Range expansion to the west was only observed through the southern corridor (Fig. 1). The first observation outside its native range was made in 1967 in the upper section of the Danube River (in Germany) (Kothé 1968). In 1993, *J. istri* was observed in the Main-Danube Canal (Tittizer 1997), in 1994 in the Main River (Schleuter and Schleuter 1995), and in 1996 in the middle section of the Rhine River (Schöll and Banning 1996). The Rhine delta was colonised

in 1997 (Kelleher *et al.* 2000b) where it inhabits solid substrates. In 1999, the species was found in the Elbe River using the central corridor (Figs. 1 and 2) for further range extension into the north-eastern part of Europe (Schöll and Hardt 2000).

DISCUSSION

The Ponto-Caspian macroinvertebrates which have expanded their range in Europe are euryhaline with an oligohaline preference. As a relict fauna of the Sarmatian or Pontian Age, these species are endemic for areas of the Black and Caspian seas with relatively low salinity (0.5-5 ‰) such as estuaries and lagoons. The colonisation success of the Ponto-Caspian macroinvertebrates that have invaded regions of Europe beyond their native range can be attributed to several biological features (Table 1). The most important are euryhaline and euryoecious characters, their non-specific food preference and the protection of juveniles (crustaceans). Relatively most successful in extending their territory in westward direction were the Crustaceans. Their expansion is considered to be attributable to shipping and their ease of mobility. Because of this, they easily can colonise a ship's hull to use it as a transport facility. This mechanism of spread is considered to be important in rivers for upstream migration and explains the successful passage of the southern corridor. Once having arrived in a new area, their mobility enables them to spread quickly.

Observations of Ponto-Caspian species outside their native range in European continental waters make clear that there are at least three main vectors for their spread westward: (a) construction of canals connecting river basins, (b) water management in some of those canals (e.g., the Main-Danube Canal), and (c) transportation attached to a vessel's hull or in ballast water. These vectors are also important in the case of secondary introductions, for those species (e.g., gammarids, mysids) that were intentionally introduced elsewhere.

Canal construction, mainly for navigation, had already started in the 17th century (Snyder *et al.* 1992). Lack of detailed information from this time period makes it difficult to reconstruct migration patterns for range extension for some species (Table 4) and to determine the main vector for their range expansion. In addition, intentional introductions in regions, particularly along the northern and central corridor, make natural migration patterns unclear.

More recently, the construction of irrigation canals and canals for drinking water supply in the former USSR can facilitate the range extension of Ponto-Caspian macroinvertebrates. These canals were mainly constructed in the second part of the last century and also serve as river basin interconnections (e.g., Muraschko and Kuksin 1984). However their importance in the range expansion of macroinvertebrates is unknown. Another difficulty in understanding migration routes in Europe is the possibility for Ponto-Caspian species to travel in ballast water of sea-going vessels using the route between the Black Sea via the Mediterranean to the coastal waters of Western Europe, and from the Baltic Sea to harbours elsewhere.

Table 4. *Summary of migration routes of some Ponto-Caspian macroinvertebrate species which successfully colonised Europe.*

Species	Corridor used northern	central	southern	Via ballast water
Cordylophora caspia		+	+	+
Dendrocoelum romanodanubiale			+	
Hypania invalida			+	
Caspiobdella fadejewi			+	
Lithoglyphus naticoides	+?	±	+?	+?
Dreissena polymorpha	+	+		+
Caspihalacarus hyrcanus			+	
Astacus leptodactylus	intentional introductions			
Hemimysis anomala		+?	+?	+?
Limnomysis benedeni			+	
Chelicorophium curvispinum		+	+	+
C. sowinskyi			+	
Dikerogammarus bispinosus			+?	
D. haemobaphes		+	+	
D. villosus			+	
Echinogammarus ischnus		+		
E. trichiatus			+	
E. warpachowskyi	intentional introductions			
Obesogammarus crassus	intentional introductions			
O. obesus			±	
Pontogammarus robustoides		+		+?
Jaera istri			+	

Note: (± = partly used; ? = migration route not clear).

The geographical invasion patterns described above were based on the years of first records combined with knowledge on years of the connection between river basins. Perhaps, the immigration routes are more complicated than is described above. Other techniques must be applied to check possible migration routes. Genetic analyses offer good possibilities for this purpose.

After the opening of a new Main-Danube Canal in 1992, connecting the Rhine and Danube basins, the southern corridor is today the most important link between the Ponto-Caspian area and Western Europe for Ponto-Caspian species to immigrate into Western Europe. This led to dramatic changes in macroinvertebrate communities in the Rhine River. In 1990 it was estimated that >95% of the macoinvertebrate density in the main distributaries of the Rhine delta consisted of nonindigenous species of which the major part originated from the Ponto-Caspian area (A. bij de Vaate, unpublished data). In 1995 the most abundant species were: *Chelicorophium curvispinum, Dikerogammarus villosus* and *Dreissena polymorpha* (Van der Velde *et al.* 2000). Other mobile species are expected to migrate into the Rhine River via the Main-Danube Canal, especially those species that have already been observed in the Upper

and Middle Danube, like the amphipods *Obesogammarus obesus, Dikerogammarus bispinosus* and *Chelicorophium sowinskyi* (Jazdzewski and Konopacka 1996; Weinzierl *et al.* 1996; Müller and Schramm 2001). However, other transport mechanisms, such as shipping, are also expected to contribute to the Ponto-Caspian species dispersal through that canal in the near future.

Knowing that each introduced species potentially can have an ecological or (and) economic impact, preventive measures against the introduction of alien species should be given high priority. For future canal constructions the installation of migration barriers of species (e.g., deterrent electrical systems) should be considered to reduce natural migration of species. Additionally, ballast water guidelines and measures to reduce the hull fouling of ships in inland services should be prepared and implemented in the near future with the aim to reduce the uncontrolled number of unintentionally transported organisms.

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CHAPTER 6

DISTRIBUTION AND ASPECTS OF POPULATION DYNAMICS

OF THE ZEBRA MUSSEL, DREISSENA POLYMORPHA (PALLAS, 1771),

IN THE LAKE IJSSELMEER AREA (THE NETHERLANDS)

Abraham bij de Vaate

DISTRIBUTION AND ASPECTS OF POPULATION DYNAMICS OF THE ZEBRA MUSSEL, DREISSENA POLYMORPHA (PALLAS, 1771), IN THE LAKE IJSSELMEER AREA (THE NETHERLANDS)

SUMMARY

The distribution, settling and growth of the zebra mussel, *Dreissena polymorpha (*Pallas), in Lake IJsselmeer and Lake Markermeer in The Netherlands were studied from 1980 to 1985. In these lakes *D. polymorpha* is the most important food source for wintering diving ducks. The study was part of an investigation into the carrying capacity of the lakes for these birds.

Key words: *Dreissena polymorpha,* zebra mussel, dispersion, growth, settlement

INTRODUCTION

The zebra mussel, *Dreissena polymorpha* (Pallas), is a bivalve that has been common in Dutch inland waters for about one and a half centuries. It was first recorded in 1827 (Van Benthem Jutting 1922). Nowadays they are found in oligotrophic to hypertrophic lakes and in waters with a certain degree of pollution. Only in seriously polluted waters the zebra mussel will be absent (Van Urk 1976). The colonisation of Lake IJsselmeer started soon after the lake was created in 1932 when a closure dam was finished, separating the Zuiderzee, an estuary of the River Rhine, from the Wadden Sea (De Jong and Bij de Vaate 1989). In about 4 years the brackish to marine Zuiderzee changed into a freshwater lake, Lake IJsselmeer (Havinga 1954). According to Wibaut-Isebree Moens (1954) the zebra mussel was already present in that region before the separation of the Zuiderzee from the sea. In the south-eastern part, near the mouth of the River IJssel (a distributary of the River Rhine), a small population was able to exist due to low chloride concentrations. The first records from the whole area were reported by Havinga (1941), based on studies made in 1939. Van Benthem Jutting (1954) suggested that Lake IJsselmeer was colonised from the small population in the south-eastern part of the former Zuiderzee.

There is no information on development of the *Dreissena* population in Lake IJsselmeer between 1943 and 1967. In 1968 (Van Soest 1970) and 1977 (Van der Wal 1979), the distribution of the zebra mussel was studied in large parts of the lake. This paper summarises studies on the occurrence and population dynamics of *D. polymorpha*, from 1980 to 1985, as part of a study on the carrying capacity of the Lake IJsselmeer area for wintering diving ducks. In that period zebra mussels were the main food for tufted duck *(Aythya fuligula)*, pochard *(A. ferina)*, scaup *(A. marila)* and goldeneye *(Bucephala clangula)*.

In the winters of 1979/1980 and 1980/1981 the maximum number of these four species was estimated to be 310,000 (Fig. 1; after Van Eerden and Bij de Vaate 1984).

STUDY AREA

Detailed information about the Zuiderzee damming, followed by land reclamation in Lake IJsselmeer, is given by Berger (1987) and De Jong and Bij de Vaate (1989). After 1975, when the construction of a dike between Enkhuizen and Lelystad was finished (Fig. 2), there were no further man-made changes in the area. At that moment the then existing Lake IJsselmeer was divided into two parts: a northern part called Lake IJsselmeer and a southern part called Lake Markermeer. The Lake IJsselmeer area is the name used for the whole area, which covers approximately 2,000 km^2.

Both lakes are very shallow. Depth of Lake Markermeer varies from 2.5 m near the west bank up to 4.5 m in the eastern part. The top layer of the bottom consists of sand (northern and southern part), clay (western part) or recently deposited silt (eastern part). In Lake IJsselmeer average depth is about 4.5 m (Berger 1987). Gullies form the deeper parts (up to 10 m), eroded sandbanks the shallow parts. As a result of wave action, some of the shallow parts are subjected to erosion and the gullies are gradually filled up.

The most important freshwater supply is the discharge of the River IJssel. Two sluices in the dike separating the lakes allow an exchange of water.

METHODS

The distribution of *D. polymorpha* was studied in a grid of sampling sites 2 km apart, aligned north/south and east/west, which gave a sampling density of one site per 4 km^2. At each site the exploring vessel was navigated in a circle and 10 bottom samples were taken at equal distances, which was possible due to a radio location system (Thomson-CSF, type Trident III) aboard the vessel. A Van Veen grab with a sampling surface of 440 cm^2 was used to sample the lake bottom. Each bottom sample was immediately washed out on a sieve with a mesh width of 1 mm aboard the vessel. The number of animals in each sample was assessed. Young mossels, generally with a shell length less than approx. 5 mm, were ignored. Samples were taken from March to December 1981.
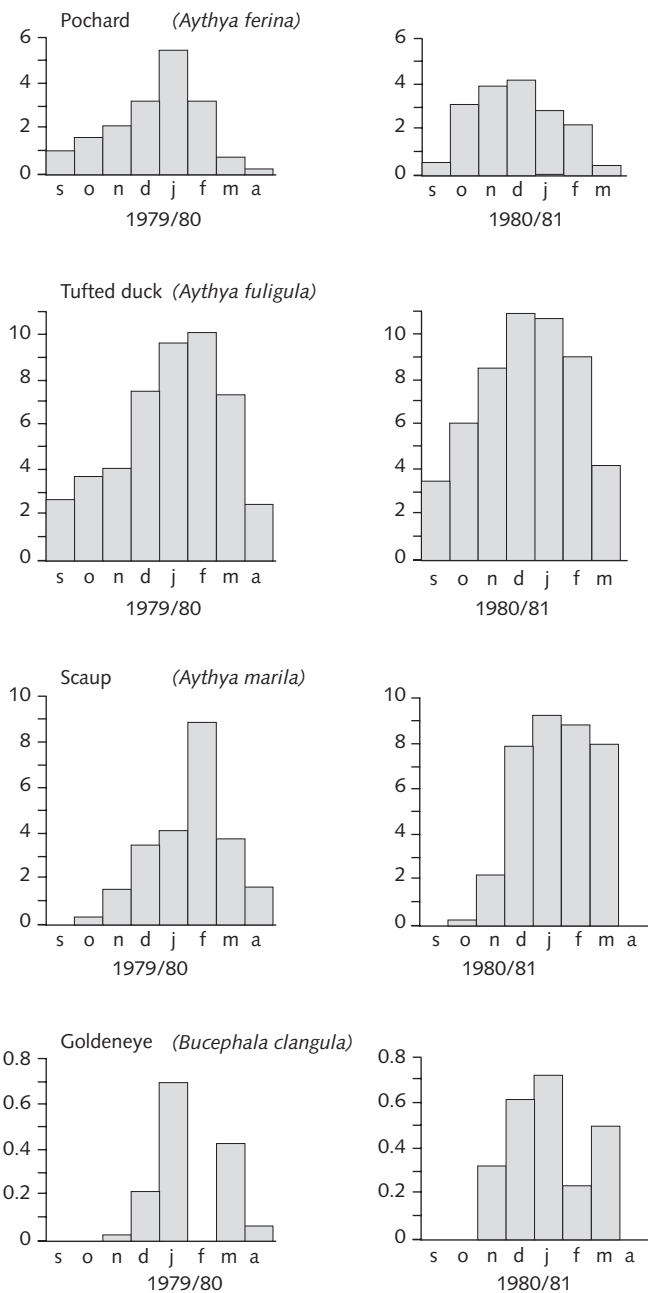
Figure 1. *Numbers (x10⁴) of benthos-feeding diving ducks in the Lake IJsselmeer area in autumn and winter of 1979/80 and 1980/81 (after Van Eerden and Bij de Vaate 1984).*
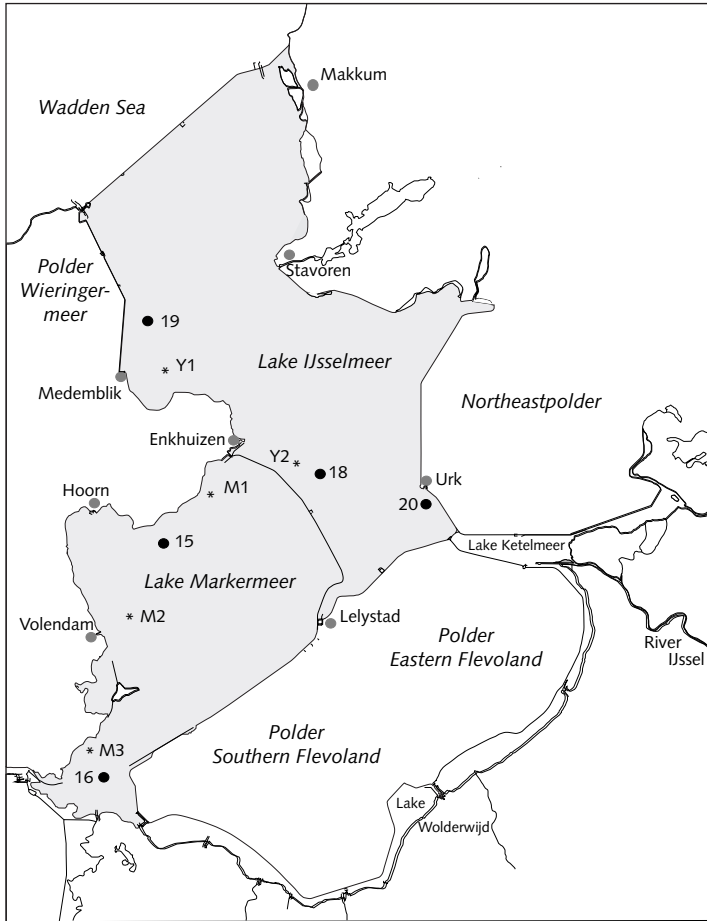
Figure 2.   *Permanent sampling sites (•) and study sites (*) in the Lake IJsselmeer area.*

Apart from this sampling, some permanent sampling sites (Fig. 2) were sampled at monthly intervals in the same way as described above. All mussels in the samples were measured to the nearest 1 mm.

Settlement of young zebra mussels on the artificial substrate PVC was investigated by fixing plates in a horizontal position on a stand which was placed on the lake bottom. The substrate was placed in the lakes in April and retrieved in November. When the settlement per unit of time was studied, the plates were carefully cleaned after each observation. Only the animals attached to the undersite of the plates were counted. The top side was mostly covered by a silt layer and therefore the young animals could not attach to that side.

Growth of the zebra mussels was calculated from interval measurements of shell length. The mussels used for growth studies were collected near the site where growth was measured. After collecting the mussles, they were removed from the substrate by carefully cutting the byssus threads. The animals were then measured to the nearest 1 mm and every 1-mm size-class (starting at 3 or 4 mm) was placed in a cage made of stainless steel wire netting with a mesh width of 2 mm. Up to a length of 20 mm at least 50 animals per length class were put in a cage together. Because it was difficult to collect sufficient larger animals, the number of animals above 20 mm was lower, with a minimum of 10 per cage. When growth was followed during the growth season, animals with a shell length of less than 10 mm were measured with a stereomicroscope to the nearest 0.1 mm. The sites at which growth was measured are shown in Fig. 2.

Dry weight of the soft body parts was measured in animals which were stored in a freezer at -20°C. Before storage, the animals were removed from the substrate and measured to the nearest 1 mm. Every length-class was frozen separately. After thawing, the soft body was removed from the shells. Dry weight was measured in duplicate in freeze dried samples of 10-100 animals. The ash content was estimated after cremating the dried material at 450°C.

RESULTS

Distribution

The distribution of *D. polymorpha* in Lake IJsselmeer and Lake Markermeer in 1981 is shown in Fig. 3, in which the density of animals with a shell length of >5 mm is given. The mussels are restricted to areas with solid substrates on the lake bottom. In general these are empty shells of marine origin such as *Mya arenaria* L. and *Cardium edule* L., the two most common species. The substrate can only be settled by zebra mussels in areas where no sedimentation of suspended materials takes place.

In the most northern and central part of Lake IJsselmeer the average density of *D. polymorpha* was very low; this was also observed in the eastern and south-eastern part of Lake Markermeer. The average density of *D. polymorpha* was estimated at 500 per m^2 in Lake IJsselmeer and 400 per m^2 in Lake Markermeer (animals with a shell length >5 mm). When only those areas where *D. polymorpha* occurs are taken into account, the average densities in both lakes were estimated at 1,000 per m^2.
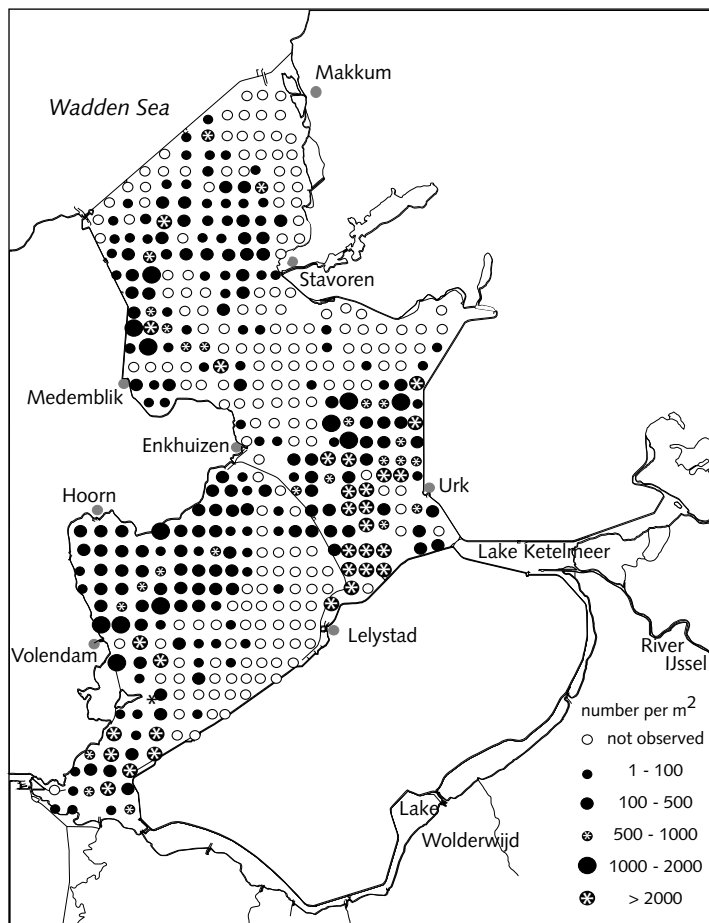
Figure 3. *Distribution of Dreissena polymorpha > approx. 5 mm in the Lake IJsselmeer area in 1981.*

Settlement

In Lake IJsselmeer and Lake Markermeer the horizontal distribution of settled young zebra mussels (one generation per year) was found to be very irregular. In 1980, when settlement was studied using an artificial substrate, the densities observed at the different study sites (Fig. 4) varied from no settlement at a site in the eastern part of Lake IJsselmeer (near Rotterdamsche hoek) to 10^5-10^6 animals per m^2 in the northern and western part. Compared with Lake IJsselmeer, settlement of young zebra mussels in Lake Markermeer was relatively low. In both lakes no relation could be found with the distribution of *D. polymorpha* in 1981.
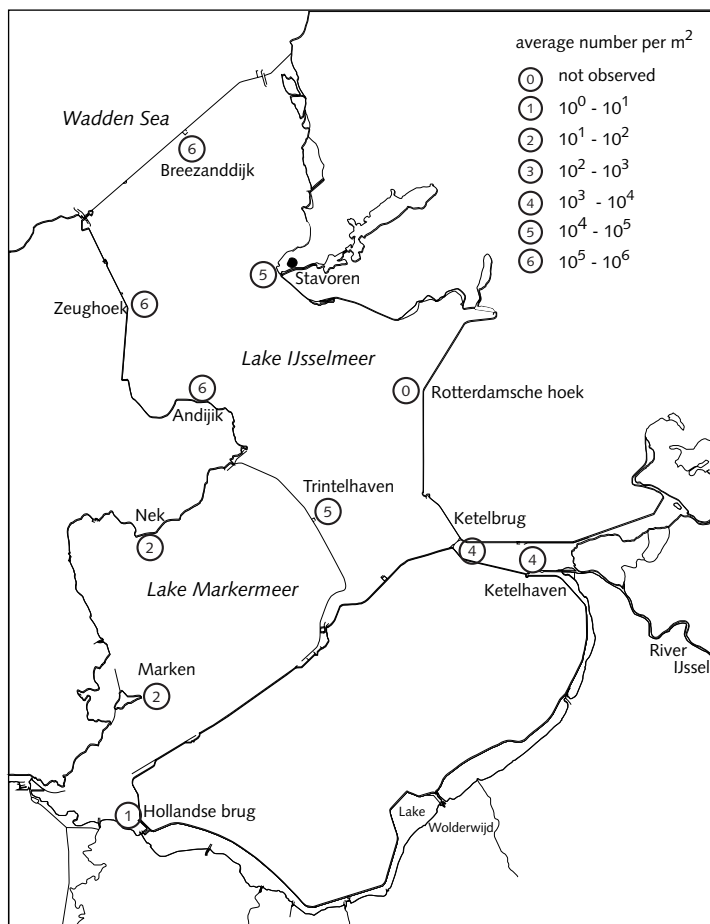
Figure 4. *Settlement of young Dreissena polymorpha on an artificial substrate (PVC) in 1980.*

The most important period of settlement of a new generation in the lake IJsselmeer area is the second part of June and the first part of August. This was not only observed on the artifical substrate in 1981, when the settlement of young mussels was studied at approximately monthly intervals, but also in the natural population in 1981-1985.

Figure 5 summarizes the results of the studies of settlement on the artificial substrate, expressed as numbers per m^2 per day. For comparison, similar data were included collected from Lake Maarsseveen, a small oligotrophic man made lake in the centre of the Netherlands. Here, in contrast, settlement started earlier, and the main period of settlement was found to be in September.
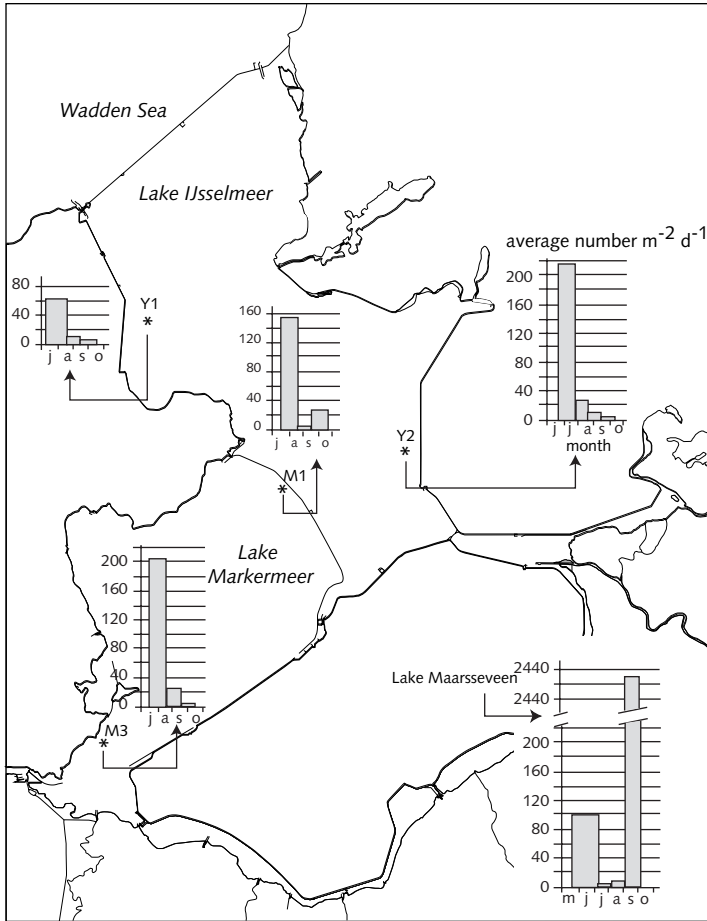
Figure 5. *Settlement of 0+ Dreissena polymorpha on an artificial substrate (PVC) in relation to the time of the year (1981).*

Settlement of young mussels in the natural population is illustrated in Fig. 6, in which the density of mussels younger and older than 1 year at 2 sampling sites is shown. The two age groups were distinguished on the basis of the results of growth studies.

Changes in densities of the settled young mussels in the successive years are also shown in Fig. 6. Yearly maxima of the 0+ generation in the natural populations on different sites were not always found in the same period. For example in 1982 a maximum was found in October at the sampling site in Lake IJsselmeer and in 1983 in November at the sampling site in Lake Markermeer (Fig. 6). However, in both cases maximum density of the 0+ animals was relatively
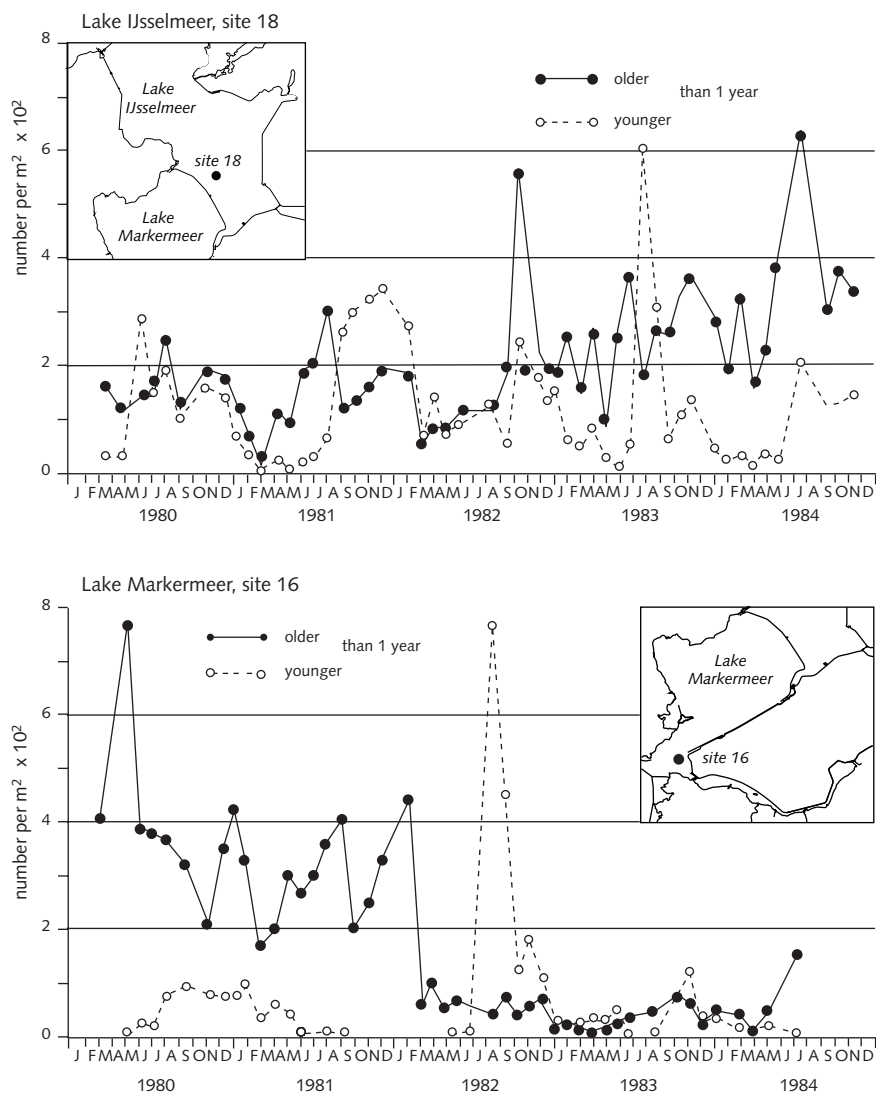
Figure 6. *Settlement of mussels in the natural population of Dreissena polymorpha at two sampling sites.*

low which indicates no settlement just after the spawning period, but active migration of the young mussels.

Population structure

Measurements of shell growth indicated that in general four generations can be found in the Lake IJsselmeer area. In shell length/frequency diagrams only the most recent generation can be distinguished clearly (Fig. 7). The overlap between the generations only gives one subsequent peak in most of the diagrams.

To eliminate deviations in length/frequency because of too few animals per length class sampled, the results of monthly population composition analysis were lumped for four successive months (November to February) (Fig. 7). It was assumed that shell length does not increase in autumn and winter.
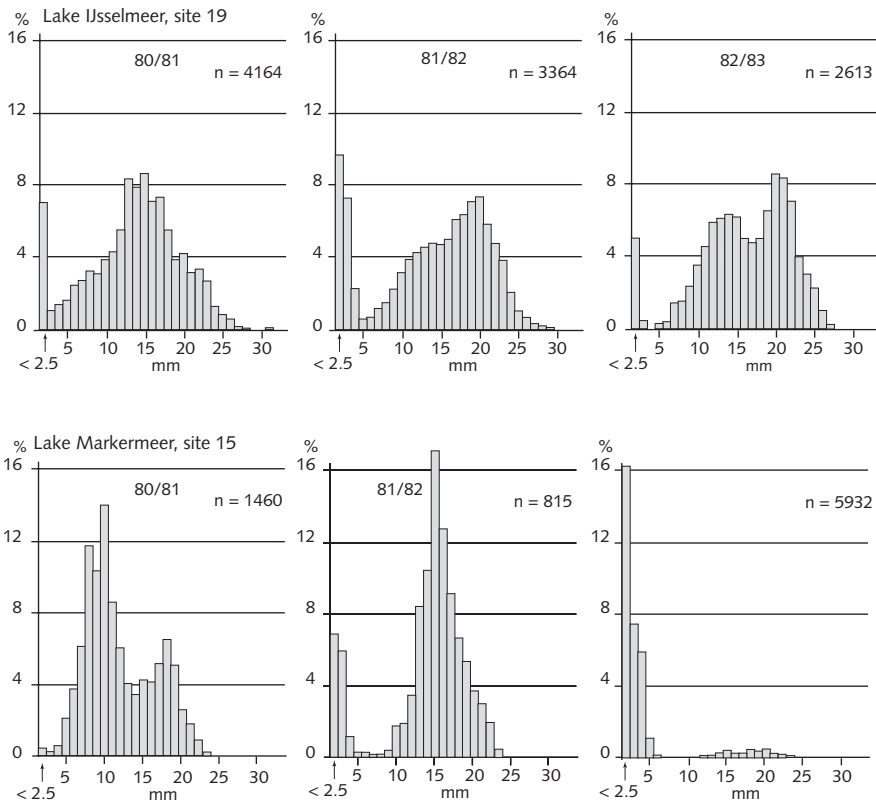
Figure 7. *Shell length/frequency distribution of the natural population of Dreissena polymorpha on two sampling sites (combined data of samples taken monthly from November through February).*

Only at site (Fig. 2) 19 in Lake IJsselmeer in 1982/1983 and at site 15 (Fig. 2) in Lake Markermeer in 1980/1981 are two peaks in the shell length distribution of 1[+] and older mussels visible, representing the second and third generation. Young mussels reach a maximum shell length of about 6 mm in their first growth season, but in general the average shell length does not exceed 3 mm.

Growth

Because it was hardly possible to calculate growth rate from shell length frequency distributions, the increase of shell length of selected animals, kept in cages, was measured. Shell length increase takes place over a relatively small part of the year. In the Lake IJsselmeer area it starts in the first half of April, when water temperature is about 6°C (Fig. 8). By the end of August, when water temperature is decreasing, the increase of shell length stops. The slight increase of shell length of the mussels in Lake Markermeer in 1984 after August was not significant.

Results of measurements of shell length growth (L_i) in relation to shell length at the beginning of the growth season (L) can best be described by the second order equation:

$L_i = aL^2 - bL + c$. In Table 1 the values for *a, b* and *c* are given for the measurements in the period 1980-1985.

Figure 9 shows the increase of shell length of *D. polymorpha* in Lake IJsselmeer on site Y2 (Fig. 2) and in Lake Markermeer on site M2 (Fig. 2) for the different years.

Maximum increase of shell length in both lakes can be described by the relations for 1982, minimum increase by the relation for 1984 in Lake IJsselmeer and 1985 in Lake Markermeer (the corrsponding values for *a, b* and *c* are given in Table 1).

As it appears from Table 1, shell length growth was measured in 1983 in two separate cage stands. When increase of shell length is calculated using both equations obtained, it seems that the differences are small (Table 2). When the results of the measurements from both stands are combined, the relation between increase of shell length and shell length of the mussels at the beginning of the growth season can be described as:

$L_i = 0.006L^2 - 0.56L + 12.1$ *($r^2=0.994$)*

Growth of the soft body of *D. polymorpha* was measured in samples taken from the wild population. The ash-free dry weight of the soft body was used as the index of body weight. The relation between ash-free dry weight and shell length can be described by the general equation: $W = aL^b$; in which W is ash-free dry weight of the soft body (mg) and L is the shell length (mm). In 1983 and 1984 values for a and b were obtained at monthly intervals in samples from site Y2 (Fig 2) in Lake IJsselmeer (Table 3). The increase of soft body weight begins in the second part or February or the first part of March. Weekly averages of water temperature rose from 1.0 to 5.6 and 2.0 to 4.9°C in this period, in 1983 and 1984 respectively. After May there was a sharp decrease in the soft body weight of the mussels which continued until September.
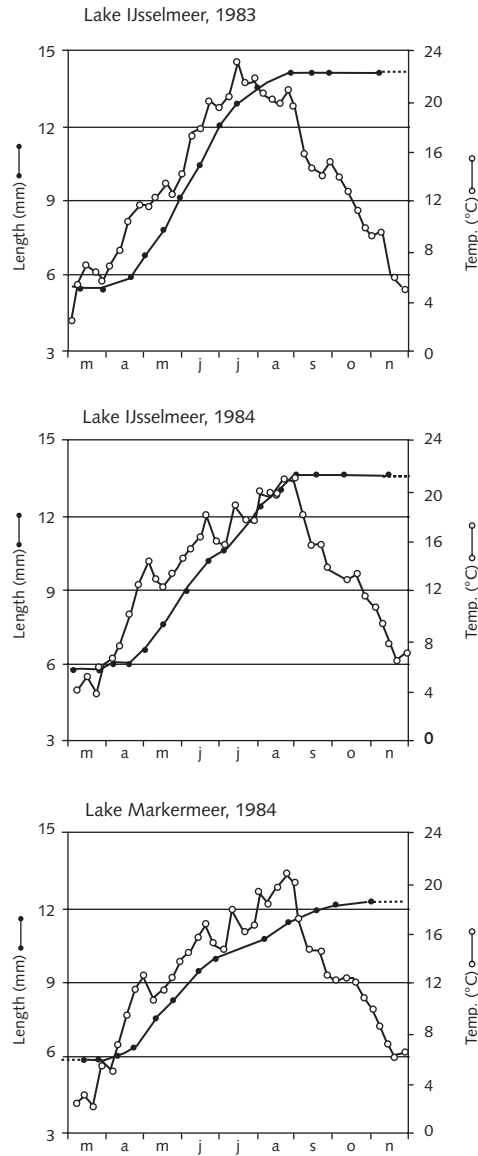
Figure 8. *Average shell length increase of Dreissena polymorpha and weekly averages of water temperature in Lake IJsselmeer and Lake Markermeer during the growth seasons of 1983 and 1984.*

Table 1. *Values for a, b and c in the equation $L_i=aL^2-bL+c$.*
Samples from Lake IJsselmeer (Y1 and Y2) and Lake Markermeer (M1, M2 and M3).

| Year	Site	*a*	*b*	*c*	**Range** *(L)* (mm)	r²
1980	Y1	0	0.59	13.2	6-20	0.980
1981	Y1	0.015	0.93	15.1	6-22	0.976
	Y2	0.024	1.19	16.8	6-21	0.968
	M1	0.029	1.35	17.4	6-23	0.980
	M3	0.036	1.44	16.9	6-19	0.952
1982	Y1	0.009	0.74	14.6	3-29	0.945
	Y2	0.012	0.80	14.5	3-24	0.977
	M1	0.014	0.95	16.7	3-27	0.945
	M2	0.026	1.27	17.1	3-22	0.977
1983	Y2	0.008	0.60	12.1	5-23	0.980
	Y2[1]	0	0.38	10.6	5-23	0.966
	M1	0.013	0.82	13.2	5-26	0.992
	M2	0.012	0.78	13.0	5-25	0.986
1984	Y1	0.007	0.57	9.9	6-24	0.954
	Y2	0.011	0.71	11.8	5-25	0.980
	M2	0.015	0.80	11.3	5-24	0.949
1985	Y2	0.014	0.92	14.7	5-25	0.960
	M2	0.016	0.78	10.6	5-24	0.958

[1] duplicate

Table 2. *Calculated average shell length increase of some length classes of Dreissena polymorpha in two identical stands with cages in Lake IJsselmeer.*

Length (mm)	Increase of shell length (mm)	
	Stand A	**Stand B**
5	9.4	9.2
10	7.0	6.7
15	4.8	4.7
20	2.9	3.2

Table 3. *Values for a and b in the equation: W = aL^b. Samples from site Y2 in Lake IJsselmeer.*

Date	a	b	r2	Range of L (mm)
19-01-83	0.013	2.447	0.988	4-26
16-02	0.018	2.272	0.990	5-26
14-03	0.018	2.307	0.986	5-29
20-04	0.024	2.417	0.966	4-28
16-05	0.017	2.456	0.988	5-26
15-06	0.018	2.532	0.981	5-28
13-07	0.015	2.491	0.994	5-25
12-09	0.007	2.600	0.998	6-26
05-10	0.018	2.299	0.998	5-25
03-11	0.019	2.273	0.996	6-25
12-12	0.024	2.281	0.994	5-26
12-01-84	0.011	2.420	0.972	6-27
09-02	0.019	2.251	0.986	7-25
07-03	0.031	2.186	0.994	6-26
05-04	0.038	2.237	0.998	6-27
01-05	0.029	2.410	0.986	6-26
05-06	0.031	2.339	0.970	6-25
03-07	0.017	2.480	0.976	5-25
01-08	0.017	2.398	0.988	5-26
04-09	0.013	2.402	0.984	5-25
08-10	0.018	2.328	0.976	5-26
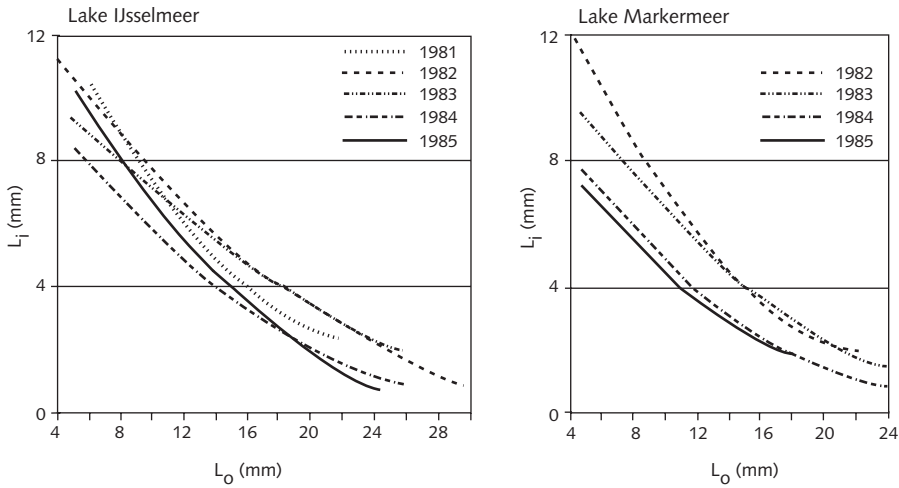
Figure 9. *The relation between shell length increment (L) and shell length (L) of Dreissena polymorpha at the beginning of the growth season.*

DISCUSSION

Distribution

The zebra mussel must have started to colonise the whole Lake IJsselmeer area in 1936. In the first months of that year the average chloride concentration in the lake dropped below a value of 5‰ (Havinga 1954). This value can be seen as the upper limit of the chloride concentration at which a population of *D. polymorpha* can develop optimally (Janssen and Janssen-Kruit 1967; Wolff 1969).

Because their occurrence is limited to solid substrates, to which the animals need to attach themselves, their distribution is strongly related to the amount of attachable materials on the bottom of inland waters. In the Lake IJsselmeer area all these materials are overgrown with zebra mussels. This means that substrate is the limiting factor in the distribution and density of the mussels in this area. Waterplants can serve as a substate for the attachment of zebra mussels as well, particular the submerged species. In the Lake IJsselmeer area only two species of the genus *Potamogeton (P. perfoliatus* L. and *P. pectinatus* L.) occur (Van Eerden and Zijlstra 1986). Both species have mainly been found in the shallow western part of Lake Markermeer. Because these plants have an annual growth cycle, they can only serve as a temporary settling place for the 0^+ generation (Oldham 1930).

In Lake IJsselmeer, population densities up to about 10,000 animals per m^2 were found. At maximum densities the animals had built up a closed layer; at lower densities the animals occur in aggregations. For comparison, maximum average densities in other lakes are summarized in Table 4. The estimated average density of *D. polymorpha* in the Lake IJsselmeer area is comparable with densities found in a large group of Masurian lakes in Poland (Stańczykowska 1964; Stańczykowska *et al.* 1975).

Densities of zebra mussels of different locations can vary very strongly within one year. There is no obvious reason for their decline in the winter of 1982 at the sampling site in lake Markermeer (Fig. 6). The most likely explanation is predation by diving ducks which were seen in thousands near the sampling site that winter.

Table 4. *Maximum average densities of Dreissena polymorpha in different lakes.*

Area	Average density Per m^2	Reference
Lake Zurich	30,000	Burla and Lubini-Ferlin (1976)
Lake Neuenburg	2,600-2,800	Pedroli (1981)
Lake Garda	20,000	Franchini (1978)
Lake Dojran	4,000-5,000	Sapkarev (1975)
Lake Constance	21,000	Suter (1982)
Dneprodzerzhinsk Reservoir	25,000-36,000	Gaidash and Lubanov (1978)
Szczecin lagoon	114,000	Wiktor (1963)

From other lakes comparable variations in abundance are also reported. In Lake Mikolajskie (Stańczykowska 1975, 1978) average density in the littoral zone decreased from 2,200 per m^2 in 1959 to <5 per m^2 in 1960. No explanation was given for this dramatic decrease. Decrease of the *Dreissena* population in Lake Constance, observed in 1972 (Walz 1974), was suggested to be caused by diving ducks at some sites and in general as a result of the extreme low water level in the previous winter. Predation by diving ducks and coots could be an important factor at different locations, in view of the numbers observed that winter (Jacoby and Leuzinger 1972) and their feeding behavior (Suter 1982).

Settlement

From studies made by Walz (1973) it is known that PVC is a good substrate for the attachment of young zebra mussels. Better colonisation of the underside of test plates was considered to be the effect of negative phototaxis by the young animals (Leentvaar 1943). Young zebra mussels in Lake IJsselmeer area settled in the same period as in some Polish inland waters (Lewandowski 1983; Piesik 1983). On the other hand, Walz (1975) found a maximum in Lake Constance in 1973 in October and in the first week of November (in May and June no observations were made). This means that the observation in Lake Maarsseveen (Fig. 5) was not exceptional. How far this relatively late spawning affects subsequent predation on the larvae is unknown. Water temperature is an important factor for the start and the length of the reproduction period. Stańczykowska *et al.* (1988) observed that the reproductive period was twice as long in lakes receiving heated water from two power plants.

The number of young mussels in the population depends on predation of the previous larval stage and the success in finding a good place (solid substrates) for settlement during the postveliger stage. Mortality in the larval stage is estimated at 20% in the veliger stage and 99% in the postveliger stage (Stańczykowska *et al.* 1988). Predators of the larvae are mainly the larvae and young stages of several species of freshwater fish. A summary of larval predators is given by Lewandowski (1982). In the Lake IJsselmeer area predators like smelt *(Osmerus eperlanus (L.))* pike perch *(Stizostedion lucioperca (L))*, ruffe *(Gymnocephalus cernuus (L.))* and roach *(Rutilus rutilus (L.))* are common.
For the postveliger stage wind velocity is an important factor in the Lake IJsselmeer area. In the shallow lakes bottom materials like detritus and silt particles are resuspended by wave action, followed by sedimentation when the action has been diminished. After sedimentation, attachable substrate can be covered for shorter or longer periods and the larvae are not able to settle. Attached postveligers can be covered as well and will die soon, when oxygen concentration in the interstitial water decreases to zero. Under anaerobic conditions 100% mortality of adult mussels is reached after 12 and 7 days at a water termperature of 10° and 19°C respectively (Walz 1973). Since relative oxygen consumption of the animals decreases as size increases (Mikheyev 1964), younger mussels will die first.

Population structure

Maximum shell length of *D. polymorpha* does not exceed 27 mm in Lake Markermeer, 31 mm in Lake IJsselmeer except the south-eastern part, or 36 mm in the south-eastern part of lake IJsselmeer (number of mussels measured: 145,600; 79,100 and 47,500 respectively). The difference in maximum shell length between the two lakes can be explained by slower shell growth and a shorter life span of the mussels in Lake Markermeer. The difference in maximum shell length between the two regions in Lake IJsselmeer can be explained by differences in water currents. In the south-eastern part of the lake water currents are more pronounced due to the discharge of the River IJssel, and this may lead to better food availability at sites with water currents. The effect of water currents could be demonstrated by the observation that young mussels grew better on a buoy than on a cage stand on the bottom of the lake. Jenner and Mommen (1985) also observed more rapid growth of young mussels in lotic environments.
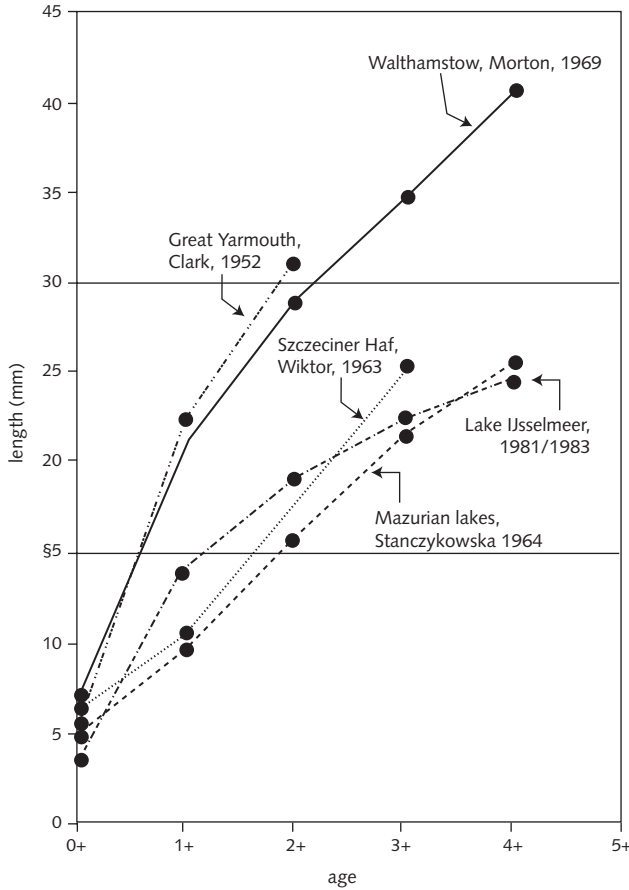
Growth

Growth in molluscs can be measured by three principal methods: measuring the distance between growth-interruption lines, calculations from size/frequency distributions, and the use of marked animals. All of these methods have their special advantages and disadvantages. In *D. polymorpha* it is very difficult to distinguish the annual growth-interruption lines. On shells of an important part of a population the lines are not clear and mistakes can be made very easily. During the growth season shell length increment can not be studied by this method. According to Morton (1969) two growth-interruption lines are formed each year: one line in the winter and the other during reproduction. Stańczykowska (1963, 1964) calculated the age of the zebra mussels in the Masurian lakes on the assumption that one growth-interruption line represented 1 year of the mussels life. Later observations on ground-down shells, however, led her to correct these ages by a factor of 2 (Stańczykowska 1976; Morton 1969).
Growth calculations from size/frequency distributions are only useful when there is only a small overlap in size between the different generations. The method used in this study can be seen as a method in which marked animals are used to assess growth of the zebra mussels. No individual mark was used, but a size class was marked as a group by putting them in a cage. Natural mortality of the mussels in the cages was ≤10% under normal conditions. In a few cases mortality was much higher due to the accumulation of mud in the cages. Growth data from cages where mortality was >50% were not used.
Growth of *D. polymorpha* in the Lake IJsselmeer area is comparable with data from Polish inland waters. In Fig. 10 shell growth is compared with data summarized by Morton (1969), who discussed differences between U.K. and Polish populations. The most important factor causing the difference is the late summer and autumn growth of the mussels in the United Kingdom, which was not found in the Lake IJsselmeer area (Fig. 8).
No significant differences in shell growth of mussels placed in water with different trophic levels were found. In Fig. 11, results of shell growth measured in the oligotrophic Lake Maarsseveen, the eutrophic Lake Markermeer and the hypertrophic Lake Wolderwijd (one of

the border lakes between the polder Southern Flevoland and the former Zuiderzee coast; Fig. 2) in 1981 are translated into growth of mussels with a given shell length.

Figure 10. *Growth of Dreissena polymorpha in different regions (completion of a figure given by Morton 1969).*

The shell growth period in the Lake IJsselmeer area differs from that observed in other regions. Kachanova (1962) and Morton (1969) observed shell growth throughout the period when water temperature was above 12° and 11°C respectively. This minimum temperature for shell growth is much higher than found during these investigations.

On the other hand, in the Lake IJsselmeer area shell growth stopped when temperatures were still above 11-12°C. It is not clear why growth stopped at a higher temperature.

From growth data, as summarized in Fig. 8 and Table 3, the biomass change of the soft body during the growth season can be calculated. In Fig. 12 an example is given for zebra mussels with shell lengths of 5.5 and 20 mm. After the growth season they will have reached a shell length of 14.7 and 23.3 mm respectively (data from Lake IJsselmeer from 1983). Decrease of the soft body weight must be the result of spawning which takes place during that period (Fig. 5). Walz (1978) observed spawning in zebra mussels from a shell length of 9.4 mm. For the population in the Lake IJsselmeer area this means that the animals become sexually mature during the 1^+ age.
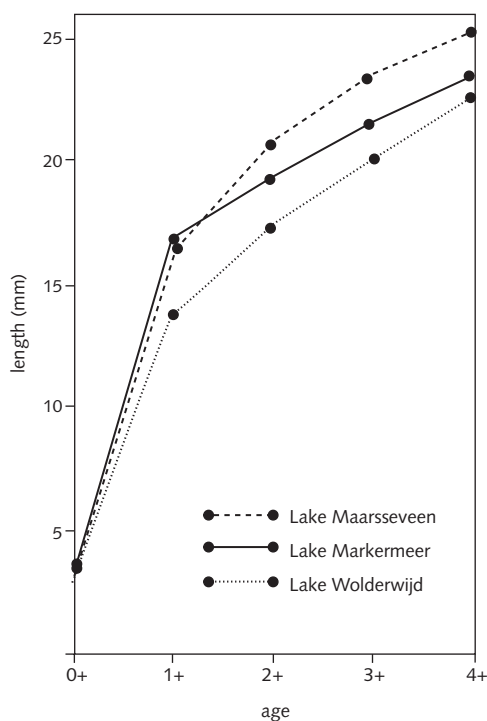
Figure 11. *Growth of Dreissena polymorpha in the oligotrophic Lake Maarsseveen, the eutrophic Lake Markermeer and the hypertrophic Lake Wolderwijd (data from 1981).*
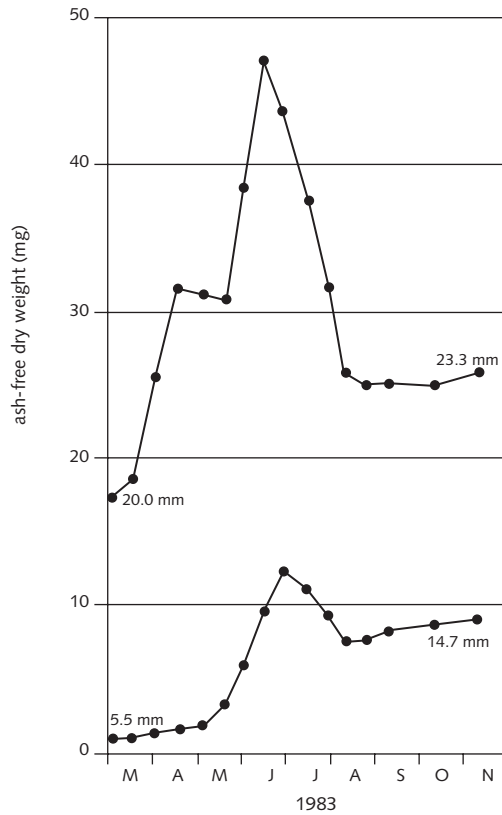
Figure 12. *Average changes in soft body weight (ash-free dry weight) of Dreissena polymorpha of two different sizes in Lake IJsselmeer in 1983.*

ACKNOWLEDGEMENTS

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CHAPTER 7

SEA TROUT MIGRATION IN THE RHINE DELTA,

THE NETHERLANDS

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Gerard de Laak and Camiel Dijkers, accepted.
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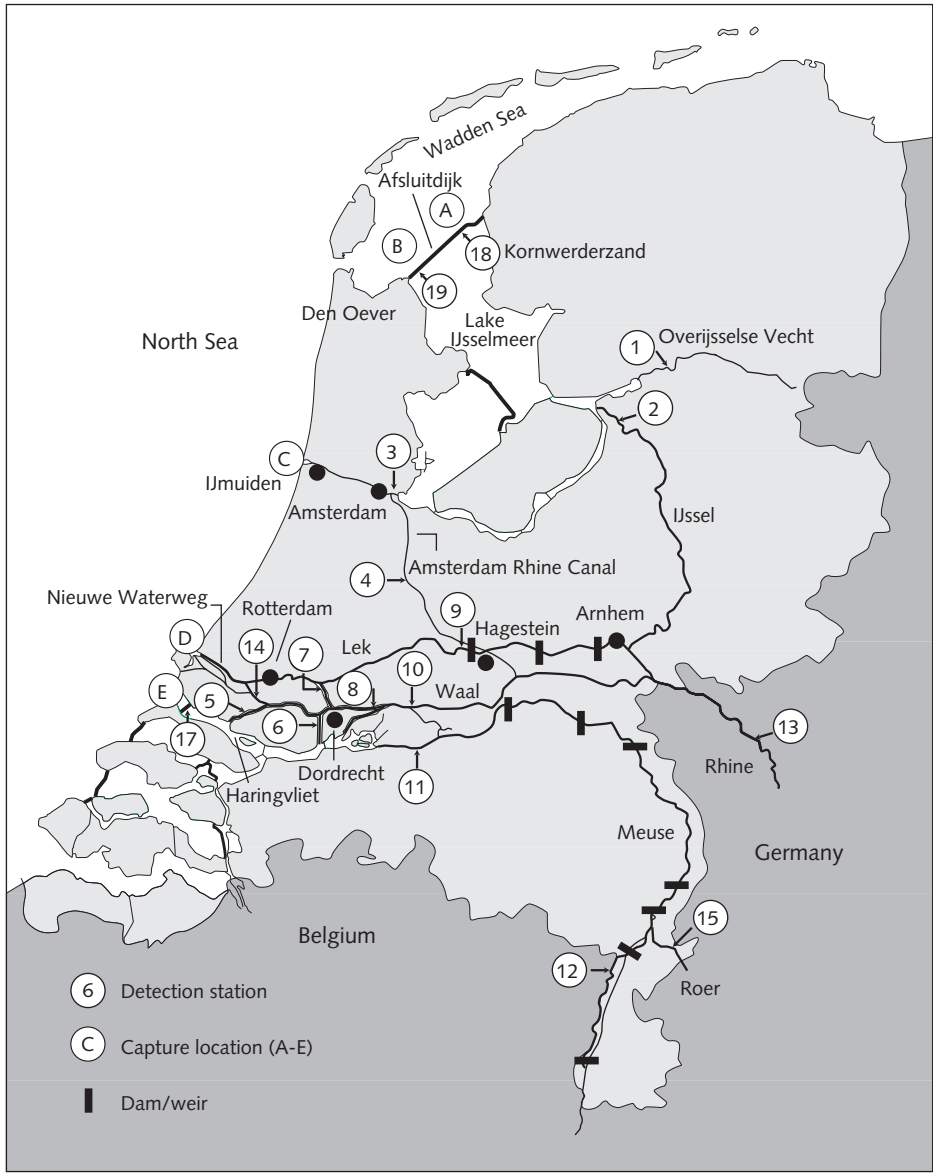# SEA TROUT MIGRATION IN THE RHINE DELTA,

THE NETHERLANDS

ABSTRACT

Sea trout, *Salmo trutta* L., migration in the Rhine delta, The Netherlands, was studied within the framework of the ecological rehabilitation of that river. The study made use of the NEDAP TRAIL System®, consisting of a chain of fixed detection stations and transponders, each transmitting an unique code. During the period 16 December 1996 - 31 December 2000, 195 (34%) out of 580 sea trout tagged were detected. Inland migration of sea trout was observed through the sluices in the dam between the Wadden Sea and Lake IJsselmeer (called Afsluitdijk), the Nieuwe Waterweg, and the sluices in the Haringvliet dam. 75% were detected for the first time at one of the detection stations within 30 days after tagging. Inland migration through the sluices in the Afsluitdijk, the Nieuwe Waterweg, and the sluices in the Haringvliet dam was observed for 34, 103 and 70 sea trout respectively. However, based on the number of tagged fish released in the adjacent coastal areas, migration through the Afsluitdijk was most important. During migration in freshwater, sea trout was predominantly active during the daylight period. Fish entering the Rhine delta through the Nieuwe Waterweg or the sluices in the Haringvliet dam chose eight and six different routes respectively for upstream migration. Differences in current velocity in the Rhine distributaries seemed to be an important factor in the choice of migration routes.

Key words: sea trout, *Salmo trutta*, Atlantic salmon, *Salmo salar*, migration, telemetry, inductive coupling, transponder, Rhine, Meuse.

INTRODUCTION

In 1987 an international plan for the ecological rehabilitation of the Rhine River was accepted after a severe pollution calamity in an upstream section, in the vicinity of Basel, Switzerland (ICPR, 1987). Most important aims of the plan were: (a) reintroduction to a self sustainable level of 'higher animal species' that had become extinct (e.g., Atlantic salmon), (b) water quality improvement to a level that it can safely be used for drinking water production, and (c) further reduction of sediment adsorbed harmful substances (ICPR, 1987; Anon., 1988). The Atlantic salmon (*Salmo salar* L.) was chosen as an indicator for the ecological rehabilitation of the river. The typical Rhine breed of this species became extinct in the first part of the 20th century (De Groot 1992). A combination of (a) damming of tributaries,

Figure 1.   *Tagging locations at the potential entrances for sea trout to enter the Rhine delta,
including the locations of the fixed detection stations.*

(b) water quality deterioration, and (c) silting up of the redds was the main cause. In addition, migration of anadromous fish species from the North Sea into the River Rhine was strongly reduced by damming of the Rhine-Meuse estuary (Haringvliet, Fig. 1) in the 1970s, and other distributaries, starting as early as the 12th century (Kalweit, 1993; Middelkoop, 1997). However, within the framework of the ecological rehabilitation of the Rhine River, improvements of inland migration possibilities are executed or under study (Admiraal *et al.*, 1993; Paalvast *et al.*, 1998).

The Atlantic salmon not only serves as an indicator but is one of the so-called 'higher animal species' that has been reintroduced in the Rhine basin. Because this species does not spawn in the Rhine delta, the Dutch contribution to reintroduction programs focuses on (a) improvement of possibilities to enter the river from the North Sea and (b) migration possibilities through the distributaries of the Rhine delta (Fig. 1). Aim of the study was to gain a clear understanding of the main migration routes the Atlantic salmon is likely to follow in the altered Rhine delta during their journey from the North Sea to the spawning areas. Subsequently, this knowledge can be introduced in relevant river management options.

In the absence of the now extinct typical Rhine salmon, sea trout (*Salmo trutta* L.) was selected as a representative species in this study. Sea trout was never extinct from the Dutch coastal zone and inland waters (De Groot, 1990, 1992), and is present now in reasonable numbers in the Dutch part of the Rhine and Meuse Rivers (Cazemier, 1994).

MATERIALS & METHODS

Study area

About 60% of The Netherlands belongs to the Rhine basin. Nearly the whole area can be considered as the Rhine delta since the first bifurcation is located 5 km west of the German-Dutch border (Fig. 1). At that point the name of the river changes into Waal and Pannerdensch Canal for the distributaries flowing west and northwestward respectively. On average 80% of the Rhine discharge flows through the Waal River. The next bifurcation, in the Pannerdensch Canal, is east of Arnhem. The northward flowing IJssel River empties in Lake Ketelmeer, an artificial lake being part of the Lake IJsselmeer area which is, in its turn, part of the former Zuiderzee, an inland sea dammed in 1932 (De Jong & Bij de Vaate, 1989). Westward flows the Nederrijn River (further downstream called Lek River) in which three weirs and accompanying locks were built for discharge control and to allow navigation in both distributaries during periods of low discharge in the Rhine River. Discharge distribution between the IJssel and Nederrijn Rivers is 4:1 on average.

In the western part of the Rhine delta the river empties in the North Sea through the Nieuwe Waterweg and the Haringvliet, both connected through a network of distibutaries with the Nederrijn and Waal Rivers (Fig. 2). The Nieuwe Waterweg is a man-made canal constructed in the 1860s to improve the connection of the Rotterdam harbours with the North Sea, and forms the only open connection with the sea. The Haringvliet, a former estuary, was

dammed in the 1970's after a severe flooding in the south-western part of The Netherlands in 1953. In both the dam separating Lake IJsselmeer from the Wadden Sea (called 'Afsluitdijk') and the Haringvliet dam, sluices were built for the discharge of river water.
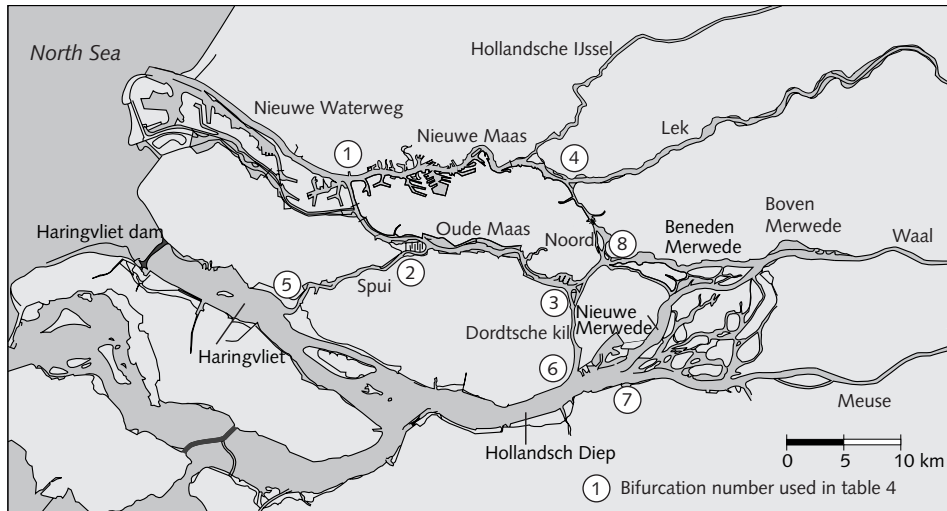
Figure 2. *The western part of the Rhine delta.*

Tagging

Sea trout (total length >39 cm, Fig. 3) were collected in the coastal area of the North Sea and in the Wadden Sea (Fig. 1), tagged with a transponder and released at the same location. Most of the fish were caught in the coastal area in front of the Haringvliet dam (Fig. 1, location E) where they appear to gather after being attracted by the freshwater discharge through the sluices in the Haringvliet dam. Professional fishermen caught the fish needed in the study with coarse-mesh fyke nets at three locations in the North Sea coastal area and two locations in the Wadden Sea (Fig. 1). Additionally a trawl net was used in June and/or July (in 1998 also in November) in the coastal area in front of the Haringvliet dam, to increase the catches (Table 1). At each tagging location, the fish were immediately after landing transferred into a 1200-1500 l container provided with a sea water circulation system for continuous refreshment. In general, the fish were kept in captivity for two days at maximum.

Table 1. *Number of sea trout tagged and catching efforts (the capital letters in the first column refer to the tagging locations in figure 1).*

	Location	Number	Catching gear	Catching effort (weeks)				
				1996	1997	1998	1999	2000
A	Wadden Sea, Kornwerderzand	61	fyke net		16	27	23	6
B	Wadden Sea, Den Oever	9	fyke net		8			8
C	North Sea, mouth North Sea canal	2	fyke net		13	12		
D	North Sea, mouth Nieuwe Waterweg	5	fyke net		16	10		
E	Haringvliet, coastal area	275	fyke net	4	13	36	27	11
		230	trawl net		2	3	2	14
	total	582						
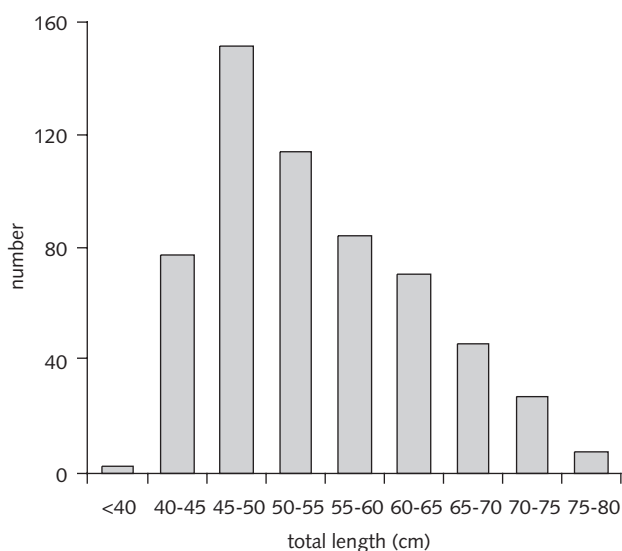
Figure 3. *Length frequency distribution of the tagged sea trout.*

Tagging started in December 1996 and ceased in June 2000. No tagging took place when water temperature had risen above 19°C. Most of the sea trout were tagged in June and July (Table 2). The tagging procedure started with measurement of total and fork length, and weight. Exceptional external characteristics were also recorded. Fish age was determined by scale readings (Anon., 1984; Shearer, 1989).

A transponder was implanted in the abdominal cavity after the trout had been anaesthetised with benzocaine (ethyl-4-aminobenzate) (Lucas, 1989; Vriese, 1995). Capture, storage and marking of the fish were approved by the Ministry Agriculture, Fisheries and Nature Conservation and the Dutch Commission for the Control of Animal Experiments (DEC).

Table 2. *Monthly number of sea trout tagged.*

Month				Year			
	1996	1997	1998	1999	2000	Total	
January			15	1		16	
February			2	5	3	10	
March		7	7	12	13	39	
April		13	2	12	13	40	
May		12	1	15	21	49	
June		8	21	106	110	245	
July		80	15	25		120	
August			1			1	
September			1			1	
October		2	7	3		12	
November		3	14			17	
December	17	8	7			32	
Total	17	133	93	179	160	582	

Telemetry system

The NEDAP TRAIL System® was used to observe migration patterns of the sea trout tagged (Breukelaar *et al.*, 1998; 2000). Fixed detection stations, constructed on the banks of watercourses that had been identified as part of a likely migration route (Fig. 1), picked up the transponder signal, unique for each fish, when a fish passed. Migration route of each fish was derived from the sequential passages past detection stations. Life time of the transponders was at least 3.5 years in the case of about 10 detections per year.

Transmission time of the transponder signal was 24 seconds followed by a mute period of two minutes to prevent the batteries from running down if a tagged fish should stop for a longer time within the reach of an antenna. In the case of a detection series at a single detection station, with intervals between the detections of three minutes or less, all detections were pooled and considered to be one registration. To describe migration routes of the tagged fish, the assumption was made that in a sequence of registrations at one detection station swimming direction turns after each registration. Such assumption was needed because swimming direction cannot be determined with the NEDAP TRAIL System®. In 92% of the cases, the animals reached the next detection station as was deduced from the sequence of registrations at a particular detection station.

Calculation of dominant flow

As a result of the combined effects of the tidal movement in the North Sea and the river discharge management through (a) the sluices in the Haringvliet dam and (b) the weirs in the Nederrijn/Lek and Meuse Rivers (Fig. 1), the flow rate ratio between the distributaries continually changes. Around high tide in the North Sea, a reversed flow rate occurs in some of them. Dominant flow was defined as the percentage of time the flow rate in one of both upstream distributaries at a bifurcation was highest during the period without flow reversion. The model 'ZWENDL' (Voogt *et al.*, 1991) was used for the dominant flow calculation, which was only made for those bifurcations where the fish had to continue upstream swimming (at some bifurcations the water in one of the two distributaries flows in downstream direction). Taking into account the average travel speed of the fish and the relatively short distance between the bifurcations and the nearest detection stations, the time each fish passed a bifurcation was equated with the time of the first detection at the nearest detection station.

Statistical analysis

The Student t-test was used to calculate statistical significance between population means, and a one-way ANOVA to test the hypothesis that the portion detected sea trout was constant over all length classes (Fowler *et al.,* 1998).
The Fulton index (Anderson & Gutreuter, 1983) was used as a metric for the condition of the fish. A correction for total fish length was made if the period between tagging and first detection was more than one month (Winter *et al.*, 2001).

RESULTS

The relationship between weight and length of the tagged sea trout (n=578) could be described with the equations: $W = 0.0038\ TL^{3.270}$ ($R^2 = 0.934$) and $W = 0.0065\ FL^{3.151}$ ($R^2 = 0.938$), in which TL and FL is total and fork length (cm) respectively, and W is weight (g). Portion of detected sea trout per length class (class width 1 cm) showed a slight but significant increase with total fish length (slope=0.08; R^2=0.085, $F_{1,35}$=4.34 and $p<0.05$).
During the period 16 December 1996 - 31 December 2000, 195 (34%) sea trout passed at least one detection station; nine fish were reported after being recaptured in Lake IJsselmeer without passing a detection station. Most of the registrations took place in June and July with 90 and 107 fishes registered respectively in these months over all years (Fig. 4). In both months, 87 % of the fish were registered during upstream migration. In December, the portion of downstream migrating fish (69%) exceeded the upstream migrating fish, while in January both portions were equal (number of registered fish was 18 and 27 for January and December respectively). In February, March and April, minimum numbers of fish were

registered; 5, 8 and 11 respectively. Because most of the sea trout (87%) were tagged in the south-western coastal zone (Fig. 1, location E), the study mainly focused on the western part of the Rhine delta. Some sea trout (n=27) travelled up and down between the coastal area and the Rhine delta before migrating upstream or disappearing. In the presentation of the results below, only the first upstream migration attempt was taken into account unless otherwise indicated.
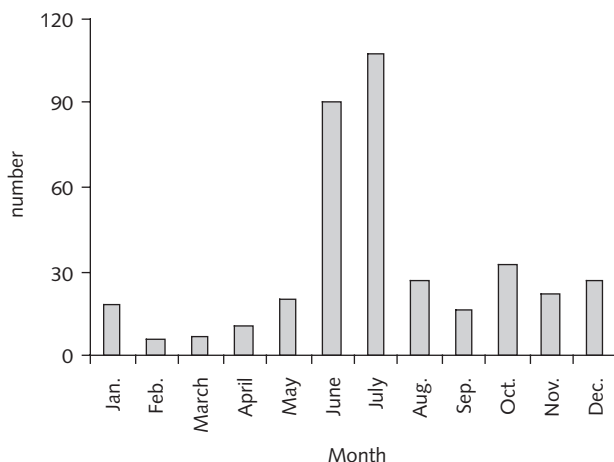
Figure 4. *Number of sea trout detected in each month in the period 1997-2000.*

Inland migration

Inland migration of sea trout was observed through the sluices in the dam between the Wadden Sea and Lake IJsselmeer (Afsluitdijk), the Nieuwe Waterweg, and the sluices in the Haringvliet dam (Fig. 2). No inland migration was observed through the North Sea Canal (Fig. 1). Although most of the sea trout entered the inland waters through the Nieuwe Waterweg or the sluices in the Haringvliet dam, inland migration through the sluices in the Afsluitdijk (n=34) was relatively more important: 49% of the sea trout tagged in the Wadden Sea (Fig. 1, locations A and B) were observed in inland waters, while 20% of the sea trout tagged in the southwestern coastal areas (Fig. 1, locations D and E) entered the Rhine delta through the Nieuwe Waterweg and 14% through the sluices in the Haringvliet dam (Table 3).

Of the inland migrating sea trout, 75% were registered for the first time at one of the

detection stations within 30 days after tagging. No significant differences (p<0.05) were found between the number of sea trout per tagging weight class at different time intervals determined by the period between tagging and the first detection.

If the tagged sea trout are split into three groups: (a) not observed in freshwater (sea group), (b) only observed in the Rhine delta (delta group), or (c) migrated further upstream (river group) (criterion for upstream migration is passage of the detection stations at Kampen [2], Nieuwegein [9], Vuren [10] or Capelse Veer [11]), it was concluded that the condition (Fulton index), the corrected total length and the age of the sea group differed significantly (p<0.05) from the delta and the river group.

Table 3. *Inland migration from the coastal areas, based on detections and recaptures in inland waters.*

From → To ↓	Haringvliet coastal area	Mouth Nieuwe Waterweg	Wadden Sea near the IJsselmeer dam
Haringvliet	70	0	1
Nieuwe Waterweg (through the North Sea)	99	3	0
Lake IJsselmeer (through the Wadden Sea)	2	0	33
Unknown (either through the Haringvliet or the Nieuwe Waterweg)	5	0	0

Effects of river discharge on inland migration was observed in the Waal River, using the results derived from the detection station at Vuren [10]. In a frequency of discharge classes, the portion of days on which upstream migration was observed differed significantly (p<0.05) from the portion of days without detection of upstream migration. At a discharge of <3000 $m^3.sec^{-1}$ (measured at the German-Dutch border) the relative number of days with fish detection was lower than without, while at a discharge of >3000 $m^3.sec^{-1}$ the opposite was observed (Fig. 5).

Difference between sea water and river water temperature was also considered a factor controlling inland migration. Assuming that sea trout, in upstream direction passing the detection station at Spijkenisse [14] in the Oude Maas River entered the freshwater the same day in June and July 1998 and 1999 (no temperature data available in 2000), predominant inland migration (p=0.054) was observed when sea water temperature was lower than the river water temperature.
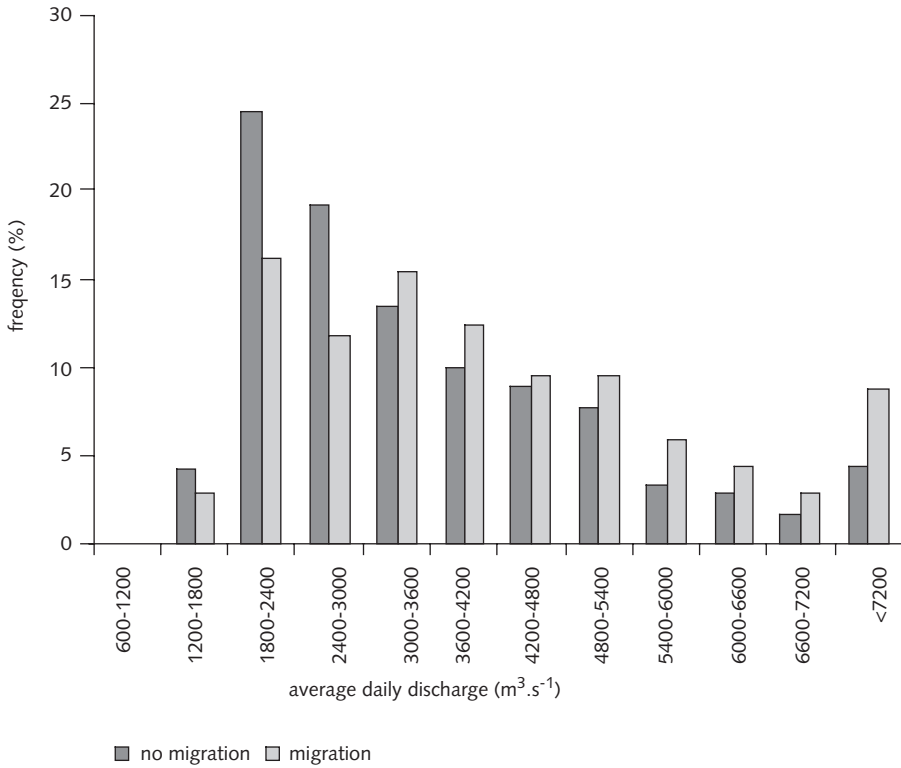
Figure 5. *Frequency of discharge at the detection station Vuren [10] (Waal River) during days with and without upstream migrating fish in the period 1998-2000.*

Upstream migration

In comparison with the complex situation in the western part of the Rhine delta, sea trout entering Lake IJsselmeer only have to navigate through this stagnant water to find the mouth of the IJssel River. Different migration routes are possible in the network of distributaries in the western part of the Rhine delta (Fig. 2). A sequence of some of them can be identified as the shortest routes to the lower Rhine or Meuse (both rivers share the Haringvliet as their former estuary). From the registrations at the detection stations at Nieuwegein [9][1] (Lek

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[1] The number is equal to that given in Figure 1.

River), Vuren [10] (Waal River) and Capelse Veer [11] (Meuse River), it was concluded that the chance to make a detour was double for sea trout entering the Rhine delta through the Nieuwe Waterweg compared with those entering through the sluices in the Haringvliet dam. Inland migration through the Nieuwe Waterweg was observed for 103 sea trout. About 20 km inland, the animals met the first decision point for the continuation of their inland journey: 27 (26%) fish chose the Nieuwe Maas River and 76 (74%) the Oude Maas River (Fig. 2, bifurcation 1). For the continuation of upstream migration from this bifurcation, eight routes were chosen by 82 sea trout during their first attempt and by twelve fish during another attempt. Second attempts were only taken into account if not occurring in the same season. Sea trout opting for the Nieuwe Maas River (n=27), met next decision point after 23 km, where they could choose between the Lek or Noord distributaries (Fig. 2, bifurcation 4). To reach this point, the fish had to travel through the city of Rotterdam. The Lek River, including the upstream stretch called Nederrijn (Fig. 1), is the only dammed Rhine distributary of which the most downstream of the three weirs is passable during 30 days per year on average. The median time the sea trout (n=14) stayed in the 5 km stretch between the detection station at Nieuwegein [9] and the most downstream weir was 55 days (range: 0.2 - 342 days). When the Noord River was chosen for upstream migration, the next decision point was the bifurcation with the Beneden Merwede and the Oude Maas Rivers (Fig. 2, bifurcation 8), 8 km upstream of the previous one. Fish traversing the 14.5 km long Beneden Merwede River entered the Waal River and after that the Lower Rhine when navigating in upstream direction.

Most of the sea trout (n=76) entering inland waters through the Nieuwe Waterweg chose the Oude Maas River at the decision point formed by the bifurcation with the Nieuwe Maas River (Fig. 2, bifurcation 2). Three km after this point, the bifurcation with the Spui River was met, 15 km further upstream the bifurcation with the Dordtsche Kil River (Fig. 2, bifurcation 3), and again 4 km upstream the bifurcation with the Beneden Merwede and Noord Rivers (Fig. 2, bifurcation 8). 59% of the sea trout entering the Oude Maas River swam into the Dordtsche Kil River, being a detour to the lower Rhine (the shortest route is through the Beneden Merwede River). The Waal River was reached by 68% of the sea trout, which chose the Oude Maas River at the decision point in the Nieuwe Waterweg, 46% reached the Lower Rhine.

Although the Haringvliet dam forms a serious obstacle for inland migratory fish, 70 (14%) of the sea trout tagged were able to pass the sluices in this dam (Fig. 2). Traversing the Rhine delta, 53 sea trout followed six different routes during their first upstream migration attempt. 84% and 14% reached the Waal and Meuse Rivers respectively.

In the western part of the Rhine delta (Fig. 2), sea trout have the possibility to deviate from the direct route to the lower parts of the Rhine and Meuse Rivers. The Dordtsche Kil River was visited by 61% of all the tagged sea trout, indicating its attraction for the upstream migration of sea trout entering the freshwater through the Nieuwe Waterweg or the sluices in the Haringvliet dam. The choice of the upstream migration route in this part of the Rhine delta seemed to be influenced by the dominant flow rate at some of the bifurcations, however, not for each discharge class distinguished (Table 4). If the route choice of more than five fish in each discharge class is compared with the dominant flow rate at the

bifurcations, the averages of dominant flow rates and choice for the upstream distributary clearly correspond to the bifurcations 1, 3, 4 and 6 given in Table 5. In the comparison, the relative contribution of each discharge class was taken into account. At the bifurcation Oude Maas-Dordtsche Kil (Fig. 2, bifurcation 3), the averages of dominant flow and upstream migrated fish only correspond at a Rhine discharge of <3000 $m^3.sec^{-1}$ that occurs 80% of the time.

Table 4. *Dominant river flow rate towards the downstream river stretch at the bifurcation points in the Rhine delta, and the upstream migration of sea trout (n).*

		Rhine discharge ($m^3.sec^{-1}$) at the German-Dutch border							
		1200-1700	1700-2200	2200-3000	3000-6000	1200-1700	1700-2200	2200-3000	3000-6000
Bifurcation		Dominant flow rate (% of the time)				Upstream migrated fish (%)			
Downstream	Upstream								
1. Nieuwe Waterweg	-Nieuwe Maas	23	31	31	31	35	42	27	8
	-Oude Maas	77	69	69	69	65	58	73	92
	n					**23**	**33**	**22**	**12**
2. Oude Maas (west)	-Oude Maas (east)	35	46	35	85	94	78	72	100
	-Spui	65	54	65	15	6	22	28	0
	n					**17**	**23**	**18**	**13**
3. Oude Maas (west)	-Oude Maas (east)	31	38	38	96	25	47	31	8
	-Dordtsche Kil	69	62	62	4	75	53	69	92
	n					**16**	**17**	**13**	**12**
4. Nieuwe Maas	-Lek	35	35	46	100	27	50	50	50
	-Noord	65	65	54	0	73	50	50	50
	n					**11**	**8**	**8**	**2**
5. Haringvliet (west)	-Haringvliet (east)	27	35	38	77	89	83	77	69
	-Spui	73	65	62	23	11	17	23	31
	n					**9**	**29**	**26**	**13**
6. Hollandsch Diep (west)	-Hollandsch Diep (east)	31	31	38	35	38	46	35	33
	-Dordtsche Kil	69	69	62	65	62	54	65	67
	n					**8**	**24**	**20**	**9**
7. Hollandsch Diep	-Nieuwe Merwede	92	100	100	100	33	50	44	100
	-Meuse	8	0	0	0	67	50	56	0
	n					**3**	**18**	**9**	**13**

Sea trout entering Lake IJsselmeer from the Wadden Sea (Fig. 1) in the northern part of The Netherlands, were relatively successful in finding a route through this stagnant water body to the mouth of the IJssel River: 25 (74%) fish that passed the Afsluitdijk were registered at Kampen [2], and 20 (59%) in the lower Rhine at Xanten [13].

Upstream migration speed, expressed as travel distance per unit of time, could be derived from sequential passages of detection stations. Median values, derived from at least ten observations, varied between 19.0 and 21.8 km d^{-1} for routes with a length of 10-25 km (4 routes); 11.2-19.2 km d^{-1} at a route length of 25-50 km (3 routes), and 19.4-21.0 km d^{-1} when the length was 125-165 km (2 routes). Based on all observations (n=314) the median upstream travel speed was 19.1 km d^{-1}, independently of the average flow rate in the distributaries, which varies from ± 1 m s^{-1} in the Rhine and Waal Rivers to < 0.5 m s^{-1} on average in the Dordtsche Kil and Meuse Rivers. The median travel speed found in this study is comparable to other studies (Bij de Vaate & Breukelaar, 2000).

During upstream migration, sea trout were predominantly active during daylight. Based on all registrations (n=1433), the highest migration activity was observed between 09.00 and 17.00 hour (Middle European Time + 1 hour) and the lowest during the dark, the period between 21.00 and 04.00 hour. Differences between the daylight and dark period, and between the combined registrations at dawn and dusk (the periods 04.00-09.00 and 17.00-21.00 hour) and the dark period were significant (p<0.01).

Downstream migration

Downstream migration was observed in 64 sea trout, of which seven fish migrated twice up and down. In 32% of all upstream migration attempts, downstream migration route was similar, especially if the fish migrated into the Lek River. Three out of five sea trout migrating into the lower Rhine (Xanten [13]) via the IJssel River, took the same downstream migration route despite an average of 80% of the Rhine discharge flowing through the Waal distributary.

Although the network of detection stations was designed for the study of upstream migration, the relatively low number of fish detected during downstream migration was obvious. The main reason was the disappearance of fish after the passage (in upstream direction) of the detection stations upstream the main bifurcations (Table 5). Relatively many fish disappeared or were recaptured after passing the detection station in the Rhine River at Xanten. Compared to the Nederrijn/Lek and Waal Rivers, upstream migration through the IJssel River caused fewer losses.

Table 5. *The number of sea trout detected at the given detection station (A), the number that only passed in upstream direction (B), and the number of reported recaptures (C).*

Detection station	A	B	C
Kampen [2] (IJssel River)	5[a]	4	0
Nieuwegein [9] (Lek River)	12[a]	7	1
Vuren [10] (Waal River)	35[a,b]	25	3
Xanten [13] (Rhine River)	89	68	8
Capelse Veer [11] (Meuse River)	24	12	3

[a] not detected at Xanten (Rhine River)
[b] including downstream swimming sea trout after passing the detection station at Xanten

Recaptures

During the study, 117 (21%) sea trout were reported after being recaptured; 24 of them were detected previous to the recapture and another 22 sea trout were released again of which five were detected afterwards. Most of the recaptures (70%) were reported from locations within a radius of 25 km from the tagging location, 6% between 25 and 100 km, and 24% from locations with a distance >100 km. Recaptures from the latter group were, among other locations, reported from the Rhine River and its tributaries in Germany (n=13), the Seine River (n=1), the Channel coastal area near Dieppe in France (n=3), and the Norwegian North Sea coastal area near Lindesnes (n=1).

DISCUSSION

Although the general aim was the identification of potential migration problems for Atlantic salmon during spawning runs in the Rhine delta, the collection of sufficient numbers of this species was not feasible in the definition phase of the project. Therefore sea trout was chosen as an alternative. From the first half of the 1930's, commercial Atlantic salmon fishing in the Rhine delta had stopped and two decades later the typical Rhine breed was considered extinct (De Groot, 1992). Incidental observations were reported in the period 1960-1990 (Cazemier, 1994), the result of either dummy runs or strays (De Nie, 1996). From the first half of the 1990's onwards, the number of observations of Atlantic salmon in the Rhine delta steadily increased due to upstream reintroductions in potential spawning areas (Raat, 2001). By the end of the 1980's, when the ecological rehabilitation of the Rhine River started, the main bottlenecks for the return of the Atlantic salmon and improvement of sea trout stocks were (a) inaccessibility of a major part of the former spawning and nursery areas (Kalweit, 1993), (b) the reduced accessibility of the river from the North Sea (De Haas, 1991),

(c) relatively high silt load in accessible spawning areas (Ingendahl, 1999), (d) low water quality (Lelek & Bushe, 1992), (e) fishery mortality at sea (Mills, 1989; Shearer, 1992), and (f) construction of hydro-electric power plants.

During the process of ecological rehabilitation, some of these bottlenecks have been reduced (e.g., improvement of the accessibility of spawning and nursery areas, reduction of pollutants, decrease of mortality at sea), however, they all still exist (Schmidt, 1996; Ingendahl, 1999; Raat, 2001).

Fish Sampling

The number of sea trout tagged in the coastal area at the main discharge points of the Rhine River was planned to be in proportion with the discharge rate. In practice, it was impossible to collect sufficient sea trout at most of the discharge points because of: (a) lack of or insufficient commercial fishery in the right period (Fig. 1, location A and B), (b) a combination of steep banks, relatively deep water and intensive navigation making commercial fishing unattractive (Fig. 1, location D), or (c) unsuitable fishing gear used by the commercial fishermen (Fig. 1, location C). These problems were not met in the coastal area in front of the Haringvliet dam (Fig. 1, location E), moreover, anadromous fish gather in that area foraging on sprat (*Sprattus sprattus* (L.)) (Vriese & Wiegerinck, 1991) or are attracted by the freshwater discharge and waiting for a chance to pass the sluices in the dam. In this area, 87% of the sea trout used in the study were tagged, resulting in an unequal relationship between that part of the sea trout tagged and the part of the Rhine discharge (27%) through the sluices in the Haringvliet dam.

Loss of tagged fish

Several factors could explain the disappearance of 51% of the sea trout after being tagged. Some tagged specimens were born or introduced in other river basins and thus not migrating to the Rhine or Meuse Rivers for spawning. Moreover, in contrast to the Atlantic salmon, sea trout normally stays in coastal areas during their sea phase (Elliott *et al.*, 1992). Travelling along the West-European coasts in their search for food, allochthonous fish are also expected to visit the sampling locations, especially those in the North Sea (Fig. 1, locations C, D and E). Recaptures of tagged sea trout in France and in Norway illustrate what distances are traversed at sea. A smaller portion of allochthonous sea trout in the Wadden Sea catches could explain the relatively more successful inland migration from this area into Lake IJsselmeer compared with inland migration through the Nieuwe Waterweg and the sluices in the Haringvliet dam. Migration in coastal areas increases capture risk since fishery pressure in the North Sea is relatively high. Loss of tagged sea trout was expected also to be the result of partial reporting of recaptured fish.

Malfunctioning of the telemetry system used can be ignored since all detection stations were

(a) programmed to check the electronic circuit with a twelve hours interval and (b) periodically checked with a hand-transponder.

An adverse effect of tagging on the fish cannot be neglected, however, information on post-implantation mortality or transponder expulsion was not available. In 1999, during an intensive search operation in the coastal area in front of the Haringvliet dam (Fig. 1, location E) with a portable detection device and an antenna fixed between two vessels, three transponders were detected. At that time, 419 tagged sea trout were released in the area. Previous to the field study, implantation effects were studied with dummy transponders in 25 rainbow trout (*Oncorhynchus mykiss* Walbaum), kept in captivity. They did not show any significant difference in growth and behaviour to a control group of the same size during a half year period after implan-tation. Transponder expulsion was not observed, although histological analyses showed some encapsulation of the transponder in two cases, most probably the effect of insufficient cleaning. None of the implanted fishes died as result of implantation (Vriese, 1995).

Inland migration

Inland migration through the sluices in the Afsluitdijk and the Haringvliet dam, which are opened if seawater level is lower than freshwater level at the other side of each dam, is only possible during a 10 to 20 minutes period after opening or before closing, when stream velocity is low enough due to small differences between both water levels. During these two periods sea trout (total length >40 cm) must be able to pass the 50 and 60 m long sluices in both dams respectively (Colavecchia *et al.*, 1998). If the sluices are partly lifted, the two periods given above are extended because the maximum flow velocity in the sluices is then reduced to a stretch of some metres and in this situation sea trout must be able to overcome a flow velocity of 9 times its body length at burst speed (Videler, 1993). An unknown factor is the effect of the turbulent zone on the navigation of fish attempting to pass the barrier from the sea. Greater problems for smaller fish to pass the sluices explains the slight but significant increase of the portion of detected sea trout per length class at increasing total fish length.

The registrations did not allow a distinction between motivated (spawning migration) and non-motivated upstream migration (e.g., dummy runs). Non-motivated upstream migration during their first attempt could be the reason that 15 sea trout showed more than one attempt. However, the main reason that four of them returned back to the North Sea after their first attempt, could also be the wrong choice of the upstream migration route, which was blocked by a weir. The remaining number of 11 dummy runs seems rather underestimated, taking into account that 63% of the tagged sea trout stayed at most one year at sea before tagging, and that it is specifically grilse that makes dummy runs (Shearer, 1955). In the absence of detection stations at the Nieuwe Waterweg and, for most of the study period, at the sluices in Lake IJsselmeer and the Haringvliet, relatively short dummy runs, if occurring, were not recorded.

In general, river discharge seems to play a dominating factor for inland migration of Atlantic

salmon and sea trout (e.g., Smith *et al.*, 1994; Jensen *et al.*, 1998). High flows facilitate river entry (Hayes, 1953; Brayshaw, 1967; Alabaster, 1970), while periods of low flow could be associated with delayed river entry (Hayes, 1953; Alabaster, 1970; Potter, 1988; Clarke *et al.*, 1991).

Upstream migration

In general the choice of the upstream migration route in the western part of the Rhine delta seemed to be influenced by the dominant flow rate at the bifurcations. Deviations can be attributed to local circumstances (Fig. 2, bifurcations 2 and 5), or preference for another stream (Fig 2, bifurcation 7). The bifurcation Oude Maas-Spui (Fig. 2, bifurcation 2) is situated on an outside curve of the Oude Maas River. If the fish mainly migrates through inside curves to avoid locally higher current velocities, the attracting flow from the Spui River will probably not be detected by most of the fish. On the other hand, attracting flow brings water from the semi-stagnant Haringvliet into the Oude Maas River. Although <70% on average of the water in the semi-stagnant Haringvliet originates from the Rhine River, its quality (odours and flavourings) is considered to be affected by autonomous phytoplankton development in the growing season which differs from phytoplankton growth in the Rhine distributaries (De Hoog *et al.*, 1997). This phenomenon could be an important reason for the sea trout to avoid the Spui River, despite its potential attraction through its dominant flow velocity. Width ratio between the Haringvliet and the Spui river is about 12:1 at the bifurcation (Fig. 2, bifurcation 5). This imbalance, and the fact that the bifurcation is situated at the northern Haringvliet bank, while the fish will enter the Haringvliet along the south bank due to the management scheme of the Haringvliet sluices at Rhine discharge <3000 $m^3.sec^{-1}$, may explain why the attractive flow from the Spui River is not detected by most of the fish. At the bifurcation Hollandsch Diep-Nieuwe Merwede-Meuse (Fig. 2, bifurcation 7) the fish had to choose between the Rhine and Meuse Rivers. Homing is considered to be the main decision factor at that location and explains the discrepancy between dominant flow rates and the choice for the upstream river section.

Recaptures

Supplementary to detections, tagged fish were also observed after being recaptured (n=117). However, only few of them contributed to the understanding of their migration pattern. Most of the fish reported (68%) was recaptured within two months after tagging. Recaptures reported from the Norwegian south coast, the German part of the Wadden Sea and the Channel near Dieppe illustrate the sea trout's stay in coastal areas during their sea phase (Elliott *et al.*, 1992; Mills, 1989). A combination of a relatively high fishing pressure in the coastal zone in front of the Haringvliet dam and the aggregation of fish, after being

attracted by freshwater discharge through the Haringvliet sluices without having the possibility to pass them, is considered to be responsible for the relatively high number (46%) of the recaptures reported from that area in which 87% of the fish was released after tagging.

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CHAPTER 8

RIVER RESTORATION: A MIRAGE!

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INTRODUCTION

Exponential increase of anthropogenic stress in European rivers started several centuries ago when inhabitants of floodplains attached an increasing number of functions to them. In the Rhine delta this type of stress began approximately about 11 centuries ago with the construction of levees. Step by step, the river basins lost their naturalness and ecological integrity (Smits *et al.* 2000). In general, river regulation was a first step (e.g., Petts *et al.* 1992, Dynesius & Nilsson 1994). Floodplains in the lower parts were narrowed by the construction of levees and dikes for land reclamation and to protect inhabitants against floods. Standard relations between channel width and depth *versus* discharge were completely disrupted due to the functions assigned to the main channel (e.g., navigation, rapid discharge of water and ice). In a natural river, all three variables are supposed to increase in a downstream direction. Classical diagrams (Church 1992) show, for example, a channel width of 500 m at a discharge of 1500 $m^3.s^{-1}$, the average discharge of the River Waal. Nowadays this main distributary of the River Rhine, which is an important shipping route between the harbours of Rotterdam and industrial areas in Germany and Switzerland, has an average channel width of only 170 m (Nienhuis & Leuven 2001). Rivers channels were shortened and normalised for discharge improvement, canalised for the purpose of navigation and regulated by weirs and sluices for water resource control and flood defence. From the early 1900s, major dam building activities started for hydroelectric power, drinking water supply and irrigation. In North America, Europe and the former Soviet Union, 71% of the large rivers (mean annual discharge >350 $m^3.s^{-1}$ before regulation) are affected by dams and reservoirs, inter-basin diversion and water abstraction (Dynesius & Nilsson 1994). Around 90% of the rivers in the United Kingdom have been regulated, while in a densely populated country like The Netherlands this percentage is close to a hundred percent (Nienhuis & Leuven 2001). Later on, rivers were also used for the downstream transport of wastes and waste water from the urban environment (Walsh 2000). River pollution particularly manifested, following the industrial revolution in Europe (Nienhuis & Leuven 2001).

River engineering

Main effects of river regulation were (a) the disappearance of riverine habitats like side channels, (b) sand and gravel bars and banks, and (c) incision of the main channel, causing a drastical reduction of the ecological functioning of aquatic/terrestrial transition zones (e.g., Van Urk & Smit 1989, Dister 1994, Gore & Shields 1995, Sparks 1995, Galat *et al.* 1998, Dohle *et al.* 1999). An opposite effect of river engineering, mainly on macroinvertebrates, in

the Rhine Delta and the lower sections of the River Meuse, was caused by the construction of groynes and the protection of banks in the summer bed. With these activities, lithal habitats were introduced in the littoral of river sections where under natural circumstances only psammal and/or pelal habitats are present. This habitat type houses, in general, a diverse macroinvertebrate community (e.g., Allan 1995). In contrast, the bottom of large natural river channels in alluvial plains, consists of a monotonous sequence of slowly moving sand dunes uncolonisable for most of the benthic macroinvertebrates. If they can live there, it is only in relatively low densities (Morris *et al.* 1968). However, due to the introduction of artificial lithal habitats, macroinvertebrate diversity and density increased in the littoral zone of the main channels of the Rhine distributaries and the lower sections of the River Meuse. Water quality improvement during the last two decades of the 20th century (chapter 1) strongly contributed to both increases as well (chapter 2).

Water quality

Data on water quality improvement in the Dutch part of the rivers Rhine and Meuse are given in chapter 1. The Rhine and Meuse Action Programmes, launched in 1987 and 1997 respectively, initially focused on additional water quality improvement. The countries in the Rhine basin, united under the International Commission for Protection of the River Rhine against Pollution (ICPR), agreed upon a target reduction of at least 50% of the pollution caused by priority compounds by the year 1995 (compared with the situation in 1985). Furthermore, water quality targets for the river Rhine were set for about 50 priority compounds, based not only on requirements for drinking water production and the protection of aquatic life, but also on human tolerance levels for fish consumption (Van Dijk *et al.* 1995). The International Commission on protection of the River Meuse (ICPM), in which the countries in the Meuse basin have been united from 1994, did not set specific targets for pollution reduction and improvement of the ecological quality (ICPM 1997).

River bottom quality

To determine the quality level of the river bed, effects of pollutants were extensively studied in a sedimentation area of the lower Rhine, the western part of the Rhine delta. Sediment quality in this area still does not meet a no observed effect level. Based on a "Triade approach" (Chapman 1986, Van de Guchte 1992) about 55% of the locations examined in 1992 and 1993 were identified as areas where pollution could be held responsible for effects observed in the field (Den Besten *et al.* 1995). According to Reinhold-Dudok van Heel & Den Besten (1999), sediment toxicity in the same area was positively correlated with concentrations of heavy metals, mineral oil, hexachlorobenzene and/or endrin. Peeters (2001) pointed out that 13.8% of contaminants explained macroinvertebrate variation in the area in the period 1992-1995. 14.7% of the variation was explained by the covariation between ecological variables and contaminants, while ecological factors explained another 17.3%.

RIVER RESTORATION

Under the aim of improving the ecological integrity of large rivers, restoration has become an important issue since the late 1980s (Boon *et al.* 1992, Sparks 1995, Nienhuis & Leuven 1999, Pedroli & Postma 1999). Important general aspects are (a) improvement of the lateral and (b) longitudinal connectivity and (c) the connectivity with the groundwater. Dutch policy for river restoration is aiming to reduce habitat fragmentation, since river valleys are considered to be important corridors for the migration and dispersal of aquatic and terrestrial animal species, and for biodiversity conservation (Anon. 1998). As a consequence of this policy, structure and functioning of ecological networks need to be improved in order to create viable populations of target species (ICPR 1998, Foppen & Reijen 1998, Chardon *et al.* 2000). However, restoration of geomorphological processes to improve connectivity in the Rhine distributaries and in the lower sections of the River Meuse is only possible in a very limited way because of the functions assigned. Impaired discharge of water and ice as well as the economy related functions, remain more important than their ecological functions, due to safety and socio-economic reasons, respectively. In practice, possibilities for restoration of large rivers in The Netherlands are thus mainly possible in aquatic/terrestrial transition zones in the Rhine delta and in the Grensmaas stretch of the River Meuse by lateral connectivity improvement (Van Dijk *et al.* 1995, Heiler *et al.* 1995, Simons *et al.* 2001, Buijse *et al.* 2002). Several large ecologically important reaches (1000-6000 ha each), with smaller areas in between, were identified along the Rhine distributaries, of which approximately 7500 ha of floodplain area have an important ecological function (Van Dijk *et al.* 1995). In the Dutch part of the River Meuse, improvement of the lateral connectivity is the main goal for the Grensmaas stretch (Helmer *et al.* 1991). Longitudinal connectivity for fish has been achieved by the construction of fish ladders at the weirs in the Dammed Meuse. In the forelands of this river section and the Tidal Meuse, secondary channels and wetlands have been created to improve storage capacity of the river (ICPM 2002).

NONINDIGENOUS SPECIES

Recent developments in macroinvertebrate communities show an increased importance of nonindigenous species in the Rhine distributaries and in the lower Meuse. A list of exotic macroinvertebrate and fish species recently found in the freshwater sections of these water bodies is given in table 1. Main part euryhaline and/or thermophilous, which clearly indicates effects of an increased chloride concentration and/or thermal pollution on macroinvertebrate communities. A relevant number is of Ponto-Caspian origin. Most of these species were able to colonise the River Rhine after construction of the Main-Danube canal, opened in September 1992. From that date, mainly introductions of native species from the Ponto-Caspian area have been observed (e.g., Schleuter *et al.* 1994, Bij de Vaate & Klink 1995, Schleuter & Schleuter 1995, Klink & Bij de Vaate 1996, Reinhold & Tittizer 1998, Schleuter & Schleuter 1998, Schmidt *et al.* 1998, Schöll & Behring 1998,

Table 1. *Nonindigenous macroinvertebrate and fish species recently (after 1950) reported from the Rhine distributaries and the Dutch part of the river Meuse.*

Species	Origin	Rhine delta	Lower Meuse	References
Tricladida				
Dendrocoelum romanodanubiale	E-Europe	+		Bij de Vaate & Swarte 2001
Dugesia tigrina	N-America	+	+	Van der Velde 1975
Bivalvia				
Corbicula fluminalis	E-Asia	+	+	Bij de Vaate 1994[A]
Corbicula fluminea	E-Asia	+	+	Bij de Vaate & Greijdanus-Klaas 1990, Bij de Vaate 1994[B]
Musculium transversum	N-America	+		Van der Velde 2002
Gastropoda				
Helisoma nigricans	N-America			Gittenberger *et al.* 1998
Menetus dilatatus	N-America		+	Wallbrink & De Vries 1996
Physella heterostropha	N-America		+	Keulen 1998
Potamopyrgus antipodarum	New Zealand	+	+	Gittenberger *et al.* 1998
Annelida				
Branchyura sowerbyi	E-Asia	+	+	Van der Velde 2002
Caspiobdella fadejewi	E-Europe	+		Bij de Vaate *et al.* 2002
Hypania invalida	E-Europe	+		Klink & Bij de Vaate 1996
Limnodrilus maumeensis	N-America	+	+	Van Haaren 2002
Acari				
Caspihalacarus hyrcanus danubialis	E-Europe	+		Bij de Vaate *et al.* 2002
Crustacea				
Astacus leptodactylus	E-Europe	+		Adema 1989
Atyaephyra desmarestii	S-Europe	+	+	Van den Brink & Van der Velde 1986
Bythotrephes longimanus	N&E-Europe	+	+	Van der Velde *et al.* 2000
Chelicorophium curvispinum	E-Europe	+	+	Van den Brink *et al.* 1989, 1993[A]
Crangonyx pseudogracilis	N-America	+		Bij de Vaate & Klink 1995
Dikerogammarus villosus	E-Europe	+	+	Bij de Vaate & Klink 1995
Echinogammarus ischnus	E-Europe	+		Van den Brink *et al.* 1993[B]
Echinogammarus trichiatus	E-Europe	+		Van der Velde 2002
Gammarus tigrinus	N-America	+	+	Pinkster *et al.* 1992, Platvoet & Pinkster 1995
Hemimysis anomala	E-Europe	+		Ketelaars *et al.* 1999
Jaera istri	E-Europe	+		Kelleher *et al.* 2001
Limnomysis benedeni	E-Europe	+	+	Kelleher *et al.* 1999
Orconectes limosus	N-America	+	+	Geelen 1975, Hadderingh *et al.* 1983
Procambarus clarkii	N-America	+		Adema 1989

Table 1: continued

Species	Origin	Rhine delta	Lower Meuse	References
Osteichthyes				
Abramis sapa	E-Europe		+	Winter, H.V., Inst. Fisheries Research, IJmuiden, unpublished observation in 2002
Acipenser baeri	E-Europe	+		De Nie 1997
Acipenser gueldenstaedti	E-Europe	+		De Nie 1997
Acipenser ruthenus	E-Europe	+		De Nie 1997
Aspius aspius	E-Europe	+	+	De Nie 1997
Ctenopharyngodon idella	E-Asia	+	+	De Nie 1997
Hypophtalmichthys molitrix	E-Asia	+	+	Nijssen & De Groot 1987
Hypophtalmichthys nobilis	E-Asia	+	+	Nijssen & De Groot 1987
Lebistes reticulatus	N&S-America	+	+	De Nie 1997
Proterorhinus marmoratus	E-Europe	+		Winter 2002
Pseudorasbora parva	E-Asia		+	De Nie 1997
Vimba vimba	E-Europe	+	+	De Nie 1997

Bij de Vaate & Swarte, 2001, Bij de Vaate *et al.* 2002). Some of the allochthonous species that recently colonised the rivers Rhine and Meuse, the amphipods *Gammarus tigrinus*, *Dikerogammarus villosus* and *Chelicorophium curvispinum*, the isopod *Jaera istri*, the bivalves *Corbicula fluminalis* and *C. fluminea*, and the polychaete worm *Hypania invalida* soon became dominant in macroinvertebrate communities in several biotopes in the Rhine distributaries and in dammed and tidal sections of the Lower Meuse (chapter 1). Range extension patterns of Ponto-Caspian species in the Dammed and Tidal Meuse showed that they had mainly migrated through the Maas-Waal Canal, a man-made connection between the Rivers Waal and Meuse in the vicinity of Nijmegen, to colonise the River Meuse.

ENDPOINTS OF RIVER RESTORATION

Talking about river restoration one has firstly to consider what the artificial endpoints are. Environmental quality assessments are based on indicator species, target species, target communities, diversity indices, or indices of biological integrity, under the assumption that the presence of specific species or a high biodiversity is the endpoint of the rehabilitation. Aims for river rehabilitation are translated in references usually derived from periods with less or with an acceptable amount of man-made disturbance. While the idea of a reference state seems straightforward, it is actually the question whether communities arising after river rehabilitation are predictable enough to strive to reference communities or specific species. The answer is no, because of the stochastically occurring disturbance events that determine the assembly of communities. According to Neumann (2002) macroinvertebrate

communities in the River Rhine did not reach a balanced state during the process of ecological rehabilitation because of the ongoing introductions of non-indigenous species and alterations in habitat structure. He suggested that fluctuations in dominant species have always been typical for post-glacial large European rivers. A stochastically changing relationship between water level fluctuations and the seasonally restricted reproduction periods of species, and as the result also changing influences of predators and competitors, are considered to be the main factors.

Obviously, the idea of a fixed "endpoint" of restoration is rather unrealistic. Beside the problem of defining what we aim at, these are also problems in restoring past regimes. Firstly, it is important to note that the scale of the remaining part of the floodplain strongly limits the effects of river rehabilitation. Natural riverine landscapes in The Netherlands were characterised by extensive flood plains and high hydraulic connectivity, resulting in a successional landscape mosaic with high habitat heterogeneity and a complex land-water coupling and exchange. Secondly, the interplay between landscape elements has a direct bearing on the generation, distribution and maintenance of riverine biodiversity (Junk 2000, Tockner *et al.* 2000, Robinson *et al.* 2002). Thirdly, the riverine fauna also provided important feedbacks that, in turn, influenced spatio-temporal dynamics of the landscape over long time periods (Naiman *et al.* 2000).
Embankments of the lower Rhine, its distributaries, and the lower Meuse, strongly reduced these fluvial hydrosystems (Petts & Amoros 1996). The normalised and canalised main channels and the joining forelands are the only remains. Compared to the pristine situation, the forelands are not wide enough to accommodate the fauna that belongs to such a situation. Nonetheless, the forelands are the only parts of the river valley available for river restoration or nature development and conservation.

Another important problem for river restoration is the fact that key elements for the relatively high biodiversity in the aquatic/terrestrial transition zones are flood controlled disturbances and geomorphological processes (Junk *et al.* 1989, Naiman & Décamps 1990, Bayley 1995, Ward 1998, Schiemer 1999). These disturbances and processes create characteristic small scale dynamics, resulting in spatial heterogeneity and differentiation in succession stages, and thus in a maximum number of functional habitats (Naiman *et al.* 1988, Décamps & Tabacchi 1994, Décamps 1996, Harper *et al.* 1998). However, possibilities for flood controlled disturbances in the forelands are restricted due to safety reasons (i.e., danger of dike bursts), and as a consequence, river dynamics which drive natural geomorphological processes are also restricted. Only human controlled disturbances in nature development areas are allowed, resulting locally in a small scale increase of spatial heterogeneity due to gradients in sediment types, bank slope, bank vegetation cover and flow gradients after construction of secondary channels. Despite its small scale and the limited discharge through these channels, a relatively broad range of functional habitats is present, in comparison with the main channel (Schropp & Bakker 1996, Grift 2001, Grift *et al.* 2001, Simons *et al.* 2001).
In addition to strongly reduced riverine landscapes and flood controlled disturbances in the aquatic/terrestrial transition zones, West-European rivers house an increased number of

nonindigenous species, mainly due to the interconnection of river basins, deliberated releases and intercontinental transport (Bij de Vaate *et al.* 2002). Recolonisation after reduction of pollution in rivers, modified by human activities seems to favour invaders more than indigenous species. These invaders then suppress the development of populations of indigenous species, however, local biodiversity increases (Van der Velde *et al.* 2002). Although the link between the biodiversity of communities and their vulnerability to invasions remains to be identified, invasibility is known to increase if a community lacks certain species, which ought to be present under normal conditions (Van der Velde *et al.* 2002). A hypothesis linking the various explanations of increased invasibility is that of fluctuating resource availability such as an increased amount of unused resources (Davis *et al.* 2000). The River Rhine is a good example in which an increased amount of unused resources occurs due to its rehabilitation. Pollution over a long period weakened the original communities and caused loss of species, initially creating open niches for pollution-tolerant invaders (Den Hartog *et al.* 1992).

The problem of invasive species is part of a final fundamental problem we should consider, namely that of the irreversibility of change in many ecosystems. While alternative stable states create difficulties for the recovery of ecosystems such as coral reefs, lakes and dry forests (Scheffer 2001), biological communities are thought to have such stable states on a more subtle scale. Drake (1990), who defined a community as the ensemble of species in a specific area whose limits are determined by the practical extent of energy flow, summarised the concept of "assembly rule" to describe the mechanics of how species of a community fit together in its present state. This state is one of those that exists between alternative states. The mechanisms and processes behind the production of alternative states are the devices of assembly rules. These rules produce communities that are, for example, differentially vulnerable to invasions of autochthonous or allochthonous species. The invasibility itself can be considered as an emergent property of the community, being the expression of the set of assembly rules. Stochastic events such as water pollution, caused by calamities, can bring the community in an alternative state by wiping out part of the species (Scheffer *et al.* 2001). The way back is determined by the assembly history from which the assembly rules operate and the real time effect of interactions and ensemble effects (Drake 1990).

With respect to water pollution, Matthews *et al.* (1996) presented the "community conditioning" hypothesis, stating that ecological communities retain information about events in their history. Effects were made visible after multivariate analysis of the results of standardised microcosm toxicity tests. Toxicants depressed the *Daphnia* populations which resulted in algal blooms. In the later part of the test, the populations appeared to have recovered due to dose/response differences that reappeared as the result of density differences in other consumers (rotifers, ostracods, ciliates) or algae that are normaly not consumed (filamentous algae and cyanobacteria). In fact, Matthews *et al.* (1996) explained with their community conditioning hypothesis the same process indicated by Drake (1990) in which the assembly history governs the assembly rules.

In conclusion, current artificial endpoints of river restoration, on the level of target species or target communities, are strongly influenced by methodological choices. They create the illusion of repairability of an unbalanced state from the past, which suggests stability. It should not be surprising that environmental policies, aiming to create stable ecosystems, may actually result in the loss of biodiversity rather than the intended gain (Reice 1994). Improvement of the water and river bed quality will improve quality of life of the aquatic organisms, but assembly rules will determine the community structures in which nonindigenous species are included as full members of trophic guilds. Nature development in the aquatic/terrestrial transition zones, such as the construction of secondary channels, increases the number of functional habitats and thus biodiversity. However, without unlimited flood controlled disturbances, the driving forces behind geomorphological processes, also needed to maintain these channels, real river restoration is absolutely out of question. In addition, assembly rules will also determine the community structures. The endpoint of river rehabilitation in The Netherlands should therefore not strive for target communities or target species (in desired densities), but locally for habitat diversity and a maximum number of trophic guilds. River rehabilitation with such an aim is not a mirage, of which everyone has their own image, but does justice to the possibilities there are without harming safety and socio-economic developments in the former floodplains of the rivers Rhine and Meuse.

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SUMMARY

Exponential increase of anthropogenic stress in European rivers, like Rhine and Meuse, started several centuries ago when inhabitants of floodplains used them for an increasing number of purposes. Step by step, the river basins lost their naturalness and ecological integrity. Usually, river regulation was a first step. Floodplains in the lower parts were narrowed by the construction of levees and dikes for land reclamation and to protect inhabitants against floods. Rivers channels were shortened and normalised for discharge improvement, canalised for the purpose of navigation and regulated by weirs and sluices for water resource control and flood defence. Later on, rivers were also used for the downstream transport of wastes and waste water from the urban environment. River pollution became particularly manifest following the industrial revolution in Europe.

The implementation of national laws against pollution and protection of the environment, and the establishment of the International Commission for Protection of the River Rhine marked a turning point in river pollution. Calamitous pollution accidents in the River Rhine caused political reveilles needed for the rehabilitation of both the rivers Rhine and Meuse. Results of water quality improvement were clearly visible from the second part of the 1970s. The Rhine and Meuse Action Programmes, launched in 1987 and 1997 respectively, not only focused on further water quality improvement but on restoration and reconstruction of physical riverine habitats as well, in order to improve lateral and longitudinal connectivity. This thesis focusses on ecosystem change over the resulting period of improving water quality in both the rivers Rhine and Meuse.

In chapter 2, long-term changes in the macroinvertebrate fauna of the littoral riprap in the River IJssel are described for the period 1975-1991. The changes in species richness and densities observed were thought to be caused by water quality improvement only. However, from later studies it was concluded that community changes after that period were dominantly induced by two nonindigenous species, the mass invader *Chelicorophium curvispinum* and *Dikerogammarus villosus* respectively.

In chapter 3 macroinvertebrate communities in the main biotopes in the Grensmaas stretch of the River Meuse are described for the period 1981-1990. In total, 51 taxa were found: 31 on stones in the littoral zone, 38 on/in the river bottom in the littoral zone of the unnavigable section, and 20 on/in the deeper river bottom in the navigable section. Typical species for the River Meuse were not observed, and the number and density of Ephemeroptera, Trichoptera, Crustacea, Hirudinea and Tricladida species appeared to be strongly reduced relative to the 'original' situation. The study provides a framework to assess effects of nature development which should be combined with gravel extraction on the river banks. An environmental risk assessment of such interventions was started recently.

Chapter 4 deals with the question how the ecological recovery in a river may be measured. Benthic macroinvertebrate community structure has become an important element in many

water quality assessments. Advantages of benthic macroinvertebrates in biological assessments include their abundance, sedentary nature, suitable life spans, diversity of phyla and trophic levels, sensitivity and swift response to various pollution types and the many sampling methods available. However, available ways to derive a measure for water and ecological quality from the composition of the macroinvertebrate fauna tend to be limited to particular systems. We assessed the practicability of the Index of Trophic Completeness (ITC). This index is based on the trophic functions of macroinvertebrates, and is independent of the presence of particular species. The index overcomes problems and drawbacks of using conventional diversity or biotic indices in biological assessments of running waters, such as limitation to distinct geographical regions or the focus on species richness without regard for the functioning of the ecosystem functioning. By applying the ITC to various data sets from rivers exposed to different degree of anthropogenic pressure, we showed the robustness of the index. However, because the index is only a metric for the functioning of the macroinvertebrate community, we recommend to combine it with other indices to cover aspects, such as biodiversity, in environmental quality assessment procedures.

Range expansion into western direction of 22 Ponto-Caspian macroinvertebrate species is reviewed chapter 5. The chapter focusses on reconstruction of their expansion routes. Insight in these routes and in the mechanisms of spread are important to assess the expansion potential of such animals in and outside Europe. The rivers Rhine and Meuse can be regarded as models for Western European rivers in which deterioration followed by ecological rehabilitation have led to a large number of invasions precluding ecological restoration to its pristine state. Invasions of nonindigenous species in the Dutch part of both rivers mainly took place unintentionally via ballast water of vessels, through canals connecting river basins, or as non-target species associated with intentionally introduced fish species. The interconnection of river basins by numerous canals, constructed during the last two centuries in Europe as a result of industrial and economical activities, has facilitated the range expansions of many species in Europe. The new connection between the Rhine and Danube basins, the Main-Danube Canal which was opened in 1992, is nowadays the most important route for freshwater nonindigenous species to enter The Netherlands. Some of these species of Ponto-Caspian origin caused dramatic changes in macroinvertebrate communities in the Rhine delta. An important lesson that can be learned from the studied introductions of Ponto-Caspian species outside their natural range of distribution is that some of them show pronounced shifts in impact and behaviour (e.g., *Chelicorophium curvispinum* and *Dikerogammarus villosus* in the River Rhine, and *Dreissena polymorpha* in North America). *D. villosus*, for example, shows a pronounced carnivorous character in the River Rhine, while it is an omnivorous species in the River Danube. This implies that extrapolation of information on original ecological niches may not always be sufficient to predict the impact of such organisms in a new environment.

Chapter 6 deals with one of the best studied Ponto-Caspian invaders, the zebra mussel *(D. polymorpha)*. The zebra mussel was already recorded in The Netherlands in 1827. Colonisation of Lake IJsselmeer started soon after the lake was created in 1932 when a

closure dam was finished, separating the Zuiderzee, an estuary of the River Rhine, from the Wadden Sea. Lake IJsselmeer became an important area for wintering tufted duck *(Aythya fuligula)*, pochard *(A. ferina)*, scaup *(A. marila)* and goldeneye *(Bucephala clangula)*, because zebra mussels are their main food source in that period of the year. Our work shows that the spread of the zebra mussel in the Lake IJsselmeer area has been habitat limited. Its presence appears largely regulated by the availability of solid substrates on the lake bottom. Growth rate, measured in terms of shell length and soft body weight increase, was analysed and appeared comparable with populations from the Mazurian lake district in Poland. The results of our study were used for calculations on the possible use of zebra mussels in biomanipulation, which became after that an important item in eutrophication control in shallow lakes.

Chapter 7 deals with the question how our rivers can be recolonised by fishes such as the salmon which migrate between riverine and marine systems during their life cycle. Although an international approach on water quality improvement in the River Rhine started in the 1960s, its ecological rehabilitation started after a severe pollution calamity in the vicinity of Basel (Switzerland) in November 1986. Among other things, the Atlantic salmon *(Salmo salar)* was chosen as an indicator for the ecological rehabilitation of the river. The typical Rhine breed of this species became extinct in the first part of the 20th century (De Groot, 1992), due to a combined action of (a) damming of tributaries, (b) water quality deterioration, and (c) silting up of the redds. In addition, migration of anadromous fish species from the North Sea into the River Rhine became strongly reduced by damming of the Zuiderzee in the 1930s and the Rhine-Meuse estuary (called Haringvliet) in the 1970s. Because this species does not spawn in the Rhine delta or in the lower section of the River Meuse, the Dutch contribution to reintroduction programs has been focused on (a) improvement of possibilities to enter both rivers from the North Sea and (b) migration possibilities through the distributaries of the Rhine delta. To gain a clear understanding of the main potential migration routes the Atlantic salmon is likely to follow in the altered Rhine delta during their journey from the North Sea to the spawning areas, sea trout *(Salmo trutta)* was selected as a representative species to study migration possibilities. Inland migration of sea trout was observed through the sluices in the dam between the Wadden Sea and Lake IJsselmeer (called Afsluitdijk), the Nieuwe Waterweg, and the sluices in the Haringvliet dam. The main upstream migration route at the current discharge management of the rivers Rhine and Meuse through the sluices in the Haringvliet dam is formed by: Nieuwe Waterweg → Oude Maas River → Dordtsche Kil River → Beneden Merwede River → Waal River. Differences in current velocity at bifurcations in the Rhine distributaries seemed to be an important factor in the choice of migration routes. Main inland migration periods were June-July and October-November. The coastal area in front of the Haringvliet dam is an important area where the fish gather after being attracted by the freshwater discharge through the sluices in the dam. Discharge management adjusted to improve inland migration through the sluices in the main migration periods is needed to facilitate passage through the dam and to reduce captures. Knowing the main migration routes through the Rhine delta, river managers can use this information in management plans for the ecological rehabilitation of the Rhine

delta and the lower River Meuse. In this way they contribute to a self sustainable population of the Atlantic salmon in both rivers.

In chapter 8 the possibilities and the endpoints of river ecological restoration are discussed. Due to the functions the Rhine distributaries and the lower River Meuse have in the modern society, river restoration and/or nature development are mainly possible in their forelands. In fact, the way back to a pristine situation was already blocked about 10 centuries ago when settlers in the Rhine delta started to construct levees to protect themselves against floods. If there could be a way back from the point of view of hydrology and morphology, communities would never be the same on species level compared to those belonging to pristine conditions because of the presence of nonindigenous species and stochastic elements in the community assemblage processes.

SAMENVATTING

De blijvende vestiging van de mens in de vloedvlaktes van de Rijn en de Maas kan gezien worden als het begin van antropogene stress op het rivierecosysteem. Deze nam in de loop der eeuwen exponentieel toe. Geconcludeerd kan worden dat de rivierlopen toen stap voor stap hun natuurlijkheid en hun ecologische integriteit begonnen te verliezen. Het reguleren van beide rivieren, om een zekere mate van bescherming tegen hoogwater te bewerkstelligen, kan gezien worden als een eerste stap op een weg die leidde naar een sterke aftakeling van hun ecologische waarden. Ter bescherming werden dijken opgeworpen wat er toe leidde dat de vloedvlakten sterk werden ingeperkt. Een bijkomstig voordeel hierbij was overigens dat vruchtbare kleigronden beter benut konden worden voor agrarisch gebruik, waardoor de bevolkingsdichtheid kon toenemen. Veel later ging men er toe over om meanders kort te sluiten en werd de hoofdgeul (het zomerbed van de rivier) vastgelegd met behulp van kribben. Deze activiteiten waren noodzakelijk voor een verbetering van de afvoer en de scheepvaart. Ten behoeve van de scheepvaart werden in de Maas en in de Nederrijn tevens stuwen gebouwd. De rivieren werden voorts gebruikt voor de afvoer van afval en afvalwater, met name uit verstedelijkte gebieden. Met de industriële revolutie kwam daar ook nog eens in sterke mate het aspect van de chemische verontreiniging bij.

Als een keerpunt in de historie van de waterverontreiniging kan worden beschouwd de implementatie van nationale wetgeving, gericht op de bestrijding van de milieu-verontreiniging en op het gebied van de natuurbescherming op niveau, en het in werking treden van het internationale verdrag inzake de bescherming van de Rijn tegen verontreiniging. Calamiteiten, zoals de endosulfanramp in 1969 en de Sandoz-ramp in 1986 zorgden voor politieke reveilles die nodig waren om te komen tot een herstel van de integriteit van de Rijn en de Maas. De resultaten van activiteiten op het gebied van waterkwaliteitsverbeteringen begonnen zichtbaar te worden in de tweede helft van de 1970er jaren. De internationale herstelprogramma's voor de Rijn en de Maas, die gelanceerd werden in respectievelijk 1987 en 1997, richtten zich niet alleen op een verdere verbetering van de waterkwaliteit, maar ook op het herstel van typische rivierbiotopen die, als gevolg van normalisatie en kanalisatie, verloren waren gegaan. Realisatie van dergelijke biotopen werd voornamelijk gerealiseerd door middel van de aanleg van nevengeulen. Hiermee werd tevens zowel de laterale als de longitudinale connectiviteit binnen de overgebleven vloedvlakte verbeterd. De onderzoeksresultaten zoals die in dit proefschrift zijn beschreven hebben vooral betrekking op de periode waarin een sterke verbetering van de waterkwaliteit optrad en waarin een begin werd gemaakt met natuurontwikkeling in de uiterwaarden van de Rijn en de Maas.

In hoofdstuk 2 worden veranderingen beschreven binnen de levensgemeenschap van ongewervelde dieren op stenen in de oeverzone van de IJssel in de periode 1975-1991. Ongewervelde dieren vormen een goede indicator voor de waterkwaliteit in stromende wateren. De soortenrijkdom is hierbij een belangrijk aspect. Deze is relatief groot in levensgemeenschappen op harde substraten, zoals stenen in de oeverzone (vaak aanwezig

als oeverbescherming of ter verdediging van kribben). De waargenomen toename in de soortenrijkdom en in de dichtheid van de betreffende levensgemeenschap in de IJssel werd geacht uitsluitend het resultaat te zijn van een verbetering van de waterkwaliteit. Echter uit latere studies bleek dat veranderingen na 1991 vooral te danken waren aan de kolonisatie van deze Rijntak door achtereenvolgens de slijkgarnaal *Chelicorophium curvispinum* en de vlokreeft *Dikerogammarus villosus*, twee allochtone soorten uit het Ponto-Kaspische gebied.

In hoofdstuk 3 is een reconstructie gemaakt van de levensgemeenschap van ongewervelde dieren in de belangrijkste biotopen in de Grensmaas, het gedeelte van de Maas dat de grens vormt tussen België en Nederland. Deze reconstructie was voornamelijk gebaseerd op ongepubliceerde resultaten (alleen in rapporten beschikbaar) van onderzoek uit de periode 1981-1990 en diende als referentie om de resultaten van te verwachten grootschalige ingrepen in dat riviertraject te kunnen evalueren. Het betreft een combinatie van grindwinning en natuurontwikkeling waarvoor uiteindelijk in 2002 een milieu-effect rapportage van start is gegaan. Van 51 taxa kon met zekerheid worden vastgesteld dat ze in de genoemde periode in de Grensmaas leefden: 31 taxa op stenen in de oeverzone, 38 taxa op of in de ondiepe bodem van het onbevaarbare gedeelte en 20 taxa op of in de diepere bodem van het bevaarbare deel.

Hoofdstuk 4 heeft betrekking op de indicatorfunctie die ongewervelde dieren hebben in stromende wateren. De structuur van een levensgemeenschap van benthische soorten is daarbij een belangrijk aspect. Verschillende eigenschappen maken ongewervelde dieren bijzonder geschikt om informatie over het voorkomen ervan te gebruiken in beoordelingsmethoden. Zo komen ze in het algemeen in voldoende hoge dichtheden voor om te kunnen volstaan met relatief eenvoudige bemonsteringsmethoden, ze zijn plaatsgebonden, hebben een generatieduur van geschikte lengte en reageren relatief snel op verschillende typen van antropogene stress. Daarnaast is de diversiteit in ongestoorde stromende wateren relatief hoog en is een scala aan bemonsteringsmethoden beschikbaar. Geschikte manieren om, op basis van de samenstelling van levensgemeenschappen in bemonsterde biotopen, een algemene maat te construeren voor de mate van de milieuvervuiling of voor de ecologische status lijken echter beperkt.
In hoofdstuk 4 is de bruikbaarheid getest van de ITC (Index of Trophic Completeness). Deze index is gebaseerd op het onderscheid van trofische relaties binnen een biocoenose. Soorten van ongewervelde dieren met dezelfde trofische relatie vormen een gilde. Alle onderscheiden gilden horen per definitie in een ongestoorde levensgemeenschap aanwezig te zijn. Verstoring van de levensgemeenschap leidt tot een afname van het aantal aanwezige gilden. De index scoort niet op de aan- of afwezigheid van individuele soorten die voor specifieke verstoringen indicatief zijn. Allochtone soorten worden echter op gelijke wijze meegenomen in de beoordeling als de autochtone soorten. Belangrijk is tevens dat de toepassing van de index zich niet behoeft te beperken tot bepaalde geografische regio's.
De bruikbaarheid van de ITC werd vastgesteld door deze toe te passen op gegevens die zijn verzameld in rivieren met verschillende vormen van antropogene druk in een aantal geografische regio's. Omdat de ITC alleen een graadmeter is voor het functioneren van een

levensgemeenschap is het, in een beoordelingsmethodiek, noodzakelijk de index te combineren met graadmeters die ook andere aspecten van de levensgemeenschap belichten. De territoriumuitbreiding in westelijke richting van een 22-tal allochtone soorten van ongewervelde dieren uit het Ponto-Kaspische gebied is beschreven in hoofdstuk 5. Ingegaan wordt op de routes die deze dieren gevolgd hebben en wat de mechanismen achter de verspreiding waren. Dit om te kunnen inschatten in hoeverre migratie buiten Europa verwacht kan worden.

De Rijn en de Maas staan model voor West-Europese rivieren waarin de verslechtering van het milieu, gevolgd door een ecologisch herstel, geleid heeft tot de invasie van een groot aantal allochtone diersoorten die de terugkeer van levensgemeenschappen horende bij ongestoorde situaties onmogelijk maken. Invasies in beide rivieren vonden voornamelijk onbedoeld plaats via ballastwater afkomstig uit zeegaande schepen, via kanalen die stroomgebieden met elkaar verbinden en met vissoorten die opzettelijk vanuit andere stroomgebieden werden uitgezet. Een relatief groot aantal vissoorten werd daarnaast overigens bewust geïntroduceerd. Voor de gebiedsuitbreiding van de Ponto-Kaspische soorten was vooral belangrijk de aanleg van een netwerk van kanalen in Europa gedurende de afgelopen twee eeuwen, als gevolg van industriële en economische activiteiten. De nieuwe verbinding tussen de stroomgebieden van de Rijn en de Donau, het Main-Donaukanaal dat in 1992 werd geopend, is tegenwoordig de belangrijkste route voor deze dieren om Nederland te kunnen bereiken. Een aantal soorten zorgde voor sterke veranderingen in levensgemeenschappen in de Rijndelta. Een belangrijke les die uit onderzoek getrokken kan worden is dat Ponto-Kaspische soorten buiten hun verspreidingsgebied een sterke verandering in hun invloed of gedrag vertonen zoals *Chelicorophium curvispinum* en *Dikerogammarus villosus* in de Rijn en *Dreissena polymorpha* (driehoeksmossel) in Noord-Amerika. *D. villosus* bijvoorbeeld vertoont een uitgesproken carnivoor gedrag in de Rijn, terwijl het in de Donau vooral een omnivore soort is. Verandering van het gedrag in nieuw gekoloniseerde gebieden maakt het moeilijk in te schatten wat het effect van invasies zal zijn op de aanwezige levensgemeenschappen.

Hoofdstuk 6 heeft betrekking op een van de best onderzochte indringers van Ponto-Kaspische komaf, de driehoeksmossel (*D. polymorpha*). Deze soort werd in 1827 al in Nederland aangetroffen. Vrij snel na de afsluiting van de Zuiderzee in 1932, toen het gebied veranderde in een zoet binnenmeer genaamd IJsselmeer, begon de kolonisatie van het gebied vanuit het oostelijk deel, waar zich voor de afsluiting van de Zuiderzee al een bescheiden populatie kon handhaven. Het IJsselmeergebied werd een belangrijk overwinteringsgebied voor duikeenden zoals de kuifeend (*Aythya fuligula*), tafeleend (*A. ferina*), toppereend (*A. marila*) en brilduiker (*Bucephala clangula*) omdat de driehoeksmosselen in het gebied de voornaamste voedselbron vormden in die periode. Uit het onderzoek naar de verspreiding van de driehoeksmossel in het IJsselmeergebied bleek dat deze substraat gelimiteerd was. Dat komt omdat de dieren zich moeten vasthechten op harde voorwerpen die niet overal in dezelfde mate op de bodem aanwezig waren. De groeisnelheid, uitgedrukt in lengtetoename van de schelp en toename van het vleesgewicht, werd vergeleken met die van driehoeksmosselen uit het Mazurische

merengebied. De resultaten van het onderzoek vormden naderhand een belangrijke bron van informatie in haalbaarheidstudies voor de toepassing van driehoeksmosselen in actief biologisch beheer.

In hoofdstuk 7 zijn de resultaten samengevat van een onderzoek naar de migratie van de zeeforel (*Salmo trutta*) door de Rijndelta en de benedenloop van de Maas. Dit onderzoek hangt nauw samen met de rekolonisatie van deze rivieren door vissen die op zee opgroeien, maar het zoete water nodig hebben om te paaien. Het betreft de groep van de anadrome vissoorten, waartoe niet alleen de zeeforel, maar ook de Atlantische zalm (*Salmo salar*) behoort. Het onderzoek werd uitgevoerd in het kader van het internationale herstelprogramma voor de Rijn dat in 1987 werd gelanceerd en o.a. tot doel had een permanente terugkeer te bewerkstelligen van de Rijnzalm, een subpopulatie van de Atlantische zalm die in de eerste helft van de 20ste eeuw uit de Rijn was verdwenen. Belangrijkste oorzaken voor het verdwijnen van de Rijnzalm waren: de verstuwing van de zijrivieren waardoor paaiplaatsen onbereikbaar werden, verslechtering van de waterkwaliteit en het verslibben van de paaibedden. Bovendien werd de intrek van anadrome vissen vanuit zee sterk gehinderd door de aanleg van dammen in de mondingen van de rivier (o.a. de Afsluitdijk en de Haringvlietdam). Omdat de Atlantische zalm niet paait in de benedenloop van de Rijn, richtte de Nederlandse bijdrage aan het herintroductieprogramma zich op de verbetering van zowel de intrekmogelijkheden vanuit zee als de doortrek via de delta. Om een beeld te krijgen van potentiële migratieroutes van de Atlantische zalm door Nederland werd met behulp van telemetrie de trek bestudeerd van zeeforellen die in de kustzone waren gemerkt. Gekozen werd voor de zeeforel als representatief "proefdier" omdat die nauw verwant is aan de Atlantische zalm en in voldoende aantallen de Rijn binnentrekt. Intrek werd waargenomen via de uitwateringssluizen in de Afsluitdijk en de Haringvlietdam en via de Nieuwe Waterweg. De belangrijkste stroomopwaartse migratieroute werd gevormd door: Nieuwe Waterweg → Oude Maas → Dordtsche Kil → Beneden Merwede → Waal. Verschillen in stroomsnelheid bij splitsingspunten in het benedenrivierengebied bleken een belangrijke factor in de keuze van het te volgen traject. De perioden juni-juli bleek jaarlijks de belangrijkste intrekperiode te zijn, gevolgd door de periode oktober-november. Tevens bleek uit het onderzoek dat de kustzone voor de Haringvlietdam, de buitendelta, een gebied is waar zeeforellen zich verzamelen. Ze worden aangetrokken door het zoete water dat vanuit het Haringvliet wordt gespuid, maar ze zijn niet bij machte de Haringvlietdam te passeren. Het spuibeheer van de Haringvlietsluizen zou daarom in de belangrijkste trekperioden gericht moeten zijn op een verbetering van de intrek van anadrome vissen, terwijl de rivierbeheerder de verkregen kennis over de migratieroutes dient te integreren in plannen voor het ecologische herstel van de grote rivieren. Op die manier wordt bijgedragen aan de terugkeer van een zichzelf instandhoudende populatie van de Atlantische zalm in de Rijn en mogelijk ook in de Maas.

In hoofdstuk 8 worden tenslotte de eindpunten van rivierherstel bediscussieerd. Geconstateerd werd dat in onze huidige samenleving de rivieren zoveel functies hebben dat ecologisch rivierherstel of natuurontwikkeling slechts mogelijk is in de uiterwaarden en dus

niet in het zomerbed. In feite werd de weg terug naar een ongestoorde situatie al ongeveer 10 eeuwen geleden geblokkeerd toen de bewoners van de Rijndelta begonnen met het opwerpen van dijken om zich te beschermen tegen overstromingen. Maar stel dat er een weg terug zou zijn, dan nog zullen op soortsniveau de levensgemeenschappen van 10 eeuwen geleden niet meer kunnen terugkeren. Niet alleen vanwege het relatief grote aantal allochtone soorten dat zich inmiddels blijvend in de Rijn en de Maas heeft gevestigd, maar ook vanwege stochastische processen die van invloed zijn bij de vorming van levensgemeenschappen.

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Timur Pavluk, you realised that the functioning of macroinvertebrates on a number of trophic levels is an important determinant of ecosystem health. During our co-operation you were able to work out your ideas of an index based on the trophic relations between macroinvertebrates within a benthic community. In the Ural mountain streams we were able to test the index. The trips to these streams belong to my best memories on practical river ecology, and Russian hospitality. I also would like to acknowledge the assistance of your co-workers in the fieldwork and in the identification of the macroinvertebrates.

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Om een beeld te krijgen van de verspreiding en de populatiedynamica van de driehoeksmossel in het IJsselmeergebied moest, gezien de omvang van het gebied, heel wat werk worden verzet, Hierbij werd niet op een uurtje gekeken ook al dreigde het soms laat te worden vanwege de lange terugreis die met de onderzoeksvaartuigen moest worden afgelegd. Een woord van dank aan de van bemanningen van de onderzoeksvaartuigen Flevo (gezagvoerder De Haan), De Blocq van Kuffeler (gezagvoerder Van der Meer), Flevomeer (gezagvoerder Bakkus), Markermeer (gezagvoerder De Ronde), Noord-Holland (gezagvoerder Witten) en Elise (gezagvoerder Burggraaff), voor hun enthousiaste inzet tijdens de bemonsteringsreizen, ook als het weer wat minder goed was, is hier dan ook zeker op z'n plaats. In dit verband moeten ook Cees Berkeveld en zijn medewerkers worden genoemd die zorgden voor de logistieke ondersteuning en de planning van de onderzoeksvaartuigen. Om de verspreiding van de mosselen in kaart te kunnen brengen hebben we in 1981 naar schatting 5.000 bodemmonsters genomen en aan boord uitgespoeld. Jan Muller heeft er daarvan minstens 1.500 voor zijn rekening genomen. Wolter Eenkhoorn droeg zijn steentje bij aan de dataverwerking, terwijl Jaap Bottenberg met zijn medewerkers een belangrijk deel van de biomassabepalingen voor hun rekening namen.

Als het gaat om telemetrisch onderzoek naar het migratiegedrag van de zeeforel moet ik in de eerste plaats André Breukelaar in het bijzonder bedanken voor zijn onvermoeide inzet om de detectiestations te realiseren en in de lucht te houden. In het project was jij mijn rechterhand en wellicht daardoor is het een van de leukste onderzoeksprojecten geworden die ik ooit uitgevoerd heb. Maar dat kwam natuurlijk ook door de speciale techniek die we konden toepassen, hoofdzakelijk ontwikkeld door Koos Fockens. Als motor achter die ontwikkeling fungeerden Jan Hogen Esch, Kim Sun en Gerben Slob. De directie van de Nedap dank ik hartelijk voor het feit dat op basis van "no cure no pay" de ontwikkeling van het detectiesysteem mogelijk werd gemaakt. Velen zijn betrokken geweest bij de voorbereidingen en het daadwerkelijke onderzoek. Herman Sips deed een vooronderzoek naar de mogelijkheden van telemetrisch onderzoek. De Meetkundige Dienst van

CURRICULUM VITAE

Abraham bij de Vaate werd op 6 september 1945 geboren in Zierikzee. Na het doorlopen van de MULO trad hij op 13 mei 1963 als leerling-analist in dienst van de kunstzijdespinnerij "Nyma" te Nijmegen. Na een aantal jaren werkzaam te zijn geweest op het waterleidinglaboratorium van de Openbare Nutsbedrijven in diezelfde plaats trad hij in 1968 als analist in dienst van het Rijksinstituut voor de Volksgezondheid in Bilthoven waar hij onderzoek verrichtte naar mogelijkheden voor het kweken van mens-pathogene virussen in continuculturen ten behoeve van de bereiding van vaccins.

De kans om aquatisch ecologisch onderzoek te gaan verrichten werd met beide handen aangegrepen toen hij in 1970 in dienst trad bij de Rijksdienst voor de IJsselmeerpolders te Lelystad. Door middel van diverse vakopleidingen bekwaamde hij zich vervolgens in diverse aspecten van de aquatische ecologie. In de periode 1980-1986 was hij als werkgroepleider actief binnen de werkgemeenschap "Aquatische Oecologie" van het BION. Van deze werkgemeenschap was hij in de periode 1983-1986 tevens bestuurslid. In 1986 maakte hij de overstap naar zijn huidige werkgever, het Rijksinstituut voor Integraal Zoetwaterbeheer & Afvalwaterbehandeling (RIZA) in Lelystad, waar hij projectleider werd voor aquatisch ecologisch onderzoek in de grote rivieren, een baan die hij nog steeds met alle plezier uitvoert. Van 1996-2003 was hij bestuurslid van de Nederlandse Malacologische Vereniging.

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