Impact of hydrology on floodplain lake ecosystems along the lower Rhine and Meuse

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IMPACT OF HYDROLOGY ON FLOODPLAIN LAKE ECOSYSTEMS ALONG THE LOWER RHINE AND MEUSE

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Voorwoord

Overstromingen zijn ín, getuige de gebeurtenissen in de VS, waar vorig jaar de Mississippi op grote schaal buiten haar oevers trad, terwijl rond de jaarswisseling de Maas in Limburg voor soortgelijke problemen zorgde. Dit pleit voor de actualiteit van het proefschrift dat nu voor u ligt. Het bevat de voornaamste resultaten van het onderzoek dat ik de afgelopen jaren verricht heb, geconcentreerd rond het thema: "Invloed van overstromingen op uiterwaardplassen langs de Rijn en Maas". Dit onderzoek werd gefinancierd door Rijkswaterstaat-RIZA (1987-1990) en door het Sandoz Rijnfonds (1990-1994).

Aanleiding voor dit onderzoek was de toenemende belangstelling voor grote riviersystemen en hun overstromingsvlakten, die overal ter wereld sterk door menselijke aktiviteiten onder druk staan. In eigen land was de sanering van de Rijn en Maas vanaf de 70-er jaren op gang gekomen en in eerste instantie gericht op verbetering van de waterkwaliteit in de stroomgeul. Pas later begon het besef door te dringen dat riviersystemen meer omvatten dan louter de stroomgeul en werd de aandacht ook gevestigd op de uiterwaarden en de rivierbegeleidende wateren hierin. Het ecologisch herstel van de Nederlandse grote rivieren kwam in een stroomversnelling na de brand bij Sandoz in 1986, die de aanleiding was voor het Rijn Aktie Programma. In het kader van dit programma werd onderzoek geïnitieerd door Rijkswaterstaat-RIZA en de afdeling Aquatische Oecologie van de KUN om de oecologische betekenis van de rivierbegeleidende plassen te achterhalen in relatie tot de rivierdynamiek. Tijdens de afronding van dit onderzoek bleken er nog tal van vragen onbeantwoord. Door subsidie uit het Sandoz-Rijnfonds kon het project een vervolg krijgen en werden diverse vragen verder uitgediept. Gelijkertijd ontstond het idee om de belangrijkste onderzoeksgegevens uit beide projecten tot één geheel in een proefschrift samen te smeden.

Het moge duidelijk zijn dat dit proefschrift – en met name het onderzoek dat eraan ten grondslag ligt – nooit het resultaat van één persoon kan zijn. Verschillende personen hebben mij met raad en daad bijgestaan. Op de eerste plaats zijn dit mijn ouders, die mijn belangstelling voor de natuur altijd gestimuleerd hebben. Aan hen draag ik dit proefschrift op.

Mijn beide promotoren, Prof. Dr. C den Hartog en Prof. Dr. G van der Velde, bedank ik hier voor het in mij gestelde vertrouwen en voor de snelheid waarmee zij al mijn manuscripten van kritische kanttekeningen voorzien hebben. Gerard van der Velde wil ik hier speciaal bedanken voor de ruimte en de vrijheid die ik kreeg om mijn eigen ideeën te verwezenlijken, zijn deskundige inbreng op het brede onderzoeksterrein, en voor zijn gezelschap tijdens buitenlandse symposia.

Mijn collega's en ex-collega's van de Vakgroep Oecologie, en met name die van de werkgroepen Aquatische Oecologie en Milieubiologie, bedank ik voor de plezierige sfeer en de stimulerende discussies.

Medewerkers van Rijkswaterstaat-RIZA te Lelystad bedank ik voor de plezierige samenwerking. Hierbij wil ik Eric Marteijn en Bram bij de Vaate speciaal noemen voor hun begeleiding van het Ecostag-projekt en het constructieve overleg, ook na de Ecostag-periode. Eric Marteijn wil ik tevens bedanken voor de bijdrage van het RIZA in de drukkosten van dit proefschrift.

Aan mijn ouders
Voor Cecile, Eline en Katharina

...Water that was formerly allowed to spread over many thousand square miles of low lands is becoming more and more confined to the immediate channel of the river, and is, therefore, compelled to rise higher and flow faster...

Charles Ellet, civil engineer (1853)

VIII

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CHAPTER 1

General introduction

Impact of hydrology on floodplain lake ecosystems along the Lower Rhine and Meuse: a general introduction

River ecosystems: a holistic perspective

Rivers play an important part in the global water cycle through the transport of runoff water, via surface and subsurface routes, from the continents to the sea. River discharge typically varies during the annual cycle and from year to year. At low water levels, rivers flow in well-defined channels, but at high discharge rates, wide floodplains are recurrently inundated, illustrating that river ecosystems are more than the sum of their lotic components: the main and side channels. In fact, for a holistic approach, river ecosystems should be considered in four dimensions (Fig. 1): the longitudinal dimension, the lateral or transversal dimension, the vertical dimension and the temporal dimension (Amoros et al., 1987a; Junk et al., 1989; Ward, 1989; Smock et al., 1992).
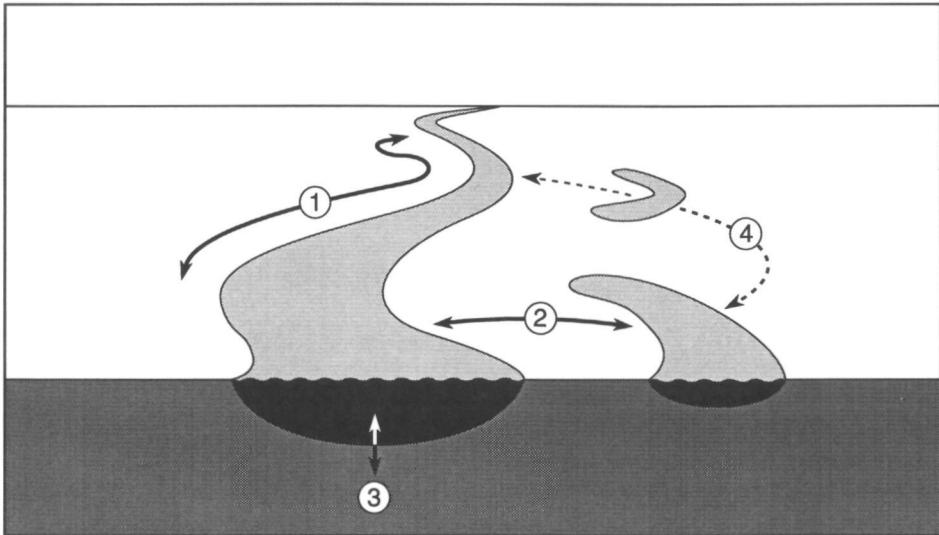
Figure 1. *Schematic view of spatio-temporal dimensions within a river-floodplain system. 1 = longitudinal dimension (upstream-downstream); 2 = transversal dimension (stream-floodplain); 3 = vertical dimension (surface water-groundwater); 4 = temporal dimension; normal line = spatial scales; broken line = time scale.*

Longitudinal dimension

Considerable attention has been paid to longitudinal zonation patterns in biological communities and abiotic parameters in streams. Along the longitudinal dimension rivers are usually classified into three main zones: the crenon (spring region), the rithron (highland brooks) and the potamon (lowland courses) (Illies, 1961). Macroinvertebrate, fish and riparian bird communities may show clear zonation patterns along the longitudinal axis of large rivers (Huet, 1949; Illies, 1961; Rochét and Frochot, 1993). Important abiotic criteria underlying these zonation patterns are annual temperature profiles, current velocities and available substrates (Hawkes, 1975). This idea of a distinct zonation pattern evolved into one which assumed a more gradual and continuous zonation: the River Continuum Concept (RCC) (Vannote et al., 1980). According to this theoretical concept, which was based on small temperate streams and extrapolated to rivers in general, there exists a continuous gradient of physical conditions from the headwater(s) to the mouth of a river. The biological communities of a given river reach are adjusted to the dynamic physical conditions of that reach, so that these form a continuum of species replacements. The input of energy, organic matter transport and storage, and use by macroinvertebrate functional feeding groups is largely regulated by fluvial geomorphological processes. One of the major assumptions of the RCC is that downstream communities are fashioned to capitalize on upstream processing inefficiencies (Vannote et al., 1980). Later studies have made suggestions to clarify, expand and refine the concept (e.g. Cushing et al., 1983; Ward and Stanford, 1983; Bruns et al., 1984; Cummins et al., 1984; Townsend and Hildrew, 1984; Minshall et al., 1985; Naiman et al., 1987), or have found anomalies which appeared contradictory to the predictions of the RCC (e.g. Sedell and Froggatt, 1984; Statzner and Higler, 1985, 1986; Perry and Schaeffer, 1987; Junk et al., 1989; Sedell et al., 1989). Large river ecosystems in particular were found difficult to fit into the RCC, and comments on this concept stressed the importance of streamside forests, floodplain lakes and river-floodplain interactions for the structure and functioning of large river systems (Sedell and Frogatt, 1984; Triska, 1984; Junk et al., 1989; Sedell et al., 1989).

Lateral dimension

A characteristic component of large rivers is their floodplain area. The floodplain area includes a variety of biotopes, which range from aquatic to terrestrial, and from permanent to temporary, depending on hydrological, geomorphological and climatological circumstances. Hydrology has a clear impact on the permanence of these biotopes, mainly via floods and via percolation of river water through the floodplain sediment, and to a lesser degree via local atmospheric input and evaporation. Temporary and permanent floodplain waters can be regarded as aquatic biotopes. Temporary floodplain waters are small and shallow stagnant water bodies which carry water only for part of the year (Williams, 1987). They usually run dry during the season with low river discharges, which in temperate lowland regions is often the summer and autumn. Permanent floodplain waters carry water throughout the year, although their depths and sizes vary over the seasons, depending on the hydrological regime.
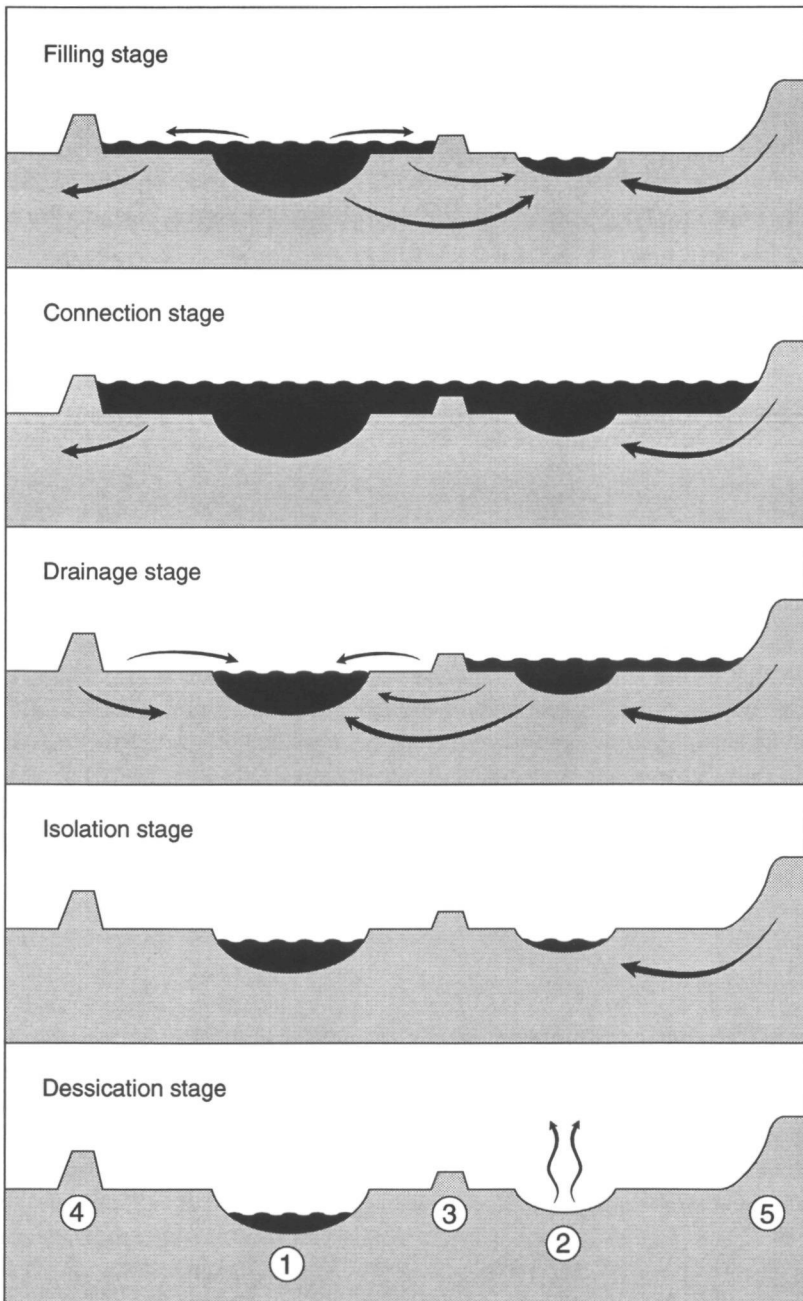
Figure 2. *Hydrological stages of a floodplain lake during a flood pulse. Arrows indicate directions of (ground)water flow.*
1 = stream bed; 2 = floodplain lake; 3 = low summer dike; 4 = main dike; 5 = moraine hill.

These hydrologically different types of water bodies may have distinct communities, because the running dry of temporary waters requires special biotic adaptations (Gladden and Smock, 1990; Neckles et al., 1990; Boulton and Lloyd, 1992; Smock et al., 1992). Hydrology exerts its impact on the floodplain lake communities by its direct physical influence on the water level and water volume, and by its indirect chemical influence on the water and sediment quality of the floodplain lakes. During a flood pulse, five hydrological stages can be distinguished, each with a different impact on the floodplain lake communities (Fig. 2):

a. the filling stage
As river water discharge increases, the water level of the floodplain lake rises and the lake volume increases, initially via percolation of ground water, later via floods. As a result the area of inundated littoral increases, which may affect the biota. Immobile terrestrial and semi-aquatic biota, such as terrestrial macrophytes and helophytes, are usually adapted to withstand partial submergence. Their tolerance against prolonged total submergence, however, varies with the species and depends on the depth, frequency, duration and season of the inundations (Blom et al., 1990; Brändle, 1991). Mobile aquatic and semi-aquatic biota, such as invertebrates, fish and birds, may migrate into the inundated areas for foraging and reproduction (Welcomme, 1979; Schiemer, 1985; Reimer, 1991; Schiemer and Zalewski, 1992).

b. the connection stage
At high water discharges, the water level in the river may reach and exceed the connection level, i.e., the level at which the lake water is connected with the main channel water. Depending on the proximity to the main channel and the lake morphology, throughflow of river water can take place. At this stage, exchange of water, chemicals, sediment, particulate organic matter and biota occurs between the main channel and its associated floodplain lake. During inundations dissolved nutrients (N and P) may enter the floodplain water bodies, which may function as nutrient sinks (Hamilton and Lewis, 1987; Forsberg et al., 1988; Pedrozo et al., 1992; Van den Brink et al., 1993e). Conversely, nutrient-laden sediments may be washed away to the channel by scouring during throughflow. Furthermore, the input of river water may lead to a dilution of ions in the floodplain lake water. Riverine fish may migrate into connected floodplain waters for reproduction, foraging and refuge during periods of high river discharge (Welcomme, 1979; Schiemer, 1985; Reimer, 1991; Schiemer et al., 1991; Schiemer and Zalewski, 1992). At falling water levels organic matter (plant material, phyto- and zooplankton, macroinvertebrates, juvenile fish) may be washed out of the floodplain and enter the foodwebs of the main channel (Eckblad et al., 1984; Hamilton and Lewis, 1987; Amoros and Roux, 1988; Van der Velde et al., 1990; Schiemer et al., 1991).

c. the drainage stage
At decreasing water discharge the water level in the floodplain lake falls and the lake volume decreases, initially via water flowing back directly to the channel and later via seepage out of the lake to the main channel. Direct exchange processes are inhibited again in disconnected lakes, and the inundated littoral area decreases.

d. the isolation stage

At low water discharges, the lake volume decreases further, until it becomes relatively stable in permanent lakes during hydrologically normal years. As the water level is stable, sedimentation of previously resuspended clay particles occurs. At this stage, the water chemistry of the lake becomes strongly divergent from that in the main channel. For example, nutrients generally become limited due to uptake by primary producers (Hamilton and Lewis, 1987). The running dry of the lake littoral stimulates the germination of some wetland plants (Keddy and Ellis, 1985; Brock et al., 1987). Furthermore, mineralization processes become accelerated at this stage, due to oxygenation of the sediment.

e. the desiccation stage

Depending on the climate and geomorphology the floodplain waters may run dry during the isolation stage. In semi-arid regions it is not only large floodplain lakes (billabongs), but entire river stretches which run empty during the dry season (Walker, 1986; Boulton and Lloyd, 1992). In the temperate belt, only the small temporary floodplain lakes run dry each year. The large permanent floodplain lakes along the Lower Rhine and Meuse run dry only during exceptionally dry and hot summers, when the lake volume decreases further through evaporation. Since river regulation has resulted in the floodplains of the Lower Rhine and Meuse being situated at relatively high levels above the stream bed, the lakes which have an open connection with the main channel simply empty themselves during years with very low river discharges. In response to this, fish and mobile invertebrates migrate to the channel. Running dry has enormous consequences for the biota, especially in the disconnected lakes. Aquatic macrophytes desiccate and may survive by means of generative and vegetative diaspores. Small invertebrates, such as cladocerans, may enter also a resting stage (Boulton and Lloyd, 1992). While the lake volume is decreasing fish and mussels become an easy prey for birds and mammals. When the lake runs dry fish and mussels become trapped and die. An invasion of semi-aquatic and terrestrial animals and vegetation occurs over the whole lake bottom in response to its drying up (Brock et al., 1987; Williams, 1987).

The duration of a flood pulse strongly depends on the river's hydrological regime, which in turn is influenced by climate, geomorphology and regulation efforts. For example, the 'pristine' tropical rivers Amazon, Paraná and Orinoco have predictable flood pulses of relatively long duration (Bonetto, 1986; Day and Davies, 1986; Junk et al., 1989). The regulated rivers Rhine and Meuse, which are situated in a temperate climatic belt, have less predictable flood pulses of relatively short duration. The largest flood pulses occur outside the growth season along these rivers, unlike the situation in the tropical rivers, which receive one major long-lasting flood pulse during and after the rainy season (Bonetto, 1986; Day and Davies, 1986). The predictability, season and extent of floodplain inundation influence the possibilities for the use of the floodplain by riverine species. In the Amazon River the regular flood pulses are essential for the survival of many fish species which are adapted to feed on fruits from trees on the floodplain. Such highly specialized adaptations are unknown for fish in European rivers, where floodplain inundation usually occurs in winter and spring, i.e., outside the growth

season. Fish which migrate to the inundated floodplains outside the growth season have been found to feed on terrestrial macroinvertebrates (Reimer, 1991).

The long-term average annual frequency, duration and extent of floodplain inundation may also vary within a particular river-floodplain ecosystem and depend on local geomorphological and hydrological conditions, provided by the presence of natural levees, dikes, sluices and dams, and on the horizontal distance between the lake and the main channel. In addition, the floodplain inundation frequency and duration depend on seasonal and year-to-year climatic variations (Amoros et al., 1987a; Amoros and Roux, 1988; Junk et al., 1989; Van den Brink, 1990; Van den Brink et al., 1993e).

Over the lateral dimension within a particular river stretch, the river's discharge regime influences the grain size of the sediment and the degree of siltation of the floodplain lake bottom via scouring floods, and hence also the possibilities for water exchange via seepage fluxes to and from the main channel. For example, cut-off channels, situated close to the main channel, sometimes still connected with the main channel at one end, are less silted up than the older, more isolated oxbow lakes, which have a thick sapropelium layer (Rostan et al., 1987). The amplitude of water-level fluctuations and the rate of filling in and running dry are therefore smallest in the 'isolated' oxbow lakes. Thus, hydrology forms a gradient over the lateral dimension of the floodplain and is recognized as the main environmental parameter influencing the aquatic as well as the semi-aquatic and 'terrestrial' communities (Amoros et al., 1987a; Junk et al., 1989; Blom et al., 1990; Van den Brink, 1990).

Floodplain waters along the Upper Rhône have been classified into four hydrological categories: eupotamon (large flowing waters: main stream and side channels), parapotamon (former channels, semi-stagnant waters, still connected with the main channel at the downstream end: dead arms and backwaters), plesio- and paleopotamon (stagnant waters connected with the main channel only during floods: cut-off channels and oxbow lakes). The plesio- and paleopotamon differ with respect to their geomorphological origin and their degree of connection with the main channel. The plesiopotamon includes abandoned braided channels, situated close to the main channel and thus frequently flooded. The paleopotamon includes abandoned anastomosed and meander channels, situated at a greater distance from the main channel and thus rarely flooded (Amoros et al., 1987a).

Interactions along the lateral dimension include active and passive transport of organisms, and exchanges of nutrients and organic matter between the channel and its floodplain (Ward, 1989). Initially, the importance of floodplain vegetation for the input of organic matter (energy) was recognized for small streams only (e.g. Kaushik and Hynes, 1971; Cummins, 1974; Vannote et al., 1980). Human activities in the past, such as the removal of trees from the stream bed (snagging), dredging, diking and regulation have changed the original vegetation and have reduced the original floodplain area of many rivers (Sedell and Frogatt, 1984; Triska, 1984; Sedell et al., 1989; Ward, 1989), thereby reducing the level of organic matter input into the channel. However, under pristine circumstances large rivers generally have extended floodplains that contribute significantly to the production of main channel biota (Junk et al., 1989).

Seasonally inundated floodplains constitute large aquatic-terrestrial transition zones, or ecotones, which border alluvial rivers. Along the borders of the relatively pristine tropical rivers these ecotones may extend for 10 km or more on either side of the channel. Habitat diversity within such land-water ecotones is related to the regular and repeated rejuvenation of successions associated with disturbance caused by floods. The biodiversity within these ecotones can therefore be very rich (Naiman and Décamps, 1990). Along the upper Amazon River channel dynamics were found to play a major role in creating and maintaining high biological diversity within the ecotone (Salo et al., 1986; Salo, 1990).

Based on research in pristine large rivers in South and North America (e.g. Amazon, Upper Mississippi) Junk et al. (1989) formulated the Flood Pulse Concept (FPC) as a complementary concept to the RCC in order to explain the relationships between the biota and the environment of an unmodified, large river-floodplain system. According to the FPC, the flood pulse is the principal driving force for the existence, productivity, and interactions of the major biota in river-floodplain systems. The predictability and duration of the flood pulse creates possibilities for biotic adaptations and strategies for efficiently using the floodplain area, resulting in a high biotic diversity. The flood pulse is associated with a 'moving littoral' throughout the floodplain. As this 'moving littoral' prevents prolonged stagnation and allows rapid recycling of organic matter, a high productivity in active floodplain areas is to be expected (Junk et al., 1989). It has been emphasized that the FPC is distinct from concepts that stress the continuous processes in flowing water, such as the RCC, since the flood pulse is a discontinuous process. Furthermore, floodplains do not depend on upstream inefficiencies of organic matter processing and the position of a floodplain within the river network is not a primary determinant of the processes that occur (Junk et al., 1989).

Vertical dimension

The exchange area between the river channel and its hyporheic zone, the area of groundwater beneath the streambed, encompasses the vertical dimension, which may include a lateral component (Stanford and Ward, 1988; Williams, 1989). The hyporheic zone functions as a refuge for benthic macroinvertebrates from disturbances such as spates and droughts (Strommer and Smock, 1989; Griffith and Perry, 1993), but it may harbour a distinct community of groundwater animals too (Danielopol, 1989). Exchanges of water, organic matter, and organisms between the superficial and subterranean habitats are dependent on the grain size of the sediment, together with the degree and nature of substrate siltation, which in turn depends on the geomorphology of the floodplain. The functioning of the hyporheic zone is therefore related to the longitudinal zonation, since the sediment grain size of the river bed of upstream zones varies from large stones and gravel to coarse sand, whereas that of downstream zones varies from coarse sand to fine sand and clay. The functioning of the hyporheic zone is also related to the lateral dimension of the floodplain. For example, the accumulation of silt and organic matter in isolated oxbow lakes impedes the exchanges between the surface and the groundwater. On the other hand, when a cut-off former meander is connected with the main

channel again at both ends, the exchanges are enhanced, because the fine sediments are flushed away and the superficial water is reconnected to the interstitial water (Amoros et al., 1987a).

Temporal dimension

Both natural evolution and human impact are major determinants of the present status of river ecosystems (Bravard et al., 1986). The present geomorphology of a river is therefore clearly related to its historical development. Within the ecological successions, the life span of pioneer and transient stages may be several years or decades. Hydro- and morphodynamics, water chemistry, population dynamics, competition and grazing all have their influence on the time scale of the ecological successions. Moreover, these ecological successions may be impeded or reversed under human impact (Amoros et al., 1987b).

Study area: The Lower Rhine and Meuse

The River Rhine originates in the Swiss Alps from two sources, Lake Toma (altitude 2344 m a.s.l.) and the Paradies Glacier (altitude 2216 m a.s.l.), and flows through Switzerland, France, Germany and the Netherlands. In the Netherlands the river divides into three branches: the river Waal/Merwede, which is the main branch, discharging 65% of the Rhine water; the river Nederrijn/Lek which discharges about 21%, and the river IJssel, which discharges only 14%. The river Meuse originates in France near Pouilly-Bassigny on the Plateau de Langres (altitude 410 m a.s.l.) and flows through France, Belgium and the Netherlands. In the Netherlands the rivers Rhine and Meuse enter a lowland area, where they form a river delta before they flow into the North Sea. An essential difference between the rivers Rhine and Meuse is their water source: the river Rhine is a combined glacier-rainwater river, whereas the river Meuse is fed by rainwater only. As a result the Rhine has a more stable discharge pattern over the seasons. However, the flooding regime of both rivers is generally rather similar, with highest river discharges normally occurring in winter and spring, and lowest discharges in autumn. Hydrological characteristics of both rivers are presented in table 1.

Table 1. *Hydrological characteristics of the rivers Rhine and Meuse (Data from RIZA, the Netherlands).*

	Rhine	Meuse
Total drainage area (km^2)	185,000	33,000
Total length (km)	1,250	890
Length in the Netherlands (km)	385	251
Mean discharge ($m^3 s^{-1}$)	2,200 (a)	250 (b)
Extremes of discharge ($m^3 s^{-1}$)	600–13,000 (a)	2–3,000 (b)

Discharges values over 1901-1985, measured at (a) Lobith and (b) Eijsden, the Netherlands.

Table 2. *Total number of (semi-)stagnant water bodies within the floodplains of the Lower Rhine and Meuse in the Netherlands, categorized by geomorphological water type (Smits, 1989).*

	Lower Rhine	Meuse
Cut-off channels/oxbow lakes	108	30
Break-through lakes	31	16
Clay-pit lakes	78	6
Sand- and gravel-pit lakes	98	65

Floodplains of the alluvial rivers Rhine and Meuse in the Netherlands harbour several hundreds of relatively large water bodies (1-200 ha), which have originated from spontaneous diversions of the streams (former meanders, silted-up side channels, oxbow lakes), from dike bursts in the past (break-through lakes, the so-called 'wielen'), and more recently from gravel, sand and clay extraction (gravel-, sand- and clay-pit lakes) (Table 2).

Apart from these relatively large permanent water bodies there are also many small temporary waters. Depending on geomorphological and hydrological circumstances, floodplain waters are subject to different inundation regimes. Normally, the Dutch floodplain lakes are inundated during winter and spring, i.e. outside the vegetation season, although the incidence of summer spates has increased over the last decades (Brock et al., 1987). Floodplain lakes along the Lower Rhine and Meuse become isolated from the river during the summer and autumn, except for those which have a permanent open connection with the main channel. In addition to these lakes, which are situated in the 'active' floodplain, there are many lakes situated behind the main dike, in the 'ancient' floodplain. The latter lakes are influenced by the river via seepage only during high water levels in the main channel (Fig. 3).

Present state and historical changes

Running waters have been used as natural discharge routes for sewage since ancient times. Evidence of early (organic) pollution can be found in the following quotation (Velsen, 1768):

'Our people have always been utterly indifferent to a vital part of this country, the rivers. We used them and abused them as we pleased, without any supervision whatsoever. If the rivers were to die tomorrow not a soul would care or be grieved. Instead of worshipping them as gods or saints, we treat them as sewers, in which anyone may freely dispose of his wastes. This is what has caused their abominable state.'

The present water quality of the main channels of the Lower Rhine and Meuse differs considerably from the original situation (Table 3), with increased levels of nutrients (nitrate and phosphate), salts (chloride, sodium, sulphate) and heavy metals (cadmium, mercury, lead, zinc) (Zuurdeeg, 1980; Van der Weijden and Middelburg, 1989; Van der Velde et al., 1991; Van den Brink et al., 1991a, 1993b). The water is also contaminated with an increasing
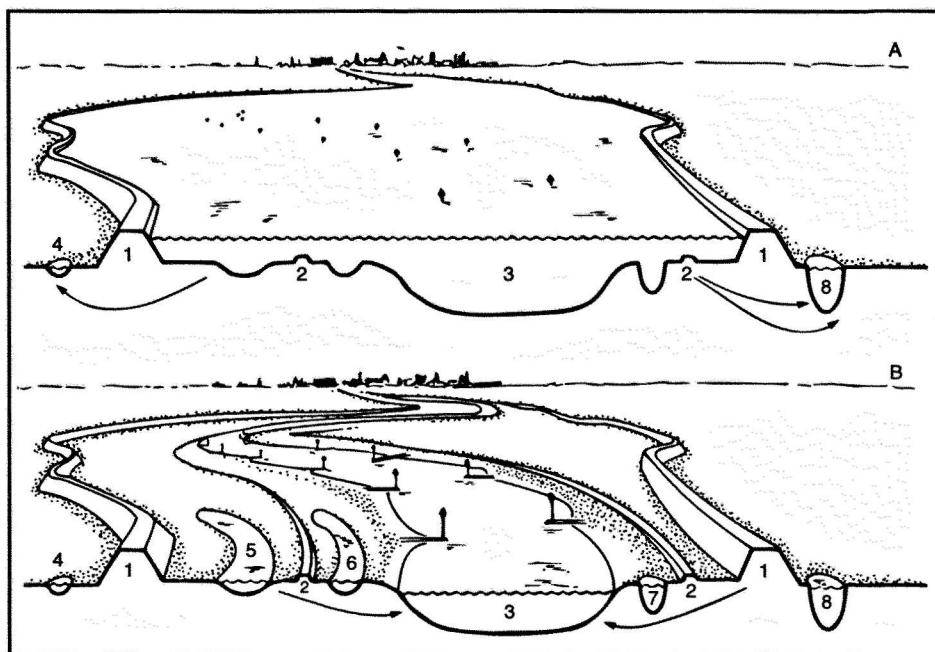
Figure 3. *Schematic view of the floodplain waters within the regulated Lower Rhine and Meuse rivers, during winter (A) and summer (B).*
1 = main dikes; 2 = summer dikes; 3 = river bed; 4, 8 = lakes protected against floods by main dike; 5 = lake protected by summer dikes or river levees; 6, 7 = unprotected lakes; 4-6 = shallow lakes; 7, 8 = deep lakes. Arrows indicate directions of groundwater fluxes.

amount of system-foreign compounds, organic micropollutants, such as PCB's, PAH's, insecticides and herbicides (Freudenthal, 1988). The Lower Rhine and Meuse are the most polluted stretches of the rivers Rhine and Meuse, because they are situated at the 'end of the pipe'.

Water quality was very poor in the 1960s-1970s, when pollution was high and oxygen levels were extremely low (Table 3). After the introduction of sewage purification plants, the oxygen levels increased again to normal levels in the Lower Rhine. The river Meuse still suffers from low oxygen levels during low water discharges in summer. The levels of ammonium have decreased again, but levels of nitrate have increased at the same time, due to an improved microbial activity in response to a reduction of the toxicity of the river water (Admiraal and Botermans, 1989). The increased sodium chloride levels in the Lower Rhine and Meuse have changed the relative ionic composition of both rivers (Fig. 4). At present, the water of the Lower Rhine is dominated by sodium chloride, instead of calcium bicarbonate, which was the original situation in this river and which is the global average situation (Webb and Walling, 1992). Although the levels of several heavy metals and organic micropollutants in the surface water of both rivers have been reduced over the last decades, the sediments of depositional areas in the main channels (Biesbosch, Haringvliet, Nieuwe Waterweg, Ketel-

Table 3. *Water quality parameters of the Lower Rhine and Meuse over the years. Annual means of at least weekly measurements are presented for 1971 and 1991 (Data from RIZA, RIWA, The Netherlands); historical data include measurements and calculations of natural background values in addition to historical water analysis (Zuurdeeg, 1980; Van der Weijden and Middelburg, 1989).*

		Lower Rhine (a)			Meuse (b)		
		<1900	1971	1991	<1900	1971	1991
Temp.	°C	10.9	13.3	14.0	<10	14.3	14.5
O_2	mg l^{-1}	-	4.4	10.2	-	8.5	7.4
pH	-	-	7.4	7.8	7.5	7.8	7.5
HCO_3	mg l^{-1}	160	157	167	172	-	185
Cl	mg l^{-1}	13	236	201	15	45	62
SO_4	mg l^{-1}	35	75	78	28	70	52
Na	mg l^{-1}	5	-	103	7	-	36
K	mg l^{-1}	5	-	7	4	-	4
Ca	mg l^{-1}	50	-	89	59	-	79
Mg	mg l^{-1}	10	-	12	6	-	8
NO_3	mg l^{-1}	0.3	2.5	3.9	-	1.9	2.7
NH_4	mg l^{-1}	0.2	2.9	0.4	-	1.6	0.7
PO_4	mg l^{-1}	0.05	0.30	0.08	0.07	0.67	0.37
t-P	mg l^{-1}	0.15	0.95	0.27	0.22	0.94	0.49
Zn	ug l^{-1}	-	301	30	24	330	78
Pb	ug l^{-1}	3	34.7	5	-	53.5	9
Hg	ug l^{-1}	<0.05	3.11	0.05	<0.05	0.29	0.05
Cd	ug l^{-1}	<0.04	5.00	0.10	<0.04	6.12	0.50
PCB's	ug kg^{-1}	0	-	24	0	-	22
PAH's	mg kg^{-1}	0	-	0.98	0	-	0.11

Data measured at (a) Lobith and (b) Eijsden, the Netherlands; -: no data available.

meer) and the sediments in the river forelands are still highly contaminated with these toxic substances (Demon and Van Broekhoven, 1989; Biekart and Leuven, 1991; Van de Guchte, 1993). Since 1900 the water temperature of the Lower Rhine and Meuse has increased by 2-4 °C as a result of thermal pollution by power plants and other industries.

The present geomorphology of the alluvial plains of the Lower Rhine and Meuse has also been drastically changed under human impact. The first documented human influence on these rivers occurred in the Roman Era and encompassed canal construction in order to regulate the discharge of the Dutch Rhine tributaries (Van der Ven, 1976; Van Urk and Smit, 1989). Embanking of the Dutch river sections started in the early Middle Ages. However, up to the 18th century the main channels were meandering and many river islands, riverside forests and drowned trees (snag) were still present (Fig. 5). The river banks were sandy and clayey, with natural slopes. The floodplain area must have been tens of kilometres wide, bound only by the ridges of moraine hills, formed in the ice age (Van Urk and Smit, 1989; Klink, 1989, 1991). River regulation and normalization started in the 19th century and was
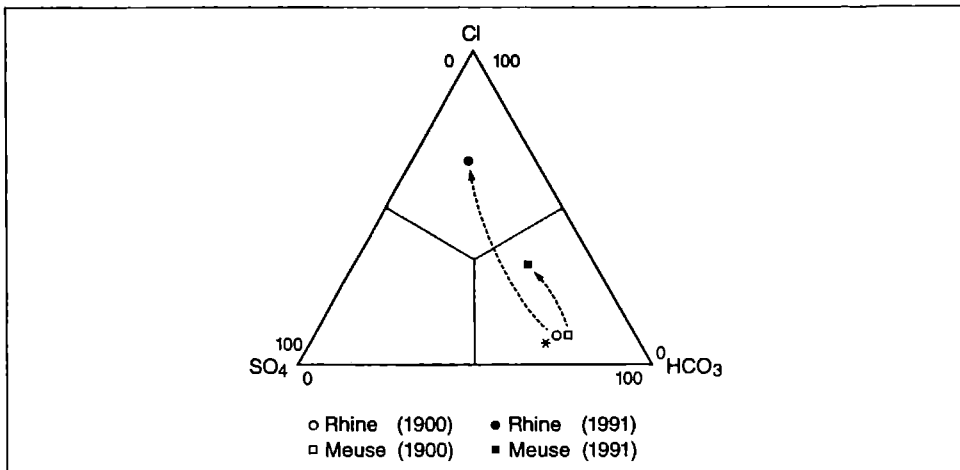
Figure 4. *Shift in relative anion ratios (percentages) of the Lower Rhine and Meuse during the period 1900-1991. The relative anion concentrations are expressed as percentages (0-100%) of the total anion concentrations in equivalents, which is set to 100%. See table 3 for sources. Asterisk = mean relative anion ratio of large European rivers (Golterman, 1975).*

completed in the present century (Van Urk and Smit, 1989). The original estuarine river mouths of the Lower Rhine and Meuse were provided with dams and sluices for sea flood protection. At several upstream locations dams were built in the main channel for river regulation and for energy supply. The river bed was fixed by groynes and dikes, which impede meandering and the formation of side channels, cut-off channels and oxbow lakes. Other consequences of this fixation are that the total floodplain area has become drastically reduced to a narrow zone of only a few kilometres wide, that the river bed has become deeper and narrower and that the river forelands have silted up and have been raised. From the 14th to the 19th century, dike bursts occurred regularly during periods of high river discharge in combination with the formation of ice dams in the river. These dike bursts resulted in deep (up to 20 m) water bodies, the break-through lakes. Large-scale clay digging and sand and gravel extraction occurred in the present century, leading to many new water bodies. Clay-pit lakes are generally shallow (up to 6 m), whereas sand- and gravel-pit lakes may be fairly deep (up to 60 m).

Not surprisingly, the biological communities in the rivers Rhine and Meuse have changed remarkably in response to the deterioration of water quality and habitats. Nearly all floodplain forests have been cut and snag has been removed from the channels in order to accelerate river discharge during high water levels. Figure 5 illustrates the changes in habitats along the banks of the Lower Rhine branch the R. IJssel over the years. At present, riparian and aquatic vegetation in the main channels of the Lower Rhine and Meuse is very sparse and more abundant only in the downstream reaches and in associated floodplain lakes (Coops and Smit, 1988; Maenen, 1989; Van den Brink et al., 1991a). The total plankton biomass in the river channels of the Lower Rhine and Meuse has increased over the years (Peelen, 1975; Tubbing, 1993).
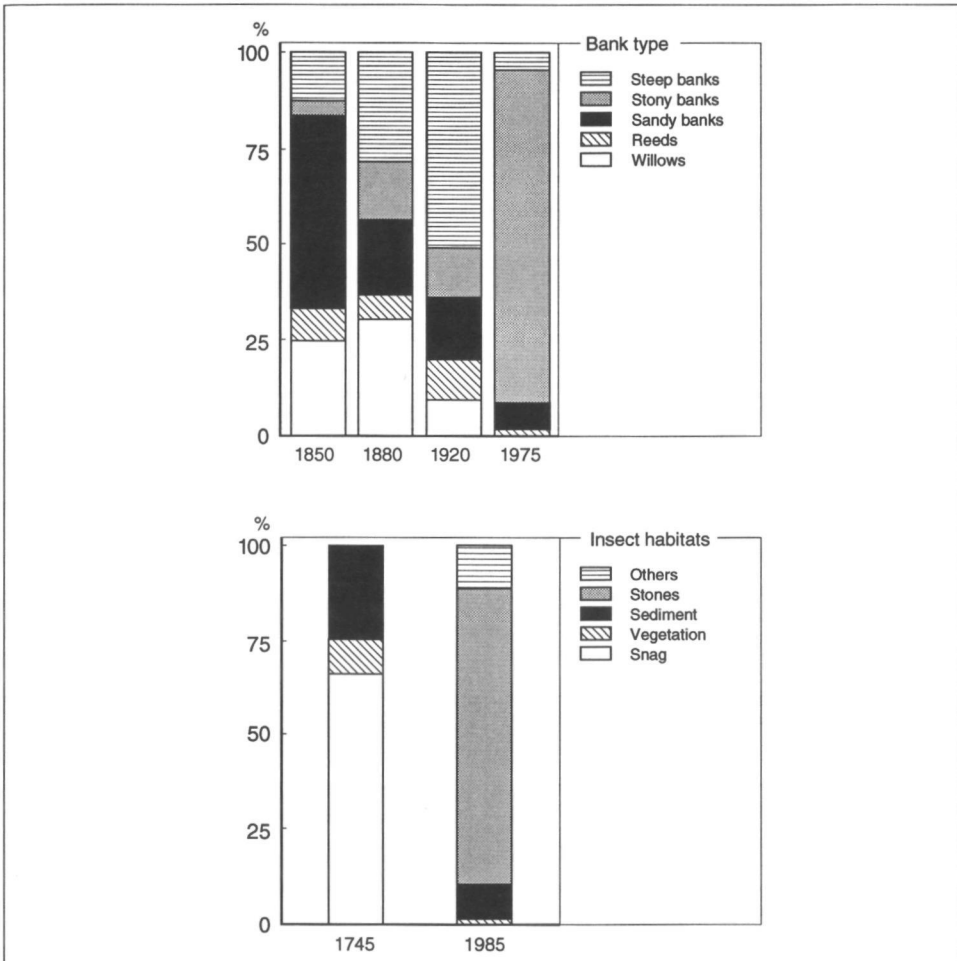
Figure 5. *Above: changes in habitats along the banks of the river IJssel, a Lower Rhine branch, during the 19th and 20th centuries. Bank length with a particular habitat is plotted as a percentage of the total bank length (Data based on river maps; after Beekmans and Verbraak, 1991).*
Below: changes in the aquatic insect fauna in the Lower Rhine.
The number of taxa associated with a particular habitat is plotted as a percentage of the total number of taxa (Data based on palaeoecological information from dated sediment cores (1745) and from recent surveys (1985); after Klink, 1991).

The present plankton communities in the main channels consist of a few dominant ubiquitous centric diatom species, in addition to ubiquitous green algae (De Ruyter van Steveninck et al., 1990; Admiraal et al., 1993); the relative abundance of benthic pennate diatoms has greatly decreased (Klink, 1991). The macroinvertebrate communities are nowadays dominated by a

few immigrant species instead of the original species. The invading species, originating from other water systems, are all brackish-water and high temperature tolerant r-strategists (Van den Brink and Van der Velde, 1986a, 1986b, 1992; Van den Brink et al., 1988, 1989, 1990, 1991b, 1991c, 1993a, 1993b, 1993c, 1993d; Den Hartog et al., 1989, 1992; Van der Velde et al., 1990; Bij de Vaate and Greijdanus, 1990, 1991; Bij de Vaate, 1991). In addition, the macro-invertebrate communities presently consist mainly of pollution-tolerant species. Large numbers of typically riverine insects, such as Ephemeroptera, Plecoptera and Trichoptera, which are all sensitive to pollution, have disappeared, as has the fauna of calm river reaches (Van Urk, 1984; Klink, 1989, 1991; Van den Brink et al., 1990). The fauna in the rivers Rhine and Meuse has deteriorated not only in response to water quality, but also to the change in habitats. For example, the phytophilous species have disappeared with the decline of the riverine vegetation (Fig. 5). The present fish fauna is dominated by euryoecious cyprinids (Fig. 6). Anadromous and rheophilous species have declined in numbers or have become entirely extinct (Cazemier, 1988; De Groot, 1988, 1989a, 1989b, 1989c, 1989d, 1990a, 1990b, 1990c, 1991a, 1991b, 1992a, 1992b, 1992c; Van den Brink et al., 1990; Van der Velde et al., 1990; Bergers, 1991; Admiraal et al., 1993). The last two decades clear signs of recovery have been noticed in the rivers Rhine and Meuse. At present the numbers of macroinvertebrate and fish species are increasing again, after a nadir in the early 1970s (Fig. 6) (Van den Brink et al., 1990; Tittizer et al., 1994). Among the native invertebrates spectacular reoccurrences were noted for the caddisfly *Hydropsyche contubernalis* McL. in 1978 (Van Urk, 1981) and for the mayfly *Ephoron virgo* (Ol.) in 1991 (Bij de Vaate and Oosterbroek, 1992) in the Lower Rhine.
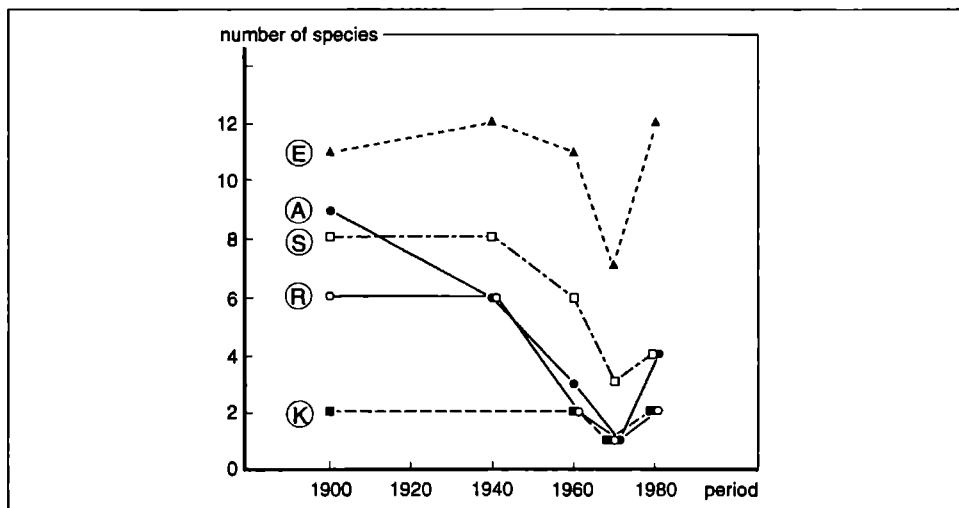
Figure 6. *Changes in fish communities in the Lower Rhine during the present century (after Van den Brink et al., 1990).*
E = euryoecious species; A = anadromous species; S = stagnophilous species;
R = rheophilous species; K = katadromous species.

Restoration measures

At the end of last century, problems with the exploitation of the salmon (*Salmo salar* L.) stocks led to the 'Salmon Treaty' between the states bordering the Rhine. However, large scale restocking attempts did not prevent the complete extinction of the Rhine salmon (De Groot, 1989a). In the 1960s-1970s, when the water quality of the rivers Rhine and Meuse was extremely poor, problems arose in the preparation of river water for drinking water. At the end of the 1970s sewage purification plants were built in order to improve the water quality. The industrial discharge of heavy metals and organic micropollutants into the river was also re-stricted. For the river Rhine, the most recent sanitation initiatives were taken by the states bor-dering the Rhine in response to the Sandoz accident in Basel (Switzerland) in November 1986. Measures included a more drastic reduction of the load of pollutants and investigations with respect to possibilities for an ecological restoration of the river. This ecological restora-tion is a new element in the Rhine management. As part of the so-called 'Rhine Action Pro-gramme' the Dutch government started the research programme 'Ecological Rehabilitation of the River Rhine'. Within this research programme, a project was carried out in order to study the ecological values and the overall impact of hydrology on aquatic communities within floodplain lakes along the rivers Rhine and Meuse in the Netherlands from 1987-1990, under the authorization of the Institute for Inland Water Management and Waste Water Treatment, RIZA, Lelystad, the Netherlands (Van den Brink, 1990). A grant from the Sandoz Rhine Fund allowed for more detailed investigations on the impact of hydrology on the aquatic floodplain ecosystems to be carried out in a follow-up project, during 1990-1994. The main results from both projects are presented here.

Outline of the thesis

The present thesis is focused on the lateral dimension, which is of major importance in large river ecosystems. The theme was also selected because information on the structure and func-tioning of floodplain waters along the rivers Rhine and Meuse was very sparse, scattered and dated (Janse, 1986, and literature therein). Previous studies on structural and functional as-pects of floodplain water bodies along the Lower Rhine and Meuse have focused on the vege-tation and plankton communities, and have been carried out in a few water bodies only (Van der Velde, 1980; Brock, 1985; Roijackers, 1985; Janse, 1986). So far, no attempt has been made to relate structural and functional aspects of the aquatic and semi-aquatic vegetation, phyto- and zooplankton and macroinvertebrates to the hydrology of lakes in floodplains of heavily eutrophicated and regulated rivers, such as the Lower Rhine and Meuse. Detailed in-formation on channel-floodplain interactions in regulated rivers is recognized as one of the major knowledge gaps in present river ecology (Ward and Stanford, 1993). Such information, however, is of extreme relevance if we wish to understand the ecological functioning of such river systems. Furthermore, it is an essential prerequisite for predicting and evaluating the im-pact of changes in hydrology on floodplain lakes due to embanking, regulation or nature res-

toration (Roux, 1982; Bravard et al., 1986; Amoros et al., 1987a; Van den Brink and Klink, 1991; Klink et al., 1991; Van den Brink et al., 1993b, 1993c). In fact, the restoration of connections between the main channel and its associated floodplain lakes and the reactivation of former side channels are two of the main measures planned for an ecological rehabilitation of the river Rhine, as formulated in the "Integrated Ecological Concept" (ICPR, 1989). But what are the ecological consequences of restoration of connections? In order to study the impact of hydrology on floodplain lake ecosystems along the Lower Rhine and Meuse, the aquatic and semi-aquatic vegetation, phyto- and zooplankton and macroinvertebrates, have been selected for study, because these communities form the basis of the foodwebs in the floodplain lakes and because they have proved to be good environmental descriptors (e.g. Roux, 1982; Castella et al., 1984).
Three lines of approach were chosen:

1. A statistical analysis of the community composition of selected biotic groups in 100 floodplain lakes along the Lower Rhine and Meuse in relation to hydrology, water and sediment chemistry, geomorphology and other environmental parameters. Multivariate analyses (classification using TWINSPAN and FLEXCLUS, and ordination using PCA and DCA) and simple correlations (i.e. Pearson and Spearman rank correlations) were used to detect the major environmental parameters which determine the distribution of the biota in the floodplain lakes. Such a statistical approach has proved to be very suitable for an improved understanding of the complexity and interactivity of biotic and abiotic variables (Jongman et al., 1987).

2. Detailed investigations were carried out on seasonal fluctuations of water chemistry and biota in a few selected water bodies which form a flood frequency gradient in the Lower Rhine floodplain, in order to study the spatio-temporal variation in physico-chemical parameters and abundance of biota in relation to hydrology.

3. An experimental approach was chosen in order to search for causality with respect to the impact of hydrology and water and sediment chemistry on the performance of (semi-) aquatic macrophytes.

The impact of hydrology on the water chemistry and phytoplankton biomass in floodplain lakes along the Lower Rhine and Meuse is discussed in *chapter 2*. An analysis of the spatial variation in physico-chemical parameters of the superficial water, interstitial water and sediment of 100 floodplain waters was made in relation to hydrology and geomorphology. In addition, the seasonal fluctuations in water chemistry and phytoplankton development were followed in the Lower Rhine channel and in five associated floodplain lakes which form an inundation gradient. *Chapter 3* deals with the impact of hydrology on the structure of zoo- and phytoplankton communities. The relative abundance of phyto- and zooplankton species was related to the degree of connection of 100 floodplain waters with the main channels of the Lower Rhine and Meuse, and to other environmental parameters such as nutritional resources and habitat characteristics. A historical perspective of the influence of hydrology on aquatic

and semi-aquatic macrophytes in Dutch floodplain lakes is presented in *chapter 4*. The species richness of (semi-) aquatic macrophytes in 75 permanent floodplain lakes was related to the longterm average annual flood frequency. In addition, the current presence of six aquatic macrophytes and seven helophytes in a large number of former channels was compared with their presence in 1954. The impact of the increased salinity of the Lower Rhine on the growth of four aquatic macrophytes is discussed in *chapter 5*. In *chapter 6* the combined influence of substrate parameters and water depth on the performance of eight helophyte species commonly occurring in European floodplains is discussed. *Chapter 7* deals with the impact of hydrology on the structural and functional aspects of macrozoobenthos in floodplain lakes. The macroinvertebrate assemblages in 100 floodplain lakes were related to flood frequency, nutritional resources and habitat characteristics via statistical analysis. *Chapter 8* discusses spatio-temporal variation in density and biomass of macroinvertebrates in three floodplain lakes with varying inundation regimes. The influence of lake hydrological regime, season and habitat on the abundance of various macroinvertebrate groups and dominant taxa was analyzed. In *chapter 9* a synthesis of the results is provided, together with suggestions for an ecological management of floodplain lakes along eutrophicated and regulated rivers, such as the Lower Rhine and Meuse.

Acknowledgements

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Impact of hydrology on the chemistry and phyto-plankton development in floodplain lakes along the Lower Rhine and Meuse

Abstract

The impact of hydrology (floods, seepage) on the chemistry of water and sediment in floodplain lakes was studied by a multivariate analysis (PCA) of physico-chemical parameters in 100 lakes within the floodplains in the lower reaches of the rivers Rhine and Meuse. In addition, seasonal fluctuations in water chemistry and chlorophyll-a development in the main channel of the Lower Rhine and five floodplain lakes along a flooding gradient were monitored. The species composition of the summer phytoplankton in these lakes was studied as well.

At present very high levels of chloride, sodium, sulphate, phosphate and nitrate are found in the main channels of the rivers Rhine and Meuse, resulting from industrial, agricultural and domestic sewage. Together with the actual concentrations of major ions and nutrients in the main channel, the annual flood duration determines the physico-chemistry of the floodplain lakes. The river water influences the water chemistry of these lakes not only via inundations, but also via seepage. A comparison of recent and historical chemical data shows an increase over the years in the levels of chloride both in the main channel of the Lower Rhine and in seepage lakes along this river. Levels of alkalinity in floodplain lakes showed an inverse relationship with annual flood duration, because sulphur retention and alkalinization occurred in seepage waters and rarely-flooded lakes. The input of large quantities of nutrients (N, P) from the main channel has resulted, especially in frequently flooded lakes, in an increase in algal biomass and a shift in phytoplankton composition from a diatom dominated community towards a community dominated by chlorophytes and cyanobacteria.

Introduction

The large rivers Rhine and Meuse are major European waterways which connect the Dutch sea ports with a highly industrialized hinterland. Most European rivers and their floodplains have been subjected to geomorphological changes since Roman times and probably even earlier (Petts, 1989). In the Netherlands the large floodplain areas of the rivers Rhine and Meuse have been dramatically reduced by means of embankment and river engineering since the Middle Ages. The water quality of these rivers has deteriorated since that time, although major changes in water chemistry did not take place until the present century. The rivers Rhine and Meuse have been severely polluted with salts, fertilizers, heavy metals and organic micropollutants as a result of high population densities, extensive agriculture, and a high level of industrialization in their drainage basins. Water quality became very bad during the sixties and seventies. Since that time improvements have been made with respect to levels of oxygen, ammonium, heavy metals and some organic toxicants. By contrast, the concentra-

tions of sodium, chloride, sulphate, phosphate and nitrate have not been improved at all and are still extremely high (Anonymous, 1989). It should be realized that the rivers Rhine and Meuse are nowadays among the most eutrophic rivers in the world (Admiraal and Botermans, 1989). Salinity is also very high, due to mining activities in the drainage basins. Mining effluents have shifted the ionic composition of the lower reaches of the rivers Rhine and Meuse from a calcium bicarbonate dominance, which is the normal situation in most rivers, towards a sodium chloride dominance (Kempe et al., 1991; Van der Velde et al., 1991). During periods of low river discharge the water of the Lower Rhine can no longer be considered "fresh". As a consequence of all these changes, the riverine vegetation, zoobenthos and fish communities in the main channels became impoverished, especially in the lower reaches (Van den Brink et al., 1990, 1991a, 1991b; Van der Velde et al., 1990).

The importance of river-floodplain interactions for the functioning of large river ecosystems has been recognized relatively recently (e.g. Minshall et al., 1985; Amoros et al., 1987; Amoros and Roux, 1988; Junk et al., 1989). During floods, there is an exchange of water, sediment, chemicals and biota between the main channel and the floodplain lakes. Information on the influence of flooding on the water chemistry of floodplain lakes is poor and concerns mainly some pristine tropical rivers (e.g. Hamilton and Lewis, 1987; Forsberg et al., 1988; Junk et al., 1989; Pedrozo et al., 1992). Studies on the impact of inundations on the water chemistry of floodplain lakes in highly eutrophic river ecosystems, which are mostly found in temperate zones (Peierls et al., 1991), are very sparse. Such studies, however, are extremely relevant for an understanding of the ecological functioning and hence for an ecological management of these river ecosystems (Bravard et al., 1986).

Although some influence of flooding on the water chemistry of floodplain lakes along the highly eutrophic rivers Rhine and Meuse might be expected (Van den Brink and Van der Velde, 1991), it was not clear which parameters are most affected by the hydrology. Furthermore, it was unknown to what extent the inundation regime affects the water chemistry. In the present study the impact of hydrology on the chemistry (major ions, nutrients, heavy metals) of the ambient and interstitial water of floodplain lakes was examined by (1) a multivariate analysis of physico-chemical parameters of 100 floodplain lakes within the lowland reaches of the rivers Rhine and Meuse, and (2) an analysis of seasonal fluctuations in the water chemistry of the main channel and five floodplain lakes along an inundation gradient in the basin of the Lower Rhine. As phytoplankton development has a pronounced effect on physico-chemical parameters of the water and sediment, and vice versa (e.g. Admiraal et al., 1990), the impact of hydrology on phytoplankton biomass and species composition in floodplain lakes was studied as well.

Sites and methods

Study sites

Within the floodplains of the rivers Rhine and Meuse lentic water bodies can be categorized according to their geomorphology and hydrology. Sites were selected within the floodplains of the lowland reaches of the rivers Rhine and Meuse in the Netherlands, outside tidal influence (Fig. 1). During July-August of 1987 and 1988 the water, sediment and phytoplankton of 28 oxbow lakes, 22 break-through lakes, 23 clay-pit lakes and 27 sand-pit lakes were each sampled once.

In order to study the impact of hydrology on the water chemistry in more detail, five floodplain lakes along the Lower Rhine were selected on the basis of inundation regime, depth and river distance (Table 1; Fig. 2). During 1990-1991 seasonal fluctuations in physico-chemical parameters and chlorophyll-a were monitored by monthly sampling of the water of the main channel and three shallow (2-5 m) and two deep (8-15 m) floodplain lakes along an inundation gradient. The studied lakes were Lake Ewijk (shallow) and Lake Waaienstein (deep), which are not protected against flooding by dikes or levees and which are frequently
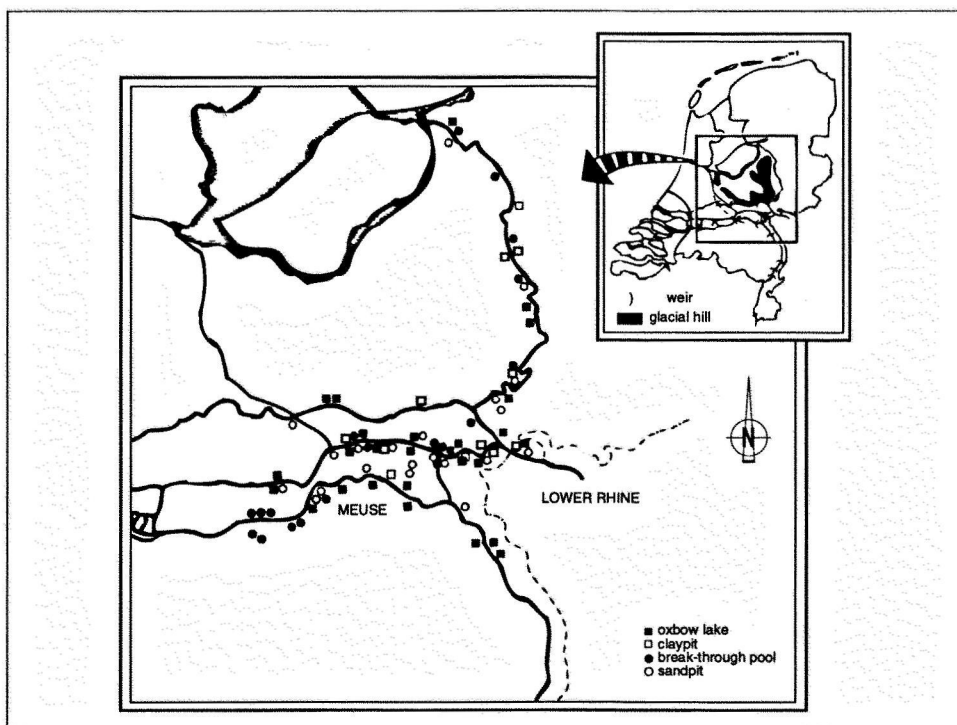
Figure 1. *Map of the sampling sites.*

inundated; Lake Oude Waal (shallow), which is protected by a small summer dike and hence is rarely inundated; and Lake Duivelswaai (deep) and Pond G (shallow), which both receive seepage water if there are high water levels in the main channel and which are protected against inundation by the main dike (Table 1; Fig. 2).

Table 1. *Topographical, geomorphological, hydrological, and vegetational characteristics of five floodplain waters along the Lower Rhine where the water chemistry was monitored monthly. Location in km's from the source of the river. Flood duration: the calculated long-term average annual flood duration in days per year (1901-1985). Floods/seepage: periods of inundation and/or seepage during 1990/1991.*

	Lake Ewijk	Lake Waaienstein	Lake Oude Waal	Lake Duivelswaai	Pond G
Coordinates	N 51°53' E 5°45'	N 51°53' E 5°51'	N 51°51' E 5°55'	N 51°52' E 5°48'	N 51°52' E 5°54'
Location (km)	893	887	882	888	882
Surface area (ha)	10	9.5	16	6	0.6
Maximum depth (m)	3	15	5	8	2
Distance from river (m)	10	100	500	650	1150
Flood duration	67	23	3	0	0
Floods	Feb/Nov-Jan	Feb/Jan	Feb/Jan	–	–
Seepage	idem	idem	idem	Feb/Jan	Feb/Jan
Submerged vegetation	absent	absent	sparse	dominant	dominant
Nymphaeid vegetation	sparse	absent	dominant	dominant	dominant

Hydrology

A hydrological characterization of the main channels of the rivers Rhine and Meuse has been presented in Van den Brink et al. (1991b). Major differences in hydrology between these river systems are the drainage areas and discharge characteristics. The total drainage area of the River Rhine measures 185,000 km^2, while the total drainage area of the River Meuse is 33,000 km^2. According to long-term measurements (1901-1985) the discharge of the R. Rhine at the Dutch-German border averages 2,200 m^3 s^{-1}, while the discharge of the R. Meuse at the Dutch-Belgian border averages 250 m^3 s^{-1}. Water-level fluctuations in the main channels of these rivers vary from 2 to 6 m in the sections under study.

Normally, the Dutch floodplain lakes are inundated during winter and spring, i.e., outside the vegetation growth season. Most lakes become isolated from the river during the rest of the year, except for water bodies which have a permanent open connection with the main channel. The duration and frequency of inundation of the lakes is largely dependent on the presence and height of summer dikes and natural levees, together with actual water-level fluctuations in the main channel. In general, the flood duration and flood frequency of the lakes decreases with increasing distance from the main channel. The water bodies behind the main dikes are
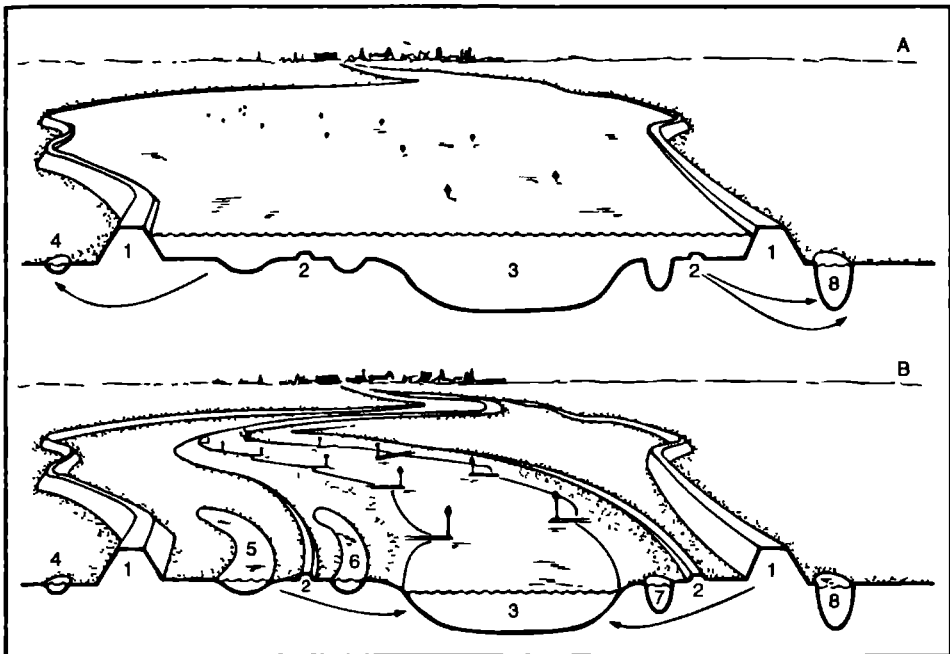
Figure 2. *Schematic view of hydrology of floodplain lakes, during A. high river discharges and B. normal river discharges.*
1 = main dikes, 2 = summer dikes, 3 = river bed, 4, 8 = seepage lakes, 5 = infrequently flooded lake, 6, 7 = frequently flooded lakes, 4-6 shallow lakes, 7, 8 = deep lakes. Arrows indicate directions of ground water fluxes.

never flooded, except during very rare catastrophes, and are normally influenced by river water via seepage only (Fig. 2).

In order to quantify the hydrological situation of the floodplain lakes, the annual flood duration was calculated as follows. Firstly, river maps were used to estimate the inundation level for each site, i.e., the lowest water level of the river at which the part of the floodplain which includes that specific site is inundated. Next, the long-term (1901-1985) annual mean number of days on which the water level in the main channel reached this level of inundation was calculated (= annual flood duration). Hydrological data were obtained from the Institute for Inland Water Management and Waste Water Treatment (RIZA, The Netherlands).

Sampling, measurements and physico-chemical analyses

At each site a mixed sample (2 liter) of the ambient water was taken, at a depth of 20 cm below the water surface in the open water compartment, i.e., outside the vegetation belt. Three samples of 100 ml each were taken out of this mixed sample. One sample was used immediately for measurements of pH, alkalinity and acidity. The other two samples were passed through a

Whatman GF/C filter (1.2 μm), and after addition of 0.5 ml of a 200 mg l⁻¹ HgCl₂ solution, stored in iodated polyethylene bottles and frozen at -27 ˚C until further analysis. In one of the latter samples a few grains of citric acid were added in order to prevent precipitation of metals. pH was measured with a Radiometer Combined pH electrode, connected to a PHM82 Standard pH meter. Alkalinity was determined by titration of a subsample of 50 ml with 0.01 N HCl down to pH 4.2, while acidity was determined by titration of another subsample of 50 ml by adding 0.01 N NaOH up to 8.2 (modified from Stumm and Morgan, 1981). The fractions of carbon dioxide and bicarbonate were calculated from equations for the inorganic carbon equilibria and pH, derived from Stumm and Morgan (1981). Conductivity was measured with an YSI model 33 SCT meter, turbidity with a Dentan model FN5 turbidity meter. Both measurements were carried out in the field. Chlorophyll-a determination was based on an ethanol extraction method according to Roijackers (1985).

Sediments were collected from below the water layer in the littoral zone, by means of a metal tube with a diameter of 7 cm. The upper 10 cm layer of sediment was sampled. Because of the inhomogeneity of the sediment, eight samples were collected and mixed. Sediment-water extracts were made for the assessment of the chemical composition of the interstitial water. 70 g wet sediment was thoroughly mixed with 200 ml twice distilled demineralized water for one hour at room temperature. The supernatant was separated from the extract by centrifugation (20', 12,000 rpm). Further treatment of the supernatant was similar to that of the water samples. Subsamples of the wet sediment were dried at 105 ˚C for 24 hours. The percentage organic matter in the sediment was calculated from the weight loss of 50 g dried sediment after 4 hours heating at 550 ˚C (= loss on ignition).

Chemical analyses of the water and sediment extracts were carried out according to Technicon Auto-analyzer Methodology (1981). Na and K were determined by flame-photometry. Colorimetrical measurements were used for chloride (with ferri-ammonium sulphate according to O'Brien 1962), sulphate (with barium chloride), phosphate (with ammonium molybdate and ascorbic acid, according to Hendrikson, 1965), nitrate/nitrite (with hydrazine sulphate, according to Kamphake et al., 1967) and total ammonia (with salicylate and hypochloride, according to Kempers and Zweers, 1986). Fe, Ca, Mg, Zn, Al and Si were analyzed using an Inductively Coupled Plasma Spectrophotometer type IL Plasma 200. Climatological data on daily solar radiation and monthly precipitation were obtained from the Dutch Meteorological Institute (KNMI, De Bilt, The Netherlands).

In order to study the species composition of the summer phytoplankton, three samples per water body were taken by drawing a net (diameter of net opening: 20 cm, mesh width: 60 μm) over a distance of 10 m through the water in a horizontal direction towards the shore, about 50 cm below the water surface.

Statistical analysis

A principal component analysis of the physico-chemical parameters (standardized values) of the ambient and interstitial water and the sediment was performed, in order to illustrate: 1. the influence of differences in the water chemistry between the main channels of the rivers Rhine

Table 2. *Pearson correlation coefficients between the loadings of the sampling sites on PC1, PC2 and PC3, and some physico-chemical parameters of the water, interstitial water and sediment of the floodplain lakes.*
n = 100 sites. *** = p < 0.001; ** = 0 001 < p < 0.01; * = 0.01 < p < 0.05.

	PC1	PC2	PC3
	water		
Na	0 86***	0 13	0 11
Cl	0 87***	0 14	0 03
EC	0 68***	0 61***	0 09
K	0 57***	0 23*	0 14
Mg	0 54***	0 39***	–0 45***
SO$_4$	0 52***	–0 21*	–0 02
Ca	0 08	0 83***	0 06
HCO$_3$	–0 08	0 82***	–0 09
Acidity	–0 26**	0 48***	0 25*
pH	0 20	–0 59***	–0 32***
NO$_3$	0 20*	–0 01	0 38***
NH$_4$	0 27**	0 21*	0 42***
d-PO$_4$	0 08	0 16	0 42***
Si	–0 22*	0 61***	0 26**
Fe	–0 22*	0 23*	0 03
Zn	–0 13	0 51***	0 31***
Al	0 18	0 16	–0 01
	interstitial water		
Na	0 89***	–0 02	0 01
Cl	0 85***	–0 02	0 10
K	0 36***	–0 28***	–0 08
Mg	0 56***	–0 17	–0 54***
Ca	0 40***	0 03	–0 50***
HCO$_3$	0 26**	0 49***	–0 36***
pH	0 40***	0 04	–0 22*
NO$_3$	0 38***	–0 25*	0 20*
NH$_4$	0 21*	–0 22*	0 01
d-PO$_4$	0 37***	–0 13	0 51***
Si	0 43***	–0 19	0 29**
Fe	–0 00	–0 34***	0 41***
Zn	0 26**	–0 07	0 35***
Al	0 27**	–0 47***	0 27**
	sediment		
Loss on ignition	–0 12	0 49***	–0 22
% Variance	20	15	9

and Meuse on the water chemistry of the floodplain lakes, and 2. the relationship between the hydrology (floods, seepage) and the water chemistry of the floodplain lakes. The parameters on which the PCA was based are presented in Table 2. In order to correlate site scores on the most important principal components (PC1, PC2 and PC3) with real values of physico-chemical parameters, Pearson correlation coefficients were calculated. A Wilcoxon test (Sokal and Rohlf, 1981) was used to test groups of floodplain lakes of the rivers Rhine and Meuse for significant differences in water chemistry and sediment characteristics. In order to detect correlations between major ions in the ambient water, and in order to relate the flooding regime to physico-chemical parameters of water and sediment, a Spearman rank correlation test was performed. All calculations were made on an IBM 3090 mainframe, using the Statistical Analysis System (SAS Institute Inc., 1989).

Results

Ordination and correlations

A multivariate analysis of physico-chemical parameters of the water and sediment of 100 lakes within the floodplains of the rivers Rhine and Meuse in The Netherlands reveals the major environmental factors affecting the water chemistry. The ordination of physico-chemical parameters visualizes the position of the sampling sites in a vector space of data (Fig. 3). The position of these sites reflects similarities and dissimilarities: sites with very similar physico-chemical parameters are grouped together, while dissimilar sites appear further apart from each other in the PCA-plot. The first three principal components (PC1, PC2 and PC3) account for 44% of the total variation in the physico-chemical data (Table 2). The eigenvalues of PC1, PC2 and PC3 were 7.6, 5.7 and 3.3 respectively. A plot of the first and second principal component axes shows that the sites are arranged along the first axis by the drainage basins in which they are located (R. Rhine or R. Meuse). A plot of the first and third principal component axes shows that the sites are arranged along both axes by their annual flood duration (Fig. 3).

Table 2 shows the Pearson correlation coefficients between the loadings of the sampling sites on the first three principal components and the physico-chemical parameters of the water, the interstitial water and the sediment of the sampling sites. The scores of the sites on PC1 show highly significant positive correlations ($p < 0.001$) with the major ions (e.g. sodium, chloride, potassium, magnesium, sulphate) of the ambient and interstitial water and with nutrients (nitrate, dissolved phosphate, silicate) of the interstitial water. The scores of the sites on PC2 show highly significant positive correlations ($p < 0.001$) with the calcium and bicarbonate concentrations of the ambient water, with the interstitial bicarbonate concentration and the organic matter content (as loss on ignition) of the sediment of the water bodies. The scores of the sites on PC3 show highly significant positive correlations ($p < 0.001$) with the levels of nutrients (nitrate, dissolved phosphate) in the ambient and interstitial water, and with the concentrations of heavy metals (Fe, Zn) in the interstitial water (Table 2).
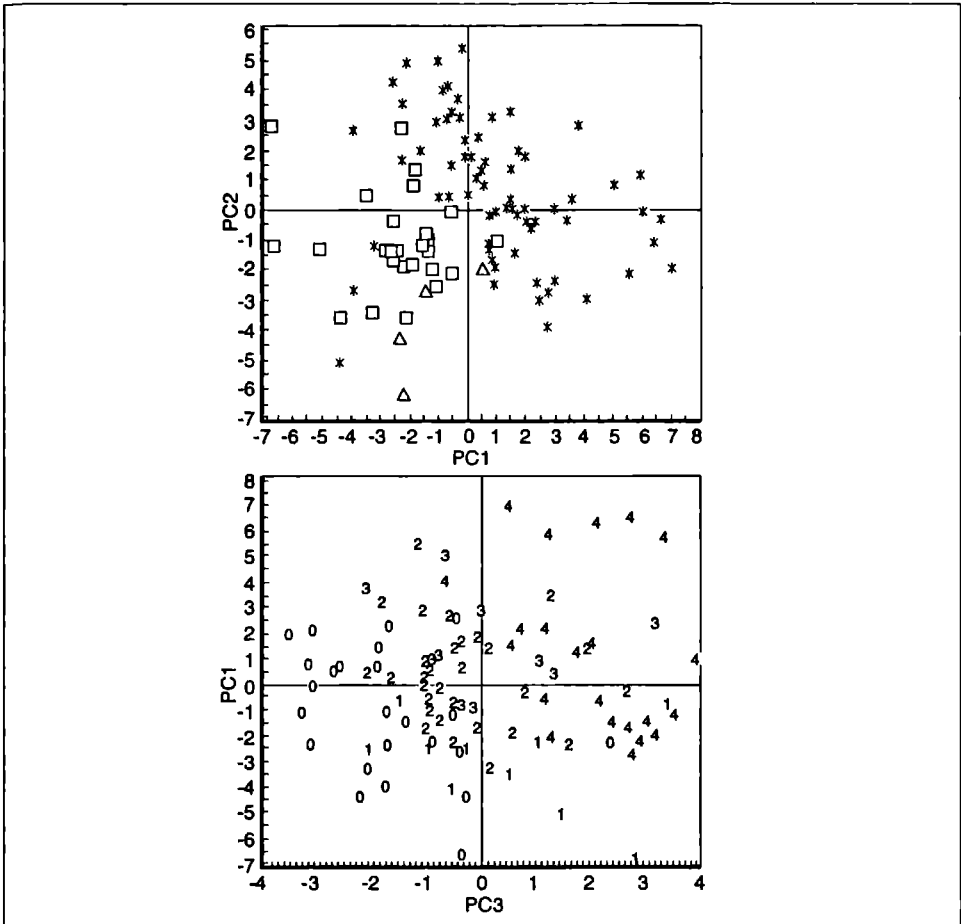
Figure 3. *Ordination plots of the sampling sites, based on physico-chemical data of water, interstitial water and sediment.*
Above: Plot of first (PC1) and second (PC2) principal component axis. Stars represent sites along the Lower Rhine; squares represent sites along the river Meuse; triangles represent sites in ancient floodplains, no longer influenced by rivers.
Below: Plot of first (PC1) and third (PC3) principal component axis. Numbers represent the long-term (1901-1985) average annual flood duration of the sites (0: 0, 1: 0-3, 2: 3-20, 3: 20-40 and 4: 40-365 days year[-1]).

Table 3 shows the interrelations between the major ions in the floodplain lakes studied. Highly positively correlations ($p < 0.001$) were found among concentrations of sodium, potassium, magnesium, chloride and sulphate. The same was true ($p < 0.001$) among the concentrations of calcium, magnesium and bicarbonate. A clear negative correlation ($p < 0.01$) was found between bicarbonate and sulphate concentrations (Table 3).

Table 3. *Spearman rank correlations among major ions in the superficial water of 100 floodplain lakes along the rivers Rhine and Meuse.*
*** = p < 0.001; ** = 0.001 < p < 0.01; * = 0.01 < p < 0.05; n = 100 observations.

	Na	K	Mg	Ca	Cl	HCO$_3$
K	0.53***					
Mg	0.43***	0.23*				
Ca	0.11	0.05	0.43***			
Cl	0.98***	0.52***	0.48***	0.14		
HCO$_3$	−0.01	−0.04	0.43***	0.87***	0.00	
SO$_4$	0.45***	0.38***	0.22*	−0.08	0.46***	−0.31**

In order to test for significant differences in chemistry between the floodplain lakes of the R. Rhine and those of the R. Meuse, a Wilcoxon test was applied (Table 4). Because major differences in chemistry could also be attributed to the annual flood duration (Fig. 3), a Wilcoxon test was applied both for a group of very frequently flooded lakes and for a group of seepage lakes. Differences in water chemistry between the floodplain lakes of the river Rhine and those of the river Meuse concerned concentrations of chloride, sodium, magnesium, sulphate, potassium, calcium and bicarbonate (alkalinity), all of which were significantly higher in the ambient water and/or in the interstitial water of the R. Rhine floodplain lakes. Sodium and chloride had their highest concentrations in the ambient as well as in the interstitial water of the R. Rhine floodplain lakes (Table 4).

Spearman rank correlation tests between the annual flood duration and the physico-chemical parameters (Table 5) show that the concentrations of sodium, chloride, nitrate and dissolved phosphate of the ambient water, and the concentrations of sodium, chloride, dissolved phosphate, silicate, iron, zinc and aluminium of the interstitial water in the floodplain lakes of the lowland reaches of the rivers Rhine and Meuse increase with increasing flood duration.

Seasonal fluctuations

Seasonal fluctuations in solar radiation, wet precipitation and fluctuations in hydrological and physico-chemical parameters of the Lower Rhine and five floodplain lakes along a flooding gradient are presented in figures 4, 5 and 6. Because the levels of chloride are highly positively (p < 0.001) correlated with those of sodium and potassium, and because the levels of bicarbonate are highly positively (p < 0.001) correlated with those of calcium and magnesium (Table 3), only the fluctuations of the major anions are presented here.

During 1990 peaks in solar radiation occurred in May and July. Water temperature strongly increased during spring and showed maximum values in August. Precipitation was highest in February and June, and lowest during the summer period. The hydrology of the Lower Rhine showed the normal situation for the Netherlands, with high water levels occurring mainly during the winter period, viz. February 1990 and January 1991 (Fig. 4).

Table 4. *Mean values (± S.D.) of physico-chemical parameters of the superficial water and interstitial water in two hydrologically contrasting groups of floodplain lakes along the rivers Rhine and Meuse during 1987/1988. Only parameters which are significantly different (Wilcoxon test) within the groups of lakes between these river systems have been indicated. n = number of lakes. *** = p < 0.001; ** = 0.001 < p < 0.01; * = 0.01 < p < 0.05.*

	unit	R. Rhine		R. Meuse		p
		river influence via very frequent inundations				
		Mean (n = 12)	(S.D.)	Mean (n = 12)	(S.D.)	
		superficial water				
Cl	μmol l^{-1}	2700	(500)	1400	(100)	***
Na	μmol l^{-1}	2300	(500)	1200	(200)	***
Mg	μmol l^{-1}	420	(30)	290	(20)	***
SO$_4$	μmol l^{-1}	680	(120)	510	(60)	***
K	μmol l^{-1}	110	(20)	90	(10)	**
EC	μS cm^{-1}	570	(100)	420	(50)	***
		interstitial water				
Cl	μmol l^{-1}	3100	(1000)	1500	(500)	***
Na	μmol l^{-1}	4000	(1200)	1700	(500)	***
Mg	μmol l^{-1}	1100	(350)	560	(160)	***
Ca	μmol l^{-1}	6300	(1010)	4500	(1500)	**
HCO$_3$	μmol l^{-1}	17300	(6400)	9500	(3400)	**
K	μmol l^{-1}	840	(350)	440	(180)	**
		river influence via seepage				
		(n = 16)		(n = 4)		
		superficial water				
Cl	μmol l^{-1}	1800	(700)	800	(300)	*
Na	μmol l^{-1}	1400	(600)	700	(300)	*
Mg	μmol l^{-1}	460	(60)	260	(120)	*
Ca	μmol l^{-1}	1600	(600)	1100	(150)	*
EC	μS cm^{-1}	470	(120)	300	(60)	*
		interstitial water				
Cl	μmol l^{-1}	2000	(800)	1000	(500)	*
Na	μmol l^{-1}	2300	(900)	1100	(500)	*

Table 5. *Spearman rank correlation coefficients between the long-term average annual flood duration and physico-chemical parameters of water and sediment in floodplain lakes along the rivers Rhine and Meuse.*
*n = number of floodplain lakes. *** = $p < 0.001$; ** = $0.001 < p < 0.01$; * = $0.01 < p < 0.05$.*

	R. Rhine	R. Meuse
n	70	26
superficial water		
Na	0.46***	0.74***
Cl	0.39***	0.85***
EC	0.24*	0.63***
K	0.41***	0.11
SO$_4$	0.32**	0.32
Mg	−0.28*	0.56**
Ca	−0.14	0.49*
HCO$_3$	−0.29**	0.09
Acidity	−0.24*	0.19
pH	0.06	0.04
NO$_3$	0.46***	0.62***
NH$_4$	0.37***	0.30
d-PO$_4$	0.43***	0.66***
Si	−0.21	0.21
Turbidity	0.39***	−0.10
Fe	−0.08	−0.42*
Zn	0.03	0.12
Al	0.24*	−0.40*
interstitial water		
Na	0.53***	0.44*
Cl	0.45***	0.59***
K	0.40***	−0.42*
Mg	0.14	−0.31
Ca	−0.03	−0.29
HCO$_3$	0.34**	0.15
pH	0.15	0.10
NO$_3$	0.22	0.12
NH$_4$	0.26*	0.08
d-PO$_4$	0.65***	0.68***
Si	0.48***	0.62***
Fe	0.37***	0.53**
Zn	0.30**	0.61***
Al	0.34**	0.45*
sediment		
Loss on ignition	−0.14	−0.39*
Grain size	0.09	0.49**
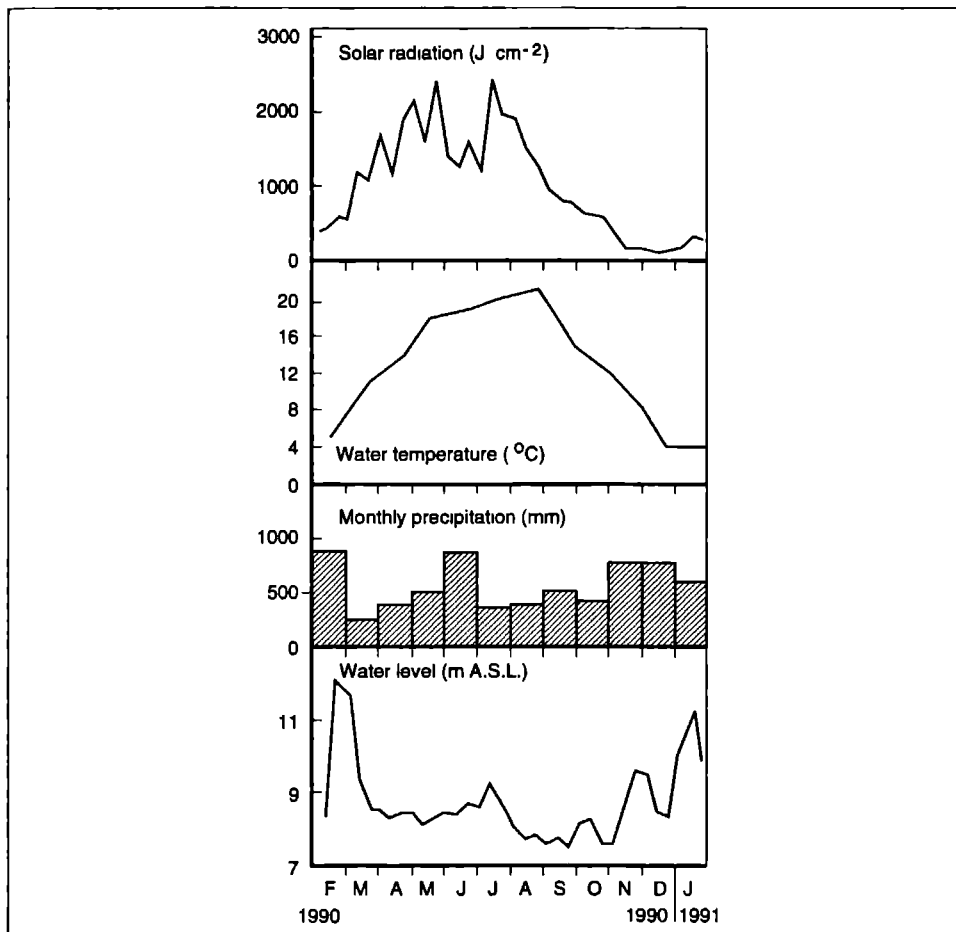
Figure 4. *Seasonal fluctuations in solar radiation (ten day means, measured at De Bilt), water temperature of the Lower Rhine at Nijmegen, wet precipitation (monthly totals, measured near Nijmegen) and water level of the Lower Rhine at Nijmegen.*

Chlorinity exhibited strong seasonal fluctuations in the main channel, but minor fluctuations in the floodplain lakes (Fig. 5). The chlorinity of the main channel was negatively correlated with the water level in the river (Spearman correlation coefficient: -0.77, $p < 0.001$). Figure 5 shows that chloride levels were higher in frequently flooded lakes than in infrequently flooded lakes and seepage lakes for most of the year, except during floods, when levels of chlorinity in flooded lakes were as high as those in the main channel. Fluctuations in alkalinity were relatively large in the shallow seepage Pond G and low in the main channel. In the seepage waters Lake Duivelswaai and Pond G alkalinity strongly increased at times with high water levels in the main channel, during February 1990 and January 1991, when the water
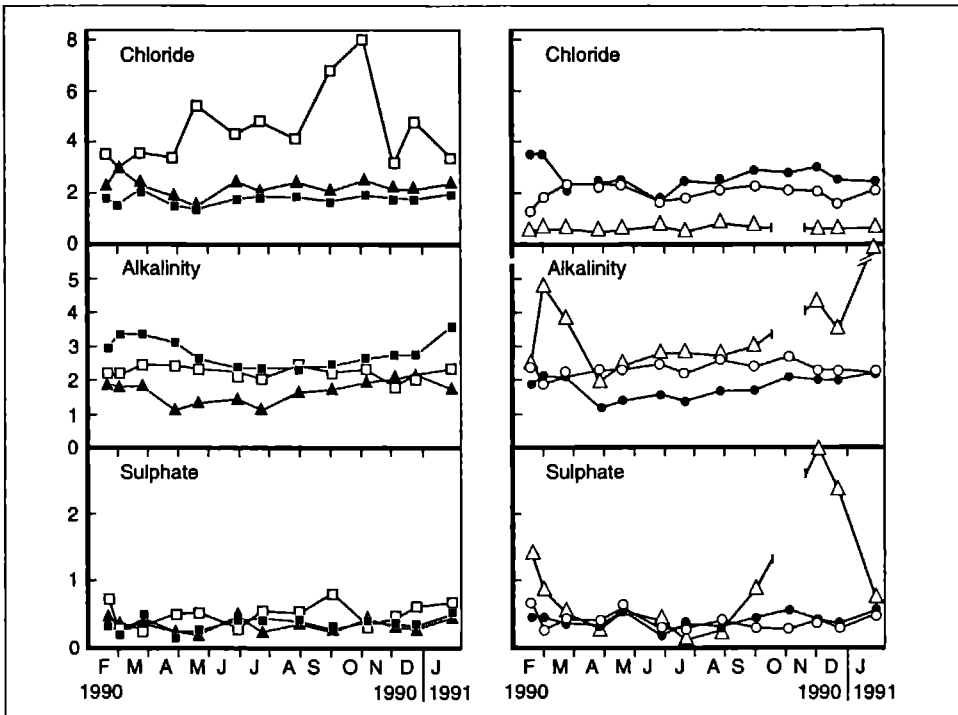
Figure 5. *Seasonal fluctuations in chlorinity, alkalinity and sulphate levels (in mmol l^{-1}) in left: the main channel of the Lower Rhine (open squares), Lake Waaienstein (closed triangles) and Lake Duivelswaai (closed squares), and right: Lake Ewijk (closed circles), Lake Oude Waal (open circles) and Pond G (open triangles).*

level of these lakes rose considerably as a result of seepage. Sulphate showed its greatest fluctuations in the shallow seepage Pond G, with extremely high levels in November when the pond was filled by inflow of phreatic water after a period of drought when the sediment dried out.

Large seasonal fluctuations also occurred in the concentrations of the plant nutrients nitrate, dissolved phosphate and dissolved silicate (Fig. 6). Dissolved silicate in the main channel was inversely correlated (Spearman correlation coefficient: -0.93, p < 0.001) with the phytoplankton biomass (as chlorophyll-a). Concentrations of nitrate and dissolved phosphate in the main channel were slightly reduced from April until September, which is the growing season, but not depleted, as was the case with silicate (Fig. 6). Nitrate and dissolved phosphate in the floodplain lakes Waaienstein, Ewijk, and Oude Waal showed their highest concentrations during periods of flooding (Fig. 6), indicating riverine input of these nutrients. In the frequently inundated lakes Ewijk and Waaienstein silicate depletion occurred during April-May and during July-August, unlike the other lakes and the main channel, where silicate depletion occurred only during February-April or not at all (Pond G).
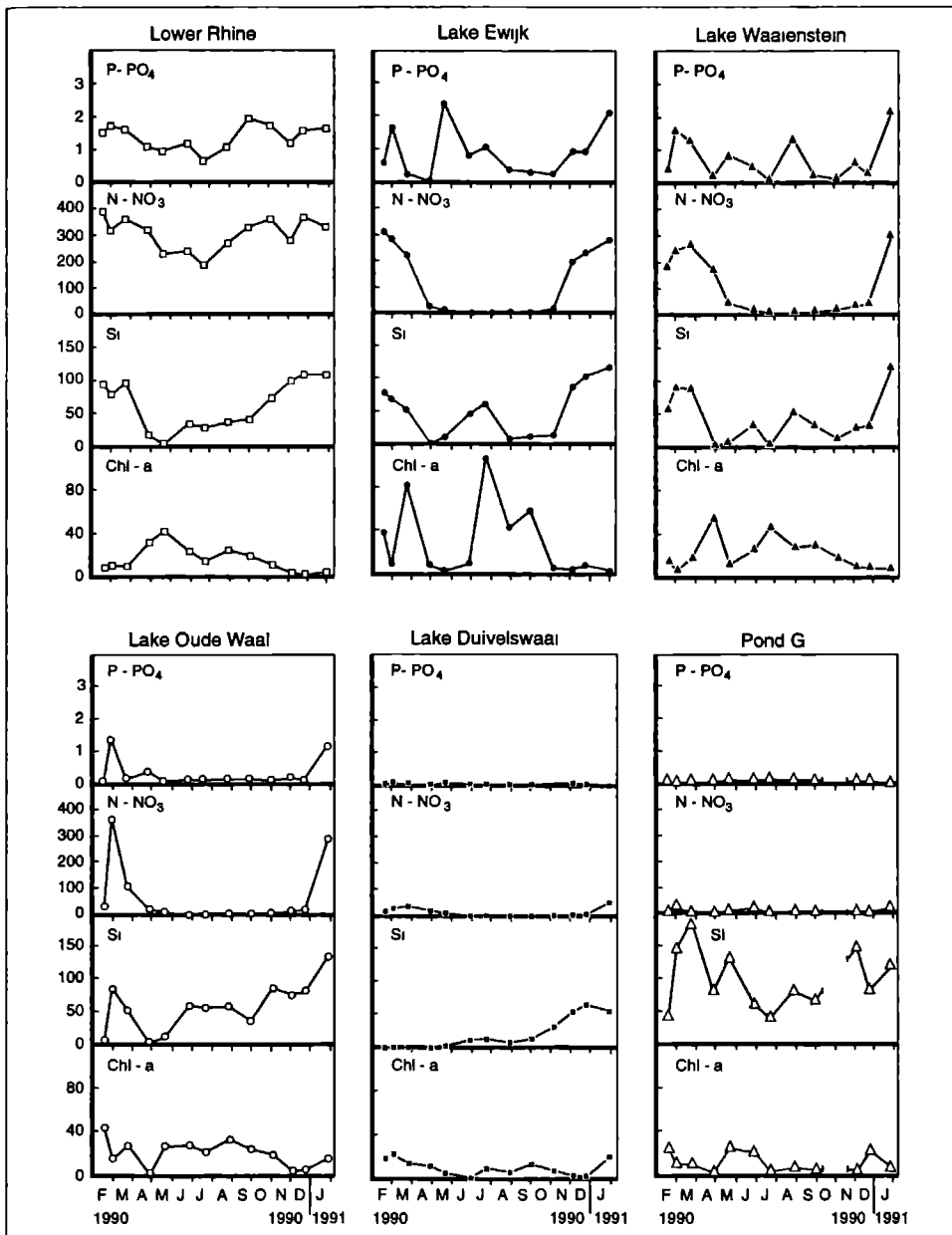
Figure 6. *Seasonal fluctuations in nutrients (in μmol l⁻¹) and chlorophyll-a (in μg l⁻¹) of the main channel of the Lower Rhine, Lake Ewijk, Lake Waaienstein, Lake Oude Waal, Lake Duivelswaai and Pond G.*

Table 6 shows the annual mean concentrations of major ions, nutrients, chlorophyll-a and nutrient ratios in the main channel of the Lower Rhine and five lakes along an inundation gradient. It can be seen that the annual mean levels of (dissolved inorganic) N and P and the annual mean chlorophyll-a concentrations in the floodplain lakes increase with increasing flood duration, whereas the annual mean Si/N and Si/P ratios decrease (Table 6). The annual mean N and P concentrations in the floodplain lakes showed a clear positive correlation with annual mean chlorophyll-a levels (Spearman correlation coefficients: 0.97 and 0.99, $p < 0.001$) and with the annual flood duration (Spearman correlation coefficients: 0.99 and 0.97, $p < 0.001$). The annual flood duration of the lakes was inversely correlated with the annual mean Si/N and Si/P ratios (Spearman correlation coefficients: -0.79, $p < 0.10$ and -0.87, $p < 0.05$). The composition of the phytoplankton in the frequently flooded lakes Ewijk and Waaienstein in August showed a dominance of chlorophytes, euglenophytes and cyanobacteria, instead of diatoms, which were dominant in less frequently flooded lakes at that time (Table 7).

Table 6. *Annual mean values ($\pm$ S.D., n = 12) of physico-chemical parameters for the main channel and five floodplain waters along a flooding gradient of the Lower Rhine during 1990. Flood duration = longterm average annual flood duration in days per year (1901-1985). All parameters in $\mu mol\ l^{-1}$, except pH (pH-units) and Chlorophyll-a (in $\mu g\ l^{-1}$).*

	R. Lower Rhine	Lake Ewijk	Lake Waaienstein	Lake Oude Waal	Lake Duivelswaai	Pond G
Flood duration	–	67	23	3	0	0
Na	3900 (1300)	2100 (500)	1700 (300)	1600 (300)	1500 (200)	520 (100)
Cl	4400 (1500)	2600 (500)	2100 (400)	2000 (400)	1700 (200)	590 (100)
EC	800 (160)	580 (80)	520 (130)	520 (40)	560 (130)	570 (260)
K	180 (40)	140 (30)	150 (30)	130 (30)	110 (10)	70 (30)
SO$_4$	520 (160)	420 (100)	350 (90)	410 (130)	370 (90)	860 (900)
Mg	440 (70)	400 (70)	340 (100)	400 (100)	410 (90)	580 (130)
Ca	1700 (200)	1100 (300)	1000 (300)	1400 (200)	1200 (400)	1900 (1200)
HCO$_3$	2200 (200)	1800 (300)	1800 (400)	2300 (200)	2800 (400)	3700 (1900)
pH	7.8 (0.1)	8.1 (0.5)	8.0 (0.3)	7.9 (0.2)	8.0 (0.2)	7.8 (0.3)
NO$_3$	310 (60)	120 (130)	110 (110)	70 (120)	15 (15)	10 (20)
NH$_4$	20 (10)	30 (30)	30 (20)	20 (20)	15 (15)	20 (20)
d-PO$_4$	1.4 (0.4)	0.9 (0.7)	0.8 (0.7)	0.3 (0.4)	0.1 (0.0)	0.2 (0.2)
Si	60 (40)	50 (40)	40 (40)	60 (40)	20 (20)	110 (60)
Chl-a	16 (12)	29 (35)	26 (20)	19 (10)	10 (7)	11 (9)
Si/N	0.2 (0.1)	0.3 (1.0)	0.3 (0.2)	4.4 (8.7)	1.0 (1.0)	10.6 (13.9)
Si/P	40 (20)	70 (60)	60 (40)	300 (200)	400 (700)	2400 (2900)

Table 7. *Relative abundance (%) of the major phytoplankton groups in the main channel and five floodplain waters along an inundation gradient of the Lower Rhine. Data from August (three samples per water body). Flood duration = longterm average annual flood duration in days per year (1901-1985). Miscellaneous includes Pyrrhophyta, Cryptophyta and Chrysophyta.*

	R. Lower Rhine	Lake Ewijk	Lake Waaienstein	Lake Oude Waal	Lake Duivelswaai	Pond G
Flood duration	–	67	23	3	0	0
Year of sampling	1987	1988	1987	1987	1988	1988
Cyanobacteria	5	20	12	4	8	9
Bacillariophyceae	65	5	27	68	55	60
Euglenophyta	0	20	4	4	4	3
Chlorophyta	28	50	54	21	30	24
Miscellaneous	2	5	3	3	3	4

Discussion and conclusions

Impact of drainage basin

The ordination of physico-chemical parameters of 100 floodplain lakes along the lower reaches of the rivers Rhine and Meuse reveals differences in chemistry between these lakes according to the drainage basin in which they are located (Fig. 3). These differences in chemistry are most pronounced in the ambient and interstitial water of frequently flooded lakes and concern concentrations of major ions, such as sodium, chloride, magnesium, potassium and sulphate, all of which are highest in the lakes along the Lower Rhine. The levels of these ions in the rivers Rhine and Meuse have increased enormously since 1900, as a result of domestic and industrial sewage (Zuurdeeg, 1980; Van der Weijden and Middelburg, 1989). At present the highest concentrations of the major ions are found in the main channel of the Lower Rhine, due to the more extensive mining activities in its drainage basin, compared with those in the River Meuse (Van den Brink et al., 1991b). Concentrations of sodium and chloride in particular have increased enormously over the years, especially in the Lower Rhine. Levels of sodium and chloride in the main channel of this river are nowadays sixteen times as high as those measured a century ago, whereas the levels of sulphate have increased by a factor of two during this period (Van den Brink et al., 1991b).

Both in the frequently flooded lakes and in the seepage lakes the highest concentrations of sodium and chloride were found in the ambient and interstitial water of the river Rhine floodplain lakes (Table 4). This must be due to the present differences in water chemistry between the rivers Rhine and Meuse with respect to sodium and chloride concentrations, as the original levels in these rivers were similar (Zuurdeeg, 1980). Because differences with respect to sodium and chloride concentrations between lakes in different drainage areas have also been found for seepage lakes, it is very likely that these ions are transported not only via flood water, but also via groundwater fluxes from the main channel towards the water bodies be-

hind the main dike. This view is further corroborated by a comparison between recent (Anonymous, 1989; own measurements) and historical data (Van Heusden, 1945) on chloride levels in the main channel and seepage lakes along the Lower Rhine. From 1938 to 1988 the annual mean chloride concentration in the main channel increased by a factor of 2, from 1.9 to 4.2 mmol l^{-1} (Van Heusden, 1945; Anonymous, 1989). Over the same period the mean chloride concentrations measured in seepage lakes along the Lower Rhine (summer measurements) increased by approximately the same factor, from 1 to 1.8 mmol l^{-1} (Van Heusden, 1945; Table 4).

Gradients and seasonal fluctuations of major anions

Chloride concentrations show major fluctuations in the main channel of the Lower Rhine, as a result from seasonal differences in river discharges. By contrast, minor fluctuations in the floodplain lakes have been found over the year, which indicates that chloride is a conservative ion in these water bodies. In the floodplain lakes of the rivers Rhine and Meuse, the levels of chloride show a clear positive correlation with the annual flood duration ($p < 0.001$) (Table 5). As a result of the longer period of connection between the river water and that of the floodplain lakes, the input of chloride is largest in frequently inundated lakes. Because chloride is a conservative ion the higher input of chloride in the frequently inundated lakes results in higher concentrations in these lakes (Table 6; Fig. 5). Alkalinity (or bicarbonate) shows the opposite trend: levels are higher in seepage waters than in frequently flooded lakes (Table 6; Fig. 5). The relatively higher levels in the seepage waters cannot be entirely explained by an input of carbonate-rich groundwater during high river discharges via seepage, as the alkalinity of the phreatic aquifer (2 meq l^{-1}) is much lower than the levels measured during seepage (3.5 meq l^{-1} in the deep Lake Duivelswaai; 5-9 meq l^{-1} in the shallow Pond G). Most probably alkalinity is generated in these seepage waters via the sulphate reduction process (Stumm and Morgan, 1981; Giblin et al., 1990; Kling et al., 1991). It is assumed that sulphate enters seepage lakes via percolation of river water through the main dike and is retained in the sediment as sulphide. Because the sediment of seepage lakes is not removed via flooding, there is a net retention of sulphur in these lakes, unlike the situation in frequently flooded lakes, where sulphur is removed with the sediment via strong currents which occur during the floods. Evidence for a major contribution of sulphate reduction to the alkalinity generation is provided by the decreases in sulphate levels in Pond G after periods of seepage and the simultaneous increases in alkalinity (Fig. 5). Moreover, the increases in alkalinity during February 1990 and December 1990-January 1991 (respectively 2 and 6 meq l^{-1} HCO_3^-) were about twice as high as the decreases in sulphate concentrations during these periods (respectively 0.9 and 3.2 meq l^{-1} SO_4^{2-}), which is in agreement with the ratio [produced HCO_3^-]/[reduced SO_4^{2-}] of the sulphate reduction process (Stumm and Morgan, 1981). Levels of sulphate and alkalinity were particularly high in the shallow seepage pond G when it was refilled via seepage after a period of drought, during which the pond ran dry. Because of its shallowness and the accumulation of sulphides in the sediment of this pond, large fluctuations in sulphate concentrations and alkalinity occur as a result from oxidation-reduction processes in response to running dry

and refilling. After the spring floods, a decrease in alkalinity was observed in all floodplain lakes, which can be attributed to calcium carbonate precipitation, a common phenomenon in hardwater lakes (Wetzel, 1975; Moss and Balls, 1989).

Loading and seasonal depletion of nutrients: impact on phytoplankton

In the main channel of the eutrophic Lower Rhine the concentrations of nitrate and dissolved phosphate are extremely high all the year round, as a result of sewage and agricultural runoff in the drainage areas (Van der Weijden and Middelburg, 1989; Kempe et al., 1991), so that depletion of these nutrients by growth of phytoplankton or aquatic macrophytes does not occur (Fig. 6). The riverine phytoplankton, which is dominated by diatoms, is limited by silicate and light (Friedrich and Viehweg, 1984; Admiraal et al., 1990).

In the lentic floodplain waters the concentrations of nitrate and dissolved phosphate show a flooding gradient: highest levels have been measured in the most frequently flooded lakes (Tables 5, 6). Because levels of nitrate and dissolved phosphate in the main channel are extremely high all the year round, a high riverine input of these nutrients in the floodplain lakes might be expected during floods. The levels of nitrate and dissolved phosphate in the floodplain lakes indeed showed highest concentrations during floods (Fig. 6). During the growing season, when no floods occurred, nitrate became depleted in all floodplain lakes studied. During the same period dissolved phosphate was depleted in Lake Oude Waal, Lake Duivelswaai and Pond G, but not in the frequently flooded Lakes Ewijk and Waaienstein (Fig. 6). Although floodplain lakes often function as nutrient traps (Hamilton and Lewis, 1987; Forsberg et al., 1988; Junk et al., 1989; Pedrozo et al., 1992), our results indicate that there are differential losses of N and P. In the frequently flooded lakes peaks in chlorophyll-a and dissolved phosphate repeatedly occurred after each other, suggesting a regeneration of phosphate from the P-loaded sediments of these lakes after depletion by phytoplankton. The observation that the levels of exchangeable P in the sediment were highest in frequently flooded lakes is in good agreement with this (Table 5).

In eutrophic river systems, hydrology has a dramatic impact on the phytoplankton development in floodplain lakes: during 1990 the annual mean chlorophyll-a concentrations in the frequently inundated Lake Ewijk (29 μg l^{-1}) and Lake Waaienstein (26 μg l^{-1}) were much higher than that in the main channel (16 μg l^{-1}) or in the infrequently inundated Lake Oude Waal (19 μg l^{-1}). Annual mean chlorophyll-a levels were lowest in the seepage waters (10-11 μg l^{-1}). The annual maximum chlorophyll-a level of Lake Ewijk (120 μg l^{-1}) occurred during the summer (Fig. 6). During this period the chlorophyll-a level in this lake was four to ten times higher than the levels in the other floodplain lakes. The high summer chlorophyll-a levels in Lake Ewijk, and to a lesser extend those in Lake Waaienstein resulted from blooms of cyanobacteria (e.g. *Aphanizomenon flos-aquae*) and chlorophytes (e.g. *Scenedesmus* spec.). In the other floodplain lakes the summer phytoplankton was dominated by diatoms (e.g. *Cymbella, Diatoma, Fragilaria, Melosira, Synedra*). The higher chlorophyll-a levels in frequently flooded lakes most probably result from the input of relatively large quantities of nitrate and phosphate during floods, in addition to a shift in the nutrient ratios (Si/N and Si/P), due to sili-

cate depletion as a result of diatom blooms. Such shifts in nutrient ratios have been related to eutrophication processes, which can be observed as a shift in phytoplankton communities from a diatom dominance towards a dominance of cyanobacteria, often resulting in higher chlorophyll-a levels (Officer and Ryther, 1980; Moss and Balls, 1989; Admiraal and Van der Vlugt, 1990, Horn and Horn, 1990). Indeed, the annual mean N and P levels in the floodplain lakes showed a clear positive correlation with annual mean chlorophyll-a levels ($p < 0.001$) and with the average annual flood duration ($p < 0.001$). Hence, it can be stated that the increased levels of riverine N and P are responsible for the eutrophication of floodplain lakes along the rivers Rhine and Meuse in The Netherlands.

Impact of hydrology

The present study shows that the water chemistry and phytoplankton development in floodplain lakes along the eutrophic and polluted rivers Rhine and Meuse are strongly related to the water chemistry in the main channels, as well as to the hydrology (Tables 4, 5, 6; Figs. 3, 5, 6). This was also found to be true for the more pristine tropical river-floodplain ecosystems, such as the Amazon (e.g. Forsberg et al., 1988), the Orinoco ((e.g. Hamilton and Lewis, 1987), and the Parana (e.g. Pedrozo et al., 1992), and may be a general phenomenon of large river-floodplain systems (Junk et al., 1989), despite strong differences in water chemistry and hydrology among river-floodplain systems.

In figure 7 a conceptual model is presented about the relationship between the fluxes of ions via floods and seepage on the one hand, and the levels of ions and the development of micro- and macrophyte communities in floodplain lakes on the other hand. Because of the high concentrations of major ions, nutrients and (heavy) metals in the main channels of anthropogenically influenced river-floodplains, such as the Lower Rhine and Meuse (Zuurdeeg, 1980; Van der Weijden and Middelburg, 1989), there is a net input of these chemicals in the lentic floodplain waters, mainly via inundations. The longer the annual flood duration, the longer the period of connection between the river and the lake water, and the higher the concentrations of salts, nutrients and (heavy) metals in the water and/or sediment of these lakes. Apart from an input of chemicals via flood water fluxes there is a transport of several water-soluble ions, such as sodium, chloride and sulphate, via groundwater fluxes (Fig. 7). In seepage lakes and infrequently flooded lakes sulphate reduction processes are responsible for the high levels of alkalinity in these lakes. These alkalinization processes are probably triggered via the input of sulphate from the main channel by seepage and floods.

The hydrology of the eutrophic rivers Rhine and Meuse clearly exercises its impact on the phytoplankton development, and consequently on the development of macrophytes, in the lentic floodplain systems, through the input of large quantities of nutrients (N, P) via inundations (Figs. 6, 7). Especially in frequently flooded lakes high chlorophyll-a levels occur as a result of blooms of cyanobacteria and chlorophytes (Tables 6, 7), which hinder the development of submerged macrophytes (Table 1; Fig. 7). Restoration of connections between the main channels of the eutrophic Lower Rhine and Meuse and associated floodplain lakes will inevitably result in hypertrophic conditions in these lakes. In order to maintain the well de-

Figure 7. *Conceptual model of the impact of hydrology on the ion fluxes, and the algal and macrophyte development within floodplain lakes along polluted and eutrophic rivers. +/- indicates a major increase or decrease along the direction of the arrows.*

veloped aquatic vegetation (and the associated fauna) in infrequently flooded lakes, and in order to restore these communities in frequently flooded lakes, a low input of nutrients, salts and other pollutants is essential (Van den Brink and Van der Velde, 1991). Hence rehabilitation of the degraded river-floodplain ecosystems of the Lower Rhine and Meuse should not merely focus on restoration of connections, but should also include water quality measures which reduce the loads of nitrogen, phosphate, sulphate, chloride and sodium.

Acknowledgements

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Impact of hydrology on phyto- and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse

Abstract

Floodplain lakes along the rivers Lower Rhine and Meuse in The Netherlands can be categorized according to their hydrology and geomorphology. The impact of hydrology on the summer plankton community composition in 100 floodplain lakes was studied by multivariate analyses (TWINSPAN, FLEXCLUS, DCA) of relative abundance data of plankton. The phyto- and zooplankton community composition in floodplain lakes is clearly related to hydrology, relevant nutritional resources and habitat characteristics, mainly via input of N and P from the eutrophic main channels during floods. The plankton species richness was related to the complexity of habitats formed by the presence of aquatic vegetation. There was a good agreement between the ecological and the environmental characterization of site groups. Cyanobacteria, Chlorophyta, and filter-feeding zooplankton taxa associated with open water are characteristic for floodplain lakes with a long annual flood duration, low Si/N and Si/P ratios, and a poorly developed aquatic vegetation. Bacillariophyceae and scraping zooplankton taxa associated with aquatic macrophytes are characteristic for floodplain lakes with a short annual flood duration, high Si/N and Si/P ratios, and a well-developed aquatic vegetation. It is concluded that restoration of connections between rarely flooded lakes and the highly eutrophic main channels of the Lower Rhine and Meuse will result in hypertrophic conditions and a reduced plankton diversity in these lakes.

Introduction

Floodplain lakes are important refuge and reproduction sites for riverine and wetland species (Amoros and Roux, 1988; Junk et al., 1989). The flood pulse is considered to be the principal driving force for the existence, productivity and interactions of the biota in these ecosystems (Junk et al., 1989; Schiemer and Zalewski, 1992). Depending on hydrological and geomorphological conditions, the frequency, duration and extent of floodplain inundation may vary among floodplain lake ecosystems (Amoros and Roux, 1988; Junk et al., 1989; Van den Brink, 1990). Floods allow an exchange of biota, chemicals, organic matter and sediment between lotic and lentic fluvial subsystems, so that an impact of the hydrology on the plankton communities in floodplain lakes can be expected. In floodplains of highly eutrophic rivers, the water quality of the main channel has been found to exert a strong influence on the floodplain lake communities via the hydrological regime (Moss and Balls, 1989; Moss et al., 1989; Van den Brink and Van der Velde, 1991; Van den Brink et al., 1991, 1993a). In floodplain lakes along the Lower Rhine and Meuse, positive correlations have been found between the annual flood duration and the concentrations of dissolved nutrients and chlorophyll-a, indi-

cating a major impact of hydrology on phytoplankton biomass within these lakes (Van den Brink et al., 1993a).

Information on the role of hydrology on phyto- and zooplankton community composition in floodplain lakes is very sparse and concerns the phytoplankton mainly (e.g. Huff, 1986; Hamilton and Lewis, 1987; Moss and Balls, 1989; Moss et al., 1989; Pedrozo et al., 1992; Van den Brink et al., 1993a). Such knowledge, however, is extremely relevant in order to understand and predict changes in floodplain lake communities resulting from hydrological changes in these lakes. Such hydrological changes might arise from river regulation, embankments or river-floodplain restoration programmes which aim at an enhancement of river dynamics and the restoration of connections between the main channel and its isolated floodplain lakes (e.g. Bravard et al., 1986; Amoros and Roux, 1988; Klink et al., 1991; Van den Brink et al., 1993b).

Plankton studies in the river systems of the Rhine and Meuse have focussed on the main channels (e.g. Peelen, 1975; Friedrich and Viehweg, 1984; Descy, 1987; Descy et al., 1987; Admiraal et al., 1990; Friedrich, 1990; De Ruyter van Steveninck et al., 1990a, 1990b, 1992). Surprisingly little attention has been paid to plankton communities in the floodplain lakes along these eutrophic rivers (Leentvaar, 1958; Wibaut-Isebree Moens, 1965; Berndt and Neumann, 1985; Roijackers, 1985, 1986; Roijackers and Kessels, 1986), despite the fact that phyto- and zooplankton production may reach higher values in backwaters and in very slowly flowing side channels than in the main channels (Wissmar et al., 1981; Berndt and Neumann, 1985; Ertl, 1985; Amoros and Roux, 1988; Van den Brink et al., 1993a). In order to study the impact of hydrology on the phyto- and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse multivariate analyses were performed on the summer plankton species composition in 100 floodplain lakes in relation to annual flood duration and other environmental parameters. Our study addresses the following questions: 1. Does hydrology affect the species composition of plankton communities in floodplain lakes along the Lower Rhine and Meuse? 2. Which plankton taxa assemblages characterize various hydrologically-different categories of floodplain lakes? 3. Is there agreement between the environmental characterization of floodplain lakes and the ecological characteristics of the plankton taxa in these lakes with respect to their use of nutritional resources and their habitat association?

Sites and methods

Study sites

Floodplain lakes associated with the Lower Rhine and Meuse in The Netherlands can be categorized according to their geomorphology and hydrology. Sites were selected in the lowland reaches of both rivers, beyond brackish water and tidal influences (Fig. 1). During the periods July-September of 1987 and 1988 28 oxbow lakes, 22 break-through lakes, 23 clay-pit lakes and 27 sand-pit lakes were each sampled once for phyto- and zooplankton, combined with
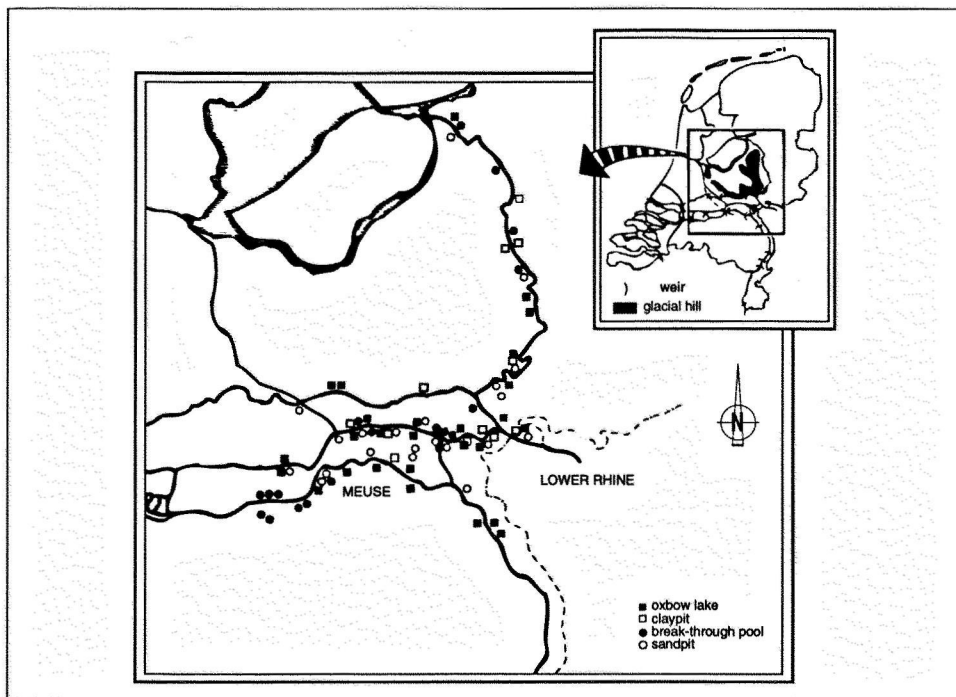
Figure 1. *Map of the sampling sites.*

measurements of physico-chemical parameters of water and sediment. The presence of sub-merged and nymphaeid aquatic macrophyte stands was recorded. During the sampling periods the sites were not flooded by the river.

Hydrology

A hydrological characterization of the main channels of the rivers Rhine and Meuse has been presented in Van den Brink et al. (1991). Major hydrological differences between these river systems include the drainage areas and discharge characteristics. The total drainage area of the River Rhine measures 185,000 km², while the total drainage area of the River Meuse is 33,000 km². According to long-term measurements (1901-1985) the discharge of the R. Rhine at the Dutch-German border averages 2,200 m³ s⁻¹, while the discharge of the R. Meuse at the Dutch-Belgian border averages 250 m³ s⁻¹.

Normally, the Dutch floodplain lakes are inundated during the winter and spring, i.e., out-side the vegetation growth season. Most lakes are isolated from the river during the rest of the year, except for water bodies which have a permanent open connection with the main channel. The duration and frequency of inundation of the lakes largely depends on the presence and height of summer dikes and natural levees, together with actual water-level fluctuations in the
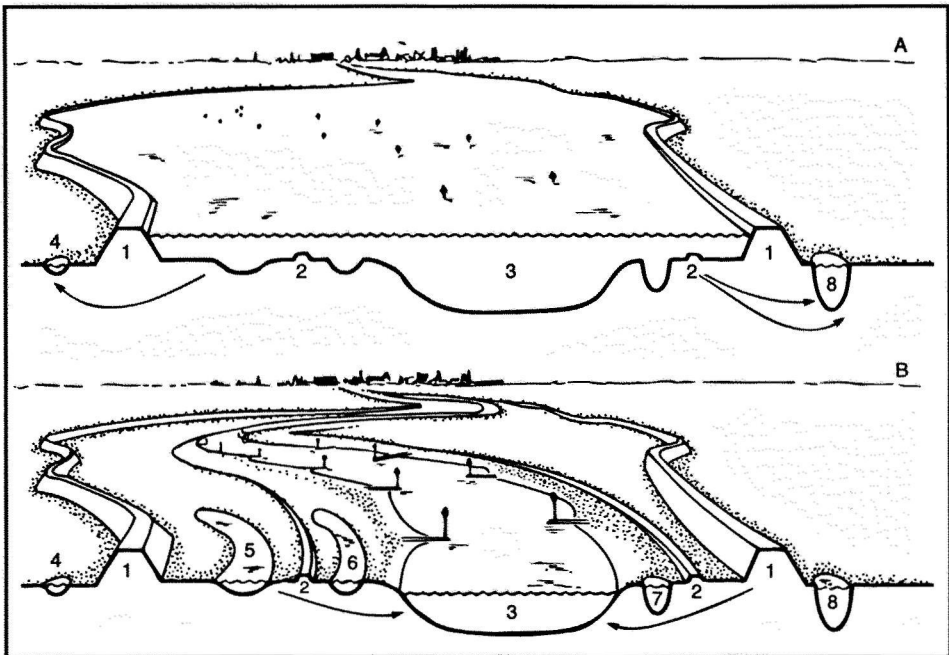
Figure 2. *Schematic view of the floodplain waters within a regulated river system, during winter (A) and summer (B). 1 = main dikes, 2 = summer dikes, 3 = river bed, 4, 8 = seepage lakes, 5 = rarely-flooded lake, 6, 7 = frequently-flooded lakes, 4-6 = shallow lakes, 7, 8 = deep lakes. Arrows indicate directions of groundwater fluxes.*

main channel. In general, the flood duration and flood frequency of the lakes decrease with increasing distance from the main channel. The water bodies behind the main dikes are never flooded and are influenced by river water through seepage only (Fig. 2).

In order to quantify the hydrological situation of the floodplain lakes, the annual flood duration was calculated as follows. First, river maps were used to estimate the inundation level for each site, i.e., the lowest water level of the river at which the part of the floodplain which includes that specific site is inundated. Next, the long-term (1901-1985) annual mean number of days on which the water level in the main channel reached this level of inundation was calculated (= annual flood duration). Hydrological data were obtained from the Institute for Inland Water Management and Waste Water Treatment (RIZA, The Netherlands).

Plankton

In order to study the species composition of the summer plankton, one mixed sample per water body was taken by drawing a net (diameter of net opening: 20 cm, mesh width: 60 µm) three times through the water over a distance of 10 m, in a horizontal movement directed towards the shore, about 50 cm below the water surface and at least 1 m above the sediment sur-

face. Samples were immediately fixed in 4 % formol (as in Roijackers, 1985). By sampling this way, the relative abundances of some very small sized species are likely to have been underestimated. However, for a study of the major similarities and dissimilarities of the plankton composition between lakes, a reasonably complete species list satisfies. In the laboratory, the samples were concentrated to a volume of about 15 ml. After thoroughly mixing, three to five 0.05 ml drops of this concentrated sample were examined under a normal light microscope in order to determine the species composition. All plankton taxa were identified to species level (where possible) and the relative abundance of the taxa was estimated on the following scale: 0: absent; 1: rare taxon, 1-10 specimens per drop; 2: frequent taxon, 11-100 specimens per drop; 3: dominant taxon, > 100 specimens per drop.

Physico-chemical parameters

At each site a mixed sample (2 l) of the surface water was taken, for an analysis of the water chemistry. This water sample was a mixture of ten 200 ml subsamples, randomly taken at a depth of about 20 cm below the water surface and at least 1 m above the sediment surface in the open water compartment, i.e., outside the vegetation belt. Sediments were collected from below the water layer in the littoral zone, by means of a metal tube with a diameter of 7 cm. The upper 10 cm of sediment was sampled. Because of the heterogeneity of the sediment, eight samples were collected and mixed. Sediment-water extracts were made for the assessment of the chemical composition of the interstitial water. A detailed account of the methods of analysis is presented in Van den Brink et al. (1993a). In order to relate the physico-chemical parameters of the water bodies to the planktonic communities, a selection of these parameters was made, based on co-variation (Van den Brink et al., 1993a) and relevance for plankton. The following parameters were selected: turbidity (TURB), DIN (= NO_3^- + NO_2^- + NH_4^+), DIP (= oPO_4), Fe, Si, DIN/DIP-ratio (N/P), Si/DIN-ratio (Si/N) and the Si/DIP-ratio (Si/P) of the surface water, DIP of the interstitial water (Psed) and percentage organic matter of the sediment (POM). The maximum depth of the water bodies (DEPTH) was recorded as deep (> 6 m) or shallow (< 6 m).

Data analysis

The 100 sampling sites were classified and ordinated on the basis of the zoo- and phytoplankton taxa composition (abundance scores). Taxa were used in the analyses only when at least present in 5 % of these sites; 150 taxa were so recorded.

Initial clustering of sites was performed using two-way indicator species analysis (TWIN-SPAN), which is based on reciprocal averaging (Hill, 1979). This initial clustering was improved by fusing and dividing clusters, using FLEXCLUS (Van Tongeren, 1986). The criteria applied to this improvement were stability and homogeneity of clusters, combined with ecological insight.

Differences in physico-chemical parameters among site groups were tested for significance using the Wilcoxon test (Sokal and Rohlf, 1981). In order to relate the annual flood dura-

tion to other physico-chemical parameters a Spearman rank correlation test was used (Sokal and Rohlf, 1981).

Detrended correspondence analysis (DCA) was used to ordinate the 150 taxa found in the 100 samples and to analyse the importance of the environmental gradients along which the taxa and the sites were plotted. The option to downweight rare taxa was used, thus avoiding the tendency of rare taxa to distort the analysis (Ter Braak, 1987). Abiotic environmental parameters were log-transformed because they were log-normally distributed. The biotic environmental parameters (the presence or absence of submerged (SUBM) and nymphaeid (NYMP) macrophyte stands) were used in the present study in order to relate the species composition of the phyto- and zooplankton to the presence and growth form of the aquatic vegetation.

Fisher's exact test (Sokal and Rohlf, 1981) was used in order to test clusters for characteristic taxa, i.e. taxa which are significantly more present or absent in any site group. Common taxa are defined here as taxa which occur in at least 76% of the sites within a site group. For an ecological characterization of the site groups only these characteristic and common plankton taxa were used.

In order to describe the site groups in terms of habitat associations of the characteristic and/or common phytoplankton and zooplankton taxa, these taxa were categorized as open water species, macrophyte associated species and sediment associated species (Redeke, 1948; Hutchinson, 1967; Gliwicz and Rybak, 1976; Round, 1981; Reynolds, 1984; Streble and Krauter, 1988). In order to describe the site groups in terms of feeding mechanism (nutritional resources) of the characteristic and/or common zooplankton taxa (Copepoda, Cladocera and Rotifera), these taxa were assigned to the functional feeding groups of predator, filter-feeder, scraper and (herbivorous) sucker according to Gliwicz and Rybak (1976). Taxa which belonged to more than one category were assigned to all categories involved. For each site group the number of taxa per category was expressed as the percentage of the total number of characteristic (see Tables 5 and 6) and/or common (see Tables 7 and 8) taxa within that site group. All calculations were performed on an IBM 3090 mainframe using the Statistical Analysis System (SAS Institute Inc., 1989).

Results

Classification of the 100 water bodies on the basis of relative abundance data of 150 phyto- and zooplankton taxa shows a division into four major site groups (Tables 1-8). Seven water bodies were discarded from further analysis of the site groups, because they could not be assigned to any group and were very heterogeneous as a whole. They can be considered as transition sites, as suggested from their intermediate position between the four site groups as presented in the DCA plot of the sites (Fig. 3).

A hydrological, geomorphological and vegetational characterization of the site groups is presented in table 1. It is very clear that the four site groups form a flood duration gradient. Group A sites nearly all (82%) have a permanent open connection to the main channel. Group
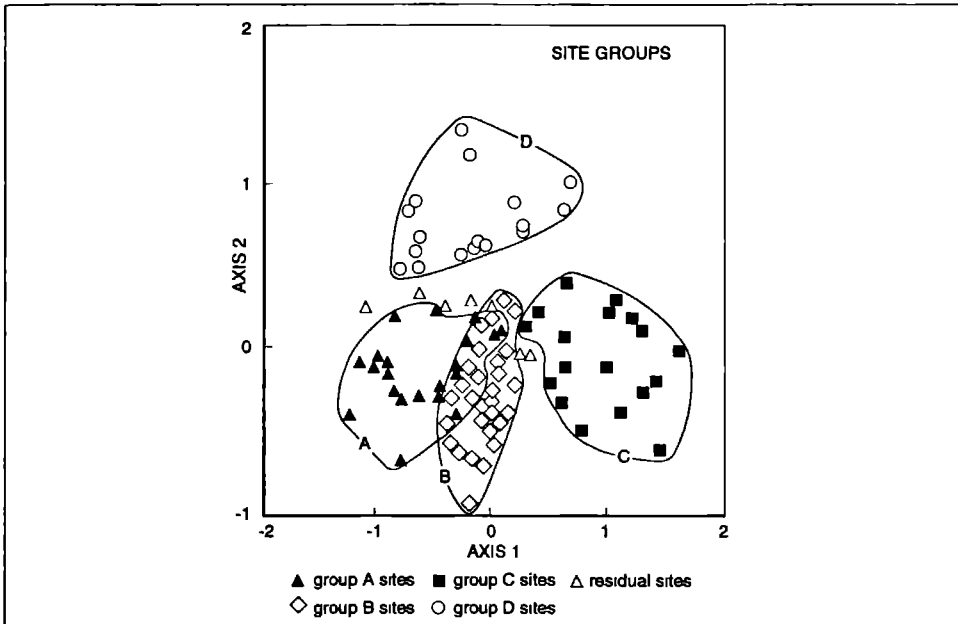
Figure 3. *DCA ordination plot of the sites and site groups, based on relative abundance of plankton taxa.*

B and C sites are mostly (75-97%) situated in the river forelands and are connected with the main channel only during floods. Group D sites are predominantly (94%) situated behind the main dike and only receive river water via seepage. Apart from a flood duration gradient the four site groups also differ in the maximum depth of their water bodies. Site groups A and D predominantly (82%) include relatively deep water bodies (maximum water depth > 6 m, up to 30 m); site groups B and C predominantly (69-71%) enclose shallow water bodies (maximum water depth < 6 m, mostly up to 3 m). In addition, the presence or absence of aquatic vegetation and the dominant growth form of the vegetation varied for the four site groups. Aquatic vegetation was scarcely present (22%) in group A sites; nymphaeids were most common (63-75%) in the site groups B and C, whereas submerged vegetation was most common (82%) in the sites of group D (Table 1).

Pphysico-chemical characterization of the site groups and the results of a Wilcoxon test for significant differences between physico-chemical parameters of these groups revealed that all parameters selected, except the N/P ratio, showed significant differences between the four site groups (Table 2). The longterm average annual flood duration of the site groups was the single environmental parameter to show significant differences (p < 0.001, Wilcoxon test) between all site groups (Table 2), indicating a flood duration gradient ranging from sites which are in permanent open connection with the main channels (group A) to sites which are situated behind the main dike and which are influenced by the river via seepage only (group

Table 1. *Hydrological, geomorphological and vegetational characteristics of the site groups from the improved TWINSPAN clustering as relative occurrence of sites (%) per group.*

Site group	A	B	C	D
Number of sites	(22)	(38)	(16)	(17)
HYDROLOGY				
sites in open connection	82	0	0	0
isolated sites in river forelands	18	97	75	6
isolated sites behind main dike	0	3	25	94
GEOMORPHOLOGY				
deep sites (> 6 m)	82	29	31	82
shallow sites (< 6 m)	18	71	69	18
AQUATIC VEGETATION				
sites with submerged macrophytes	22	37	50	82
sites with nymphaeid macrophytes	0	63	75	47
sites without aquatic macrophytes	78	29	0	0

D). The Si/P ratios of site groups A and B were significantly (p < 0.05, Wilcoxon test) lower than those of site groups C and D (Table 2). Si/P and Si/N ratios were both negatively correlated (p < 0.001) with the annual flood duration of the sites (Table 3). The levels of DIN, DIP and exchangeable P in the sediment (P-sediment) were positively correlated (p < 0.001) with the annual flood duration of the sites (Table 3).

A DCA plot based on the relative abundance of the plankton taxa shows the major environmental gradients which are correlated with the axes 1 and 2 (Fig. 4). The percentages of variance accounted for by axes 1 and 2 are 19 and 14 %; their eigenvalues are 0.25 and 0.17 respectively. The first axis is positively correlated with the silicate concentration, the Si/P-ratio, the Si/N-ratio and the presence of nymphaeids, and negatively correlated with the annual flood duration and the maximum depth of the water bodies. The second axis is positively correlated with the presence of submerged vegetation and the maximum water depth and negatively correlated with the annual flood duration and the turbidity (Fig. 4). In this figure the phytoplankton and the zooplankton taxa are plotted as symbols which indicate the taxonomic group to which they belong. In contrast to the zooplankton groups, the major phytoplankton groups appear as more or less separated clusters. Cyanobacteria and Chlorophyta are for the greater part separated from the Bacillariophyceae along the arrow which points into the direction of an increase in annual flood duration and which points in the opposite direction from the increase in Si/N and Si/P ratios and the presence of submerged macrophytes (Fig. 4).

Table 2. *Means (and extremes) of physico-chemical parameters of water and sediment of the water bo-dies per site-group from the improved TWINSPAN clustering of plankton composition. Means with the same letter are not significantly different (Wilcoxon test, p < 0.05). Concentrations in μmol l^{-1}, turbidity in ppm, organic matter content of sediment in % dry weight, and annual flood duration in number of days year^{-1}. P-sediment (= water exchangeable P in sediment).*

Site group	A	B	C	D
HYDROLOGY				
Annual flood duration	303[a]	14[b]	4[c]	0[d]
	(25-365)	(0-67)	(0-10)	(0-1)
WATER				
DIN	56[a]	14[b]	9[b]	11[b]
	(8-203)	(2-84)	(2-51)	(0-57)
DIP	2.2[a]	0.8[b]	0.9[b]	0.3[c]
	(0.1-8.9)	(0.1-4.3)	(0.1-3.0)	(0.1-2.5)
Si	23[b]	30[b]	98[a]	15[b]
	(3-65)	(0-140)	(8-210)	(2-64)
Fe	0.5[c]	2.1[b]	5.3[a]	0.4[c]
	(0-2.7)	(0-29)	(0.3-32)	(0-1.3)
Si/N	1[c]	4[b]	15[a]	10[ab]
	(0-3)	(0-28)	(1-80)	(0-70)
Si/P	30[b]	60[b]	310[a]	120[a]
	(1-110)	(0-310)	(9-1280)	(5-640)
N/P	70[a]	30[a]	60[a]	80[a]
	(2-690)	(1-210)	(1-410)	(1-570)
Turbidity	6[b]	14[a]	8[b]	3[c]
	(1-14)	(2-71)	(1-10)	(1-7)
SEDIMENT				
P-sediment	24[a]	12[b]	5[c]	3[c]
	(4-120)	(1-130)	(1-17)	(1-7)
Organic matter	3[b]	7[a]	8[a]	6[b]
	(1-6)	(1-21)	(1-26)	(1-25)

Table 3. *Spearman rank correlation coefficients between the annual flood duration and physico-chemical parameters (n = 100 sites).*
***: p < 0.001, **: p < 0.01, n.s.: not significant.

	Annual flood duration
P-sediment	0.64 ***
DIN	0.54 ***
DIP	0.52 ***
Turbidity	0.28 **
N/P	−0.01 n.s.
Si	−0.03 n.s.
Fe	−0.11 n.s.
Organic matter sediment	−0.16 n.s.
Si/N	−0.38 ***
Si/P	−0.46 ***
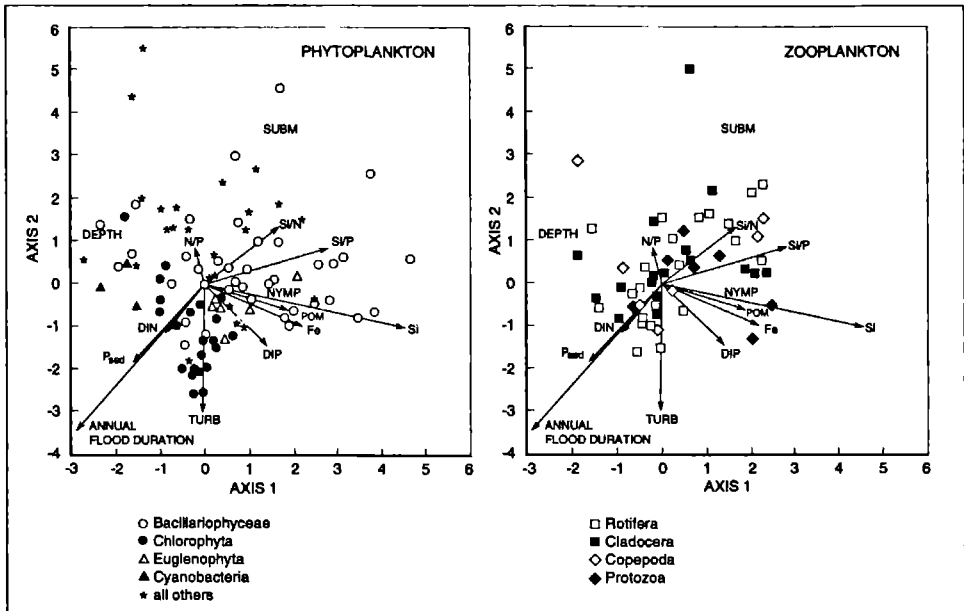
Figure 4. *DCA ordination plots of environmental parameters and the phytoplankton and zooplankton taxa as translated into taxonomic main groups. Abiotic environmental parameters (arrows) are plotted as biplot scores, biotic environmental parameters (NYMP, SUBM) are plotted as centroids. TURB: turbidity; NYMP: nymphaeids; SUBM: submerged aquatic macrophytes; Psed: exchangeable P in the sediment; POM: percentage organic matter in the sediment.*

The mean species richness of the phyto- and zooplankton calculated for each of the four site groups (Table 4) was lowest for the group A sites and rather similar for the other three groups. The latter three groups showed differences in the mean number of taxa of Bacillariophyceae, Euglenophyta and Chlorophyta (Table 4).

Characteristic phytoplankton taxa of site group A were Cyanobacteria and some Bacillariophyceae and Chlorophyta, while those of site group B included predominantly Euglenophyta and Chlorophyta, those of site group C almost exclusively Bacillariophyceae, and those of site group D predominantly Bacillariophyceae and Pyrrhophyta (Table 5). Characteristic zooplankton taxa of site groups A and D were few; site group B was characterized by Cladocera and Rotifera, and site group C by Protozoa (Table 6).

Table 4. *Means (and extremes) of the number of plankton taxa of the site groups from the improved TWINSPAN clustering. Miscellaneous includes Chrysophyta, Pyrrhophyta and Cryptophyta.*

Site group	A	B	C	D
Plankton taxa	35 (23-70)	52 (30-82)	50 (32-81)	51 (32-72)
Phytoplankton taxa	23 (13-47)	33 (15-53)	32 (13-51)	32 (21-51)
Zooplankton taxa	12 (6-27)	19 (11-32)	18 (10-30)	19 (9-33)
Cyanobacteria	3 (1-5)	3 (0-5)	1 (0-4)	3 (1-5)
Bacillariophyceae	11 (3-25)	11 (1-25)	19 (5-30)	13 (6-25)
Euglenophyta	0 (0-2)	4 (0-10)	2 (0-5)	2 (0-5)
Chlorophyta	8 (3-17)	14 (5-22)	8 (1-15)	11 (4-20)
Protozoa	1 (0-5)	3 (0-6)	4 (1-6)	3 (0-5)
Copepoda	2 (1-4)	2 (1-4)	3 (0-4)	2 (1-4)
Cladocera	5 (1-11)	6 (0-12)	5 (1-11)	6 (2-12)
Rotifera	4 (1-12)	8 (3-13)	6 (1-15)	8 (3-13)
Miscellaneous	1 (0-3)	1 (0-4)	2 (0-3)	3 (0-6)

When the plankton taxa present in the DCA plots are characterized by their substrate association and position in the water layer as open water taxa (limnoplankton), benthos or epiphyton, it appears that the benthic and epiphytic taxa were mainly present at sites with a short annual flood duration and absent from sites with a long annual flood duration (Fig. 5).

A characterization of the site groups based on the habitat association of the characteristic (Tables 5, 6) and common (Tables 7, 8) plankton taxa points into the same direction (Fig. 6): the relative species richness of taxa associated with open water is highest in sites of groups A and B, which have a relatively long annual flood duration, whereas the relative species richness of the macrophyte and sediment associated species is highest in the rarely-flooded and non-flooded sites of groups C and D.

A characterization of the site groups based on the numbers of the characteristic and common zooplankton species categorized as functional feeding groups shows that the relative species richness of filter-feeders was highest in lakes with a long flood duration, i.e. site groups A and B, whereas the relative species richness of scrapers was highest in hydrologically more isolated lakes, i.e. site groups C and D (Fig. 6).

Table 5. *Relative frequency of occurrence of characteristic phytoplankton taxa within the site groups from the improved TWINSPAN clustering. Only species which are significantly more frequently (+++, ++, +) or less frequently (——, —, –) present (Fisher's exact test) within a site group as compared to all other site groups have been indicated.*
+++/——: p < 0.001, ++/—: p < 0.01, +/–: p < 0.05.

Site group	A	B	C	D
CYANOBACTERIA				
Anabaena spiroides	++		–	
Aphanizomenon flos-aquae	++	++	—-	
Microcystis aeruginosa	+++		—-	
BACILLARIOPHYCEAE				
Asterionella formosa	++			
Aulacoseira granulata	+			——
Caloneis amphisbaena			+++	
Cocconeis pediculus			+++	——
Cyclotella/Stephanodiscus spec	+++			——
Cymbella cistula			++	
Cymbella lanceolata	—-		+++	
Cymbella prostrata				+
Cymbella ventricosa	–		+	
Eunotia pectinalis			+++	
Fragilaria capucina		–		
Fragilaria construens			+	
Fragilaria crotonensis		–		+
Gomphonema acuminatum			+++	
Gomphonema constrictum	—-		+++	+
Gyrosigma acuminatum			+	
Gyrosigma attenuatum				+++
Melosira varians			++	–
Rhopalodia gibba				+
Surirella elegans				+
Synedra capitata	–		+++	
Synedra pulchella			+++	
Synedra ulna			+	
CHRYSOPHYTA				
Chrysococcus spec.	—-	+++		
Dinobryon divergens	—			+++
Synura spec			+++	
EUGLENOPHYTA				
Euglena spec	—-	+++		
Phacus longicauda	——	+++		——
Phacus pleuronectes	—-	++		
Trachelomonas hispida	——	++		
Trachelomonas volvocinopsis	——	+++		
PYRRHOPHYTA				
Ceratium hirundinella		—	—	+++
Peridinium spec	–			+++
CRYPTOPHYTA				
Cryptomonas erosa			+++	

Table 5. *Continued*

Site group	A	B	C	D
CHLOROPHYTA				
Actinastrum hantzschii		+++		–
Ankistrodesmus falcatus	–––	+++		—
Crucigenia apiculata	—	+++	–	
Crucigenia quadrata		+++		
Dictyosphaerium pulchellum		+++		——
Eudorina elegans	++	——		
Pediastrum boryanum	–	+++	–	
Pediastrum duplex	+	++		——
Pediastrum tetras	——	+++		
Scenedesmus acuminatus		+++		–
Scenedesmus arcuatus	–	+++		
Scenedesmus dimorphus		+++	+	——
Scenedesmus quadricauda	–	+++		–––
Selenastrum westii	–	+++		
Tetraedron minimum		+++		
Tetraedron regulare	–	+++		
Closterium acutum		++		
Staurastrum planctonicum	+++		–	
Spirogyra spec.				+++
Zygnema spec.				+++

Table 6. *Relative frequency of occurrence of characteristic zooplankton taxa within the site groups from the improved TWINSPAN clustering. Only species which are significantly more frequently (+++, ++, +) or less frequently (———, —, –) present (Fisher's exact test) within a site group as compared to all other site groups have been indicated.*
+++/———: $p < 0.001$, ++/—: $p < 0.01$, +/–: $p < 0.05$.

Site group	A	B	C	D
PROTOZOA				
Arcella gibbosa			+++	
Arcella vulgaris	——		+++	
Centropyxis aculeata		–		+
Difflugia spec.	–––			
Epistylus spec.		+		
Halteria spec.			+	
Tintinnopsis lacustris		+++	+++	
COPEPODA				
Cyclops spec.	+			
Cyclops strenuus		++		
Eucyclops serrulatus	–			
Harpacticidae		–	+	

Table 6. *Continued*

Site group	A	B	C	D
Mesocyclops hyalınus				–
Mesocyclops leuckartı		——	–	+++
CLADOCERA				
Alona guttata				——
Alonella exigua		–		+++
Bosmına longırostrıs	——	+++		
Cerıodaphnıa pulchella	——	+++		
Chydorus sphaerıcus			+	
Daphnıa cucullata	+	+	—	–
Dıaphanosoma brachyurum	+++	–	———	
Eurycercus lamellatus			++	
Graptoleberıs testudınarıa			+	
Pleuroxus truncatus	–			
Scapholeberıs mucronata	–	+++		
Sıda crystallına		+		
Sımocephalus vetulus	–		+++	
ROTIFERA				
Asplanchna prıodonta	———	+++	–	
Brachıonus angularıs	——	+++		
Brachıonus calycıflorus	—	+++		——
Brachıonus dıversıcornıs		++		
Brachıonus quadrıdentatus		++		
Fılınıa longıseta	———	+++		–
Kellıcottıa longıspına			–	+
Keratella cochlearıs	———	+++	–	
Lecane spec		——	+	+
Lepadella spec		+++	+	
Platyıas quadrıcornıs	–		+++	
Polyarthra dolıchoptera	–	+++		
Polyarthra euryptera		++	——	
Polyarthra vulgarıs	+			
Rotıfer neptunıus				++
Trıchocerca porcellus			+	

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Figure 5. *DCA ordination plots of environmental parameters and the phytoplankton and zooplankton taxa as translated into habitat association groups. Abiotic environmental parameters (arrows) are plotted as biplot scores, biotic environmental parameters (NYMP, SUBM) are plotted as centroids. TURB: turbidity; NYMP: nymphaeids; SUBM: submerged aquatic macrophytes; Psed: exchangeable P in the sediment; POM: percentage organic matter in the sediment.*

Table 7. *Absolute frequencies of occurrence of common phytoplankton taxa. Frequency of occurrence: *:1-25%, **:26-75%; ***:76-100% of the sites within one site group.*

Site group	A	B	C	D
CYANOBACTERIA				
Aphanizomenon flos-aquae	***	***	*	*
Microcystis aeruginosa	***	**	*	*
BACILLARIOPHYCEAE				
Amphora ovalis	**	**	***	***
Asterionella formosa	***	**	**	**
Aulacoseira granulata	***	***	**	*
Cyclotella/Stephanodiscus spec.	***	**	**	
Cymbella lanceolata		*	***	*
Gomphonema constrictum	*	*	***	**
Gyrosigma attenuatum	*	**	*	***
Melosira varians	**	**	***	*
Navicula spec.	***	***	***	***
Nitzschia spec.	**	***	***	***
Synedra acus	**	**	***	**

Table 7. *Continued*

Site group	A	B	C	D
Synedra capitata		*	***	*
Synedra pulchella	*	*	***	*
CHRYSOPHYTA				
Dinobryon divergens	*	*	**	***
EUGLENOPHYTA				
Euglena spec.	*	***	**	**
Phacus longicauda	*	***	*	
Trachelomonas hispida	*	***	**	**
Trachelomonas volvocinopsis	*	***	**	**
PYRRHOPHYTA				
Ceratium hirundinella	**	**	*	***
CHLOROPHYTA				
Ankistrodesmus falcatus	*	***	**	*
Pediastrum duplex	***	***	*	**
Scenedesmus quadricauda	**	***	**	**
Mougeotia spec.	**	**	**	***
Spirogyra spec.	*	**	**	***

Table 8. *Absolute frequencies of occurrence of common zooplankton taxa. Frequency of occurrence: *:1-25%, **:26-75%; ***:76-100% of the sites within one site group.*

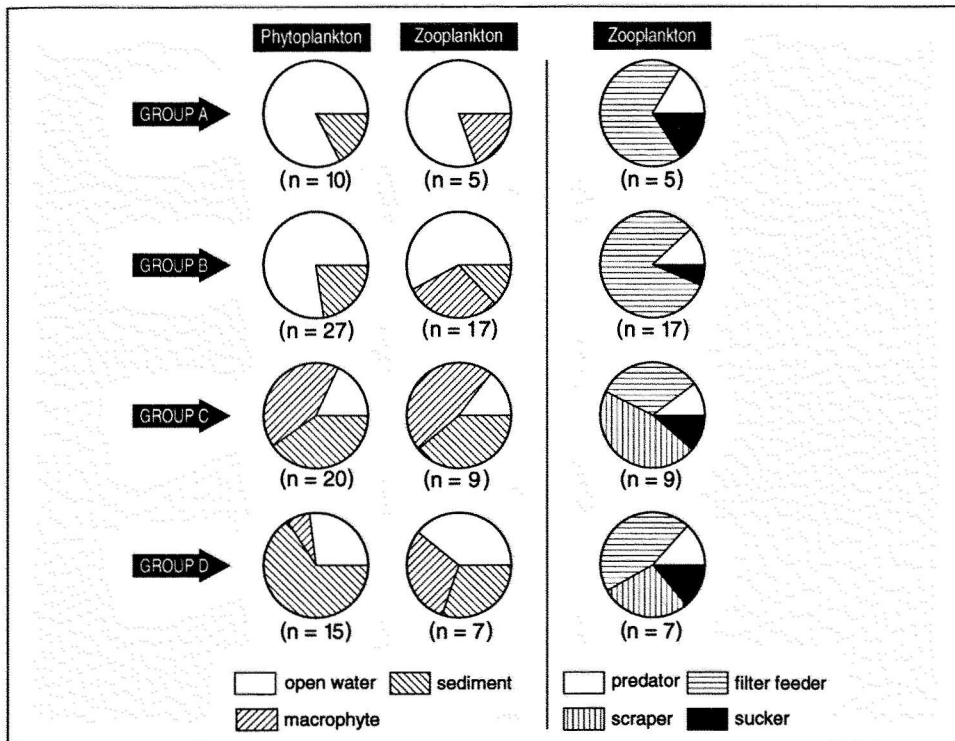| Site group	A	B	C	D
PROTOZOA				
Centropyxis aculeata	**	*	**	***
Difflugia spec.	*	**	**	***
COPEPODA				
Cyclops strenuus	**	***	**	**
Mesocyclops leuckarti	*	*		***
CLADOCERA				
Bosmina longirostris	*	***	**	**
Daphnia cucullata	***	***	**	**
ROTIFERA				
Asplanchna priodonta	*	***	**	**
Brachionus angularis	*	***	**	**
Keratella cochlearis	**	***	**	***
Keratella quadrata	***	***	**	**
Polyarthra dolichoptera	**	***	**	**

Figure 6. *Characterization of the site groups A, B, C and D by a conversion of phyto- and zoo-plankton species into habitat association groups (**left**) and by a conversion of zooplankton species into functional feeding groups (**right**). Both conversions are based on numbers of characteristic (Tables 5, 6) and/or common (Tables 7, 8) species. Total number of taxa involved in brackets.*

Discussion

Classification, ordination and abiotic interrelations

Both classification and ordination of the 100 floodplain waters, based on the relative abundance of the phytoplankton and zooplankton taxa, show the overall importance of the hydrology for the composition of the plankton communities in these waters (Tables 1-3, Figs. 4-6). Classification of the floodplain waters based on the relative abundance of plankton taxa resulted in the identification of four major site groups, forming a flood duration gradient (Tables 1-2). Physico-chemical parameters underlying the division into these groups were hydrological ones, such as the connectedness to the main channel and the longterm average annual flood duration, and co-varying parameters such as nutrient concentrations (N, P, Si) and nutrient ratios (Si/N, Si/P), as well as habitat characteristics, such as the maximum depth and the

vegetation structure of the water bodies (Tables 1-3). Ordination of the plankton abundance data points in the same direction: major parameters most closely related to the pattern of variation in plankton composition were annual flood duration, silicate concentration, Si/N and Si/P ratios, turbidity, presence of submerged vegetation, and maximum water depth (Fig. 4). The positive correlations between the annual flood duration and the levels of nutrients (DIN, DIP) and nutrient ratios (Si/N and Si/P) in the surface water and levels of DIP in the interstitial water (Table 3; Fig. 4) can be explained by the very high levels of DIN and DIP presently occurring in the Lower Rhine and Meuse. Via floods these nutrients enter the floodplain lakes, where nutrient loading takes place (Van den Brink et al., 1993a). The negative correlations between the water depth and the levels of Si and P in the surface water of the lakes (Fig. 4) can be related to the geomorphology of the sites. In an earlier study it was found that the influence of the sediment on the lake water chemistry generally increases with decreasing water depth: in shallow floodplain lakes regeneration of nutrients (Si, P) from the sediment was found to be more important than in deep lakes (Van den Brink et al., 1993a).

Nutritional relations

Phytoplankton taxa which belong to the Cyanobacteria, Chlorophyta and Euglenophyta were most frequently found in water bodies with low Si/N and Si/P ratios and a relatively long annual flood duration (14 days year[-1] or more), whereas taxa which belong to the Bacillariophyceae and Pyrrhophyta were most frequently found in water bodies with high Si/N and Si/P ratios and a short annual flood duration (4 days year[-1] or less) (Tables 2, 3; Fig. 4). A relationship between Cyanobacteria and Chlorophyta dominance over Bacillariophyceae on the one hand, and nutrient ratios on the other, has frequently been reported in studies on eutrophication processes in lentic water bodies (e.g. Sommer, 1986; Moss and Balls, 1989; Admiraal and Van der Vlugt, 1990; Horn and Horn, 1990; Van der Velde et al., 1991). The resource competition theory (Tilman, 1977), which has been experimentally corroborated (e.g. Tilman et al., 1982, 1986; Sommer, 1986, 1988, 1993) may at least partially explain the differences observed in the phytoplankton communities of hydrologically-different categories of water bodies. According to this theory, different relative supply rates of two or more limiting resources (e.g. N, P, Si or light) should result in phytoplankton communities dominated by different species (Tilman et al., 1982, 1986). High Si/N and Si/P ratios have been associated with a dominance of Bacillariophyceae, whereas low ratios have been associated with a dominance of Cyanobacteria and Chlorophyta (Tilman et al., 1986). Consequently, an increase in the concentrations of N and P in floodplain lakes from the main channels during floods may change the Si/N and Si/P ratios in favour of Cyanobacteria and Chlorophyta. It is possible that a long period of connection with the main channel affects the phytoplankton community composition by inducing Si-limitation in floodplain lakes. Evidence for this possibility comes from an earlier study, in which we found Si-depletion occurring during spring and summer in floodplain lakes with a long annual flood duration, and occurring during spring only or not occurring at all in rarely-flooded or isolated lakes (Van den Brink et al., 1993a). In this context it is interesting to note that Lake IJsselmeer, which receives Rhine water (with low Si/N and Si/P

ratios), regularly shows blooms of Cyanobacteria in the summer, unlike Lake Markermeer, which has been hydrologically isolated from Lake IJsselmeer by a dam (Berger and Sweers, 1988; Van der Velde et al., 1991). In addition to the actual levels of N, P and Si in the water column, regeneration of these nutrients from the sediments may strongly influence the phytoplankton community composition as well. The phosphate-laden sediments of frequently-flooded lakes along the Lower Rhine and Meuse have indeed shown regeneration of P after depletion of this nutrient from the water layer, thereby lowering the Si/P ratio, unlike the situation in hydrologically more isolated floodplain lakes (Van den Brink et al., 1993a).

The presence of centric diatoms (i.e. *Aulacoseira granulata*, *Cyclotella* spec., *Stephanodiscus* spec.) and the pennate diatom *Asterionella formosa* in floodplain lakes in open connection with the main channel (82% of the group A sites) (Tables 1, 5) indicates a strong influence from the main channel, since these taxa dominate the present phytoplankton communities in the main channels of the Lower Rhine and Meuse (Friedrich and Viehweg, 1984; De Ruyter van Steveninck et al., 1990a). So, it is possible that their abundance in the connected lakes result from a larger input of these biota during the longer periods of mixing of main channel water with lake water. On the other hand, the centric diatoms are relatively strong competitors for Si at high P levels, and *A. formosa* is a very opportunistic species (Tilman et al., 1982; Moss and Balls, 1989), which might explain their frequent occurrence at sites with low Si/P ratios, such as with the main channel connected lakes, too.

The categorization of the characteristic and common zooplankton species within each site group into functional feeding guilds, as described by Gliwicz and Rybak (1976), illustrates the importance of the food source for the composition of the zooplankton communities in the four site groups (Fig. 6). The relative species share of filter-feeding zooplankton was highest in lakes with a poor vegetation and hence a poor epiphyton community (group A) and in lakes with a high turbidity (group B), partly caused by phytoplankton blooms (Van den Brink et al., 1993a). The relative species share of scraping zooplankton was highest in site groups C and D, with a well developed vegetation and epiphyton (Fig. 6; Table 1). It is worth mentioning that a similar relationship between feeding guilds, nutritional resources and hydrology has been found for macrozoobenthos communities in these floodplain lakes (Van den Brink and Van der Velde, 1991).

Habitat relations

The complexity of habitats formed by the presence of aquatic vegetation can be related to the species richness of plankton taxa in the floodplain lakes. The scarcity of vegetation in the floodplain lakes in open connection with the main channels is associated with a relatively low plankton species richness. This is further illustrated by the relation between the availability of particular substrates (e.g. vegetation, sediment) and the phyto- and zooplankton community composition (Figs. 5, 6; Tables 1, 5-8). Epiphytes and benthic taxa (heleoplankton, e.g., *Gomphonema constrictum*, *Cymbella lanceolata*, *Simocephalus vetulus*) which are associated with the presence of macrophytes and/or sedimentary detritus, were predominantly found in lakes with an extensive aquatic vegetation, such as the group C and D sites. Open water taxa

(limnoplankton, e.g., *Asterionella formosa*, *Daphnia cucullata*) were most common and abundant in lakes with a poorly developed aquatic vegetation, such as the group A and B sites. The decrease in abundance of aquatic vegetation with increasing annual flood duration might arise from an impoverishment of the underwater light climate as a result of blooms of algae (input of N and P) and resuspension of fine sediment particles (Hough et al., 1989; Van den Brink et al., 1993a), from physical disturbance of plants (Van den Brink et al., 1991) and from an increase in salinity (Van den Brink and Van der Velde, 1993) during floods and may be responsible for the poorly developed microphyto- and microzoobenthos and epiphyton in lakes with a long flood duration.

The influence of water depth may be related to the occurrence of summer stratification: species such as *Ceratium hirundinella* and *Microcystis aeruginosa*, characteristic of the deep sites of respectively group D and group A (Table 1), may bloom in water bodies which are deep enough to show thermal stratification (Leentvaar, 1958; Steinberg and Hartmann, 1988).

Impact of hydrology

Hydrology clearly exerts an overall impact on the phyto- and zooplankton community composition in floodplain lakes of the Lower Rhine and Meuse, via its effects on the lake water chemistry, the exchange of plankton organisms during floods, the hydraulic retention time, and the aquatic vegetation. The longer the period of connection between the floodplain lakes and the main channels, the longer the period of input of main channel water with low Si/N and Si/P ratios into these lakes, favouring Cyanobacteria and Chlorophyta at the cost of most Bacillariophyceae (Van den Brink et al., 1993a). In the highly eutrophic tidal river-floodplain system of the R. Bure, England, hydrology was found to exert an influence on phytoplankton composition via the input of nutrients (P) and thereby changing Si/P ratio's as well (Moss et al., 1989). Apart from its effects on the lake water chemistry, an increase in annual flood duration probably increases the input of main channel plankton species in adjacent floodplain lakes too, because of the longer period of mixing of main channel water with lake water. Moreover, an increase in connectedness to the main channel means a decrease in the hydraulic retention time, and thus, a decrease in the time available for potential structural maturation of the plankton communities to take place, favouring opportunistic and short-living forms (Moss and Balls, 1989). Finally, an indirect result of an increase in connectedness is that the aquatic vegetation declines (by impoverishment of the underwater light climate, physical disturbance and/or osmotic stress). This hydrology-induced change from a macrophyte dominated community towards one which is dominated by planktonic microphytes has a clear impact on higher trophic levels in the floodplain lakes, i.e. zooplankton (this study), macrozoobenthos (Van den Brink and Van der Velde, 1991), and probably also fish (Lammens, 1989; Moss and Timms, 1989).

From the results presented here it can be predicted that rehabilitation of river floodplains by restoration of connections between isolated, infrequently-flooded lakes and the main channels of highly eutrophic river systems, such as the Lower Rhine and Meuse, will inevitably result in hypertrophic conditions in these lakes, and hence in an impoverishment of ecological

values. Restoration of connections are less deleterious in disconnected, frequently-flooded lakes (annual flood duration > 20 days year[1]), because these already have an impoverished aquatic vegetation and associated macroinvertebrate fauna (Van den Brink et al., 1991; Van den Brink and Van der Velde, 1991). However, in order to restore these communities a further isolation is recommended as long as the Lower Rhine and Meuse contain the present high levels of N and P.

Acknowledgements

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The (semi-) aquatic vegetation of still waters within the floodplains of the rivers Rhine and Meuse in The Netherlands: historical changes and the role of inundation

Abstract

The floristic composition of (semi-) aquatic macrophytes in floodplain lakes along the Lower Rhine and Meuse was studied in historical perspective. The actual presence of six aquatic macrophytes (*Nuphar lutea* (L.) Sm., *Nymphaea alba* L., *Nymphoides peltata* (Gmel.) O. Kuntze, *Potamogeton natans* L., *P. lucens* L. and *Stratiotes aloides* L.) and seven helophytes (*Equisetum fluviatile* L., *Oenanthe aquatica* (L.) Poiret, *Polygonum amphibium* L., *Ranunculus lingua* L., *Sparganium erectum* L., *Typha angustifolia* L. and *T. latifolia* L.) in a large number of former channels was compared with their presence in 1954. The presence of the aquatic species was found to be considerably reduced, especially in the summerbed waters. The present species richness of (semi-) aquatic macrophytes in 75 floodplain waters was related to the inundation frequency and co-varying parameters. Species richness was found to decrease with increasing annual inundation frequency. The relevance of stress factors as inundation frequency, salinity and eutrophication for the observed decline in species richness is discussed.

Introduction

The impact of human activities over the last decades on the ecosystems of the rivers Rhine and Meuse has lead to an impoverishment of ecological values (e.g. Admiraal et al., 1989; Van Urk and Smit, 1989). Due to the increased industrialization the waste water discharge and the shipping traffic on these rivers have increased enormously. The consequences of these changes for the various functional aquatic components of the ecosystems have been worked out for macroinvertebrates (Klink, 1989; Van den Brink et al., 1990), fish (Cazemier, 1988; Van den Brink et al., 1990; Van der Velde et al., 1990) and plankton (Peelen, 1975; De Ruyter van Steveninck et al., 1989). Within the scope of a research programme on the ecological rehabilitation of the large rivers in The Netherlands (Anonymous, 1988) the aquatic and semi-aquatic vegetation in the floodplains of the rivers Rhine and Meuse has recently been studied.

Floodplains of the alluvial rivers Rhine and Meuse in The Netherlands harbour a large number of still water bodies which have originated from spontaneous diversions of the streams (e.g. oxbow lakes) (Van Urk and Smit, 1989), from dike bursts in the past, and more recently from sand and clay extraction. Depending on geomorphological and hydrological circumstances, these still waters are subject to different inundation regimes: some water bodies are always in open connection with the main stream and frequently inundated, whereas other waters are only flooded during high river discharges. Normally, high river discharges

occur in winter and spring, although summer spates have become more numerous over the last decades (Van de Steeg, 1984; Brock et al., 1987).

This paper surveys historical changes in the aquatic and semi-aquatic vegetation of still waters within the floodplains of the rivers Rhine and Meuse since the early fifties and discusses the role of inundation.

Sites and methods

In order to study the floristic composition, 75 permanent, relatively large (1-200 ha) still waters located in the floodplains of the rivers Rhine and Meuse (Fig. 1) were selected on the ground of geomorphological and hydrological characteristics.

In The Netherlands the rivers are regulated and normalized, which means that the river bed is fixed by the main dikes during winter (Fig. 2A) and by the small summer dikes during summer (Fig. 2B), whereas the banks are protected by breakwaters. Within the riverine area several still water bodies can be distinguished. Some of the water bodies are in open connection with the river during the greater part of the year. These waters are entirely or partly lo-
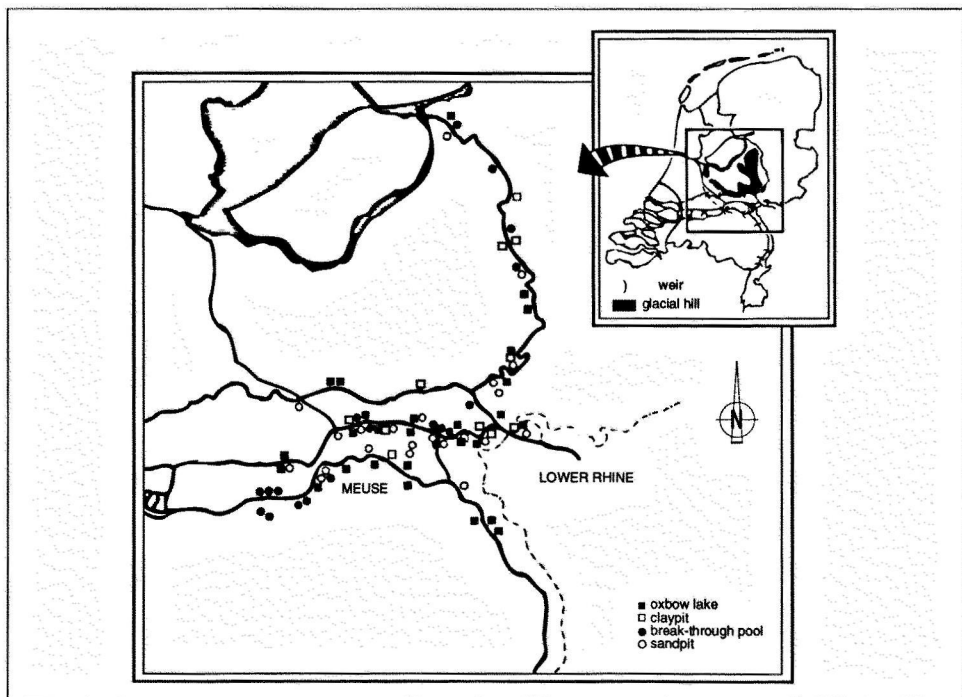

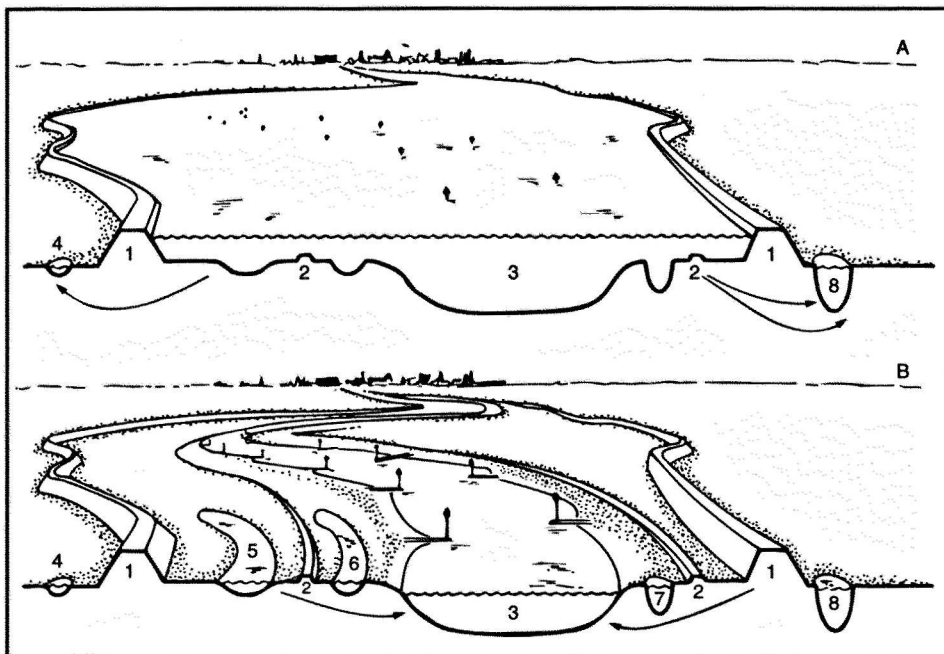**Figure 1.** *Map of study area with sampled localities.*

Figure 2. *Schematic view of water bodies within a river system, during winter (A) and summer (B).*
1 = main dikes, 2 = summer dikes, 3 = river bed, 4-8 = floodplain waters. Arrows indicate
direction of seepage.

cated between the small summer dikes, i.e. within the summer bed of the river, and are subject
to relatively frequent inundations. In the forelands, the areas between the summer bed and the
main dikes, the inundation frequency is largely dependent on local hydrological circumstan-
ces such as the height of the summer dikes and natural levees, together with actual water level
fluctuations in the river. In general, the still waters located on higher grounds in the river fore-
lands are flooded only during high river discharges. The still waters behind the main dikes are
never flooded although they are influenced by river water via seepage.

The floristic composition of the selected water bodies was investigated during the sum-
mer periods of 1987 and 1988. The presence of aquatic macrophytes and helophytes was re-
corded in each water body. Water and sediment samples were taken from each locality and
analysed using standard laboratory procedures (Leuven, 1988). In order to relate species rich-
ness to various physico-chemical parameters (e.g. inundation frequency, chemical composi-
tion of ambient and interstitial water, morphological parameters) a Spearman rank correlation
test (Sokal and Rohlf, 1981), performed with the Statistical Analysis System (SAS Institute
Inc., 1985), was applied.

In order to compare the present floristic composition of the vegetation of the still waters
with historical data, 13 common macrophyte species characteristic of different inundation
regimes (Van der Voo and Westhoff, 1961) were selected. Only oxbow lakes were used for

this comparison, because historical data of the vegetation of the other water types were scarce. As all the selected species are perennials, all the still water bodies are oxbow lakes and the vegetation in both studies was investigated for at least two successive summers, the data are supposed to be reliable and comparable. Hydrological data for the rivers and still water bodies were obtained from the Institute for Inland Water Management and Waste Water Treatment (DBW/RIZA, Arnhem). Historical and recent physico-chemical data for the River Rhine at Lobith and the River Meuse at Eijsden were derived from Zijlstra (1980), Scholte Ubing (1980), Zuurdeeg (1980), Anonymous (1985) and Maenen (1989). The nomenclature of the macrophytes follows that of Heukels and Van der Meijden (1983).

Results

A physico-chemical characterization of the rivers Rhine and Meuse (Table 1) shows the major differences between these river systems, such as discharge characteristics, water level fluctuations and median salinity, all of which are higher in the River Rhine. The difference with respect to salinity can be attributed largely to the higher sodium and chloride content of the River Rhine, due to the discharge of large quantities of salt by mines in France and Germany.

Over the last decades the ten-yearly mean discharge of the River Rhine at Lobith has increased by about 10 % (Table 2). Moreover, the ten-yearly mean discharge amplitude, defined as the difference between the highest and lowest mean monthly discharges, is nowadays almost twice that of the first half of the century, which means that at present water level fluctuations in this river are larger than they used to be.

Apart from an increase in the total amount of water discharged, an increase over the years in the concentrations of dissolved nutrients and chlorinity can be observed for both rivers (Table 3).

Table 1. *Geographical, hydrological and physicochemical characteristics of the rivers Rhine and Meuse. For references see text.*

	Rhine	Meuse
Total drainage area (km^2)	185,000	33,000
Drainage area in The Netherlands (km^2)	25,000	6,000
Total length (km)	1,250	890
Total length in The Netherlands (km)	385	251
Mean discharge (m^3 s^{-1})	2,200[*]	250[**]
Extremes of discharge (m^3 s^{-1})	600–13,000[*]	1–3,000[**]
Median water level fluctuations (m)[***]	5.9	2.2
Maximum water level fluctuations (m)[***]	9.4	8.3
Median salinity (mmol l^{-1})[***]	11.3	6.7

* measured at Lobith over 1901-1985; ** measured at Borgharen over 1911-1988; *** own data (1988)

Table 2. *Longterm changes in discharge characteristics of the River Rhine at Lobith.*
Mean, minimum and maximum monthly mean discharge in $m^3 s^{-1}$. For references see text.

Period	Mean	Minimum	Maximum	Max-Min
1901-1910	2105	1597	2684	1087
1956-1965	2154	1608	2613	1005
1966-1975	2278	1667	2856	1189
1976-1985	2403	1614	3485	1871

Table 3. *Changes over the years in trophic level (N, P and C), sulphate and chlorinity of the River Rhine (= R) at Lobith and the River Meuse (= M) at Eijsden. Yearly mean concentrations in $mg\ l^{-1}$. For references see text.*

Year	NO₃		o-PO₄		t-P		HCO₃		SO₄		Cl	
	R	M	R	M	R	M	R	M	R	M	R	M
<1900	0.3	n.d.	0.05	n.d.	0.15	0.22	160	172	35	28	13	15
1985	4.5	2.9	0.39	0.37	0.60	0.59	140*	110*	81	46	207	65

n.d.= not determined; *own data (1988)

Concurrently with these changes in abiotic parameters, there was a decline in the occurrence of selected macrophyte species in oxbow lakes within the floodplains of the rivers Rhine and Meuse in The Netherlands (Table 4). The changes in the frequency of occurrence were found to be different for the various species. The species *Stratiotes aloides* L. and *Ranunculus lingua* L. disappeared from the habitats under study. The nymphaeids *Nuphar lutea* (L.) Sm., *Nymphaea alba* L., *Nymphoides peltata* (Gmel.) O. Kuntze and *Potamogeton natans* L., the submersed aquatic macrophyte *Potamogeton lucens* L. and the helophytes *Oenanthe aquatica* (L.) Poiret, *Sparganium erectum* L., *Equisetum fluviatile* L. and *Typha angustifolia* L. all showed a reduced frequency of occurrence, whereas *Typha latifolia* L. and *Polygonum amphibium* L. did show no change at all over the years. The aquatic macrophytes located in the summer bed showed the largest decline (Table 4).

In order to relate the present species richness with the inundation frequency, the still waters were divided into five inundation classes (Table 5; Fig. 3). A clear negative correlation was found between the aquatic and semi-aquatic macrophyte species richness in the still waters and the frequency of inundation (Spearman rank correlation test, $p < 0.001$). An inundation frequency of 20 days per year or more (classes 3 and 4) leads to a significant decrease in the species richness (Table 5), which was most apparent for aquatic macrophytes (Fig. 3). From this frequency onwards, summer inundations occur more often in addition to the normal winter floodings. Apart from this negative correlation between species richness and the frequency of inundation, there were also significant negative correlations (Spearman rank correlation test) between species richness and orthophosphate concentrations of the interstitial water ($p < 0.001$), between species richness and the nitrate ($p < 0.01$), orthophosphate ($p < 0.05$), sodium ($p < 0.01$), chlorinity ($p < 0.01$) and turbidity ($p < 0.05$) of the ambient water,

Table 4. *Changes in the presence of selected macrophyte species in oxbow lakes along the rivers Rhine and Meuse in The Netherlands. 0= not present; 1=present in 1-20 %, 2= 21-40 %, 3=41-60 %, 4=61-80 %, 5=81-100 % of water bodies.*
Source: 1954: Van der Voo and Westhoff (1961); 1988: present study.

Location	winter bed		summer bed	
Year of study	1954	1988	1954	1988
Number of water bodies	69	27	16	41
AQUATIC MACROPHYTES				
Nuphar lutea (L.) Sm.	5	3	5	2
Nymphaea alba L.	3	2	3	1
Nymphoides peltata (Gmel.) O. Kuntze	5	3	5	1
Potamogeton natans L.	3	1	2	0
Potamogeton lucens L.	4	2	4	1
Stratiotes aloides L.	2	0	1	0
HELOPHYTES				
Equisetum fluviatile L.	3	1	2	1
Oenanthe aquatica (L.) Poiret	4	2	3	1
Polygonum amphibium L.	3	3	4	4
Ranunculus lingua L.	1	0	1	0
Sparganium erectum L.	4	2	2	1
Typha angustifolia L.	3	2	1	1
Typha latifolia L.	1	1	1	1

Table 5. *Mean (N) and maximum (Nmax) numbers of (semi-) aquatic macrophyte species present in floodplain waters of the rivers Rhine and Meuse in The Netherlands (n = number of waters).*

Inundation class	Inundation frequency*	Rhine			Meuse		
		N±S.D.	Nmax	n	N±S.D.	Nmax	n
0 not inundated	0	16.1±4.3	23	15	18.3±2.6	22	5
1 low inundation frequency	0–2	17.7±3.1	23	6	15.7±4.3	22	6
2 moderate inundation frequency	3–20	15.5±6.3	26	22	12.5±4.0	18	4
3 high inundation frequency	21–40	10.2±3.3	16	6	n.p.		0
4 very high inundation frequency	>40	5.9±1.6	9	8	9.0±2.9	13	5

* in days per year (long-term annual average), n.p. = not present.

and positive correlations between species richness and the alkalinity ($p < 0.05$) of the ambient water. These parameters were also correlated with the inundation frequency.

The frequency of the selected macrophyte species in three inundation classes is different for the various taxa listed (Table 6). Most species are intolerant to high inundation frequencies, except *Nymphoides peltata*, which occurs in the Rhine system under a regime of moderate to high inundation frequencies, and *Polygonum amphibium*, which appears to be indifferent with respect to this factor.
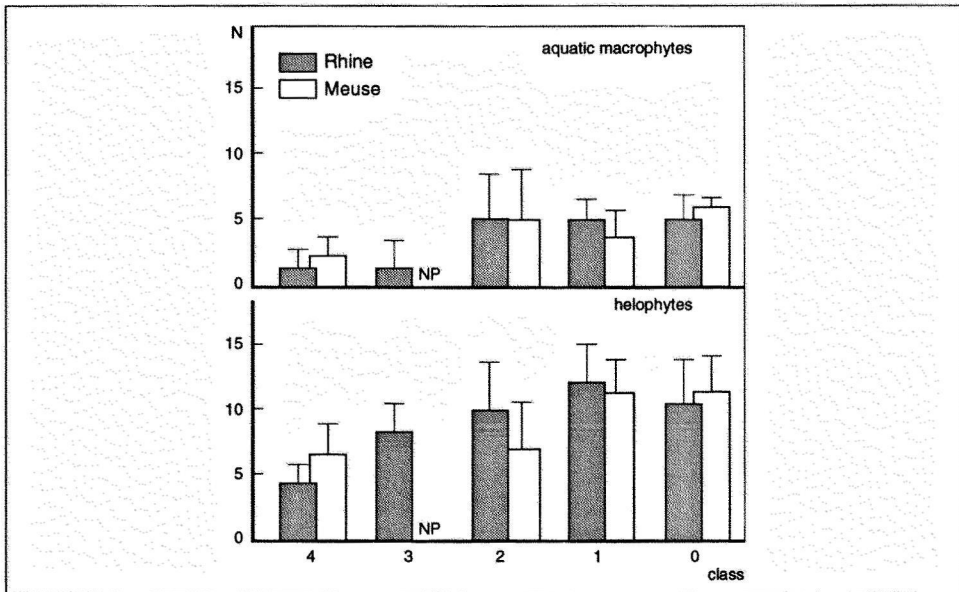
Figure 3. *Mean numbers (N) ± S.D. of aquatic macrophytes and helophytes present in still waters within the floodplains of the rivers Rhine and Meuse in The Netherlands classified to decreasing inundation frequencies (see Table 5 for further explanation).*

Table 6. *The occurrence of selected macrophyte species in floodplain waters along the rivers Rhine and Meuse in relation to the frequency of inundation. For explanation of inundation classes and frequencies of occurrence, see Tables 5 and 4, respectively.*

	Rhine			Meuse		
Inundation class	0	1+2	3+4	0	1+2	3+4
Number of water bodies	14	28	14	5	10	5
AQUATIC MACROPHYTES						
Nuphar lutea	3	4	1	4	3	1
Nymphaea alba	2	2	1	2	2	0
Nymphoides peltata	1	3	2	1	1	0
Potamogeton lucens	2	3	0	1	0	0
HELOPHYTES						
Equisetum fluviatile	1	1	0	2	1	0
Oenanthe aquatica	1	2	0	0	2	0
Polygonum amphibium	4	4	4	3	3	3
Sparganium erectum	2	2	0	2	3	0
Typha angustifolia	3	2	0	1	2	2
Typha latifolia	1	1	0	1	2	1

Discussion and conclusions

The present aquatic and semi-aquatic vegetation in oxbow lakes within the floodplains of the rivers Rhine and Meuse was compared with the results of a large-scale floristic investigation of similar water bodies which was carried out from 1954 to 1956 (e.g. Van der Voo and West-hoff, 1961). In order to obtain a reliable comparison, 13 common species were selected which are more or less characteristic of different inundation regimes. Van der Voo and Westhoff (1961) observed that *Stratiotes aloides* and *Equisetum fluviatile* both predominantly in-habited waters with a very low frequency of inundation, that *Ranunculus lingua*, *Nymphaea alba*, *Typha angustifolia* and *Sparganium erectum* were characteristic for water bodies with a moderate frequency of inundation, and that *Nymphoides peltata*, *Oenanthe aquatica* and *Polygonum amphibium* f. *natans* occurred more frequently in waters with higher frequencies of inundation. In the present study the general pattern of occurrence of the selected species in relation with the frequency of inundation was found again (Table 6). However, the occurrence was found to be considerably reduced for nearly all these species, especially for aquatic mac-rophytes within the summer bed (Table 4).

Most obviously the present species richness of aquatic macrophytes and helophytes in still waters (Table 5, Fig. 3) was negatively correlated with the frequency of inundation. High inundation frequencies, e.g. inundation regimes including summer floodings (classes 3 and 4), are probably more detrimental for aquatic macrophytes than for helophytes because the re-duction in species richness was largest for the aquatic species (Fig. 3). This is not surprising as aquatic macrophytes are more directly related to physico-chemical parameters of the ambient water than helophytes. Correlations of species richness with interstitial and ambient ortho-phosphate, nitrate, sodium and chloride concentrations were less significant and possibly in-direct. The increased dynamics of the river and the changes in the water chemistry of the river water (nutrients and chlorinity) over the last decades are probably the prime factors respon-sible for the changes in the species frequency, as well as for the present species richness of still water bodies within the area studied.

A relationship between the frequency, duration and season of inundation and the floristic composition of still waters in Dutch river forelands has been reported previously (Van der Voo and Westhoff, 1961; Van Donselaar, 1961; Van de Steeg, 1984; Brock et al., 1987; Van der Sman et al., 1988). These studies have emphasized the deleterious effects of floodings during the summer, which is the growth period. Summer inundations are detrimental for the vegeta-tion because non-rooting and weakly rooting macrophytes may be washed away. Further-more, the primary productivity of submersed plants or plant parts is hindered by an increase in turbidity, due to resuspended clay particles or nutrient enrichment after the floodings (Brock et al., 1987). Winter inundations are a normal ecological factor in the Dutch river stretches, which prevent the succession of the vegetation in the open water towards a marsh vegetation by erosion of the sediment. However, an increase in the river discharge over the years, leading to an increase in the inundation frequency of the still waters during winter and summer, has probably resulted in a deterioration with respect to water level fluctuations of the habitats for

most species, except for *Polygonum amphibium*, which showed more resistance against these changes (Table 4).

Apart from the increased water level fluctuations it is probably the changed nutrient status (Table 3) which is mainly responsible for the decline in occurrence of submersed macrophytes such as *Potamogeton lucens* and macrophytes with a submersed phase of development such as *Stratiotes aloides*. An increase in the concentrations of nitrate and orthophosphate leads to an impoverished underwater light climate due to an enhanced growth of phytoplankton and epiphytes, which reduces photosynthesis of the submersed macrophytes (Hough et al., 1989).

A third possible factor which may have contributed to the decline of macrophytes in the still waters is the increased salinity of the river water. In a large-scale correlative study on the occurrence of aquatic and semi-aquatic macrophytes in relation to environmental parameters in about 600 still waters in The Netherlands De Lyon and Roelofs (1986) found that *Nuphar lutea*, *Nymphaea alba*, *Potamogeton natans*, *P. lucens*, *Stratiotes aloides*, *Equisetum fluviatile*, *Typha angustifolia* and *T. latifolia* occurred most frequently in waters with a moderate salinity (6.3-8.2 mmol l^{-1}), whereas *Oenanthe aquatica*, *Sparganium erectum*, *Polygonum amphibium* and *Nymphoides peltata* were found at higher salinities (9.0-10.8 mmol l^{-1}). The present mean salinity of the River Rhine (11.3 mmol l^{-1}; Maenen, 1989), however, is above the optimum salinity for the species listed above.

Although some key factors have been delineated in the present study, it is clear that more detailed information on the occurrence of aquatic and semi-aquatic macrophytes in relation to the factors inundation and salinity is needed. Because these factors are often correlated in the field situation, information on the responses of the various plant species to the factors inundation (frequency, duration and season of flooding) and salinity could be provided by an experimental approach to the subject. Such information is extremely relevant for recent initiatives with respect to the rehabilitation of the ecological values of the rivers Rhine and Meuse, which includes among others the conservation of the vegetation of still waters in the river forelands, and also the restoration of the vegetation of the river-banks.

Acknowledgements

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Growth and morphology of four freshwater macrophytes under the impact of the raised salinity level of the Lower Rhine

Abstract

The growth and morphology of *Potamogeton lucens* L., *P. perfoliatus* L., *P. nodosus* Poir. and *Ranunculus circinatus* Sibth. were studied in relation to salinity. Plants were grown for eight weeks in microcosms under ambient climatic conditions at (sodium) chloride concentrations which presently occur in the main channel of the Lower Rhine and its connected lakes (7.0 mmol l^{-1} Cl$^-$), which have a poorly developed vegetation, and at concentrations which presently occur in infrequently flooded lakes (1.4 mmol l^{-1} Cl$^-$) within the floodplain of the Lower Rhine, which are rich in aquatic macrophytes.

The sodium chloride level of the main channel negatively affected biomass production and growth rates for all three *Potamogeton* species, but not for *R. circinatus*. The reductions in biomass and growth rates of the *Potamogeton* species, concurred with a decline in their leaf area ratios, suggesting that the growth reduction might be related to a reduced leaf cell expansion. Root:shoot ratios increased in all selected species, whereas flowering decreased in response to higher salinity. The relevance of salinity as a stress factor is discussed in relation to the occurrence of these macrophytes in the Lower Rhine and its floodplain lakes.

Introduction

The aquatic vegetation in the Lower Rhine and its floodplain lakes has become impoverished under human impact. In addition to changes in the morphology and hydrology of the river as a result of normalization and regulation efforts, the water quality of the Lower Rhine has been drastically changed as a result of salt-mining, agricultural effluents, and industrial and domestic sewage in its drainage basin (Van den Brink et al., 1991a; Van der Velde et al., 1991; Admiraal et al., 1993). Apart from an increase in nutrient levels in the river water, which has resulted in eutrophication of Rhine-water receiving water bodies (Admiraal et al., 1989; Van der Velde et al., 1991; Van den Brink et al., 1993), the levels of sodium and chloride in particular have greatly increased during this century (Van der Weijden and Middelburg, 1989). Yearly mean chloride concentrations of 4.2-7.0 mmol l^{-1} Cl$^-$, with maxima of 11.8 mmol l^{-1} Cl$^-$, have been measured over the last two decades in the Lower Rhine (Heymen and Van der Weijden, 1991). These chloride concentrations are ten to twenty times the original levels (Van der Weijden and Middelburg, 1989). Mining effluents have shifted the ionic composition in this river from a calcium bicarbonate dominance, which was the normal situation, towards a sodium chloride dominance (Kempe et al., 1991). This shift in ionic composition was not restricted to the main channel of the Lower Rhine, but was also found in water bodies connected with the main channel and in frequently inundated lentic floodplain waters (Van den Brink et

al., 1993). Effects of the raised sodium and chloride levels of the Lower Rhine are known for planktonic and macroinvertebrate communities in the main channel and its associated floodplain lakes (Friedrich and Viehweg, 1984; Den Hartog et al., 1989; Van den Brink et al., 1990; Van den Brink et al., 1991b; Van den Brink and Van der Velde, 1991; Admiraal et al., 1993). Remarkably, long-term effects of mining effluents on aquatic vegetation have received very little attention (e.g. Rabe et al., 1982; Maenen, 1989).

Correlative studies have emphazised the possible importance of sodium chloride concentrations in relation to the occurrence of aquatic macrophytes in the Lower Rhine and its floodplain lakes (Maenen, 1989; Van den Brink et al., 1991a; Admiraal et al., 1993). However, sodium chloride levels in these floodplain lakes are also interrelated with co-varying chemical parameters such as N and P, as well as with hydrological ones, such as the annual flood duration (Van den Brink et al., 1993). Causal relationships between salinity and the growth of freshwater macrophytes have been found for only a very few species, and mostly concern salinity values above 15.5 mmol l^{-1} Cl (about 1 ‰ S) (e.g. McCahee and Davis, 1971; Haller et al., 1974; Rabe et al., 1982; Van Wijk, 1989; Twilley and Barko, 1990). Information on the effects of sodium chloride on the morphology of aquatic macrophytes is completely absent.

In order to study the impact of the raised sodium chloride levels on the occurrence of aquatic macrophytes in the Lower Rhine and its floodplain lakes, four species were cultured in microcosms. The effects of sodium chloride on plant growth and morphology have been examined in a functional growth analysis. Species were selected on the basis of their presence in water bodies along an inundation and chlorinity gradient within the Lower Rhine floodplain: *Potamogeton nodosus* Poir., occurring locally in the river channel; *P. lucens* L., commonly occurring in infrequently flooded lakes; and *P. perfoliatus* L. and *Ranunculus circinatus* Sibth., predominantly occurring in isolated floodplain lakes along the Lower Rhine (Maenen, 1989; Van den Brink, 1990; Van den Brink et al., 1991a; Coops et al., 1994).

Materials and methods

Species

Plant material was sampled from water bodies within the floodplain area of the Lower Rhine in The Netherlands at the end of May 1990 (Table 1). Apical stem segments (20 cm stem length) of *P. lucens*, *P. perfoliatus* and *R. circinatus*, and young intact plants of *P. nodosus* (total length of above ground parts: 20 cm) were taken from the sampled plant material. For each species, 24 stem segments or plants were used in the experiments.

Experimental design and measurements

Selected plant material was randomly and equally distributed over four artificial outdoor ponds, which were filled with tap water (2000 l, water depth: 70 cm). The plant segments were then planted in sediment-filled PVC pots (diameter 14 cm; height 13 cm), in such a way

that the lower 10 cm portion of each stem segment was buried under the sediment, to allow them to root for a period of two weeks. Before planting the sediment-filled PVC pots were submerged for one week. The sediment consisted of a mixture of river sand and river clay (1:1 v/v) collected from the river forelands near Nijmegen, The Netherlands. In order to prevent turbidity of the water column due to phytoplankton growth, 1 kg *Daphnia* (fresh weight) was added to each pond. At the onset of the experiment sodium chloride was added to the water to obtain a final concentration of 1.4 mmol l^{-1} Cl$^-$ in the control ponds and 7.0 mmol l^{-1} Cl$^-$ in the experimental ponds. After eight weeks of growth (from 11 June 1990 to 6 August 1990) under ambient climatic conditions the following parameters were measured: fresh and dry weights of leaves, stems and roots, numbers of inflorescences and leaves, and leaf area. Fresh weights were determined after blotting the plant material for 1 minute with blotting paper. Dry weights were determined by weighing after drying at 105 °C for 24 h. Leaf area was determined by photocopying 20 randomly selected fresh leaves per plant, after which the surface areas of the photocopied leaves were measured using a planimeter (Kotron Messgeräte, MOP.AMO 3), followed by calculation of the mean leaf area. Total leaf area per plant was calculated by multiplying the mean leaf area by the number of leaves.

Salinity and calcium bicarbonate levels were monitored daily through measurements with an YSI model 33 SCT salinity meter and through estimation of the bicarbonate alkalinity via titration of a 50 ml sample with 0.01 N HCl down to pH 4.2 (Stumm and Morgan, 1981). Since evaporation exceeded precipitation during the experiment, the salinity was adjusted bi-weekly by adding tap water to each pond. Calcium bicarbonate alkalinity was adjusted weekly to a level of 2 meq l^{-1}, by separately adding sodium bicarbonate and calcium chloride (1:1 equivalent ratios) to each pond. Other chemical parameters of the water were analysed at the end of the experiment, according to standard laboratory procedures (Van den Brink et al., 1993).

Table 1. *Occurrence of selected macrophytes and annual mean concentrations (and ranges) of sodium and chloride (in mmol l^{-1}) at the sampling stations during 1990 (n = 12 measurements, monthly samples). +: present, -: absent, *: present and sampled at that location. P.l. = P. lucens, P.n. = P. nodosus, P.p. = P. perfoliatus, R.c. = R. circinatus.*

Water body	Location	P.l.	P.n.	P.p.	R.c.	Na$^+$	Cl$^-$
R. IJssel	Lat. N 52°31'; Long. E 5°57'	-	*	-	-	4.5 (2.1-7.0)	4.8 (2.4-7.3)
Wolderwijd	Lat. N 52°20'; Long. E 5°36'	-	-	*	-	2.8 (2.1-3.5)	3.0 (2.8-3.9)
Oude Waal	Lat. N 51°51'; Long. E 5°55'	*	-	+	+	1.6 (1.2-2.5)	2.0 (1.2-3.1)
Duivelswaai	Lat. N 51°52'; Long. E 5°48'	+	-	+	*	1.5 (1.2-1.9)	1.7 (1.3-2.1)

Growth analysis

The relative growth rate (RGR) (Fisher, 1921; Hunt, 1982) of each individual plant was calculated using the formula RGR $=(\ln W_t - \ln W_0)/t$ where W_0 and W_t are the dry weights of the plants after 0 and t days respectively. Fresh weight-dry weight relationships were used to calculate the dry weights of the plants at the start of the experiment (W_0).

For a further analysis of RGR, the specific leaf area, the leaf area ratio, the net assimilation rate, and the root:shoot ratio were calculated (Hunt, 1982; Poorter, 1989). The specific leaf area (SLA) is the leaf area (LA) per unit leaf weight (WL): $SLA = LA/WL$. The leaf area ratio (LAR) is the ratio between leaf area (LA) and the total plant weight (W): $LAR = LA/W$. The net assimilation rate (NAR) is the increase in plant weight (W) per unit leaf area (LA) and per unit of time (t) (Hunt, 1982). Thus

$$NAR = (W_t-W_0)/t \times (\ln LA_t - \ln LA_0)/(LA_t-LA_0)$$

where LA_0 and LA_t are the total leaf areas per plant after 0 and t days. The RSR is the ratio between the dry weight of the below- (W_B) and above-ground parts (W_A): $RSR = W_B/W_A$. Means of growth parameters (RGR, SLA, LAR, NAR, RSR) and numbers of inflorescences per species per treatment were statistically compared using a least significant difference (LSD) test (Sokal and Rohlf, 1981), with the help of the Statistical Analysis System (SAS, 1989).

Results

The main differences in chemical parameters of the water between the experimental and the control ponds concerned sodium and chloride concentrations (Table 2).

Table 2. *Physicochemical characteristics of the culture media. Mean values ($\pm$ S.D.) of parameters are given, except for pH (ranges) (n = 4 measurements at the end of the experiment). All parameters in mmol l^{-1}, except for NO_3, NH_4 and d-PO_4 (in μmol l^{-1}) and pH (pH-units).*

	control		experimental	
pH	7.5-8.5		7.5-8.5	
HCO_3	2.0	(0.5)	2.0	(0.5)
Na	2.4	(0.4)	8.0	(0.4)
K	0.15	(0.02)	0.14	(0.04)
Ca	0.7	(0.05)	0.7	(0.05)
Mg	0.1	(0.01)	0.1	(0.03)
Cl	1.4	(0.2)	7.0	(0.2)
SO_4	0.4	(0.01)	0.4	(0.01)
NO_3	30	(8)	20	(8)
NH_4	6	(1)	6	(1)
d-PO_4	0.3	(0.1)	0.2	(0.1)

Total biomass production in response to increased sodium chloride concentrations was significantly reduced (p < 0.05) for *Potamogeton lucens*, *P. nodosus* and *P. perfoliatus*, but not for *Ranunculus circinatus* (Table 3). It was found that the relative leaf and root biomasses, unlike the relative stem biomasses, of the *Potamogeton* species were most affected by salinity (Fig. 1). The relative growth rates showed the same pattern: a decrease in RGR was found for the three *Potamogeton* species, but not for *R. circinatus* (Fig. 2). The leaf area ratio (LAR), i.e. the ratio between the total leaf area (measure of total photosynthetic area) and the total plant biomass, was also clearly reduced (p < 0.05) for the *Potamogeton* species, but not for *R. circinatus* (Fig. 2). The reduction in LAR resulted from a reduced production of leaves per plant, whereas the surface area of the leaves was also reduced. The specific leaf area (SLA), i.e. the ratio between the total leaf area and the total leaf biomass, also showed a decrease with increasing salinity, but was only significantly reduced (p < 0.05) for *P. nodosus* and for *R. circinatus* (Fig. 2). Under salinity stress the net assimilation rate (NAR) significantly increased (p < 0.05) for all *Potamogeton* species, but not for *R. circinatus* (Table 4).

Table 3. *Mean total dry weight (in g ± S.D.) of selected species after eight weeks growth at control (1.4 mmol l^{-1} Cl⁻) and experimental (7.0 mmol l^{-1} Cl⁻) sodium chloride concentrations. * = significantly different, p < 0.05 (LSD test).*

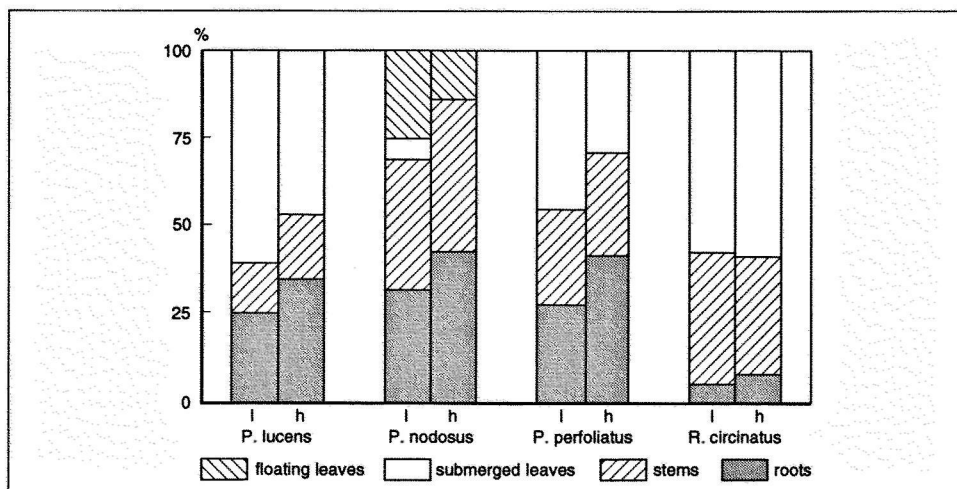|	control	experimental
Potamogeton lucens	3.91 (1.01)	1.78 (1.06)*
Potamogeton nodosus	5.19 (1.26)	1.74 (0.72)*
Potamogeton perfoliatus	6.33 (2.80)	2.34 (0.69)*
Ranunculus circinatus	10.60 (3.00)	11.35 (4.67)

Figure 1. *Relative biomasses (%) of leaves, stems and roots of selected macrophytes in response to control, low (l) (1.4 mmol l^{-1} Cl⁻) and experimental, high (h) (7.0 mmol l^{-1} Cl⁻) chlorinities.*

Table 4. *Mean net assimilation rates (in g m^{-2} day^{-1} ± S.D.) of selected species after eight weeks growth at control (1.4 mmol l^{-1} Cl$^-$) and experimental (7.0 mmol l^{-1} Cl$^-$) sodium chloride concentrations.*
* = significantly different, p < 0.05 (LSD test).

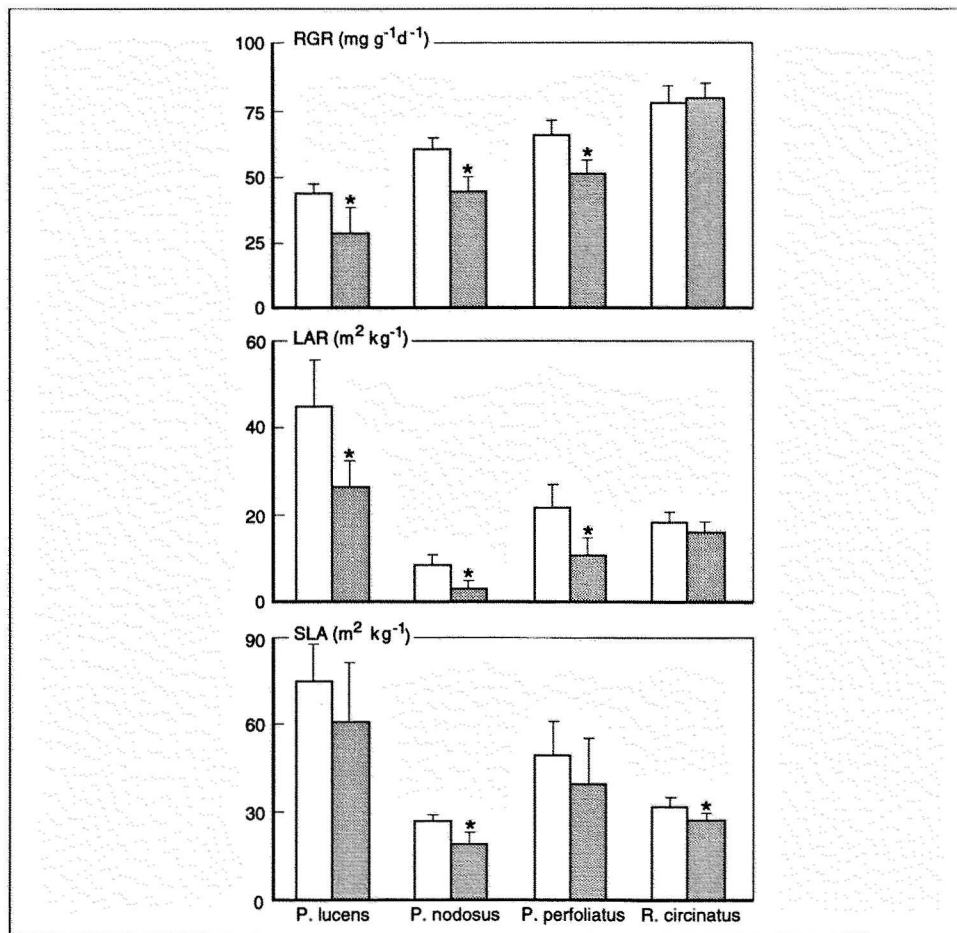|	control	experimental
Potamogeton lucens	1.7 (0.5)	2.4 (0.9)*
Potamogeton nodosus	6.7 (1.0)	13.7 (4.2)*
Potamogeton perfoliatus	4.0 (0.8)	7.1 (1.8)*
Ranunculus circinatus	5.9 (0.6)	6.6 (1.1)

Figure 2. *Above: Relative Growth Rates (RGR), middle: Leaf Area Ratios (LAR) and below: Specific Leaf Areas (SLA) of selected macrophytes in response to control (1.4 mmol l^{-1} Cl$^-$) (clear) and experimental (7.0 mmol l^{-1} Cl$^-$) (shaded) chlorinities. Asterisks indicate significant differences between responses at the two chlorinities (p < 0.05; LSD-test).*

In response to salinity, all four species showed an increased RSR (Fig. 3). Species which flowered during the experiment (*P. nodosus*, *P. perfoliatus* and *R. circinatus*) showed a reduced number of inflorescences at the highest sodium chloride concentration (Fig. 4).

Figure 3. *Root:shoot ratios of selected macrophytes in response to control (1.4 mmol l⁻¹ Cl⁻) (clear) and experimental (7.0 mmol l⁻¹ Cl⁻) (shaded) chlorinities. Asterisks indicate significant differences between responses at the two chlorinities (p < 0.05; LSD-test).*

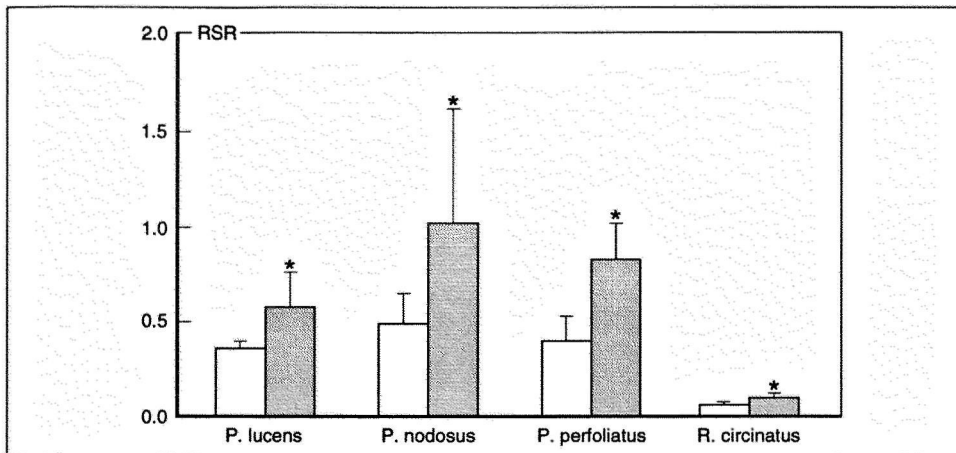**Figure 4.** *Mean number of inflorescences of selected macrophytes in response to control (1.4 mmol l⁻¹ Cl⁻) (clear) and experimental (7.0 mmol l⁻¹ Cl⁻) (shaded) chlorinities. Asterisks indicate significant differences between responses at the two chlorinities (p < 0.05; LSD-test).*
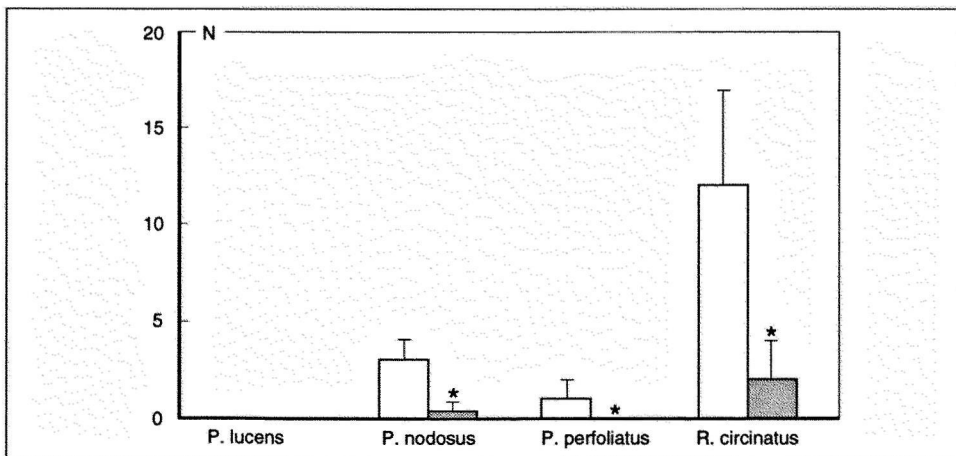
Discussion and conclusions

The morphology and growth of all macrophytes under study were clearly affected by a chlorinity of 7.0 mmol l^{-1} Cl^{-}, which is in the range of the sodium chloride concentrations presently occurring in the Lower Rhine (Figs. 1-4, Table 3). Biomass production and RGR of *Potamogeton lucens*, *P. nodosus* and *P. perfoliatus* declined in response to this sodium chloride concentration, unlike biomass production and RGR of *Ranunculus circinatus* (Table 3, Fig. 2). The relative biomasses of the leaves of the *Potamogeton* species decreased, whereas those of the roots of all selected species increased in response to increased sodium chloride concentrations (Fig. 1), indicating similar phenoplastic responses for the various species. The reduction in RGR of the *Potamogeton* species concurred with a reduction in LAR, which indicates that the decline in growth was caused by a decrease in the total photosynthetic area of the plants (Fig. 2). Most likely this decrease in total photosynthetic area was not compensated for by an increase in the chlorophyll-a content of the leaves. In a study of the impact of salinity on the growth of four freshwater macrophytes (including *P. perfoliatus*) Twilley and Barko (1990) did not find any significant change in leaf chlorophyll-a content in response to salinities up to 12 ‰ S. As the reduced growth rate can be attributed to a reduction in the relative leaf area (LAR) (Fig. 2), the effect of increased salinity on the growth of the *Potamogeton* species might be the result of a reduced leaf cell expansion, which might be purely an osmotic effect (Greenway and Munns, 1980; Rozema and Van Diggelen, 1991). Since we did not measure concentrations of potential osmotica inside the plants, this explanation remains hypothetical.

The value of SLA, i.e. the ratio between the leaf area and the leaf weight, declined significantly ($p < 0.05$) for *P. nodosus* and for *R. circinatus*, but not for the other investigated *Potamogeton* species (Fig. 2). A reduction in SLA is an indication for the occurrence of leaf succulence, the production of smaller and thicker leaves, and can be induced by an increased osmolarity of the growth medium (Greenway and Munns, 1980; Rozema and Van Diggelen, 1991). The decrease in SLA of *Potamogeton nodosus* resulted partly from a loss of the thin submerged leaves, whereas its thicker floating leaves were still present (Fig. 1). For *R. circinatus* succulence of the same leaf type occurred, which may be an adaptation to increased salinity. It is of interest to note that both *P. nodosus* and *R. circinatus* are capable of surviving periods of drought by producing land forms. Both increased salinity and drought cause water stress in plants and may induce succulence by way of adaptation.

The tendency of all species under study to reduce their SLA (Fig. 2) with increasing salinity might suggest a general adaptation mechanism, related to leaf morphology. In this context it is of interest to note that most salt-tolerant freshwater macrophytes and all brackish water macrophytes have relatively small, finely dissected or narrow leaves. In the present study for example, *R. circinatus* with its relatively small, finely dissected leaves was found to be more salt tolerant than the broad-leaved *Potamogeton* species. In fact, within the genus *Potamogeton* the brackish water tolerant species are all narrow-leaved species (e.g. *P. pectinatus* L., *P. mucronatus* Schrader ex Sonder and *P. pusillus* L.) (Van Wijk and Verbeek, 1986), as are all brackish water macrophyte species (e.g. *Ruppia* spp., *Zannichellia* spp.). This suggests

that the growth form of aquatic macrophytes might be of adaptive value with respect to salinity tolerance.

The relative root biomass increased in response to salinity in all four species ($p < 0.05$) (Figs. 1, 3). An increase in RSR has been found for a number of freshwater macrophytes in response to increased sodium chloride levels, and is probably a response which overcomes a water deficit by increasing the relative root surface area (Haller et al., 1974; Twilley and Barko, 1990).

The reduced RGR of the *Potamogeton* species in response to salinity could not clearly be related to changes in the NAR (Table 4). The increased NAR of the *Potamogeton* species in response to salinity may suggest a more economic carbon assimilation (Causton and Venus, 1981; Hunt, 1982) or may result from an allocation of biomass to non-photosynthetic plant parts, such as the stems and roots (Lambers et al., 1989). Direct measurements of the photosynthetic and respiration rates are needed to provide more insight in this matter (Lambers et al., 1989).

The mean number of inflorescences per plant was markedly reduced in response to salt stress (Fig. 4) for all flowering species. Even the most salt tolerant species, *R. circinatus*, produced fewer flowers under salt stress compared with normal conditions. A reduction in flowering in response to salinity has also been reported for *P. perfoliatus* and for *Myriophyllum spicatum* L. (Twilley and Barko, 1990). However, it is not very likely that generative reproduction plays an important role in the persistence of the species selected. Wiegleb and Brux (1991) state that the reproductive strategies of *Potamogeton lucens*, *P. nodosus* and *P. perfoliatus* are mainly vegetative, irrespective the degree of either stress or disturbance. Vegetative reproduction is also very common for *R. circinatus* (Hoogers, 1966).

The differences in sodium chloride tolerance between the *Potamogeton*-species and *Ranunculus circinatus* are in agreement with differences in distributional limits between these species in the Netherlands (De Lyon and Roelofs, 1986). In a study of 600 water bodies in the Netherlands it was found that *P. lucens* and *P. perfoliatus* predominantly occurred in waters with a moderate chlorinity (range: 0.6-5.0 mmol l^{-1} Cl⁻; mean: 2.0 mmol l^{-1} Cl⁻), whereas *R. circinatus* was also frequently found in waters with higher chlorinities (range: 0.6-9.0 mmol l^{-1} Cl⁻; mean: 3.0 mmol l^{-1} Cl⁻) (De Lyon and Roelofs, 1986). During a study of the riverine vegetation in the Netherlands *Potamogeton nodosus* was found at moderate chlorinities (range: 1.3-3.1 mmol l^{-1} Cl⁻; mean: 2.0 mmol l^{-1} Cl⁻) (Maenen, 1989). In a branch of the Lower Rhine, the R. IJssel, with a mean chlorinity of 4.8 mmol l^{-1} Cl⁻ in 1990, *Potamogeton nodosus* was found to occur less frequently and in lower densities than in the R. Meuse (mean 1990 chlorinity: 1.8 mmol l^{-1} Cl⁻), which suggests that the species is living under salinity stress in the R. IJssel. In fact, the species has disappeared from many locations along the main channel of the Lower Rhine since the early 1940s (Maenen, 1989), which might be attributed to increased salinity. From 1940 to 1990 the annual mean chlorinity of the Lower Rhine increased from 1.7 to 5.4 mmol l^{-1} Cl⁻ (Van der Weijden and Middelburg, 1989). Whether or not the negative impact of the salinity of the Lower Rhine on the occurrence of *P. nodosus* is partly counteracted by the very high nitrogen levels, which might be utilized in osmoregulation (Twilley and Barko, 1990), is an item for further study.

The absence of *P. lucens* and *P. perfoliatus* from the main channel and from connected floodplain lakes along the Lower Rhine might be related to salinity as well, since the maximum sodium chloride concentrations occurring there in 1990 (7.5 mmol l^{-1} Cl^{-}) (Heymen and Van der Weijden, 1990) negatively affected the growth of these species too. However, the absence of *R. circinatus* in these waters must be related to factors other than salinity, as this species is tolerant to the maximum salinities occurring in those waters. The absence of *R. circinatus* from the main channel and from connected floodplain lakes along the Lower Rhine might be the result of the impoverished underwater light climate due to frequent algal blooms and suspension of clay particles, or of the more dynamic hydrology, as this species does not tolerate strong currents (Van den Brink et al., 1991a; Van den Brink and Van der Velde, 1991).

Acknowledgements

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Effects of substrate parameters on growth responses of eight helophyte species in relation to flooding

Abstract

The interactive effects of substrate parameters (redox potential, organic matter content) and flooding depths on growth responses and field distribution of eight helophyte species, common in European floodplains, were studied. These species (*Acorus calamus, Carex acuta, Equisetum fluviatile, Sagittaria sagittifolia, Scirpus lacustris, Sparganium erectum, Typha angustifolia* and *Typha latifolia*) showed distributional differences, which could be related to the hydrological regime and to the redox potential and organic matter content of the submerged sediment in the littoral of floodplain lakes. The growth responses of these helophyte species were studied in relation to flooding (plants partially flooded versus totally submerged) and sediment characteristics (mineral, moderately reductive sediment versus organic, highly reductive sediment) for eight weeks during the growth season in outdoor artificial ponds under ambient climatic conditions. Flooding conditions were found to exert a clear impact on helophyte growth responses. In response to total submergence, most species showed shoot length extensions and restored contact between leaves and air. Shoot fractions were generally lower under submerged conditions, as a result of growth reduction at prolonged submergence. The impact of sediment characteristics on growth responses of the species under study depended partly on the flooding conditions. All species under study tolerated prolonged anoxic and toxic sediments, provided the plants grow emergent. When growing emergent on organic, highly reductive sediments, these species increased their growth rate and allocated biomass to above-ground plant parts, which suggests a general adaptation mechanism to hypoxic and toxic conditions. Prolonged submergence on organic, highly reductive substrates resulted in a growth reduction of all species selected.

Our results indicate that the decline of the helophyte vegetation in moderately dynamic floodplain lakes along the Lower Rhine and Meuse can be related to the combination of the organic, highly reductive sediments and the increased incidence of summer floods there in particular. Besides shared growth responses, species-specific differences in flooding tolerance and field distribution were observed between the selected helophyte species. The experimentally established flooding tolerances and tolerances to highly reductive substrates were generally larger than predicted by the observations on the distribution of the species in the field, suggesting that additional factors which restrict the occurrence of these species are involved.

Introduction

Helophytes are wetland plants which are normally emergent, i.e. they root in the bottom and their basal parts are often continually submerged, but their leaves and inflorescences emerge far above the water surface (Den Hartog and Van der Velde, 1988). As helophytes inhabit the aquatic-terrestrial ecotone, they are by definition adapted to partial flooding conditions. When these plants become partially flooded during the growth season, with most of their photosyn-

thetic surface still emergent, oxygen is transported to their rooting zones to overcome the an-
oxic conditions in the submerged sediment. Flood events which lead to the total submergence
of helophytes hinder the oxygenation of the sediments by the plants and thereby their growth
(Armstrong, 1969; Brändle, 1991). The tolerance of helophytes against total submergence
varies with the species and may depend on the depth, frequency, duration and season of floods
(e.g. Brock et al., 1987; Grace, 1989; Blom et al., 1990; Brändle, 1991; Coops and Smit,
1991; Coops et al., 1991; Van den Brink et al., 1991; Squires and Van der Valk, 1992).

Differences in flooding tolerance between helophyte species may lead to changes in the
marsh vegetation of lakes in response to changes in the hydrological regime. As a result of
river regulation, 'improved' drainage in the entire river basin, and floodplain deterioration,
the marsh vegetation bordering floodplain lakes along the Lower Rhine and Meuse has se-
verely declined. This decline has been attributed in particular to an increased frequency, dura-
tion and depth of summer floods over the last decades, leading to prolonged submergence of
helophyte stands in these lakes during the summer season (Van de Steeg, 1984; Brock et al.,
1987; Van den Brink et al., 1991). Field observations suggest that the impact of summer
floods on the survival of helophytes depends not only on the species, and the frequency, dura-
tion and depth of the inundations, but also on substrate parameters, such as the organic matter
content and related parameters like the redox potential and the presence of natural potentially
toxic ions like sulphide in the sediment (Brock et al., 1987; Grace, 1988; McKee et al., 1989;
Weisner and Granéli, 1989; Coops and Smit, 1991; Coops et al., 1991). Submerged reductive
sediments may cause a greater oxygen stress than oxidative sediments, since the oxygen de-
mand of the former sediments is much greater (Armstrong, 1967). Moreover, a combination
of low redox potentials with the presence of natural toxins in the sediment may cause an even
greater stress (Ernst, 1990).

Due to interrelations between hydrology and sediment parameters of floodplain lakes
(Rostan et al., 1987; Van den Brink et al., 1993), field observations can only make a limited
contribution to an understanding of the changes in the helophyte vegetation bordering these
lakes. Experimental evidence for an impact of substrate parameters on helophyte growth re-
sponses under flooding conditions is poor; it deals mostly with nutrient limitation, and is
available for a few species only (Grace, 1988, 1989; Pearson and Havill, 1988; Weisner and
Granéli, 1989; Neill, 1990, 1993).

In the present study we tested the hypothesis that the combination of summer floods and
organic, highly reductive sediments may severely hinder the growth of helophyte species bor-
dering floodplain lakes. In order to study species-specific differences in performance and
tolerance to submergence and substrate characteristics, eight helophyte species, common in
European alluvial floodplains, were selected. The combined effects of sediment parameters
and flooding depths on the growth responses and flooding tolerances of *Acorus calamus* L.,
Carex acuta L., *Equisetum fluviatile* L., *Sagittaria sagittifolia* L., *Scirpus lacustris* L., *Spar-
ganium erectum* L., *Typha angustifolia* L. and *Typha latifolia* L. were examined by: 1. a study
of the field distribution of these species in floodplain lakes in relation to flooding regime and
sediment parameters (organic matter content, redox potential), and 2: mesocosm experiments
on the impact of these sediment parameters on growth responses (relative growth rate, shoot

length extension, biomass allocation) of the species selected at contrasting flooding depths (partially flooded versus totally submerged).

Methods

Field distribution

In order to study the occurrence of the species selected in relation to hydrological and sediment parameters, 114 lakes located in the floodplains of the Lower Rhine and Meuse in the Netherlands were selected on the basis of their geomorphology and hydrology. These floodplain lakes were categorized according to their inundation regime: A = isolated lakes, protected against inundations by the main dike; B = moderately dynamic lakes, protected against summer inundations by low dikes or levees, but subjected to winter floods; C = very dynamic lakes, unprotected by dikes or levees and hence frequently inundated with long-lasting floods, in summer as well as in winter (Van den Brink, 1990; Van den Brink et al., 1993). These three categories form an inundation gradient over the lateral dimension of the Lower Rhine and Meuse floodplains. Group A lakes show only minor water-level fluctuations during the growth season. Group B lakes show minor water-level fluctuations during the growth season too, under normal hydrological circumstances. However, the last decades, abnormal high river discharges during summer occasionally occur within the study area. These high river discharges lead to exceptionally large water-level fluctuations and to complete submergence of helophyte stands in group B lakes. Group C lakes show large water-level fluctuations during winter and summer. Within each floodplain lake, the presence of the species selected was recorded during the vegetation periods of 1987 and 1988.

Sediments were collected from below the water layer in the littoral zone, close to the vegetation stands, by means of a metal tube with a diameter of 7 cm. The upper 10 cm layer of sediment was sampled. Because of the heterogeneity of the sediment, eight samples per site were collected and mixed. Sediments were dried at 105 °C for 24 hours. The percentage of organic matter in the sediment was calculated from the weight loss of the dried sediment after 4 hours heating at 550 °C (=loss on ignition).

The redox potential of the sediment was measured in a selected number of lakes within abundant monospecific vegetation stands (10-12 stands per species). Redox potential was recorded using a platinum redox electrode and a Metrohm 6.0701.100 calomel reference electrode connected to a Consort P914 mV/pH meter. Calibration occurred with a Metrohm 6.2306.020 redox standard solution. Recordings were read after 10 min. equilibration at a sediment depth of 10-15 cm. Eight recordings were made per vegetation stand.

Mesocosm experiments

Species
All species were collected during the period 1-8 July 1990 in the forelands of the river Rhine near Nijmegen (The Netherlands). Individual plants (= one shoot with a rhizome (when present) and roots) were transplanted to PVC pots (diameter 18 cm; height 20 cm) containing either mineral or organic sediment. A shoot is defined here as the entire set of aboveground plant parts emerging from one node of the rhizome or roots, including stems and leaves. Shoot height is defined as the maximum length of leaves. For *E. fluviatile* and *Scirpus lacustris* the tallest 'stems', i.e. the above-ground photosynthetic erect stem-like structures, were measured. Although these structures are not stems in the exact meaning, but include peduncles and leaves as well, we use here the term stem for practical reasons. Due to genotypic and phenotypic variation, the species selected showed variable shoot heights. For each species, 32 plants were selected with more or less uniform shoot heights (variation: ± 10%). These heights were as follows: *Acorus calamus*: 65 cm; *Carex acuta*: 25 cm; *Equisetum fluviatile*: 45 cm; *Sagittaria sagittifolia*: 40 cm; *Scirpus lacustris*: 70 cm; *Sparganium erectum*: 60 cm; *Typha angustifolia*: 65 cm and *Typha latifolia*: 65 cm. The rooted rhizomes of *A. calamus, E. fluviatile, Scirpus lacustris, Sparganium erectum, T. angustifolia* and *T. latifolia* were clipped to a length of 10 cm, the very short rhizomes of *C. acuta* to a length of 2 cm. *Sagittaria sagittifolia* has no rhizome: individually rooted specimens were used. The experiments were carried out between 23 July and 18 September 1990, in outdoor ponds on the university grounds, under ambient climatic conditions. The nomenclature of the species follows that of Van der Meijden (1990).

Sediments
The mineral sediment consisted of river sand mixed with river clay and the organic sediment consisted of a mixture of river clay and organic mud. These sediments were collected in river forelands near Nijmegen. PVC pots (diameter 18 cm; height 20 cm) were filled with either mineral or organic sediment. Subsequently, one g of a controlled NPK release fertilizer (Osmocote Plus; Sierra Chemical Company) was added per pot. Before the start of the transplantation experiments these sediment-filled pots were submerged for one week in tap water.

For a physico-chemical characterization of the sediments used in the experiments, the percentage of organic matter, the redox potential and the chemical composition of the interstitial water were analyzed at the end of the experiment. For these analyses four pots containing mineral sediment and four pots containing organic sediment were used, in which no plants had been potted. Redox potential was measured as described above. The other parameters were measured according to standard laboratory procedures (Van den Brink et al., 1993).

Experimental design
At first, the potted helophytes were randomly distributed over two large artificial ponds (length: 8 m; width: 2.5 m; depth: 1 m), which were filled with tap water up to a level of 30 cm (= partial flooding), so that only the lower 10 cm of the stems were flooded. Two series of

eight species of helophytes were randomly distributed over each pond; one series with the mineral and the other with the organic sediment. After transplantation the helophytes were allowed to adapt to this flooding depth in both ponds for two weeks. Subsequently, one pond was completely filled, so that the water level was 80 cm above the sediment surface and all helophytes in this pond were totally submerged. The water depth in the other pond was kept at 10 cm above the sediment surface. In this way four experimental treatments were obtained: mineral sediment, partially flooded; mineral sediment, totally submerged; organic sediment, partially flooded; and organic sediment, totally submerged. The following parameters were measured at the start of the experiment and after two, four and eight weeks: length of the leaves (for *E. fluviatile* and *Scirpus lacustris*: length of stems) and number of leaves (for *E. fluviatile* and *Scirpus lacustris*: number of stems). For each specimen, dry weight biomasses of aboveground (stems, leaves) and belowground (rhizomes, roots) parts were measured at the end of the experiment (eight weeks of treatment). These biomasses were determined by weighing after drying at 105 °C for 24 h.

Growth analysis
In order to study the initial growth responses of the eight species, shoot length extensions over the first two weeks were analyzed by measuring the shoot length increase. In order to compare growth responses over the entire experimental period (= eight weeks) the relative growth rate (=RGR in mg g^{-1} day^{-1}) was calculated for each individual plant, using Hunt's (1982) formula RGR =(ln W_t - ln W_0)/t where W_0 and W_t are the dry weights of the shoots after 0 and t days, respectively. In order to calculate the dry weight of the shoots, total shoot length-dry weight relationships were used. A good correlation between total shoot length and dry weight of the shoots was obtained for each species by regression analysis. The correlation coefficients (r) of these regressions ranged from 0.84 to 0.97. Effects on biomass allocation were studied by calculating the shoot fraction, i.e. the shoot dry weight biomass as a percentage of the total dry weight biomass at the end of the experiment.

Statistical analysis

In order to relate the hydrological regime of the floodplain lakes with sediment parameters of these lakes, and in order to relate the redox potential of the sediment with the percentage of organic matter in the sediment of these lakes, a Spearman rank correlation test (Sokal and Rohlf 1981) was applied.

Experimental data, i.e., the initial shoot length extension, relative growth rates after the first 4 weeks (RGR$_{0-4}$) and after the next 4 weeks (RGR$_{4-8}$), and final shoot fraction were analyzed using a three-way factorial analysis of variance (ANOVA), with species, flooding depths, sediment types and interactions as the sources of variance (Sokal and Rohlf, 1981). Statistical analyses were performed using the SAS statistical package (SAS Institute Inc., 1989).

Results

Field observations

The redox potential showed a clear negative correlation with the percentage of organic matter in the sediment of the selected floodplain lakes (Spearman rank correlation test; $p < 0.001$), indicating that organic substrates within these floodplain lakes were more reductive than mineral substrates. The organic matter content and redox potential in the sediment in the lake littoral were related to the flooding regime of the floodplain lakes (Fig. 1). In general, organic, reductive sediments were absent from very dynamic floodplain lakes. Highly organic and highly reductive sediments were found to occur in moderately dynamic lakes only, which were only occasionally flooded during the growth season (Fig. 1).

The distribution of the selected species in the 114 floodplain lakes showed a transversal zonation pattern of species over the inundation gradient of lakes (Fig. 2), suggesting a difference in flooding tolerance among these species. *Acorus calamus* and *Carex acuta* were about equally present in all three hydrological categories of lakes. Although *Sagittaria sagittifolia*, *E. fluviatile*, *Scirpus lacustris* and *T. angustifolia* were found in each hydrological category too, there was a gradual shift towards less dynamic lakes in which these species were most frequently found. *Equisetum fluviatile* and *Sagittaria sagittifolia* were most frequently found in moderately dynamic lakes. *Scirpus lacustris* and *T. angustifolia* were seldomly found in very dynamic lakes. *Sparganium erectum* and *T. latifolia* were not found at all in very dynamic floodplain lakes (Fig. 2).

The distribution of the selected species in relation to the field redox potential showed a zonation pattern too (Fig. 3). *C. acuta* was most frequently found on moderately reductive to oxidative sediments (100 to 250 mV) and not found at all on highly reductive sediments. *Sagittaria sagittifolia*, *E. fluviatile*, *T. latifolia*, *Sparganium erectum* and *A. calamus* were most frequently found on reductive sediments (-100 to 100 mV). *Scirpus lacustris* and *T. angustifolia* were both found at the lowest sediment redox potentials and occurred on reductive to highly reductive sediments (-200 to 100 mV) (Fig. 3).

Mesocosm experiments

Table 1 shows a physico-chemical characterization of the sediments used in the experiments. Apart from the percentage of organic matter (expressed as loss on ignition), the main differences between the organic and mineral sediments were the redox potentials and the levels of exchangeable sulphur, iron and manganese in the soil. The organic sediment showed the lowest redox potential, and the highest concentrations of exchangeable sulphur, iron and manganese. Free sulphides were detected only in the organic sediment under highly reductive conditions. The dominant form of nitrogen was also different: nitrate under moderately reductive conditions and ammonium under highly reductive conditions (Table 1).

The results of a three-way ANOVA with species, flooding depths and sediment types and their interactions as sources of variance (Table 2) showed that growth responses varied with
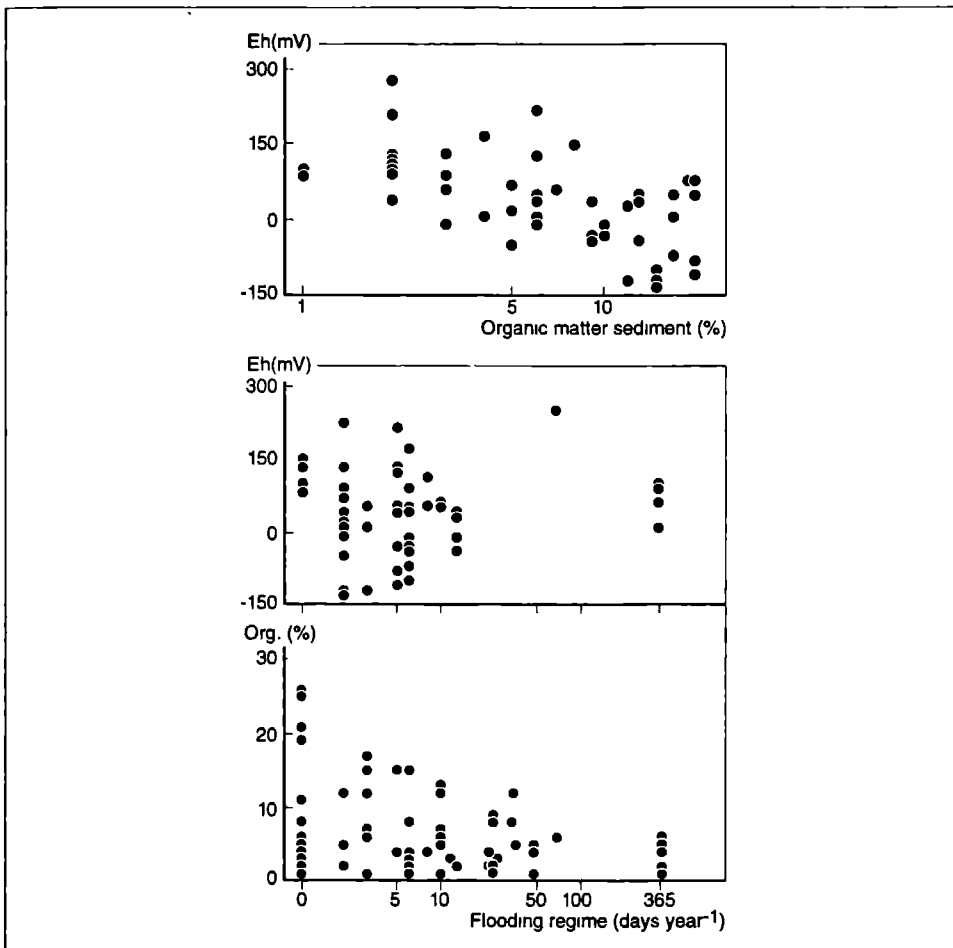
Figure 1. *Relationships between (above) organic matter content and redox potential (Eh) of the sediment, (middle) redox potential (Eh) and the flooding regime, and (below) organic matter content (Org.) in the sediment and the flooding regime of floodplain lakes. Flooding regime is expressed as the average number of flooding days per year.*

species, flooding depths and sediment types. Interactive effects of sediment type and flooding treatment were clear for initial shoot length extensions and relative growth rates (Table 2).
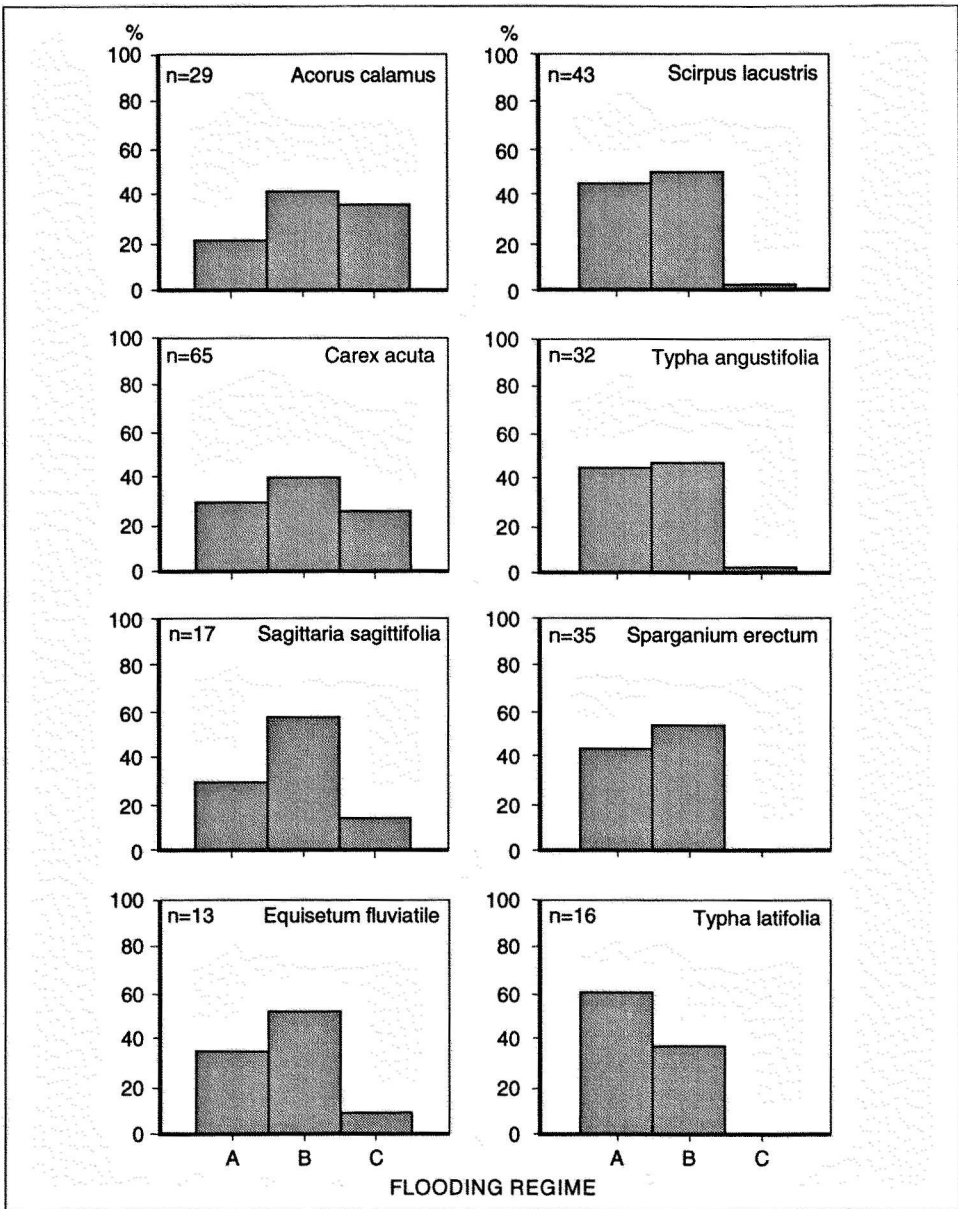
Figure 2. *Relative occurrence (in %) of selected helophyte species in relation to the flooding regime. n = number of lakes in which the species was found. A: isolated lakes; B: moderately dynamic lakes, normally flooded only during winter, outside the vegetation season; C: very dynamic lakes, flooded during summer and winter.*
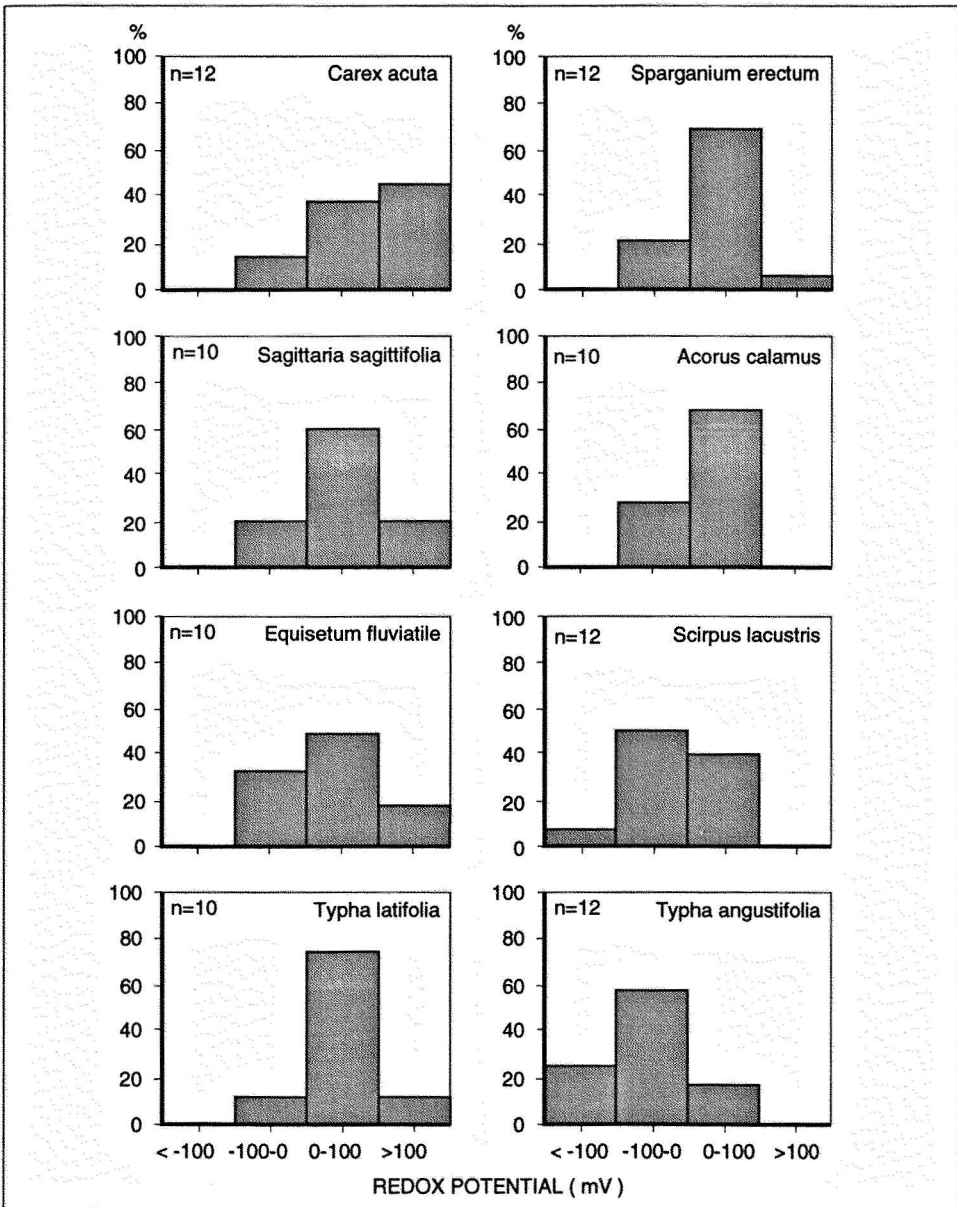
Figure 3. *Relative occurrence (in %) of selected helophyte species in relation to the redox potential (Eh in mV) of the sediment. n = number of vegetation stands at which the redox potential was measured.*

Table 1. *Physicochemical characteristics of the submerged sediments used in the experiments. Values of parameters given are means (± S.D.), except for pH (ranges) (n = 8 measurements).*

Sediment type		mineral		organic	
Grain size		sand/clay		clay	
Redox potential (mV)		+160	(30)	−180	(20)
Moisture content (%)		20	(2)	65	(12)
Loss on ignition (%)		2	(1)	11	(5)
pH		6.5-7.0		6.5-7.0	
K^+	$\mu mol\ l^{-1}$	460	(30)	380	(40)
NO_3^-	$\mu mol\ l^{-1}$	240	(40)	20	(10)
NH_4^+	$\mu mol\ l^{-1}$	120	(10)	100	(5)
t-P	$\mu mol\ l^{-1}$	4	(4)	4	(1)
t-S	$mmol\ l^{-1}$	2	(1)	46	(2)
Ca^{2+}	$mmol\ l^{-1}$	7	(2)	9	(3)
Fe^{2+}	$\mu mol\ l^{-1}$	3	(1)	35	(10)
Mn^{2+}	$\mu mol\ l^{-1}$	1	(1)	80	(10)

Table 2. *Effects of flooding depth, sediment type and interactions on initial shoot length extension, relative growth rates and final shoot fraction of eight helophyte species after flooding treatments. P-values of an ANOVA with species, flooding depth, sediment type and their interactions as sources of variance.*
*** = $p < 0.001$; ** = $0.001 < p < 0.01$; * = $0.01 < p < 0.05$; n.s.= not significant.*

		Dependent variables			
Independent variables	df	initial shoot length extension	RGR 0-4 weeks	RGR 4-8 weeks	final shoot fraction
species (sp)	7	***	***	***	***
flooding depth (fl)	1	***	**	***	***
sediment type (se)	1	n.s.	***	n.s.	*
sp x fl	7	***	***	***	***
se x sp	7	n.s.	**	*	n.s.
se x fl	1	***	***	***	n.s.

Initial shoot length extensions were clearly related to flooding depths and varied with the species (Table 2; Fig. 4). Shoot length extensions were generally largest at the totally submerged treatment. All species reached the water surface after two weeks of submergence, except *C. acuta* and *E. fluviatile* which remained completely submerged during the entire experimental period. The influence of sediment type on initial shoot length extensions varied with flooding depths (Table 2). Under partially flooded conditions shoot length extensions for most species were highest on organic sediments, whereas under submerged conditions vari-
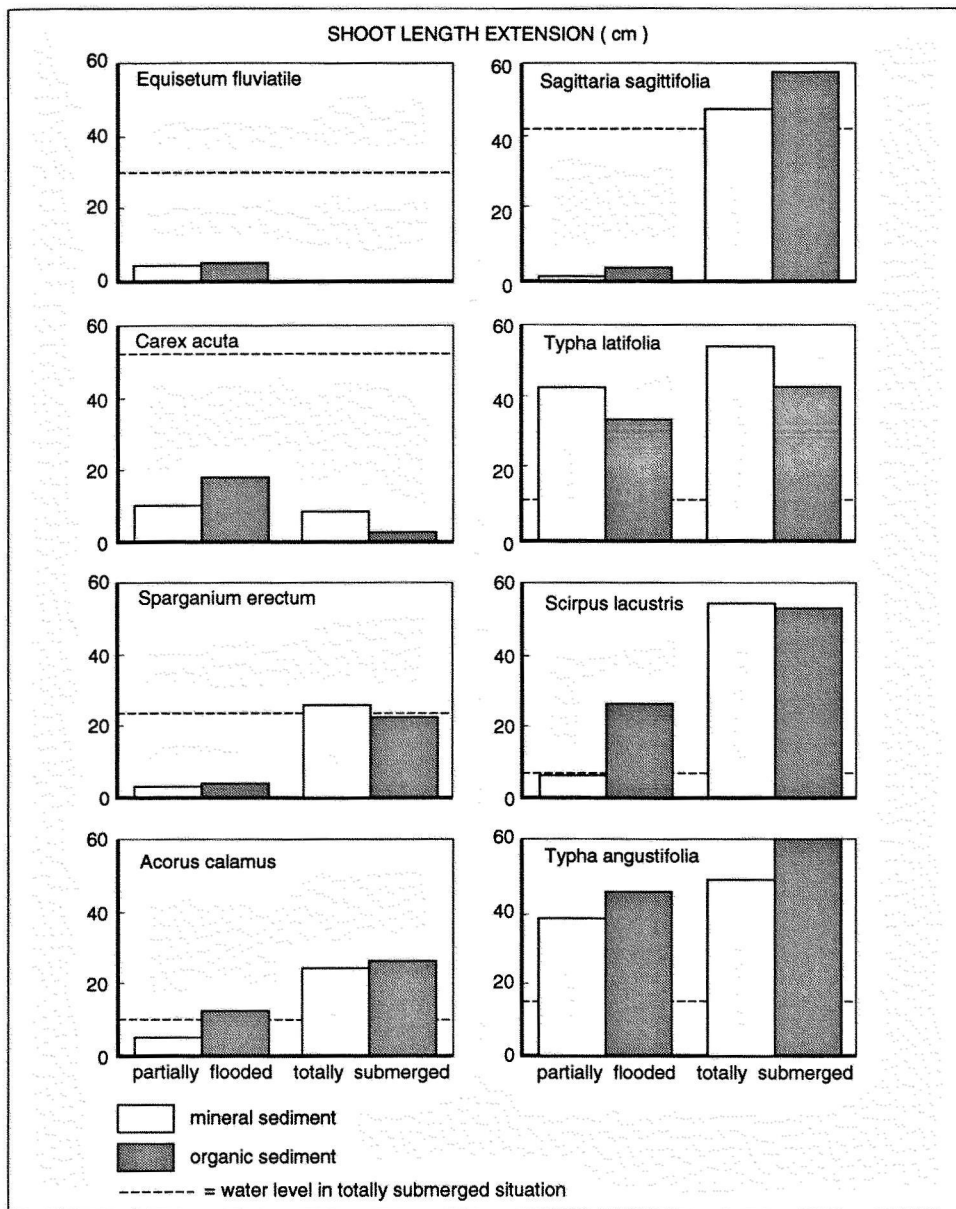
SHOOT LENGTH EXTENSION (cm)

Figure 4. *Initial shoot length extension (in cm, after two weeks of flooding) of selected helophyte species in relation to substrate and flooding condition.*

ation in shoot length extension due to sediment type was less clear and varied from one species to another (Fig. 4).

Sediment type had a clear effect on the relative growth rates during the first four weeks of growth (RGR_{0-4}); its effect on the relative growth rates during the second growth period (RGR_{4-8}) varied with flooding depths (Table 2). Initial relative growth rates (RGR_{0-4}) were generally higher on organic sediments (Fig. 5), indicating that growth was faster on the organic, highly reductive sediments than on the mineral, moderately reductive sediments. Relative growth rates were generally lower during the second part of the experiment (RGR_{4-8}) than during the initial part (RGR_{0-4}), but were again highest on organic sediments under partially flooded conditions. During the second growth period relative growth rates (RGR_{4-8}) were lowest on the organic sediments under totally submerged conditions (Fig. 5).

The RGRs at the various experimental treatments showed a specific pattern for each species (Fig. 5). Based on these growth patterns four species groups could be distinguished. *A. calamus*, *T. angustifolia* and *Scirpus lacustris* showed only minor variations in RGRs at the various treatments. *Sagittaria sagittifolia* had its lowest RGRs under partially flooded conditions. This species lost part of its erect emergent leaves during the experiment and produced floating leaves only under totally submerged conditions. This explains the lower growth reduction of *Sagittaria sagittifolia* under such conditions when compared with prolonged partially flooding conditions (Fig. 5). *C. acuta* and *E. fluviatile* had their highest RGRs on organic sediments under partially flooded conditions and their lowest RGRs on the same sediments under totally submerged conditions. The same was true for *Sparganium erectum* and *T. latifolia*. The growth pattern of the latter species differed from the former ones in showing high negative growth rates on both sediments under prolonged submerged conditions (Fig. 5).

The shoot fractions at the end of the experiment varied with species, flooding depths and sediment types (Table 2; Fig. 6). Shoot fractions of *A. calamus*, *T. angustifolia*, *Scirpus lacustris* and *Sagittaria sagittifolia* did not show much variation in response to flooding depth. Those of *C. acuta*, *E. fluviatile*, *Sparganium erectum* and *T. latifolia* were lower under submerged conditions. In general, shoot fractions were highest for plants growing on organic, highly reductive sediments, indicating that more biomass was allocated to above-ground plant parts on organic, highly reductive sediments than on mineral, moderately reductive sediments (Fig. 6).
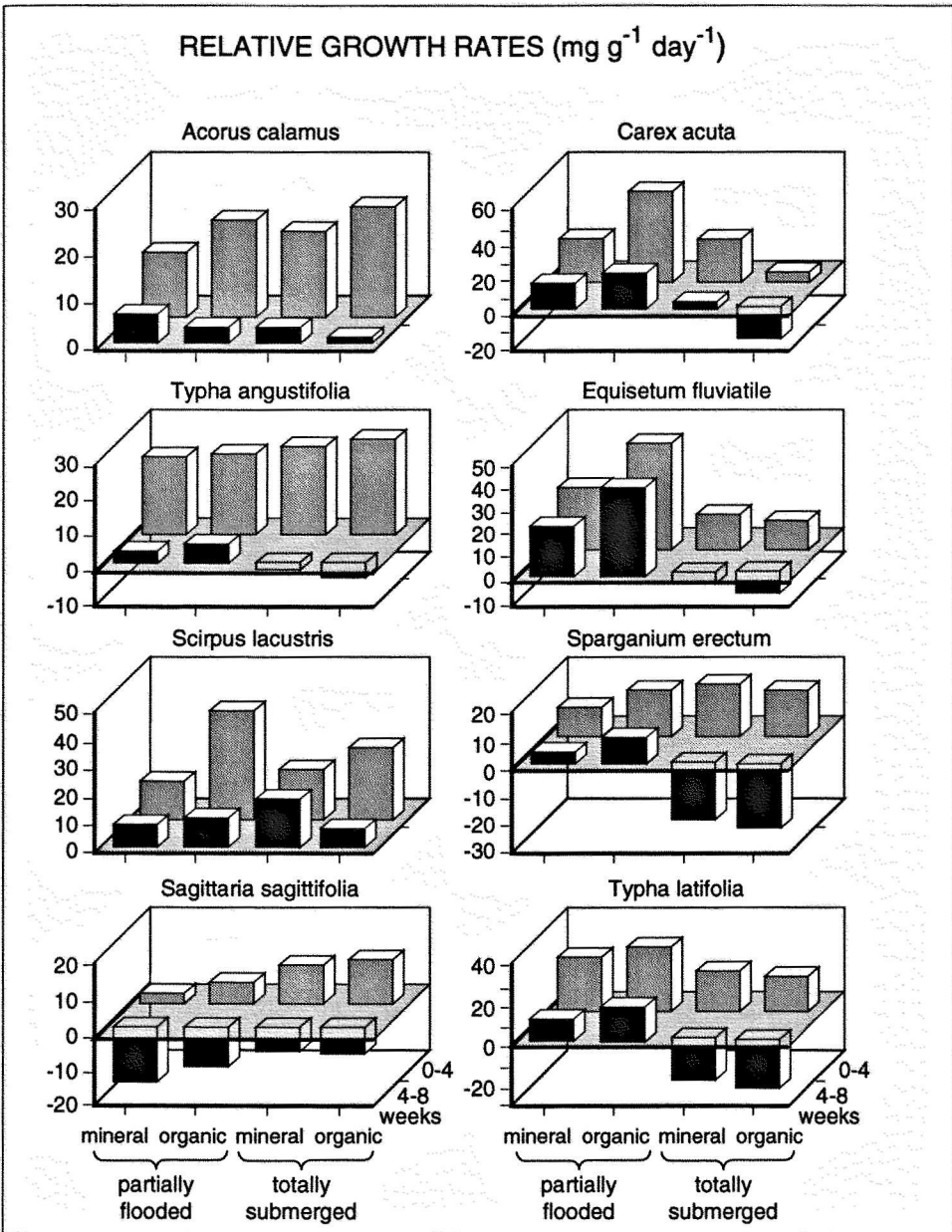
Figure 5. *Relative growth rates (in mg g⁻¹ day⁻¹) of eight helophyte species after the first (0-4) and after the second (4-8) four weeks of growth at two flooding levels and two contrasting sediments.*
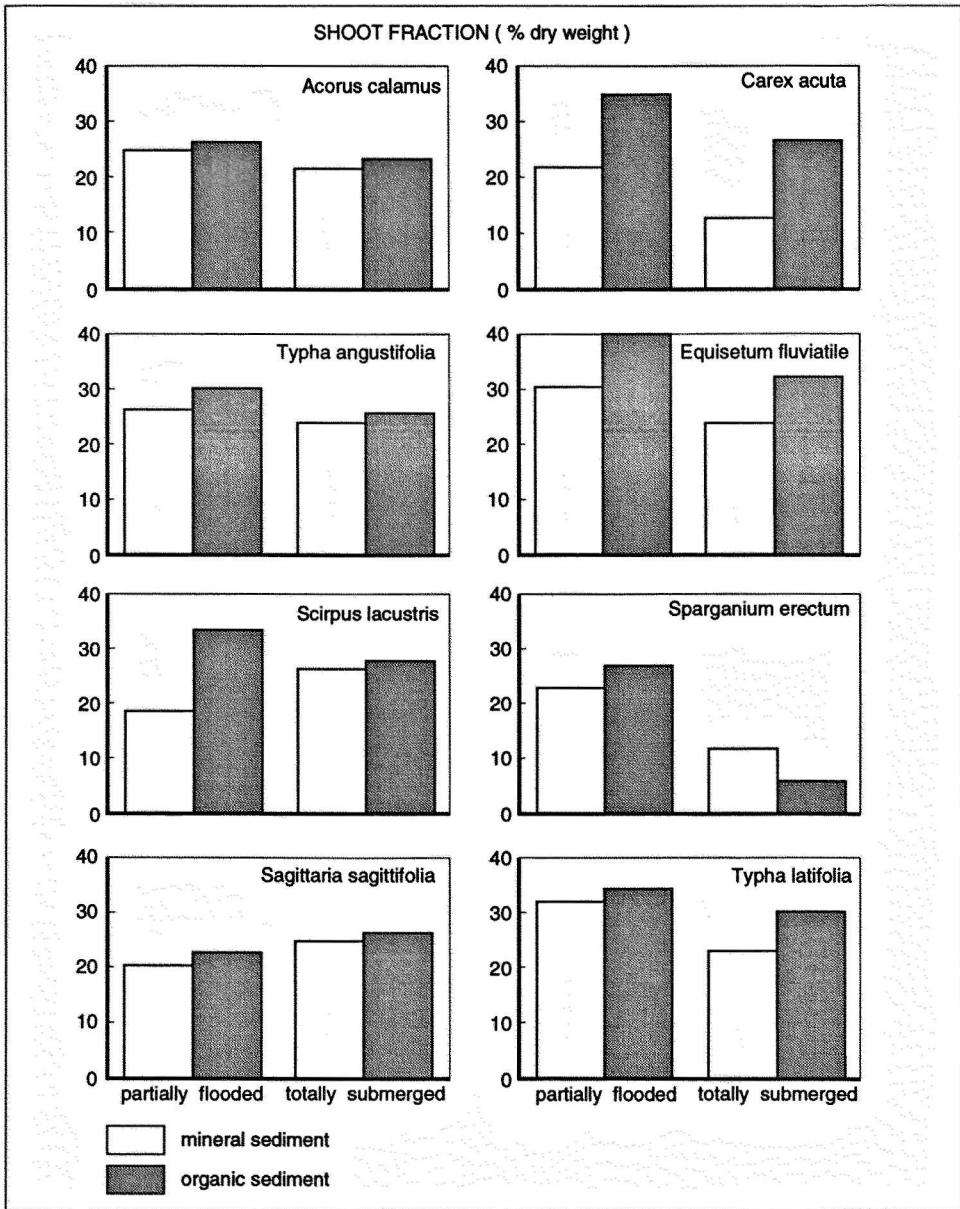
Figure 6. *Shoot fraction (= the dry weight biomass of the above-ground plant parts as a percentage of the total plant dry weight biomass) of selected helophyte species after eight weeks of flooding treatment in relation to substrate and flooding condition.*

Discussion

The mesocosm experiments demonstrated a clear combined effect of flooding treatment and sediment type on the growth responses of helophytes from floodplain areas. Under conditions normal to helophytes, i.e. partially flooded conditions, shoot length extensions, relative growth rates and biomass allocation to above-ground plant parts were highest on organic, highly reductive substrates (Figs. 4, 5, 6). The higher growth rates on the organic substrate under the partially flooding conditions could not be attributed to a better nutrient supply, as both substrates were well supplied with nutrients from Osmocote, and concentrations of NH_4^+, P and K in the interstitial water of the two sediments were rather similar, whereas NO_3^- was highest in the mineral sediment (Table 1). The concentrations measured in these sediments were within the range of those recorded in the field (Van den Brink, 1990). The difference in redox potential between the two sediments is a factor more likely to be involved. The organic sediment showed the lowest redox potential (Table 1), putting a greater oxygen demand on the roots of the helophytes (Armstrong, 1967), whereas it also showed the highest levels of sulphide and manganese, which are toxic under these circumstances (Pearson and Havill, 1988; McKee et al., 1989; Ernst, 1990; Koch et al., 1990; Gambrell et al., 1991). Because all species selected possess intercellular lacunae in their shoots, rhizomes and roots, oxygen can be transported from the ambient air to their root zones for respiration and detoxification, as long as the plants are largely emergent (Barclay and Crawford, 1982; Smirnoff and Crawford, 1983; Studer and Brändle, 1984; Brändle, 1991). This means that it is extremely important for these species to have enough shoot (stems, leaves) biomass above the water level to deal with the anoxic and toxic conditions in their rooting zones caused by the highly reductive flooded sediments. Both growth rate increase and biomass allocation to shoots can be seen as adaptations to these conditions, which all the species apparently tolerated well. An increase in plant growth rate in response to reductive and toxic sediment conditions has also been found in other wetlands plants (*Oryza sativa, Aster tripolium*) (Tolley et al., 1986; Pearson and Havill, 1988), so it may be a general strategy among such plants.

Under submerged conditions, the plants suffered from severe oxygen stress, because flooded sediments are anoxic (Armstrong, 1967). Prolonged complete submergence on oxidative to moderately reductive substrates is well tolerated by *Acorus calamus, Carex acuta, Typha angustifolia, Scirpus lacustris, Sagittaria sagittifolia*, and not tolerated by *Equisetum fluviatile, Sparganium erectum* and *T. latifolia* (Fig. 5). In response to submergence all species, except *C. acuta* and *E. fluviatile*, increased their shoot lengths and restored contact with the ambient air (Fig. 4). Shoot length extension is a common adaptation of wetland plants to avoid anoxia (Armstrong, 1969; Blom et al., 1990; Brändle, 1991), but is in itself not a guarantee for flood tolerance. For example, the restoration of the leaf-air contact by shoot length extension did not prevent the decay of *Sparganium erectum* and *T. latifolia* under prolonged submerged conditions. Moreover, other adaptations to submergence are also possible. For example, *C. acuta* survived the prolonged anoxic conditions on the mineral substrate during complete submergence by growth retardment, which can be seen as an adaptation to flooding conditions too.

During prolonged submergence all species selected showed their lowest RGRs on the organic, highly reductive substrate, indicating that they suffered most from oxygen stress on these highly oxygen demanding and toxic sediments when the air-leaf contact is impaired. A combination of high water levels leading to prolonged submergence of helophyte stands and organic, highly reductive substrates is an exceptional situation in the Dutch river forelands. Normally, high water levels during the growth season occur in the unprotected, very dynamic floodplain lakes only, where organic, highly reductive substrates are absent (Fig. 1). However, the last decades abnormal high water levels during the growth season have occurred more and more frequently in the Lower Rhine and Meuse floodplains (Van de Steeg, 1984; Brock et al., 1987; Van den Brink et al., 1991). It has been suggested that this change in flooding regime is responsible for the decline of the helophyte vegetation in the moderately dynamic floodplain lakes, especially on the organic sediments (Van de Steeg, 1984; Brock et al., 1987). The present results clearly show that a combination of prolonged submergence and highly reductive substrates leads to a growth reduction in all species selected.

Species-specific differences in growth responses and tolerance to flooding and substrate parameters can be related to the distribution patterns of the selected species in the field. The species which occur over the entire flooding gradient, *Acorus calamus* and *Carex acuta*, both showed tolerance to anoxic conditions when they are experimentally subjected to floods leading to submergence. *A. calamus* showed no significant change in growth rate at all under the various experimental treatments. *C. acuta* on the other hand, was found to be intolerant to a combination of prolonged anoxia and the presence of toxins. This intolerance may explain why *C. acuta* occurred mainly on mineral, oxidative to moderately reductive sediments in the Dutch river forelands (Fig. 3). Along the Lower Rhine and Meuse, *Equisetum fluviatile, Sagittaria sagittifolia, Scirpus lacustris, Sparganium erectum, Typha angustifolia* and *Typha latifolia* were absent or very sparse in dynamic floodplain lakes (Fig. 3). *Sagittaria sagittifolia, Scirpus lacustris* and *T. angustifolia* showed tolerance to prolonged submergence on mineral and organic substrate types, unlike *E. fluviatile, Sparganium erectum* and *T. latifolia*, which were intolerant to prolonged submergence on both substrate types (Fig. 5). The absence of *E. fluviatile, Sparganium erectum* and *T. latifolia* from very dynamic lakes might be related to their intolerance to anoxic conditions caused by prolonged submergence, irrespective of substrate conditions (Figs. 2, 5; Table 3). The absence of *Sagittaria sagittifolia, Scirpus lacustris* and *T. angustifolia* from very dynamic floodplain lakes might result from an intolerance to the very large water-level fluctuations which occur in these lakes. Apart from an influence on the air-leaf contact, water dynamics exercise a mechanic influence on these plants, leading to breakage of culms, or uprooting of entire plants (Coops et al., 1991). In addition, frequent disturbance of the sediment as a result of scouring during floods might prevent the establishment of these species in very dynamic floodplain lakes. Furthermore, the influx of eutrophic river water during floods results in an impoverished underwater light climate (Van den Brink et al., 1993) which hinders the photosynthesis of submerged plant parts and thereby their growth.

Table 3. *Synthesis of field and experimental observations on distribution and tolerance of eight selected helophyte species with respect to flooding conditions and substrate parameters.*

	DISTRIBUTION in lake categories			EXPERIMENTAL TOLERANCE prolonged submergence		DISTRIBUTION on sediments
	A	B	C	mineral moderately reductive sediments	organic highly reductive sediments	organic highly reductive sediments
Scirpus lacustris	++	++	+	+	+	+
Typha angustifolia	++	++	+	+	+	+
Sagittaria sagittifolia	++	++	+	+	+	-
Acorus calamus	++	++	++	+	+	-
Carex acuta	++	++	++	+	-	-
Equisetum fluviatile	++	++	+	-	-	-
Sparganium erectum	++	++	-	-	-	-
Typha latifolia	++	++	-	-	-	-

A = isolated lakes; B = moderately dynamic lakes; C = very dynamic lakes;
++ = very common; + = present/tolerant; - = absent/intolerant.

Conclusions

The present study clearly demonstrates that all selected helophyte species show tolerance to highly reductive and toxic substrates, provided enough shoot biomass is present above the water surface. Long-term inundations of floodplain areas during the growth season, which result in partial flooding of these plants, increase growth rates and induce biomass allocation to above-ground plant parts when they grow on reductive and toxic sediments. Short-term inundations leading to complete submergence are well tolerated on such substrates. Prolonged total submergence of helophytes on organic, highly reductive sediments results in a growth reduction for all species selected. This is in accordance with observations of the deterioration of the helophyte vegetation in the Lower Rhine and Meuse floodplain lakes, in particular on the organic, highly reductive sediments in response to summer floods.

Besides these shared growth responses the present study clearly demonstrates differences between the eight selected species with respect to their field distribution and experimental tolerance to flooding levels and redox potentials of the submerged sediments (Table 3). *Scirpus lacustris* and *Typha angustifolia* are tolerant to prolonged submergence on mineral, moderately reductive sediments and on organic, highly reductive sediments. These species occur in isolated as well as in very dynamic floodplain lakes, but predominantly in isolated and in moderately dynamic lakes, on mineral to organic, reductive to highly reductive sediments. *Sagittaria sagittifolia* is tolerant to prolonged submergence, on mineral, moderately reductive sediments and on organic, highly reductive sediments. It is distributed in the floodplain in isolated as well as in very dynamic lakes, but mainly in moderately dynamic lakes on mineral to organic, oxydative to reductive sediments. *Acorus calamus* is tolerant to prolonged

submergence on mineral, moderately reductive sediments and on organic, highly reductive sediments. It occurs in isolated as well as in very dynamic floodplain lakes, although it is less common in isolated lakes. It can be found on mineral to organic reductive sediments. *Carex acuta* is tolerant to prolonged submergence on mineral, moderately reductive sediments but intolerant to prolonged submergence on organic, highly reductive sediments. It occurs in isolated as well as in very dynamic floodplain lakes, on mineral to low organic, moderately reductive to oxidative sediments. *Equisetum fluviatile*, *Sparganium erectum* and *Typha latifolia* are intolerant to prolonged submergence, irrespective the sediment type. These species occur in isolated and in moderately dynamic floodplain lakes, on mineral to organic, oxydative to reductive sediments. *E. fluviatile* occurs rarely in very dynamic lakes.

Besides these species-specific tolerances and distribution patterns, discrepancies between the field distribution and the experimental growth responses were found. For example, *Scirpus lacustris*, *T. angustifolia*, *Sagittaria sagittifolia*, *A. calamus* and *C. acuta* were found to tolerate prolonged submergence when growing on a mineral, moderately reductive sediment, but only the latter two species were commonly found in very dynamic floodplain lakes in which summer floods are a normal phenomenon (Table 3). Prolonged submergence on organic, highly reductive sediments were tolerated by *Scirpus lacustris*, *T. angustifolia*, *Sagittaria sagittifolia* and *A. calamus*, but only the first two species were found to occur on highly reductive organic sediments in the floodplain lakes (Table 3). The observed discrepancies between the field situation and the experimental results suggest that apart from flooding depth, flooding duration, flooding season and sediment characteristics other factors (e.g. germination requirements, competition, herbivory) which also restrict their occurrence are involved in the distribution of helophyte species in river floodplain lakes.

Acknowledgements

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CHAPTER 7

Macrozoobenthos of floodplain waters of the rivers Rhine and Meuse in The Netherlands: a structural and functional analysis in relation to hydrology

Abstract

The river systems of the Rhine and Meuse include a large number of floodplain waters showing differences in hydrology and geomorphology. A classification of 100 water bodies based on their macroinvertebrate communities has been worked out as a tool for ecological management. Analyses were performed on structural (species composition) and functional (trophic relations) aspects of macrozoobenthos in relation to hydrological, vegetational and physicochemical parameters. Based on the classification of macroinvertebrate communities, three major groups of water bodies can be distinguished, which are related to the frequency of inundation. The annual flood frequency constitutes the major environmental gradient which structures the zoobenthos communities in the Dutch floodplain waters. Faunal composition is mediated by substrate availability, water chemistry, and the availability of nutritional resources. This typology serves as a basis for the prediction of the impact of hydrology changes on the macrozoobenthos communities of floodplain waters of highly eutrophic and otherwise polluted rivers.

Introduction

Many large European rivers have been subjected to anthropogenic influences since Roman times. Up to the Middle Ages the rivers Rhine and Meuse were natural, meandering streams, with side channels, cut-off channels, and oxbow lakes. Today these rivers are for the greater part embanked and regulated, and as a consequence the total floodplain area is fixed and greatly reduced (Van Urk and Smit, 1989). As a result of both former river activity and human activities the Netherlands floodplains harbour numerous 'lentic' water bodies, which have different degrees of connectedness with the main channel. In addition to the changes in geomorphology, the water chemistry in the main channels of the rivers Rhine and Meuse has also been drastically altered. Major changes since the beginning of this century include a five to sixteen-fold increase in chlorinity as a result of mining activities, and a four to fifteen-fold increase in nutrients (P and N) due to increased inputs of agricultural fertilizers, sewage, and industrial effluents (Van den Brink et al., 1991). In addition to these chemicals, the river water has also been severely polluted by heavy metals and organic micropollutants (Anonymous, 1988).

It is now generally accepted that large river ecosystems include the entire floodplain area and not only the lotic component (e.g. Minshall et al., 1985; Amoros et al., 1987; Junk et al., 1989). However, up to now, studies on the zoobenthos of the rivers Rhine and Meuse have focused on the main channel (e.g. Peeters, 1988; Schiller, 1990; Tittizer et al., 1990; Van den

Brink et al., 1990; Van der Velde et al., 1990; Van Urk and Bij de Vaate, 1990; and references therein). Except for a few studies in some selected water bodies along the German Upper River Rhine (e.g. Biss and Palm, 1990; Halbfass, 1990; Neugebauer, 1990; Obrdlik et al., 1990), there is no extensive information on the macrozoobenthos in floodplain waters within these river systems in relation to hydrology and other physicochemical parameters. Such basic knowledge is necessary in order to understand the ecological functioning of the entire river system. Furthermore it serves as a background in assessing the impact of changes in hydrology on floodplain waters due to human interferences (Bravard et al., 1986; Amoros et al., 1987).

Macroinvertebrates are frequently used to describe structural and functional aspects of the lotic parts of river ecosystems (e.g. Cummins, 1974; Vannote et al., 1980; Cummins et al., 1984; Ward et al., 1986). However, relatively few attempts have been made to describe structural and functional relationships within the macroinvertebrate assemblages in 'lentic' floodplain waters. Most of these studies cover only specific animal groups and emphasize the use of characteristic species as environmental descriptors (e.g. Richardot-Coulet et al., 1983; Castella et al., 1984; Castella and Amoros, 1988; Foeckler, 1990), whereas attempts to describe habitats in terms of nutritional resources based on the total macrozoobenthos composition have been extremely rare (Gladden and Smock, 1990).

In order to determine the impact of hydrology on the structure and function of Dutch floodplain waters, the species composition of the macrozoobenthic communities was studied in relation to environmental parameters. The specific aims of this study were to describe the relation between the annual flood frequency and (a) structural (species composition, habitat assemblages) and (b) functional (trophic relationships) aspects of the macrozoobenthic communities.

Study sites and methods

Study sites

Within the floodplains of the rivers Rhine and Meuse 'lentic' water bodies can be categorized according to their geomorphology and hydrology. Sites were selected within the floodplains of the lowland reaches of the rivers Rhine and Meuse in the Netherlands outside the tidal influence (Fig. 1). Normally, the Dutch floodplain waters are inundated only during winter and spring (Fig. 2A). Most waters become isolated from the river during the rest of the year (Fig. 2B), except for water bodies which are in permanently open connection with the main channel. The latter waters are entirely or partly located between the low summer dikes, i.e. within the summer bed of the river. Water levels in these water bodies follow the fluctuations in the main channel, resulting in relatively frequent inundations. In the forelands, the areas between the summer bed and the main dikes, the inundation frequency is largely dependent on local hydrological circumstances such as the height of summer dikes and natural levees, together with actual water-level fluctuations in the main channel. Water-level fluctuations in these water

bodies decrease with increasing distances from the main channel. In general, the water bodies located on higher grounds in the river forelands are flooded only during high river discharges. The water bodies behind the main dikes are never flooded, except in very rare catastrophes, and are normally influenced by seepage only.

Hydrology

A hydrological characterization of the main channels of the rivers Rhine and Meuse is presented in Van den Brink et al. (1991). In the Dutch sections of the rivers Rhine and Meuse, water-level fluctuations vary from 0.5 to 9.5 m; in the sections under study from 2 to 6 m. In order to quantify the hydrological situation of the floodplain waters, the frequency of inundation by river water was calculated as follows. Firstly, based on river maps, the inundation level for each site was estimated, which is the lowest river level at which that part of the floodplain is inundated. Next, the long term (1901-1985) average annual number of days on which the water level in the main channel reaches this level of inundation was calculated (= frequency of inundation). Hydrological data for the floodplain waters were derived from the Institute for Inland Water Management and Waste Water Treatment (RIZA, Arnhem, The Netherlands).

Sampling and identification

In order to study the macrozoobenthos, 100 'lentic' water bodies located on the floodplains of the rivers Rhine and Meuse in the Netherlands (Fig. 1) were selected on the basis of geomorphological and hydrological characteristics. The littoral zone of each water body was sampled for macrozoobenthos with a triangular pond-net (base: 50 cm; height: 30 cm; length: 50 cm; mesh size: 0.5 mm; length of handle: 110 cm) during the summer period (August-September). Any macroinvertebrates living on fixed substrates such as stones were sampled by scraping the substrate. Sampled material was put in plastic bags which were kept cool and transported to the laboratory. After washing over a 0.5 mm mesh sieve the macroinvertebrates were sorted out in white trays and preserved in 70 per cent ethanol or in Koenike-solution (water mites), except for flatworms and leeches, which were identified alive. All specimens were identified to species level if possible. The following groups were identified: Tricladida, Oligochaeta, Hirudinea, Bivalvia, Gastropoda, Chelicerata (Araneida and Actinedida), Crustacea (Isopoda, Amphipoda, and Decapoda) and Hexapoda (Ephemeroptera, Odonata, Heteroptera, Coleoptera, Megaloptera, Diptera, Trichoptera, and Lepidoptera). The nomenclature used in this paper follows that of Mol (1984). At each site the (semi-) aquatic vegetation was described. Physicochemical parameters of the water and sediment were obtained by standard laboratory procedures (Van den Brink, 1990).

Data analysis

To assess the similarity of the macroinvertebrate species composition between sites, based on the presence or absence of taxa, samples were classified by hierarchical clustering with the average linkage between merged groups technique, using Jaccard coefficients (Pielou, 1984; Jongman et al., 1987). Taxa which occurred in less than 5 per cent of the sites were omitted in this procedure. Site groups resulting from hierarchical clustering were compared for characteristic taxa, i.e. taxa which occurred significantly relatively more frequent in one of the site groups, with the use of Fisher's exact test (Sokal and Rohlf, 1981).

In order to describe the site groups in terms of relative species composition, the species were divided into three categories: faunal groups, habitat association groups, and functional feeding groups. For each faunal group the mean number of species per site was calculated. In order to show the relative importance of the different habitats and nutritional resources for the macroinvertebrates within the site groups, the calculations for these two categories were based on the characteristic taxa within the site groups (Table 1) in addition to the common taxa which occurred in more than 50 per cent of the sites within one site group (Table 2). Species which belonged to different categories with respect to habitat preference or feeding
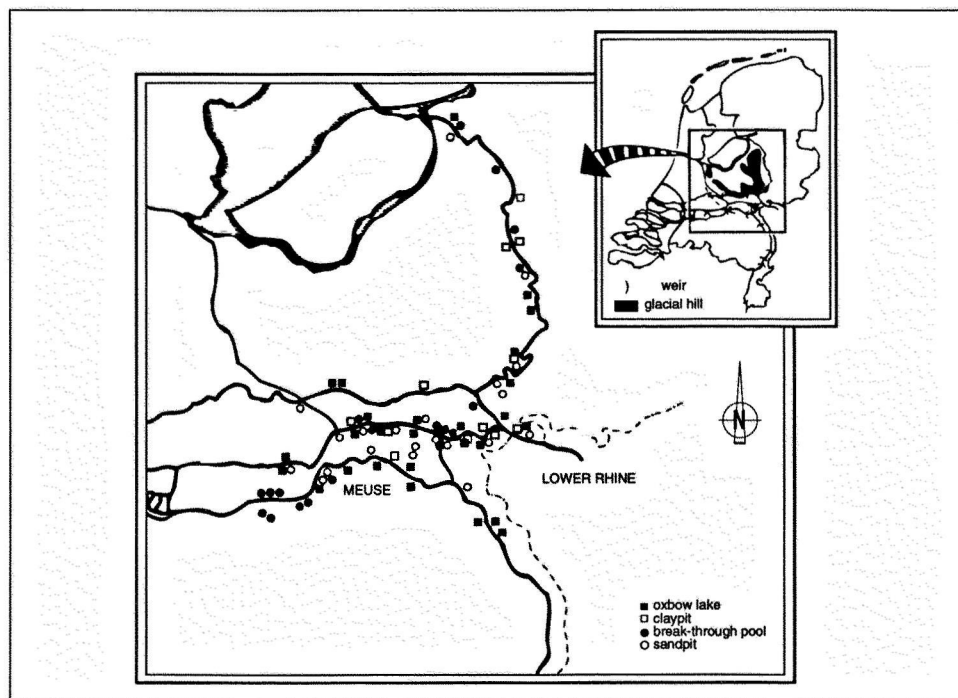
Figure 1. *Map of the sampling sites.*
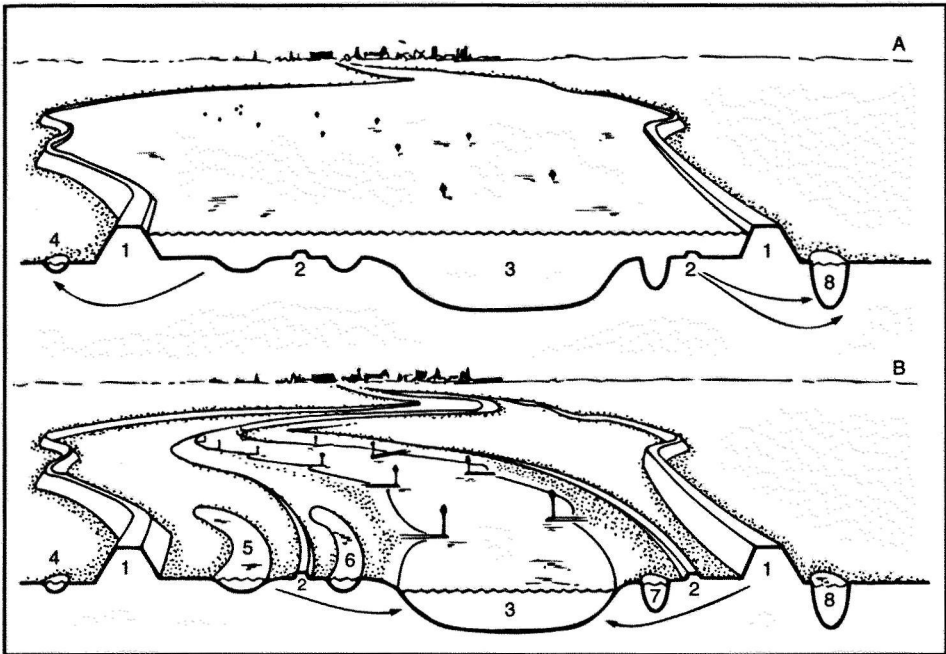
Figure 2. *Schematic view of water bodies within a river system, during winter (A) and summer (B). 1 = main dikes, 2 = summer dikes, 3 = river bed, 4-8 = floodplain waters. Arrows indicate direction of seepage.*

mechanism were included in both categories. The percentages of species per category were then calculated for each site group.

Results

A hierarchical classification of the sites based on the species composition of the macro-zoobenthos shows a division into three major site groups (Fig. 3). Characteristic species, i.e. species which occur significantly more frequently (Fisher's exact test) in a particular site group are listed in table 1. A physicochemical characterization of these site groups shows that there are distinct differences with respect to their frequency of inundation and related physicochemical parameters, such as N, P, Cl and alkalinity (Table 3). Sites of group I are located outside the 'active' floodplain, viz. on the land side of the main dike. These sites are no longer flooded, but receive seepage water when river discharges are high. The sediment of these sites consists of a mixture of sand and clay. The helophyte zone is well developed. The aquatic vegetation is diverse and consists of submerged macrophytes and nymphaeids. Sites of group II are located in the active floodplain and are subject to infrequent inundations. The annual

Table 1. *Relative frequency of occurrence of characteristic macroinvertebrates within the site groups from Hierarchical clustering. n = number of sites per group. Only species which are significantly more frequently (+++, ++, +) or less frequently (——, —, -) present (Fisher's exact test) within any site group are indicated.*
+++/——: p < 0.001, ++/—: p < 0.01, +/-: p < 0.05.

Site group	I	II	III	Site group	I	II	III
n	24	42	34	n	24	42	34
TRICLADIDA				**GASTROPODA** (cont.)			
Dugesia tigrina	++			*Bithynia tentaculata*			—
Dugesia polychroa	-	+++	-	*Physella acuta*	——	-	+++
Polycelis tenuis		++	——	*Potamopyrgus antipodarum*		——	+++
Dendrocoelum lacteum			-	*Lithoglyphus naticoides*			++
OLIGOCHAETA				**ACTINEDIDA**			
Nais pardalis		+		*Hydrodroma despiciens*	+++		—
Psammoryctides albicola		+		*Limnesia undulata*	++		—
Tubificidae		+		*Neumania vernalis*	++		
Lumbriculus variegatus			——	*Piona longipalpis*	++		
Limnodrilus claparedeanus	—			*Hydrachna cruenta*	+		-
HIRUDINEA				*Hygrobates longipalpis*	+		
Glossiphonia heteroclita		+++	——	*Limnesia maculata*	+		
Helobdella stagnalis		+++	—	**CRUSTACEA**			
Erpobdella testacea		++		*Proasellus meridianus*	+		
Erpobdella octoculata		+	-	*Asellus aquaticus*		++	—
Hemiclepsis marginata		+		*Gammarus tigrinus*	——		+++
BIVALVIA				*Atyaephyra desmaresti*			+
Pisidium milium	+			**EPHEMEROPTERA**			
Pisidium obtusale	+			*Caenis luctuosa*	+++	—	
Dreissena polymorpha		——	+++	*Cloeon simile*	+++	-	
Unio pictorum			++	*Caenis horaria*	++		
Anodonta anatina			++	**ODONATA**			
Sphaerium solidum			++	*Enallagma cyathigerum*	++		
Pisidium supinum			++	*Erythromma najas*	++		——
Unio tumidus			+	*Coenagrion pulchellum*	+		-
Pisidium casertanum			+	*Ischnura elegans*		+++	-
Pisidium henslowanum			+	Coenagrionidae		++	-
GASTROPODA				*Coenagrion puella*			-
Planorbis planorbis	—	+++		*Coenagrion* spec.			-
Bithynia leachi		+++	—	**HETEROPTERA**			
Anisus vortex		+++	—	*Ilyocoris cimicoides*	++		—
Acroloxus lacustris		++	-	*Plea minutissima*	++		—
Physa fontinalis		++	——	*Gerris thoracicus*		+++	
Gyraulus albus		++	—	*Notonecta glauca*		+++	——
Bathyomphalus contortus		++	——	*Callicorixa praeusta*		++	
Planorbarius corneus		++	—	*Corixa punctata*		++	-
Hippeutis complanatus		++	——	*Hesperocorixa linnei*		++	
Valvata cristata		++	——	*Gerris argentatus*		++	
Segmentina nitida		+		*Nepa cinerea*		++	
Planorbis carinatus			——	*Mesovelia furcata*		+	

Table 1. *Continued*

| Site group	I	II	III	Site group	I	II	III
n	24	42	34	n	24	42	34
HETEROPTERA (cont.)				**DIPTERA** (cont.)			
Sigara falleni		+	—	*Polypedilum uncinatum*	+		
Sigara lateralis		+		*Tanypus kraazi*	+		–
Gerris odontogaster	–			*Cladotanytarsus* spec	+		
COLEOPTERA				*Clinotanypus nervosus*		++	———
Haliplus flavicollis	+++	–	–	*Metriocnemus hirticollis*		+	
Hyphydrus ovatus	++		——	*Chaoborus flavicans*		+	——
Haliplus immaculatus	++		—	*Ptychoptera* spec		+	
Haliplus lineolatus	++			*Chironomus thummi*			—
Haliplus varius	++			*Microtendipes chloris*			——
Ilybius fenestratus	+			*Paratanytarsus* spec			———
Helophorus brevipalpis		++		*Dicrotendipes nervosus*			–
Hygrotus versicolor		++	——	*Cricotopus sylvestris*	——		
Hygrotus decoratus		+		*Glyptotendipes* spec	–		
Laccophilus minutus		+	—	**TRICHOPTERA**			
Enochrus testaceus		+		*Cyrnus crenaticornis*	+++		—
Hydrobius fuscipes		+		*Molanna angustata*	+++	–	
Peltodytes caesus		+		*Cyrnus flavidus*	++		
Haliplus ruficollis		+		*Athripsodes aterrimus*	++		—
Laccophilus hyalinus		—		*Mystacides nigra*	++		
Noterus crassicornis		—		*Triaenodes bicolor*	++		——
Haliplus gr ruficollis		—		*Agraylea multipunctata*	+		
MEGALOPTERA				*Agrypnia pagetana*	+		
Sialis lutaria	++		—	*Oecetis furva*			—
DIPTERA				*Phryganea grandis*			–
Psectrocladius psilopterus	+++	—		*Oecetis ochracea*			++
Psectrocladius obvius	++			**LEPIDOPTERA**			
Ablabesmyia phatta	++			*Acentropus niveus*	+++	—	
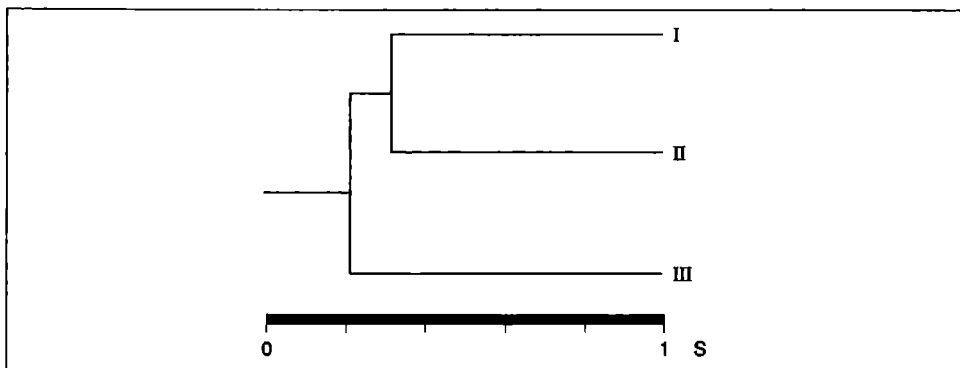
Figure 3. *Dendrogram showing site groups from cluster analysis. S = similarity (Jaccard coefficient).*

Table 2. *Absolute frequencies of occurrence of macroinvertebrate taxa which occur in at least 50 per cent of the sites within any site group.*
Frequency of occurrence: *: 1-25%, **: 26-50%, ***: 51-100% of the sites within one site group.

Site group	I	II	III	Site group	I	II	III
OLIGOCHAETA				**ACTINEDIDA** (cont.)			
Tubificidae	**	***	**	Limnesia maculata	***	***	***
HIRUDINEA				**CRUSTACEA**			
Glossiphonia heteroclita	***	***	*	Asellus aquaticus	***	***	***
Piscicola geometra	***	***	**	Gammarus pulex	***	**	**
Erpobdella testacea	**	***	*	Gammarus tigrinus		**	***
Hemiclepsis marginata	**	***	*	**EPHEMEROPTERA**			
Theromyzon tessulatum	**	***	*	Caenis luctuosa	***	*	*
Glossiphonia complanata	**	***	**	Caenis horaria	***	**	**
Helobdella stagnalis	***	***	***	**ODONATA**			
Erpobdella octoculata	***	***	***	Coenagrionidae	***	***	**
BIVALVIA				**HETEROPTERA**			
Sphaerium corneum	*	***	**	Sigara falleni	***	***	**
Pisidium casertanum	**	**	***	Sigara striata	***	***	***
Pisidium subtruncatum	**	**	***	**COLEOPTERA**			
Pisidium supinum	*	*	***	Haliplus immaculatus	***	*	*
Dreissena polymorpha	*	*	***	Laccophilus hyalinus	***	***	*
GASTROPODA				Hygrotus versicolor	***	***	**
Bathyomphalus contortus	**	***		**DIPTERA**			
Bithynia leachi	***	***	*	Microtendipes chloris	***	***	**
Hippeutis complanatus	***	***	*	Polypedilum gr. sordens	***	***	**
Planorbis carinatus	***	***	*	Chironomus thummi	**	***	*
Anisus vortex	***	***	*	Endochironomus albipennis	***	***	***
Acroloxus lacustris	**	***	*	Glyptotendipes spec	***	***	***
Physa fontinalis	**	***	*	Polypedilum nubeculosum	***	***	***
Valvata cristata	**	***	*	Procladius spec	***	***	***
Gyraulus albus	***	***	**	Cladotanytarsus spec	***	*	***
Bithynia tentaculata	***	***	***	Tanytarsus spec	***	**	***
Radix auricularia	***	***	***	Cricotopus sylvestris	**	***	***
Radix peregra	***	***	***	Cryptochironomus spec	**	**	***
Potamopyrgus antipodarum	***	**	***	Dicrotendipes nervosus	**	**	***
Valvata piscinalis	***	***	***	**TRICHOPTERA**			
Planorbis planorbis		***	*	Athripsodes aterrimus	***	*	
Physella acuta		*	***	Molanna angustata	***	*	*
ACTINEDIDA				Cyrnus flavidus	***	**	*
Hydrodroma despiciens	***	*	*	Mystacides longicornis	***	**	***

average frequency of inundation is less than 20 days per year. These sites are flooded during winter, but (very) rarely during the growing season. The sediment consists mainly of clay covered with a sapropelium layer (organic matter content up to 21 per cent). A broad littoral helophyte zone is present. Nymphaeids are dominant in the water compartment. Sites of

Table 3. *Physicochemical parameters, sediment characteristics and vegetational aspects of the site groups from the Hierarchical clustering of the sites based on the presence or absence of macrozoobenthos species. Inundation frequency in days per year; NO_3^- and oPO_4^{3-} in $\mu mol\ l^{-1}$; Cl^- and HCO_3^- in mmol l^{-1}; organic matter content in % (all ranges).*

Site group	I	II	III
HYDROLOGY			
Geographical location	land side	river side	river side
Inundation frequency	0	1-20	21-365
CHEMISTRY			
Trophic level	medium	high	very high
NO_3^-	< 5	5-10	10-100
oPO_4^{3-}	< 0.5	1-5	1-5
Chlorinity	medium	high	very high
Cl^-	0.5-1.5	1-2	2-4
Alkalinity	high	high	high
HCO_3^-	2-4	2-4	1-2
SEDIMENT			
Sediment type	sand/clay	clay	sand/clay
Organic matter content	1-26	1-21	1-15
VEGETATION			
Helophyte zone	rich	rich	poor
Submerged macrophytes	dominant	present	absent
Nymphaeid macrophytes	present	dominant	present

group III are located in the active floodplain and are subject to (very) frequent inundations. The annual average frequency of inundation is more than 20 days per year. Floodings occur during winter and summer. The sediment consists mainly of sand with a small amount of clay. The helophyte zone is poorly developed and aquatic macrophytes are sparse or absent (Table 3).

In the Dutch floodplain waters relatively high numbers of (semi-) aquatic insect (especially Diptera) and mollusc species were found (Fig. 4A). Apart from a decrease in the total number of macrozoobenthos species in site group III, the entire species composition alters with changing flood frequencies. In general, the relative numbers of mollusc species increase with increasing inundation frequencies, whereas the relative numbers of water mites and insects (especially Coleoptera and Trichoptera) decrease (Fig. 4B). Although the absolute number of Diptera species also decreases with increasing flood frequencies (Table 1), the percentage of Diptera species increases, because the decline in numbers of other insect groups is larger.

A characterization of the three site groups based on the substrate association of the contributing macrozoobenthos species is presented in figure 5A. It shows that the species composition of site groups I and II, with abundant vegetation, is characterized by phytophilous
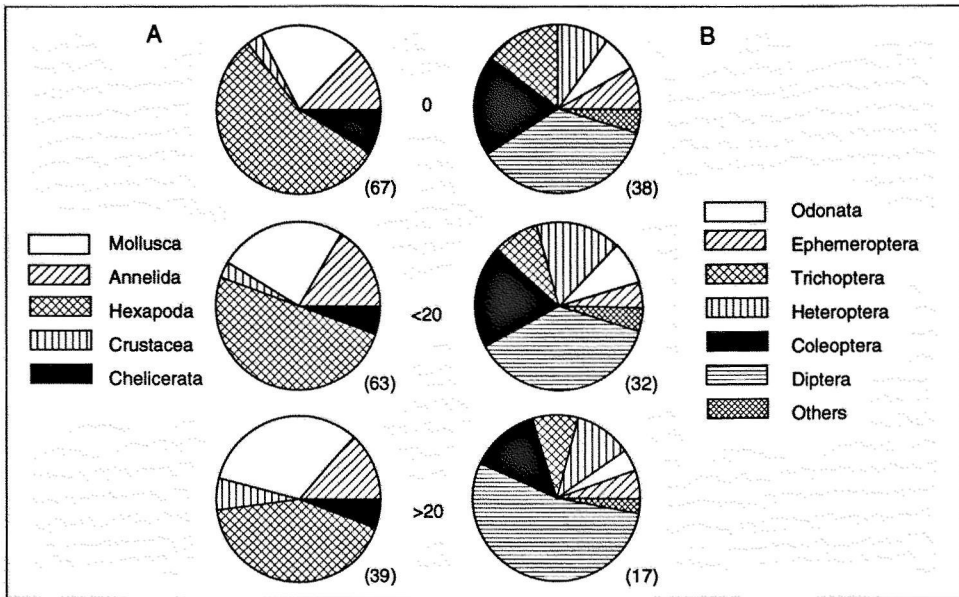
Figure 4. *Relative composition of major fauna groups (A) and insect groups (B) within the site groups, based on macroinvertebrate species composition. Numbers of species are given in brackets. 0, < 20, > 20: inundation frequencies of the site groups.*

species, whereas the species composition of site group III, with sparse vegetation, is characterized by psammophilous species. In addition to phytophilous species, site group II shows a relatively high number of pelophilous species, which correlates with the high organic matter content in the clayish sediment of these sites.

Figure 5B shows the relative species compositions of the three site groups based on the functional feeding categories distinguished by Cummins (1974). Most species in site groups I and II are predators, whereas the species composition of site group III is characterized by filter-feeding species. The percentages of shredding and scraping species are highest in site groups I and II respectively; that of collector-gatherers or deposit-feeders in site group III.

Discussion

Species composition and habitat characterization

Classification of the Dutch floodplain waters, based upon the presence or absence of macrozoobenthos species, results in the identification of three major site groups (Fig. 3; Table 1). Abiotic parameters underlying the division of the floodplain waters into these site groups are the frequency of inundation and interrelated physicochemical parameters, such as the contents of sodium, chloride, phosphate, and nitrate (Table 3; Van den Brink, 1990). As the flood
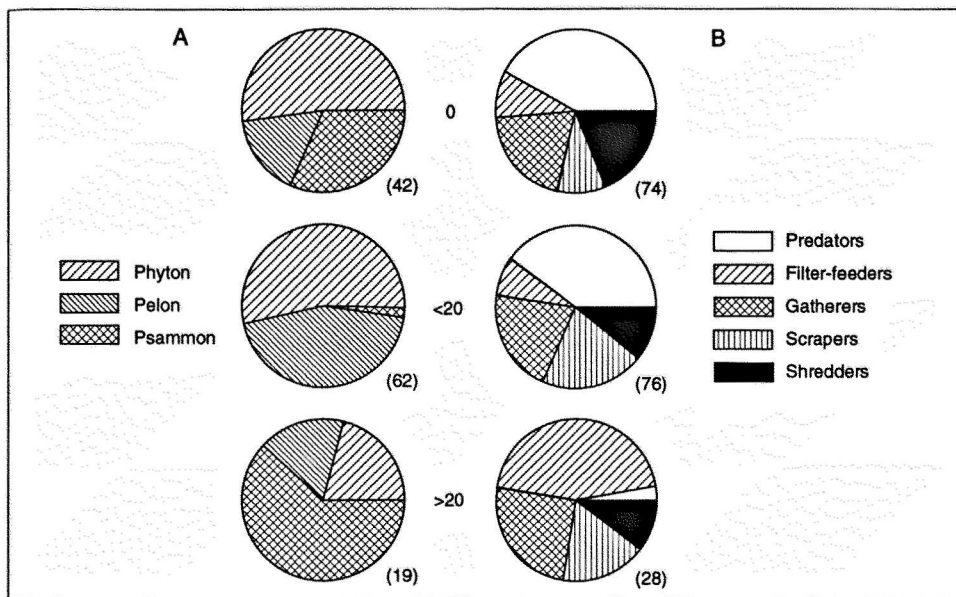
Figure 5. *Relative importance of habitats (A) and functional feeding groups (B) within the site groups, based on macroinvertebrate species composition. Numbers of species are given in brackets. 0, < 20, > 20: inundation frequencies of the site groups.*

frequency increases, the concentrations of these ions in the 'lentic' water bodies increase as well, due to a relatively high input of salts and nutrients from the main channel during floods (Van den Brink et al., 1991). A structural analysis of the three site groups (Fig. 4) shows that the mean number of macroinvertebrate taxa per site group decreases with increasing flood frequencies (Fig. 4A). Moreover, it was found that with changing flood frequencies the percentages of various faunal groups change. In non-flooded and infrequently flooded waters the species composition of the insect fauna is more diverse and the relative contributions of the various insect groups are more evenly distributed (Fig. 4B). In frequently or very frequently flooded water the entire macroinvertebrate community is impoverished. Among the (semi-) aquatic insects, it are especially the Trichoptera and Coleoptera which decrease in species richness with increasing frequencies of inundation, while a few Diptera species characterize the insect fauna (Fig. 4B; Table 2).

Several species which are characteristic of one of the site groups (Table 1) can be related to the presence or absence of specific substrates within such a site group. For example, the presence in site group I of *Cloeon simile, Enallagma cyathigerum, Ilyocoris cimicoides, Plea minutissima, Haliplus flavicollis* and *Acentropus niveus* is associated with the occurrence of submerged aquatic macrophytes (Macan, 1965; Seeger, 1971a, b; Kimmins, 1972; Geijskes and Van Tol, 1983). Characteristic species of site group II, such as *Ischnura elegans, Notonecta glauca, Metriocnemus hirticollis,* are associated with a broad helophyte zone (Macan,

1965; Geijskes and Van Tol, 1983; Moller Pillot and Buskens, 1990). The presence in site group III of *Pisidium supinum, P. casertanum, P. henslowanum, Sphaerium solidum, Potamopyrgus antipodarum, Lithoglyphus naticoides*, and *Oecetis ochracea* is associated with sandy substrates (Janssen and De Vogel, 1965; Wallace, 1981; Kuiper, 1986) (Table 3).

A characterization of the three site groups based on the substrate associations of the species is presented in figure 5A. Phytophilous species are relatively most numerous in site groups I and II, which are not or infrequently inundated (Fig. 5A). Due to several factors correlating with the frequency of inundation, such as water-level fluctuations, salinity, and eutrophication, the (semi-) aquatic vegetation of frequently flooded backwaters is sparse or absent (Van den Brink et al., 1991). As a consequence, this substrate is of minor importance for the macrozoobenthos in those waters. Besides phytophilous species, site group II waters are characterized by a large number of pelophilous species, which are associated with muddy substrates, such as a clay and sapropelium layer (Fig. 5A; Table 3). Site group III is characterized by a large number of psammophilous species (Fig. 5A), which are associated with the sandy substrates of the site group III waters (Table 3).

In addition to relations with the available substrates of the sites, there are relations with the water chemistry, e.g. trophic level and chlorinity. For example, chironomid species characteristic of site group I, such as *Psectrocladius psilopterus, P. obvius* and *Polypedilum uncinatum* occur predominantly in mesotrophic waters, whereas dominant chironomids of site group III, such as *Cricotopus sylvestris* and *Dicrotendipes nervosus*, are most frequently found in hypertrophic waters in the Netherlands (Moller Pillot and Buskens, 1990). Several species characteristic of site group III, such as *Dreissena polymorpha, Physella acuta, Potamopyrgus antipodarum, Gammarus tigrinus* and *Atyaephyra desmaresti* are euryhaline immigrants (Van den Brink and Van der Velde, 1986; Den Hartog and Van der Velde, 1987; Den Hartog et al., 1989), nowadays occurring in high numbers in the main channels of the rivers Rhine and Meuse (Peeters, 1988; Van den Brink et al., 1990; Van Urk and Bij de Vaate, 1990). At present, high concentrations of salts and nutrients resulting from anthropogenic sources occur in the Dutch main channels, favouring the occurrence of euryhaline opportunistic species (Van den Brink et al., 1990).

From the correlations between species assemblages and the available habitats it can be concluded that macroinvertebrates are good structural descriptors. Because of the correlations between the species composition and the water chemistry of the backwaters, the characteristic species can be used as physicochemical descriptors too (Castella et al., 1984). However, in order to understand the ecological meaning behind these correlations, more autecological and ecophysiological data are needed.

Functional feeding groups

According to the River Continuum Concept (Vannote et al., 1980), the relative importance of macroinvertebrate functional feeding groups changes along the longitudinal course of a river. In the lowland reaches of the large rivers Rhine and Meuse the faunal composition is dominated by collectors (filter-feeders and deposit-feeders) (Peeters, 1988; Van den Brink et al.,

1990), which is consistent with the RCC (Vannote et al., 1980). Aquatic macrophytes are nearly absent (Maenen, 1989), whereas phytoplankton is well developed in the Dutch main channels (De Ruyter van Steveninck et al., 1990), creating good conditions for collectors. However, because the RCC focuses on the longitudinal processes, it neglects the role of the transversal river-floodplain interactions, which are of major importance in large river ecosystems (Junk et al., 1989).

In the present study a change in macroinvertebrate functional feeding groups was found along the transversal dimension of the floodplain (Fig. 5B), which shows a flooding gradient (Fig. 2). Shredder species, which feed on coarse particulate organic matter (CPOM; mainly leaf litter, particle size greater than 1 mm), are most numerous in non-flooded waters (site group I; Fig. 5B), which are mesotrophic with a high diversity and a high production of the (semi-) aquatic vegetation (Van den Brink et al., 1991). Filter-feeding species, which use fine particulate organic matter (FPOM; particle size less than 1 mm), are most numerous in the frequently and very frequently flooded waters (site group III; Fig. 5B), which are hypertrophic causing phytoplankton blooms due to a high input of nutrients from the main channel (Table 3). As a result of large water-level fluctuations, high flood frequencies, phytoplankton blooms, and high concentrations of salts, vegetation is poorly developed (Van den Brink et al., 1991), so that the possibilities for shredders are limited. Collector-gatherers or deposit-feeding species, which use FPOM as sedimentary detritus, also increase their relative numbers with increasing flood frequencies (Fig. 5B). Scrapers, or grazing species which feed on epiphyton, are most numerous in site groups II and III (Fig. 5B) which are more eutrophic than site group I (Table 3). Predatory species are scarcely present in site group III (Fig. 5B), which can be linked to the monotonous habitat, probably resulting in a low prey diversity.

From this functional analysis it appears that energy pools within the floodplain waters change along the transversal flooding gradient, and are affected directly by the hydrology. These results are in agreement with the Flood Pulse Concept (Junk et al., 1989), in which the hydrology (the flood pulse) is the primary factor which controls the composition, productivity, and interactions of the biota in river-floodplain systems.

Impact of hydrology

From the present study it is clear that the species composition of the macrozoobenthos within the Dutch floodplain waters can be attributed to a complex of factors which are related to hydrology. With changing flood frequencies, the magnitude of physical parameters such as water-level fluctuations, erosion, sedimentation, turbidity, and chemical parameters such as salinity and the concentrations of plant nutrients change in the backwaters as well. All these physicochemical changes have their influence on the macrozoobenthos. Active migrations, drift, and erosion of macroinvertebrates can occur during high water levels, when the floodplain is inundated. During dry periods shallow water bodies can fall dry, which is detrimental to immobile and non-drought-resistant macroinvertebrates. Sedimentation affects the grain size of the sediment and consequently the substrate availability for the psammon and pelon. A high water turbidity can hinder predatory species which hunt their preys on sight. A high sa-
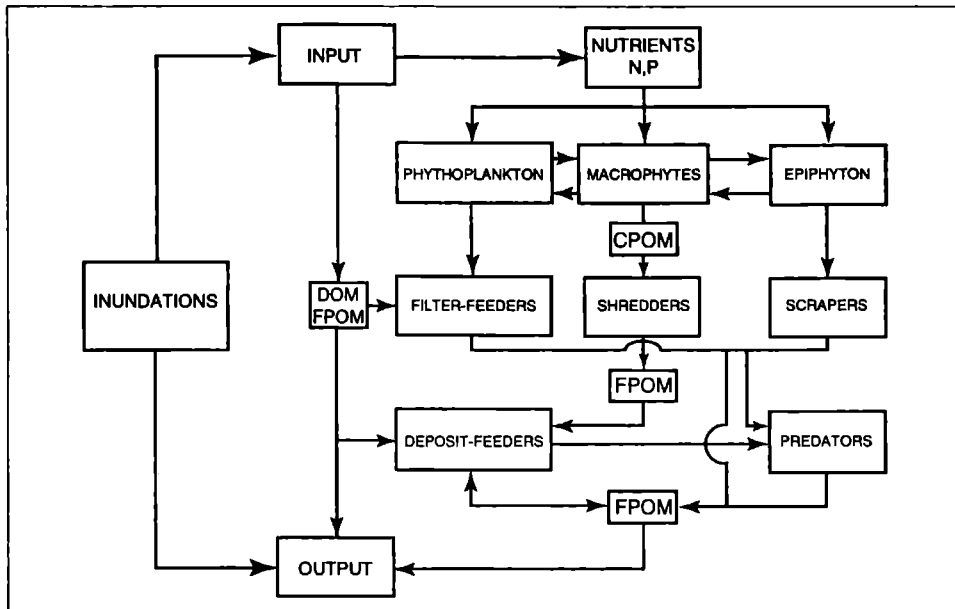
Figure 6. *Schematic diagram of the impact of inundations on energy fluxes within floodplain waters.*

linity of the water means an osmotic stress for freshwater macroinvertebrates, but favours the occurrence of euryhaline species. High concentrations of plant nutrients affect the phyton substrate and nutritional resources.

Because floodplain waters are open systems it is clear that inundations influence the energy fluxes within the floodplain waters as a whole (Fig. 6). This is especially true for the floodplains of highly eutrophic rivers, such as the rivers Rhine and Meuse in the Netherlands. Inundation results in a large input of plant nutrients (N, P) from allochthonous sources. As inundation frequencies increase, the competition between microphytes and macrophytes will shift towards a phytoplankton-dominated community, thereby influencing the available nutrient resources for macroinvertebrates (Fig. 6).

Conclusions

Flood frequency constitutes the major environmental gradient which structures the macrozoobenthos communities in floodplain waters of the highly eutrophicated rivers Rhine and Meuse. The species composition is mediated by substrate availability, water chemistry, and nutritional resources. As the vegetation declines with increasing flood frequencies, species related to the phyton habitat decrease in relative importance. With increasing inundations, the trophic level and chlorinity in the backwaters increase too, favouring the occurrence of tolerant and opportunistic species. A division of the macroinvertebrate fauna into functional feed-

ing groups shows that the percentage of shredding species is highest in non-flooded waters, whereas that of filter-feeders is highest in frequently and very frequently flooded sites. The relationship between the frequency of inundation and the functional feeding groups shows that the faunal composition is at least partly mediated by the availability of the nutritional resources: in non-flooded waters aquatic vegetation is well developed, providing food (CPOM) for shredders; in frequently flooded waters vegetation is sparse, but phytoplankton, which provides food (FPOM) for filter-feeders, is abundant.

From results of the present study it can be predicted that the faunal composition of the Dutch floodplain waters will change if the frequency of inundation changes. Restoration of the connections between former meanders and the eutrophicated main channels of the rivers Rhine and Meuse in the Netherlands will probably lead to hypertrophic waters with an impoverished, collector-dominated macroinvertebrate fauna. Such restoration measures must go hand in hand with water quality improvements and should maintain a flooding gradient in order to get a maximum diversity in the macroinvertebrate communities.

Acknowledgements

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CHAPTER 8

Macrozoobenthos abundance and community composition in three Lower Rhine floodplain lakes with varying inundation regimes

Abstract

The relative importance of lake inundation regime, littoral substrate and season for macrozoobenthos abundance and community composition was studied in three Lower Rhine floodplain lakes situated along a flood duration gradient. In each lake the macrozoobenthos density, biomass and community composition were determined monthly over one year in two contrasting littoral substrates (sandy-mineral sediments and clayey-organic sediments). The influence of the lake inundation regime on the macrozoobenthos abundance was tested against those of littoral substrate and season with a three-way analysis of variance (ANOVA). Between-lake variation in macrozoobenthos abundance was clear for Bivalvia, Ephemeroptera, Heteroptera and Trichoptera. Bivalvia (*Pisidium* spec.) were most abundant in the frequently flooded lake, Heteroptera (*Micronecta* spec., *Sigara falleni* (Fieber), *S. striata* (L.)) in the rarely flooded lake, and Trichoptera (*Mystacides longicornis* (L.), *M. nigra* (L.)) and Ephemeroptera (*Caenis horaria* (L.), *C. luctuosa* Burmeister) in the isolated, non-flooded lake, suggesting an impact of inundation regime on the abundance of these dominant taxa in Lower Rhine floodplain lakes. In each lake the annual average abundance of macrozoobenthos was dominated by Gastropoda (*Bithynia tentaculata* (L.), *Potamopyrgus antipodarum* (Gray), *Valvata piscinalis* (Müller)).

Between-lake variation in the relative densities of macrozoobenthos functional feeding groups suggests an impact of the inundation regime on the macrozoobenthos communities via the availability of nutritional resources. Relative densities of filter-feeders (e.g. *Pisidium* spec.) were highest in the frequently flooded lake with its high phytoplankton biomass and poorly developed vegetation. Shredders (e.g. *Mystacides* spec.) were most numerous in the non-flooded lake with its well-developed aquatic vegetation and low phytoplankton biomass.

Within-lake variations in macrozoobenthos abundance could be attributed to littoral substrate and season. The importance of substrate on macrozoobenthos abundance was most clear for Oligochaeta and Trichoptera. The importance of season on macrozoobenthos abundance was clear for the total macrozoobenthos and for all taxonomic groups, except Oligochaeta. Correlations between the total macrozoobenthos abundance and seasonally fluctuating parameters, i.e., flood pulse duration, water level, water temperature and vegetational coverage in the lakes, suggest that hydrological parameters were most important in the frequently flooded lake, whereas vegetational coverage and water temperature were most important in the isolated, non-flooded lake.

Introduction

The importance of floodplains for the structure and functioning of large river ecosystems has been widely recognized (Minshall et al., 1985; Schiemer, 1985; Amoros et al., 1987; Amoros and Roux, 1988; Junk et al., 1989; Ward, 1989; Reimer, 1991). The flood pulse is regarded as

the major environmental parameter influencing the existence, productivity and interactions of biota in large river ecosystems. During floods exchanges of water, chemicals, sediment and biota occur between the channel and its associated floodplain lakes (Amoros and Roux, 1988; Chauvet and Décamps, 1989; Junk et al., 1989; Van den Brink et al., 1993a).

Macroinvertebrates constitute an important link in the trophic dynamics of river-floodplain systems by cycling nutrients and by providing food for higher trophic levels, like fish and birds. The duration, frequency and timing of the flood pulses exert a clear impact on the macroinvertebrate assemblages in floodplain lakes (Castella et al., 1984; Amoros et al., 1987; Junk et al., 1989; Van den Brink and Van der Velde, 1991; Bournaud et al., 1992). During floods, macroinvertebrates are washed out of the floodplain lakes and enter foodwebs in the main channel, whereas at the same time riverine species enter these lakes for foraging, feeding and/or reproduction (Eckblad et al., 1984; Shaeffer and Nickum, 1986; Junk et al., 1989; Van der Velde et al., 1990).

Studies on the relation between the flood pulse duration and macrozoobenthos abundance in floodplain waters are very sparse and deal mainly with temporary and semi-permanent waters along relatively pristine rivers (Gladden and Smock, 1990; Neckles et al., 1990; Boulton and Lloyd, 1992; Smock et al., 1992). Information on the relation between the flood pulse duration and macrozoobenthos communities in permanent floodplain lakes along regulated, polluted and otherwise deteriorated river-floodplain systems, like the Lower Rhine, is entirely sparse (Van den Brink and Van der Velde, 1991). Such knowledge, however, is very important if we wish to restore such degraded river-floodplains (Amoros and Roux, 1988).

Studies of macrozoobenthos communities in the Rhine river system have focused on the main channel (Kinzelbach and Friedrich, 1990, and references therein; Bij de Vaate and Greijdanus-Klaas, 1991; Van den Brink et al., 1991, 1993b; Dudok van Heel et al., 1992; Van der Velde and Van den Brink, 1994). So far, studies of macrozoobenthos abundance in floodplain lakes along this river have been carried out in only two water bodies in the Upper Rhine valley (Obrdlik and Castella, 1991; Obrdlik and Garcia-Lozano, 1992). Recently, the importance of flood pulse duration for the macrozoobenthos species composition in floodplain lakes along the Lower Rhine has been analyzed (Van den Brink and Van der Velde, 1991).

Like most European rivers, the River Rhine underwent considerable changes under human impact, especially in its lower reaches. Since the Rhine flows through a densely populated, strongly industrialized, and an intensive agricultural area, the levels of nutrients, salts and micropollutants in the main channel water are highest in its downstream section, which is the Lower Rhine (Van der Weijden and Middelburg, 1989). Due to regulation efforts, embankments and floodplain deterioration, the Lower Rhine floodplains lost much of their original character (Van Urk and Smit, 1989). Historical changes in river hydrology and floodplain geomorphology have influenced the inundation regime of the lakes, whereas the changed river water quality has influenced the water quality in the floodplain lakes via floods and percolation (Van den Brink et al., 1993a). The presence of high main dikes and low summer dikes are the cause of a relative sharp zonation of floodplain lakes with respect to their inundation regime.

An earlier classification of 100 floodplain lakes along the Lower Rhine (and Meuse) based upon their macrozoobenthos species assemblages showed that the floodplain lakes could be categorized in three major groups according to their inundation regime (Van den Brink and Van der Velde, 1991). In order to study the impact of inundation regime on the macrozoobenthos abundance and community composition, three permanent water bodies, each representative for one of these hydrological classes, were sampled monthly for macrozoobenthos over one year. Since habitat and season strongly affect the abundance of (semi-)aquatic macrozoobenthos (e.g. Soszka, 1975; Benke et al., 1984; Cyr and Downing, 1988, 1989; Findlay et al., 1989; Van der Velde and Brock, 1991), the spatio-temporal variation in macrozoobenthos density and biomass within these lakes was also taken into account. The present paper focusses on the following questions: 1. What is the relative importance of lake inundation regime, littoral substrate and season on the abundance of macrozoobenthos (total macrozoobenthos, taxonomic main groups, functional feeding groups) in Lower Rhine floodplain lakes? 2. What is the impact of the inundation regime on the macrozoobenthos community composition (relative densities of dominant species and functional feeding groups) in these lakes? 3. What is the impact of seasonal fluctuations in hydrological parameters (occurrence and duration of flood pulses, water level) on the total macrozoobenthos abundance in these lakes?

Sites and methods

Study sites

The study area is situated on the left bank of the Lower Rhine (the main branch, the River Waal, which receives 67% of the River Rhine discharge; river km 876-894) in the Netherlands (Fig. 1). In the Lower Rhine the highest water levels usually occur during winter and spring, i.e., outside the vegetation growth season. Over the years, water level fluctuations of 6 m frequently occur in this river stretch. At a water level of 12 m above sea level (a.s.l.) all water bodies in the study area are connected to the main channel, except for those which are situated behind the main dike. Many types of water bodies with varying inundation regimes occur along this meandering lowland section of the river Rhine. The lakes studied were Lake Ewijk, which is not protected against flooding by dikes and which is frequently inundated (connection level above 8 m a.s.l.); Lake Oude Waal, which is protected by a low summer dike and hence is infrequently inundated (connection level above 11.5 m a.s.l.), and Lake Duivelswaai, which is protected against inundation by the main dike (height 15 m a.s.l.) and which is influenced by the river exclusively via seepage at high water levels in the main channel. Due to differences in hydrological and geomorphological conditions between these lakes, in combination with the highly eutrophic main channel, these lakes differ in their trophic status as well (Tables 1, 2). Lake Ewijk is a former side channel of the Lower Rhine which silted up at its upstream end around 1900 and at its downstream end about 20 years ago. The sediment consists predominantly of sand (95%), except for a small littoral zone at the up-

stream end which is clayey. Lake Oude Waal is a former meandering channel, cut off in the 15th century. The sediment consists predominantly of clay with a thick sapropelium layer, except at sites where dike bursts have occurred. These sites are sandy (wash-over deposits) and make up about 10% of the lake surface area. Lake Duivelswaai originated from a dike burst before the 18th century. About 60% of the littoral zone consists of sandy sediment (wash-over deposits). The rest of the littoral zone consists of clay with a sapropelium layer.
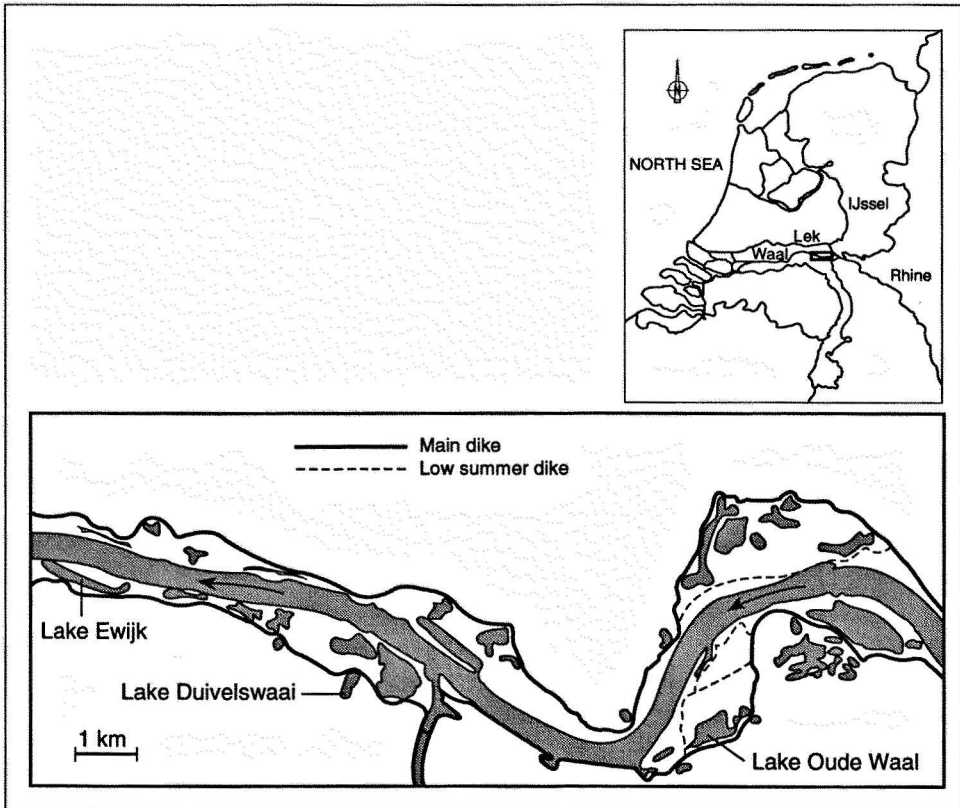

Figure 1. *Map of the Lower Rhine near Nijmegen (Waal branch), between river km 876 and river km 894, showing the study sites.*

Table 1. *Topographical, geomorphological, hydrological and habitat characteristics of three Lower Rhine floodplain lakes with varying inundation regimes. Location in km's from the source of the river. Annual flood duration in days per year (average over 1901-1985). Sediment is expressed as a proportion of the lake surface area (in %). Organic matter content in sediment in percentage of dry weight (ranges are given).*

Lake	Ewijk	Oude Waal	Duivelswaai
Coordinates	N 51°53'	N 51°51'	N 51°52'
	E 5°45'	E 5°55'	E 5°48'
Location (km)	893	882	888
Surface area (ha)	10	16	6
Maximum depth (m)	3	5	8
Distance from river (m)	10	500	650
Annual flood duration	67	3	0
Sandy-mineral sediment	95	10	60
Clayey-organic sediment	5	90	40
Organic matter in sediment	2-10	4-16	4-14
Submerged vegetation	absent	sparse(2a)	dominant(3a)
Nymphaeid vegetation	sparse(1b)	dominant(2b)	dominant(3b)
Emergent vegetation	sparse(1c)	abundant(2c)	abundant(3c)

(1b): *Nymphoides peltata* (Gmel.) O. Kuntze; (1c): *Carex acuta* L.;
(2a) *Ranunculus circinatus* Sibth., *Potamogeton lucens* L., *P. pectinatus* L.; (2b): *Nuphar lutea* (L.) Sm., *Nymphaea alba* L., *Nymphoides peltata*; (2c): *Glyceria maxima* (Hartman) Holmberg, *Phragmites australis* (Cav.) Trin. ex Steudel, *Scirpus lacustris* L., *Typha angustifolia* L.;
(3a): *Chara vulgaris* L., *Ch. globularis* Thuill., *Hippuris vulgaris* L., *Potamogeton crispus* L., *P. lucens, P. pectinatus, P. perfoliatus* L., *Ranunculus circinatus, Elodea nuttallii* (Planchon) St. John; (3b): *Nuphar lutea, Nymphaea alba*; (3c): *Hippuris vulgaris, Phragmites australis*.

Table 2. *Annual mean values (± S.D.) of monthly recorded physico-chemical parameters of the surface water in three Lower Rhine floodplain lakes with varying inundation regimes during 1990 (n= 12 observations). All parameters in $\mu mol\ l^{-1}$, except for pH (pH-units) and chlorophyll-a ($\mu g\ l^{-1}$).*

Lake	Ewijk		Oude Waal		Duivelswaai	
Na	2100	(500)	1600	(300)	1500	(200)
K	180	(40)	130	(30)	110	(10)
Ca	1100	(300)	1400	(200)	1200	(400)
Mg	400	(70)	400	(100)	410	(90)
Cl	2600	(500)	2000	(400)	1700	(200)
HCO_3	1800	(300)	2300	(200)	2800	(400)
SO_4	420	(100)	410	(130)	370	(90)
NO_3	120	(130)	70	(120)	15	(15)
NH_4	30	(30)	20	(20)	15	(15)
$o-PO_4$	0.9	(0.7)	0.3	(0.4)	0.1	(0.0)
pH	8.1	(0.5)	7.9	(0.2)	8.0	(0.2)
chlorophyll-a	29	(35)	19	(10)	10	(7)

Sampling, measurements and physico-chemical analyses

In order to analyze the importance of the littoral substrates for the densities and biomasses of the macrozoobenthos, one site with a sandy-mineral sediment and one with a clayey-organic sediment was selected in each lake for monthly sampling over one year (October 1991 up to September 1992). At low water levels, the littoral zone within these sites down to a depth of 1 m was sampled for macrozoobenthos with a pondnet (as described in Van den Brink and Van der Velde, 1991). Although this procedure was probable less accurate than taking grabs or sediment cores, it had several advantages above these methods, such as a larger sampling area and hence a more complete picture of the benthic fauna as larger and very mobile macroinvertebrates are easier collected. The net was quickly pushed through the upper 2 cm of the lake sediment over a randomly selected surface of approximately 2 m². From April to November, during the growing season, when vegetation was present in the selected habitats, sampling occurred between patches of submerged and nymphaeid macrophytes, avoiding sampling of vegetation, although vegetational debris was sampled this way. At high water levels sampling was done with the same net by pushing the net through the sediment, using a small rubber boat. Wooden fences in the landscape, close to the sampling sites, were used as orientation marks, so that the same areas could be recognized and sampled even when they were flooded. Sampled material was put in plastic bags which were kept cool and transported to the laboratory. After washing over a 500 μm mesh sieve the macrozoobenthos was sorted out in white trays, preserved in 70 % ethanol, identified and counted. Densities were expressed as numbers of individuals per m². All specimens belonging to Hirudinea, Gastropoda, Crustacea (Isopoda, Amphipoda, Decapoda), Ephemeroptera, Odonata, Heteroptera, Coleoptera and Trichoptera were identified to species level where possible. Bivalvia and Nematocera were identified to genus level; Oligochaeta and a rest group including Actinedida, Megaloptera, Brachycera and Lepidoptera, were not identified any further. All taxa were categorized into functional feeding groups based on available information (Cummins, 1973, 1974). Taxa which use more than one feeding mode were assigned to more than one group. Average density was then allocated equally among the functional groups to which they had been assigned. Of course this procedure involves approximations based on incomplete information and cannot be presumed to result in functional group allocations as accurate as would have been provided by studying food habits of all taxa sampled.

Macrozoobenthos biomass was assessed by taking samples in the littoral zone of the lakes in a similar way as outlined above during the months of February, April, July and September 1991. Dry weight biomasses were measured in unpreserved macrozoobenthos material, by drying to constant weight at 105 °C for 24 h. Unionid mussels and crayfish (*Orconectes limosus* (Raf.)) were excluded from the weight analysis because they had not been sampled adequately.

The relative abundance of vegetation in the sampling sites was recorded via an estimation of the percentage coverage of the submerged aquatic macrophytes and the nymphaeid macrophytes within a 3 x 3 m plot.
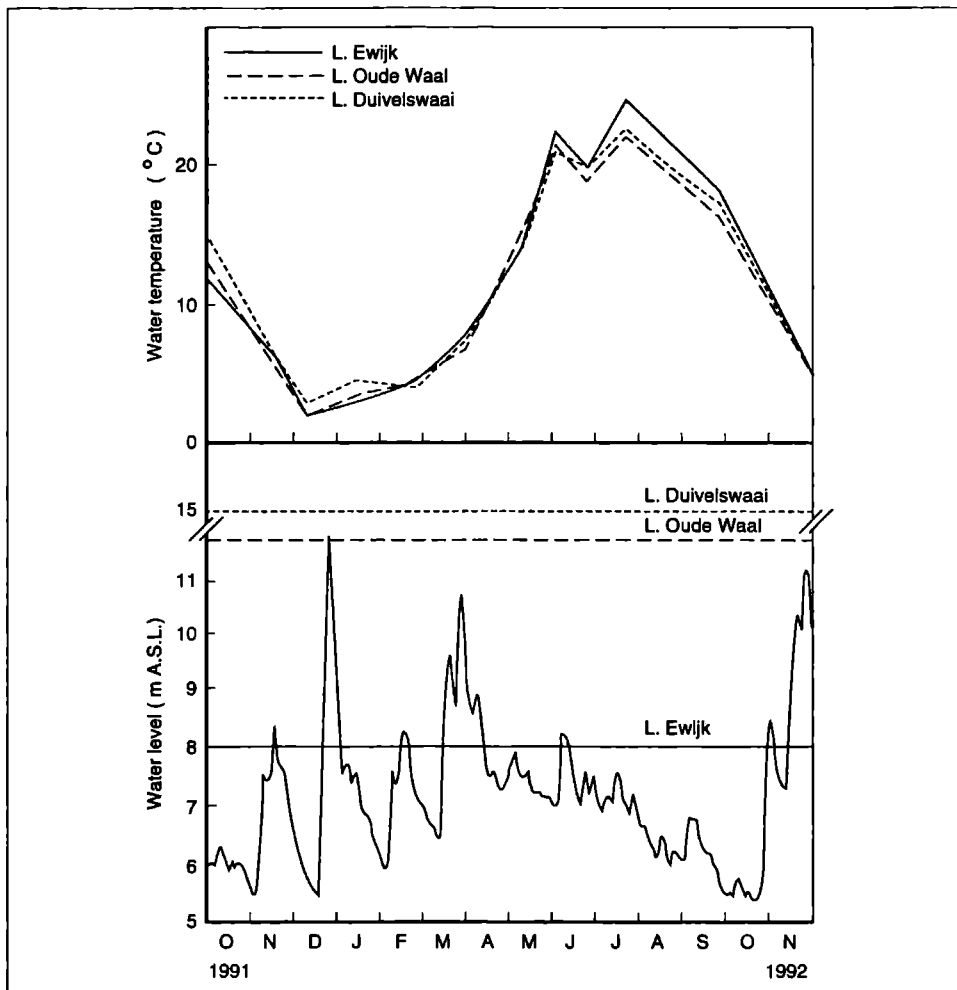
Figure 2. *Seasonal fluctuations in water temperature (above) and water level (below) of three flood-plain lakes with varying inundation regimes. Connection levels are indicated by horizontal lines.*

Physico-chemical parameters of the surface water (temperature, pH, alkalinity, concentrations of chloride, sodium, calcium, potassium, sulphate, magnesium, nitrate, ammonium, dissolved phosphate and chlorophyll-a) were obtained by standard laboratory measurements (Van den Brink et al., 1993a). Data on water levels of the Lower Rhine at Nijmegen were obtained from The Institute for Inland Water Management and Waste Water Treatment (RIZA-Lelystad, The Netherlands). In order to obtain data on the flood pulse duration of the three floodplain lakes within the study period, river maps were used to estimate the connection

level for each lake, i.e., the lowest water level of the river at which the part of the floodplain which includes that specific lake is inundated (plotted in Fig. 2). Next, the number of days was calculated on which the water level in the main channel reached or exceeded this connection level during a flood pulse (= flood pulse duration).

Statistical analysis

The relative importance of lake hydrological regime, littoral substrate and season on macrozoobenthos densities and biomasses, and on densities of macrozoobenthos functional feeding groups were analyzed by three-way analysis of variance (ANOVA) models (Sokal and Rohlf, 1981). Densities and biomasses were log(n+1) transformed for the ANOVA, because these were log-normally distributed.

In order to analyze the role of seasonal fluctuating parameters as flood pulse duration, water level, water temperature and the abundance of aquatic vegetation within the lakes for the total macrozoobenthos density and biomass, a Spearman rank correlation test was applied (Sokal and Rohlf, 1981).

Annual and seasonal mean densities were compared with the help of a Wilcoxon test (Sokal and Rohlf, 1981). Statistical analyses were performed with the General Linear Models (GLM) procedure, the Correlation (CORR) procedure and with the Nonparametric (NPAR1WAY) procedure available in the Statistical Analysis System (SAS) software package (SAS Institute Inc., 1989).

Results

Environmental conditions

The three floodplain lakes clearly differed with respect to their hydrological regime (Table 1). During the hydrologically normal years 1991 and 1992 Lake Ewijk was frequently flooded, with floods lasting several weeks, while Lake Oude Waal was flooded only once for a few days and Lake Duivelswaai was not flooded at all (Fig. 2). Water level fluctuations occurred in all lakes, due to seepage of river water through the bottom of the lakes. Due to hydrological differences, in combination with the high nutrient levels of the main channel water, the three lakes also differed in their water chemistry, their phytoplankton biomass and the relative proportion of the main habitats provided by the type of sediment (sandy-mineral sediment or clayey-organic sediment) and type of aquatic vegetation (submerged macrophytes or nymphaeid macrophytes) (Tables 1, 2). Lake Ewijk is more eutrophic than Lake Oude Waal, which in turn is more eutrophic than Lake Duivelswaai. Thus, apart from a hydrology gradient, the three lakes also form a trophic gradient. During the study period there were no clear differences in water temperature between the sites (Fig. 2). Water temperature was lowest during winter (3-4 °C) and highest during summer (20-24 °C). Aquatic vegetation was present from April to November, with highest coverages during August.

Between-lake variation

The total macrozoobenthos abundance showed no significant differences between the lakes, although there was a tendency that annual average total macrozoobenthos densities were highest in the most dynamic and most eutrophic Lake Ewijk, whereas annual average total macrozoobenthos biomasses were highest in the least dynamic and least eutrophic Lake Duivelswaai (Tables 3, 4). Significant between-lake variation in macrozoobenthos abundance (ANOVA; $p < 0.001$) was found for Bivalvia, Ephemeroptera, Heteroptera and Trichoptera. Highest annual mean densities and biomasses of Bivalvia were recorded in the frequently flooded Lake Ewijk, those of Heteroptera in the rarely flooded Lake Oude Waal and those of Ephemeroptera and Trichoptera in the non-flooded Lake Duivelswaai (Table 4). After adjustment for relative substrate proportion (Table 1) it was found that Gastropoda (density: 39%, biomass 65%) and Bivalvia (density: 39%, biomass: 26%) were the dominant groups in Lake Ewijk, that Gastropoda (density: 35%, biomass 51%) and Heteroptera (density: 13%, biomass: 19%) were the dominant groups in Lake Oude Waal, and that Gastropoda (density: 36%, biomass 58%), Trichoptera (density: 19%, biomass: 33%) and Ephemeroptera (density: 19%, biomass: 2%) were the dominant groups in Lake Duivelswaai (Table 4; Fig. 3).

Table 3. *P-values of the ANOVA model for the influence of lake, substrate and season on macro-invertebrate densities (N) and dry weight biomasses (B).*
***: $p < 0.001$; **: $0.001 < p < 0.01$; * $0.01 < p < 0.05$.

| | Independent variables | | | | | |
| | Lake | | Substrate | | Season | |
Dependent variables	N	B	N	B	N	B
Oligochaeta	0.672	0.844	0.003**	0.004**	0.279	0.884
Hirudinea	0.073	0.072	0.357	0.267	0.000***	0.181
Gastropoda	0.050	0.840	0.687	0.618	0.000***	0.033*
Bivalvia	0.000***	0.044*	0.975	0.641	0.045*	0.004**
Crustacea	0.086	0.723	0.411	0.709	0.014*	0.007**
Ephemeroptera	0.000***	0.000***	0.962	0.486	0.016*	0.028*
Odonata	0.034*	0.318	0.003**	0.060	0.000***	0.101
Heteroptera	0.000***	0.127	0.003**	0.051	0.050*	0.009**
Coleoptera	0.321	0.593	0.002**	0.136	0.011*	0.315
Nematocera	0.447	0.340	0.036*	0.272	0.000***	0.071
Trichoptera	0.000***	0.000***	0.000***	0.000***	0.034*	0.014*
Total	0.151	0.912	0.213	0.620	0.000***	0.031*

	Taxonomic groups		Feeding guilds
	density	biomass	density

L. Ewijk

L. Oude Waal

L. Duivelswaai

Legend:
- Gastropoda
- Bivalvia
- Crustacea
- Ephemeroptera
- Odonata
- Heteroptera
- Nematocera
- Trichoptera
- Miscellaneous
- Predators
- Filter-feeders
- Deposit-feeders
- Scrapers
- Shredders
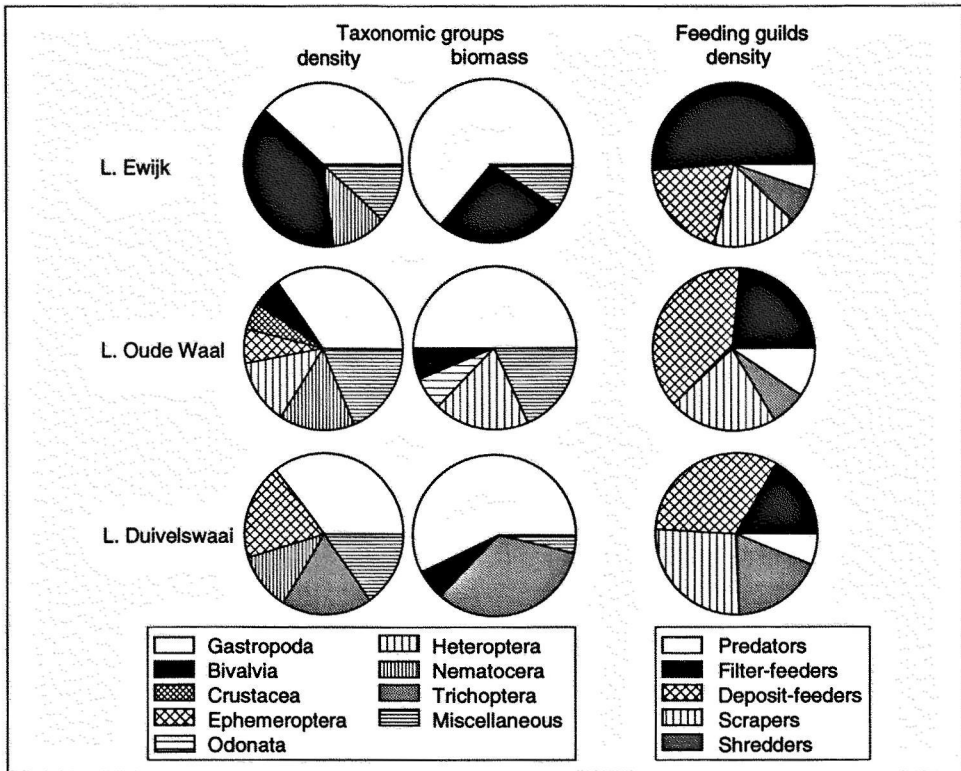
Figure 3. *Macroinvertebrate community composition in three floodplain lakes with varying inundation regimes, adjusted for the relative proportion of sandy and clayey substrates.*
Left: relative densities (%) of macroinvertebrate taxonomic main groups; centre: relative biomasses (%) of macroinvertebrate taxonomic main groups; right: relative densities (%) of macroinvertebrate feeding groups.

A total of 175 taxa were recorded in this study, divided over the following groups: Hirudinea: 9; Gastropoda: 23; Bivalvia 5 (only genus level); Crustacea: 7; Ephemeroptera: 6; Odonata: 8; Heteroptera: 24; Coleoptera: 41; Trichoptera: 25; and Nematocera: 27 taxa (only genus level). The highest number of taxa (132) was found in Lake Oude Waal, followed by Lake Duivelswaai (100), while the lowest number of taxa (79) was found in Lake Ewijk. Only 23 taxa show annual mean densities of more than 10 specimens per m^2 and were considered dominant (Table 5). These dominant taxa were not evenly distributed over the lakes and habitats, but showed clear preferences. Species such as *Physella acuta* (Drap.) and *Oecetis ochracea* (Curtis) were found exclusively in Lake Ewijk, whereas *Caenis luctuosa* and *Mystacides nigra* were found in Lake Duivelswaai only. *Caenis horaria* was not observed in Lake Ewijk. *Potamopyrgus antipodarum* and Tanytarsini were not recorded in Lake Oude Waal, while *Gammarus tigrinus* Sexton was not collected from Lake Duivelswaai (Table 5). Several

Table 4. *Annual mean density (N; individuals m⁻²) and annual mean biomass (B; in mg DW m⁻²) of macroinvertebrates in three lakes with varying inundation regimes, adjusted for the relative proportions of sandy and clayey substrates (extremes in parentheses).*

Lake		Ewijk	Oude Waal	Duivelswaai
Oligochaeta	N	15	18	8
		(0-1237)	(0-59)	(0-37)
	B	2	23	4
		(0-43)	(0-82)	(0-16)
Hirudinea	N	3	8	5
		(0-295)	(0-60)	(0-24)
	B	2	19	5
		(0-9)	(0-133)	(0-32)
Gastropoda	N	229	144	158
		(0-2302)	(2-934)	(1-1019)
	B	615	731	1010
		(97-5435)	(154-2091)	(41-2211)
Bivalvia	N	228	24	13
		(0-1028)	(2-107)	(0-160)
	B	243	86	110
		(13-358)	(0-228)	(0-414)
Crustacea	N	24	19	17
		(0-272)	(0-89)	(0-83)
	B	16	10	23
		(0-103)	(0-52)	(0-87)
Ephemeroptera	N	3	31	82
		(0-73)	(0-147)	(6-337)
	B	<1	8	23
		(0-6)	(0-18)	(7-58)
Odonata	N	1	19	4
		(0-77)	(0-99)	(0-25)
	B	3	87	15
		(0-183)	(0-273)	(1-41)
Heteroptera	N	12	54	7
		(0-253)	(0-271)	(0-48)
	B	12	273	26
		(0-324)	(2-902)	(1-84)
Coleoptera	N	3	11	7
		(0-42)	(0-41)	(0-52)
	B	2	11	6
		(0-84)	(0-35)	(0-12)
Nematocera	N	71	71	47
		(0-278)	(1-770)	(0-145)
	B	21	22	20
		(3-47)	(3-97)	(3-85)
Trichoptera	N	20	13	83
		(0-75)	(0-120)	(0-323)
	B	22	58	581
		(0-69)	(0-870)	(18-2697)
Total	N	591	416	441
		(49-3722)	(66-1940)	(32-1262)
	B	939	1429	1739
		(118-5988)	(271-3224)	(117-3850)

dominant species showed increasing or decreasing densities in the lakes along the inundation gradient. For example, the annual mean densities of *Pisidium* spec., *Valvata piscinalis* and *Gammarus tigrinus* were highest in Lake Ewijk and lowest or even zero in Lake Duivelswaai. Conversely, the annual mean densities of *Caenis horaria* and *Mystacides longicornis* were lowest in Lake Ewijk and highest in Lake Duivelswaai (Table 5).

Table 5. *Annual mean density of dominant macroinvertebrate taxa (individuals m⁻²) in three lakes with varying inundation regimes, adjusted for the relative proportion of sandy and clayey substrates. S: preference for sandy habitats (psammon), P: preference for clayey and organic substrates (pelon), V: preference for vegetation (phyton), -: no preference.*

Lake	Ewijk	Oude Waal	Duivelswaai	
Gastropoda				
Bithynia tentaculata (L.)	2	22	12	-
Physella acuta (Draparnaud)	17	0	0	-
Potamopyrgus antipodarum (Gray)	118	0	103	S
Valvata piscinalis (Müller)	92	19	15	-
Bivalvia				
Pisidium spec.	225	24	12	-
Crustacea				
Gammarus tigrinus Sexton	22	5	0	-
Asellus aquaticus (L.)	1	13	12	-
Ephemeroptera				
Caenis horaria (L.)	0	5	27	-
Caenis luctuosa Burmeister	0	0	40	-
Cloeon dipterum (L.)	1	15	9	-
Odonata				
Ischnura elegans (Van der Linden)	1	15	1	V
Heteroptera				
Micronecta spec.	3	14	1	-
Sigara falleni (Fieber)	3	20	4	V
Sigara striata (L.)	1	9	1	V
Nematocera				
Chironomus spec.	3	17	1	P
Endochironomus spec.	1	12	3	P/V
Glyptotendipes spec.	4	12	8	P/V
Microtendipes spec.	0	4	11	S
Polypedilum spec.	16	3	7	-
Tanytarsini	28	0	4	S
Trichoptera				
Oecetis ochracea (Curtis)	18	0	0	S
Mystacides longicornis (L.)	2	4	54	S/V
Mystacides nigra (L.)	0	0	17	S/V

The macrozoobenthos densities expressed on the basis of functional feeding group composition show that the relative densities of shredders and filter-feeders vary between the lakes (ANOVA; p < 0.05) (Table 6). If the densities of the macrozoobenthos functional feeding groups are adjusted for habitat proportion per lake (Fig. 3), it appears that the relative density (based on annual mean densities) of filter-feeders (e.g. *Pisidium* spec.) was highest in the frequently flooded Lake Ewijk and lowest in the non-flooded Lake Duivelswaai. Conversely, the relative abundance of shredders (e.g. *Mystacides longicornis, M. nigra*) was highest in the non-flooded Lake Duivelswaai and lower in the other lakes (Fig. 3).

Within-lake variation

Within-lake variation in abundance and community composition could be attributed to both substrate and season. Densities and biomasses of Oligochaeta and Trichoptera were clearly related to substrate (Table 3). Highest annual mean densities and biomasses of Oligochaeta were found on the clayey-organic sediment; highest annual mean densities and biomasses of Trichoptera (*Oecetis ochracea, Mystacides longicornis* and *M. nigra*) were recorded on the sandy-mineral sediment.

Table 6. *P-values of the ANOVA model for the influence of lake, littoral substrate and season on relative densities of macroinvertebrate functional feeding groups.*
***: p < 0.001; **: 0.001 < p < 0.01; * 0.01 < p < 0.05.

	Independent variables		
Dependent variables	Lake	Substrate	Season
Predators	0.280	0.020*	0.026*
Shredders	0.000***	0.141	0.074
Scrapers	0.488	0.832	0.189
Gatherers	0.019*	0.526	0.096
Filterers	0.000***	0.330	0.725

Clearly, the seasonal variation in total macrozoobenthos abundance was larger than the variation between the lakes or between the littoral substrates. Highest seasonal total macrozoobenthos densities and biomasses were recorded in the frequently flooded Lake Ewijk (Tables 3, 4). There was a distinct impact of season on abundance of all taxonomic main groups, except for Oligochaeta (Table 3).

A pattern in seasonal fluctuations of macrozoobenthos abundance was found for each lake with highest densities occurring during July-August, which is the summer period, and lowest densities occurring during winter and early spring (January-April) (Fig. 4). However, in detail there were differences in this pattern between the lakes. A similar seasonal pattern was found for macrozoobenthos biomasses in lakes Ewijk and Oude Waal, unlike Lake Duivelswaai,
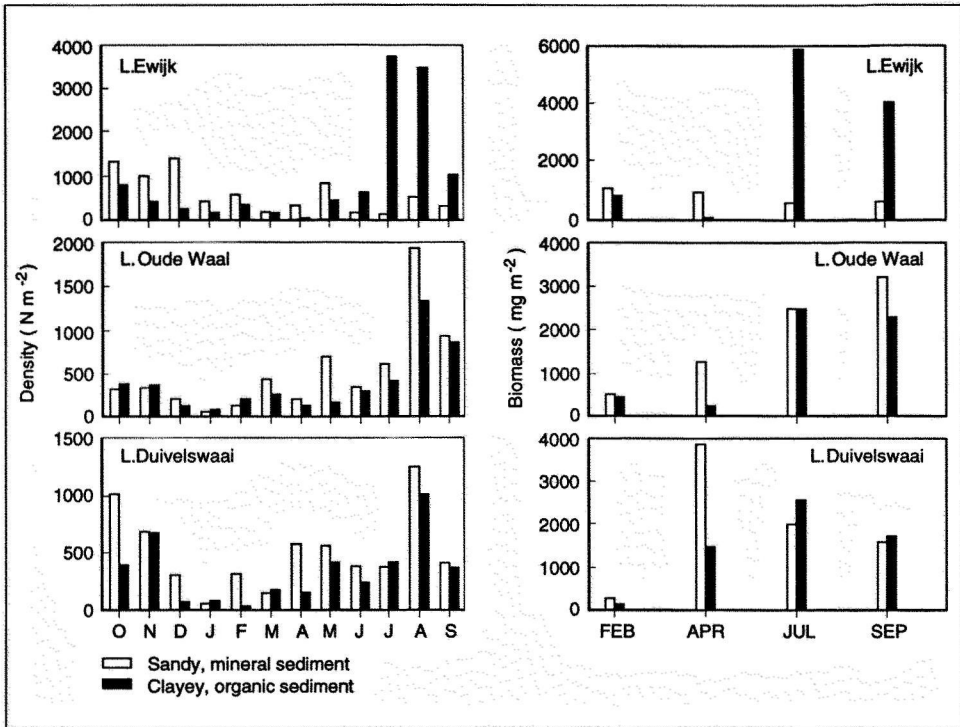
Figure 4. *Seasonal fluctuations in total macroinvertebrate density and biomass in contrasting littoral substrates within three floodplain lakes with varying inundation regimes.*

where highest biomasses occurred in April (Fig. 4). The importance of the seasonal fluctuations in flood pulse duration, water level, water temperature and vegetational coverage for the macrozoobenthos density and biomass varied between the three lakes (Table 7). In the frequently flooded Lake Ewijk total macrozoobenthos density was most clearly negatively correlated (Spearman rank correlation; $p < 0.001$) with the duration of the flood pulses shortly before the sampling dates, and with the water level during the sampling dates. In the infrequently flooded Lake Oude Waal the same negative correlations were found, although less clear ($p < 0.05$), whereas no such correlations were found for the non-flooded Lake Duivelswaai. In the latter two lakes positive correlations were found between macrozoobenthos density and water temperature, and between macrozoobenthos density and vegetational abundance. In Lake Duivelswaai the latter correlation was found to be strongest ($p < 0.001$) (Table 7).

Table 7. *Spearman rank correlation coefficients between total macrozoobenthos density (data from both substrates have been pooled for each lake; N; individuals m⁻²; n = 24) and biomass (B; in mg DW m⁻²; n = 8) on the one hand and flood pulse duration, water level, water temperature and vegetational development on the other, in three lakes with varying inundation regimes.* ***: $p < 0.001$; **: $0.001 < p < 0.01$; * $0.01 < p < 0.05$.

Lake	Ewijk		Oude Waal		Duivelswaai	
	N	B	N	B	N	B
Flood pulse duration	−0.66***	−0.31	−0.50**	0.0	0.0	0.0
Water level	−0.63***	−0.31	−0.42*	−0.51	−0.19	0.34
Water temperature	0.20	0.10	0.55**	0.79**	0.50**	0.52
Vegetational abundance	0.41*	0.38	0.52**	0.81**	0.63***	0.49

Discussion

The impact of lake hydrological regime on the macrozoobenthos abundance in Lower Rhine floodplain lakes became clear on the community level. Between-lake variation in density and biomass was highly significant for Bivalvia, Ephemeroptera, Trichoptera, and for Heteroptera densities (Table 3). The densities of the dominant species within these groups as well as those of some Gastropoda and Crustacea species were found to change over the horizontal zonation of lakes according to their hydrological regime (Table 4). This observation suggests that the lake hydrological regime influences the abundance of these groups and thereby the community composition of the macrozoobenthos. The densities of *Pisidium* spec., *Valvata piscinalis*, *Physella acuta*, *Gammarus tigrinus* and *Oecetis ochracea* increased over the gradient with increasing flood duration, or were exclusively found in Lake Ewijk, with the highest annual flood duration. All these dominant taxa are nowadays abundant in the main channel of the Lower Rhine too, predominantly on the sandy and silty flats of the depositional, slow-flowing or semi-stagnant areas (Smit and Snoek, 1989; Dudok van Heel et al., 1992), habitats which are morphologically, hydrologically and physico-chemically comparable to those found in Lake Ewijk. In the Netherlands, *Physella acuta*, *Potamopyrgus antipodarum* and *Gammarus tigrinus* are euryhalinous immigrants, which were formerly absent from the Lower Rhine (Van den Brink et al., 1990), so their presence in the frequently flooded Lake Ewijk must have resulted from a migration of these biota from the main channel to this floodplain lake, most probably through floods. In contrast with the above-mentioned species, the densities of *Caenis horaria*, *C. luctuosa*, *Mystacides longicornis* and *M. nigra* decreased over the gradient of lakes with increasing annual flood duration, all being predominantly found in the isolated, non-flooded Lake Duivelswaai (Table 5). These species are nowadays absent or extremely sparse in the main channel of the Lower Rhine (Smit and Snoek, 1989; Van den Brink et al., 1990; Bij de Vaate and Greijdanus-Klaas, 1991), although they were formerly very common in the depositional main channel areas (Klink, 1989; Van den Brink et al., 1990; and literature therein). For phytophilous species like *Mystacides longicornis* and *M. nigra* the deterioration of the phyton habitat in particular may be the cause of their absence in the main

channel. Besides habitat deterioration the changed water quality is assumed to have affected the native macrozoobenthos in the main channel of the Lower Rhine too, especially insect groups, such as Ephemeroptera, Plecoptera and Trichoptera (Klink, 1989; Van den Brink et al., 1990; Van den Brink and Van der Velde, 1991; Admiraal et al., 1993).

In the Lower Rhine floodplain lakes, Gastropoda made up an important part of the total densities and biomass of macrozoobenthos, just as in the Upper Rhine floodplain lakes, with the same dominant species, i.e., *Bithynia tentaculata*, *Potamopyrgus antipodarum* and *Valvata piscinalis* (Table 5; Orblik and Castella, 1991). These species are opportunistic deposit-feeders which live on sedimentary detritus. However, they may also feed themselves by filtering suspended matter from the water column or by scraping epiphytes from solid substrates (Fretter and Graham, 1975). This unselective foraging behaviour may explain their high densities and their general occurrence in the sediments of floodplain lakes and depositional main channel sections (Fretter and Graham, 1975; Kolodziejczyk, 1984; Hoffman and Neumann, 1990; Foeckler, 1991; Van den Brink and Van der Velde, 1991; Dudok van Heel et al., 1992).

The species composition found in the three Lower Rhine floodplain lakes shows much resemblance to those found in other floodplain lakes along the rivers Rhine, Meuse, Rhône and Danube (Castella et al., 1984; Obrdlik et al., 1990; Foeckler, 1991; Van den Brink and Van der Velde, 1991). In the floodplain lakes of these rivers a gradual change in the species composition was found over the lateral dimension, suggesting hydrology to be the main environmental parameter structuring the communities. However, the composition of the macrozoobenthos communities, which characterize hydrologically different groups of water bodies, varies in the different river systems, which might be related to differences in parameters co-varying with hydrology, such as water chemistry. Compared with the other rivers, the Lower Rhine and Meuse are highly eutrophic, so that in their floodplain lakes a trophic gradient is positively correlated with the hydrological gradient, thereby influencing nutritional and habitat resources (Van den Brink and Van der Velde, 1991; Van den Brink et al., 1993a). A comparison of the macrozoobenthos commmunity composition, based on relative densities of the functional feeding groups (Fig. 3), between the three Lower Rhine floodplain lakes stresses the importance of this trophic gradient by suggesting that the impact of hydrology on the macrozoobenthos communities is mediated by the availability of nutritional resources. The community in the frequently flooded Lake Ewijk was numerically dominated by filter-feeding collectors (e.g. *Pisidium* spec.), which feed on fine particulate organic matter, such as phytoplankton. Indeed, Lake Ewijk showed the highest annual mean phytoplankton biomass, but the lowest abundance of aquatic vegetation (Tables 1, 2). Conversely, the relative importance of shredders (e.g. *Mystacides* spec.), which feed on coarse particulate organic matter, such as vegetational debris, was highest in the non-flooded Lake Duivelswaai. The latter lake showed the highest abundance of aquatic vegetation and the lowest annual phytoplankton biomass (Tables 1, 2). It is of interest to note that a similar relationship between feeding guild composition, nutritional resources and hydrology has been found in studies on the zooplankton and macrozoobenthos communities within 100 lakes in flooding gradients along the Lower Rhine and Meuse (Van den Brink and Van der Velde, 1991; Van den Brink et al., 1994). In these studies, however, the relationship was not based on the relative densities of the feeding guilds,

but on the relative number of taxa which were assigned to the various feeding guilds. Thus, the relative number of filter-feeding macroinvertebrate and plankton taxa was found to be highest in frequently flooded lakes and lowest in infrequently and non-flooded lakes, whereas the opposite was found to be true for the relative number of shredding taxa (Van den Brink and Van der Velde, 1991; Van den Brink et al., 1994). The similar results obtained from these different studies suggest a general transversal zonation pattern of invertebrate feeding guilds in lakes along flooding gradients within eutrophic river-floodplain systems. Future studies on invertebrate functional feeding guild zonation patterns over the lateral dimension of other river-floodplain systems are needed to test the generality of these results.

Within-lake variation in density and biomass was clearest for Oligochaeta, predominantly occurring on clayey-organic habitats and for Trichoptera, predominantly occurring on sandy-mineral habitats. Oligochaeta are often associated with clayey-organic soft sediments in floodplain lakes and sedimentation areas in main channels (e.g. Anderson and Day, 1986; El-stad, 1986; Schleuter and Tittizer, 1988; Orbdlik and Castella, 1991; Dudok van Heel et al., 1992), whereas an association of Trichoptera with sandy-mineral habitats can be related to the fact that all three dominant Trichoptera species (*Oecetis ochracea, Mystacides longicornis, M. nigra*) are psammophilous species (Table 5).

For the total macrozoobenthos abundance the seasonal variation was found to be more important than the spatial variation (ANOVA; $p < 0.05$). Although a general pattern was found for seasonal changes in total macrozoobenthos density, with highest densities occurring during summer and lowest densities during winter months (Fig. 4), the relative importance of seasonally fluctuating environmental parameters for the total macrozoobenthos density was found to vary among the three lakes (Table 7). In the frequently flooded Lake Ewijk total macrozoobenthos densities were most strongly correlated ($p < 0.001$) with the flood pulse duration, suggesting the role of this hydrological factor to be more important than parameters as water temperature and vegetational abundance in this lake. In the rarely flooded Lake Oude Waal factors as flood pulse duration, water temperature and vegetational abundance were all well correlated ($p < 0.01$) with macrozoobenthos abundance, suggesting an equal importance among these parameters in this lake. In the isolated, non-flooded Lake Duivelswaai total macrozoobenthos densities were correlated with vegetational abundance and water temperature only, and not with hydrological parameters (Table 7), despite the fact that the water level in this lakes fluctuated by about 2 m, due to inflow and outflow of seepage water through the floodplain sediment. The observation that the correlations between total macrozoobenthos abundance and seasonal fluctuating hydrological parameters, such as flood pulse duration and water level, were most clear for Lake Ewijk, which is the most dynamic lake under study, suggests that the monthly total macrozoobenthos abundance in floodplain lakes is negatively influenced by inundations.

Conclusions

The present results indicate that the restoration of connections between the main channel and infrequently flooded lakes within large eutrophic regulated river systems will lead to an impoverishment of the macrozoobenthos fauna in these lakes, whose fauna will then resemble the present impoverished fauna of the semi-stagnant depositional main channel areas. Such an impoverishment will not be compensated for by a significant increase in total macrozoobenthos abundance. Restoration of degraded river ecosystems like the rivers Rhine and Meuse should therefore focus on water quality parameters, reducing the concentrations of major ions and nutrients in these systems. The present attempts to restore floodplain habitats, which aim at an increase in channel-floodplain lake interactions, should only be carried out in frequently flooded lakes which already have an impoverished macroinvertebrate fauna.

Acknowledgements

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CHAPTER 9

Synthesis

Impact of hydrology on floodplain lake ecosystems along the Lower Rhine and Meuse: a synthesis

Introduction

Floodplain lakes contribute significantly to the structure and functioning of large river eco-systems (Amoros et al., 1987a, 1987b; Junk et al., 1989; Chapter 1). The flood pulse constitutes the overall parameter which influences the existence and productivity of biota in large river-floodplain systems. Floods offer possibilities for exchange of biota and abiotic substances between 'terrestrial' and 'aquatic' and between 'lentic' and 'lotic' parts of large river eco-systems. The extent of this exchange capacity is mainly governed by the duration and frequency of the floods. Hydrology constitutes an environmental gradient over the lateral dimension of the floodplain, thereby influencing the zonation of biota in the aquatic and terrestrial subsystems (Amoros et al., 1987a; Amoros and Roux, 1988; Junk et al., 1989; this thesis). In the eutrophicated and otherwise polluted Lower Rhine and Meuse floodplains a transversal gradient in water and sediment quality runs parallel with the hydrological gradient (Demon and Van Broekhoven, 1987; Van der Velde et al., 1991; Van den Brink et al., 1993a), thus forming an additional factor which affects the zonation of communities in floodplain lakes. The present thesis deals with the extent to which and the various mechanisms by which hydrology exerts its influence on floodplain lake communities, in particular those along the eutrophic and regulated Lower Rhine and Meuse. The scope of this thesis has been presented in chapter 1. The following sections summarize the most important conclusions of the preceding chapters and discuss relevant results of other studies with respect to the impact of hydrology on floodplain lakes.

Impact on water and sediment chemistry (Chapter 2)

Hydrology exerts its influence on the floodplain lake water and sediment chemistry via seepage and floods (Chapter 1). At increasing river discharges main channel water percolates through porous floodplain sediments, so that dissolved chemicals may enter floodplain lakes via the interstitial water compartment. At high river discharges floodplain lakes may become connected with the main channel, resulting in an exchange of water masses, dissolved chemicals and suspended sediment particles. Generally, the main source of water and most dissolved and suspended substances is the main channel, which in turn reflects the entire catchment area. Thus, under pristine conditions, floodplain lakes derive their basic fertility from the main channel, via the input of dissolved and particle-bound nutrients in floods (Junk et al., 1989). In floodplain lakes along industrially, agriculturally, and otherwise anthropogenically influenced rivers, such as the rivers Rhine and Meuse, floods provide an enormous additional input of nutrients, especially in the downstream river sections (Van den Brink et al., 1993a).

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The duration of the period of connection with the heavily eutrophicated main channels was found to be of overriding importance for the annual mean levels of nutrients in the water and sediment compartments of the associated floodplain lakes (Van den Brink et al., 1993a). In general, the concentrations of N and P, the main limiting nutrients, in floodplain lakes during floods are as high as those in the main channel. After the floods, when lakes are disconnected, the concentrations of these nutrients decrease again because of uptake by primary producers -phytoplankton and (semi-)aquatic macrophytes (Hamilton and Lewis, 1987; Forsberg et al., 1988; Van den Brink et al., 1993a)- and sedimentation to the lake bottom. In floodplain lakes which are permanently connected with the main channel, depletion of nutrients may or may not occur, depending on the nutrient level in the main channel and the exchange rate between the main channel and its associated floodplain lake. This exchange rate depends in turn on the geomorphological situation, such as the width of the connection opening and the distance between the lake and the channel. In the abandoned channels and sand pits in open connection with the Lower Rhine and Meuse, depletion of nutrients does not occur, because of the very high nutrient levels in the main channel (Chapter 1). Differential losses of N and P may occur within and between floodplain lakes. By decomposition of biota and sedimentation of suspended particles, these nutrients may enter the sediment of floodplain lakes during stable water periods. During this isolation stage they are at least partially recycled via mineralisation processes. Depending on the reducing capacity and biological activity of the lake sediments, N may be transported to the atmosphere by denitrification processes. Another possibility is that N is removed with the sediment during throughflow (Howard-Williams, 1985). Although N is normally imported into floodplain lakes by floods, additional N may be imported through seepage, through fixation of atmospheric N by biota, and by atmospheric precipitation. In the relatively nutrient-poor Orinoco floodplain lakes, fixation of atmospheric nitrogen into the lake was found to occur by N-fixing Cyanobacteria such as *Anabaena* spec. and *Anabaenopsis* spec. (Hamilton and Lewis, 1987). Whether or not this also occurs in eutrophic floodplain lakes is unknown. P is generally retained in the sediment and may be partially transported to the main channel again via throughflow (Howard-Williams, 1985). Conversely, P may be regenerated from the floodplain lake sediment after depletion of this nutrient by primary producers (Forsberg et al., 1988; Van den Brink et al., 1993a). Regeneration of N and P from the lake sediment might be enhanced during bioturbation by macroinvertebrates and fish. Floodplain lakes along the Lower Rhine and Meuse were found to act as nutrient traps (Van den Brink et al., 1993a), just like those along the relatively 'pristine' rivers Amazon, Orinoco and Parana (Hamilton and Lewis, 1987; Forsberg et al., 1988; Pedrozo et al., 1992; Furch and Junk, 1993). In the Orinoco river system there appears to be a net retention of N (27% of annual input) and P (39% of annual input) in floodplain lakes, through conversion of riverine input of inorganic N and P to organic forms (Hamilton and Lewis, 1987). Along the Lower Rhine and Meuse, net retention of these nutrients occurs as well, since the levels of N and P in the interstitial water of the sediment were found to be highest in the most frequently flooded lakes, further illustrating the overriding importance of floods in combination with the highly eutrophic main channels for the eutrophication processes in the floodplain lakes (Chapter 2; Van den Brink et al., 1993a).

Floodplain lakes along the industrialized rivers Rhine and Meuse contain extremely high amounts of dominant ions (Na^+, K^+, Ca^{2+}, Cl^-, SO_4^{2-}), heavy metals (Cd, Hg, Pb, Zn) and organic micropollutants (PCB's, PAH's, insecticides, herbicides) in their water and sediment compartments (Chapter 2; Demon and Van Broekhoven, 1987). The concentrations of these anthropogenically introduced chemicals in the water and/or sediment of the floodplain lakes were found to increase with increasing flood frequency and duration (Chapter 2, Demon and Van Broekhoven, 1987). It is especially in the Lower Rhine that the input of the dominant ions Na^+ and Cl^- has increased the salinity of the surface and the interstitial water of the river and its associated floodplain lakes (Chapter 2). Indeed, within the Lower Rhine floodplain a shift in ionic composition has been found over the hydrological gradient: the water of frequently flooded lakes is dominated by sodium chloride, just as in the main channel, whereas that of rarely-flooded and non-flooded lakes is dominated by calcium bicarbonate, which is the normal situation in most rivers (Chapter 1; Golterman, 1975; Webb and Walling, 1992). Due to the industrial pollution in the Rhine and Meuse catchment area, which reached a peak in the 1960s-1970s, the levels of heavy metals and organic micropollutants in floodplain sediments have reached values that are detrimental to public health, especially in frequently flooded sediments along downstream river sections (Demon and Van Broekhoven, 1987; Rang and Schouten, 1989; Anonymous, 1991; Van der Perk et al., 1992).

Impact on phytoplankton and zooplankton (Chapters 2, 3)

As floodplain lakes derive their basic fertility from the main channel, it can be expected that the phytoplankton development is influenced by hydrology. Indeed, phytoplankton productivity is enhanced by nutrient replenishment via floods, as has been found in floodplain lakes along the eutrophic Lower Rhine and Meuse (Chapter 2; Van den Brink et al., 1993a). Disturbance of the sediment by floods may initially reduce phytoplankton productivity via shading by resuspended clay particles (Wissmar et al., 1981; Cuker et al., 1990). This may explain why chlorophyll-a levels are generally highest during the isolation phase, when stagnation of water and sedimentation of clay particles occur (Hamilton and Lewis, 1987; Van den Brink et al., 1993a; Chapter 2).

In floodplain lakes along the Lower Rhine and Meuse an increase in annual mean phytoplankton biomass has been found with increasing annual flood duration (Chapter 2; Van den Brink et al., 1993a). Increasing annual flood duration and flood frequency correlate with increasing levels of P and N in the water and sediment, so that a trophic gradient runs parallel to the inundation gradient over the lateral dimension of the floodplains of these rivers. In frequently flooded lakes it was found that P is regenerated from the sediment, after depletion of this nutrient from the water column by algae, unlike the situation in rarely-flooded and non-flooded lakes. Because of regeneration of P from the sediment, P-limitation in the water column is cancelled out, favouring the occurrence of phytoplankton blooms. Indeed, chlorophyll-a levels were highest in frequently flooded lakes, after P-regeneration during the retention period. Phytoplankton and zooplankton productivity are generally higher in associ-

ated floodplain lakes than in the main channels of lowland rivers (Wibaut-Isebree Moens, 1964; Wissmar et al., 1981; Berndt and Neumann, 1985; Van den Brink et al., 1993a; Vásquez and Rey, 1992, 1993; Neumann et al., 1994; Van den Brink and Van der Velde, 1994), because of the more stable environmental conditions. A combination of high nutrient levels and semi-stagnant water in downstream river sections contributes to high phyto- and zooplankton densities in semi-stagnant depositional main channel areas as well as in floodplain lakes (De Ruyter van Stevenink et al., 1990; Van den Brink, 1990).

Besides an impact on zoo- and phytoplankton productivity, hydrology was also found to influence the phyto- and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse (Chapter 3; Van den Brink et al., 1994). During floods, when the lake water is connected with the main channel water, dispersal of very small suspended biota, such as zoo- and phytoplankton organisms, may easily occur (Vásquez and Rey, 1993). The phytoplankton communities of frequently flooded lakes showed an abundance of the same centric diatom species which are presently dominant in the main channels (i.e. *Cyclotella* spec., *Stephanodiscus* spec., *Aulacoseira granulata* (Ehr.) Sim.), suggesting the impact of exchange of these biota on the community composition (Chapter 3; Neumann et al., 1994; Van den Brink et al., 1994). The impact of floods was also illustrated by a study of the phytoplankton communities in different parts of the floodplain lake "Oude Waal" along the Lower Rhine (Roijackers, 1985). Shortly after a flood event, the plankton communities showed great resemblance, unlike the situation after a longer period of retention, when habitat structures provided by water plants became important (Roijackers, 1985). Apart from the levels of N and P in the water compartment and the regeneration of nutrients from the lake sediment, nutrient ratios, i.e., the Si/N- and Si/P-ratios, influence the phytoplankton community composition. The summer phytoplankton composition of frequently flooded lakes along the Lower Rhine and Meuse is dominated by Cyanobacteria (*Aphanizomenon flos-aquae* (L.) Ralfs, *Microcystis aeruginosa* Kütz.), Chlorophyta (*Crucigenia* spec., *Pediastrum* spec., *Scenedesmus* spec.), and a few centric diatoms (*Aulacoseira granulata, Stephanodiscus* spec., *Cyclotella* spec.), all favoured by the low Si/N- and Si/P-ratios occurring there. The summer phytoplankton composition of the hydrologically more isolated lakes is dominated by pennate diatoms (*Cymbella* spec., *Gomphonema* spec., *Gyrosigma* spec., *Synedra* spec.), which are favoured by the high Si/N- and Si/P-ratios in these lakes. In these hydrologically more isolated lakes the chrysophyte *Dinobryon divergens* Imhof, associated with mesotrophic environments, was more frequently found than in the other lakes (Chapter 3; Van den Brink et al., 1994). The complexity of zooplankton and phytoplankton habitats, resulting from the presence of aquatic macrophytes, can be related to species diversity and community composition. The highest plankton diversity (species richness) has been found in hydrologically isolated lakes, with a well developed aquatic vegetation. The relative abundance of sediment-dwelling species and epiphytes (heleoplankton) was also highest in these lakes. Plankton diversity was lowest in lakes connected with the main channel, which also have a sparse aquatic vegetation. The plankton community in these lakes is dominated by open water species (limnoplankon). The zooplankton community feeding guilds were found to change in response to hydrology (Van den Brink et al., 1994; Chapter 3). Filter-feeding zooplankton taxa such as the cladocerans

Bosmina longirostris (Müll.) and *Daphnia cucullata* Sars were most frequently found in connected and frequently flooded lakes with a high annual phytoplankton biomass and a poorly developed vegetation, while scraping zooplankton taxa such as the cladocerans *Simocephalus vetulus* (Müll.) and *Eurycercus lamellatus* (Müll.) were most frequently found in rarely-flooded lakes with a well-developed vegetation but a low annual phytoplankton biomass (Van den Brink et al., 1994).

Impact on vegetation (Chapters 4, 5 and 6)

The diversity (species-richness) of the aquatic and semi-aquatic macrophytes of floodplain lakes along the Lower Rhine and Meuse was found to decrease with increasing annual flood duration and flood frequency (Chapter 4; Van den Brink et al., 1991a), suggesting an impact of hydrology on the distribution of these plants in the floodplain. Hydrology exerts its influence on floodplain lake vegetation via physical and chemical disturbance. Summer floods are most detrimental to vegetation, because they occur in the growth season (Brock et al., 1987). Inundations may lead to the complete submergence of rooted aquatic macrophytes with floating leaves, such as nymphaeids, and to partial or total submergence of the emergent littoral vegetation (e.g. annuals, helophytes, trees). Although these plants are equipped with various adaptation mechanisms for water-level fluctuations, the frequency, duration, depth and season of the inundations largely determine their establishment, growth and survival (Brock et al., 1987; Blom et al., 1990; Brändle, 1991; Van den Brink et al., 1991a; Chapters 4, 6). Physical disturbance caused by inundations may include water currents, i.e., throughflow, and disturbance of the sediment by scouring, so that weakly rooted macrophytes may be uprooted and transported downstream. This type of disturbance was found to be an important dispersal mechanism for the helophyte *Ranunculus lingua* L. (Johansson and Nilsson, 1993), and may be important for the vegetative dispersal of other macrophytes too. Via physical disturbance floods may set back the succession of the wetland vegetation to pioneer stages.

Inundations may lead to an impoverishment of the under water light climate, through resuspension of clay particles and the occurrence of long-lasting phytoplankton blooms, in response to nutrient input. This may severely hinder the development of submerged aquatic vegetation. At very low river discharges, large littoral areas of floodplain lakes may fall dry, leading to desiccation of vegetation, which is most detrimental to several submerged aquatic macrophytes. Via deposition and erosion hydrology influences the grain size and the nutritional state of the sediment, and thereby the establishment, growth and survival of macrophytes. In a study of the impact of hydrology on eight helophyte species, commonly occurring in European alluvial plains, it was found that the abundance of several species increased with increasing organic matter content and decreased with annual flood duration (Van den Brink, unpublished), suggesting an impact of floods via the floodplain lake sediment.

Hydrology may induce chemical disturbance of vegetation through inflow of polluted river water during floods (Chapters 4, 5; Van den Brink et al., 1991a; Van den Brink and Van der Velde, 1993). This is very clear for floodplain lakes along the industrial rivers Rhine and

Meuse. The present high levels of N and P in the main channel water lead to eutrophication of the floodplain lakes, favouring the planktonic microphytes at the cost of the submerged aquatic macrophytes. The high levels of Na^+ and Cl^- in the Lower Rhine have shifted the ionic composition of frequently flooded lakes from a calcium bicarbonate towards a sodium chloride dominance, which means an osmotic stress for freshwater plants. Although the present high levels of Na^+ and Cl^- in the Lower Rhine are not acutely lethal to *Potamogeton lucens* L., *P. nodosus* Poir. and *P. perfoliatus* L., experimental studies have shown a reduced productivity of these macrophytes under salinity stress, which could be attributed to a reduced photosynthetic capacity (Van den Brink and Van der Velde, 1993; Chapter 5). Such a reduced productivity may have contributed to the disappearance of several freshwater macrophytes from the main channel and its connected floodplain lakes over the last decades (Maenen, 1989; Van den Brink et al., 1991a).

The present high levels of sulphate in the Lower Rhine and Meuse may have contributed to the concentration of sulphides in floodplain lake sediments (Van den Brink et al., 1993a). Sulphides are natural toxins for many aquatic organisms (Ernst, 1990; Van Wijck et al., 1992; Chapter 6). Wetland plants usually have adaptations in order to survive anaerobic and potentially toxic conditions, provided they are only partially flooded, so that air can be transported to their root zones for the oxidation of toxic compounds and for root respiration (Brändle, 1991). In an experimental study of the impact of sediment characteristics on the flooding responses of eight helophyte species, it was found that the possible impact of toxins on growth rate was most evident when the plants were entirely submerged during floods (Chapter 6).

Impact on macroinvertebrates (Chapters 7 and 8)

The impact of hydrology on macroinvertebrate abundance and community composition in floodplain lakes is very complex (Van den Brink and Van der Velde, 1991). Hydrology affects macroinvertebrate habitat structures, possibilities for dispersal, water and sediment quality and nutritional resources, all of which have their influence on the community composition.

Through inundations, hydrology directly influences the area with floating and emergent structures, such as nymphaeid and emergent vegetation, which constitute the aquatic-terrestrial transition zone for many semi-aquatic macroinvertebrates, such as Ephemeroptera, Odonata and Diptera, by providing important oviposition and emergence sites (Van der Velde, 1980, 1988). Disturbance of the sediment by floods influences sediment inhabitants. The sediment grain size and the amount of siltation is influenced by the frequency and duration of the floods, together with the occurrence and rate of throughflow, when the sediment is scoured by the currents and fine sediments are washed away (Amoros et al., 1987a).

The period of connection of floodplain lakes with the main channel is of interest for the exchange of macroinvertebrates between these 'lentic' and 'lotic' subsystems. Macroinvertebrates may be washed out to the main channel by floods. There they may enter the main channel foodwebs (Eckblad et al., 1984). Floodplain lakes may also serve as reservoir and refuge areas during periods of disturbance of the main channel biota (Junk et al., 1989; Kinkopf,

1993). During the 1960-1970s the water quality of the Lower Rhine and Meuse was very poor, which led to the disappearance of many species from the main channels. During the 1980s, when the water quality improved, a repopulation of the main channels occurred with biota from refuge areas, such as floodplain lakes and tributaries (Van den Brink et al., 1990). Calamities, such as the Sandoz pollution in the river Rhine in 1986, have illustrated the importance of these refuge areas for the entire river system (Klaffke and Abbott, 1992). However, the present macroinvertebrate communities in the Lower Rhine and Meuse main channels are dominated by exotic species, such as *Corophium curvispinum* Sars, *Gammarus tigrinus* (Sexton), and *Dreissena polymorpha* (Pallas) (Van den Brink et al., 1993d). The immigration of these not strictly rheophilous allochthonous species have reduced the existing populations via interspecific competition, not only in the main channel (e.g. Van den Brink et al., 1990; 1991b, 1991c, 1993d; Van der Velde et al., 1994) but also in their associated floodplain lakes (Van den Brink 1990; Van den Brink and Van der Velde, 1991). The replacement of the freshwater amphipod *Gammarus pulex* (L.) by the brackish water immigrant *G. tigrinus* in the main channel and in the frequently flooded lakes is a good example of this type of species replacement (Van den Brink, 1990; Van den Brink et al., 1990; Van den Brink and Van der Velde, 1991; Pinkster et al., 1991). *Gammarus pulex* is still present in the rarely-flooded lakes in the active floodplain and in the non-flooded lakes situated behind the main dike in the ancient floodplain (Van den Brink and Van der Velde, 1991), which have a reservoir function. Indeed, the rarely-flooded and non-flooded lakes still harbour a number of riverine species which were formerly characteristic of the slow-flowing and semi-stagnant depositional main channel areas, but which have disappeared from these areas because of the deterioration of habitats and water quality (Chapter 8; Klink, 1989; Van den Brink and Van der Velde, 1991).

The water and sediment chemistry of the Lower Rhine and Meuse floodplain lakes influences the macroinvertebrate populations via its effects on the trophic level (food availability through nutrient input), via effects on the osmoregulation (salinity level through input of sodium chloride) and via toxic effects (Chapter 7; Van den Brink and Van der Velde, 1991; Klink et al., 1991; Van de Guchte, 1993). Nutrient enrichment of floodplain lakes by highly eutrophic main channels may influence the phyto- and zooplankton abundance and species composition (Chapters 2, 3) and thereby the food availability of macroinvertebrates. The present high salinity level in the main channel of the Lower Rhine may have contributed to the dominance of oligohalinous species in the frequently flooded lakes (Chapter 7). Due to the industrial pollution of the last decades, the floodplain lake sediments have been loaded with heavy metals and organic micropollutants (PCB's, PAH's, insecticides, herbicides). These pollutants may induce deformities of the head capsules of larvae of Chironomidae, as well as a reduced productivity of their adults and hence a reduced food availability for higher trophic levels, including fish and birds (Klink et al., 1991; Van de Guchte, 1993).

Studies of the impact of hydrology on the macroinvertebrate community composition of Lower Rhine and Meuse floodplain lakes along an inundation gradient have indicated that the community composition is at least partially influenced by the availability of nutritional resources (Chapters 7, 8). Filter-feeders, which feed on fine particulate organic matter (FPOM) such as phytoplankton and suspended and dissolved organic matter, were most abundant

(densities as well as numbers of taxa) in the frequently flooded lakes with a high phytoplankton biomass and a poorly developed vegetation. Shredders, which feed on coarse particulate organic matter (CPOM) such as leaf litter, were most abundant in the non-flooded lakes which harbour a well developed aquatic vegetation and a low phytoplankton biomass (Van den Brink and Van der Velde, 1991; Chapters 7, 8). However, in each hydrological category of these floodplain lakes the macroinvertebrate community was numerically dominated by collectors, i.e., filter-feeders and deposit-feeders, both of which feed on FPOM, and subdominated by scrapers, which feed on epiphyton. Predators, which feed on other animals, and shredders, which feed on CPOM, were numerically poorly represented (Chapter 8). These results might support the findings of Hamilton et al. (1992) and Bunn and Boon (1993), who indicate that the major energy source for floodplain lake food webs is formed by phytoplankton and epiphyton. Further studies on floodplain lake foodwebs, based on, e.g., a combination of functional feeding guilds and stable isotope analysis, are required in order to confirm this idea. In the Lower Rhine and Meuse floodplain lakes the lowest species richness was generally found in the frequently flooded lakes, whereas the total macroinvertebrate density and biomass did not vary much in response to flood frequency (Chapters 7, 8).

Impact on fish

Floodplain lakes are of vital importance as reproduction and foraging sites for fish (Welcomme, 1979; Amoros and Roux, 1988; Bergers, 1991; Schiemer and Zalewski, 1992). They also offer refuge zones for riverine fish at high water discharges (high current velocities) as well as areas from which depopulated main channel sections may be restocked after heavy pollution (Amoros and Roux, 1988; Lelek, 1989). Hydrology exerts its influence on fish communities in river ecosystems by influencing the refuge zones, feeding areas and nursery grounds during periods of high river discharges, when floodplain lakes are connected with the main channels. Floodplain lakes which are connected with the main channel all year round have been reported to be of greater value for riverine fish than the disconnected, more isolated lakes which are only flooded at high river discharges (Schiemer, 1985, 1988; Amoros and Roux, 1988; Lelek, 1989). For example, the production of fish in the river Danube was found to be greatest in the connected floodplain lakes (Amoros and Roux, 1988). Along the regulated Lower Rhine and Meuse, most side channels and anastomosed channels have been silted up, so that they are connected with the main channel during floods only. Most lakes which are at present in open connection with the main channel all year round have been dug for sand and gravel extraction. These gravel- and sand-pit lakes appear to function as important foraging biotopes for riverine fish (Bergers, 1991; Staas, 1991; Staas and Neumann, 1994). Because of their high zooplankton productivity, they are especially attractive for zooplankton-foraging fish, such as juveniles of bream *Abramis brama* L. and roach *Rutilus rutilus* (L.) (Bergers, 1991). Since connected lakes offer migration possibilities between lotic and 'lentic' sites all year round, it can be expected that they are most important for opportunistic species (Staas, 1991). Indeed, strictly rheophilous species and migratory species, which are at present seri-

ously endangered in many European rivers (Schiemer et al., 1991), are more confined to side channels, tributaries and natural river banks for their reproduction (Schiemer, 1988; Copp and Penáz, 1988; Schiemer et al., 1991). Isolated, infrequently flooded lakes appear to function as biotopes for stagnophilous species, which are not characteristic river species, although they contribute to the fish diversity of the entire river-floodplain ecosystem (Böving, 1981; Schiemer, 1985, 1988; Schiemer et al., 1991).

In the Lower Rhine and Meuse floodplain lakes the species composition of juvenile and small fish was found to change over the lateral dimension of the floodplain (Table 1). Juveniles of phytophilous and stagnophilous fish species, such as *Esox lucius, Tinca tinca, Cobitis taenia, Rutilus erythrophthalmus* and *Perca fluviatilis* were predominantly caught in non-flooded and infrequently flooded clearwater lakes which harbour a well-developed aquatic vegetation. These species are associated with clear water lakes as they hunt their preys by sight (*E. lucius, P. fluviatilis*), or because they need vegetation stuctures for foraging (*R. erythrophthalmus*), refuge (*E. lucius, T. tinca*) and/or spawning (*C. taenia, E. lucius, P. fluviatilis*) (Nijssen and De Groot, 1987; Copp and Penáz, 1988). Juveniles of euryoecious, open water fish species, such as *Alburnus alburnus* and *Abramis brama*, were less restricted in their distribution, whereas those of riverine species like *Gobio gobio* and adults of *Gasterosteus aculeatus* were predominantly collected in frequently flooded and in connected lakes (Table 1), which have a sparse aquatic vegetation. Despite their preliminary nature, the data presented in table 1 clearly illustrate the importance of hydrology for the fish reproduction and nursery biotopes. Moreover, the zonation in fish fry communities depicted here shows much resemblance with more detailed studies of the ecology of fish spawning and nursery zones in the floodplain lakes along the Upper Rhône (Copp and Penáz, 1988), the Danube (Schiemer, 1985; Schiemer et al., 1991) and the German Lower Rhine (Böving, 1981). In

Table 1. *Relation between annual flood duration (in number of days per year) and the percentage of lakes where juvenile (0+ and 1+) and small (2-6 cm total body length) fish were collected with a dip-net during August-September of 1987-1991 (n = number of lakes sampled).*

Annual flood duration	0	1-20	21-364	365	
(n)	(23)	(42)	(15)	(20)	
Esox lucius L.	22	2			(m, l)
Tinca tinca (L.)	22	26	7		(m, l)
Cobitis taenia L.	22	17	13		(m, l)
Rutilus erythrophthalmus (L.)	4	17	7		(m, l)
Perca fluviatilis L.	4	5	7		(m, l)
Alburnus alburnus (L.)	9	21	33	15	(e)
Cyprinus carpio (L.)		5	7		(m, l)
Abramis brama (L.)		2	7	5	(e)
Gobio gobio (L.)			7	15	(s, r)
Gasterosteus aculeatus L.(*)				25	(a)

(*) = adults only; m = phytophilous species; s = psammophilous species; e = euryoecious species; l = stagnophilous species; r = rheophilous species; a = anadromous species.

these studies it was found that the spawning and nursery areas of phytophilous and stagnophilous species like *E. lucius* and *T. tinca* were the disconnected, well-vegetated floodplain lakes. In the connected semi-stagnant floodplain lakes, opportunistic species such as *Rutilus rutilus* (L.), *Alburnus alburnus*, *Abramis brama*, and *Blicca bjoerkna* (L.) were found to spawn. Of course, these species which do not demand much of their environment, were not confined to these habitats for breeding. The spawning and nursery areas of rheophilous species like *G. gobio*, *Chondrostoma nasus* (L.), *Leuciscus cephalus* (L.) and *L. leuciscus* (L.) were side channels and main channel areas (Schiemer, 1985, 1988; Copp and Penáz, 1988; Schiemer et al., 1991).

Transversal zonation patterns

The distribution of aquatic biota in Lower Rhine and Meuse floodplain lakes clearly shows a transversal zonation pattern, which is perpendicular to the river axis and which is related to the flood pulse duration (Fig. 1; Chapters 3, 4, 6, 7, 8). Increasing flood pulse duration was
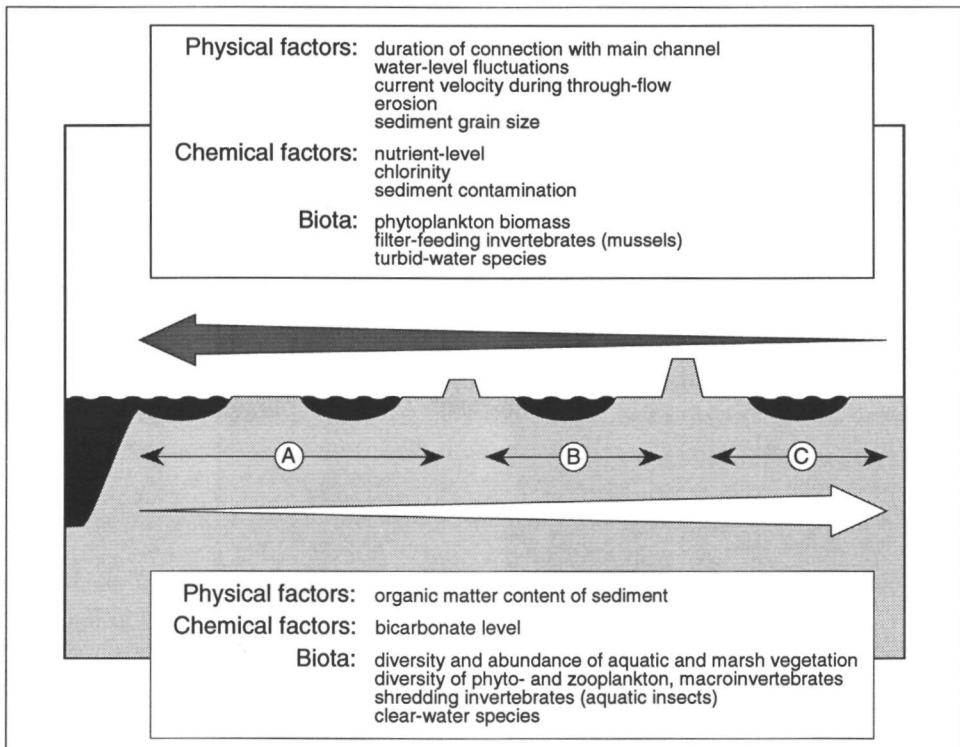

Physical factors: duration of connection with main channel
water-level fluctuations
current velocity during through-flow
erosion
sediment grain size

Chemical factors: nutrient-level
chlorinity
sediment contamination

Biota: phytoplankton biomass
filter-feeding invertebrates (mussels)
turbid-water species

Physical factors: organic matter content of sediment
Chemical factors: bicarbonate level
Biota: diversity and abundance of aquatic and marsh vegetation
diversity of phyto- and zooplankton, macroinvertebrates
shredding invertebrates (aquatic insects)
clear-water species

Figure 1. *Schematic view of transversal zonation pattern of Dutch floodplain lakes and the directions of change in physical, chemical and biotic parameters.*

found to be associated with a shift from a submerged aquatic macrophyte-dominated clear water community towards a planktonic microphyte-dominated turbid water community over the lateral dimension. Together with hydrological parameters, such as flood pulse duration, flood frequency, rate of through-flow and water-level fluctuations, the physicochemistry of the river water exerts its influence on the biota, resulting in a continuum of species replacements. Based on the species composition of phytoplankton, zooplankton, aquatic and semi-aquatic macrophytes, macroinvertebrates and juvenile fish, three major hydrological categories of floodplain lakes can be distinguished (Fig. 1).

A. very dynamic, frequently flooded lakes

These lakes are frequently flooded, with flood pulses of relatively long duration (longterm average annual flood duration more than 20 days per year). Several lakes are in open connection with the main channel all year round. Riverine input and exchange possibilities of aquatic biota are highest in these lakes, so that there is much resemblance between the communities in these lakes and the communities in the depositional main channel areas, which are both semi-stagnant riverine biotopes. Nutrient levels are highest in these lakes, supporting phytoplankton production. The phytoplankton community is dominated by Cyanobacteria (*Aphanizomenon flos-aquae*) and Chlorophyta (*Pediastrum* spec., *Scenedesmus* spec.). Zooplankton may reach high densities and consists of *Cyclops strenuus* Kozminski, *Bosmina longirostris, Dapnia cucullata*, and several Rotifera species (e.g. *Brachionus* spec., *Keratella* spec.). Aquatic vegetation is sparsely present and may consist of patches of *Nymphoides peltata* (Gmel.) O. Kuntze (Lower Rhine) and/or *Potamogeton pectinatus* L.. The helophyte zone is also poorly developed, and consists of *Phalaris arundinacea* L. and *Carex acuta* L. (Lower Rhine) or *Acorus calamus* L. (Lower Meuse). The macroinvertebrate community is numerically dominated by filter-feeders, such as small mussels (*Pisidium casertanum* (Malm), *P. henslowanum* (Sheppard), *P. nitidum* Jenyns, *P. moitessierianum* (Paladilhe), *P. supinum* Schmidt) and snails (*Valvata piscinalis* (Müll.), *Potamopyrgus antipodarum* (Gray)). Juvenile riverine psammophilous fish species such as *Gobio gobio* were collected exclusively in these lakes.

B. moderately dynamic, rarely-flooded lakes

These lakes are normally disconnected and only infrequently flooded, with flood pulses of short duration (longterm average annual flood duration less than 20 days per year). Riverine input and exchange possibilities are much lower here, although still recognizable. Nutrient levels and chlorophyll-a levels are much lower than in the more dynamic lakes. The phytoplankton community is dominated by epiphytic diatoms (e.g. *Cymbella* spec., *Melosira varians* Agardh.). The zooplankton community consists of the same species as in the frequently flooded lakes, together with benthic forms like *Simocephalus vetulus*. Aquatic vegetation is well developed and consists of large stands of nymphaeids (*Nuphar lutea* (L.) Sm.), frequently accompanied by pondweeds (*Potamogeton lucens, P. crispus* L.). The helophyte zone is

also well developed and may consist of large stands of *Glyceria maxima* (Hart.) Holmb. and *Typha angustifolia* L., frequently accompanied by many other helophytes. The macroinvertebrate communities are numerically dominated by deposit-feeders, such as snails (*Bithynia tentaculata* (L.)), water bugs (*Sigara falleni* (Fieb.), *S. striata* (L.)) and midge larvae (*Chironomus* spec., *Endochironomus* spec., *Glyptotendipes* spec.). Juvenile phytophilous fish like *Tinca tinca* were most frequently collected in these lakes.

C. isolated, non-flooded or seepage lakes

These lakes are situated in the ancient floodplain, on the land side of the main dike, and are never flooded, although their water level and water chemistry are influenced via seepage. As a result of seepage from the river to the lake through the floodplain sediments, particle-bound nutrients and toxic compounds are filtered out. Nutrient levels are lowest here, as are phytoplankton densities. The phytoplankton community consists of epiphytic diatoms, together with Pyrrhophyta, of which *Ceratium hirundinella* (Müll.) Schr. is most conspicious. The presence of the chrysophyte *Dinobryon divergens* may be related to the mesotrophic environment here. The zooplankton species *Mesocyclops leuckarti* Claus was abundantly found in these non-flooded lakes only. Aquatic vegetation is well developed and may consist of submerged aquatic macrophytes such as *Ranunculus circinatus* Sibth. and *Myriophyllum spicatum* L., together with nymphaeids like *Nymphaea alba* L. and *Nuphar lutea*, often accompanied by many other species. The helophyte zone shows much resemblance with those of the rarely-flooded lakes. Flood sensitive species such as *Typha latifolia* L. are more common here. A conspicious component of the macroinvertebrate community in these lakes are caddisflies (*Molanna angustata* Curtis, *Mystacides longirostris* (L.), *Mystacides nigra* (L.)) and mayflies (*Cloeon simile* Eaton, *Caenis horaria* (L.), *Caenis luctuosa* Burm.), both of which show their highest densities and numbers of species in these lakes. The relative abundance of shredders (e.g. *Mystacides* spec.) also reaches its peak here, and juvenile phytophilous fish as *Esox lucius* were collected most frequently in these lakes.

Biodiversity of aquatic biota in Dutch floodplain lakes

In order to estimate the contribution of floodplain lake species to the total biodiversity of the entire Lower Rhine and Meuse river-floodplain systems, historical and recent information on the plankton and macroinvertebrate species in main channels has been compared with recent data from the floodplain lakes. Such a comparison could not be made for aquatic macrophytes, since historical information about macrophytes in the main channels of the Lower Rhine and Meuse is rather incomplete. Nevertheless, it is beyond doubt that many aquatic macrophyte species formerly occurred in large stands in the Lower Rhine and Meuse main channels. For example, palaeoecological studies on sediment cores from these rivers revealed large numbers of fructifications (oögonia) of Characeae (Klink, unpublished). Historical records showed the presence of the running water species *Ranunculus fluitans* Lamk. and *Pota-*

Table 2. *The number of aquatic macrophyte taxa recently collected in the Lower Rhine and Meuse channels (Maenen, 1989) in comparison with that recently collected in their associated flood-plain lakes (Maenen, 1989; Van den Brink, 1990).*

	Lower Rhine and Meuse, recent	Floodplain waters, recent
Characeae	0	2
Nymphaeaceae	1	3
Ceratophyllaceae	1	1
Ranunculaceae	0	3
Haloragaceae	0	2
Primulaceae	0	1
Menyanthaceae	0	1
Callitrichaceae	1	4
Lentibulariaceae	0	1
Alismataceae	0	1
Hydrocharitaceae	1	4
Potamogetonaceae	6	11
Najadaceae	0	1
Lemnaceae	2	4
Total	12	39

mogeton nodosus at several locations along the large Dutch rivers (Mennema et al., 1980, 1985). Van der Ploeg (1990) mentions the former occurrence of large underwater meadows in the Lower Rhine and Meuse, consisting of *Potamogeton perfoliatus*. This species was once so abundant in the Biesbosch area that it had a bad reputation among local fishermen (Vuyck, 1895, in: Van der Ploeg, 1990). During recent intensive surveys relatively small stands of *Potamogeton nodosus, P. pectinatus* L. and *Nuphar lutea* have been found at only a few locations in the main channels, in addition to nine other species which have only incidentically been found (Maenen, 1989; Table 2). When comparing the recent main channel species list with that from the floodplain lakes, it appears that Potamogetonaceae include the largest species group in both biotopes (Table 2). Although many macrophyte species recorded from the floodplain lakes still occur abundantly there, several species have declined since the 1950s (Van der Voo and Westhoff, 1961; Van Donselaar, 1961; Van Donselaar-Ten Bokkel Huinink, 1961; Maenen, 1989; Van den Brink et al., 1991a). Among these, *Ranunculus lingua* and *Stratiotes aloides* L. have disappeared entirely from the Lower Rhine and Meuse floodplain lakes (Maenen, 1989; Van den Brink et al., 1991a). Undoubtedly, the decline of aquatic vegetation must have been largest in the main channel, because hydrological changes, habitat deterioration and water pollution are most evident there. It is therefore not surprising that at present the floodplain lakes contribute greatly to the biodiversity of aquatic macrophytes in the total river-floodplain area (Table 2). At present, about 70% of the species collected in the Lower Rhine and Meuse river-floodplain area have been found exclusively in the floodplain lakes.
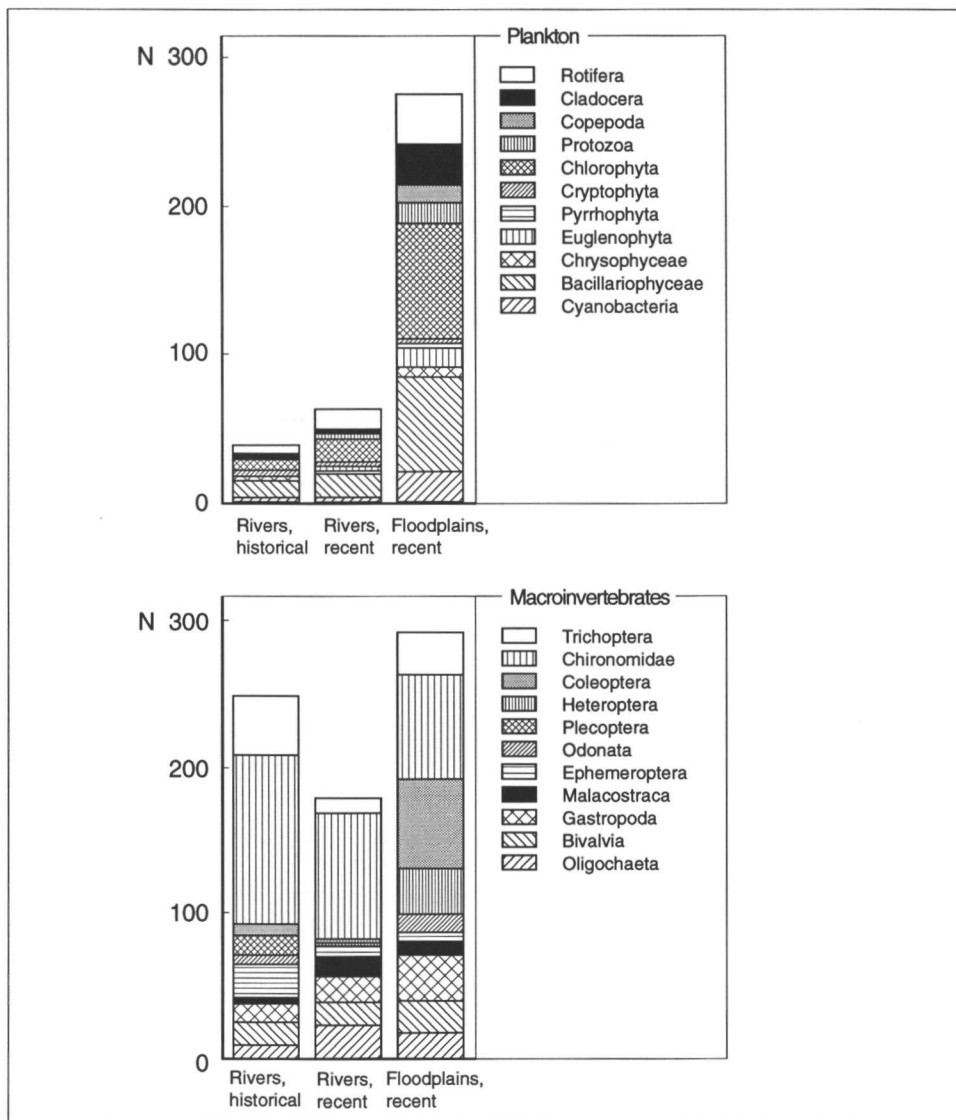
Figure 2. *Historical and present plankton (**above**) and macroinvertebrate (**below**) community composition of the Dutch main channel sections of the Lower Rhine and Meuse and present composition in their associated floodplain lakes. N = number of taxa. Only those macro-invertebrate groups were considered for which historical information was available. Data from tables 3 and 4.*

The present phyto- and zooplankton species richness in floodplain lakes along the Lower Rhine and Meuse was found to be many times higher than that recorded in the main channels

Table 3. *Numbers of plankton taxa formerly and recently collected in the Dutch sections of the Lower Rhine and Meuse channels (Peelen, 1975; and references therein) in comparison with those recently collected in their associated floodplain lakes (Van den Brink, 1990).*

	Lower Rhine and Meuse, ±1900	Lower Rhine, recent	Lower Meuse, recent	Lower Rhine and Meuse, recent	Floodplain waters, recent
Cyanobacteria	2	3	3	3	21
Bacillariophyceae	14	12	15	18	65
Chrysophyceae	2	1	0	1	6
Euglenophyta	2	3	1	3	14
Pyrrhophyta	1	1	0	1	3
Cryptophyta	0	1	0	1	2
Chlorophyta	10	15	15	17	78
Rhodophyta	0	0	0	0	1
Protozoa	0	2	3	3	15
Copepoda	0	0	0	0	11
Cladocera	2	2	2	2	27
Rotifera	6	11	13	15	34
Total	39	51	52	64	277

(Table 3; Fig. 2). Both in the main channels and in the floodplain lakes, Chlorophyta, Bacillariophyceae and Rotifera showed the highest species numbers (Fig. 2). A comparison of species lists revealed that all species occurring in the main channels had also been found in the floodplain lakes (Peelen, 1975; Van den Brink, 1990). Conversely, a large number of plankton species have exclusively been found in the floodplain lakes. Benthic and epiphytic species in particular have only sporadically been recorded from the main channels. These species have been abundantly found in the floodplain lakes along these rivers. They were probably present in the main channels of the Lower Rhine and Meuse in larger numbers before river regulation had taken place, i.e., before the 19th century. Evidence for this comes from a palaeolimnological study of sediment cores from the Rhine area (Klink, unpublished), which showed that epipsammic and epiphytic pennate diatoms dominated the spectrum of diatom frustules in the sediment deposited in the 19th century, whereas planktonic centric species were numerically dominant in sediment layers deposited in the 20th century. A striking increase in abundance from historical to recent core layers was found for the centric diatom species *Cyclotella meneghiniana* Grün. (Klink, unpublished). As this is a brackish-water species, its increased abundance can be attributed to the increased salinity of the Lower Rhine. At present, the floodplain lakes contribute 77% to the plankton taxa found in the entire Lower Rhine and Meuse river-floodplain systems.

As with macrophytes and plankton taxa, the present number of macroinvertebrate taxa in floodplain lakes along the Lower Rhine and Meuse is higher than that recorded in the main channels (Table 4). If we compare only taxa for which historical data are available (Table 4; Fig. 2), it appears that the percentage of common taxa, i.e., taxa which occur both in the main channel and in the floodplain lakes, has increased (Fig. 3). In other words, the composition of

the macroinvertebrate communities in the main channel at present shows a greater similarity to that in the floodplain lakes. The reasons behind this are the deterioration of habitats and water quality, which has led to the decline of rheophilous species of mayflies, stoneflies, caddisflies and blackflies (Fig. 2). At present, about 56% of the macroinvertebrate taxa collected in the Lower Rhine and Meuse river-floodplain area are found exclusively in the floodplain lakes. Clearly, the enormous variety of floodplain lakes, which comprise a complex array of heterogeneous habitats, contributes to the total biodiversity in the river-floodplain systems as a whole.

Table 4. *Numbers of aquatic macroinvertebrate taxa formerly collected in the Lower Rhine and Meuse channels (palaeoecological and literature data) (Klink, 1989; Van den Brink et al., 1990; and literature therein) and those recently collected in the main channels of the Lower Rhine (Hof, 1992; and literature therein) and Lower Meuse (Franzen, 1991; and literature therein) in comparison with those recently collected in their associated floodplain lakes (Van den Brink, 1990).*

	Lower Rhine and Meuse, before 1900	Lower Rhine, recent	Lower Meuse, recent	Lower Rhine and Meuse, recent	Floodplain waters, recent
Tricladida	-	3 (3)	4 (4)	6 (4)	4
Oligochaeta	10 (1)*	18(11)	13 (5)	23(13)	19
Hirudinea	-	10 (9)	10 (8)	12 (9)	10
Bivalvia	15 (12)	11 (8)	11 (9)	16(12)	21
Gastropoda	13 (12)	10(10)	15(15)	17(17)	31
Araneida	-	0 (0)	0 (0)	0 (0)	1
Actinedida	-	0 (0)	3 (2)	3 (2)	50
Malacostraca	3 (2)	14(10)	9 (8)	14(10)	9
Ephemeroptera	25 (3)	4 (1)	5 (3)	7 (3)	7
Odonata	5 (1)	2 (1)	2 (1)	2 (1)	12
Plecoptera	14 (0)	3 (0)	0 (0)	3 (0)	0
Heteroptera	1 (0)	2 (1)	1 (1)	3 (2)	31
Coleoptera	7 (0)	2 (1)	1 (0)	2 (1)	61
Megaloptera	1 (1)	1 (1)	0 (0)	1 (1)	1
Neuroptera	-	0 (0)	1 (0)	1 (0)	0
Chironomidae	116 (39)	61 (32)	64 (36)	87 (45)	72
Simuliidae	6 (0)	1 (0)	0 (0)	1 (0)	0
Chaoboridae	-	0 (0)	0 (0)	0 (0)	4
Brachycera	-	1 (0)	2 (1)	3 (1)	19
Trichoptera	40 (10)	7 (5)	10 (5)	10 (7)	29
Lepidoptera	-	0 (0)	0 (0)	0 (0)	4
Total**	>257 (81)	149 (94)	149 (94)	204 (125)	385
Total***	257 (81)	134 (81)	129 (83)	174 (112)	297

- : No data available
*: Numbers of common taxa which occur both in the main channel(s) and in the floodplain lakes are given in parentheses.
**: Based on all groups
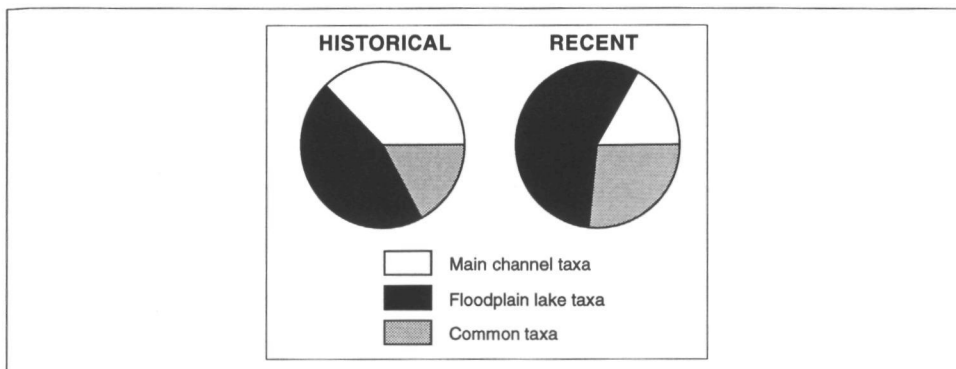***: Based on groups for which historical information is available.

Figure 3. *Relative shares of macroinvertebrate taxa in the Lower Rhine and Meuse main channels and their associated floodplain lakes in the Netherlands. Total number of taxa is 100%. A comparison of the present floodplain lake taxa (Van den Brink, 1990) with (left) historical data on main channel taxa based on dated sediment cores and literature (Klink, 1989; Van den Brink et al., 1990; and literature therein), and (right) recent data on main channel taxa based on recent surveys (Franzen, 1991; Hof, 1992; and literature therein).*

Fig. 4 illustrates the impact of hydrology on the diversity (species richness) of macroinvertebrates, plankton and aquatic macrophytes in floodplain lakes along the Lower Rhine and Meuse. In both rivers, the biodiversity of the aquatic cenoses was found to decrease with increasing flooding frequencies. Besides species richness, hydrology also clearly influences the species composition of the floodplain lakes. As can be seen in figure 4, the three hydrological categories of floodplain lakes along the Lower Rhine show great resemblance to the corresponding categories for the River Meuse. Differences between hydrological categories of floodplain lakes within one river system were much larger, indicating that the impact of hydrology on the floodplain lake communities is more important than the role of river system related parameters.

Scope for ecological management of Dutch river floodplains

In response to the Sandoz accident on 1 November 1986, the states bordering the river Rhine agreed on the Rhine Action Programme, in which for the first time an ecological goal for Rhine management was elaborated. This ecological goal is directed towards water quality criteria, i.e., a further reduction of the loads of micropollutants and nutrients, but also towards morphological and hydrological criteria, such as the development of fish passages. Two main measures have been suggested for the rehabilitation of floodplain habitats (ICPR, 1989): 1. restoration of connections between the main channels and floodplain lakes, and 2. reactivation of former side channels. The results of studies presented in this thesis provide clear information from which restrictions and recommendations can be deduced with respect to the proposed restoration measures.
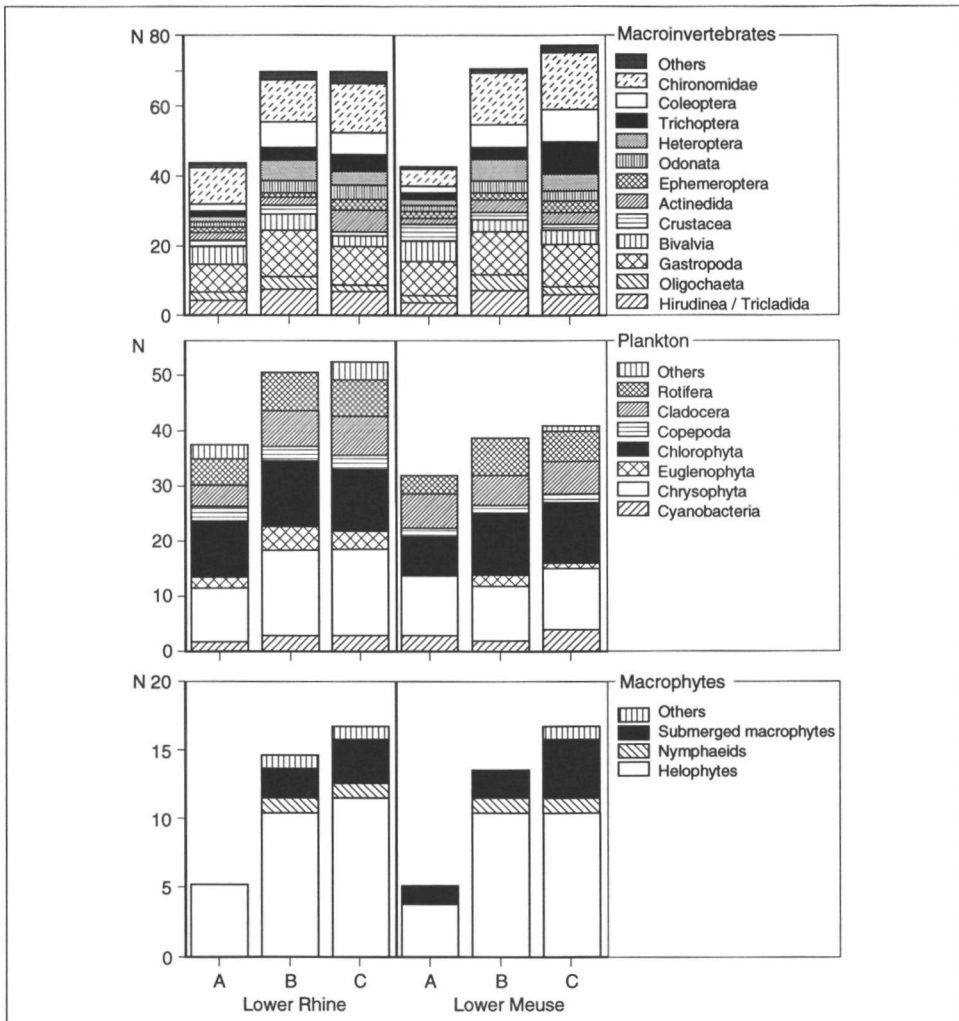
Figure 4. *Mean numbers of taxa (= N) of macroinvertebrate, plankton and macrophyte groups in three hydrological groups of floodplain lakes along the Lower Rhine and Meuse in the Netherlands. A: very dynamic lakes, unprotected against floods; B: moderately dynamic lakes, protected against average summer floods by small summer dikes or levees, un-protected against winter floods; C: isolated lakes, protected against floods by a main dike.*

In the Lower Rhine and Meuse floodplain lakes the diversity (species richness) of plankton, aquatic and semi-aquatic macrophytes and macroinvertebrates was found to decrease with increasing degrees of connection with the main channel (Fig. 4). Moreover, the entire aquatic community in the floodplain lakes was found to change from a clear-water community towards a turbid-water community with increasing flooding frequency, as a result of

the high input of nutrients from the highly eutrophic main channels through floods. Only very few macroinvertebrate species collected in a total of 100 floodplain lakes were predominantly found in frequently flooded lakes, whereas many others were characteristic of rarely flooded and non-flooded lakes (Van den Brink and Van der Velde, 1991). Moreover, the species inhabiting frequently flooded lakes were also found to occur in the main channels, and appeared to be mainly invaders from other aquatic systems, not strictly riverine species. At present, 25% of the aquatic insects, mostly phytophilous species, which formerly lived in the main channel but have disappeared from there with the decline of the vegetation, can still be found in the non-flooded and infrequently flooded lakes. The fish fauna in lakes connected with the main channel of the Lower Rhine is dominated by opportunistic fish species like bream and roach (Böving, 1981), whereas phytophilous and stagnophilous clear-water species like pike and tench are confined to isolated and infrequently flooded lakes. Hence, rehabilitation of the Lower Rhine and Meuse floodplains should initially be directed towards the protection of the ecological values of non-flooded and rarely flooded lakes (long-term average annual flood duration less than 20 days per year), by further isolation from the influx of river water and agricultural influences (Van den Brink and Klink, 1991). Protection and enhancement of ecological values in non-flooded and in rarely flooded lakes is important because these lakes may function as a reservoir in case of calamities in main channel areas. Moreover, these lakes provide a variety of wetland functions. Their well-developed aquatic and marsh vegetation provide important habitats for refuge, nesting, breeding, nursery and feeding for a variety of wetland species, including macroinvertebrates, fish, amphibians, reptiles, waterfowl and other birds, and mammals. Riverine wetlands provide corridors for amphibians and mammals. Furthermore, wetland vegetation provides organic matter in a variety of particle sizes, which may enter the main channel foodwebs via floods, thereby contributing to the variety of nutritional resources there (Maurizi and Poillon, 1992; Van den Brink et al., 1993b, 1993c).

The results of the restoration project 'Duursche Waarden' in the floodplain of the IJssel branch of the Lower Rhine point to the same direction. As predicted by previous studies, presented in this thesis, the reconnection of isolated, infrequently flooded lakes with the main channel resulted in a huge loss of aquatic macroinvertebrate species, an increase in the trophic level resulting in phytoplankton blooms, and an increase in chironomid head capsule deformations, which might be attributed to an increased sediment pollution in these lakes due to increased influx of polluted river water (Klink et al., 1991).

Consequently, restoration of connections between the main channel and floodplain lakes should concentrate on the frequently flooded lakes (long-term average annual flood duration more than 20 days per year), which already have an impoverished aquatic flora and fauna. It has been argued that connected lakes provide important foraging and nursery sites for fish which live in the main channels of the Lower Rhine and Meuse (Lelek, 1989; Bergers, 1991; Staas, 1991; Neumann and Rutschke, 1993; Molls and Neumann, 1994; Neumann et al., 1994; Staas and Neumann, 1994). This may hold true for gravel-pit lakes in particular, because these are deep enough to contain water even at very low river discharges. The shallow backwaters which are still at one end in open connection with the main channel simply empty themselves at low river discharges. The few studies which have focused on fish diets and fish

reproduction in gravel-pit lakes along the Lower Rhine suggest that these biotopes are most beneficial for opportunistic fish species like bream and roach (Bergers, 1991; Staas, 1991; Staas and Neumann, 1994). Nevertheless, connected lakes may be important as refuge areas for all riverine fish, including the juveniles of rheophilous species (Staas, 1991; Molls and Neumann, 1994; Staas and Neumann, 1994). Clearly, more research on this topic is needed in order to know whether and in which direction the riverine fish fauna is manipulated by the restoration of connections.

Instead by restoring the lake-river connection just at one end, the ecological values of floodplain lakes might be enhanced by reconnecting the lake at both ends, so that a running water biotope, a lotic side channel, is re-established. In such a lotic side channel riverine habitats may be restored which have disappeared from the main channel. These habitats include gravel, sand and clay banks, marsh and aquatic vegetation and riverside forests. It has been argued that flushing by river water prevents the accumulation of nutrients and toxic compounds in the sediment of the lotic side channels, unlike the situation in 'lentic' ones (Klink, 1991; Klink et al., 1991). Reactivation of lotic biotopes should initially be directed towards frequently flooded lakes only, because of uncertainty of success. Although the water quality of the Lower Rhine and Meuse has greatly improved over the last decades, essential further improvement may be frustated by diffuse sources and calamities. Nevertheless, it might be worthwile to start a lotic side channel project in order to study the possibilities of restoration. Of course such a project should be monitored adequately and should be used to carry out experiments that are designed to accelerate the restoration process.

Ecological research should be integrated into river management as much as possible and should not be a minor consideration. Such research should be directed at the further improvement of the water quality in the main channels, the restoration of impoverished and degraded riverine and floodplain habitats, the local improvement of floodplain lake water quality, and clean-up measures for the polluted sediments of valuable floodplain lakes. A further reduction of the pollution loads in the entire drainage basin is of overriding importance for the improvement of the Rhine and Meuse river-floodplain ecosystems. This reduction is at present focused on nutrients, heavy metals and organic micropollutants, but should include a reduction of the sodium chloride loads too. Restoration of habitats should focus on wetland vegetation, including aquatic macrophytes, helophytes and trees. Restoration of (semi-)aquatic and terrestrial floodplain vegetation can partly be achieved by fencing out cattle. For an improvement of floodplain lake water quality, retainment of the relatively clean seepage water from moraine and riverine hills, or the water from small streams which flow onto the floodplain, can be used. Dredging of the sediment of floodplain lakes can be used to clean up the polluted sediments, but also to increase the sediment variability within these lakes, and thereby the habitat diversity.

More information is needed about the historical and present occurrence of species in relation to the total array of biotopes, including small side streams and temporary floodplain waters along the entire river basins, in order to provide baseline information on the distribution of species inhabiting river-floodplain areas and the biodiversity of the entire drainage basins. In this way, refuge centres from which depopulated areas may be restocked can be located.

Furthermore, information on food-webs in the floodplain systems might provide clues for an ecological improvement of floodplain lake functioning. In fact, all these items are prerequisites for the ultimate success of the ecological restoration programmes.

Acknowledgements

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Samenvatting

Overstromingsvlakten vormen een karakteristiek onderdeel van grote rivieroecosystemen. Naast de hoofdstroomgeul kunnen nevengeulen en afgesneden meanders tot de aquatische onderdelen van een natuurlijk rivier-oecosysteem gerekend worden. Zoals zoveel grote rivieren elders in de wereld zijn de Rijn en Maas tegenwoordig gereguleerd en genormaliseerd, waardoor ze niet meer vrij kunnen meanderen en er geen nieuwe geulen meer worden gevormd. De stroomgeul is vastgelegd door kribben, het afvoerregime geregeld door stuwen en de overstromingsvlakten zijn fors gereduceerd door dijken. Binnen deze bedijkte overstromingsvlakten, ook wel uiterwaarden genoemd, bevinden zich verschillende afgesneden voormalige stroomgeulen (oude rivierlopen, strangen, hanken), plassen ontstaan door vroegere dijkdoorbraken (wielen, kolken, waaien) en gegraven plassen ten behoeve van delfstofwinning (kleiputten, zandputten, grindgaten). De meeste van deze uiterwaardplassen zijn bij lage rivierwaterstanden geïsoleerd ten opzichte van de rivier, maar worden overstroomd bij hoge rivierwaterstanden en staan dan in open verbinding met de rivier. Andere plassen staan voortdurend in open verbinding met de rivier. Tenslotte zijn er ook binnendijks gelegen plassen die door de rivier beïnvloed worden via kwel.

Dit proefschrift handelt over de invloed van overstromingen op de aquatische levensgemeenschappen in binnen- en buitendijks gelegen plassen langs de Nederlandse trajekten van de Rijn en Maas. Deze invloed geschiedt niet altijd direkt, maar verloopt vaak op een uitermate komplexe wijze, waarbij de gevolgen voor allerlei soorten verschillend kunnen zijn. Een van de belangrijkste gevolgen van overstromingen is dat er uitwisseling plaatsvindt van water, opgeloste en zwevende stoffen, sediment en biota, tussen de stroomgeul en de uiterwaardplassen. De mate waarin dergelijke uitwisseling plaatsvindt, hangt nauw samen met de overstromingsdynamiek, dat wil zeggen met de duur en de frequentie van de overstromingen. Deze overstromingsdynamiek wordt bepaald door de afvoerfluktuaties van de rivier, door de geomorfologie van de uiterwaard, door de aanwezigheid van kaden, sluizen en dijken en door jaarlijkse klimaatschommelingen.

Overstromingen beïnvloeden de aquatische levensgemeenschappen in uiterwaardplassen direkt door fysische verstoring en indirekt door chemische verstoring. Fysische verstoring treedt op door waterstandsschommelingen, door de totstandkoming van een direkte verbinding tussen de plas en de stroomgeul, door het tijdelijk optreden van stroming in de plas, en door erosie- en sedimentatieprocessen. Chemische verstoring treedt op door instroom van water uit de stroomgeul, dat veelal een andere samenstelling heeft dan dat in de plas.

Door lozingen vanuit de industrie, de landbouw en huishoudens is de waterkwaliteit van de Rijn en Maas vooral de laatste eeuw drastisch verslechterd. Hoewel het dieptepunt voorbij lijkt, bevat het water van beide rivieren nog steeds een teveel aan nutriënten, zouten, zware metalen en organische microverontreinigingen.

De waterkwaliteit van de stroomgeul beïnvloedt de water- en bodemkwaliteit in de uiterwaardplassen via direkte overstromingen en via ondergrondse kwelstromen (Hoofdstuk 2).

Hoe langer en vaker een plas door de rivier overstroomd wordt, des te hoger zijn de gehalten aan nutriënten (N, P), zouten (Na, Cl), zware metalen (Zn, Pb, Hg, Cd) en organische micro-verontreinigingen (PCB's, PAK's) in het water, het bodemwater en het bodemslib van de plas. Ook werd er een significant verband gevonden tussen de overstromingsdynamiek, het chloro-fyl-a gehalte van het water, en de vegetatiesamenstelling van de plassen. Hoe vaker en langer een plas door de rivier overstroomd wordt, des te hoger is het chlorofyl-a gehalte in het water. Omgekeerd namen de soortenrijkdom en de bedekking van ondergedoken waterplanten af bij toenemende overstromingsdynamiek. Frequente overstroming met het voedselrijke rivierwa-ter heeft langdurige fytoplanktonbloei, gedomineerd door cyanobacteriën en groenwieren, tot gevolg bij stagnatie. Als gevolg hiervan verslechtert het onderwaterlichtklimaat, waardoor ondergedoken waterplanten het op den duur afleggen tegen zwevende algen.

Door het hoge zoutgehalte van de Rijn is de watersamenstelling van frequent overstroom-de uiterwaardplassen veranderd. Oorspronkelijk werd de waterkwaliteit gedomineerd door calciumbicarbonaat maar thans door natriumchloride.

De gehalten aan zware metalen en organische microverontreinigingen in onbekade en dus frequent overstroomde uiterwaarden zijn hoger dan die in bekade uiterwaarden, die op hun beurt weer hoger zijn dan die in binnendijkse referentiegebieden. Deze ernstige vervuiling is het gevolg van afzetting van verontreinigd slib via overstromingen en is ten dele een erfenis uit de 60-er en 70-er jaren.

Behalve via overstromingen wordt de waterkwaliteit van de uiterwaardplassen ook beïn-vloed via kwel. Kwelwater afkomstig van de rivier heeft een betere kwaliteit dan het water in de stroomgeul zelf, hoewel het hogere gehalten aan natriumchloride en nitraat bevat, dan kwelwater afkomstig van stuwwallen.

De overstromingsdynamiek heeft een sterke invloed op de soortensamenstelling van het fyto- en zoöplankton van de uiterwaardplassen (Hoofdstuk 3), vooral vanwege het hoge nu-triëntengehalte (N, P) van het rivierwater. In frequent overstroomde plassen is het fytoplank-ton tijdens de zomermaanden gedomineerd door cyanobacteriën (*Aphanizomenon flos-aquae*, *Microcystis aeruginosa*) en groenwieren (*Crucigenia* spec., *Pediastrum* spec., *Scenedesmus* spec.), terwijl de fytoplanktonsamenstelling van weinig dynamische plassen gedomineerd is door pennate diatomeeën (*Cymbella* spec., *Gomphonema* spec., *Gyrosigma* spec., *Synedra* spec.). De zoöplanktonsamenstelling van frequent overstroomde plassen be-staat uit soorten van het open water, voornamelijk filtreerders als de watervlooien *Bosmina longirostris* en *Daphnia cucullata*, terwijl het zoöplankton van weinig dynamische plassen ook benthische epifyton-schrapers als de watervlooien *Simocephalus vetulus* en *Eurycercus lamellatus* omvat.

Effekten van overstromingen op water- en moerasplanten zijn beschreven in de hoofd-stukken 4, 5 en 6. De soortenrijkdom van de water- en moerasvegetatie van de onderzochte uiterwaardplassen neemt af bij toenemende overstromingsdynamiek (Hoofdstuk 4). Water-gentiaan (*Nymphoides peltata*) en Veenwortel (*Polygonum amphibium*) behoren tot de weini-ge soorten die bestand zijn tegen de dynamische omstandigheden in frequent overstroomde uiterwaardplassen. Uit een vergelijking van vroegere met recente vegetatiegegevens van ui-terwaardplassen blijkt dat een groot aantal soorten water- en moerasplanten sterk in hun ver-

spreiding achteruitgegaan is. De oorzaken van deze achteruitgang lijken te kunnen worden gezocht in de veranderde rivierdynamiek, dat wil zeggen een optreden van zomerhoogwaters gedurende een aantal opeenvolgende jaren, en in de veranderde rivierwaterkwaliteit, met name de toename van het gehalte aan eutrofiërende stoffen (N en P) en de toename van de saliniteit.

Hoofdstuk 5 beschrijft een experiment naar de invloed van de saliniteit op de groei en de morfologie van vier soorten zoetwaterplanten (*Potamogeton lucens, P. nodosus, P. perfoliatus* en *Ranunculus circinatus*). Deze planten werden in proefvijvers blootgesteld aan (natrium)chloride in concentraties als die in Rijnwater (7.0 mmol l^{-1} Cl^-) en als die in hydrologisch geïsoleerde uiterwaardplassen (1.4 mmol l^{-1} Cl^-). Bij de hoogste chlorideconcentratie resulteerde dit in een verlaagde biomassaproduktie en verlaagde relatieve groeisnelheden van de *Potamogeton*-soorten, terwijl er geen overeenkomstige effekten gevonden werden bij *R. circinatus*. Bij al deze soorten nam de wortel-spruitverhouding bij de hoogste zoutconcentratie toe en nam de bloei af. De gevonden effekten suggereren dat het huidige zoutgehalte in de Rijn een osmotische stress induceert bij de onderzochte waterplanten.

Hoofdstuk 6 beschrijft een experiment naar de rol van het sediment (organisch stofgehalte, redoxpotentiaal, gehalte aan natuurlijke toxinen, zoals sulphide en mangaan) bij de overstromingstolerantie van acht soorten moerasplanten (*Acorus calamus, Carex acuta, Equisetum fluviatile, Sagittaria sagittifolia, Scirpus lacustris, Sparganium erectum, Typha angustifolia* en *Typha latifolia*). Planten werden gepoot in potten met een organisch of een mineraal sediment, waarna deze potten over twee proefvijvers verdeeld werden. Het organisch sediment was sterker reducerend en had hogere gehalten aan natuurlijke toxinen, zoals sulfide en mangaan, dan het minerale sediment. In de ene vijver werden de planten slechts ten dele onder water gezet. In de andere vijver werden ze gedurende acht weken geheel onder water gezet. Uit dit experiment bleek dat indien de planten slechts ten dele onder water staan alle soorten op het organische sediment het snelst groeiden. Indien de planten geheel ondergedompeld werden, groeiden sommige plantesoorten nog steeds het snelst op het organische substraat, terwijl andere soorten het snelst op het minerale sediment groeiden. De verschillen in groeisnelheid kunnen worden verklaard door onderlinge verschillen in tolerantie ten aanzien van inundatie, een lage redox potentiaal en de gehaltes aan gereduceerde stoffen als sulphide en mangaan in het sediment.

De invloed van overstromingen op aquatische macro-evertebraten in uiterwaardplassen is uitermate complex (Hoofdstukken 7 en 8). Overstromingen beïnvloeden de soortensamenstelling en de dichtheden van macro-evertebraten via de waterkwaliteit, de aanwezigheid en de kwaliteit van habitats, het voedsel en de mogelijkheden tot uitwisseling van biota met de stroomgeul. Er zijn aanwijzingen gevonden dat de macro-evertebratenfauna in uiterwaardplassen van de Rijn en Maas sterk beïnvloed worden door het hoge nutriëntengehalte in de stroomgeul van beide rivieren. De relatieve soortenaantallen en de relatieve dichtheden van functionele voedselgilden vertonen een verschuiving over de overstromingsgradiënt. Filtreerders, zoals erwtemossels (bijvoorbeeld *Pisidium supinum*), die leven van fijn particulair organisch materiaal, zoals fytoplankton en gesuspendeerd en opgelost organisch materiaal, domineren de macro-evertebratengemeenschap in frequent overstroomde uiterwaardplassen, die door een hoge fytoplanktondichtheid en een lage waterplantenbedekking gekenmerkt wor-

den. Omgekeerd zijn verknippers, zoals bepaalde soorten kokerjuffers (bijvoorbeeld *Mystacides longicornis*), die leven van grof particulair organisch materiaal, zoals bladmateriaal, het meest talrijk in de hydrologisch geïsoleerde uiterwaardplassen, die door een lagere fytoplanktondichtheid en een hogere waterplantenbedekking gekenmerkt worden. De overeenkomstige resultaten met betrekking tot de aanwezigheid en de dominatie van bepaalde voedselgilden zowel bij het zoöplankton als bij de macro-evertebraten vormen een extra aanwijzing dat de soortensamenstelling van deze gemeenschappen sterk beïnvloed worden door de dominante voedselbron in de plas.

De verspreiding van alle onderzochte levensgemeenschappen (waterplanten, moerasplanten, fytoplankton, zoöplankton, macro-evertebraten en juveniele vissen) in de uiterwaardplassen van de Rijn en Maas vertoont een horizontaal zoneringspatroon, loodrecht ten opzichte van de stroomdraad van de rivier. Dit zoneringspatroon is gerelateerd aan de overstromingsdynamiek. De uiterwaardplassen binnen de onderzochte riviertrajekten kunnen op grond van de samenstelling van hun aquatische levensgemeenschappen in drie hydrologische categorieën ingedeeld worden:

A. *zeer dynamische uiterwaardplassen*: dit zijn onbedijkte plassen die frequent en langdurig overstroomd worden, gemiddeld meer dan 20 dagen per jaar;

B. *weinig dynamische uiterwaardplassen*: deze plassen zijn gelegen tussen een zomerkade en de winterdijk en worden slechts weinig frequent en gedurende korte tijd overstroomd, gemiddeld minder dan 20 dagen per jaar;

C. *geïsoleerde uiterwaardplassen*: dit zijn binnendijks gelegen plassen en worden derhalve nooit overstroomd, maar ondervinden rivierinvloeden via kwelstromen.

Met toenemende overstromingsdynamiek verschuift de biocoenose in uiterwaardplassen van een helder-water gemeenschap, gekenmerkt door ondergedoken waterplanten met geassocieërde fauna naar een troebel-water gemeenschap die gedomineerd wordt door planktonische algen met geassociceërde fauna.

Op grond van de resultaten zoals beschreven in dit proefschrift kan gesteld worden dat natuurontwikkelingsprojecten in uiterwaard(plass)en niet zonder meer volgens het 'Plan Ooievaar' kunnen worden uitgevoerd. Enige nuancering met betrekking tot de voorgestelde verhoging van de rivierdynamiek door het doorsteken van zomerkades is hier op zijn plaats. Het in open verbinding brengen van weinig dynamische plassen met de stroomgeul van de Rijn of Maas zal leiden tot een achteruitgang van de aquatische natuurwaarden en dient derhalve achterwege te blijven. Dergelijke maatregelen zijn minder schadelijk voor de natuurwaarden van uiterwaardplassen met een hoge overstromingsdynamiek, aangezien deze reeds een verarmde biocoenose bezitten. Het verdient op de eerste plaats aanbeveling de waterkwaliteit van de Rijn en Maas verder te verbeteren. Daarnaast zouden natuurontwikkelingsprojecten zich kunnen richten op habitatverbetering, zoals de aanleg van nevengeulen, een verdwenen component van het Nederlandse rivierensysteem. Of de aanleg van dergelijke geulen daadwerkelijk tot een verhoging van de natuurwaarden zal leiden bij de huidige waterkwaliteit van de Rijn en Maas dient uiteindelijk in de praktijk te worden vastgesteld.

Curriculum vitae

Fred WB van den Brink is op 1 juni 1956 te Eindhoven geboren. In 1976 behaalde hij het Atheneum-B diploma aan het Augustinianum te Eindhoven. In datzelfde jaar werd een aanvang gemaakt met de universitaire opleiding Biologie (B1g, oude stijl) aan de Katholieke Universiteit te Nijmegen. In 1980 werd het Kandidaatsexamen Biologie met als bijvak Geologie behaald; in 1984 het Doctoraalexamen Biologie met 1e-graads onderwijsbevoegdheid. Het hoofdvak werd verricht in de Aquatische Oecologie (Prof. Dr. C den Hartog, Prof. Dr. G van der Velde, Dr. JFM Geelen, Dr. F van Herp); bijvakken in de Ecotoxicologie (Prof. Dr. AP van Overbeeke, Dr. RAC Lock) en Wetenschapsfilosofie (Prof. Dr. P Scheurer). Tijdens de doctoraalopleiding was hij studentassistent bij de afdelingen Aquatische Oecologie, Microbiologie en Dierfysiologie. Van 1985-1986 was hij als volontair werkzaam op het Laboratorium voor Aquatische Oecologie onder leiding van Prof. Dr. C den Hartog en Prof. Dr. G van der Velde, alwaar een onderzoek naar samenstelling van de huidige en de historische Rijnfauna verricht werd. Van 1987 tot heden is hij als wetenschappelijk projectmedewerker verbonden aan de Vakgroep Oecologie, Werkgroep Aquatische Oecologie. De volgende projecten werden door hem uitgevoerd aan de KUN: 1987-1990: Project "Typologie en waardering van stagnante wateren langs de grote rivieren in Nederland, op grond van waterplanten, plankton en macrofauna" in opdracht van Rijkswaterstaat DBW/RIZA; 1991: Project "Hydrobiologisch onderzoek in de uiterwaarden bij Neerijnen" in opdracht van de Stichting Het Geldersch Landschap; 1990-1994: Project "Invloed van overstromingen op de levensgemeenschappen in rivierbegeleidende wateren binnen een overstromingsgradiënt langs de Rijn", gesubsidieërd door het Sandoz Rijnfonds. Momenteel is hij als projectleider werkzaam aan de ontwikkeling van een beoordelingssysteem voor verontreinigde waterbodems van strangen, in opdracht van Rijkswaterstaat, Direktie Gelderland. Naast het verrichten van wetenschappelijk onderzoek, waarvan een groot deel van de resultaten de basis van het onderhavige proefschrift vormt, vervulde hij ook een aantal onderwijstaken, waaronder colleges en practica voor doctoraalstudenten, en begeleidde hij de cursus Mariene Biologie te Roscoff (Frankrijk). Sinds 1991 is hij redaktielid van het tijdschrift De Levende Natuur.

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