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BIODIVERSITY IN THE LOWER RHINE AND MEUSE RIVER-FLOODPLAINS: ITS SIGNIFICANCE FOR ECOLOGICAL RIVER MANAGEMENT

F.W.B. VAN DEN BRINK[1], G. VAN DER VELDE[2], A.D. BUIJSE[3] and A.G. KLINK[4]

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ABSTRACT:

The diversity of aquatic biota in two large river systems of The Netherlands, *viz.* the Lower Rhine and Meuse, is discussed in order to: (1) reveal historical changes in biodiversity; (2) examine the role of river-floodplain connectivity; (3) set guide lines for ecological river management. The taxonomical diversity, or species richness, is used to describe the former and recent state of aquatic biota in these river systems. The ecological diversity, obtained by incorporating the concept of ecological groups into the concept of biodiversity, appears very useful in delineating guide-lines for ecological river management. The present species richness in the main channels still appears to be relatively low, despite major water quality improvements. Although present biodiversity is much improved compared with a few decades ago, it is evident that the present species are mainly eurytopic, including many exotics. The inhibition of a further biodiversity recovery results from river regulation and normalization, which have caused the deterioration and functional isolation of main channel and floodplain biotopes. The importance of connectivity for the diversity of aquatic biota is found to be different for various taxa. Moreover, a transversal zonation by the biota in the floodplain lakes is found, emphazising the importance of differences in the degree of connectivity for a diverse aquatic flora and fauna. It is concluded that floodplain lakes contribute significantly to the total biodiversity of the entire riverine ecosystem. The redevelopment of active secondary channels is required to restore the most typical riverine habitats and biota.

INTRODUCTION

The United Nations conference on environment and development, Rio de Janeiro 1992, made clear that much effort should be undertaken to halt world-wide species loss (VAN NIEUKERKEN and VAN LOON, 1995). In the biodiversity crisis, most attention has been focused on tropical rain forests and ocean conservation, whereas remarkably little attention has been paid to rivers and streams. Due to their economic value, large temperate rivers in particular, have experienced dramatic environmental changes which have resulted in huge species losses (*e.g.* PETTS, 1989; CALOW and PETTS, 1992, 1994). On the other hand, due to their dynamic nature, rivers and streams have shown remarkable recovery capacities, which makes them very amenable for redevelopment of their ecological values (PETERSEN and PETERSEN, 1992; ALLAN and FLETCHER, 1993).

In Western Europe, the large rivers Rhine and Meuse have been used by man since ancient times. Human impact has intensified enormously over the last century in these rivers, resulting in an ecological nadir in the 1970s. Following water quality improvement measures, a gradual increase in species richness in the Rhine and Meuse was noted during the 1980s (MEURISSE-GENIN *et al.*, 1987; VAN DEN BRINK *et al.*, 1990; FRANZEN, 1991; TITTIZER *et al.*, 1993). Presently, however, ecological improvement is stagnating, indicating that restoration measures must not consider water quality improvements alone (BIJ DE VAATE, 1994; KETELAARS and FRANZEN, 1995). This stagnation is generally considered to be due to the poor habitat diversity which presently exists in these regulated rivers. Since the Rhine and Meuse are major shipping routes, habitat restoration measures have been focused on the floodplains of these rivers. Several studies demonstrated an increase in biodiversity of the terrestrial parts of the floodplains after habitat restoration measures, such as a local increase in river dynamics and a transformation of agricultural floodplain meadows to nature reserves. In particular, the management of the more 'terrestrial' floodplain vegetation via extensive grazing by cattle and horses, to create habitat heterogeneity, has resulted in an increased diversity of terrestrial plants, invertebrates, reptiles, birds and mammals in these areas (CALS, 1994; KURSTJENS *et al.*, 1995). In order to enlarge the heterogeneity of aquatic biotopes, and thereby the biodiversity of aquatic flora and fauna, a reconnection of abandoned channels with the main channels has been suggested together with an increase in the hydrodynamics of abandoned channels (ICPR, 1989; CALS, 1994). However, the biodiversity of aquatic macrophytes and macroinvertebrates in low dynamic floodplain lakes decreased in response to the restoration of connections (KLINK *et al.*, 1991; CALS, 1994).

To provide guidelines for the ecological management of the aquatic component of the Lower Rhine and Meuse, we studied the role of connectivity between floodplain lakes and the main channel (VAN DEN BRINK, 1990, 1994, and references therein). Based on these earlier studies, a method is proposed to use biodiversity analysis for the delineation of ecological rehabilitation measures. We address the following questions:

1. How does biodiversity reflect the changes in ecological functioning that have occurred in the Lower Rhine and Meuse over the last century?
2. How does biodiversity indicate the ecological importance of floodplain lakes and their connectivity to the main channel for various aquatic biota?

In order to answer these questions, the recent biodiversity is compared with a historical reference. Next, the role of river-floodplain connectivity for aquatic biota is evaluated by comparing the recent biodiversity of hydrologically different floodplain lakes. Based on these biodiversity analyses, restoration measures are suggested. Not only taxonomical biodiversity, or species richness, is compared, but also ecological biodiversity, by arranging species into ecological groups. In this way, the quality and omissions in the main ecological functions can be indicated which have to be reactivated in order to restore the ecosystem. Due to different ecological demands it is important that ecological restoration measures should not be carried out to favour one group only, but several groups simultaneously. Therefore, our biodiversity analyses include plankton, macrophytes, macroinvertebrates and fish.

THE LOWER RHINE AND MEUSE

General river characteristics

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 R. Waal/Merwede is the main branch, discharging 65% of the water; the R. Nederrijn/Lek discharges about 21%, and the R. IJssel discharges only 14%. The R. Nederrijn/Lek is regulated by three weirs, the other two branches are free-flowing.

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. This river is highly regulated by many weirs, of which seven are located in The Netherlands.

In The Netherlands, the rivers Rhine and Meuse enter a lowland area, where they form a river delta

Table 1. Hydrological characteristics of the rivers Rhine and Meuse (Data from RIZA, Arnhem, 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]
Minimal discharge ($m^3\ s^{-1}$	600[a]	2[b]
Maximum discharge ($m^3\ s^{-1}$)	13,000[a]	3,000[b]
Median water level fluctuations (m)[c]	5.9	2.2
Maximum water level fluctuations (m)[c]	9.4	8.3

a: measured at station Lobith, The Netherlands, over 1901-1985

b: measured at station Borgharen, The Netherlands, over 1911-1988

c: measured along the Dutch river sections, over 1988 before they flow into the North Sea. At present, most Dutch sea arms are closed by huge dams; the only direct connection between the Lower Rhine/Meuse estuary and the North Sea is via the Nieuwe Waterweg near Rotterdam, a highly industrialised area with many harbours. An essential difference between the rivers Rhine and Meuse is their water source: the River Rhine is a combined glacial-rain river, whereas the River Meuse is rain-fed only. As a result, the Rhine has a relatively stable basic seasonal discharge, while the Meuse has a distinct summer minimum flow. Hydrological characteristics of both rivers are presented in Table 1. The flooding regime of both rivers is more or less comparable since both rivers have their highest river discharges occurring normally in winter and spring.

Floodplain lakes

Floodplains of the alluvial rivers Rhine and Meuse in The Netherlands contain several hundreds of relatively large water bodies (1-200 ha), which have originated from spontaneous diversions of the streams (former meanders, anastomosed channels, oxbow lakes), from dike bursts in the past (breakthrough lakes, the so-called 'wielen'), and more recently from sand, gravel and clay extraction (pits). Depending on geomorphological and hydrological circumstances, these floodplain waters are subject to different hydrological regimes. Normally, the Dutch floodplain lakes are inundated during winter and spring, *i.e.* outside the vegetational growth season, although in recent decades the incidence of summer spates has increased (MAENEN, 1989). Most lakes become isolated from the river during the summer and autumn, except for water bodies which have a permanent open connection with the main channel, the so-called anastomosed lakes. There are also isolated lakes which are located on the landward-side of the main dike, outside the active floodplain, and which are influenced by the river via seepage only (VAN DEN BRINK, 1994). Apart from floodplain lakes, there are many small, mainly temporary waters, and a limited number of brooklets, emptying into the main channels. Active secondary channels are entirely absent in the Dutch river area.

Environmental changes and present state

The geomorphology of the alluvial plains of the Lower Rhine and Meuse has been drastically changed by human impact. The first documented human influence on these rivers occurred in the Roman Era and encompassed canal construction to regulate the discharge of the Dutch Rhine distributaries. Embankment of the Dutch river sections began in the early Middle Ages. However, up to the 18th century, the main channels were meandering and many river islands, floodplain forests and snag habitats were still present (KLINK, 1989, 1991). Later, the need for timber resulted in the disappearance of floodplain forests, whereas snag was removed to facilitate shipping. River regulation and normalization began in the 19th century and was completed in the present century. The canalization of the upper R. Rhine north of Basle, the so-called Tulla correction, was carried out in the period between 1817 and 1876, and had tremendous environmental consequences. The once anastomosing river system with islands, sand and gravel flats – a highly diverse system of various habitats in a dynamic environment – was transformed into a petrified canal with high current velocities (VAN URK and SMIT, 1989). The R. Meuse was a relatively free-flowing river until 1918. In order to facilitate shipping on this rain-fed river, more than 70 weirs have since been built. As a result, the R. Meuse can be considered to be a chain of basins with long residence times in periods of extreme drought (VAN URK, 1984). The summer beds of both rivers have become fixed by groynes and dikes which impede meandering and the formation of anastomosed and secondary channels. As a result, the total floodplain area has become drastically reduced, the river has incised itself into its summer bed and the river forelands have silted up. In the 18th and 19th century, dike bursts occurred regularly during periods of high river discharges in combination with the incidence of ice in the river. These dike bursts resulted in deep (up to 20 m) holes which became filled with river water. Large-scale clay digging and sand and gravel extraction occurred in the present century resulting in many new water bodies. After the large sea-flood-disaster of 1953, plans were made to close the large estuaries of the Rhine/Meuse delta. The former main estuary, the Haringvliet, was dammed in 1970 and subsequently, the large intertidal freshwater marsh, the Biesbosch, lost its unique character (VAN URK, 1984).

The present water quality of the main channels of the Lower Rhine and Meuse differs considerably from the original situation, with increased levels of nutrients (nitrate and phosphate), salts (chloride, sodium, sulphate) and heavy metals (cadmium, lead, zinc). The water is also contaminated with an increasing amount of organic micropollutants, such as PCB's, insecticides and

Table 2. Water quality parameters of the Lower Rhine (measured at Lobith, NL) and Meuse (measured at Eijsden, NL) over the years. Annual means of at least weekly measurements are presented for 1971 and 1991 (Data from RIZA, Lelystad, and RIWA, Amsterdam, 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). –: no date available.

		Lower Rhine			Meuse		
		<1900	1971	1991	<1900	1971	1991
Temp	°C	10.9	13.3	14.0	<10.0	14.3	14.5
O_2	mg l^{-1}	>10.0	4.4	10.2	>10.0	8.5	7.4
pH		7.5	7.4	7.8	7.5	7.8	7.5
HCO_3^-	mg l^{-1}	160	157	167	172	170	185
Cl^-	mg l^{-1}	13	236	201	15	45	62
SO_4^{2-}	mg l^{-1}	35	75	78	28	70	52
NO_3^-	mg l^{-1}	0.3	2.5	3.9	0.3	1.9	2.7
NH_4^+	mg l^{-1}	0.2	2.9	0.4	0.2	1.6	0.7
PO_4^{3-}	mg l^{-1}	0.05	0.30	0.08	0.07	0.67	0.37
total -P	mg l^{-1}	0.15	0.95	0.27	0.22	0.94	0.49
Zn	µg l^{-1}	–	301	30	24	330	78
Pb	µg l^{-1}	3	35	5	–	54	9
Hg	µg l^{-1}	<0.05	3.11	0.05	<0.05	0.29	0.05
Cd	µg l^{-1}	<0.04	5.00	0.10	<0.04	6.12	0.50
PCB's	µg l^{-1}	0	–	24	0	–	22
PAH's	µg l^{-1}	0	–	0.98	0	–	0.11

Table 3. Diagram showing the ecological attributes of macrophyte, diatom, insect and fish species, which have been used for the translation of species into ecological groups, according to the indexed references. References: [a]ELLENBERG, 1974; [b]BLOEMENDAAL and ROELOFS, 1988; [c]VAN DER WERFF, 1984; [d]VAN DAM *et al.*, 1994; [e]KLINK, 1989; [f]VERDONSCHOT, 1990; [g]CUMMINS, 1973; [h]BALON, 1975a, 1975b; [i]NIJSSEN and DE GROOT, 1987

	macrophytes	diatoms	insects	fish
trophic state	+[a,b]	+[c,d]		
substrate	+[b]	+[c,d]	+[e,f]	+[h]
flow preference			+[e,f]	+[i]
feeding mode			+[f,g]	+[i]

herbicides (Table 2). Water quality was very poor during the 1960s-1970s, when oxygen levels were extremely low. After the sanitation of waste water discharges during the 1970s-1980s, oxygen levels returned to normal in the Lower Rhine. The River Meuse still suffers from low oxygen levels during low water discharges in summer. Although the levels of several heavy metals in both rivers have been reduced over the last two decennia, the sediments of depositional areas in the main channel and the sediments of the river forelands are still strongly contaminated.

HISTORICAL AND RECENT BIODIVERSITY

In order to estimate the relative contribution of the aquatic species occurring in the channels and floodplain lakes to the total species richness of the entire Lower Rhine and Meuse river-floodplains, historical and recent information on these aquatic species was gathered from our own investigations and from the literature (see Tables 4 – 7). Despite extensive literature surveys, historical information of the occurrence of riverine species is poor. Therefore, our analyses are based on the presence or absence of species and not on abundance data. In order to find possible causes for changes in ecological functioning of the present river-floodplains, the species lists were converted to lists of ecological groups with the aid of autecological data from the literature (see Table 3).

Aquatic macrophytes

The present diversity of aquatic macrophytes in the main channels of the Lower Rhine and Meuse is rather poor as compared with the former situation (Table 4) or with the present diversity in flood-plain lakes (Fig. 1). At present, about 70% of the species recorded have been found exclusively in the floodplain lakes. The other 30% can be found both in the main channel and flood-

Table 4. Number of aquatic macrophyte species formerly collected in the Lower Rhine and Meuse rivers (MENNEMA *et al.*, 1980, 1985), in comparison with those recently collected in the main channels (MAENEN, 1989) and their associated floodplain lakes (VAN DEN BRINK, 1990). *: number of species also presently occurring in floodplain lakes.

	Lower Rhine and Meuse rivers	Lower Rhine and Meuse channels	Floodplain lakes
	± 1900	recent	recent
Characeae	>2	0	2
Nymphaeaceae	3	1	3
Ceratophyllaceae	1	1	1
Ranunculaceae	5	0	3
Halogaraceae	2	0	2
Primulaceae	1	0	1
Menyanthaceae	1	0	1
Callitrichaceae	7	1	4
Lentibulariaceae	1	0	1
Alismataceae	1	0	1
Hydrocharitaceae	5	1	4
Potamogetonaceae	19	6	11
Najadaceae	2	0	1
Lemnaceae	5	2	4
Total number	>53 (39)*	12 (12)*	39
Number of exotics	4 (7%)	1 (8%)	4 (10%)

plain lake biotopes. Although historical data on the distribution of aquatic macrophytes in the large rivers and their floodplain waters are far from complete, it is beyond doubt that many species have disappeared or became rare. For example, palaeoecological studies on sediment cores from these rivers revealed large numbers of fructifications (oogonia) of Characeae (KLINK, unpublished). Historical records prove the presence of the lotic species *Ranunculus fluitans* Lamk. and *Potamogeton nodosus* Poir. at several locations along the Lower Rhine and Meuse (MENNEMA *et al.*, 1980, 1985). Although *R. fluitans* no longer maintains itself in the Dutch rivers, it is still present in some tributaries of these rivers (DE LA HAYE, 1994). VAN DER PLOEG (1990) mentions the former occurrence of large underwater meadows in the lower Rhine and Meuse, consisting of *P. perfoliatus* L.. This species was once so abundant in the Biesbosch area that it had a bad reputation among local fishermen (VUYK, 1895, in: VAN DER PLOEG, 1990). During recent intensive surveys of the main channels, small stands of *Potamogeton nodosus, P. pectinatus* L. and *Nuphar lutea* (L.) Sm. have been found at only a few relatively stagnant downstream locations (MAENEN, 1989; COOPS *et al.*, 1993). Deterioration of aquatic macrophytes in these regulated rivers is probably caused by increased river dynamics, *i.e.* enlarged differences between summer and winter water depths, increased stream velocities and a higher incidence of summer spates. This is especially likely since not only the number of species indicating oligo- and mesotrophic conditions has been reduced, but also the number of eutrophic species (Fig. 1). For example, the water-soldier *Stratiotes aloides* L., characteristic of low dynamic floodplain lakes, has disappeared from the Dutch rivers following the frequent summer floods during the 1970s-1980s. Complete stands of this floating species have been lifted up with the rising water and have been transported downstream (VAN DE STEEG, 1984). The decline of oligotrophic and mesotrophic species from the river-floodplains (Fig. 1) can be further related to the increased eutrophication over the years (Table 2).

Apart from hydrophytes, several helophytes, such as *Ranunculus lingua* L. and *Equisetum fluviatile* L., characteristic of floodplain areas with high groundwater levels, have declined in occurrence. This can be related to an overall lowering of groundwater levels in the floodplain areas as a result of river incision caused by regulation (VAN URK and SMIT, 1989).

The number of exotic aquatic macrophytes in the Lower Rhine and Meuse river-floodplains is quite low (Table 4). The only exotic macrophyte that has been frequently found is *Elodea nuttallii* (Planch.) St. J., often extremely dominant in newly created lakes, such as gravel-, clay- and sand-pits.

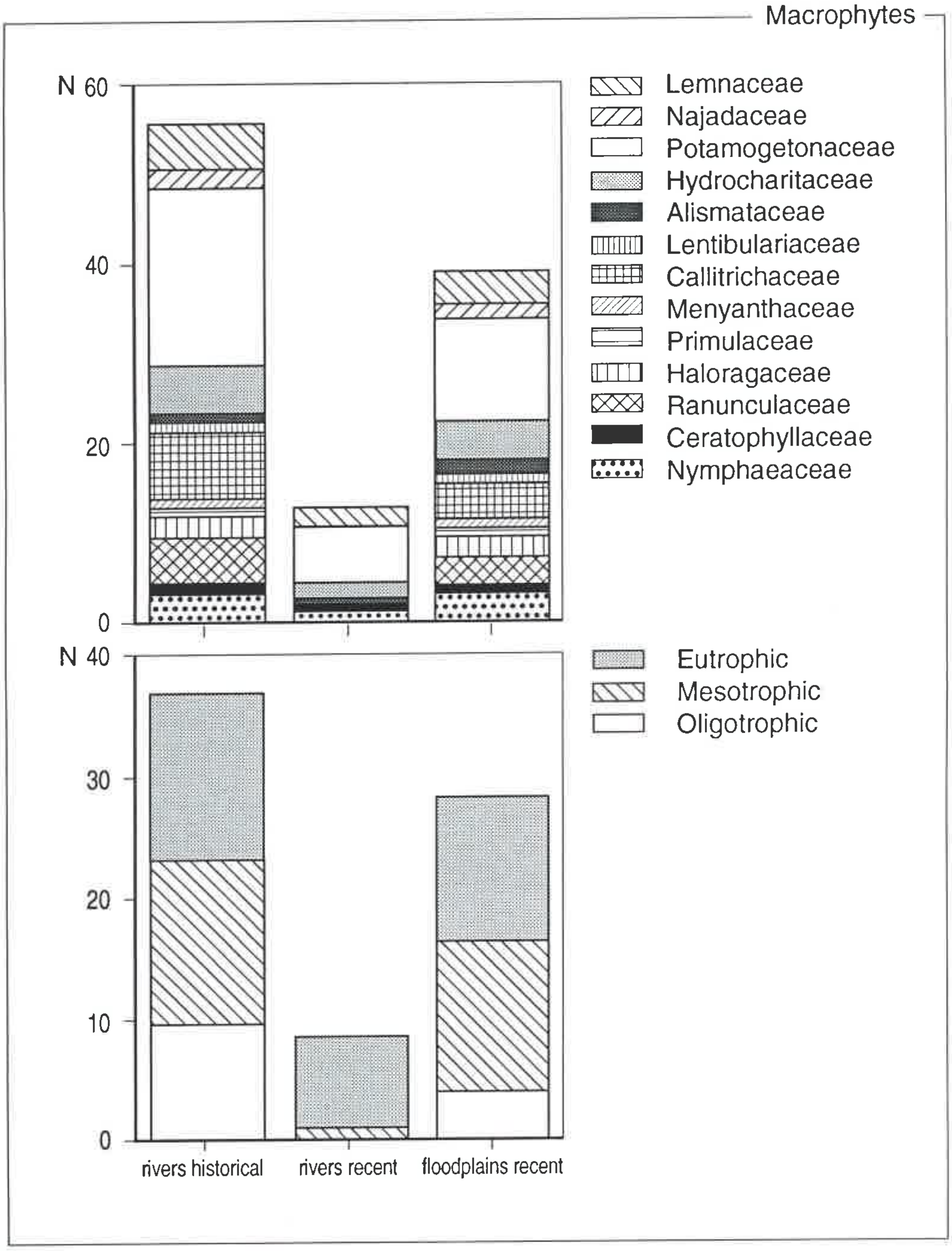

Fig. 1. Historical and recent biodiversity of aquatic macrophytes in the Lower Rhine and Meuse river-floodplains. Above: taxonomic groups, below: trophic groups. N = number of taxa.

Plankton

Unlike other groups, the diversity of plankton taxa in the Lower Rhine and Meuse main channels seems to have increased during this century (Table 5). However, this may be an artefact of improving identification techniques over the years. Benthic and epiphytic species in particular have only sporadically been recorded from the main channels in the present century, as is shown for diatoms (Fig. 2). Such species have been found 'in abundance' in the floodplain lakes (Fig. 2) and they showed a higher diversity in the main channels before river regulation took place, *i.e.*, before the 19th century. At that time, snag, vegetation and shallow sandy river stretches provided natural habitats for these species (VAN URK and SMIT, 1989). Evidence for this comes from a palaeolimnological study of sediment cores from the Rhine area (KLINK, unpublished). This study shows that epipsammic and epiphytic pennate diatoms dominated the spectrum of diatom frustules in the sediment deposited during the 19th century, whereas planktonic centric species were numerically dominant in sediment layers deposited in the 20th century. This means that complex arrays of lotic and lentic areas with snag, macrophytes and undisturbed sandy banks and river islands as habitats for benthic diatoms have vanished, due to regulation and normalisation works and heavily motorised shipping traffic. Recent studies indicate that, apart from biotope changes, the plankton diversity may be negatively influenced by the present high levels of micropollutants in the Lower Rhine and Meuse (TUBBING *et al.*, 1995).

The recent diversity of plankton in the floodplain lakes is many times higher than that in the main channels (Table 5). At present, the floodplain lakes contribute 77% to the plankton taxa recorded in the entire Lower Rhine and Meuse river-floodplain systems. A comparison of species lists proves that all species from the main channels have also been recorded in the floodplain lakes. Both in the main channels and in the floodplain lakes, diatoms, chlorophytes and rotifers show the highest species numbers (Table 5). The present phytoplankton communities in the main channels consist of a few dominant euryoecious species of centric diatoms, such as *Stephanodiscus hantzschii* Grün., *S. neoastrea* Hakansson & Hickel, *Aulacoseira granulata* (Ehrenb.) Simons and *Cyclotella meneghiniana* Kütz., and chlorophytes, such as *Pediastrum* spec. and *Scenedesmus* spec. (DE RUYTER VAN STEVENINCK *et al.*, 1990; VAN DEN BRINK, unpublished).

A distinct increase in abundance from historical to recent core layers was found for the centric diatom *Cyclotella menighiniana* (KLINK, unpublished). This is a brackish-water species, and so its increased abundance can be attributed to the increased salinity of the Lower Rhine.

The diatom species in the former and recent channels, as well as in the floodplain lakes, indicate

Table 5. Numbers of plankton taxa formerly collected in the Lower Rhine and Meuse rivers (PEELEN, 1975; and references therein) in comparison with those recently collected in the main channels (PEELEN, 1975) and in their associated floodplain lakes (VAN DEN BRINK, 1990) *: number of species also presently occurring in floodplain lakes

	Lower Rhine and Meuse rivers	Lower Rhine and Meuse channels	Floodplain lakes
	± 1900	recent	recent
PHYTOPLANKTON			
Cyanobacteria	2	3	21
Bacillariophyceae	14	18	65
Chrysophyceae	2	1	6
Euglenophyceae	2	3	14
Pyrrhophyta	1	1	3
Cryptophyta	0	1	2
Chlorophyta	10	17	78
Rhodophyta	0	0	1
ZOOPLANKTON			
Protozoa	0	3	15
Copepoda	0	0	11
Cladocera	2	2	27
Rotifera	6	15	34
Total	39 (39)*	64 (64)*	277

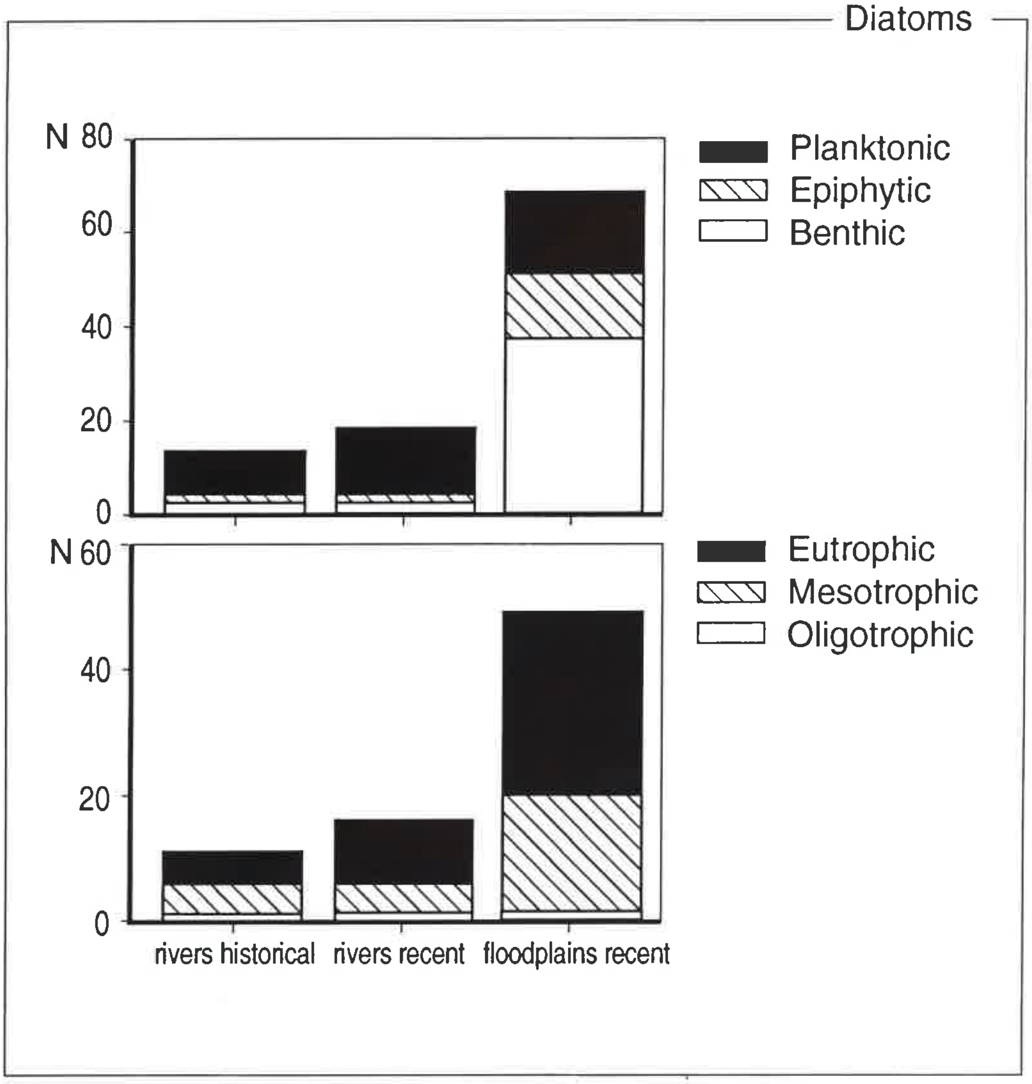

Fig. 2. Historical and recent biodiversity of diatoms in the Lower Rhine and Meuse river-floodplains. Above: habitat preference groups, below: trophic groups. N = number of taxa.

mesotrophic to eutrophic conditions. However, the number of species indicating eutrophic conditions has increased since the start of the century (Fig. 2), probably due to the increased eutrophication. Although not occurring in fast flowing river sections, zooplankton is well developed in the highly regulated R. Meuse with its many weirs, in the more stagnant downstream areas of the Lower Rhine, as well as in the floodplain lakes of both rivers (DE RUYTER VAN STEVENINCK *et al.*, 1990; VAN DEN BRINK, 1990, 1994).

Recently, some exotic diatom species have been found in the Lower Rhine and Meuse main channels (*e.g.* *Cyclotella bodanica* Eul., *Cymbella alpina* Grün., *Gomphonema ventricosum* Gregory and *Surirella spiralis* Kütz.), but only occasionally and in very low numbers (VAN DAM *et al.*, 1994).

Aquatic macroinvertebrates

As with aquatic macrophytes, the present diversity of aquatic macroinvertebrates in the Lower Rhine and Meuse main channels is rather poor. At present, 52% of the aquatic insect taxa for which historical data exist, occur exclusively in the floodplain lake biotopes, 17% exclusively in the main channels and 31% in both biotopes. Before the present century, 46% of the insect species occurred in the floodplain lakes only, 37% in the channel biotopes and only 17% in both biotopes (Table 6). This means that the biodiversity of typical riverine taxa has decreased over the years. A clear difference between lotic and lentic river sections is the (former) presence of (predominantly) rheophilous taxa (*e.g.* Ephemeroptera, Plecoptera, Coleoptera: Elmidae and Diptera: Simuliidae) in the lotic channels, and the presence of mainly stagnophilous taxa (*e.g.* most Coleoptera and Heteroptera) in the floodplain lakes (Fig. 3). Mainly rheophilous insects, such as Ephemeroptera, Plecoptera, Simuliidae and Trichoptera species, have disappeared over the years (Table 6; Fig. 3). Among these were many species inhabiting snag and vegetation, which declined in the Dutch river sections (KLINK, 1989, 1991). Although the decline occurred among species with a variety of feeding modes, the strongest decline occurred in taxa with scraping and shredding feeding modes (Fig. 3). This means that biotopes containing benthic algae and coarse particulate organic matter, provided by leaf litter, have diminished. With the deterioration of aquatic vegetation and the removal of snag and

Table 6. Numbers of aquatic macroinvertebrate taxa formerly collected in the Lower Rhine and Meuse rivers (palaeoecological and literature data; KLINK, 1989; VAN DEN BRINK *et al.*, 1990; and literature therein) and those recently collected in the main channels (FRANZEN, 1991; HOF, 1992; and literature therein), in comparison with those recently collected in their associated floodplain lakes (VAN DEN BRINK, 1990) -: no data available; *: number of species also presently occurring in floodplain lakes **: based on all groups; ***: based on groups for which historical information is available.

	Lower Rhine and Meuse rivers	Lower Rhine and Meuse channels	Floodplain lakes
	<1900	recent	recent
Tricladida	–	6	4
Oligochaeta	>10	23	19
Hirudinea	–	12	10
Bivalvia	12	16	21
Gastropoda	13	17	31
Araneida	–	0	1
Actinedida	–	3	50
Malacostraca	3	14	9
Ephemeroptera	25	7	7
Odonata	5	2	12
Plecoptera	14	3	0
Heteroptera	1	3	31
Coleoptera	7	2	61
Megaloptera	1	1	1
Neuroptera	–	1	0
Chironomidae	116	87	72
Simuliidae	6	1	0
Chaoboridae	–	0	4
Brachycera	–	3	19
Trichoptera	40	10	29
Lepidoptera	–	0	4
Total**	>253 (81)*	204 (125)*	385
Total***	253 (81)*	174 (112)*	297
Number of exotics	5 (2%)	25 (12%)	20 (5%)

Fish

Compared with the historical situation, the diversity of fish in the main channels has decreased (Table 7; Fig. 4). At present, only two fish species (6% of the total) collected in the Lower Rhine and Meuse rivers occur exclusively in the floodplain lakes and seven species (20%) exclusively in the main channel. Anadromous species, in particular, have declined over the years: Sturgeon (Acipenseridae: *Acipenser sturio* L.), Maifish (Clupeidae: *Alosa alosa* (L.))), Houting and Vendace (Salmonidae: *Coregonus oxyrinchus* (L.) and *C. albula* (L.)) and Atlantic Salmon (Salmonidae: *Salmo salar* L.)) have become entirely extinct from these rivers (Table 7; Fig. 4). Since these fish species were economically important, the long-term depletement of their stocks has been well documented. The decline of these anadromous species was already evident in the first half of the 19th century, when river engineering works resulted in the disappearance of specific spawning grounds, feeding biotopes, nursery areas and the obstruction and blockage of migrating routes (DE GROOT, 1989; VAN DEN BRINK *et al.*, 1990). During the 1960s-1970s, fish diversity was at its nadir (VAN DEN BRINK *et al.*, 1990), which coincided with low oxygen concentrations and high levels of micropollutants in the river water at that time (Table 2). The fish fauna is currently dominated by euryoecious Cyprinids, such as Bream (*Abramis brama* (L.)), White Bream (*Abramis bjoerkna* (L.)), Bleak (*Alburnus alburnus* (L.)) and Roach (*Rutilus rutilus* (L.)). Although still present in the Dutch rivers, the densities of the characteristic rheophilous Cyprinids, such as Barbel (*Barbus barbus* L.), Dace (*Leuciscus leuciscus* (L.)), Chub (*L. cephalus* (L.)) and Nase (*Chondrostoma nasus* (L.)) have been strongly reduced (VAN DEN BRINK *et al.*, 1990; VRIESE, 1992).

Pelagophils, lithophils and phytophils, and predominantly zooplanktivorous and zoobenthivorous fish species, have been reduced in diversity (Fig. 4). This means that deterioration of spawning and feeding habitats, and obstruction of migration routes are important causes for their decline.

Table 7. Numbers of fish species formerly collected in the Lower Rhine and Meuse rivers (VAN DEN BRINK *et al.*, 1990; VRIESE, 1992; and references therein), in comparison with those recently collected in the main channels (VAN DEN BRINK *et al.*, 1990; VRIESE, 1992; and references therein) and in their associated floodplain lakes (WILLINK and CUPPEN, 1993; DE LAAK *et al.*, 1994; VAN DEN BRINK, 1994, BUIJSE and VRIESE, 1996). *: number of species also presently occurring in floodplain lakes.

	Lower Rhine and Meuse rivers	Lower Rhine and Meuse channels	Floodplain lakes
	<1900	recent	recent
Petromyzontidae	3	3	2
Acipenseridae	1	0	0
Anguillidae	1	1	1
Clupeidae	2	1	0
Cyprinidae	19	17	18
Cobitidae	3	3	2
Ictaluridae	0	1	1
Siluridae	1	1	0
Esocidae	1	1	1
Osmeridae	1	1	1
Salmonidae	6	3	2
Gadidae	1	1	1
Gasterosteidae	2	2	2
Cottidae	1	1	1
Centrarchidae	0	1	1
Percidae	3	3	3
Pleuronectidae	1	1	0
Total number	46 (33)*	41 (35)*	36
Number of exotics	3 (7%)	7 (17%)	7 (19%)

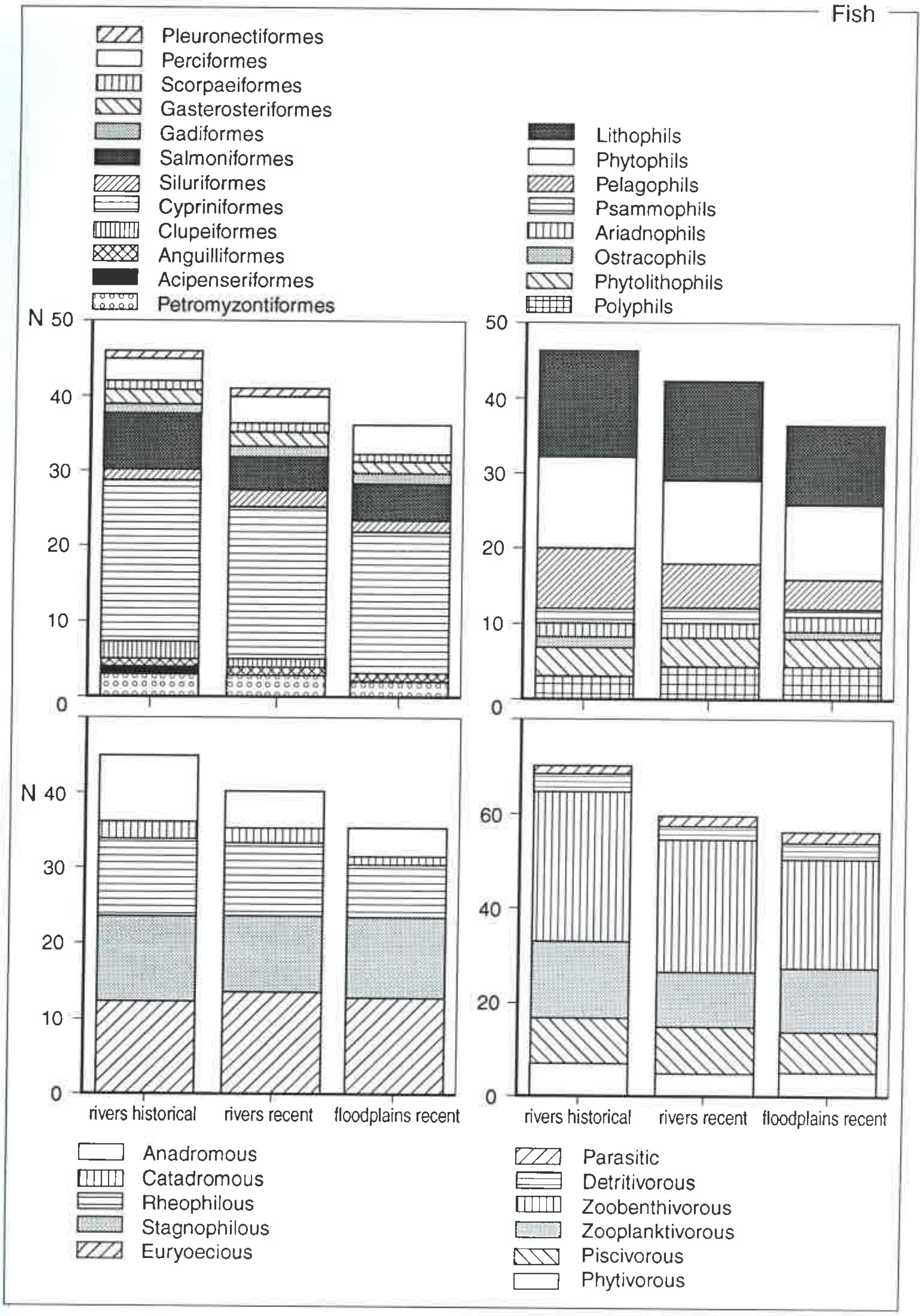

Fig. 4. Historical and recent biodiversity of fish in the Lower Rhine and Meuse river-floodplains. Above left: taxonomic groups, above right: reproduction guilds, below left: flow preference groups, below right: feeding guilds. N = number of taxa.

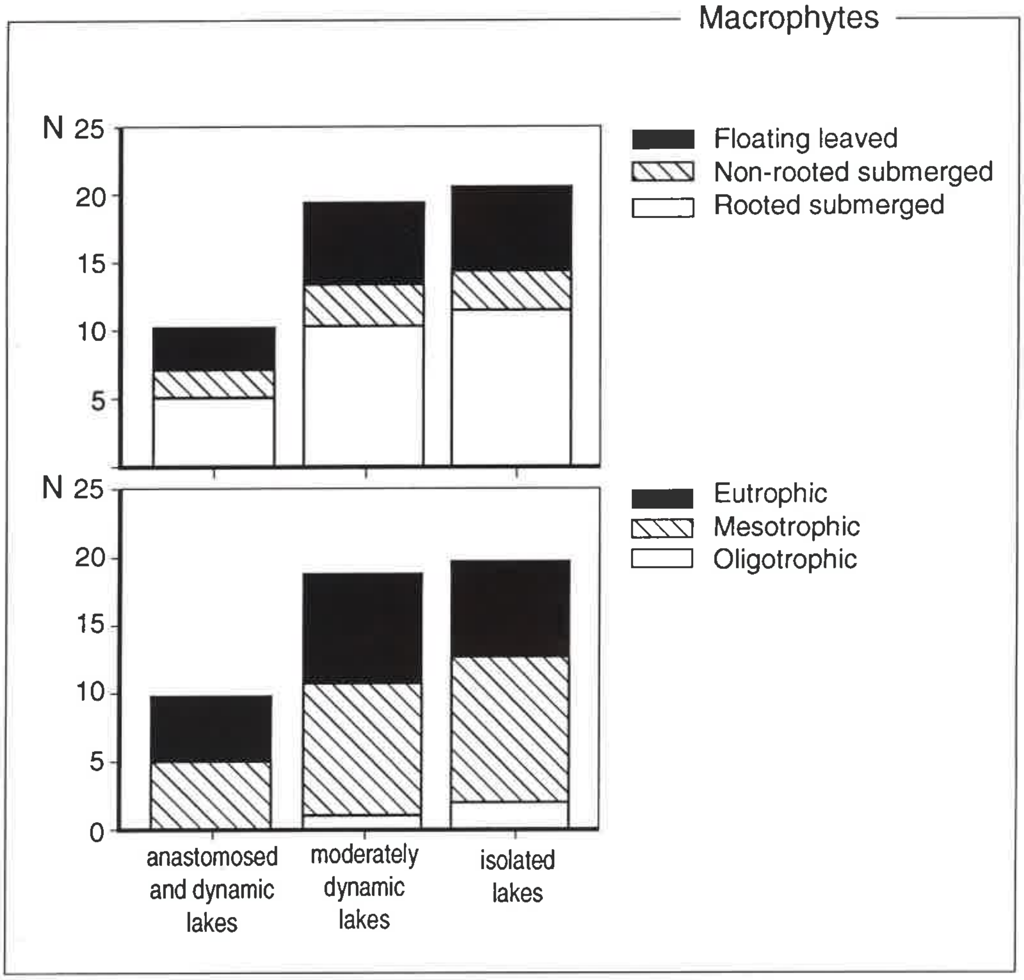

Fig. 5. Recent biodiversity of aquatic macrophytes along a hydrological gradient of lakes in the Lower Rhine and Meuse floodplains. Above: habitat groups, below: trophic groups. N = number of taxa.

The decline of taxonomical biodiversity is partly obscured by the presence of exotics. Most of them have been introduced to stop the decline of fish stocks (DE GROOT, 1985). However, only a few, like Carp (*Cyprinus carpio* L.) and Pikeperch (*Stizostedion lucioperca* (L.)) are successful and dominant.

ROLE OF RIVER-FLOODPLAIN CONNECTIVITY

The role of river-floodplain connectivity is discussed by comparing the biodiversity of aquatic biota in categories of floodplain lakes with a different hydrology. These categories are adapted from earlier typological studies on macrophyte, plankton and macroinvertebrate species composition and abundance of 100 floodplain lakes (VAN DEN BRINK, 1990, 1994 and references therein). Three categories of floodplain lakes are distinguished:

A. very dynamic floodplain lakes, which are in open connection with the main channel for more than 20 days per year on average; this category includes anastomosed channels and lakes (*e.g.* sand and gravel pits) which are permanently connected with the main channel,

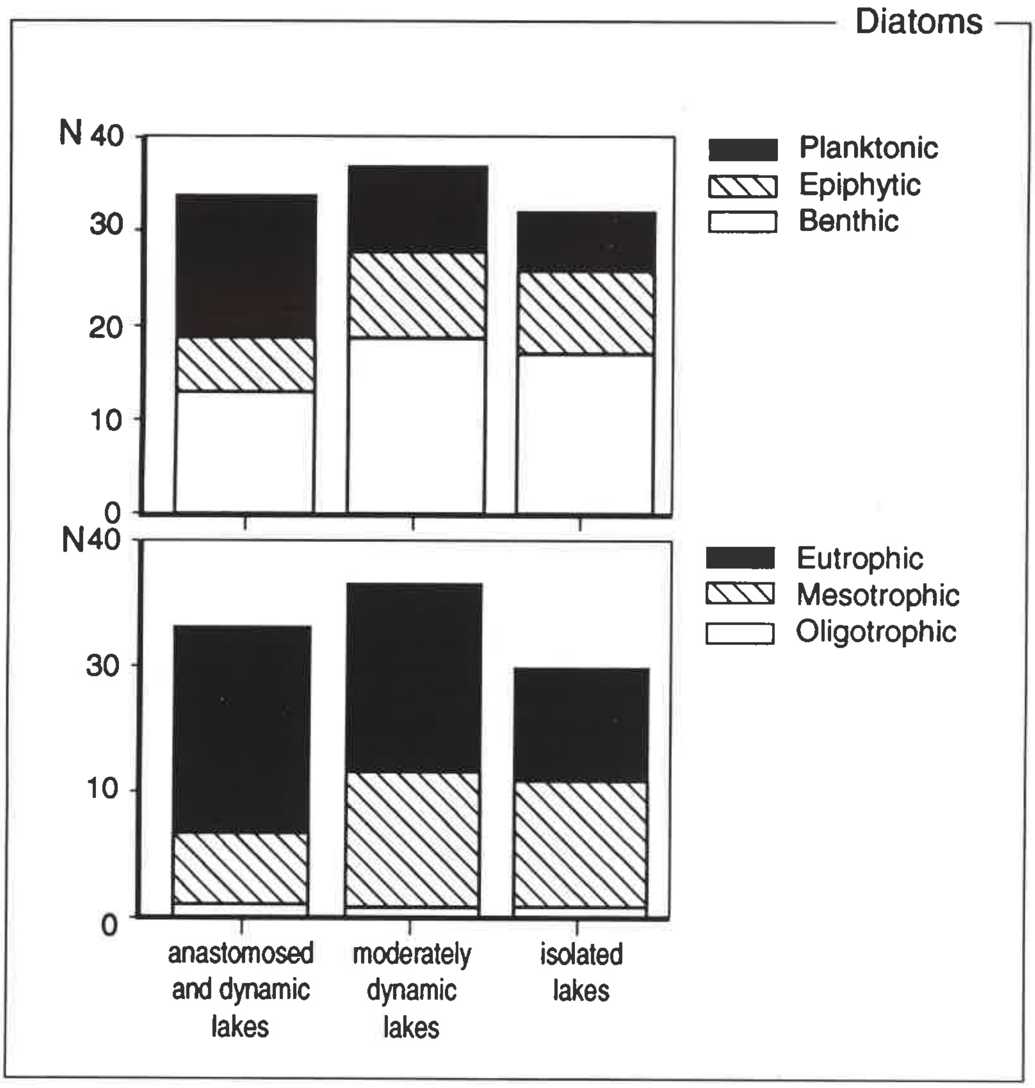

Fig. 6. Recent biodiversity of diatoms along a hydrological gradient of lakes in the Lower Rhine and Meuse floodplains. Above: habitat preference groups, below: trophic groups. N = number of taxa.

B. moderately dynamic floodplain lakes, which are in open connection with the main channel via floods during 20 or less days a year on average,

C. isolated floodplain lakes, which are situated outside the active floodplain and which are influenced by the main channel via seepage through the main dike.

For fish, category A has been divided into very dynamic disconnected lakes and anastomosed lakes, according to typological studies in other European river systems (*e.g.* SCHIEMER, 1988; COPP and PENÀZ, 1988).

Aquatic macrophytes

The biodiversity of aquatic macrophytes in floodplain lakes is lowest in very dynamic and anastomosed lakes (Fig. 5). Species with floating leaves, such as Nymphaeaceae and Lemnaceae, but

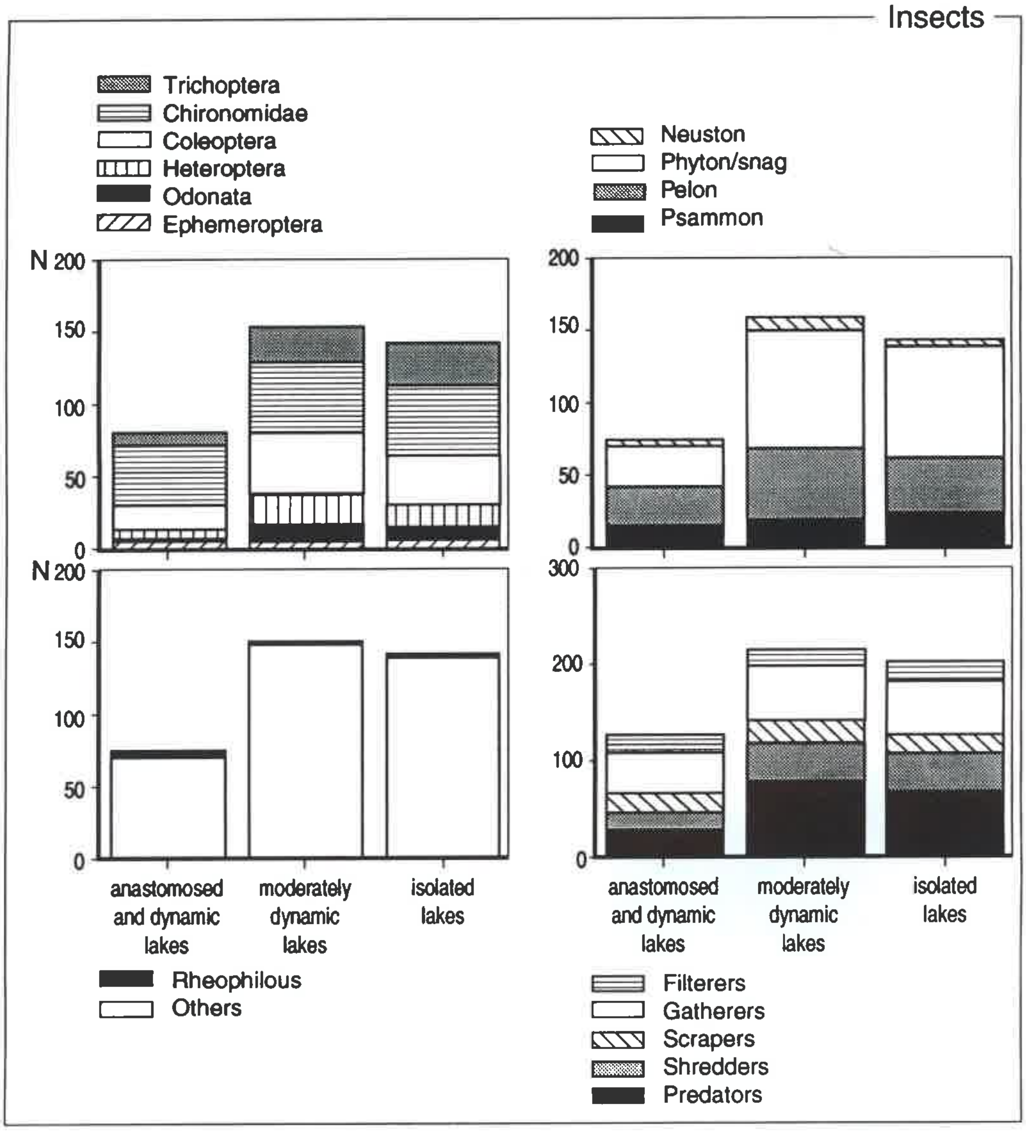

Fig. 7. Recent biodiversity of aquatic insects along a hydrological gradient of lakes in the Lower Rhine and Meuse floodplains. Above left: taxonomic groups, above right: habitat preference groups, below left: flow preference groups, below right: functional feeding groups. N = number of taxa.

also rooted submerged species, such as several Potamogetonaceae, decrease in diversity with increasing degree of connectivity. Since the biodiversity of floating leaved species, which are adapted to turbid waters, and submerged species, which need clear water, both decline with increasing flood dynamics, the poor diversity in very dynamic lakes can be attributed to hydro-dynamics (flood frequency, flooding period, current velocity during through-flow), morphodynamics (erosion and sedimentation) as well as to water quality parameters (N, P, turbidity). Regulation and normalisation of the Lower Rhine and Meuse and their tributaries have resulted in an unnaturally rapid run-off of rainwater. This causes erratic and high water-level fluctuations, sometimes even during the growth

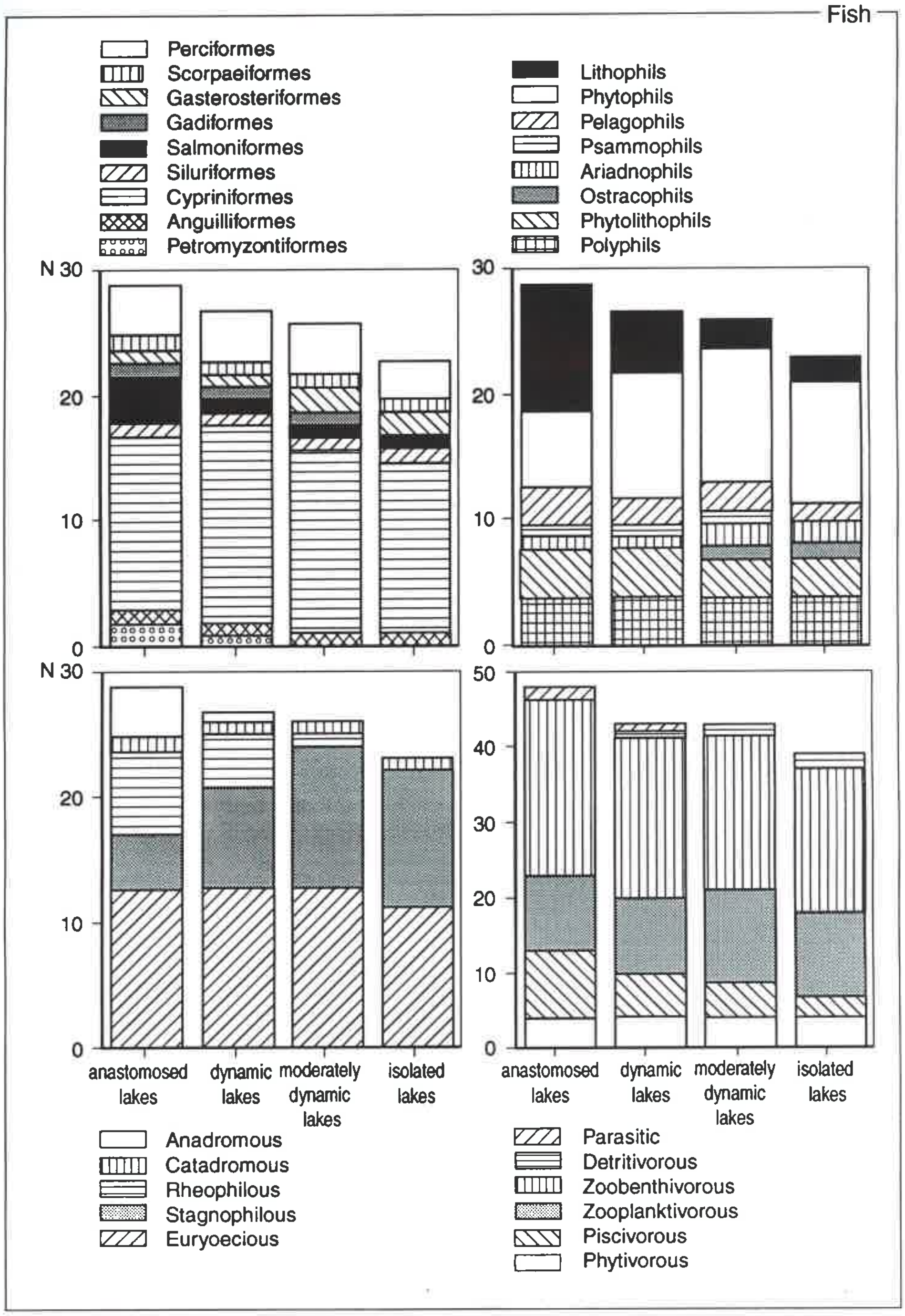

Fig. 8. Recent biodiversity of fish along a hydrological gradient of lakes in the Lower Rhine and Meuse floodplains. Above left: taxonomic groups, above right: reproduction guilds, below left: flow preference groups, below right: feeding guilds. N = number of taxa.

season (BROCK *et al.*, 1987). The extremely high intensity of shipping traffic causes strong wave action in anastomosed lakes, making the sandy substrate unstable and unsuitable for the settlement of aquatic macrophytes. The strong wave action also causes high turbidity in such lakes, due to resuspension of clay particles, which hinders the development of submerged macrophytes. Besides physical effects, the present high nutrient levels in the Lower Rhine and Meuse are probably also responsible for the low diversity of submerged macrophytes in the very dynamic lakes. The diversity of oligotrophic and mesotrophic species decrease with increasing river dynamics (Fig. 5). Eutrophic and sometimes hypertrophic conditions, causing prolonged algal blooms, in anastomosed and very dynamic floodplain lakes prevent the occurrence of these species there (VAN DEN BRINK *et al.*, 1993).

Plankton

The species richness of diatoms varies only moderately over the lateral dimension of the floodplain, although the functional groups show a clear shift (Fig. 6). The diversity of planktonic species is found to increase with increasing river dynamics, whereas the diversity of epiphytic and benthic species is found to decrease. This pattern corresponds with the pattern of macrophyte diversity (Fig. 5). The dominant planktonic species in the connected floodplain lakes are the same as those in the main channels (VAN DEN BRINK *et al.*, 1994). Species indicating eutrophic conditions are more diverse in dynamic and anastomosed lakes, whereas species indicating mesotrophic conditions are more numerous in isolated lakes (Fig. 6). The levels of nutrients found in these lakes show a similar pattern (VAN DEN BRINK *et al.*, 1993, 1994).

Aquatic macroinvertebrates

Biodiversity of aquatic insects is lowest in anastomosed and dynamic floodplain lakes (Fig. 7). Trichoptera, Coleoptera, Heteroptera and Odonata, in particular, show a low diversity in the most dynamic lakes. The numbers of rheophilous taxa are extremely low in all types of lakes, which are governed by semi-stagnant conditions. The biodiversity of species characteristic of habitats provided by vegetation, snag and organic detritus is lowest in the most dynamic lakes, which also have a low abundance and diversity of macrophytes (Fig. 5). Also the diversity of shredders and predators is found to be reduced in the most dynamic floodplain lakes (Fig. 7), and can be related to the sparse vegetation and the high turbidity of the water (VAN DEN BRINK and VAN DER VELDE, 1991). The dominant species found in the very dynamic and anastomosed lakes are the same as those recorded from the sandy banks in the semi-stagnant downstream rivers areas (VAN DEN BRINK, 1994).

Fish

In contrast with the other aquatic taxa, biodiversity of fish is highest in anastomosed lakes and lowest in isolated flood-plain lakes (Fig. 8). Several studies have reported the importance of anastomosed lakes for riverine fish as refuge zones during periods of high river discharge, as foraging areas and nursery grounds. They also act as reservoir sites, from which the river may be restocked after periods of heavy pollution (SCHIEMER, 1988; AMOROS and ROUX, 1988; JUNK *et al.*, 1989).

Along the Lower Rhine and Meuse, anadromous taxa, like Petromyzontiformes, such as Sea lamprey (*Petromyzon marinus* L.) and River lamprey (*Lampetra fluviatilis* (L.)) and Salmoniformes, such as Sea trout (*Salmo trutta trutta* L.) and Smelt (*Osmerus eperlanus* (L.)) and rheophilous species such as Dace (*Leuciscus leuciscus*), Chub (*L. cephalus*) and Nase (*Chondrostoma nasus*) are incidentally found in anastomosed lakes, but not found at all in moderately dynamic and in isolated lakes. Although anadromous and rheophilous species decrease in diversity, stagnophilous species increase in diversity with decreasing river dynamics (Fig. 8). A similar distributional pattern over the lateral dimension of the floodplain has also been observed in other river systems, such as the R. Danube (SCHIEMER *et al.*, 1991), the Upper R. Rhône (COPP and PENÁZ, 1988) and the German Lower Rhine (BÖVING, 1981), indicating a general pattern in European temperate rivers.

Reproductive guilds show that lithophils decrease, whereas phytophils increase in diversity with decreasing river dynamics (Fig. 8). This observation is in accordance with the higher diversity of aquatic macrophytes in low dynamic lakes, and the presence of gravel in the main channels and tributaries of the Lower Rhine and Meuse. In the Upper Rhône, COPP and PENÁZ (1988) found a similar distributional pattern for reproductive guilds. When converted to feeding guilds it appears that piscivorous and parasitic fish decrease, whereas zooplanktivorous species increase in diversity with decreasing river dynamics (Fig. 8). This might be related to the high fish production in connected lakes (AMOROS and ROUX, 1988) and the high zooplankton diversity in isolated lakes (VAN DEN BRINK *et al.*, 1994).

Table 8. Synoptic table showing the main causes of biodiversity losses of aquatic macrophytes, diatoms, aquatic insects and fish.

cause	macrophytes	diatoms	insects	fish
river regulation	*	*	*	*
impoverished water quality	*	*	*	*
increased shipping traffic	*	*	*	*
removal of snag		*	*	*
loss of floodplain forests			*	*
migration barriers				*

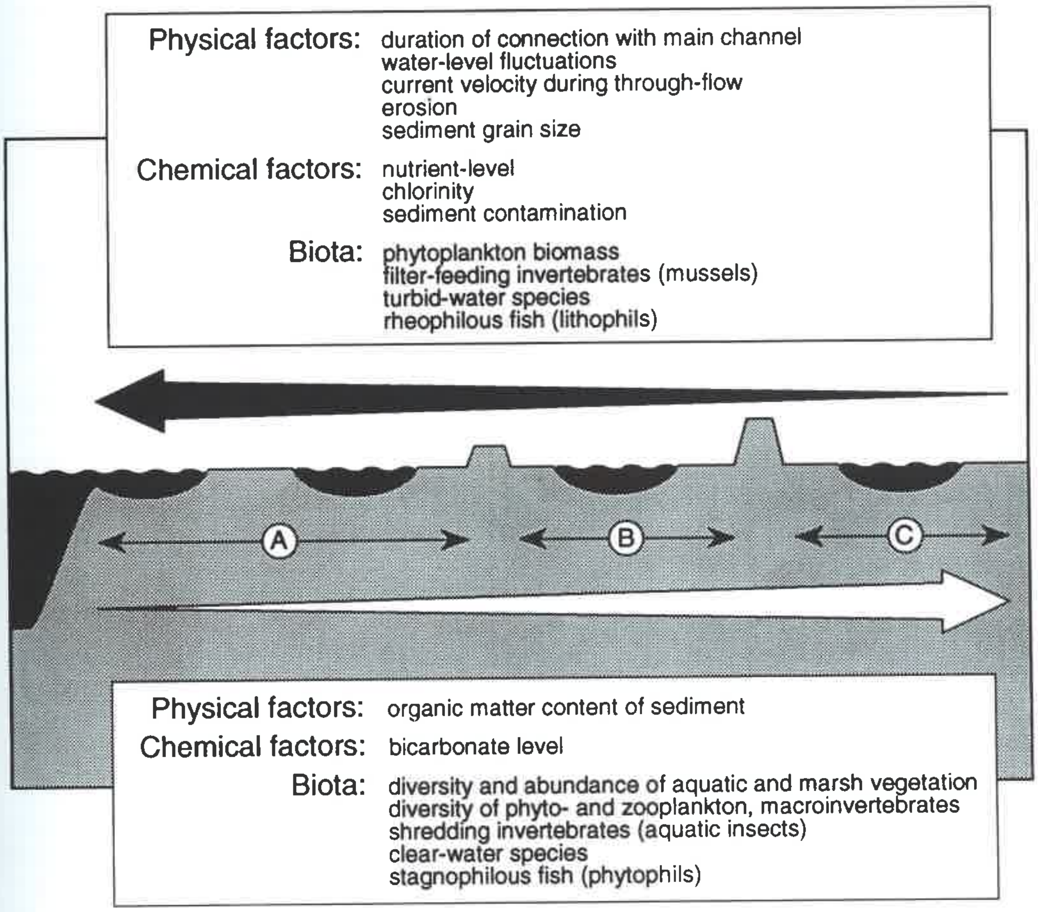

Fig. 9. Schematic view of transversal zonation patterns in Lower Rhine and Meuse floodplain lakes and the directions of changes in physical, chemical and biotic parameters. A = anastomosed and very dynamic lakes; B = moderately dynamic lakes; C = isolated lakes, outside active floodplain.

CONCLUSIONS AND RECOMMENDATIONS

In the Lower Rhine and Meuse, the present species richness of aquatic macrophytes, plankton, macroinvertebrates and fish shows a strong reduction when compared with historical references. By translating structure into function, relating species to trophic groups, habitat groups, flow preference groups and feeding groups, it becomes clear that this reduction has been caused by the destruction of many typical riverine habitats via the regulation and normalisation of the main channels and their tributaries, by water quality deterioration, by intensification in shipping traffic and by blockage of migration routes (Table 8).

The role of connectivity between main channel and floodplain lakes for the diversity of aquatic biota is different for the various taxa. A clear transversal zonation has been found with regards to species, biodiversity, functional groups and abiotic conditions (Fig. 9). This emphasises the importance of variation in hydrology, substrates, and physico-chemical parameters for a diverse aquatic flora and fauna in the floodplain lakes. Since biodiversity of aquatic macrophytes, zoo- and phytoplankton and aquatic macroinvertebrates in anastomosed channels is very reduced as compared with hydrologically more isolated lakes, a simple reconnection of moderately dynamic floodplain lakes with the main channels will result in a species loss within these biota. On the other hand, anastomosed lakes are important for fish which will find refuge and feeding grounds there.

The floodplain lakes as a whole contribute enormously to the total biodiversity of the entire river system. However, the lotic component of aquatic biota, rheophilous invertebrates and fish, which has been reduced most dramatically in the rivers Rhine and Meuse over the years, is hardly found in the floodplain lakes, owing to the semi-stagnant conditions there. So, for the re-development of a high diversity of all groups of aquatic biota, it is absolutely necessary that the natural variety in flow velocities, flood frequencies and flooding periods, geomorphological textures, water quality and nutritional resources and habitats will be restored in the river-floodplains. This variety can only be guaranteed when natural hydrological, geomorphological and ecological processes are re-established, and water quality improves further. The redevelopment of active secondary channels, accompanied by floodplain forests, is required to restore the most typical riverine habitats and biota.

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