How fish benefit from floodplain restoration

along the lower River Rhine

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R.E. Grift

Proefschrift

ter verkrijging van de graad van doctor

op gezag van de rector magnificus

van Wageningen Universiteit

Prof. dr. ir. L. Speelman,

in het openbaar te verdedigen

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des namiddags te half twee in de aula.

Hetzelfde water

Hetzelfde water dat met stormgejoel
En helse vlagen komt en wordt gevreesd,
Is ook het water dat, sereen en koel
De mensen van hun kwellingen geneest.

Ons lage land aan zee is een groot lijf
Met aderen, aorta's, bloedkanalen
En al wat zich vertakt – een druk bedrijf
Dat regelt dat we pijnloos ademhalen.

Geen netwerk dat je ongestraft verbouwt.
Het overstroomt bij elke prop meteen.
Wordt het in één arterie te benauwd,
Dan spatten duizend haarvaten uiteen.

Elk lichaam is een tijdelijke spons.
Bepleister het geval met poederdons
En kalk, van top tot teen, dan wordt dat lijf
Sneller dan je tot tien telt droog en – stijf.

Verwen de stroom die door je lichaam stuwt.
Laat bloed, bekwaam getemd, de vrije loop.
Bedenk – wie van de norse buien gruwt –

Dat ook een hart niet wordt geamputeerd
Omdat het breken kan. Wie water keert
Omdat het aanvalt doodt de biotoop

Van al wat weerloos is en wordt bedreigd.
Het lijkt wel op een gordiaanse knoop.

Het water zelf intussen, daalt en stijgt.

Gerrit Komrij.

Abstract

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The objectives of this study were to test the beneficial value of newly created secondary channels and reconnected oxbow lakes along the lower River Rhine for fish and to give advice on position, shape and character of future water bodies. These water bodies should contribute to the rebuilding of the population of rheophilic cyprinids that are endangered due to embankment and normalization of the Rhine. The functions these water bodies fulfil during the life cycle of distinct fish species, were inferred from the description of patterns of presence of fish in time and space in 25 floodplain water bodies (secondary channels, oxbows, lakes). In all water bodies, depth, flow velocity and the presence of vegetation determine the fish community present. Secondary channels and reconnected oxbow lakes do have a beneficial value for the riverine fish community. They function as nursery areas for all rheophilic cyprinids (e.g. *Barbus barbus*, *Leuciscus idus* and *Gobio gobio*). Secondary channels probably also function as spawning areas for *L. idus* and *G. gobio* but not for lithophilic species (*B. barbus*, *Leuciscus leuciscus*) since suitable substrate lacks. Eurytopic species (*Abramis brama*, *Rutilus rutilus* and *Stizostedion lucioperca*) use all types of floodplain water body to reproduce. For *A. brama*, isolated turbid clay-pits form important source areas from which juveniles recruit to the main channel during floods. The dominance of eurytopic species in the lower Rhine is caused by the large area of suitable spawning and nursery areas for these species relative to those of rheophilic species. For limnophilic species (*Tinca tinca*, *Rutilus erythrophthalmus*) suitable habitat (vegetated lakes) is also scarce and should be preserved. Within plans on flood protection, floodplain management should focus on increasing the number of secondary channels and on restoring the natural interaction between the river and its floodplains.

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Photo 1. The lower River Rhine near Wageningen.

Chapter 1

Introduction

1.1 Changing views on the importance of the River Rhine

Until the 1970s, the River Rhine and its floodplains were used as a resource for drinking water, fishing, agriculture, transport, industry and recreation without regarding ecological values. The Rhine was canalized and its discharge regulated: water quality and habitat diversity for the riverine fauna decreased dramatically which led to a poor faunistic diversity. River engineering started far before floodplain ecology and the relationship between the main channel and floodplain were sufficiently understood. At present, however, decades of experience with rivers subjected to extended river regulation works indicate serious negative side effects on both flood control and the environment (Junk, 1999). In the 1970s, plans were realized to improve the water quality and in the 1990s, ideas arose that flood protection should no longer be pursued by heightening the dykes, but by coupling the excavation of floodplains to nature development. At present, the Rhine is still an important resource for humans, but its ecological values are more important than up to the 1970s.

The importance of rivers as valuable resources has led to intense use of river basins and modifications to the courses of many rivers. Rivers have always attracted humans to settle near them and many large cities and important industries are located near to large rivers. The River Rhine, for example, is the largest river (Table 1.1) and its catchment area (185,000 km^2; Figure 1.1) the most densely populated and industrialized river basin in Western Europe, with more than 54 million inhabitants and about 10% of the world's chemical industries (Cals *et al*., 1998). Flowing for 1,320 km through the economic heartland of Western Europe, the Rhine carries more traffic than any other river in Europe. It has made Rotterdam the biggest seaport anywhere in the world and Duisburg the biggest inland port in Europe. 165,000 ships pass the Dutch/German border each year, transporting about 150 millions tons of freight. Apart from its importance for navigation, the Rhine is also important for public water supply: about 5 to 15% of its mean annual discharge is used for agriculture, industry and cooling of power plants (Garritsen *et al*., 2000). Other water-related public interests include recreation, fisheries, nature and, above all, flood protection.

Apart from providing resources and being functional, rivers also pose danger for humans. Discharge usually varies strongly, even over short periods of time, and sometimes leads to flooding of adjacent land. In the Netherlands, life is closely attuned to the danger of flooding since the land comprises the delta of the Rivers Rhine, Meuse and Schelde and a large part of the country lies below sea level. Dyke bursts from both the rivers and the sea pose a constant danger of flooding. In 1926, high discharges of the Rivers Rhine and Meuse breached some river dykes inundating large areas, and in 1995 heavy rainfall during several weeks produced high discharges which threatened

the dykes. The authorities were forced to evacuate more than 250,000 people within 36 hours. In 1953, a tremendous storm surge struck the southwestern coast of the Netherlands. Many dykes breached, thousands of hectares were inundated and over 1,800 people drowned (Huisman *et al.*, 1998).

Table 1.1 The ten largest rivers in Europe (Middelkoop & Van Haselen, 1999).

River	Length (km)	Drainage area (km^2)	Discharge at river mouth (m^3 s^{-1})
Volga	3,550	1,440,000	8,400
Danube	2,850	817,000	6,400
Wisla	1,068	194,000	1,000
Rhine	1,320	185,000	2,300
Oder	866	119,000	530
Loire	1,012	115,000	400
Rhône	812	98,000	1,700
Po	676	75,000	1,500
Meuse	935	36,000	230
Tiber	393	16,000	230

The Rhine, like most other rivers in temperate regions, has been greatly modified to facilitate navigation, produce electricity, facilitate agriculture in the floodplains and to protect the hinterland from flooding. The course of the river has been modified, floodplains disconnected from the main channel, dykes built and estuaries closed off from the sea. Moreover, water quality decreased dramatically due to industrialization and increasing population density in the basin. Modification of the main channel and its floodplains led to a loss of essential habitat for many ecological groups, including fish. Since many of the fish species that are indigenous to the lower Rhine utilize a wide range of riverine conditions over their life cycles, they are very susceptible to deterioration of both habitat and water quality. In the 1970s, however, the idea that the Rhine was only a shipping route and posed danger to humans changed, and it was realized that the environmental conditions had to improve. Above all, the current policy on river management aims at increased safety against floods, but recent insights in ways to increase safety, by coupling floodplain excavation to the development of nature areas, were implemented and at several locations, secondary channels were created and oxbow lakes reconnected to the main channel permanently. In this thesis, the beneficial value of these water bodies for the riverine fish community is evaluated.

1.2 Deterioration of the River Rhine habitat

The loss of habitats that are important for the ecological functioning of the lower Rhine occurred in three major steps: in the 15th century when the embankment of

floodplains was completed, in the 19th century when major regulation works were completed and in the 20th century when the estuaries were disconnected from the sea. The first recorded historical evidence of human impact dates back to the Roman era but it may be assumed that the lower Rhine retained an almost natural character until the early Middle ages (Van Urk & Smit, 1989).

Figure 1.1. Drainage area of the River Rhine with the study area (River Waal) indicated.

In its natural condition, the Rhine was dynamic and the course of the main channel changed continuously due to the natural morphological processes of erosion and deposition. Within the wide and shallow main channel, islands and sandbanks provided a diversity of habitats with a large variation in flow velocities and depths. The area inundated during floods must have been tens of kilometres wide, bound only by the ridges of hills formed in the ice age (Figure 1.2[a]; Van Urk & Smit, 1989). With the main channel, floodplains formed an integral part of the whole. Due to the gradual transition between water and land, floodplains were inundated frequently and were highly productive areas that were important nurseries for fish.

Figure 1.2. Changes in the riverine landscape. The lines between the ridge and the winter dyke are hatched to indicate that the width of the original floodplain is not at scale; it was up to ten times wider than indicated.

Early human modifications of the main channel and the adjacent floodplains were not only typical of the Rhine. Almost all European rivers have been subjected to modification from relatively early in the history of the continent. In the Roman era, river basins were locally deforested and streams slightly modified and canalized for water power. In the lower Rhine area for example, the Romans created the 'Drusus canal', which was an artificial connection between the Rivers Rhine and IJssel (Van Urk & Smit, 1989).

In the Middle Ages, deforestation of river basins in Europe progressed further and in some lower order streams, weirs and dams were built for waterpower. In larger streams, human interference comprised bank control and the resulting siltation led to increased meandering and braiding of the main channel. Around 1450 the Netherlands lost the greater part of its natural floodplains when the embankments along the lower River Rhine were completed (Figure 1.2[b]).

During the industrial revolution (1700-1800), agriculture in river basins intensified which sometimes led to complete deforestation. Floodplains were used more intensively and were embanked on the riverside to facilitate their use for agricultural purposes in summer (Cowx & Welcomme, 1998). In the Netherlands, from 1600 to 1850, embanked floodplain sections were enlarged for cultivation by lateral accretion, aided by the building of groynes and planting of willows (Middelkoop, 1997). As a result, the area inundated during floods was confined to a narrow zone a few kilometres wide along each side of the river. In a 32 km stretch of the Rhine, the area of the summer river bed, which inundates frequently, was reduced drastically: from 42 km^2 in 1780 to 28 km^2 in 1830 (Table 1.2; Maas *et al.*, 1997). Sedimentation of silt concentrated in this narrow zone and, as a result, the embanked floodplains were raised in height (Van Urk & Smit, 1989).

Table 1.2. Historical change of morphology of a stretch of the River Rhine (Waal branch, river km 884.5-916.3; between the cities of Nijmegen and Tiel) from 1780-1990. Habitats in the summer bed are positioned between the main channel and levees or summer dykes. Habitats in the winter bed are positioned between levees or summer dykes and the winter dyke; data from Maas *et al.* (1997).

Position	Habitat	Year		
		1780	1830	1990
Total surface (km^2)		**46.5**	**47.1**	**45.3**
In summer bed	Deep river bed	13.6	15.3	13.5
	Gravel bank	0.2	0.0	0.0
	Sand bank	1.7	0.6	0.0
	Secondary channel	0.5	1.6	0.0
	Natural levee	0.5	0.7	2.1
	Herbaceous vegetation	21.2	8.8	6.8
	Connected oxbow	1.7	0.6	0.5
	Oxbow lake	2.8	1.0	0.8
	Floodplain lake	0.1	0.1	4.3
Total summer bed		**42.3**	**28.8**	**28.0**
In winter bed	Floodplain	3.7	14.4	12.8
	Oxbow lake	0.4	3.6	2.8
	Floodplain lake	0.0	0.3	0.4
	Built-up high water free	0.0	0.0	1.3
Total winter bed		**4.1**	**18.3**	**17.3**

In the 19th century, throughout Europe, large rivers were straightened and deepened for navigation purposes. In the German part of the Rhine, river modification followed the ideas of Tulla to confine the stream to one main channel the depth of which should maintain itself automatically (Lelek, 1989). In the Netherlands, the Rhine was normalized to prevent formation of ice jams, which had caused dyke breaches in the past, and to improve navigation (Middelkoop, 1997). Sand bars were removed, channel width reduced and river banks were protected from erosion by regular arrays of groynes (Van Urk & Smit, 1989; Middelkoop, 1997; Cals *et al.*, 1998). By 1830, gravel banks had disappeared and the area of frequently inundated herbaceous vegetation had decreased. It decreased from 21 km^2 in 1780 to 9 km^2 in 1830 in the 32 km stretch of the Rhine for which the historical development of habitat was investigated (Table 1.2).

In the 20th century, European rivers deteriorated further and most were extensively modified. Main channels were deepened and straightened or sometimes reduced to concrete or earthen-banked channels only (Cowx & Welcomme, 1998). Besides decreased connectivity in the lateral direction, between main channel and the adjacent floodplains, the construction of dams and enclosure of the rivers from the sea terminated connectivity between upstream areas and the estuaries. In the Netherlands, in the 1950s three weirs were constructed in one of the three branches of the lower Rhine (River Nederrijn/Lek). In the 1980s enclosure of the estuaries from the sea, to act as flood protection, was completed.

Due to the incision of the river bed and aggradation of the floodplains, the natural, gradual connection between the main channel and its floodplains was lost. Natural water bodies with a permanent opening to the river were disconnected from it and at present the floodplains are more rarely, but abruptly when it happens, inundated than before embankment. Moreover, the original riverbed, characterized by sand and gravel beds, has cut down and nowadays has steep shorelines and low habitat variability (Buijse & Vriese, 1996; Middelkoop, 1997; Cals *et al.*, 1998). The resulting landscape is a main channel with a fringe of floodplain and little variation in frequency and duration of flooding. Remote lakes and floodplains that were seldom flooded are completely disconnected from the river by winter dykes, except for groundwater flow (Figure 1.2[c]). As a consequence, the aquatic ecosystem of the Rhine is fragmented during most of the time. It comprises the main channel, with its poor habitat diversity and strong hydrological dynamics, deep harbours and connected sand-pits, and floodplain lakes that are isolated from the main channel. The aquatic habitats in the floodplains are only connected during floods.

1.3 Deteriorating water quality

In addition to a severe impact on the morphology of river basins, humans had a tremendous effect on the water quality of European rivers, which reached its minimum in the Rhine in the 1960s. During the industrial revolution, population size in Western Europe increased rapidly. In the 19th century, rivers were used for waste water disposal and locally, pollution sometimes became severe (Cowx & Welcomme, 1998). Water quality in the Rhine deteriorated as a consequence of industrial, agricultural and household waste water disposal (Wolff, 1978). By 1880, the quality of salmon *Salmo salar* from the Rhine for example, was classified by whether it smelled of phenol, which was mainly used as a disinfectant (Lobregt & Van Os, 1977). In the 20th century, industrialization proceeded and after the Second World War, industrial activities in Western Europe increased rapidly and large quantities of untreated waste water heavily polluted the Rhine. As a consequence, dramatic diurnal fluctuations in dissolved oxygen levels occurred and the mean and minimum annual oxygen concentrations reached their all time low (Figure 1.3), causing unprecedented mass kills of fish during periods of low discharge. Toxic substances wiped out several aquatic species. As a result of the use of the Rhine as a source of cooling water, mean water temperature increased significantly, from about 11°C in the early 1900s to almost 14°C in the 1990s (Figure 1.3; Huisman *et al.*, 1998). Heavy metals and chlorinated hydrocarbons made the consumption of fish hazardous (Lelek, 1989). Press and public began to designate the Rhine as the open sewer of Europe.
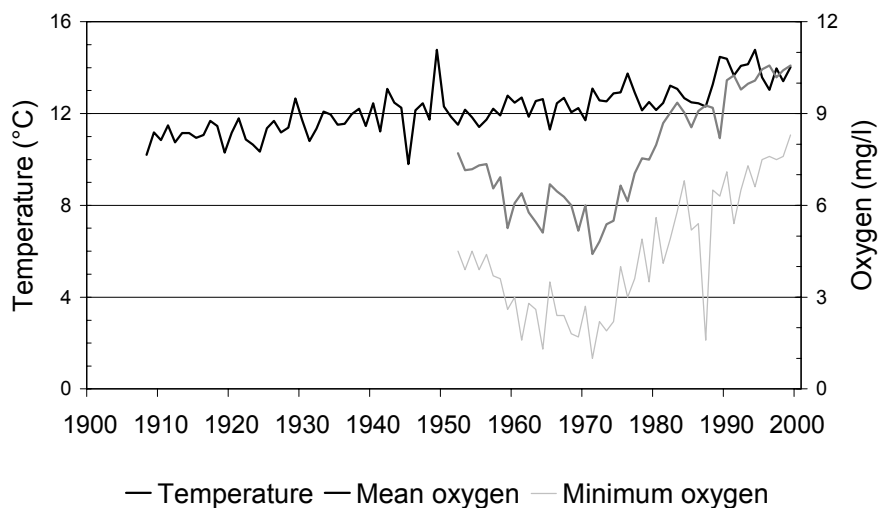

Figure 1.3. Annual mean water temperature and mean and minimum oxygen content of the River Rhine (Lobith; measured at 8.00 am).

Already in 1950, the Rhine states (Switzerland, Germany, France, Luxembourg and the Netherlands) had created the International Commission for the Protection of

the Rhine (ICPR) which started to investigate the quantities and types of pollution (Wieriks & Schulte-Wülwer-Leidig, 1997). It took until 1972, however, before the efforts of the ICPR had any effect on the water quality (Huisman *et al.*, 1998). Treatment measures for waste water from industries and municipalities were realized and the pollution loads decreased (Wieriks & Schulte-Wülwer-Leidig, 1997). By 1980, oxygen contents had exceeded the level of the 1950s, from when they were measured (Figure 1.3).

In November 1986, a fire broke out at the Sandoz Chemical Industries near Basel, Switzerland, which resulted in the discharge of fire extinguisher fluids and water, polluted with a variety of toxic chemicals, into the Rhine. Consequently, pollutants flowed downstream and caused the death of almost all aquatic life as far downstream as the Loreley Cliff near Koblenz, 430 km downstream. The Sandoz incident triggered a wave of publicity in all the Rhine states and, within ten months, three ministerial conferences resulted in the Rhine Action Programme (Heil, 1990). In 1987, the Rhine Action Programme accelerated existing programmes to enhance the water quality and set out clear goals to be reached in the year 2000: the ecosystem should be improved to such an extent that higher species such as salmon and sea trout *Salmo trutta* again became indigenous, the production of drinking water should be guaranteed for the future and the pollution of river sediments should be reduced to such an extent that at any time sludge may be used for land fill or be dumped at sea (Wieriks & Schulte-Wülwer-Leidig, 1997). The Rhine Action Programme did lead to a better water quality and at present, water quality is no longer limiting ecological rehabilitation (Admiraal *et al.,* 1993).

1.4 Deteriorating fish community

In the 20th century, the deterioration of physical habitat and the decline in water quality, led to a strong decline in the faunistic diversity of the Rhine (Lelek, 1989; Van den Brink *et al.*, 1990). At present, species diversity of aquatic macrophytes, macro-invertebrates and fish is poor (Van den Brink *et al.*, 1996).

The low habitat diversity, blocked migration routes and poor water quality were fatal for cyprinid and diadromous rheophilic fish species (Table 1.3) which require a specific array of habitats during their life cycles. According to Van den Brink *et al.* (1990), 40 fish species occurred in the Lower Rhine around 1900 which number decreased to 28 in the early 1970s, after which it increased to 36 species in the late 1980s. Especially the number of rheophilic and diadromous species had decreased (Van den Brink *et al.*, 1990).

Table 1.3. Occurrences around 1890 and from 1992-1996 of fish species occurring in the lower Rhine. Classification of the reproductive guilds according to Schiemer & Waidbacher (1992) and Quak (1994).

Guild	Species	Family	English name	Dutch name	1890[1]	1996[2]
Rheophilic A	Acipenser sturio (X)	Acipenseridae	sturgeon	steur	+++	0
	Alosa alosa (X)	Clupeidae	allis shad	elft	+++	+
	Barbatula barbatulus	Cobitididae	stone loach	bermpje	++	+
	Barbus barbus (E)[3]	Cyprinidae	barbel	barbeel	+++	++
	Chondrostoma nasus (E)	Cyprinidae	nase	sneep	+++	++
	Coregonus lavaretus	Salmonidae	common whitefish	grote marene	+	0
	Coregonus oxyrinchus (X)	Salmonidae	houting	houting	+++	0
	Cottus gobio	Cottidae	bullhead	rivierdonderpad	++	++
	Lampetra fluviatilis (V)	Petromyzontidae	river lamprey	rivierprik	+++	++
	Leuciscus cephalus (V)	Cyprinidae	chub	kopvoorn	+++	++
	Leuciscus leuciscus (V)	Cyprinidae	dace	serpeling	+++	++
	Petromyzon marinus (E)	Petromyzontidae	sea lamprey	zeeprik	+++	++
	Salmo salar (X)	Salmonidae	salmon	zalm	+++	+
	Salmo trutta (V)	Salmonidae	sea trout	beekforel/zeeforel	+++	++
	Thymallus thymallus	Salmonidae	grayling	vlagzalm	++	0
Rheophilic B	Aspius aspius[4]	Cyprinidae	asp	roofblei	0	++
	Cobitis taenia	Cobitididae	spined loach	kleine modderkruiper	++	++
	Gobio gobio	Cyprinidae	gudgeon	riviergrondel	+++	++
	Leuciscus idus	Cyprinidae	ide	winde	+++	++
	Lota lota	Gadidae	burbot	kwabaal	+++	+
Rheophilic C	Alosa fallax (X)	Clupeidae	twaite shad	fint	+++	0
	Osmerus eperlanus	Osmeridae	smelt	spiering	+++	+
	Platichthys flesus	Pleuronectidae	flounder	bot	+++	++
Eurytopic	Abramis bjoerkna	Cyprinidae	white bream	kolblei	+++	+++
	Abramis brama	Cyprinidae	bream	brasem	+++	+++
	Alburnus alburnus	Cyprinidae	bleak	alver	+++	+++
	Anguilla anguilla (S)	Anguillidae	eel	paling	+++	+++
	Carassius auratus[5]	Cyprinidae	goldfish	goudvis	+++	+
	Carassius auratus gibelio[4]	Cyprinidae	gibel carp	giebel	++	+
	Ctenopharyngodon idella[5]	Cyprinidae	grass carp	graskarper	0	+
	Cyprinus carpio[4]	Cyprinidae	common carp	karper	++	++

Guild	Species	Family	English name	Dutch name	1890[1]	1996[2]
	Esox lucius	Esocidae	pike	snoek	+++	++
	Gasterosteus aculeatus	Gasterosteidae	stickleback	driedoornige stekelbaars	+++	+
	Gymnocephalus cernuus	Percidae	ruffe	pos	+++	++
	Perca fluviatilis	Percidae	perch	baars	+++	+++
	Phoxinus phoxinus	Cyprinidae	eurasian minnow	elrits	++	
	Pseudorasbora parva[5]	Cyprinidae	stone moroko	blauwband	0	+
	Rutilus rutilus	Cyprinidae	roach	blankvoorn	+++	+++
	Silurus glanis	Siluridae	wels	meerval	+	++
	Stizostedion lucioperca[4]	Percidae	pikeperch	snoekbaars	0	+++
Limnophilic	*Carassius carassius*	Cyprinidae	crucian carp	kroeskarper	+++	++
	Leucaspius delineatus (V)	Cyprinidae	sunbleak	vetje	++	++
	Misgurnus fossilis	Cobitididae	weatherfish	grote modderkruiper	+++	0
	Pungitius pungitius	Gasterosteidae	ten spined stickleback	tiendoornige stekelbaars	++	+
	Rhodeus sericeus (V)	Cyprinidae	bitterling	bittervoorn	+++	+
	Rutilus erythrophthalmus	Cyprinidae	rudd	ruisvoorn	+++	++
	Tinca tinca	Cyprinidae	tench	zeelt	++	++

[1]: occurrence: +++: common; ++: rare; +: sporadical; 0: absent (Lelek, 1989)
[2]: occurrence: +++: common (>1 per fyke net day); ++: rare (>0.01 and <=1 per fyke net day); +: incidental (>0 and <=0.01 per fyke net day); 0: absent (Klinge *et al.*, 1998).
[3]: red list species are indicated according to De Nie & Van Ommering (1998): X: extinct as viable population; E: endangered; V: vulnerable; S: susceptible.
[4]: exotic species that has settled in the Netherlands.
[5]: exotic species.

Consequently, the fish community changed into a less diverse, eurytopic community. At present, there are 47 species known to occur, of which only four eurytopic species dominate: pikeperch *Stizostedion lucioperca*, bream *Abramis brama*, white bream *A. bjoerkna* and roach *Rutilus rutilus*. Cyprinid and diadromous rheophilic fish are extinct or present in very low numbers (Klinge *et al.,* 1998).

Gravel extraction, degradation of the river bed, intensive fisheries on spawning populations and barriers to migration have caused the decline of diadromous species (De Groot, 1990; Raat, 2001). Up to the beginning of the 20th century, diadromous species such as atlantic salmon (De Groot, 1989[a]; Martens, 1992), sea trout (De Groot, 1989[b]), allis shad *Alosa alosa* (De Groot, 1992[a]) and sturgeon *Acipenser sturio* (De Groot, 1992[b]) were abundant and commercially exploited (Figure 1.4). The Rhine was considered to be one of the largest and most important salmon rivers in Europe.

Figure 1.4. Total catches of commercial fish species in the Netherlands from 1860 onwards. Catch is the numbers per year caught (except *C. oxyrinchus* of which catch is in kg). Please note the [10]Log scale of the y-axis. (Data from De Groot, 1989[a]; 1989[b]; 1992[a]; 1992[b]; 1992[c]).

According to Schiemer (1999, 2000), the lack of riverine inshore structures is the main cause of the decline in rheophilic cyprinid species (ide *Leuciscus idus*, chub *L. cephalus* and barbel *Barbus barbus*) in regulated rivers. These structures form the spawning and nursery habitats of these species. Unfortunately rheophilic cyprinids were of no commercial interest so no historical quantitative data on their abundance is available. From the by-catches of commercial species, however, we can assume that these species were abundant in the lower reaches of the Rhine (e.g. Redeke, 1941; Lelek, 1989; Van den Brink *et al.*, 1990; De Groot, 1991; Volz & Cazemier, 1991;

Martens, 1992). In 1660, for example, barbel was mentioned as a by-catch species for which, for each basket caught, the fishermen had to pay dfl 0.05 tax. In contrast, for each basket of salmon, the fishermen had to pay dfl 6.00 in tax (Lobregt & Van Os, 1977). Their numbers, however, declined (Lelek, 1989; Van den Brink *et al.*, 1990; Van den Brink *et al.*, 1996) and most are listed as vulnerable or endangered on the Netherlands Red List of freshwater fish species (De Nie & Van Ommering, 1998). In other European rivers also, most rheophilic cyprinids have declined and are frequently considered endangered, e.g. Danube (Schiemer & Spindler, 1989; Guti, 1993), Pilica, Warta & Gwada (Penczak & Kruk, 2000), Morava (Jurajda, 1995), Havel and Spree (Wolter & Vilcinskas, 1999) and Oder (Bischoff & Wolter, 2001).

1.5 Rehabilitation of river ecosystems

Plans for river rehabilitation

Improving water quality alone is not sufficient to rehabilitate the riverine ecosystem: restoring habitats in floodplains is also essential (Schropp & Bakker, 1998). Three programmes were developed that proposed measures to rehabilitate physical habitat conditions in the Rhine. These plans have in common that they propose measures to remove bottlenecks for the riverine fish community. Each of the programmes had, however, an effect on a different group of fish. The first (Salmon 2000) focuses on removing barriers in the longitudinal direction down the river, whereas 'Black Stork' and 'Living Rivers' focus on increasing habitat diversity in the lateral direction. Removing longitudinal barriers aims at enhancing diadromous species whereas increasing habitat diversity in the lateral direction aims at enhancing rheophilic cyprinid species.

The 'Salmon 2000' project, which was initiated by the ICPR, considered the return of the salmon in the year 2000 as a symbol and indicator of success for ecosystem restoration as a whole (Wieriks & Schulte-Wülwer-Leidig, 1997). The targets to be achieved by this programme were restoration of migration routes and spawning sites for migratory anadromous fish and to protect, preserve and improve ecologically important reaches of the Rhine and the Rhine valley for a larger variety of indigenous plants and animals (Cals *et al.*, 1998).

Plan 'Black Stork' launched the idea of shifting agricultural activities inland to provide space for natural morphological processes such as erosion and sedimentation in floodplains (De Bruin *et al.*, 1987). The plan proposed to connect floodplain lakes to the main channel permanently and to restore floodplain forests. This plan was a first

and important step forwards for nature conservation and protection and towards ecological rehabilitation of the Rhine (Cals *et al.*, 1998).

'Living Rivers' (WWF, 1993) proposed the creation of secondary channels in the floodplains by means of which conflicting functions of the Rhine could be integrated. The plan stated that the re-establishment of species is dependent on restoring lost habitats such as shallow, low-flow secondary channels and large woody debris. Restoration of these types of habitat in the main channel of the Rhine is not compatible with its functions as a navigation route and transport route for water and ice. Secondary channels, that have the permanent low-flow conditions that are required for the re-establishment of typical riverine species, could be created by clay mining. The excavated clay could be sold to brick factories and used for dyke improvement. Consequently, ecological rehabilitation would be cost neutral. Moreover, due to the excavation of clay from the floodplains, their discharge capacity at periods of high water would be increased (Cals *et al.*, 1998).

National policy on river management

At present, national policy on the major rivers in the Netherlands has incorporated the above three plans and sustainable flood protection along the rivers will be achieved through a combination of measures: strengthening the dykes, retaining the water and giving the rivers more room to expand (Ministry of Transport, Public Works and Water Management, 1998). The effects of climate change point towards sea-level rise and larger variations in river discharges with more wet winters and dry summers, which puts at risk the country's safety from flooding, from both sea and river. The 1996 Flood Protection Act linked the level of protection required to the nature of the flood threat and the seriousness of the potential consequences in a given area. The safety standard for the lower Rhine area is set at an average of one flood event every 1,250 years (Middelkoop & Van Haselen, 1999).

Secondary channels have been dug at several locations in the floodplains of the Rhine and isolated oxbows have been connected with a downstream opening to the main channel (Figure 1.5; Buijse & Vriese, 1996; Cals *et al.*, 1998; Simons *et al.*, 2001). These floodplain water bodies should provide living conditions for organisms that are at present rare or endangered but are still present in the main channel (Schropp & Bakker, 1998). This holds especially true for rheophilic cyprinids the further expansion of whose populations is thought to be curtailed by scarcity of these types of water body (Buijse & Vriese, 1996; Cals *et al.*, 1998).

Figure 1.5. Examples of two newly created floodplain water bodies along the River Waal. Downstream reconnected oxbow lake 'Passewaaij' (left panel, created in 1996) and secondary channel 'Gameren' (right, created in 1996). Arrows indicate directions of flow. The secondary channel is a flow-through system. The connected oxbow lake is predominantly stagnant. Water flows during rising and falling water levels in the main channel and due to water displacement of passing ships.

1.6 Significance of floodplains for fish

The importance of floodplains for lowland rivers

More than in any other ecosystem, the riverine ecosystem is moulded and its biota influenced by abiotic factors such as discharge pattern, temperature regime and the morphology and geology of the river basin (Petts, 1994). These factors change along the course of the river and consequently, biotic processes and species composition of biotic communities change as well. Changes in nutrient processing and biological characteristics along the course of the river are described by the River Continuum Concept (Vannote *et al.*, 1980). The concept states that rivers have a longitudinal structure that results from a gradient of physical forces that changes predictably along the length of a river. These forces produce a continuum of morphological and hydrological features from the headwaters to the mouth (Johnson *et al.*, 1995). This concept was, however, mainly based on small streams, and it was found difficult to fit large floodplain rivers, like the lower Rhine, to this concept (Junk *et al.*, 1989; Sedell *et al.*, 1989; Welcomme *et al.*, 1989; Petts & Maddock, 1994). The Flood Pulse

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Concept (Junk *et al.*, 1989) proposes that the pulsing of the river discharge, the flood pulse that extends the river onto the floodplain, is the major force controlling biota in floodplain rivers. Flood pulses control biota in three ways: directly by facilitating migration of animals and indirectly by enhancing primary production and by structuring of habitats. Junk *et al.* (1989) describe the river-floodplain system analogous to a highway network with the vehicles corresponding to the fish. During floods, biota can migrate both actively and passively between different habitats in the river-floodplain system. The main channel is used principally as a route for gaining access to feeding areas, nurseries, spawning grounds or as a refuge at low water levels or low temperatures during winter (Junk *et al.*, 1989).

Productivity in floodplain water bodies is much higher than in the main channel of the river (Van den Brink, 1994; Bayley, 1995; Ward & Stanford, 1995). The moving littoral (or aquatic/terrestrial transition zone, ATTZ), which occurs as a result of the flood pulse, is the major zone for biological production in the floodplain. Junk *et al.* (1989) define the floodplain as the ATTZ because it alternates between aquatic and terrestrial environments. High turnover rates of organic matter and nutrients are predicted to occur largely as a result of this movement (Junk *et al.*, 1989; Bayley, 1995; Ward & Stanford, 1995). The main channel of the river contains nutrients that are products from upstream areas, but conditions for primary production in the main channel (high flow velocity and large depth) are poor. In shallow floodplain water bodies, however, conditions are favourable for primary production. In these water bodies, algae and macrophytes use nutrients transported by the flood pulse. Algae and macrophytes are the forage base for zooplankton, macro-invertebrates and fish. Moreover, during floods, nutrients previously mineralized during the preceding dry phase are dissolved. At present, the ATTZ along the lower Rhine is limited to the area between the winter dykes.

Apart from important driving factors for ecological processes in the riverine ecosystem, floodplains to a large extent provide habitat complexity and habitat quality (Schiemer & Zalewski, 1992). The formation of habitats, which is the result of interaction between hydrology and floodplain morphology, occurs at different spatial and temporal scales. With the flood pulse, sediment is transported from upstream areas to the floodplain. Sedimentation and erosion form bars and levees and impact on the morphology of oxbows, backwaters and secondary channels. Sand banks, for example, can be formed within a single flood event of a few days. On the contrary, succession of oxbow lakes from water to land, as a result of sedimentation, may take centuries. The spatial scales of riverine habitats and their temporal persistence are correlated: larger units persist for longer periods (Bayley & Li, 1994; Figure 1.7). With regard to disturbance and stability, microhabitats (sand bars, beds with aquatic vegetation) are

the most susceptible but also have the shortest recovery times (Petts, 1994). Heterogeneity of substratum, depth and slope of water bodies create a diversity of physical habitats in the floodplain.

The function of floodplains during the life cycle of fish

Abundance of food and habitat heterogeneity make floodplains suitable nursery areas for many riverine fish species (Bayley, 1995). In lowland sections of rivers such as the Rhine in the Netherlands, floodplains are essential for the reproductive cycle of many fish species. Fish vary enormously in size from egg to adult, and, associated with this variation in body size, they exhibit complex life cycles and patterns of habitat use (Schlosser, 1991).

Figure 1.6. The basic life cycle of riverine fish with patterns of habitat use and migration (after Schlosser, 1991).

In general, riverine fish migrate between spawning, feeding and overwintering habitats (Figure 1.6). Individual fish have daily activities (feeding, seeking refuge) during which they migrate over short distances over short periods. During longer periods or between seasons they may migrate to different habitats to utilize different resources. These time scales are two to three orders of magnitude smaller than those relating to the persistence of riverine habitats they use (Figure 1.7; Bayley & Li, 1994). Among species, their home range and the types of habitat they require during their life cycle vary strongly (Figure 1.7). A salmon, for example, utilizes a river over almost the

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entire basin. Adults migrate from sea upstream the river, through several branches, after which they lay their eggs on gravel banks in small tributaries. On the contrary, crucian carp *Carassius carassius*, remains in isolated floodplain lakes and only utilizes a single floodplain lake during its complete life cycle (Figure 1.7). Similarly, these scales also vary within species depending on age and size; larvae may utilize resources at scales in space and time different from adults.

a) Fish community

b) River Rhine habitat

Figure 1.7. Temporal and spatial scaling of fish communities (a) and of the River Rhine (b). In figure (a), values on the x-axis are left out since they vary strongly among fish species. Some species (salmon for example) complete their life cycles covering almost the entire drainage basin whereas others (crucian carp) remain in one floodplain (adapted from Bayley & Li, 1994; Petts, 1994).

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During their life cycle, many fish utilize floodplains, either temporarily or permanently, to spawn, forage or avoid harsh conditions (Welcomme, 1979; Welcomme & De Mérona, 1988; Fernandes, 1997; Molls, 1999; Saint-Paul *et al.*, 2000). In temperate lowland rivers, fish have adapted to the large spatial heterogeneity that supports a large diversity of fish species exhibiting a wide range of life cycles. The fish species in lowland rivers can be classified according to their differential use of floodplains. Due to the variation in connectivity, laterally across the floodplain, there is a lateral zonation of fish reproduction (Copp & Peñáz, 1988; Copp, 1989; Copp *et al.*, 1991). From the lotic main channel to lentic zones in the floodplains, fish reproduction in European rivers shifts from rheophilic, through eurytopic to limnophilic species (Table 1.3; Figure 1.8; Regier *et al.*, 1989; Schiemer & Waidbacher, 1992).

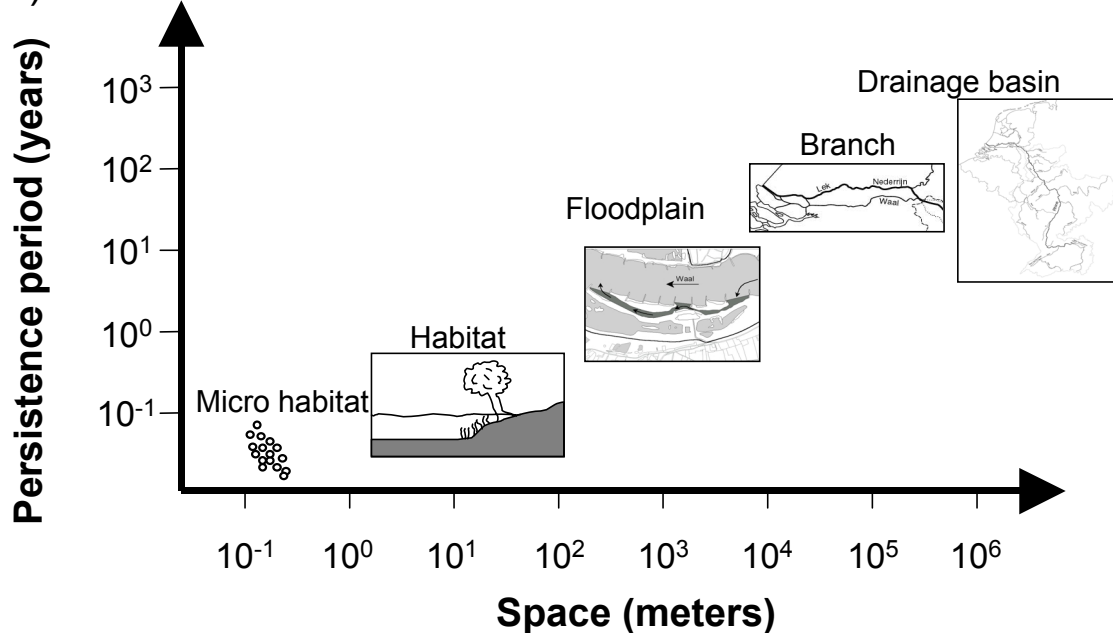During their ontogeny, rheophilic cyprinids require a specific sequence of habitat types (Schiemer *et al.*, 1991; Schiemer & Zalewski, 1992; Schiemer *et al.*, 1995). All rheophilic species lay their eggs in flowing water but the preferred spawning substrate varies (Balon, 1975; Mann, 1996). During early stages of their life cycles, they depend on inshore zones of the river or on low-flow, connected backwaters (Schiemer & Waidbacher, 1992) since their scope for optimal and critical flow velocities is very restricted (Flore & Keckeis, 1998; Schiemer *et al.*, 2001). With increasing size, habitat requirements with regard to flow velocity, substrate type and food change dramatically and a habitat shift is commonly observed in young cyprinid assemblages in large rivers (Gaudin, 2001). Salmonid rheophilic species and Rheophilic C species do not use floodplains. Salmonids complete their life cycle on a much larger scale and migrate through the Dutch part of the River Rhine to spawning and nursery areas upstream, in Germany, France, Luxembourg and Switzerland. Rheophilic C species are bound to the brackish water zones in the estuaries.

Eurytopic species are habitat generalists that occur in both the main channel and in various types of floodplain water body (Figure 1.8; Schiemer & Waidbacher, 1992). Many eurytopic species use low-flow zones and connected backwaters throughout their lives. They occur in the backwaters year-round in consistent population densities, whereas some species occur in highest densities during the spawning season (Schiemer & Spindler, 1989; Holcik, 1996; Molls, 1999).

Limnophilic species (Table 1.3) can complete their life cycle within one habitat. They remain in isolated lakes throughout their lives and require aquatic vegetation for their reproduction (Figure 1.8). They are often adapted to withstand extreme environmental conditions that occur in floodplain lakes during isolation, such as low water levels and anoxic conditions (Welcomme & De Mérona, 1988). Only to prevent inbreeding, they should leave these habitats during floods to meet other conspecifics.

Thus, an important element of the ecological status of rivers is the spatial/temporal availability and connectivity of habitats that are required during the life cycles of the fish species which are indigenous to the river (Schmutz *et al.*, 2000). It is apparent that the requirements for habitat availability and connectivity differ among species (Schiemer, 2000): the salmon requires connected habitats on a catchment scale, whereas the crucian carp needs a single floodplain lake that exists over a long period.

Figure 1.8. Differential use of habitats in floodplains along lowland rivers by four reproductive guilds. Black arrows indicate adult migration to spawning sites. Figure adapted from Schiemer & Waidbacher (1992) and Quak (1994).

Consequently, fish community structure (species and age composition) is a good indicator of the ecological condition of floodplain rivers; the various guilds integrate a wide range of riverine conditions over their life cycles, from sediment structure and flow velocities for egg development, to connectivity between spawning and nursery areas (Copp, 1989; Schiemer *et al.*, 1991; Schiemer, 2000; Gaudin, 2001).

Therefore, it is important to assess whether newly created secondary channels and reconnected oxbow lakes do function as spawning and nursery areas for endangered rheophilic fish. If they do, their construction contributes to the rebuilding of the population of rheophilic fish in the lower Rhine. The function of floodplain water bodies for rheophilic fish can be tested since, in the 1990s, in the lower Rhine, individuals of all rheophilic cyprinid species were observed (Table 1.3; Klinge *et al.*,

1998). This means that a stock, which has the potential to benefit from secondary channels and reconnected oxbow lakes, was present before these habitats were created but is probably curtailed by a scarcity of suitable habitat. From studies on less disturbed rivers in temperate regions, it is known that the types of water body that were created in the Netherlands, function as spawning and nursery areas for rheophilic fish. It is, however, not yet known which fish have colonized these new water bodies in the lower Rhine and utilize them as spawning and nursery areas. Moreover, there is limited knowledge on the occurrence of fish species in water bodies that were already present before floodplain restoration started. This limited knowledge constrains the decision making on future management.

1.7 Study objectives

The objectives of this study were to test the beneficial value of newly created secondary channels and reconnected oxbows for rheophilic fish and to give advice on position, shape and character of future water bodies (Lanters & Van Densen, 1996). These objectives were pursued by:
1. Assessing the fish community structure in various types of floodplain water body along the lower Rhine.
2. Assessing the functions that these water bodies fulfil as spawning, nursery and refuge areas during the life cycles of the various fish species.

It is the first time that the fish community in floodplains along the lower Rhine has been investigated. Numerous studies have described floodplain fish community structures and the functioning of floodplain water bodies for fish, but these were carried out on the Rhine more upstream in Germany (Molls, 1999) and in other European rivers, e.g. the Danube (Schiemer, 1985; Guti, 1996; Holcik, 1996), the Rhône (Copp & Peñáz, 1988; Copp, 1989; Copp et al., 1991), the Great Ouse (Copp, 1991) and the Garonne (Gozlan et al., 1998). Fish monitoring programmes in the lower Rhine in the Netherlands are restricted to the main channel and some deep sand-pits. So far, only the presence of fish species in floodplain lakes has been assessed in one small-scale pilot study (Buijse & Vriese, 1996). Van den Brink (1994) investigated lake ecosystems in the floodplains along the lower Rhine, predominantly for water chemistry, plankton, aquatic vegetation and macro-invertebrates and presented some preliminary data on the lateral zonation of fish species composition.

From the function that floodplain water bodies fulfil during the life cycles of the distinct fish species, their beneficial value for the riverine fish community can be assessed. This function is investigated by describing the presence and abundance of

fish species in floodplain water bodies, over time and space (Figure 1.9). The time-scale varies (days, weeks, months, years) and depends on the part of the life cycle and on the water body investigated. For habitat shifts in larvae and juveniles, for example, the time-scale is days or weeks. Moreover, the time-scale depends on the connectivity of the water body with the main channel. Permanently connected water bodies are investigated with a higher resolution in time than floodplain lakes, of which the fish community will, between floods, probably remain more constant. The scale of the spatial distribution depends mainly on the developmental stages (larvae, juveniles, adults) and may be smaller for larvae and juveniles than for adults. From the presence of stages of fish species, at various moments, at different locations, the habitats they occupy during their life cycles is known. Consequently, the role of each habitat during the life cycle of the species, and hence its function for the riverine fish community, can be inferred (Figure 1.9).

Figure 1.9. Approach to infer the function of floodplain water bodies for fish. The scale of time varies from days to years, the scale of space varies from habitat to water body (Figure based on Schiemer & Spindler, 1989). In this example, a habitat shift from Habitat A to Habitat B is observed for species A, whereas species B remains in habitat A throughout the sampling period. By sampling different developmental stages in various habitats, the habitats it uses during its life cycle can be described and the function these habitats fulfil be inferred.

This study is a first evaluation of the ecological functioning of newly created and reconnected floodplain water bodies for fish. The evaluation of the first few restoration projects should demonstrate desirable features that can be replicated on a larger scale to benefit the riverine fish community (Bayley *et al.*, 2000). To give advice on position, shape and character of future water bodies, the study should result in quantitative design tools and guidelines. These are, for example: depth, slope, flow velocity, substratum type and flooding frequency and duration.

Apart from the evaluation of restoration projects, studying dynamics of fish communities in restored floodplains also offers the opportunity to test overall concepts and hypotheses and contributes to the understanding of the functioning of floodplains

for fish in temperate lowland rivers (Bayley, 1995; Schiemer *et al.*, 1999). Major concepts regarding the functioning of large rivers have mainly been based on undisturbed, tropical rivers and little is known about the functioning of undisturbed temperate rivers (Ward *et al.*, 1999; Tockner *et al.*, 2000). This lack of baseline data may cause problems when disturbed temperate rivers are restored since it may be difficult to define restoration targets (Bayley, 1991). Moreover, there are more plans for river restoration, based on these concepts, than there are demonstrations (Gore & Douglas Shields Jr., 1995). This study could give insight into the ecological functioning of floodplain water bodies that were created as a compromise between safety, navigation and nature.

1.8 Study area and sampling

Study area

To assess how the various fish species utilize different types of floodplain water body, 25 water bodies along the lower Rhine were sampled from November 1996 to December 1999 (Figure 1.10; Table 1.5). These comprised water bodies created for floodplain restoration and water bodies that already existed before floodplain restoration had started. They varied in hydrological and morphological characteristics: connectivity, flow velocity, depth, slopes of the shorelines and substratum types. Four water bodies had permanent connections with the main channel, whereas the 21 floodplain lakes were only connected during floods.

The water bodies with a permanent connection to the main channel mainly differed in hydrological conditions. All of them were created in the 1990s for nature restoration purposes. From all these water bodies, aquatic vegetation is absent and their substratum consists of sand, silt and sometimes clay. Three of them are secondary channels that have two openings to the main channel and a continuous moderate flow. They mainly differ in shoreline complexity and, consequently, they differ in the variability of sites with flowing and stagnant water. The fourth water body is a reconnected oxbow lake, which only has one opening at its downstream end to the main channel. It is stagnant, except for the opening where passing ships cause the water to move in and out.

The 21 lakes differ in surface, depth, frequency of inundation and presence of aquatic vegetation. They comprise man-made sand and clay-mining pits and natural oxbow lakes. Lakes that lie between summer dykes and the main channel are connected with the main channel for 50-150 days per year, on average (Figure 1.11). From 1900-1999, these lakes were connected with the main channel at least once, and

sometimes several times a year. Lakes that are positioned behind summer dykes are connected less frequently, on average 2-20 days per year, usually in winter (Figure 1.11). From 1900-1999, these lakes remained isolated for one full year only nine times.

The study was carried out along the River Waal, the free-flowing main branch of the River Rhine in the Netherlands, from the Dutch/German border (Lobith; river km 860) up to the stretch where the marine tidal cycle influences water levels (Gorinchem; river km 960; Figure 1.1; 1.10).

Where the Rhine enters the Netherlands (at Lobith), the average discharge is 2,200 m^3 s^{-1} (Middelkoop & Van Haselen, 1999). Floods may occur in winter, early spring and summer (Figure 1.8) but their origins differ. High precipitation and low evaporation in the catchment area may cause peaks in winter. Melting ice and snow in the Alps may cause peaks in spring and summer (April-June). Just after crossing the border, the river splits into three branches, of which the River Waal transports 66% of the water and is less canalized than other branches (Rivers Lek and IJssel): 19% of the shoreline consists of rip-rap. The total surface of the Waal and adjacent floodplains is 150 km^2 (Table 1.4). At low water levels, which occur on more than 150 days per year (<9.6 m above sea level (a.s.l.) Lobith), the surface of the main channel (39 km^2) and water bodies that are permanently connected to the main channel (9 km^2) is 48 km^2. The frequently inundated zone of the floodplains, that is inundated 50-150 days per year (9.6 -11.2 m a.s.l. Lobith), leading to some submerged terrestrial vegetation, is only 8 km^2. 82 km^2 of the floodplain, which is mainly grassland, is inundated less than 50 days per year (>11.2 m a.s.l. Lobith). In the floodplains there are 10 km^2 of permanent lakes (clay-pits and oxbows). The data for the other branches are also given (Table 1.4).

Table 1.4 Characteristics of the three branches of the River Rhine in the Netherlands.

| Branch | River stretch (river km) | Permanent water | | Floodplain inundation (days per year) | | | | | Total |
		Main channel (km^2)	Water bodies (km^2)	150-365 (km^2)	50-150 (km^2)	20-50 (km^2)	2-20 (km^2)	<2 (km^2)	(km^2)
Waal	857-960	39.0	18.7	2.1	8.2	12.5	58.7	11.0	150.3
Nederrijn	868-989	26.8	8.3	1.8	2.1	3.1	25.2	45.5	112.9
IJssel	879-1006	14.6	10.6	0.3	8.1	17.8	44.9	24.7	121.1
Total		**80.5**	**37.6**	**4.3**	**18.4**	**33.4**	**128.9**	**81.2**	**384.3**
Waal		26%	12%	1%	5%	8%	39%	7%	100%
Nederrijn		24%	7%	2%	2%	3%	22%	40%	100%
IJssel		12%	9%	0%	7%	15%	37%	20%	100%
Total		**21%**	**10%**	**1%**	**5%**	**9%**	**34%**	**21%**	**100%**

During the sampling period (1997-1999) several peaks occurred in the discharge during which terrestrial vegetation was inundated and floodplain lakes became connected with the main channel (Figure 1.11). Compared to long term records, 1997 was an average year with discharge peaks in spring and summer, whereas 1998 was an exceptional year with low discharge in spring and summer and a peak in September, which normally has a low discharge. 1999 had a wet spring and summer in comparison with normal years. Water levels in March 1997, November 1998, March 1999 and November 1999 exceeded the height of the summer dykes and consequently all floodplains were inundated bankful.

Sampling

In all water bodies, fish community structure was assessed with seine nets, trawls and electro-fishing. To assess the relationship between species composition and the environment of each sample, a description of the micro-habitat was made: water temperature, flow velocity, depth and Secchi-disk depth were measured, substrate type determined and presence of aquatic and inundated terrestrial vegetation estimated. The scale of this habitat description depended on the gear type used.

The various types of water body were sampled on several occasions (Figure 1.11). Secondary channels and the connected oxbow lake were sampled up to 14 times per year whereas the lakes were sampled up to three times per year. The sampling programme in the lakes was adapted to floods so that they were sampled shortly after they had been connected to the main channel.

1.9 Introduction to the Chapters

A first test of the beneficial value of reconnected floodplain water bodies

In **Chapter 2**, the beneficial value of two newly created secondary channels and a reconnected oxbow lake is tested by comparing their 0-group fish communities with the fish community of an isolated floodplain lake already present. It was expected that the density of rheophilic cyprinids would be higher in secondary channels than in a reconnected oxbow lake, and lowest in the floodplain lake. In this Chapter, data are analysed with a rather low resolution regarding both habitat and fish species. On a spatial scale, fish communities are compared only among water bodies. Moreover, differences in abundance of the species are not assessed at the species level; fish species are classified into four groups (rheophilic cyprinids, eurytopic cyprinids, percids and other species).

Table 1.5. Characteristics of floodplain water bodies sampled. Numbers of water bodies refer to Figure 1.10. Types of water body: MC: main channel; GF: groyne fields; SC: secondary channel; COL: connected oxbow lake; SP: sand-pit; CP: clay-pit; OX: oxbow lake. The connectivity is the long-term (1900-1995) average duration (days per year) the water body has been connected with the main channel. Vegetation is the percentage of the water body covered and was estimated in summer 1999.

Map (Nr.)	Dutch name or floodplain	Water body	Surface (10^4 m^2)	Depth (Nov/Dec) (m)	Connectivity (days/year)	Submerse vegetation (% cover)	Floating vegetation (% cover)	Helo-phytes (% cover)
-	River Waal	MC	3900.0	4.0	permanent	0	0	0
-	Kribvak	GF	4.0	2.0	permanent	0	0	0
1	Opijnen	SC	13.6	1.5	permanent	0	0	0
2	Beneden Leeuwen	SC	26.9	1.5	permanent	0	0	0
3	Gameren	SC	8.4	1.0	permanent	0	0	0
4	Passewaaij	COL	5.4	2.5	permanent	0	0	0
5	Gendt	SP	5.0	2.0	2-20	0	0	0
6	Gendt	CP	0.7	1.5	2-20	11	5	2
7	Gendt	CP	0.6	1.5	2-20	0	10	2
8	Gendt	CP	0.7	1.0	2-20	28	9	4
9	Gendt	CP	2.0	0.8	2-20	4	0	0
10	Bemmel	CP	1.4	0.8	2-20	42	34	12
11	Bemmel	CP	0.9	0.5	2-20	0	75	20
12	Bemmel	CP	4.0	1.5	2-20	0	2	1
13	Deest	CP	8.0	1.5	50-150	0	0	0
14	Deest	CP	2.0	1.0	50-150	2	14	0
15	Heesselt	CP	0.1	0.8	2-20	60	50	6
16	Heesselt	CP	0.9	0.8	2-20	57	46	6
17	Heesselt	CP	0.3	0.4	2-20	89	0	5
18	Heesselt	CP	1.3	0.8	2-20	0	0	0
19	Ochten	CP	0.2	1.0	2-20	81	4	4
20	Lent	OX	3.5	1.5	50-150	3	0	0
21	Ewijk	OX	12.6	2.5	50-150	2	0	0
22	Heesselt	OX	0.2	1.5	2-20	0	0	0
23	Opijnen	OX	1.8	0.8	2-20	32	34	3
24	Kil van Hurwenen	OX	10.1	1.0	2-20	0.2	14	5
25	Kil van Waarden-burg	OX	4.3	1.0	2-20	5	50	3

The habitat suitability of secondary channels and reconnected oxbow lakes

Chapter 3 presents quantitative guidelines for the creation of future floodplain water bodies to enhance specific fish species. The relationship between habitat availability and the structure of the 0-group fish assemblage is investigated in three secondary channels and a reconnected oxbow lake. To assess their beneficial value, densities of individual species in these water bodies are compared with those in the groyne fields already present. Suitability of habitats is investigated by assessing the spatial distribution of the 0-group fish assemblage among and within water bodies. It is supposed that habitats with higher presence and abundance of a species are the most suitable for that species.

Figure 1.10. The River Waal with all floodplain water bodies present. Floodplain water bodies sampled are indicated. Numbers refer to Table 1.5.

Figure 1.11. Water levels of the River Rhine during the sampling years (1997-1999). In each graph, the grey line represents the mean water level in the 20 years period 1980-1999. Grey panels indicate threshold of floodplain lakes becoming connected with the main channel (lower panel: lakes connected 50-150 days/year (9.6-11.2 m a.s.l. at Lobith); upper panel: lakes connected 2-20 days/year (12.4-14.7 m a.s.l. at Lobith). Moreover, above 9.6 m a.s.l. terrestrial vegetation becomes inundated along permanently connected floodplain water bodies. Arrows indicate sampling periods: white arrows (0-group fish) and grey arrows (1+ fish) in permanently connected water bodies; black arrows in floodplain lakes.

Data are analysed at a more detailed spatial scale (65-800 m^2) than in Chapter 2 (54,000-385,000 m^2). Within the fish's life cycle, this chapter focuses on three early developmental stages (larvae, small juveniles, juveniles >3 cm) of the nine most abundant species.

How fish utilize restored floodplain water bodies

In **Chapter 4** the contribution of two secondary channels and a reconnected oxbow lake to the rebuilding of populations of rheophilic cyprinids is assessed by

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investigating their function as spawning and nursery areas. The functioning is inferred from the temporal and spatial patterns of larval, juvenile and adult fish during two consecutive years. With knowledge about the functioning of these types of water body, it can be tested whether man-made floodplain water bodies can compensate for the loss of inshore zones and connected backwaters along the lower Rhine. Moreover, advice can be given on the position, shape and characteristics of future connected floodplain water bodies. Data are analysed at a higher temporal resolution than in Chapters 2 and 3 although on a spatial scale, habitats within floodplain water bodies are not distinguished.

Migration of fish to and from floodplain lakes during floods

In **Chapter 5**, the functioning of isolated floodplain lakes for fish is investigated by assessing migration of fish between the main channel and floodplain lakes during floods. The hypothesis is tested that bream, white bream, roach and pikeperch move into these lakes during the connection stage to reproduce. During three consecutive years (1997-1999) five lakes were sampled six times and population size, the numbers of immigrants during the connection phase and the numbers that stayed resident were estimated using mark-recapture techniques. Effects of connection of floodplain lakes on the fish community present could be assessed by comparing fish community structures before and after a flood. Due to the abundance and dominance of bream, large numbers of fish could be marked and recaptured, and this chapter focuses on the migration patterns of this species.

Fish communities in isolated floodplain lakes

In **Chapter 6** fish communities in 20 lakes are described and factors that govern the species diversity and the presence and reproduction of limnophilic species are investigated. These lakes varied in surface area, depth, inundation frequency and presence of vegetation. To assess how these lakes contribute to fish species diversity in the river-floodplain system, fish communities are compared with those in the main channel and in various types of floodplain water body that are permanently connected with the main channel.

Synthesis: how fish benefit from floodplain restoration along the lower River Rhine

In **Chapter 7**, first, seven conclusions of this study are summarized. The results of Chapters 2-6 are integrated by describing the life cycles of fish in the lower Rhine and by describing how they utilize floodplains. From these patterns in time and space, the factors that determine the fish community in the lower Rhine are inferred. From a description of the current plans for floodplain management, regarding protection against flooding, it is assessed how environmental conditions for riverine fish can be improved within these plans. It is discussed which measures should be taken to rehabilitate the riverine fish community at the population level.

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Photo 2. Secondary channel 1 (nevengeul Opijnen) with the River Waal on the background.

Chapter 2

Restoration of the river-floodplain interaction: benefits for the fish community in the River Rhine

Abstract

In the River Rhine, canalization of the river and disconnection of floodplains from the river bed led to the present low diversity of habitats. Spawning conditions for especially rheophilic cyprinids have declined dramatically. Nowadays, eurytopic species dominate the riverine fish community. In 1989, river restoration started by connecting water bodies in the floodplains to the main channel permanently. To evaluate the effect of these restorations on the fish community, four floodplain water bodies, which differ in connectivity with the main channel, flow velocity and presence of aquatic vegetation, were sampled to investigate their functions as spawning and nursery areas for riverine fishes. The hypothesis that density of rheophilic cyprinids is in accordance with flow and connectivity was tested by analysis of presence-absence data, using a logistic model and by analysis of variance for abundance data using a generalized linear model. Presence and abundance of rheophilic cyprinids increased from the isolated oxbow lake (not connected, no flowing water present) to connected oxbow lake (permanently connected with the main channel, no flowing water present) and to both secondary channels (permanently connected with the main channel, flowing water present permanently). Connectivity of a water body with the main channel and the presence of flowing water are important factors driving the structure of the 0-group fish assemblage in floodplain water bodies. Only a few years after their creation, secondary channels provide a suitable habitat as nursery areas for rheophilic cyprinids.

2.1 Introduction

In lowland floodplain river systems, like the River Rhine in the Netherlands, ecosystem dynamics are dominated by lateral exchanges between the main channel and the floodplain, and are influenced by vertical exchanges between the main channel and the underlying alluvial aquifer (Petts, 1994). Lateral exchanges between main channel and floodplain, and nutrient recycling within the floodplain have more direct impact on biota than the nutrient spiralling discussed in the River Continuum Concept (Vannote *et al.*, 1980; Junk *et al.*, 1989). Besides important factors for driving ecological processes in the riverine ecosystem, floodplains for a major part provide habitat complexity and habitat quality in the river ecosystem (Schiemer & Zalewski, 1992). Therefore floodplains can fulfil the requirements for a specific sequence of habitat types of certain young fishes during their ontogeny (Amoros & Roux, 1988; Copp, 1989, Schiemer *et al.*, 1991; Schiemer & Zalewski, 1992; Schiemer *et al.*, 1995).

However, to date the floodplains along the rivers in the Netherlands are enclosed by a low summer or minor dyke and a high winter or major dyke, which has reduced its width to several hundred metres (Cals *et al.*, 1998; Schropp & Bakker, 1998). The summer dyke, situated between the river and the floodplains, enables the use of floodplains for agricultural purposes while the winter dyke prevents the hinterland from flooding. Due to the presence of the summer dyke, the aquatic/terrestrial transition zone is disturbed (Buijse & Vriese, 1996). Besides decreased dynamics in the lateral direction of the river, the original river bed, characterized by sand and gravel beds, has changed into a deep river bed with steep shore faces (Cals *et al.*, 1998). These developments led to the present poor diversity of habitats in the River Rhine in the Netherlands. As a consequence, spawning and nursing conditions for especially rheophilic cyprinids as ide *Leuciscus idus*, chub *L. cephalus* and barbel *Barbus barbus* are thought to have declined dramatically. Loss of suitable habitat together with increasing pollution and a decline in oxygen content of the river water during the 1960's, led to a severe decrease in the population of rheophilic cyprinids (Van den Brink *et al.*, 1990). Nowadays, eurytopic species as pikeperch *Stizostedion lucioperca*, roach *Rutilus rutilus* and bream *Abramis brama* dominate the riverine fish community (Bakker *et al.*, 1998; Klinge *et al.*, 1998).

However, in recent years attempts to increase the dynamics in the lateral direction were made through nature restoration projects (WWF, 1993; Cals *et al.*, 1998). At several locations in the floodplains of the Dutch River Rhine, secondary channels have been dug and isolated backwaters have been connected with a downstream opening to the main channel (Figure 2.1; Schropp & Bakker, 1998).

Beneficial effects of these newly created floodplain ecotopes on the population of riverine fishes were presumed but not demonstrated yet.

Figure 2.1. Map of the Netherlands and of the four water bodies sampled.

In the present study, the hypothesis was tested that these newly created ecotopes form suitable spawning and nursery habitats for riverine fishes, and that the density of rheophilic cyprinids is in accordance with flow and connectivity of these water bodies. We expected that the density of rheophilic cyprinids is higher in permanently connected water bodies where a continuous flow is present (secondary channels) than in permanently connected water bodies where flowing water is absent (connected oxbow lake) and stagnant water bodies which are connected only with the main channel during floods (isolated oxbow lake). This hypothesis can be tested since it is known that a population of adult rheophilic fishes does exist in the River Rhine in the Netherlands (Bakker *et al.*, 1998; Klinge *et al.*, 1998). This paper presents the preliminary results after one season (1997) of sampling.

2.2 Materials and methods

2.2.1 Sites and sampling

To test the hypothesis that secondary channels provide suitable habitats for spawning and nursing of rheophilic cyprinids, 0-group fish were sampled in four water bodies in the floodplains of the River Rhine in the Netherlands: two secondary channels, one downstream connected oxbow lake and an isolated oxbow lake (Figure 2.1). We counted all fish that were born in the year of sampling as 0-group fish. Samples were collected once every three weeks from the end of April until the beginning of October 1997.

Both secondary channels are characterized by a continuous flow with a velocity of approximately 0.3 m s^{-1} (Table 2.1). In secondary channel 1 (SC1), habitats with stagnant water are virtually absent while in secondary channel 2 (SC2) habitats with stagnant water are present in former clay-pits which have a connection with the flowing secondary channel (Figure 2.1). Both secondary channels and the connected oxbow lake (COL) have a permanent connection with the main channel which allows fish to move in and out these waters year-round. The isolated oxbow lake (IOL) is only connected with the main channel during periods of high discharge which occurs on average five days per year, which does not imply every year (Figure 2.1; Table 2.1; Van den Brink, 1995). In summer, in the isolated oxbow lake extended beds of *Nuphar lutea* and *Nymphoides peltata* cover circa 25 percent of the water surface. The shore zone is almost completely covered with reed *Phragmatis australis*.

In the surveys, trawls were used to sample the open water and seine nets to sample the shore zone. From April until the end of July, a fine meshed frame-trawl (opening 2.4 by 0.7 m, mesh size 4 mm stretched) and a 16 m seine (mesh size 1.5 mm

stretched) were used. From the first week of July onwards, a beam trawl (opening 3.5 by 0.75 m, mesh size 4 mm stretched) and a 25 m seine (mesh size 7.5 mm stretched) were used. Both trawl nets were used to fish at both the bottom and at the surface. The average towed distance of each haul of 5 minutes was estimated with a digital flow meter.

Table 2.1. Characteristics of the four water bodies in the floodplains of the River Rhine in the Netherlands.

	SC1	SC2	COL	IOL
River kilometre	929	908	917	864
River bank (Left/ Right)	R	L	R	R
Average surface during summer (km^2)	0.14	0.27	0.05	0.43
Average depth during summer (m)	1	1.5	2	1.5
Average discharge ($m^3 s^{-1}$)	5	10	0	0
Connectivity with main channel (days/year)	365	365	365	5
Year of creation	1994	1995	1996	1775

The 0-group fish were immediately preserved in 4% formalin and taken to the laboratory for identification. Pre-finfold larvae were identified by their internal and external pigmentation and the number of myomeres (Balinsky, 1948; Koblickaya, 1981; Spindler, 1988; Mooij, 1989; Urho, 1996). Fry with developed fins were identified by their fin positions and number of fin rays and the number of scales on the lateral line (Pekar, 1965; Koblickaya, 1981). If the number of fish within a group (Percidae or Cyprinidae) was large (>100), subsampling was applied. In that case, at least 100 fishes per family per group were identified. Circa 4% of the fishes were damaged or were hybrids and could not be identified further than to the family level (Table 2.2). Fork length was measured to the nearest millimetre. Age 1 and older fish were measured in the field, kept in life nets and set free at the end of each sampling day.

2.2.2 Data analysis

To analyse the abundance of juvenile fishes in the four water bodies sampled, species were classified in four groups: percids, eurytopic cyprinids, rheophilic cyprinids and other species. All percid species are considered eurytopic. The other species comprise those only seldomly caught and are not further addressed here. Classification in rheophilic and eurytopic cyprinids was done according to Schiemer & Waidbacher (1992) and Quak (1994). The number of individuals per group was summed per haul and only data on 0-group fish were analysed further.

Table 2.2. Classification of fish species by ecological guild and total number of 0-group fishes caught in the four sampling gears used. n.i. indicates that species could not be identified further than to the group level.

Percids	Numbers	Eurytopic cyprinids	Numbers
Stizostedion lucioperca	4851	*Abramis brama*	67216
Perca fluviatilis	2003	*Abramis bjoerkna*	21496
Gymnocephalus cernuus	150	*Rutilus rutilus*	5368
Percid (n.i.)	234	*Alburnus alburnus*	3703
		Cyprinus carpio	393
		Cyprinid (n.i.)	4097
Total numbers	7238		102273

Rheophilic cyprinids	Numbers	Other species	Numbers
Aspius aspius	306	*Gasterosteus aculeatus*	33
Leuciscus idus	275	*Rutilus erythrophthalmus*	12
Barbus barbus	276	*Carassius carassius*	9
Gobio gobio	204	*Rhodeus sericeus*	8
Leuciscus cephalus	55	*Esox lucius*	2
Leuciscus leuciscus	43	*Pungitius pungitius*	1
Chondrostoma nasus	42		
Cobitis taenia	2		
Cottus gobio	1		
Total numbers	1204		65

Presence-absence analysis

Since the number of zero catches was approximately 50% of the total catches per group and gear, presence-absence data were analysed using logit regression (Ter Braak & Looman, 1995). In the generalized linear model, the response variable p_{ij} was defined as:

$$p_{ij} = n_{ij}(\text{non-zero}) / (n_{ij}(\text{zero}) + n_{ij}(\text{non-zero})). \qquad (1)$$

Where: p= response variable (fraction of non-zero catches); n= number of catches; i= water body (i= 1 to 4) and j= sample week (j= 1 to 7).

The analysis was done for fish groups and gear types separately. The response variable p_{ij} has a binomial distribution (Sokal & Rohlf, 1995). A logit function g(M) was used to link the expected value of the response variable (p) to the linear predictor:

$$g(M) = \ln(p_{ij}/(1-p_{ij})). \qquad (2)$$

Where g(M)= expected value of fraction of non-zero catches and M= overall mean.

The linear predictor for the expected fraction of non-zero catches was defined using the following model:

$$g(M) = M + fwb_i + week_j. \tag{3}$$

Where fwb_i= effect of ith floodplain water body and $week_j$= effect of jth week.

The procedure was implemented using PROC GENMOD of the SAS software package (SAS Institute Inc., 1990). 95% approximate confidence limits of the fitted value were calculated as described in the GENMOD procedure manual. If a term did not reduce deviance significantly (alpha=0.05), it was removed from the model.

Abundance analysis of non-zero catches

Effects of water body and week on abundance data of non-zero catches were estimated through analysis of variance (ANOVA) on catch per haul numbers. In order to meet the assumptions for analysis of variance, catch data were natural-log transformed (Sokal & Rohlf, 1995):

$$C = \ln(CpUE). \tag{4}$$

Where CpUE= catch per unit of effort (number of fishes per haul) only non-zero catches included and C= log transformed catch per haul data.

The linear predictor for the log transformed catch per haul data was defined using the following model:

$$C(M)_{ijk} = M + fwb_i + week_j + fwb_i \text{ x } week_j + e_{jk}. \tag{5}$$

Any non-significant term (alpha=0.05) was excluded and the model was refitted with the remaining terms. Residual analysis was used to check the goodness of fit of the model and comprised a Wilk-Shapiro test of normality of the residuals (alpha=0.05). The 95% confidence limits were calculated to compare the means between groups.

2.3 Results

In the four waters sampled, in total 110,780 0-group fish of 23 species were caught. The juvenile fish communities were dominated by percids and eurytopic cyprinids. Percids were pikeperch, perch *Perca fluviatilis* and ruffe *Gymnocephalus cernuus*. The most abundant eurytopic cyprinid species were roach, bream, white bream *Abramis*

bjoerkna and bleak *Alburnus alburnus* (Table 2.2). The contribution of juvenile rheophilic cyprinids to the total catch varied among the four water bodies sampled (Table 2.3, 2.4). The most abundant rheophilic cyprinids were the exotic asp *Aspius aspius*, chub, barbel and gudgeon *Gobio gobio*. In the isolated oxbow lake, no 0-group rheophilic cyprinids were caught while in secondary channel 1 the contribution of rheophilic cyprinids to the total catch was up to 40%.

2.3.1 Percids

Presence and abundance of percids in the samples were highest in the connected oxbow lake in spring and lowest in the isolated oxbow lake in all seasons (Table 2.3, 2.4).

In each of the four gears used, a significant difference in samples between water bodies was observed (Table 2.3). This was caused only by a low number of catches with percids in the isolated oxbow lake; between the three permanently connected water bodies, no significant difference in fractions of non-zero catches of percids was observed. The moment of sampling was only significant in the fry trawl and the 1.5 mm seine, the gears used in the first part of the season (Table 2.3; Figure 2.2). This was caused by low catches of percid larvae in the first sampling week (April 29) when apparently the spawning season for percids had not started yet.

With regard to the abundance of percids, only a significant difference between water bodies in the first part of the season, i.e. in catches in the fry trawl and the 1.5 mm seine, was observed (Table 2.4). In the fry trawl, a significant effect of week and of the interaction between water body and sampling week was found. This was caused by the low catches of 0-group percids in the first sampling week (April 29), the significantly higher catches in the second sampling week (May 20) and successive significantly lower catches in the third sampling week (June 17).

2.3.2 Eurytopic cyprinids

Presence and abundance of 0-group eurytopic cyprinids were highest in the isolated oxbow lake and lowest in secondary channel 1 (Table 2.3, 2.4).

Table 2.3. Presence-absence data. Fractions of non-zero catches for the different gears and fish groups and significance levels of the factors water body (Fwb) and time (Week) in SC1, SC2, COL and IOL as predicted from the logistic model (3). Significance levels: **: p<0.01; *: p<0.05; n.s.: not significant (p>=0.05).

		Fraction non-zero catches (g(M))				Significance levels	
		SC1	SC2	COL	IOL	Fwb	Week
Percids	1.5 mm Seine	0.50	0.49	0.58	0.10	**	**
	7.5 mm Seine	0.38	0.54	0.75	0.06	**	n.s.
	Fry trawl	0.52	0.48	0.54	0.17	*	**
	Beam trawl	0.67	0.89	0.76	0.47	*	n.s.
Eurytopic cyprinids	1.5 mm Seine	0.54	0.45	0.75	0.65	*	**
	7.5 mm Seine	0.78	0.73	0.94	0.76	n.s.	**
	Fry trawl	0.43	0.40	0.67	0.61	n.s.	**
	Beam trawl	0.67	0.72	0.82	1.00	*	n.s.
Rheophilic cyprinids	1.5 mm Seine	0.54	0.37	0.39	0.00	**	**
	7.5 mm Seine	0.56	0.58	0.50	0.00	**	n.s.
	Fry trawl	0.52	0.12	0.00	0.00	**	*
	Beam trawl	0.58	0.56	0.12	0.00	**	n.s.

Table 2.4. Abundance data. Numbers per haul of non-zero catches as predicted from linear model (5), and significance levels of the factors water body (Fwb), time (Week) and interaction between water body and time (Fwb x Week) in SC1, SC2, COL and IOL. Significance levels: **: p<0.01; *: p<0.05; n.s.: not significant (p>=0.05).

		Predicted number per haul (C(M))				Significance levels (%)		
		SC1	SC2	COL	IOL	Fwb	Week	Fwb x Week
Percids	1.5 mm Seine	3.9	22.0	30.6	2.6	**	n.s.	n.s.
	7.5 mm Seine	4.6	6.5	3.4	2.0	n.s.	*	*
	Fry trawl	3.9	11.1	36.6	4.1	**	**	**
	Beam trawl	14.9	14.6	7.6	3.0	n.s.	n.s.	n.s.
Eurytopic cyprinids	1.5 mm Seine	12.3	21.3	18.2	15.0	n.s.	**	n.s.
	7.5 mm Seine	11.4	32.5	23.1	48.9	*	n.s.	**
	Fry trawl	3.4	5.9	11.4	13.6	n.s.	*	n.s.
	Beam trawl	7.4	27.7	52.5	665.1	**	**	**
Rheophilic cyprinids	1.5 mm Seine	3.9	4.1	2.0	.	n.s.	n.s.	n.s.
	7.5 mm Seine	3.7	2.4	2.9	.	n.s.	n.s.	n.s.
	Fry trawl	3.0	2.8	.	.	n.s.	n.s.	n.s.
	Beam trawl	20.9	3.9	1.7	.	n.s.	n.s.	n.s.

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Figure 2.2. Fractions of non-zero catches with 95% confidence limits for the three groups. Shore zone: 1.5 mm seine (April 29 to June 17) and 7.5 mm seine (from July 8 onwards). Open water: fry trawl (April 29 to June 17) and beam trawl (from July 8 onwards). Because of the low water level, secondary channel 1 could not be sampled with a beam trawl in September.

Among water bodies, presence of eurytopic cyprinids, was only significantly different in the 1.5 mm seine and the beam trawl (Table 2.3). The difference in the 1.5 mm seine was caused by the low fraction of catches with eurytopic cyprinids in both secondary channels. The significant effect of water body on the catches in the beam trawl was caused by the fact that in all catches of the beam trawl in the isolated oxbow lake, eurytopic cyprinids were present while these fractions in the other three water bodies were significantly lower. In the first part of the season, presence of eurytopic cyprinids varied significantly over time (Table 2.3; Figure 2.2). A significant increase

in the fraction of catches with eurytopic cyprinids in the third sampling week (June 17) was observed (Figure 2.2). This is due to bream, the dominating eurytopic cyprinid species, which had just hatched. In this week, large numbers of bream larvae were caught.

In the first part of the season, no significant difference in the abundance of eurytopic cyprinids between the four water bodies was observed. However, in the second part of the season, abundance of eurytopic cyprinids differed significantly among water bodies (Table 2.4). This was caused by the high numbers of eurytopic cyprinids in the isolated oxbow lake. In the first part of the season, abundance of eurytopic cyprinids varied significantly over time (Table 2.4). In the first sampling week (April 29) virtually no 0-group eurytopic cyprinids were caught. In the second sampling week (May 20) catches of this group were low and catches increased significantly in the third sampling week (June 17).

In the second part of the season, a second peak in the abundance of 0-group eurytopic cyprinids around August 20 occurred. As a result of a second spawning period of bream, catches in the open water sampled with the beam trawl differed significantly over time.

2.3.3 Rheophilic cyprinids

In the isolated oxbow lake, no 0-group rheophilic cyprinids were caught, neither in the open water nor in the shore zone. Only presence of rheophilic cyprinids differed significantly among water bodies (Table 2.3). Abundance of rheophilic cyprinids in non-zero catches did not differ significantly between water bodies (Table 2.4).

In all four gears used, a significant difference in presence of rheophilic cyprinids in the samples between water bodies was observed (Table 2.3). For all gears, this difference was based on the contrast between the isolated oxbow lake (no 0-group rheophilic cyprinids at all) and the three permanently connected water bodies. In the open water, rheophilic cyprinids were almost absent in the connected oxbow lake (Table 2.3). In the shore zone of both secondary channels, in more than half of the samples rheophilic cyprinids were present (Table 2.3). An almost absence of 0-group rheophilic cyprinids in the first sampling week (April 29) explains the significance of the sampling period (Figure 2.2).

Abundance of rheophilic cyprinids differed among water bodies and over time, but differences were not significant (Table 2.4). This can be attributed to the fact that zero catches were omitted in the abundance analysis. In the open water in secondary channel 1, rheophilic cyprinids were the most abundant fish species (Table 2.4).

2.4 Discussion

Connectivity of a floodplain water body with the main channel and the presence of flowing water are important factors driving the structure of the 0-group fish assemblage in floodplain water bodies. In permanently connected water bodies, where a continuous flow is present, highest presence and abundance of rheophilic cyprinids and lowest densities of eurytopic cyprinids were found (Table 2.3, 2.4; Figure 2.2). A similar increase in density of rheophilic cyprinids along a gradient of increasing flow and connectivity was found in the 'Basses Terres' floodplain of the upper Rhône (Copp & Peñáz, 1988) and in the 'Szigetköz' floodplain of the Danube (Guti, 1996). In the three permanently connected water bodies, presence and abundance of eurytopic percids and cyprinids increased with decreasing flow and connectivity (Table 2.3, 2.4; Figure 2.2). Only several years after their creation, the three newly created floodplain waters form suitable nursery areas for rheophilic cyprinids. Since abundance of rheophilic cyprinids increase, and abundance of eurytopic species decrease along a gradient of flow and connectivity, creation of new floodplain waters with a permanent connection and a constant, moderate flow, probably has the highest potential in benefitting the rheophilic fish community in the River Rhine.

Presence and abundance of percids and eurytopic cyprinids can be explained by spawning periods of various fish species like pikeperch and bream. Of the rheophilic cyprinids, no clear spawning season was observed. Almost no larvae of rheophilic cyprinids were caught so it is not proven that the sampled floodplain water bodies function as spawning areas for these species. Successive sampling will focus on identifying spawning sites of rheophilic fishes and on investigating larval drift of this group into the floodplain water bodies.

Despite the fact that no rheophilic cyprinids were caught in the isolated oxbow lake, the results of the abundance analysis showed no significant differences in abundance of rheophilic cyprinids among water bodies. Therefore, results of analyses of log transformed catch data for species that are not common, should be interpreted carefully. For these species, additional analysis of presence-absence data gives better insight in differences between water bodies and over time.

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Photo 3. Sampling juvenile fish in a reconnected oxbow lake (Wetland Passewaaij) with a 25 m seine net.

Chapter 3

Testing the suitability of habitat for 0-group fish in rehabilitated floodplains along the lower River Rhine

Abstract

To assess the suitability of rehabilitated floodplains along the lower River Rhine for rheophilic cyprinids, we investigated the spatial distribution of 0-group fish among, and within, three newly created secondary channels, an oxbow lake reconnected downstream and several groyne fields along the main channel. Fish were sampled during summer in 1997, 1998 and 1999 with seine nets and trawls and, for each sample, the micro-habitat was described. Compared to the groyne fields present originally, the additional water bodies created provide suitable habitats for 0-group fish. Their beneficial value differs, however, for different reproductive guilds and depends on the morphological and hydrological conditions. In general, among these water bodies, total fish density increased along a gradient of decreasing water movement whereas the proportion of rheophilic species (*Barbus barbus*, *Gobio gobio*, *Leuciscus idus* and *Aspius aspius*) decreased. Rheophilic fish were clearly spatially separated from eurytopic fish (e.g. *Abramis brama*, *Rutilus rutilus* and *Stizostedion lucioperca*) but species were also spatially separated within both guilds. During floods, inundated terrestrial vegetation proved to be an important habitat for the larvae of all species. To enhance the riverine fish community, floodplain water bodies should have complex shorelines, and a high variability of flow velocities. Their slopes should be moderate in order to optimize the probability of terrestrial vegetation being submerged during spring and summer. Future management of similar floodplains should focus on increasing the diversity and accessibility of aquatic habitats in order to increase overall fish species diversity, since different types of water body clearly have complementary values.

3.1 Introduction

In order to rehabilitate the interaction between the main channel of the River Rhine and the adjacent floodplains, secondary channels have recently been created and isolated oxbows have been reconnected with a downstream opening to the main channel (WWF, 1993; Buijse & Vriese, 1996; Cals *et al.,* 1998). These floodplain water bodies should provide living conditions for organisms that are at present rare or endangered but are still present in the main channel (Schropp & Bakker, 1998). Disappearance of these habitats, caused by regulation and normalization, is thought to be the limiting factor during the ontogeny of rheophilic cyprinids such as ide *Leuciscus idus*, chub *L. cephalus* and barbel *Barbus barbus*. Numbers of these species declined sharply and the fish community of the lower River Rhine and its floodplains has changed into a less diverse and eurytopic community dominated by pikeperch *Stizostedion lucioperca*, bream *Abramis brama*, white bream *A. bjoerkna* and roach *Rutilus rutilus* (Klinge *et al.,* 1998). Newly created and reconnected water bodies should provide suitable habitats for 0-group rheophilic fish and thus contribute to the rebuilding of their populations in the Netherlands.

At present, rehabilitation of floodplains along the lower Rhine is being linked to increasing the discharge capacity of the river during floods. The plan 'Living Rivers' (WWF, 1993) proposed the creation of secondary channels within the floodplains by which conflicting functions of the river could be integrated. The plan suggested that the re-establishment of species is dependent on restoring lost habitats such as shallow, low-flow areas. In the main channel, restoration of these types of habitat is not compatible with the function as a navigation route and for the discharge of water. In the floodplain, secondary channels are created by clay mining and the excavated clay can be sold to brick factories or can be used for dyke improvement. Consequently, the ecological rehabilitation is cost neutral. In addition, the discharge capacity of the floodplains at periods of high water will be increased, which is necessary to cope with the increased risk of floods (Cals *et al*., 1998). Although the overall yearly discharge will remain fairly constant, extremely high and low flows are likely to become more common as a result of climate change (Middelkoop & Van Haselen, 1999).

We investigated the relationship between habitat availability in different floodplain water bodies and the structure of the 0-group fish assemblage in order to assess the types of water body that are most suitable for increasing the habitat availability for rheophilic cyprinid fish. Three newly created secondary channels and one oxbow lake reconnected downstream were selected because at the time of sampling, they were the only ones in the rehabilitated floodplains that were permanently connected with the main channel. The approach taken for assessing

suitability was to compare 0-group fish assemblages among various types of habitat and water body, and to compare these with the assemblages in groyne fields that existed before the floodplains were rehabilitated. Habitats (water bodies) with higher densities of a species are assumed to be more suitable for that species than habitats with lower densities. Suitability of habitats was investigated by assessing the spatial distribution of the 0-group fish within and among the water bodies. The scale of the assessment was about 100 m^2 within water bodies and about 0.02-0.2 km^2 when fish assemblages were compared among water bodies and groyne fields. The spatial distribution was tested for differences in presence (number of hauls in which a species occurred) and abundance (numbers per m^2) of species among habitats.

It is imperative for sound fish stock management that the suitability of habitats for 0-group fish is assessed and this should be given attention in any rehabilitation programme (Cowx & Welcomme, 1998; Bayley et al., 2000). Numerous studies have described the habitat preferences of 0-group fish of species that are indigenous to the lower Rhine (e.g. Grossman & De Sostoa, 1994; Watkins et al., 1997; Baras et al., 1995; Gozlan et al., 1998; Bischoff & Freyhof, 1999; Jurajda, 1999) but so far no particular study had been carried out in this particulate area. Investigating ontogenetic habitat shifts in these fish is not our primary goal here: we evaluate the suitability of water bodies in a few rehabilitation projects for 0-group rheophilic fish to determine desirable features that should be replicated on a larger scale to benefit the riverine fish community at the population level.

The relationship between habitat and fish assemblages was investigated in three newly created secondary channels, one reconnected oxbow lake and several groyne fields (Figure 3.1). All these water bodies differ in their morphological and hydrological characteristics. To identify the effect of water level on habitat availability and the effect of habitat availability on the spatial distribution, fish were sampled year-round. Moreover, year-round sampling allowed habitat preferences that change quickly during early development of larval and juvenile fish (Schiemer & Spindler, 1989; Schiemer et al., 1995) to be investigated.

Study area

The River Rhine is, from its source in Switzerland to the outflow to the North Sea, 1320 km long and has a catchment area of 185,000 km^2 (Lelek, 1989), of which 25,000 km^2 are situated in the Netherlands, forming the delta area. Where the Rhine enters the Netherlands (at Lobith), the average discharge is 2200 m^3 s^{-1} (Middelkoop & Van Haselen, 1999). Floods may occur in winter, early spring and summer (Figure 3.2, lower panel) but their origin may differ. High precipitation and low evaporation in the

catchment area may cause peaks in winter. Melting ice and snow in the Alps may cause peaks in spring and summer (April-June). Just after crossing the border, the river splits into three branches, of which one (River Waal) transporting 66% of the water, is free flowing and less normalized than other branches (Rivers Lek and IJssel): 19% of the shoreline consists of rip-rap. The total surface of the Waal and adjacent floodplains is 150 km^2. At low water levels that occur more than 150 days per year (<9.6 m above sea level (a.s.l.) Lobith), the surface of the main channel (39 km^2) and water bodies that are permanently connected to the main channel (9 km^2) is 48 km^2. The part of the floodplain that is inundated 50-150 days per year (9.6 -11.2 m a.s.l. Lobith), leading to some submerged terrestrial vegetation, is only 8 km^2. 82 km^2 of floodplain, which is mainly grass land, is inundated less than 50 days per year (>11.2 m a.s.l. Lobith). In the floodplains 10 km^2 of permanent lakes exists.

All water bodies sampled are permanently connected to the main channel but differ in their morphological and hydrological conditions. In the main channel, flow velocities vary between 0.5 and 1.5 m s^{-1} and sand, apart from the boulders covering the groynes, is the only substrate. Groyne fields (GF) are hydrologically dynamic and inhospitable sites owing to marked changes in water level and strong eddies caused by ships that pass on average every three minutes. Water flows permanently through the three secondary channels (SC) at moderate rates (0.05-0.20 m s^{-1}) while the oxbow lake is only connected with the main channel downstream and is therefore almost stagnant. The secondary channels vary in their shoreline complexity (shoreline / length ratio); SC3 has the lowest shoreline complexity and SC2 the highest (Figure 3.1). Variability of hydrological conditions increases with shoreline complexity. In all water bodies sampled, aquatic macrophytes were absent. During floods, submerged terrestrial plants were the only vegetation present.

Each groyne field has an average surface area of 2 ha., groynes are about 100 m long and about 200 m apart. SC1 (river km 929; average surface 13.6 ha.) is the oldest secondary channel created in 1994. A 1 km wing dyke, built in 1984 to prevent erosion of the outer curve of the river, was opened at both ends (Figure 3.1). The former groyne fields that had been isolated from the main channel by the wing dyke were reflooded and to improve water quality in these segments during summer, all the groynes at the landward side of the wing dyke were cut through. As a result, SC1 has a well-developed, complex shoreline and flow velocities are characterized by a moderate variability. SC2 (river km 908; average surface 26.9 ha.) was created in 1997 by excavating channels between a sand-pit and an oxbow each of which was connected on one side with the main channel. Water now enters the sand-pit (depth of approximately 15 m), then out through the channel and along the former oxbow before returning to the main channel. In some former clay mining pits that have been laterally connected to

Figure 3.1. Maps of the River Rhine in the Netherlands and of water bodies sampled (surface at mean water levels indicated). Arrows indicate the direction of flow. Secondary channel 1 (SC1), secondary channel 2 (SC2) and secondary channel 3 (SC3) are flow-through systems. The connected oxbow lake (COL) is predominantly stagnant: water flows during rising and falling water levels in the main channel and due to water displacement of passing ships.

Figure 3.2. Water levels of the River Rhine (Lobith) in the three years sampled (upper three panels). The horizontal line indicates water level (9.6 m a.s.l. Lobith) above which terrestrial vegetation inundates in the floodplain water bodies sampled. Arrows indicate sampling weeks, black arrows indicate weeks in which terrestrial vegetation was inundated for more than one day. Vertical lines indicate the three sampling seasons grouped in each year for the Canoco analysis (Table 3.5). Whisker and box plots (lower panel) present minimum and maximum water levels and the percentiles per month (data from 1970-1999).

the channel, water is stagnant. This site has the greatest variability in depth and flow conditions. SC3 (river km 938; average surface 8.4 ha.), created in 1998, has the lowest shoreline complexity, variation in flow velocities is very low. COL (river km 917; average surface 5.4 ha.) was permanently reconnected to the main channel downstream in 1996 (Figure 3.1). Except at the exit, where passing ships cause water to move in and out, the water is stagnant. The dead end is the deepest part. At a water level >12 m a.s.l. (Lobith) water enters COL from upstream.

3.2 Materials and methods

3.2.1 Data collection

0-group fish were sampled every three weeks from April through September in 1997, 1998 and 1999 (weekly from April through June 1999). Different gears were applied in different habitats at different times yielding a total of 1356 hauls. Seine nets were used to sample the shore zone while trawls were used in the open water. Until the end of July, gears consisted of a fine meshed frame trawl (FT1) and a 16 m seine (SE1). From the first week of July onwards, a beam trawl (BT) and a 25 m seine (SE2) were used. A smaller frame trawl (FT2) has been used in spring 1998 and 1999 and a plankton net (PN) in spring 1999. Sizes and mesh sizes of these nets are presented in the legend of Figure 3.3. Seine hauls were standardized so that the area fished was 65 m^2 for SE1 and 140 m^2 for SE2. Trawls were towed behind a boat and used to sample both at the bottom and at the surface. The towed distance of each 5 minute haul was estimated with a digital flow meter. The trawled surfaces were approximately 70, 200, 400 and 800 m^2 for the PN, FT1, FT2 and BT respectively.

Water depth (m), flow velocity (m s^{-1}), water temperature (°C) and Secchi-disk depth (m) were measured during each haul. Flow velocity was measured with a digital portable flow meter (Marsh McBirney Flow-mate model 2000) at 0.15 m above the bottom and water temperature with a digital thermometer (WTW Oxy 330). The type of substrate was determined and the abundance of inundated terrestrial vegetation (percentage cover) was estimated. Although it was attempted to make hauls in a uniform environment, the values of environmental variables varied in practice. Therefore, depth, flow velocity and vegetation were each classified (Table 3.1). 0-group fish were preserved in 4% formalin and identified in the laboratory (Grift *et al.*, 2001). Fork length was measured to the nearest cm and to the nearest mm for fish <10 cm.

Table 3.1. Classification of habitat variables measured and estimated. Terrestrial vegetation is the percentage of the surface of the haul that was covered by inundated terrestrial vegetation.

Class	Flow (m s^{-1})	Depth (m)	Substrate	Terrestrial vegetation (%)
1	0.0	<=0.20	Silt	0
2	0.01-0.04	0.20-0.50	Clay	<1
3	0.05-0.09	0.51-1.00	Sand	1-4
4	0.10-0.14	1.01-2.00	Gravel	5-14
5	0.15-0.19	2.01-3.00	Boulders	15-24
6	0.20-0.29	3.01-5.00		25-49
7	0.30-0.49	5.01-10.00		50-74
8	>=0.50	>=10.00		75-100

3.2.2 Data analysis

0-group fish were distinguished from older fish by evaluating length-frequency distributions. These showed clear cut-off lengths for all species. To distinguish larvae from juveniles, developmental stage (larval or juvenile) and length (mm forklength) of 500 fish in total of the nine species analysed were recorded. The juvenile stage is defined as the stage in which all fins are completely differentiated (Copp, 1990). Cut-off lengths for juvenile fish were determined as the length at which 50% of the fish were in each stage. Lengths at which fish became juveniles, as measured in this study, were comparable with those found in the literature (Balinsky, 1948; Copp, 1990; 1992; Baras & Nindaba, 1999; Gozlan *et al.*, 1999). 0-group fish larger than 3 cm were considered as a separate group because at this length, all had fully developed fins.

Data on 0-group fish of the four most abundant rheophilic species (asp *Aspius aspius*, ide, barbel and gudgeon *Gobio gobio*) and of the five most abundant eurytopic species (pikeperch, roach, bream, white bream and bleak *Alburnus alburnus*) were used for statistical analysis. These species made up 95% of the total numbers present.

The statistical analysis of catch data comprised three steps. First, differences in densities among water bodies and years were analysed with linear models. To analyse the spatial distribution of the 0-group fish, catch data were pooled over all water bodies and sampling years, and explored using canonical correspondence analysis. This resulted in a set of significant explanatory environmental variables. Finally, the effects of these variables on presence and abundance of fish were tested statistically with linear models.

Linear models

At first, the probability of a sample containing a specific species was analysed using logistic regression. Thereafter, the log-normal distribution of the abundance in the non-zero fraction of the catches was analysed with ANOVA. The fraction of non-zero

catches (P_{ij}) was transformed to a linear predictor (g(M)) by logit transformation. The abundance data (A, numbers per 1000 m^2) were log-transformed to spread the distribution more evenly through its range. For a more detailed description see Grift *et al.* (2001).

A 2nd order polynomial model for day number (N) was used for each of the nine species separately to assess differences in presence and abundance of a species among water bodies (W) and sampling years (Y). This choice was made because numbers of larvae increase after spawning has started, reach a maximum, and then decrease throughout the rest of the season. This model included eight depth classes (D, Table 3.1) and eight flow velocity classes (F) as recorded at the sampling site:

$$E_{ijklm} = M + W_{im} + Y_{jm} + N(W_{im}) + N^2 + D_{km} + F_{lm}. \tag{1}$$

Where: E_{ijklm} = Expected value of presence (g(M)) or abundance (ln(A)) of a fish species (m) and M is the mean.

1998 data from GF and SC3 were excluded from the analysis of differences of densities among water bodies and sampling years because both locations had been sampled only occasionally in 1998.

For the analysis of the effects of depth and flow velocity on presence and abundance, data from the various water bodies and sampling years were pooled, but only those weeks were included in which life stages of a species were present, in any of the water bodies sampled:

$$E_{ijmn} = M + D_{imn} + F_{jmn}. \tag{2}$$

Where: E_{ijmn} = Expected value of presence (g(M)) or abundance (ln(A)) of a stage (n) of fish species (m).

To analyse the effect of inundated terrestrial vegetation (T) on presence and abundance, data from those sampling weeks in which water levels at Lobith exceeded 9.6 m a.s.l. for more than one day were analysed (Figure 3.2). This model included eight classes of coverage with terrestrial vegetation:

$$E_{imn} = M + T_{imn}. \tag{3}$$

Where: E_{imn} = Expected value of presence (g(M)) or abundance (ln(A)) of a stage (n) of fish species (m).

An estimate of the actual density (numbers per m^2) in each class of the habitat variables was based on the multiplication of the predicted fraction of non-zero catches with the predicted abundance in the non-zero catches.

The logistic models were applied using PROC GENMOD of the SAS software package (SAS Institute Inc., 1990). The 95% approximate confidence limits of the fitted values were calculated as described in the manual. F-statistics and associated p-values were calculated and if a term did not reduce deviance significantly ($p>0.05$), it was removed from the model. ANOVA was implemented using PROC GLM of the SAS software package. Residuals were checked by a Wilk-Shapiro test on normality (alpha =0.05) and non-significant terms ($p>0.05$) were removed.

Canonical correspondence analysis

Canonical correspondence analysis (Canoco software Version 4; Ter Braak & Šmilauer, 1998) was selected to explore the relationship between fish assemblage structure and the environment, because we expected a unimodal response of the species to the environmental variables. For each haul, the abundance (numbers per 1000 m^2) per species and life stage was square root transformed. The measure of water temperature for each haul was calculated by substracting the mean water temperature measured on a sampling day from the actual temperature measured on the site of the haul. Substrate was described by four binary class variables that indicated the presence or absence of silt, clay, sand or gravel in each sample. The remaining variables, flow velocity, depth, corrected temperature, Secchi-disk depth, percentage inundated terrestrial vegetation, and substrate type were included using the approach of forward selection. The effect of each variable was tested using a Monte Carlo permutation test ($p<0.10$; 1000 random permutations). The null hypothesis to be tested was that the samples were randomly linked with the environmental data (Ter Braak & Verdonschot, 1995). The analyses were done by year and by sampling period (Figure 3.2; spring: April-June; summer: July-half August; late summer: half August-September).

3.3 Results

3.3.1 Habitat description of water bodies sampled

During the investigation, several peaks in discharge occurred resulting in inundation of terrestrial vegetation (Figure 3.2). Compared to long term records, 1997 was an average year with discharge peaks in spring and summer, whereas 1998 was an exceptional year with low discharge in spring and summer and a peak in September, which has a low median discharge. Discharge in spring 1999 was relatively high in

comparison with normal years: from the end of February to the end of July, terrestrial vegetation along the water bodies was inundated continuously.

The water bodies varied strongly in hydrological and morphological conditions as can be inferred from the distributions of flow velocity, depth and substrate types observed (Figure 3.3). GF provided the most hydrologically dynamic habitats with the highest flow velocities and water level fluctuations and COL provided the least dynamic habitats. SC3 is the most dynamic and SC2 the least dynamic of the three secondary channels.

Flow velocities were in general below 0.5 m s^{-1} in all water bodies. Sites with stagnant water were most frequently observed in SC2 and COL. In SC2, the downstream connected clay-pits (Figure 3.1) formed large areas with stagnant water. In SC1 most sites had low-flow (0.01-0.10 m s^{-1}) conditions. Only in GF and SC3, sites with moderate (>0.10 m s^{-1}) flow velocities prevailed. In both, stagnant sites were only observed inshore at high water levels.

All water bodies had comparable, moderate (0.5-5 m) depths. In GF, SC1 and COL, very shallow (<0.2 m) sites also occurred because gentle slopes were present. The deepest sites (>5 m) occurred in GF, near the main channel and at the dead end of COL (Figure 3.1).

At many sites, the substrate was a combination of sand, clay and/or silt. In all water bodies, sand was the most abundant substrate type with the exception of SC2 where clay prevailed. Clay also occurred along the shoreline of COL. In SC1, silt occurred in the stagnant parts along the shorelines. Gravel was only, but not always, present in GF and then only as a thin layer over sand. Submerged vegetation was only present when the floodplain was inundated. During several samplings, grasses, herbaceous plants and sometimes willows covered almost the entire area. However, at most sites vegetation was completely absent for most of the time (Figure 3.3).

Figure 3.3. Distributions of samples taken over gear types used and habitat variables measured. Number of hauls in each water body (indicated between brackets). Gear types: PN: plankton net (0.4 x 2.5 m, mesh size 0.5 mm stretched); FT1: frame trawl 1 (2.4 x 0.7 m, mesh size 4 mm stretched); FT2: frame trawl 2 (1.25 x 0.5 m, mesh size 0.5 mm stretched); BT: beam trawl (3.5 x 0.75 m, mesh size 4 mm stretched); SE1: seine 1 (1.5 x 16 m seine, mesh size 1.5 mm stretched); SE2: seine 2 (1.5 x 25 m, mesh size 7.5 mm stretched).

Table 3.2. Numerical composition of 0-group fish assemblages in 1997, 1998 and 1999. Effort is the surface area sampled. '.': species absent, '0.0': proportion <0.05%. n.s.: not sampled. Classification into reproductive guilds according to Schiemer & Waidbacher (1992) and Quak (1994).

Guild	Species	1997					1998					1999				
		GF	SC1	SC2	SC3	COL	GF	SC1	SC2	SC3	COL	GF	SC1	SC2	SC3	COL
	Effort (x 1000 m²)	n.s.	22	36	n.s.	31	12	40	49	0.46	32	63	34	n.s.	18	42
	Numbers caught		3294	8433		10511	204	10870	49945	698	34618	4182	122342		2354	116832
	Number of species		20	18		17	8	15	14	13	15	17	19		17	17
Rheophilic A	Barbus barbus		6.8	0.4		0.2	64.7	3.3	0.0	0.1	0.2	6.5	0.6		17.0	0.6
	Chondrostoma nasus		1.0	0.1		0.0	2.0	0.0	0.0	.	.	4.6	0.0		1.7	.
	Cottus gobio			0.0												
	Leuciscus cephalus		0.5	0.3		0.2		0.0	0.0		0.0	0.3	0.0		0.1	0.0
	Leuciscus leuciscus		0.8	0.1		0.1	2.0	0.1	0.0	0.1	0.1	0.3	0.0		5.9	0.0
Rheophilic B	Aspius aspius		2.9	1.6		0.7		4.9	5.2	1.4	1.1	1.8	0.3		0.8	1.4
	Cobitis taenia		0.0													
	Gobio gobio		3.8	0.2		0.0		11.9	0.4	14.5	0.0	2.8	0.0		12.0	0.0
	Leuciscus idus		5.7	0.8		0.2	1.0	41.3	18.3	4.9	4.9	6.4	2.4		5.0	0.4
Diadromous	Coregonids											0.2	0.0		0.1	0.0
	Osmerus eperlanus												0.0			0.0
	Percentage rheophilic		**21.4**	**3.5**		**1.4**	**69.6**	**61.4**	**23.9**	**21.1**	**6.4**	**22.8**	**3.4**		**42.6**	**2.4**
Eurytopic	Abramis bjoerkna		7.9	5.8		12.9		0.3	0.1	.	0.4	2.8	0.4		5.3	15.0
	Abramis brama		6.2	8.5		20.5	3.4	3.1	5.7	2.7	16.0	55.8	66.6		22.2	71.2
	Alburnus alburnus		8.1	13.8		21.5		10.5	12.2	25.4	11.5	3.1	0.3		6.2	0.7
	Cyprinus carpio		1.1			0.0			0.0	0.1	0.0	0.1	0.0		0.3	0.0
	Esox lucius		0.1										0.0		0.3	
	Gasterosteus aculeatus		0.2			0.0		0.0		8.2	0.0	0.2	0.0			0.1
	Gymnocephalus cernuus		1.4	0.5		0.3		1.5	0.7	3.4	0.3	0.5	0.4		0.3	0.2
	Perca fluviatilis		11.7	8.6		8.1	0.5	2.3	6.7	35.2	4.5	0.8	0.2		3.7	0.3
	Rutilus rutilus		27.4	30.6		10.3	2.9	16.4	19.2	3.4	21.9	5.1	24.8		11.5	3.5
	Stizostedion lucioperca		5.6	25.6		23.6	18.6	3.7	29.8		36.5	8.0	1.2		5.8	5.5
	Hybrid cyprinid		8.5	0.1		0.2		0.0	0.1	0.0	0.0	0.0	0.0		0.0	0.1
	Unidentified		0.4	2.8		1.2	4.9	0.8	1.6		2.3	1.0	2.8		1.7	1.1
	Percentage eurytopic		**78.5**	**96.4**		**98.6**	**30.4**	**38.6**	**76.1**	**78.5**	**93.6**	**77.3**	**96.6**		**57.3**	**97.6**
Limnophilic	Leucaspius delineatus															
	Pungitius pungitius			0.0												
	Rhodeus sericeus		0.0	0.0		0.0										
	Rutilus erythrophthalmus		0.1	0.0		0.0				0.4						
	Percentage limnophilic		**0.1**	**0.1**		**0.0**	**0.0**	**0.0**	**0.0**	**0.4**	**0.0**	**0.0**	**0.0**		**0.0**	**0.0**

Water temperature and transparency hardly varied among the water bodies (Figure 3.4). Variability of water temperatures within water bodies depends on their connectivity with the main channel, being largest in COL, and smallest in GF and SC3. The largest Secchi-disk depths were observed in SC2 which is presumably caused by sedimentation of sand and silt in the deep (>15 m) sand-pit through which water enters after leaving the main channel (Figure 3.1). In the former clay-pits, transparency was however low causing the large variability in Secchi-disk depths in SC2.

Figure 3.4. Distribution of water temperature (left panel) and Secchi-disk depth (right panel) in the water bodies sampled.

3.3.2 Spatial distribution of 0-group fish among water bodies

In total 363,381 0-group fish of 25 species were caught (Table 3.2). The number of species observed by water body and years varied from 8 (GF in 1998) to 20 (SC1 in 1997). Barbel, asp, ide and gudgeon were the most abundant rheophilic species while white bream, bream, bleak, roach and pikeperch were the most abundant eurytopic species. These nine species contributed 95% to the total numbers. Diadromous rheophilic and limnophilic species were caught only occasionally.

Presence and abundance of these nine species differed significantly among the water bodies (Table 3.3). In general, total density increased along a gradient of decreasing hydrodynamics, being lowest in the hydrologically dynamic GF and SC3 and highest in the less dynamic COL and SC2 (Figure 3.5). The proportion of rheophilic fish, however, showed a contrasting pattern, with highest proportions in the dynamic GF and SC3 (Table 3.2). For most species, both presence and abundance varied significantly throughout each year, but the patterns differed between presence and abundance (Table 3.3). The presence showed a parabolic pattern in all species based on the significance of the quadratic term. In contrast, the quadratic term of day

did not contribute significantly to explaining the variance in abundance (with the exception of barbel) indicating a decrease in a log-linear fashion.

In GF and SC3, densities were generally low. The relatively high proportion of rheophilic fish (23-70% in GF and 21-43% in SC3; Table 3.2) was caused rather by lower densities of eurytopic roach, bream and pikeperch than by higher densities of rheophilic fish compared to the other water bodies (Figure 3.5). In general, densities of rheophilic fish were highest in the secondary channels. Highest densities of asp and ide occurred in SC1 and SC2 whereas highest densities of barbel and gudgeon occurred in SC1 and SC3. Eurytopic species were most abundant in SC2 and almost absent from SC3. Highest densities of eurytopic fish occurred in COL. Densities of pikeperch, roach and bream were, however, comparable to densities in SC2.

Each water body contributed differently to the riverine fish community when all data are aggregated (Table 3.4). Owing to their hydrologically dynamic environment, without shelter, GF do not seem to provide suitable habitat for many fish species: densities of ide and of all eurytopic species were lowest and only for barbel and gudgeon were densities higher than in the less hydrologically dynamic floodplain water bodies (SC2, COL). Only for barbel and gudgeon did SC3 have a clear beneficial value over and above GF. SC1, with its complex shoreline and hence a moderate variability in flow velocities, had a greater beneficial value than GF. SC2 and COL had comparable beneficial values for asp as well as many eurytopic fish species.

3.3.3 Spatial distribution of 0-group fish within water bodies

Rheophilic fish were clearly spatially separated from eurytopic fish but also the species within each guild were spatially separated (Figure 3.6). In each year and season analysed (spring, summer and late summer), species composition varied significantly among habitats which differed in flow velocity and depth (Table 3.5). Flow velocity, water temperature and Secchi-disk depth were negatively correlated with depth. The fish assemblage in shallow, warmer habitats with higher flow velocities was characterized by rheophilic species while eurytopic species were concentrated in deeper, slower flowing habitats. Within the rheophilic guild, barbel and gudgeon were caught in the habitats with highest flow velocities whereas ide and asp prevailed in deeper habitats with lower flow velocities. Within the eurytopic guild, species also were spatially separated by flow velocity. Bleak occurred in the habitats with higher flow velocities than pikeperch and bream. Larvae of asp, bream, white bream, roach, ide and barbel, dominated in habitats that were covered by inundated terrestrial vegetation when available (Table 3.5; Figure 3.6).

Table 3.3. Results analysis presence-absence data (Table a) and abundance data (Table b; model 1) for 0-group fish to test differences among sampling years and water bodies (1329 samples). Dev.: Reduction in deviance. P_r>Chi (presence-absence) and P_r>F (abundance): ***: $p<=0.0001$; **: $p<=0.01$; *: $p<=0.05$; n.s.: non significant ($p>0.05$).

Table 3.3a	Presence-absence							
	Non-0	Wb	Year	Day(Wb)	Day^2	Depth	Flow	Dev
Barbel	201	***	n.s.	n.s.	***	***	n.s.	0.09
Asp	214	**	***	***	***	***	**	0.22
Ide	268	**	***	***	***	***	*	0.15
Gudgeon	135	***	***	***	***	n.s.	**	0.29
Roach	439	***	***	***	***	***	*	0.14
Bream	527	***	***	***	***	n.s.	**	0.16
White bream	161	***	*	***	***	n.s.	*	0.23
Bleak	275	***	***	***	***	n.s.	n.s.	0.34
Pikeperch	525	***	n.s.	***	***	n.s.	n.s.	0.16

Table 3.3b	Abundance						
	Wb	Year	Day(Wb)	Day^2	Depth	Flow	R^2
Barbel	*	n.s.	***	*	***	n.s.	0.34
Asp	**	**	**	n.s.	***	n.s.	0.34
Ide	**	**	**	n.s.	***	**	0.34
Gudgeon	**	**	n.s.	n.s.	***	n.s.	0.37
Roach	**	**	***	n.s.	***	*	0.27
Bream	***	***	***	n.s.	***	***	0.39
White bream	**	*	n.s.	n.s.	***	n.s.	0.41
Bleak	n.s.	n.s.	**	n.s.	***	n.s.	0.36
Pikeperch	***	*	***	n.s.	***	***	0.39

Table 3.4. Relative abundance of nine species in groyne fields (GF), secondary channels (SC) and a reconnected oxbow lake (COL) along the lower Rhine from 1997-1999. Numbers given per species are densities over all samples relative to the water body with the lowest densities (=1).

		GF	SC3	SC1	SC2	COL
Rheophilic	Barbel	4	17	6	1	3
	Asp	2	1	6	9	6
	Ide	1	1	5	4	2
	Gudgeon	6	30	22	5	1
Eurytopic	Roach	1	3	12	14	10
	Bream	1	2	6	2	8
	White bream	1	3	4	6	11
	Bleak	1	3	5	10	13
	Pikeperch	1	1	2	7	12

Figure 3.5. Densities of 0-group fish of the nine species in the five water bodies sampled in 1997, 1998 and 1999. 'x' is not sampled. Densities are the product of the fraction of non-zero catches and the mean abundance per non-zero catch (please note the log-scale). Water bodies are ordered along a gradient of decreasing connectivity with the main channel.

Depth and flow velocity often had statistically significant effects on the presence and abundance of the different stages of the nine species (Table 3.6), which largely supported the findings based on canonical correspondence analysis: rheophilic fish prevailed in shallow habitats with moderate flow whereas eurytopic fish were prevailed in deeper habitats with less flow.

Depth and flow velocities at which larvae occurred at highest densities, varied among species (Figure 3.7, 3.8) but of all species (except gudgeon) densities of larvae were significantly higher at sites with vegetation then at sites without (Figure 3.9, 3.10). Asp, bream and bleak larvae were found in shallow (<0.4 m deep) stagnant habitats. Larvae of barbel, ide and gudgeon occurred in highest densities in shallow habitats where water flowed with a moderate velocity (<0.20 m s^{-1}). On the contrary, larvae of white bream, roach and pikeperch were most abundant in deeper (>0.5 m) habitats. Roach larvae were present in highest densities in habitats with stagnant water while larvae of pikeperch and white bream occurred in habitats with flowing water as well.

As was observed for larvae, depth and flow velocities at which juveniles occurred at highest densities, varied among species (Figure 3.7, 3.8), but regarding cover of vegetation, densities of all species (except gudgeon and white bream) were, in general, highest in habitats with intermediate cover (1-50%; Figure 3.9, 3.10). Densities of barbel (<3 cm) were highest in shallow (<0.5 m deep), stagnant habitats but densities of barbel >3 cm were highest in habitats with low (0-0.05 m s^{-1}) flow conditions. Juveniles of asp, ide and roach occurred in habitats with various flow velocities (0-0.40 m s^{-1}) but were limited to shallow (<1 m deep) areas. In contrast, pikeperch and bream occurred at any depth but were limited to habitats with flow velocities <0.05 m s^{-1}. Juveniles of white bream and bleak were most abundant in shallow (<0.5 m deep) habitats with low flow velocities (<0.05 m s^{-1}). Ide, pikeperch, bream and bleak preferred shore zones with little (1-5%) cover, whereas asp, barbel, roach and white bream preferred moderate cover (5-50%).

Figure 3.6. Distribution of 0-group fish in groyne fields and floodplain water bodies along the River Rhine. Canonical correspondence analysis ordination diagram with fish stages and species, water bodies, substrate types and environmental variables. Data are results from analysing all data together (Table 3.5) but results are presented for rheophilic (upper panel) and eurytopic (lower panel) species separately. First and horizontal axis explains 0.054 of variance in species data, second axis 0.015. Species are abbreviated with their first two letters of genus and species name and their stage (1: larval; 2: juvenile <=3 cm; 3: juvenile >3 cm).

Rheophilic species

Figure 3.7. Occurrence of 0-group rheophilic fish along flow and depth gradients. The bubble size represents relative density at a site with a certain flow velocity (x-axis) and depth (y-axis). The sum of the surface of the bubbles in each chart is 100%. Densities were estimated by multiplying predicted fractions of non-zero catches and abundance in the non-zero catches for each class of flow and depth. Axes were used to symbolize significance: the horizontal for flow, the vertical for depth. Bold axes represent variables that were significant ($p<0.05$) in both the presence-absence and in the abundance model, normal axes represent variables that were significant in either of both models, dashed axes represent variables that were not significant in both models. The lower right panel presents distribution of depth and flow velocities at sites sampled.

Figure 3.8. Occurrence of 0-group eurytopic fish along flow and depth gradients. The bubble size represents relative density at a site with a certain flow velocity (x-axis) and depth (y-axis). The sum of the surface of the bubbles in each chart is 100%. Densities were estimated by multiplying predicted fractions of non-zero catches and abundance in the non-zero catches for each class of flow and depth. Axes were used to symbolize significance: the horizontal for flow, the vertical for depth. Bold axes represent variables that were significant (p<0.05) in both the presence-absence and in the abundance model, normal axes represent variables that were significant in either of both models, dashed axes represent variables that were not significant in both models.

Rheophilic species

Figure 3.9. Preference 0-group rheophilic fish for inundated terrestrial vegetation. Densities are the products of the fraction of non-zero catches and the mean abundance per non-zero catch. Of each stage and species, significance levels of the term 'percentage terrestrial vegetation' are given (presence-absence /abundance; model 3): P_r>Chi and P_r>F: ***: $p<=0.0001$; **: $p<=0.01$; *: $p<=0.05$; n.s.: $p>0.05$. Data of species and stages of which none of the variables in none of the models were significant are not presented. 'x'= value not represented in the analysis.

Eurytopic species

Figure 3.10. Preference 0-group eurytopic fish for inundated terrestrial vegetation. Densities are the products of the fraction of non-zero catches and the mean abundance per non-zero catch. Of each stage and species, significance levels of the term 'percentage terrestrial vegetation' are given (presence-absence /abundance; model 3): P_r>Chi and P_r>F: ***: p<=0.0001; **: p<=0.01; *: p<=0.05; n.s.: p>0.05. Data of species and stages of which none of the variables in none of the models were significant are not presented. 'x'= value not represented in the analysis.

Table 3.5. Results canonical correspondence analysis per sampling period. Sampling periods are indicated in Figure 3.2. Per habitat variable, the fraction of variance explained is presented. 'x': values for the habitat variable zero in each sample.

Year	Season	Samples	R²model	Terrestrial vegetation	Flow	Depth	Ctemp	Secchi	Gravel	Sand	Clay	Silt
1997	Spring	144	0.18	0.08	0.02	0.02	0.01	0.03	x	n.s.	n.s.	n.s.
	Summer	112	0.11	0.03	0.02	0.02	n.s.	0.02	x	0.02	n.s.	n.s.
	Late summer	81	0.19	x	n.s.	0.03	0.06	0.03	x	n.s.	0.02	0.03
1998	Spring	116	0.27	x	0.02	0.04	0.04	0.04	x	0.03	0.02	0.08
	Summer	103	0.13	x	0.02	0.05	n.s.	0.02	x	n.s.	0.03	0.02
	Late summer	85	0.25	0.03	0.07	0.06	n.s.	n.s.	x	n.s.	0.05	0.06
1999	Spring	452	0.15	0.04	0.03	0.02	0.01	0.01	n.s.	0.01	0.02	0.01
	Summer	151	0.17	0.02	0.02	0.02	n.s.	0.01	0.04	n.s.	0.05	0.02
	Late summer	106	0.18	x	0.03	0.02	0.04	0.05	n.s.	n.s.	n.s.	0.04
Total	1997-1999	1351	0.09	0.05	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.01

Table 3.6. Results analysis presence-absence data and abundance data (model 2) of 0-group fish for the factors flow velocity and depth. Dev.: Reduction in deviance. P_r>Chi (presence-absence) and P_r>F (abundance): ***: p <= 0.0001; **: p <= 0.01; *: p<=0.05; n.s.:p>0.05.

| Spec | Stage | Total | Non-0 | Presence-absence | | | Abundance | | |
				Flow	Depth	Dev	Flow	Depth	R^2
Barbel	Larvae (<=18 mm)	650	147	***	n.s.	0.05	***	**	0.32
	Juv1 (>18 mm)	591	56	**	**	0.13	n.s.	n.s.	-
	Juv2 (>30 mm)	498	37	n.s.	**	0.09	n.s.	*	0.21
Asp	Larvae (<=25 mm)	219	23	n.s.	*	0.11	n.s.	n.s.	-
	Juv1 (>25 mm)	326	16	n.s.	**	0.17	n.s.	n.s.	-
	Juv2 (>30 mm)	721	191	**	***	0.13	*	***	0.27
Ide	Larvae (<=24 mm)	404	56	*	*	0.09	**	**	0.47
	Juv1 (>24 mm)	279	28	n.s.	***	0.19	**	n.s.	0.36
	Juv2 (>30 mm)	780	212	n.s.	***	0.09	*	***	0.23
Gudgeon	Larvae (<=13 mm)	217	18	n.s.	n.s.	-	n.s.	n.s.	-
	Juv1 (>13 mm)	533	80	***	n.s.	0.09	*	*	0.26
	Juv2 (>30 mm)	596	100	***	n.s.	0.08	*	***	0.39
Roach	Larvae (<=16 mm)	446	92	n.s.	***	0.07	*	n.s.	0.16
	Juv1 (>16 mm)	524	135	n.s.	**	0.04	*	***	0.28
	Juv2 (>30 mm)	616	278	***	***	0.11	*	***	0.20
Bream	Larvae (<=19 mm)	689	264	**	*	0.04	***	***	0.29
	Juv1 (>19 mm)	613	173	***	n.s.	0.07	**	***	0.31
	Juv2 (>30 mm)	647	257	***	*	0.07	***	*	0.15
White bream	Larvae (<=19 mm)	456	62	n.s.	n.s.	-	*	**	0.37
	Juv1 (>19 mm)	526	93	**	*	0.07	n.s.	***	0.37
	Juv2 (>30 mm)	426	62	n.s.	n.s.	-	n.s.	**	0.27
Bleak	Larvae (<=12 mm)	648	132	n.s.	n.s.	-	n.s.	**	0.14
	Juv1 (>12 mm)	596	121	n.s.	n.s.	-	n.s.	**	0.19
	Juv2 (>30 mm)	425	192	n.s.	*	0.02	n.s.	***	0.13
Pikeperch	Larvae (<=18 mm)	529	183	*	n.s.	0.03	*	***	0.20
	Juv 1 (>18 mm)	569	151	***	*	0.08	**	**	0.23
	Juv2 (>30 mm)	750	313	*	**	0.03	***	***	0.20

3.4 Discussion

Newly created and reconnected floodplain water bodies provide suitable habitats for 0-group fish. Their value is greater than that of habitats in the main channel present originally, but depends on the type of water body and differs among reproductive guilds of fish. Secondary channels provided the best habitats for rheophilic fish while the reconnected oxbow lake provided the best habitat for eurytopic fish. Rheophilic and eurytopic 0-group fish were clearly spatially separated according to flow and depth, but species also showed different habitat preferences within each guild. Flow

velocity, depth and the presence of inundated terrestrial vegetation at a site determined the species assemblage. This offers the opportunity of designing floodplain water bodies with optimal environmental conditions for 0-group rheophilic fish. Future management should, however, focus on a diversity of habitat types and water bodies since each of the water bodies studied, had clear complementary values for specific species.

The five water bodies sampled had clear differences in their fish species composition that can be attributed to the observed habitat preferences of the fish and to differences in habitat characteristics. The most important habitat characteristics were water depth and flow velocity, as was also observed in the River Garonne, France (Gozlan *et al.*, 1998) and the River Danube, Austria (Schiemer & Spindler, 1989). Our findings, that rheophilic fish prefer shallow sites with moderate flow, corroborate the habitat preferences of these species found in other European Rivers (Copp, 1992; Watkins *et al.*, 1997; Baras *et al.*, 1995; Garner & Clough, 1996; Gozlan *et al.,* 1998; Bischoff & Freyhof, 1999; Jurajda, 1999). Species composition shifted along a gradient of flow and connectivity: the highest proportion of rheophilic fish in the hydrologically dynamic GF and SC3 and the highest proportions of eurytopic fish in the less dynamic SC2 and COL. Our results show, however, that within these guilds, habitat preference varies among species along a gradient of flow and connectivity also: barbel and gudgeon preferring sites with higher flow velocities than ide and asp. Consequently, barbel and gudgeon prevailed in SC3 and GF whereas ide and asp prevailed in SC2 and COL. A comparable pattern was observed among the eurytopic species: bleak occurring at sites with higher flow velocities in the more dynamic water bodies, pikeperch and bream occurring in stagnant habitats in SC2 and COL.

The pattern of spatial distribution of the different fish species observed in our man-made secondary channels and reconnected oxbow lake resembles the spatial occupation observed in natural floodplains along other European rivers with comparable environmental conditions and a comparable fish fauna. The abundance of rheophilic fish decreased with decreasing flow velocities in secondary channels and connected oxbow lakes in the Szigetköz floodplain along the River Danube. In a slow flowing secondary channel, 0-group rheophilic species (barbel, nase *Chondrostoma nasus*, dace *Leuciscus leuciscus*, chub *L. cephalus* and ide) dominated whereas eurytopic species (bream, roach, white bream and perch *Perca fluviatilis*) dominated a downstream connected oxbow lake (Guti, 1996). Rheophilic species (nase, dace, gudgeon and chub) were abundant in a secondary channel in the Basses Terres floodplain along the Upper Rhône while they were absent from a downstream connected oxbow lake. Eurytopic species (roach, bream and white bream) occurred in

both types of water body (Copp & Peñáz, 1988) but bream and white bream were most abundant in connected oxbow lakes (Copp, 1989).

During floods, submerged terrestrial vegetation determined the spatial distribution of the 0-group fish. In addition to its importance as a spawning substrate, submerged vegetation probably provides food and shelter for 0-group fish. During floods, terrestrial organisms will also be part of the floodplain foodweb (Winemiller, 1996) and the abundance of macro-invertebrates is usually higher among submerged vegetation (Swales, 1979; Brock & Van der Velde, 1996). In dense vegetation, there will be lower flow velocities that will better suit the poor swimming capacities of larvae (Lightfoot & Jones, 1979; Copp, 1990). During early life stages, larvae may be severely affected by high flow velocities that limit feeding and growth (Flore & Keckeis, 1998) and optimal flow velocities are critical during these stages (Schiemer *et al.*, 1991). For juveniles, that obviously swim more strongly than larvae, low-flow conditions among submerged vegetation could be of less importance than shallow areas which provide daytime refuges from potential predators (Copp, 1990; 1992; Copp & Jurajda, 1993). At present, permanent aquatic vegetation is, however, completely absent from the water bodies sampled. It is unlikely that aquatic vegetation will develop in these water bodies due to their frequent and large water level fluctuations and their low transparency. Thus the presence of submerged vegetation depends completely on the flooding of terrestrial plants.

Permanently connecting floodplain water bodies to the main channel significantly increases the probability of terrestrial vegetation being inundated, in all months of the growing season (Figure 3.11). At the moment, at low discharge, habitat variability in the main channel is low and, for most fish species, suitable spawning and nursery areas are lacking. Flooding of terrestrial vegetation increases habitat diversity but, the aquatic/terrestrial transition zone is only small. Due to the presence of summer dykes, inundation of large areas in the floodplains during the spawning or nursery season depends on erratic floods that do not occur every year. Consequently, for most fish species, availability of suitable habitat during the spawning and nursery season is unpredictable. It has been shown that, in lowland rivers, discharge stochasticity sometimes strongly controls population size (Welcomme, 1979; Grossman *et al.*, 1982; Schiemer & Zalewski, 1992; De Mérona & Gascuel, 1993; Spindler, 1995; Winemiller, 1996). For most fish species, the unpredictable availability of habitat in the lower River Rhine might be an important factor limiting year-class strength. Rehabilitating floodplains by removing summer dykes will increase the probability of suitable habitat for fish during the spawning and nursery season and could contribute significantly to rebuilding fish populations.

At present, the national policy concerning major rivers in the Netherlands provides the opportunity to improve the environmental conditions for rheophilic species on a larger scale, in more floodplains. The policy aims at sustainable flood protection along the rivers that will be achieved through a combination of measures: strengthening the dykes, retaining the water and giving the rivers more room to expand (Ministry of Transport, Public Works and Water Management, 1998). The secondary channels investigated, that were also aimed to give the river more room in the floodplain, seem to combine improved safety with improved environmental conditions for fish. They did provide suitable habitat and clearly had a beneficial value for the riverine fish community above that provided by the groyne fields originally present. On a local scale, these water bodies thus provide riverine fish with habitats whose absence is thought to limit their population sizes, and they seem to compensate for the lack of natural floodplain water bodies with a permanent connection to the river. Therefore, the type of water body assessed in this study could be replicated on a larger scale, within the framework of sustainable flood protection. Since we only compared fish assemblages among the newly created floodplain water bodies, they may not be

Spawning season Nursing season

Probabilities of submerged terrestrial vegetation (%)		
	Before rehabilitation	After rehabilitation
Water level	(>11.2 m)	(>9.6 m)
March	31	65
April	32	74
May	20	68
June	22	73
July	8	60
August	2	34
September	1	19

Figure 3.11. Probabilities of water levels in the spawning season (left panel) and nursing season (right panel). The vertical lines indicate water levels at which large areas with terrestrial vegetation get inundated in the present situation (11.2 m a.s.l.) and in connected floodplain water bodies with moderate slopes (9.6 m a.s.l.). Probabilities of these water levels per month are indicated in the table.

optimal for rebuilding the population of rheophilic fish in the lower Rhine. From the analysis of spatial distribution at the habitat level (1×10^{-4} km^2), however, some guidelines for the design of optimal floodplain water bodies for fish can be given.

Generally speaking, floodplain water bodies should have complex shorelines with a high variability of flow velocities and moderate slopes where terrestrial vegetation can develop that has a high probability of being submerged during spring and summer. The morphology and hydrology of floodplain water bodies can probably be designed to enhance specific groups of fish species. For example, to enhance rheophilic species such as barbel and gudgeon, floodplain water bodies should have shallow (<1 m) areas with moderate flow velocities of 0.05-0.15 m s^{-1}. Shallow (<1 m) areas are also important for other rheophilic species such as ide and asp, but for these species, flow velocities should be less than 0.10 m s^{-1}. These types of water body will also enhance the eurytopic bleak that preferred comparable habitats. Permanently connected water bodies with stagnant water deeper than 2 m are probably beneficial for eurytopic species such as bream, roach and pikeperch. As described above, for almost all fish species, submerged terrestrial vegetation is important as a spawning substrate in spring and as refuge and foraging areas in summer. Therefore, the slopes of these water bodies should be moderate and balanced between too steep (terrestrial vegetation will develop but will seldom be submerged) and too shallow (the shore zone will be flooded too frequently and no terrestrial vegetation can develop).

Future management of floodplains should focus on increasing the diversity of aquatic habitats in order to increase species diversity and restore the fish community of the lower River Rhine, since different types of water body had clear complementary values for the riverine fish community. In rivers, as elsewhere, biodiversity is in general attributable to habitat heterogeneity (Hildrew, 1996; Ward, 1998) and preservation of a high biodiversity is preferred above active management for a single species (Tockner *et al.*, 2000). Our results give insight into the habitat preferences of 0-group fish but, more importantly, they explain why, and prove, that newly created and reconnected floodplain water bodies do have a beneficial value for the riverine fish community. Moreover, they show that morphological and hydrological characteristics of the floodplain water body directly determine the species composition of the 0-group fish assemblage. Consequently, restoration of the river-floodplain interaction, combined with sound development of various types of habitat, can contribute significantly to ecological restoration of the river-floodplain system.

Acknowledgements

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Photo 4. Measuring the catch in a reconnected oxbow lake (Wetland Passewaaij).

Chapter 4

How fish utilize restored floodplain water bodies along the lower River Rhine

Abstract

This study presents a first description of the structure of the fish community that is present year-round in floodplain water bodies that were created for nature restoration purposes. These water bodies should compensate for the loss of low-flow zones and connected backwaters along the lower River Rhine. Their contribution to the restoration of populations of endangered rheophilic cyprinids was assessed by investigating the extent to which they function as spawning and nursery areas for these species. The functioning is inferred from patterns of occurrence over time of larval, juvenile and adult fish during two consecutive years. Of the 47 species observed in the Rhine in the Netherlands, 30 occurred in the floodplain water bodies. Of 23 species, 0-group fish were present. The water bodies function as short-term nursery areas for rheophilic species of which densities peaked in summer. The secondary channels may also function as spawning areas for ide *Leuciscus idus* and gudgeon *Gobio gobio*, but this could not be demonstrated unambiguously. For the lithophilic species (barbel *Barbus barbus* and asp *Aspius aspius*) they do not function as spawning areas since suitable substrate is lacking. Eurytopic species (bream *Abramis brama*, roach *Rutilus rutilus* and pikeperch *Stizostedion lucioperca*) use these water bodies both as spawning and nursery areas. We conclude that the colonization of these new water bodies has been rapid and that their functioning for fish resembles that of natural water bodies as described for less degraded rivers elsewhere. However, stock rehabilitation of Rheophilic A species in the lower reaches of the Rhine may be constrained by lack of suitable upstream spawning areas and the opportunities for larvae to passively reach downstream nursery areas. Restoration of lateral connectivity is probably most important for their rehabilitation, because longitudinal connectivity between spawning and nursery areas is not limiting.

4.1 Introduction

Floodplain rehabilitation along the River Rhine in the Netherlands is aimed at restoring habitats that were prevalent in ancient times when there was strong interaction between the hydrodynamics of the river and the adjacent floodplains (Van Urk & Smit, 1989; WWF, 1993; Middelkoop & Van Haselen, 1999). At several locations in the floodplains, secondary channels have been dug and isolated oxbows have been connected to the main channel by a downstream opening (Buijse & Vriese, 1996; Cals *et al.,* 1998). These water bodies should compensate for the loss of low-flow zones and connected backwaters, and should provide living conditions for rare or endangered organisms in the lower Rhine (Schropp & Bakker, 1998).

In many rivers, fish migrate between the main channel and the floodplains to spawn, forage or avoid harsh conditions (Welcomme, 1979; Welcomme & De Mérona, 1988; Fernandes, 1997; Molls, 1999; Saint-Paul *et al.,* 2000). They have adapted to the variation in connectivity, and this leads to a lateral zonation of fish reproduction in floodplain water bodies (Copp & Peñáz, 1988; Copp, 1989; Copp *et al.*, 1991; Guti, 1993). From the lotic main channel to the lentic zones in the floodplains, reproduction of different fish species in European rivers ranges from rheophilic, through eurytopic to limnophilic (Regier *et al.*, 1989; Schiemer & Waidbacher, 1992). Of those three guilds, only rheophilic and eurytopic species require low-flow zones or water bodies during certain parts of their life-history. Limnophilic species, such as tench *Tinca tinca* and weatherfish *Misgurnus fossilis*, remain in the temporarily isolated lakes throughout their lives.

During their ontogeny, rheophilic cyprinids such as barbel *Barbus barbus* and ide *Leuciscus idus*, require a specific sequence of habitat types (Schiemer *et al.*, 1991; Schiemer & Zalewski, 1992; Schiemer *et al.*, 1995). All rheophilic species lay their eggs in flowing water but the preferred spawning substrate varies (Balon, 1975; Mann, 1996). During early stages of their life cycles, they depend on inshore zones of the river or on low-flow, connected backwaters (Schiemer & Waidbacher, 1992) since their range of optimal and critical flow velocities is very restricted (Flore & Keckeis, 1998; Schiemer *et al.*, 2001[a]). With increasing size, habitat requirements with regard to flow velocity, substrate type and food change dramatically and habitat shifts are commonly observed in young cyprinid assemblages in large rivers (Gaudin, 2001).

Eurytopic species, such as bream *Abramis brama* and roach *Rutilus rutilus*, are habitat generalists that occur in the main channel as well in various types of floodplain water body (Schiemer & Waidbacher, 1992). Many eurytopic species use low-flow zones and connected backwaters throughout their lives. Either they occur consistently

in high densities in the backwaters year-round or they are present only in high densities during the spawning season (Schiemer & Spindler, 1989; Holcik, 1996; Molls, 1999).

In the Rhine, regulation of flow has led to a loss of inshore habitat, a lowered water table, siltation of the floodplains and a reduction in river-floodplain connectivity. In the main channel, only groyne fields provide low-flow zones but, because of the intensive shipping, water level in these fields fluctuates almost continuously and strong reversing currents create a highly dynamic environment. Natural water bodies with a permanent connection to the main channel have mostly been disconnected and the floodplains inundate more abruptly and less frequently than before embankment. The resulting landscape is a fixed main channel with a fringe of floodplains, with little variation in frequency and duration of flooding (Buijse & Vriese, 1996; Cals *et al.*, 1998).

Poor habitat diversity, in combination with the poor water quality in the 1960s led to a dramatic decline in species diversity of the Rhine fish community. At present, 47 species occur in the River Rhine in the Netherlands dominated by four eurytopic species; pikeperch *Stizostedion lucioperca*, bream, white bream *Abramis bjoerkna* and roach (Klinge *et al.*, 1998). Abundance of rheophilic species declined strongly (Lelek, 1989; Van den Brink *et al.*, 1990; Van den Brink *et al.*, 1996) and most species are listed as vulnerable or endangered on the Netherlands red list of fresh water fish species (De Nie & Van Ommering, 1998). In other European rivers also, most rheophilic cyprinids have declined and are often considered endangered, e.g. the Danube (Schiemer & Spindler, 1989; Guti, 1993), Pilica, Warta & Gwada (Penczak & Kruk, 2000), Morava (Jurajda, 1995), Havel and Spree (Wolter & Vilcinskas, 1999) and Oder (Bischoff & Wolter, 2001[a]). The main cause of their decline in regulated rivers is, according to Schiemer (1999, 2000), the lack of inshore river structures, which form the spawning and nursery habitats of these species. A potential stock of rheophilic cyprinid species is, however, currently present in the lower Rhine (Klinge *et al.*, 1998) and ecological rehabilitation is no longer limited by water quality (Admiraal *et al.,* 1993). Expansion of their populations is therefore thought to nowadays be curtailed by scarcity of suitable habitats (Buijse & Vriese, 1996; Cals *et al.,* 1998). The restored floodplain habitats should provide suitable habitat for spawning and nursery areas and contribute to rebuilding the population of rheophilic fish.

Riverine fish have proven to be remarkably persistent under environmental change, probably because they are adapted to intense and frequent natural disturbances such as extreme floods and droughts (Bayley & Li, 1994). They are, for example, able to exploit new habitats such as a newly created side arm of the Danube (Schmutz *et al.*, 1994), flooded areas that had not been accessible for decades (Bayley *et al.*, 2000) and pools along the lower Oder that were formed by a dyke breach (Bischoff & Wolter,

2001[b]). Within a few years after the creation of two secondary channels and a connected oxbow lake along the lower Rhine, 0-group rheophilic fish were observed in these new habitats (Grift *et al.*, 2001; Simons *et al.*, 2001) but it is as yet unknown which function these types of water body fulfil and whether they contribute to the rehabilitation of the riverine fish community. In this study, their functioning as spawning and nursery areas is inferred from the temporal patterns of occurrence of larval, juvenile and adult fish during two consecutive years. With knowledge about the functioning of these types of floodplain water body, their contribution to restoration of the riverine fish community may be assessed and advice on the location, shape and character of future floodplain water bodies might be given.

Numerous studies have described the ecological functioning of floodplain water bodies for fish in the German reaches of the lower Rhine (Molls, 1999) and other European rivers, e.g. Danube (Schiemer, 1985; Guti, 1996; Holcik, 1996), Rhône (Copp & Peñáz, 1988; Copp, 1989; Copp *et al.*, 1991), the Great Ouse (Copp, 1991) and Garonne (Gozlan *et al.*, 1998). It is, however, the first time that the fish community structure in floodplain water bodies along the lower Rhine has been described year-round. Moreover, our results are a first test of the functioning of these newly created and reconnected floodplain water bodies along the Rhine.

Study area

The Rhine, from its source in Switzerland to the outflow to the North Sea, is 1320 km long and has a catchment area of 185,000 km^2 (Lelek, 1989), of which 25,000 km^2 are situated in the Netherlands, forming the delta area. Where the Rhine enters the Netherlands (at Lobith; Figure 4.1), the average discharge is 2200 m^3 s^{-1} (Middelkoop & Van Haselen, 1999). Floods may occur in winter, early spring and summer (Figure 4.2) but their origin may differ. High precipitation and low evaporation in the catchment area may cause peaks in winter. Melting ice and snow in the Alps may cause peaks in spring and early summer (April-June). Just after crossing the border, the river splits into three branches, of which one (River Waal) transporting 66% of the water, is free flowing and less canalized than other branches (Rivers Lek and IJssel): 19% of the shoreline consists of rip-rap. In the main channel, flow velocities vary between 0.5 and 1.5 m s^{-1} and sand, apart from the boulders covering the groynes, is the only substrate. Only groyne fields provide areas where flow velocity is moderate but strong eddies occur that are caused by ships passing, on average, every three minutes. At moderate water levels, the main channel has an average depth of 4 m and the groyne fields have average depths of 2-3 m.

Figure 4.1. Maps of the River Rhine in the Netherlands and of the floodplain water bodies sampled. Arrows indicate the direction of flow. Secondary channel 1 (SC1) and secondary channel 2 (SC2) are both flow-through systems. The connected oxbow lake (COL) is predominantly stagnant. Water flows during rising and falling water levels in the main channel and due to water displacement of passing ships.

Figure 4.2. Water levels and water temperatures of the River Rhine near Lobith in 1997 (solid lines) and 1998 (dashed lines). The hatched horizontal line in the water level figure indicates the water level above which terrestrial vegetation in floodplains is inundated (>9.6 m a.s.l. at Lobith). Arrows indicate sampling periods in 1997 (top panel) and 1998 (bottom panel): white arrows sampling of 0-group fish; black arrows of 1+ fish. Minimum and maximum water levels and the percentiles per month are presented in the middle panel (data from 1970-1999).

At present, there are 62 water bodies with a permanent connection to the main channel, along the three branches of the lower Rhine, of which three along the River Waal were sampled in the present study (Figure 4.1). They were the only secondary channels and reconnected oxbow lake along the River Waal at the time of sampling and are all part of floodplain restoration projects. The other 59 water bodies are man-made sand-pits or harbours.

Both secondary channels (SC1 and SC2) are very dynamic and flowing water is permanently present. In the less dynamic reconnected oxbow lake (COL), water is predominantly stagnant and water only flows when the water level in the main channel rises and falls, or due to water displacement by passing ships. The distance between the most upstream and most downstream water body sampled is 21 km. Aquatic macrophytes were absent from all the water bodies and, during floods (water level >9.6 m above sea level (a.s.l.) at Lobith), inundated terrestrial plants were the only vegetation present.

SC1 (river km 929; average surface 13.6 ha.) was created in 1994, the first in the Netherlands. A 1 km wing dyke, built in 1984 to prevent erosion of an outer curve of the River Waal, was opened at both ends and all the groynes were cut through (Figure 4.1). The resulting complex outline means that SC1 has a well developed shoreline and a moderate variation in flow velocities. Average flow velocity in the secondary channel, that has a depth of about 1.5 m at moderate water levels, is 0.1-0.4 m s^{-1} and the substrate is sand. In the former groyne fields, which are less than 1.5 m deep, flow velocity is close to zero and the substrate is sand and silt. Slopes in the area are moderate except at the wing dykes and former groynes, which are covered by boulders of 15-20 cm.

SC2 (river km 908; average surface 26.9 ha.) was created in 1997 by excavating channels between a sand-pit and an oxbow, each of which was connected on one side to the main channel. Water now enters the sand-pit, which has a depth of approximately 15 m, then flows out through the secondary channel and along the oxbow before returning to the main channel. In this secondary channel, flow velocities vary between 0.1 and 0.4 m s^{-1}, the average depth is 1.5 m and the substrate is sand. In the former clay-pits, which have been laterally interconnected, water is stagnant, depth varies between 1 and 2.5 m and the substrate consists of clay and silt.

COL (river km 917; average surface 5.4 ha.) was created in 1996 by permanently reconnecting an oxbow to the main channel at its downstream end (Figure 4.1). Except at this connection point, where passing ships cause water to move in and out, COL is stagnant. Occasionally, less than 50 days per year, (water level >12 m a.s.l. at Lobith), water from upstream enters the lake. The deepest part (3-4 m deep) is at the

upstream end and has almost vertical slopes. In the other parts, slopes are moderate and depths vary from 0.5-2.5 m. Apart from some patches of clay, the substrate is sand.

Between 1997 and 1998 water levels in the Rhine exhibited widely different patterns, while water temperatures exhibited a similar pattern (Figure 4.2). In both years, there were several peaks in the discharge during which terrestrial vegetation was inundated. Compared to long term records, 1997 was an average year with discharge peaks in spring and summer, whereas 1998 was an exceptional year with low discharge in spring and summer and a peak in September, which has a low long-term median discharge (Figure 4.2). In March 1997 and November 1998 the floodplains were inundated bankful. At these water levels, fish could not be sampled effectively.

4.2 Materials and Methods

4.2.1 Data collection

1-group and older (1+) fish were sampled every seven weeks from March to December 1997 and 1998 (Figure 4.2) with a 100 m seine net and a 7 m trawl (Table 4.1), except in September 1998, when only COL was sampled due to logistic reasons. All seine hauls were made in a standardized manner so that the area fished was approximately 3000 m^2. The fish were measured (fork length, to the nearest cm) in the field, kept in 'life-nets' and released at the end of each sampling day. In addition to the seine net and trawl, electro-fishing (150 V DC, 5 A) was used in some parts of the water bodies such as the wing dyke of SC1 and among inundated terrestrial vegetation when it was available.

Table 4.1. Overview of nets used.

Gear type		Mesh size (mm stretched)	Width	Height	Area covered (m^2)	Period	Years
Seine nets	100 m seine	14.0	100.0	3.0	3000	Mar-Dec	97, 98
	Seine net 1	1.5	16.0	1.5	65	Apr-Jul	97, 98
	Seine net 2	7.5	25.0	1.5	140	Jul-Sep	97,98
Trawls	Trawl 1	17.0	7.0	1.0	1400	Mar-Dec	97,98
	Frame trawl 1	4.0	2.4	0.7	200	Apr-Jul	97,98
	Frame trawl 2	0.5	1.3	0.5	400	Apr-Jul	98
	Beam trawl	4.0	3.5	0.75	800	Jul-Sep	97,98

0-group fish were sampled approximately every three weeks from April to September in both years (Figure 4.2) with two fine meshed seine nets and three types of trawl (Table 4.1). Hauls with both seine nets were made in a standardized manner so that the area fished was 65 m^2 and 140 m^2 respectively. Trawls were towed behind a

boat and were used to sample both at the bottom and at the surface. The towed distance of each 5 minute haul was estimated with a digital flow meter. The surface sampled was calculated by multiplying the distance towed by the width of the trawl. 0-group fish were preserved in 4% formalin and identified in the laboratory as described in Grift *et al.* (2001). Fork length was measured to the nearest mm for fish smaller than 10 cm and to the nearest cm for larger fish.

4.2.2 Data analysis

Densities of fish were expressed as numbers per 1000 m^2 sampled. For 1+ fish, only samples from the seine net were used. In all the water bodies, nearly the whole surface could be sampled well with the seine. For 0-group fish, samples from seine nets and trawls were combined. Data were analysed in detail for one Rheophilic A cyprinid species (barbel), three Rheophilic B cyprinid species (asp *Aspius aspius*, gudgeon *Gobio gobio* and ide) and five eurytopic species (pikeperch, white bream, bream, roach and bleak *Alburnus alburnus*). These nine species comprised the four most abundant rheophilic species and the five most abundant eurytopic species. Their numbers comprised 92% of both the 0-group and 1+ fish assemblages.

Fish species were classified into reproductive guilds according to Schiemer & Waidbacher (1992) and Quak (1994). 0-group fish were distinguished from older fish by evaluating length-frequency distributions that gave clear cut-off lengths for most species. For gudgeon, this distinction was less clear and all gudgeon >5 cm were considered 1+ (Mann, 1980). To distinguish larvae from juveniles, developmental stage (larval or juvenile) and length (mm fork length) of 500 fish of the nine species analysed were recorded in total. The juvenile stage is defined as the first stage in which all fins are completely differentiated (Copp, 1990). Cut-off lengths for juvenile fish were determined as the length at which 50% of the fish were in each stage. Lengths at which fish became juveniles, as measured in this study, were comparable with those found in the literature (Balinsky, 1948; Copp, 1990; 1992; Baras & Nindaba, 1999; Gozlan *et al.*, 1998).

We decided to pool length-frequency distributions over water bodies because, for the nine species, the pattern in time hardly varied among the water bodies. Moreover, mean length of 0-group fish hardly varied among water bodies and between years. Only for asp, ide and white bream, did growth differ significantly (ANOVA, p>0.05) among water bodies but the differences were small.

4.3 Results

4.3.1 Species composition and size distributions

In total 30 fish species were caught and 0-group fish were caught of 23 species. Within the 1+ fish assemblage, species richness was highest in SC1 (22 and 24 species in 1997 and 1998 respectively) and lowest in COL (16 and 19 species; Table 4.2). Within the 0-group fish assemblage, however, species richness hardly varied among water bodies (Table 4.2). In all water bodies, the majority of the 1+ fish belonged to the eurytopic guild (93-99%); rheophilic species contributed only 1-6% (Table 4.2). The most abundant eurytopic species were bream, bleak, roach, white bream and perch *Perca fluviatilis* and the most abundant rheophilic species were ide, chub *Leuciscus cephalus*, asp and gudgeon. Species composition within the 0-group fish assemblage was different: the proportion of eurytopic fish varied from 39 to 99% whereas rheophilic species contributed from 1 to 61% (Table 4.2). In both guilds, the same species (and barbel) were most abundant as in the 1+ assemblage. Limnophilic species and diadromous rheophilic species were present, but their proportions in both the 0-group and the 1+fish assemblages were very low.

4.3.2 Patterns in time of asp, ide, gudgeon and barbel

Throughout the sampling period, 1+ asp occurred in the floodplain water bodies but their densities were low, except in summer/ early autumn (July-October) 1997 (Figure 4.3). Most of them were <25 cm and probably sub-adults. Patterns in time of 0-group asp were comparable in all water bodies in both years: an almost absence of larvae, appearance of juveniles of 3-5 cm in June after which juveniles were continuously present and grew to an average length of 10 to 11 cm in autumn (Figure 4.5; 4.7).

1+ ide were observed in low densities throughout the sampling period, except in December 1998 when, in addition, 22 adult ide were caught in SC1. 0-group ide were abundant from spring to autumn. Some larvae were observed during the first two sampling occasions in SC2, in April and May 1997 (Figure 4.5). From June 1997 onwards, they occurred in all the water bodies and stayed during the rest of the year. During the first sampling in 1998 (in May), larvae occurred at all sites but their densities varied among the three water bodies: 1583, 156 and 1 per 1000 m^2 in SC2, COL and SC1 respectively. In June, however, densities in COL and SC1 had increased sharply to 965 and 3048 per 1000 m^2 respectively, whereas densities in SC2 decreased (to 362 per 1000 m^2). From June onwards, densities generally decreased in all water bodies. By September, their mean length was 10 cm.

In 1997, 0-group gudgeon were first observed in June (in SC1), and in 1998 they were first observed in May (in SC1 and COL; Figure 4.5). From these dates onwards, larvae occurred almost continuously until August but the total numbers decreased from June onwards and became zero after August in both years. The presence of larvae from May through August (Figure 4.7) may reflect the multiple spawning periods of this species. 1+ gudgeon were observed occasionally in low densities (Figure 4.3).

In all three water bodies, larvae of barbel were present at low densities during the second sampling, in May 1997 (2, 4 and 5 per 1000 m^2 in SC1, SC2 and COL respectively). Only in SC1 had their numbers increased sharply in June (240 per 1000 m^2) when the majority of barbel was 2-4 cm. In 1998, barbel appeared also in May (at the first sampling) but only in SC1 and COL where they occurred in comparable densities (22 and 25 per 1000 m^2 in SC1 and COL respectively). From June onwards, 0-group barbel occurred in SC2 also and at all locations their numbers decreased. As from August, 0-group barbel had disappeared from the floodplains in both years. Only a few 1+ barbel were caught of which none was larger than 10 cm nor could be considered adult (Figure 4.3).

4.3.3 Patterns in time of roach, bream, white bream, bleak and pikeperch

In both years, roach showed similar patterns over time: sub-adults resided in the floodplains year-round whereas in spring, adults moved in after which 0-group roach became abundant and remained so (Figure 4.4, 4.6, 4.8). Throughout the sampling period, sub-adult roach were present in rather constant densities, also during winter of 1997/1998. Adults were also present year-round, but their densities varied over time (Figure 4.4). In winter (December-March), their densities were almost zero but in spring (April) adult roach moved into the floodplains after which their densities became low during summer. After the adults had immigrated, 0-group roach became abundant and remained throughout the rest of the year (Figure 4.6) while their mean lengths increased (Figure 4.8).

Sub-adults and adults of bream were present throughout the entire sampling period; densities of sub-adults were, however, low in winter (December-March) and the numbers of adults increased sharply in spring (April). After adult bream had immigrated, 0-group bream became abundant and remained throughout the rest of the year (except in SC1 in 1997; Figure 4.6), while their mean lengths increased (Figure 4.8).

Table 4.2. Numerical composition of the 1+ and 0-group fish assemblage in three floodplain water bodies in 1997 and 1998. Data on 1+ fish are from surveys for 1+ fish only; data for 0-group fish from the surveys for 0-group fish only.

| | | 1+ fish | | | | | | | 0-group fish | | | | | | |
| | | SC1 | | SC2 | | COL | | | SC1 | | SC2 | | COL | | |
Guild	Year	1997	1998	1997	1998	1997	1998	Average	1997	1998	1997	1998	1997	1998	Average
	Numbers caught	**1403**	**2557**	**3522**	**1589**	**2854**	**2745**		**3294**	**10870**	**8433**	**49945**	**10511**	**34618**	
	Number of species	**22**	**24**	**16**	**16**	**16**	**19**		**20**	**15**	**18**	**14***	**17**	**15**	
Rheophilic A	Barbus barbus (E)*	0.1	.	.	.	.	.	0.0	6.8	3.3	0.4	0.0	0.2	0.2	1.8
	Chondrostoma nasus (E)	0.1	0.0	.	.	.	0.0	0.0	1.0	0.0	0.1	.	0.0	.	0.2
	Cottus gobio	0.1	.	0.0	.	.	.	0.0	.	.	0.0	0.0	.	.	0.0
	Lampetra fluviatilis (V)	0.1	.	.	.	.	.	0.0	.	.	.	.	.	.	0.0
	Leuciscus cephalus (V)	0.4	2.5	.	.	0.0	0.1	0.5	0.5	0.0	0.3	0.0	0.2	0.0	0.2
	Leuciscus leuciscus (V)	0.2	0.0	.	.	.	0.1	0.1	0.8	0.1	0.1	0.0	0.1	0.1	0.2
Rheophilic B	Aspius aspius	0.4	0.5	0.9	0.5	0.7	0.3	0.5	2.9	4.9	1.6	5.2	0.7	1.1	2.7
	Cobitis taenia	.	0.0	.	.	.	.	0.0	0.0	.	.	.	.	.	0.0
	Gobio gobio	0.6	0.9	.	0.1	.	0.2	0.3	3.8	11.9	0.2	0.4	0.0	0.0	2.7
	Leuciscus idus (S)	1.1	1.2	0.1	0.1	0.2	0.4	0.5	5.7	41.3	0.8	18.3	0.2	4.9	11.8
Diadromous	Coregonid sp.	.	0.0	.	.	.	.	0.0	.	.	.	.	.	.	0.0
	Platichthys flesus	0.8	0.2	0.1	0.1	.	0.0	0.2	.	.	.	.	.	.	0.0
	Total rheophilic	**4.0**	**5.5**	**1.1**	**0.8**	**0.9**	**1.2**	**2.2**	**21.4**	**61.4**	**3.5**	**23.9**	**1.4**	**6.4**	**19.7**
Eurytopic	Abramis bjoerkna	6.1	2.9	8.8	2.8	11.1	7.9	6.6	7.9	0.3	5.8	0.1	12.9	0.4	4.6
	Abramis brama	41.5	56.1	42.9	64.2	61.7	56.9	53.9	6.2	3.1	8.5	5.7	20.5	16.0	10.0
	Alburnus alburnus	11.5	6.5	24.3	10.6	12.0	13.1	13.0	8.1	10.5	13.8	12.2	21.5	11.5	12.9
	Anguilla anguilla (S)	2.9	1.3	0.1	0.7	1.0	3.1	1.5	.	.	.	.	.	.	0.0
	Cyprinus carpio	0.1	0.1	.	.	.	0.1	0.1	1.1	.	.	0.0	0.0	0.0	0.2
	Esox lucius	0.1	0.1	0.3	0.6	0.3	0.1	0.2	0.1	.	.	.	.	.	0.0
	Gasterosteus aculeatus	.	0.1	.	0.2	.	.	0.1	0.2	.	.	.	0.0	0.0	0.0
	Gymnocephalus cernuus	2.3	1.1	1.7	0.8	0.7	1.4	1.3	1.4	1.5	0.5	0.7	0.3	0.3	0.8
	Perca fluviatilis	2.6	1.5	0.4	0.3	0.6	0.5	1.0	11.7	2.3	8.6	6.7	8.1	4.5	7.0
	Pseudorasbora parva	.	.	.	0.0	.	.	0.0	.	.	.	.	.	.	.
	Rutilus rutilus	20.4	20.6	16.6	13.0	6.0	5.6	13.7	27.4	16.4	30.6	19.2	10.3	21.9	21.0
	Stizostedion lucioperca	4.6	2.3	2.7	5.7	3.9	9.1	4.7	5.6	3.7	25.6	29.8	23.6	36.5	20.8
	Hybrid	0.4	0.2	0.7	0.1	0.4	0.4	0.4	8.5	0.0	0.1	0.1	0.2	0.0	1.5
	Unidentified	.	.	.	.	.	.	0.0	0.4	0.8	2.8	1.6	1.2	2.3	1.5

		1+ fish							0-group fish						
		SC1		SC2		COL			SC1		SC2		COL		
Guild	Year	1997	1998	1997	1998	1997	1998	Average	1997	1998	1997	1998	1997	1998	Average
	Numbers caught	**1403**	**2557**	**3522**	**1589**	**2854**	**2745**		**3294**	**10870**	**8433**	**49945**	**10511**	**34618**	
	Number of species	**22**	**24**	**16**	**16**	**16**	**19**		**20**	**15**	**18**	**14***[*]	**17**	**15**	
	Total eurytopic	**92.5**	**92.8**	**98.4**	**98.9**	**97.8**	**98.3**	**89.8**	**78.5**	**38.6**	**96.4**	**76.1**	**98.6**	**93.6**	**75.7**
Limnophilic	*Carassius carassius* (V)	.	0.0	.	.	.	.	0.0	.	.	.	.	.	.	0.0
	Leucaspius delineatus (V)	2.6	0.8	0.2	0.3	0.4	0.4	0.8	.	.	.	.	.	.	0.0
	Pungitius pungitius	.	.	.	.	.	.	0.0	0.0	.	0.0	.	.	.	0.0
	Rhodeus sericeus (V)	.	.	.	.	.	.	0.0	0.0	.	0.0	.	.	.	0.0
	Rutilus erythrophthalmus	0.9	0.7	0.2	0.1	0.8	0.1	0.5	0.1	.	0.0	.	0.0	.	0.0
	Tinca tinca	.	0.1	0.1	.	0.0	.	0.0	.	.	.	.	.	.	0.0
	Total limnophilic	**3.5**	**1.7**	**0.5**	**0.4**	**1.3**	**0.5**	**1.3**	**0.1**	**0.0**	**0.1**	**0.0**	**0.0**	**0.0**	**0.0**

[*]Red list species are indicated (De Nie & Van Ommering, 1998): E: Endangered; V: Vulnerable; S: Susceptible.

Figure 4.3. Length-frequency distributions of asp, ide, gudgeon and barbel in three floodplain water bodies in 1997 and 1998. Fork length (lower value of 5 cm classes) on the x-axis and numbers per 1000 m² on the y-axis. Data from the 100 m seine net only. 0-group (white bars), sub-adults (grey bars) and adults (black bars) indicated (stages are based on their lengths and are only indications).

Figure 4.4. Length-frequency distributions of roach, bream, white bream, bleak and pikeperch in three floodplain water bodies in 1997 and 1998. Fork length (lower value of 5 cm classes) on the x-axis and numbers per 1000 m² on the y-axis. Data from the 100 m seine only. 0-group (white bars), sub-adults (grey bars) and adults (black bars) indicated (stages are based on their lengths and are only indications; data from Molls, 1997).
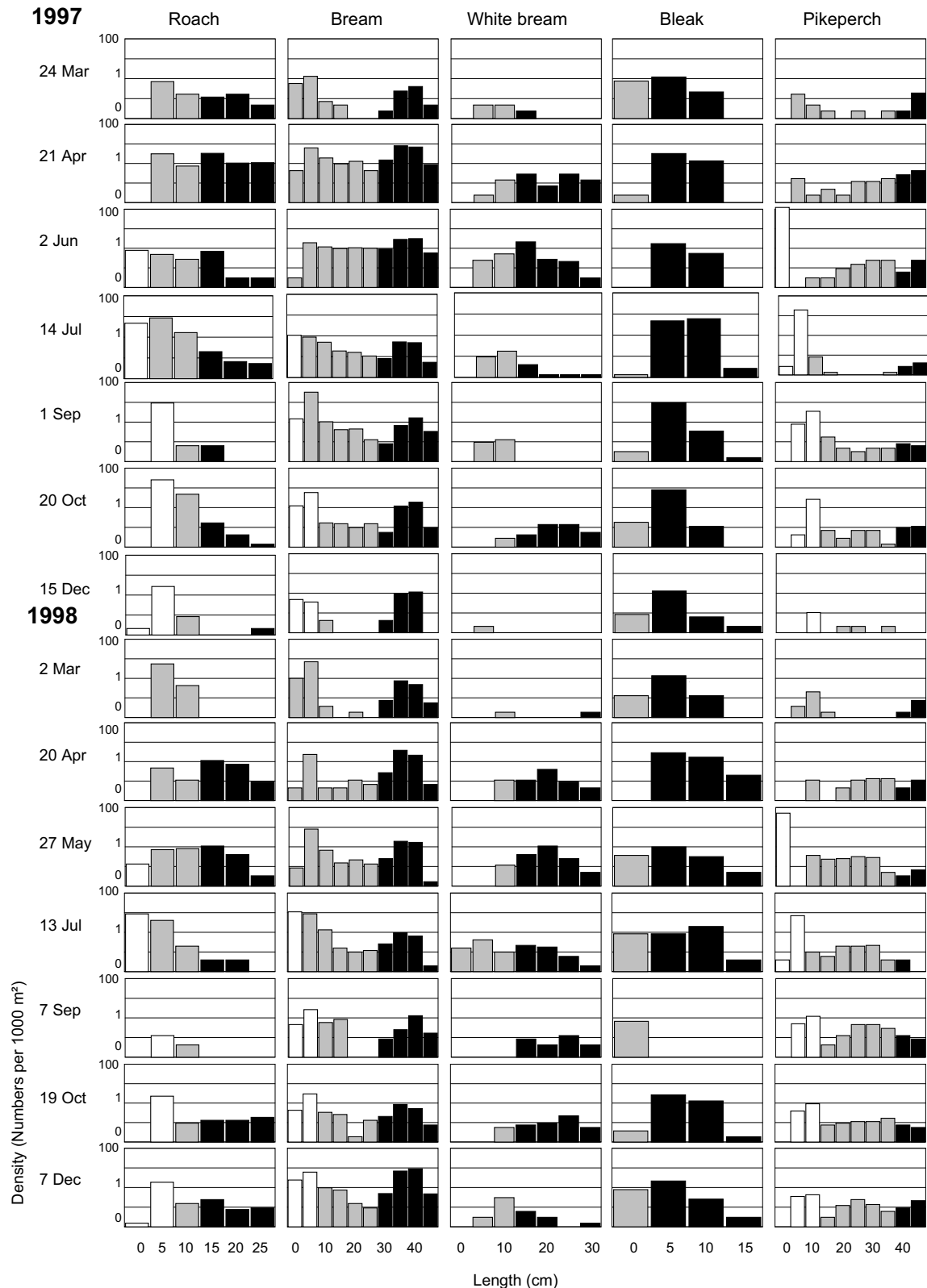
In SC1, densities of bream peaked in July 1997, probably as a result of a second spawning (Figure 4.6). In March 1997 and winter 1997/1998 (December-March), 0-group and adult bream were present whereas sub-adults were not. It appears as if 0-group and adult bream overwintered in the floodplains whereas the sub-adults avoided the floodplains in winter.

In winter (December-March) white bream had almost disappeared from the floodplains whereas during spring 1997 (April-June) and from spring through autumn 1998 (April-October) adults were present. Densities of adults peaked in June after which 0-group white bream were observed until autumn. Densities of larvae were however low and varied from 0.4-1.0 per 1000 m^2 in 1997 and 1-20 per 1000 m^2 in 1998.

Densities of 1+ bleak were almost constant throughout the sampling period (Figure 4.4). In June of both years, 0-group bleak appeared in all water bodies but few larvae were caught in SC1 as early as May 1998. From June onwards, their densities remained rather constant (Figure 4.6) while their mean length increased (Figure 4.8). Larvae did, however, occur in the floodplains from May through August that may reflect the multiple spawning of this species.

Sub-adult and adult pikeperch occurred in the floodplains throughout the year except in winter (December-March) and July 1998 (Figure 4.4). Their densities were rather constant. In all water bodies, 0-group pikeperch were first observed in May (Figure 4.6; 4.8), except in SC2 where a few larvae were caught as early as April 1997. From May onwards, densities of 0-group pikeperch decreased while their mean length increased to 10.1 in 1997 and to 12.0 cm in 1998. Densities of 0-group pikeperch were always lower in SC1 than in the other two water bodies.

4.4 Discussion

In the newly created secondary channels and the reconnected oxbow lake, a total of 30 fish species, and 0-group fish of 23 species, were recorded. From the patterns of eurytopic and rheophilic larvae, juveniles and adults (summarized in Figure 4.9), we may infer how the species that were analysed utilize the types of water body sampled and extrapolate the results to other species.

Species that, according to Balon (1975), are lithophilic (barbel, asp), utilize floodplain water bodies that are permanently connected to the main channel of the lower Rhine, as nursery areas but probably not as spawning areas, since suitable substrate is lacking. The late appearance of 0-group asp, six weeks after the first survey, at a length of 3 cm, indicates that asp spawned elsewhere, entered the floodplains as juveniles and utilized them as nursery areas. Larvae of barbel occurred

in low densities, whereas densities of juveniles peaked when they were 2-4 cm, after which they disappeared from the floodplains. This pattern agrees with the ontogenetic shift in habitat use by barbel as described for other rivers. Adults deposit eggs on shallow (0.2 m deep) gravel banks with high flow velocities (0.4 m s^{-1}; Baras, 1994), whereas larvae prefer low-flow, shallow bays in the littoral zone, which they leave at 5 cm to migrate to riffles with higher flow velocities (Schiemer & Spindler, 1989; Bischoff & Freyhof, 1999). In our water bodies, nase *Chondrostoma nasus*, chub and dace *Leuciscus leuciscus* showed similar temporal patterns to barbel and asp: juveniles occurred at low densities while larvae occurred only occasionally and adults were completely absent (Figure 4.9). According to Balon (1975), dace is a phyto-lithophilous species but according to Mann (1996), there appear to be no published reports of this species spawning on substrates other than gravel. This fits in with the pattern of the presence of dace in our floodplain water bodies and supports our conclusion that dace does not spawn there. For these lithophilic species, absence of suitable spawning substrate is probably limiting completion of the reproductive cycle within the Netherlands. At present this type of coarse substrate is absent from the floodplains and main channel of the lower Rhine in the Netherlands but prior to river regulation, at the end of the 18th century, there were some gravel banks (Maas *et al.,* 1997). Connected water bodies in floodplains of the lower Rhine probably only form suitable habitat for short periods in the life cycles of these species (Figure 4.9).

Other rheophilic cyprinids (ide and gudgeon), probably utilize secondary channels and connected backwaters along the lower Rhine as nursery areas, and they could utilize secondary channels as spawning areas since environmental conditions seem suitable, but we were unable to demonstrate this. Larvae of ide were observed in all the water bodies in 1998. According to Balon (1975), ide is phyto-lithophilous and deposits its eggs on submerged plants and spawns at water temperatures of 4-15°C (Cala, 1971; Mann, 1996). In March 1997, and several periods from March through May 1998, terrestrial vegetation (which is, when available, the only vegetation present) was inundated along the secondary channels during periods with water temperatures >8°C. Environmental conditions thus seemed favourable for the spawning of ide in both years. Larvae of gudgeon were present almost continuously from June through August which reflects the intermittent spawning of this species (Mann, 1980). According to Balon (1975), gudgeon is a psammophilic species and its eggs hatch in flowing water on the surface of sandy bottoms. Both sandy bottoms and flowing water are present in both secondary channels at all times, so habitat is suitable for reproduction of the gudgeon also. Juveniles of ide and gudgeon may also have entered the secondary channels from spawning locations elsewhere, since their densities increased at later stages (Figure 4.9). Since flowing water is absent from the

downstream connected oxbow lakes, rheophilic species will probably not spawn in these types of floodplain water body, and only utilize them as nursery areas.

Figure 4.5. Patterns in time of 0-group asp, ide, gudgeon and barbel in three floodplain water bodies in 1997 and 1998. Sampling date on the x-axis and density (numbers per 1000 m^2) on the y-axis.

Figure 4.6. Patterns in time of 0-group roach, bream, white bream, bleak and pikeperch in three floodplain water bodies in 1997 and 1998. Sampling date on the x-axis and density (numbers per 1000 m^2) on the y-axis.

Figure 4.7. Length-frequency distributions of 0-group asp, ide, gudgeon and barbel in three floodplain water bodies in 1997 (black bars) and 1998 (grey bars). Fork length on the x-axis; numbers per 1000 m^2 on the y-axis. Sampling week and date are given on the left hand side. Mean length (L) and total numbers caught (n) are given in the figures. Dashed line indicates length at which fish became juveniles (cm forklength, indicated in bold on top of the line).

Figure 4.8. Length-frequency distributions of 0-group roach, bream, white bream, bleak and pikeperch in three floodplain water bodies in 1997 (black bars) and 1998 (grey bars). Fork length on the x-axis; numbers per 1000 m^2 on the y-axis. Sampling week and date are given on the left hand side. Mean length (L) and total numbers caught (n) are given in the figures. Dashed line indicates length at which fish became juveniles (cm forklength, indicated in bold on top of the line).

Most eurytopic species utilize the secondary channels and the reconnected oxbow lake as nursery areas and most probably as spawning areas also. Larvae, juveniles and adults were found of roach, bream, white bream and pikeperch and most larvae appeared a few weeks after adults migrated into the floodplains (Figure 4.9). Juveniles resided in the floodplains year-round. The migration of adult roach, bream and white bream into floodplain water bodies in the spawning season is fully in line with the observations of Molls (1999) in a German stretch of the Rhine, 20 km upstream of the Dutch border. Adult roach, bream and white bream entered a connected oxbow to spawn after which white bream and roach moved back to the main channel, whereas bream remained present during summer and autumn (Molls, 1999). In our water bodies, 1+ roach and bream were resident throughout the year whereas white bream left after the spawning season. Our results corroborate those of Schiemer & Spindler (1989), that 0-group eurytopic fish remain in the backwaters of large rivers. In a natural secondary channel along the Upper Rhône, 0-group bleak and roach were also present continuously from June to September, and so were 0-group roach, bream and white bream in a natural connected oxbow lake (Copp & Peñáz, 1988). Copp & Peñáz (1988) assume that most 0-group fish remain in the spawning area and use it as a nursery. For eurytopic species, our results support their assumption.

When a rheophilic fish species only utilizes water bodies in restored floodplains as nursery areas, its stock rehabilitation in the lower reaches of the Rhine might be constrained by lack of suitabl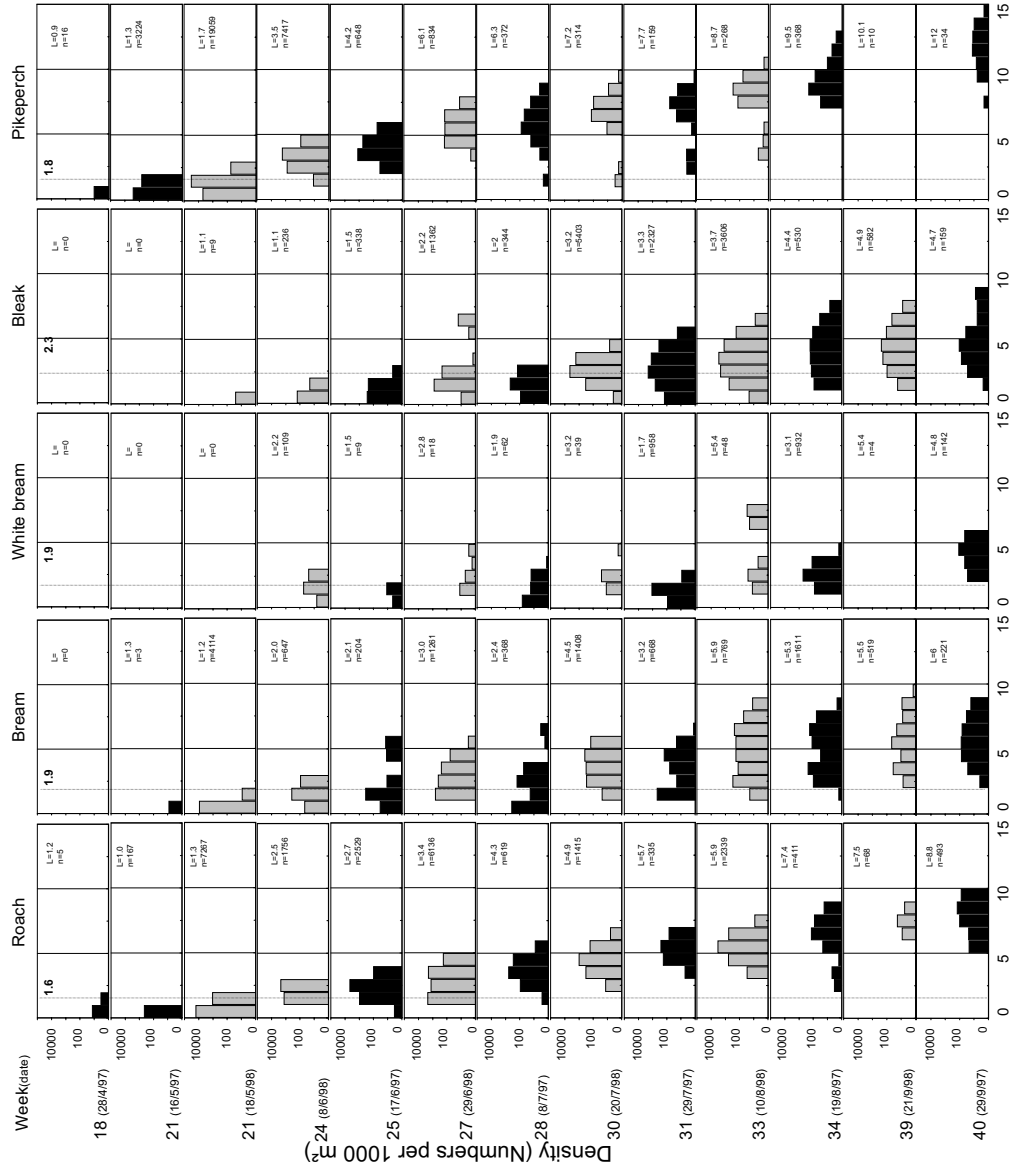e upstream spawning areas. Barbel and asp are common species in two German stretches of the Rhine (river kms 674-705 and 818-856) upstream of the Dutch border. In a seine netting and electrical fishing survey of those areas from 1992 to 1994, 0-group barbel occurred in more than 50% and 0-group asp in 20-50% of the samples (Staas & Neumann, 1995). Staas & Neumann (1995) concluded that these two, as well as other rheophilic species such as dace, chub, ide and nase, reproduced successfully in this part of the Rhine. The Rhine is free flowing between that stretch and our water bodies (River km 908-929), so larvae can reach the floodplains passively. For many riverine species, larval drift is an important process by which they reach suitable nursery areas in their early life stages (Gale & Mohr jr., 1978; Northcote, 1984; Jurajda, 1998; Schmutz & Jungwirth, 1999) and has been observed for many species, both eurytopic and rheophilic, that occurred in our floodplain water bodies (e.g. Nezdoliy, 1984; Jurajda, 1998; Reichard et al., 2001). Larval drift was the most important factor in the initial colonization of a recently created secondary channel along the Danube (Schmutz et al., 1994). 0-group fish can also leave connected backwaters and consequently, the population of 0-group fish in a nursery area is not stable but an assemblage determined by imports from upstream and exports downstream (Schiemer et al., 2001[b]) as well as by spawning and hatching in

the water body itself. This is not in line with the view expressed by Copp & Peñáz (1988) that most 0-group fish remain in the spawning area and use it as a nursery. They conclude that the reproductive potential of a floodplain ecosystem for fish may be evaluated from a single estimate in late summer, based on the relative abundance and total biomass of 0+ fish. Our data, as an example for lowland rivers, question their proposal and subsequent conclusion. 0-group fish of most species were present throughout the summer (June-August). Conclusions about whether eggs were spawned locally may be deduced only from the presence of adult fish and the youngest larval stages. Rheophilic A species, particularly, used the water bodies for only a short period. The approach of Copp & Peñáz (1988) tends to underestimate the relevant but temporal function of the connected water bodies.

Figure 4.9. Summarizing figure of the patterns in time of three groups of fish. Graphs present combined densities of 0-group and 1+ fish of: Rheophilic A species (nase, dace, chub, barbel) and asp; Rheophilic B species (ide and gudgeon) and eurytopic species (roach, bream, white bream, bleak, pikeperch, perch and ruffe *Gymnocephalus cernuus*). Data of 1997 and 1998 over the three water bodies combined. Please note the difference in the scaling of the y-axis among species and between 0-group and 1+ fish.

We conclude that the colonization process of these new water bodies has been rapid and that their functioning for fish resembles that of natural water bodies as described for less degraded rivers elsewhere. Almost all species that might have been expected, were observed and of most of these species, juveniles utilized these water bodies at some stage of their life cycles. However, our expectation for the functioning of the secondary channels and connected oxbow for especially rheophilic species has become more modest. Rheophilic A species (barbel, chub, nase and dace) did not spawn and even made limited use of them as a nursery. Also asp did not spawn locally. For most Rheophilic B species (ide, gudgeon), secondary channels appeared to fulfil the requirements of all early life-stages (eggs, larvae, juveniles). For all rheophilic species, the reconnected oxbow lake appeared to function as a nursery area. For eurytopic species, both types of water body appeared to function as both spawning and nursery areas, while some species (bream, bleak, pikeperch) seem to be resident all year. Limnophilic species occurred in low densities at all times at all sites, and we assume that they do not make much use of the types of water body sampled. Of the 47 species that have been observed in the lower Rhine (Klinge *et al.*, 1998), 17 species have not been observed, of which the majority of these would not be expected to utilize lowland floodplains. Riverine species such as eurasian minnow *Phoxinus phoxinus*, grayling *Thymallus thymallus* and stone loach *Barbatula barbatulus*, for example, are typical of brooks or lower order streams. Diadromous species, such as salmon *Salmo salar*, sea trout *S. trutta* and sea lampern *Petromyzon marinus*, occur in the lower Rhine but they will only pass through the main channel to spawn in upstream reaches. The only indigenous species that might have been expected but were not found, were burbot *Lota lota* and wels *Siluris glanis* that are both endangered species that occur in very low numbers.

Restoration of lateral connectivity will probably contribute to the rehabilitation of the population of rheophilic fish in the lower Rhine, since longitudinal connectivity is currently not limiting, at least not in the branches Waal and IJssel. Both lateral and longitudinal connectivity, in their complex interactions with hydrology, are vital requirements for diverse fish communities and high productivity (Amoros & Roux, 1988; Schmutz & Jungwirth, 1999; Schiemer, 2000). Our findings show that, on a local scale, man-made water bodies can compensate for lost habitats along the lower Rhine. Since all rheophilic fish spawn in flowing water, their larvae face the risk of being swept away from the spawning areas (Bardonnet, 2001), from which they need to reach suitable nursery areas (Schiemer & Spindler, 1989). In these restricted areas, the population of 0-group fish is determined by both imports and exports (Schiemer *et al.*, 2001[b]). Therefore, the distance between spawning and nursery areas should support early settling of the larvae, and the probability of retention in the nursery areas should

be optimized. A high retention will benefit recruitment (Schiemer *et al.*, 2001[b]), especially in regulated rivers such as the Rhine where nursery areas are scarce: only three secondary channels and four reconnected oxbow lakes exist. The other permanently connected water bodies are deep (up to 20 m) sand-pits and harbours with steep slopes along the shores. At present, floodplain management along the lower Rhine foresees the creation of more secondary channels, coupled to flood protection using increased discharge capacity (Ministry of Transport, Public Works and Water Management, 1998). Numbers of gudgeon, asp, burbot and nase increased significantly from 1993 to 1999 in a national monitoring programme, in which catches from fyke nets of professional fishermen are recorded (Winter *et al.*, 2000). This confirms our assumption that there is a stock of rheophilic fish present in the lower Rhine which has the ability to grow and has the potential to profit from the types of secondary channel and reconnected oxbow lake we have studied.

Acknowledgements

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Photo 5. Sampling with the 200 m seine net in a turbid clay-pit (Gendt).

Chapter 5

Migration of bream between the main channel and floodplain lakes along the lower River Rhine during the connection phase

Abstract

The dynamics of three cyprinid species (bream *Abramis brama*, roach *Rutilus rutilus*, white bream *A. bjoerkna*) and one percid (pikeperch *Stizostedion lucioperca*)*,* were studied in floodplain lakes along the lower River Rhine in the Netherlands to assess lateral migration during the connection phase. During three successive years (1997-1999) five lakes were sampled six times with seine nets and electro-fishing. Population size, the numbers of immigrants during the connection phase and the numbers that stayed resident, were estimated using mark-recapture techniques. Mature bream (>30 cm forklength) dominated the fish communities, in terms of biomass, in all lakes at all times. In some lakes bream made up 99% of the total fish biomass. While immature, medium-sized bream (10-30 cm) and white bream and roach were abundant in the main channel of the river, these species were almost absent from the floodplain lakes. Inundation of the floodplains did not lead to spatial homogenization of species and length distributions. Small bream (<10 cm) leave the floodplains to become resident in the main channel until maturity. Once mature (at about 30 cm), they return to the lakes during the next inundation and stay there. Mature bream that moved into the lakes were significantly smaller and had a lower condition than the resident bream. Turbid clay-pits are probably important sources of bream for the lower Rhine and the recruitment of 0-group bream to the riverine population is influenced by the discharge pattern.

5.1 Introduction

Winter dykes have been built along the main channel of the River Rhine in the Netherlands, to prevent flooding of the hinterland and summer dykes facilitate agriculture in the floodplains. Owing to the presence of these dykes, the floodplains are at present disconnected from the main channel and the typical aquatic/terrestrial transition zone of lowland rivers (Junk *et al.*, 1989; Bayley & Li, 1994), has been lost (Buijse & Vriese, 1996). The main channel of the river has been fixed by groynes and consequently, habitat diversity is low. Several fish species that occur in the main channel depend on floodplain water bodies for reproduction but, owing to the presence of the summer dykes, these isolated floodplain water bodies are infrequently and abruptly inundated (Buijse & Vriese, 1996). Only during their inundation is random or directed exchange possible, within the riverine fish community, between floodplains and main channel. In many rivers, fish migrate between the main channel and floodplain lakes to spawn, forage or avoid harsh conditions (Welcomme, 1979; Welcomme & De Mérona, 1988; Fernandes, 1997; Molls, 1999; Saint-Paul *et al.*, 2000) but this is rarely possible in the Lower Rhine.

From 1992-1996, 47 fish species were observed during a bottom trawl and electro-fishing monitoring programme that covered the main channel and some deep sand-pits (Klinge *et al.*, 1998). Of these, bream *Abramis brama*, roach *Rutilus rutilus*, white bream *A. bjoerkna* and pikeperch *Stizostedion lucioperca* contributed 95% to the total biomass present (Wiegerinck *et al.*, 1997; Hartgers *et al.*, 1998; Stam *et al.*, 1999). For these four dominant species, the main channel with its low habitat diversity provides poor spawning habitat and floodplain lakes are much more suitable. There are approximately 300 of these lakes along the branches of the River Rhine in the Netherlands (Van den Brink, 1994).

According to Balon (1975) and Mann (1996), bream and roach are phytolithophilic species that deposit eggs on submerged plants or on rocks, logs and gravel, white bream is a phytophilic species that scatters or deposits eggs with an adhesive membrane which sticks to submerged aquatic plants or to flooded terrestrial plants, and pikeperch is a nest spawner that lays its eggs on hard substrates that are clear from silt and mud. Except for submerged plants, suitable substratum for eggs is present in the main channel but these eurytopic species prefer lower flow velocities and their larvae cannot withstand flow velocities higher than about 0.1 m s^{-1} (Vriese *et al.*, 1994). In the main channel, only groyne fields provide areas where flow velocity is moderate but, because of intensive shipping, the water level in these fields fluctuates almost continuously and strong reversing currents create a highly dynamic environment. In contrast, all floodplain lakes have stagnant waters and in many oxbow

lakes submerged vegetation is abundant because transparency is high. Moreover, food conditions for zooplanktivorous juvenile fish will probably be better in floodplain lakes than in the main channel. Chlorophyll-a concentrations were higher in floodplain lakes along the River Rhine than in the main channel (Van den Brink, 1994) and in lowland rivers in general, zooplankton biomass increases with decreasing connectivity (Amoros & Roux, 1988).

Migration to these lakes is only possible during inundation when they become temporarily connected to the main channel. We investigated lateral migration of the four dominant fish species between the main channel and floodplain lakes and tested the hypothesis that bream, white bream, roach and pikeperch migrate to these lakes during the connection phase. We describe changes in the species and size composition of the fish communities in five lakes based on six samplings over a period of three years, during which the floodplains were inundated, and thus connected with the main channel, twice. Quantitative data on migration patterns of bream and pikeperch were obtained from mark-recapture data.

5.2 Materials and methods

5.2.1 Sites and sampling

The River Rhine, from its source in Switzerland to the outflow to the North Sea is now 1320 km long and has a catchment area of 185,000 km^2 (Lelek, 1989) of which 25,000 km^2 are situated in the Netherlands, forming the delta area. Where the Rhine enters the Netherlands (at Lobith, Figure 5.1), the average discharge is 2200 m^3 s^{-1} (Middelkoop & Van Haselen, 1999). On average, there are two peaks in the discharge every year. High precipitation and low evaporation in the catchment area cause a peak in winter. Melting ice and snow in the Alps cause a peak in spring (April-June). This mixed discharge regime results in a more or less stable pattern (Cals *et al.,* 1998; Middelkoop & Van Haselen, 1999) although floods may occur at any time. Just after crossing the border, the river splits into three branches, of which one (the River Waal), transporting 66% of the water, is free flowing and is less 'normalized' than other branches of the Rhine in the Netherlands: 19% of the shoreline consists of rip-rap. In the main channel, flow velocities vary between 0.5 and 1.5 m s^{-1} and, apart from the boulders covering the groynes, sand is the only substratum.

From March 1997 to December 1999, five isolated floodplain water bodies (Table 5.1; Figure 5.1), two man-made clay-pits and three oxbow lakes along the River Waal, were sampled during six periods of approximately three weeks each (Figure 5.2). The two clay-pits were created approximately 50 years ago. The substratum is

clay and silt, the slopes along the shore are steep (>45°) and aquatic vegetation and helophytes are absent (Table 5.1). Both are turbid (Secchi-disk depths of about 0.3 m). The substratum of the oxbow lakes consists of silt and organic debris and the shore zones have gentle slopes (<10°). In summer, extended beds of *Nuphar lutea* and *Nymphoides peltata* cover circa 75% of the water surface in oxbow 2 and oxbow 3, and the shore zone is almost completely covered with reeds, *Phragmatis australis*. Both are relatively clear (Secchi-disk depths of about 0.9 m). Oxbow 1 has a morphology comparable to that of the other two oxbows but vegetation is almost absent. Mean depth of all the lakes normally varies between 1 and 2.5 m depending on water level, which is influenced, through seepage and infiltration, by the main channel.

Table 5.1. Characteristics of the floodplain lakes sampled. Inundation duration is the long term (1900-1995) average number of days per year during which a floodplain lake was connected with the main channel.

Floodplain lake	Position	Surface	Distance from main channel	Maximum depth	Macrophytes	Inundation threshold	Inundation duration
	(river km, bank)	($\times 10^4$ m²)	(m)	(m)	(% cover)	(m a.s.l. at Lobith)	(days per year)
Clay-pit 1	898 (L)	8.0	73	2.5	0	12.3	50-150
Clay-pit 2	874 (R)	2.0	1082	1.5	0	13.5	2-20
Oxbow 1	892 (L)	12.6	25	5.0	0	10.3	50-150
Oxbow 2	932 (L)	10.1	690	2.0	15	14.8	2-20
Oxbow 3	932 (R)	4.3	700	1.5	50	13.9	2-20

During the sampling period, all the floodplain lakes sampled were connected with the main channel at least twice, in November 1998 and in January 1999. Moreover, water levels exceeded the inundation threshold of oxbow 1 and clay-pit 1 many times (Figure 5.2). The sampling programme was adapted to take advantage of the floods so that the lakes were sampled shortly after they had been connected with the main channel. The oxbow lakes were sampled only once during each period (except in March 1997) whereas both clay-pits were generally sampled twice (Table 5.2).

Fish were collected with seine nets of 100 and 200 m (bag stretched mesh 14 mm). Because of local conditions (aquatic vegetation) oxbow 2 and oxbow 3 were also sampled by electro-fishing (approximately 150 V DC, 5 A). Catches were sedated in a chloride-butanol solution and species were identified and fork length measured to the nearest centimetre. All fish were kept in 'life nets' (4x4x1.5 m) and set free at the end of each survey.

Figure 5.1. Maps of the five floodplain lakes sampled along the River Waal (arrows indicate direction of flow).

Figure 5.2. Water levels of the River Rhine near Lobith in 1997-1999 and inundation thresholds above which the five floodplain lakes become connected to the main channel (solid lines). Grey arrows indicate marking campaigns, and white arrows censuses in Clay-pit 1 and/or 2. These coincide with the samplings in other lakes.

To estimate population size and migration and mortality rates, bream, roach and pikeperch were marked (Table 5.2). White bream were excluded because they were not caught in the lakes (Table 5.3). In March 1997 fish were marked by clipping the top of the caudal fin. From November 1997 to April 1999, fish larger than 15 cm were marked permanently with a batch mark. A batch mark was used since it was assumed that the probability of fish migrating between sampling sites was negligible. Bream and roach were marked by injecting alcian blue between fin rays of the pelvic and pectoral fins. Pikeperch was marked permanently by cutting fin rays of the dorsal fin in 1997 and 1998 and with alcian blue in 1999. During the second of the two censuses, unmarked fish were also marked. In April 1999, it was decided to sample clay-pit 1 only once because the water temperature rose above 12°C and this might result in differential mortality of marked and unmarked fish. Approximately 200 bream >30 cm could be measured and marked per hour, by two persons. In late 1997, probably due to errors in recording the numbers of recaptures, the estimated population had to be corrected using recaptures from early 1998. This was only possible because the marks used were permanent.

Table 5.2. Overview of sampling periods and marks applied to bream, roach and pikeperch in each period. Pelvic and pectoral fins were marked by injecting alcian blue between fin rays. Dorsal fins of pikeperch marked by cutting the 2nd or 4th fin ray. When lakes were sampled twice in the same period, census followed two weeks after marking during which all unmarked fish caught were also marked. Marks: C: caudal; L: left; R: right; pect: pectoral fin; pel: pelvic fin. Marking: M: marking; C: census; n.s.: not sampled; S: sampling without marking.

Period	Marks			Sampling and marking				
	Bream	Roach	Pikeperch	Clay-pit 1	Clay-pit 2	Oxbow 1	Oxbow 2	Oxbow 3
Mar 1997	C, clip	C, clip	C, clip	M,C	M,C	S	S	S
Nov 1997	L, pect	L, pect	2nd fin ray	M,C	M,C	M	M	M
Mar 1998	R, pect	R, pect	4th fin ray	M,C	M,C	M	M	M
Jan 1999	L, pel	L, pel	L, pel	M,C	M,C	M	M	M
April 1999	R, pel	R, pel	R, pel	M	M,C	n.s.	n.s.	n.s.
Dec 1999	-	-	-	S	S	S	n.s.	S

To assess differences in condition, three bream per cm class were weighed during all samplings in the two clay-pits and during the samplings in March 1997, November 1997 and January 1999 in the three oxbow lakes. In addition, marked and unmarked bream were weighed in January and April 1999, after the inundation, to investigate possible differences between resident and immigrant bream. To compare the condition of the bream in the lakes and in the main channel, length weight data from other surveys in secondary channels and connected oxbows and sand-pits during the same periods were also used. Because these water bodies are permanently connected with the main channel, the condition of fish caught there is regarded as being representative for the main channel.

5.2.2 Data analysis

To compare the species composition of fish communities among floodplain lakes, data collected in November 1997 were used, since this was the only occasion during which all floodplain lakes were sampled at the end of the growing season. 0-group fish were distinguished from older fish by evaluating length-frequency distributions that gave clear cut-off lengths for all species. We counted all fish that were born before the year of sampling as 1+ fish, and fish that were born in the year of sampling as 0-group fish.

The population at moment t was estimated with the Lincoln-Petersen method which assumes that the ratio of marked fish (M_t) to the population (N_t) is equal to the ratio of recaptured fish (R_t) to the catch taken for census (C_t) (Ricker, 1975; Pollock *et al.*, 1990):

$$N_t = (M_t+1) \times (C_t+1) \times (R_t+1)^{-1}. \tag{1}$$

To calculate 95% confidence limits (N_{t95}), R was treated as a binomial variable when low numbers (<25) of fish were recaptured. For larger values of R, Pearson's formula was used (Ricker, 1975):

$$N_{t95} = R_t + 1.92 +/- 1.96 \times (R_t + 1)^{0.5} \tag{2}$$

Because the marks applied remained visible during the entire period, the population of resident fish (fish that were already present before the connection phase: $N_{t,res}$) after the connection phase could be estimated as:

$$N_{t,res} = (R_{t-1}/C_t) \times N_t \times (N_{t-1}/M_{t-1})^{-1}. \tag{3}$$

Where t refers to the period after inundation and t-1 to the period before inundation.

The size of the resident population was estimated based on the mark most recently used before connection and checked with the other marks that were applied before. To estimate the size of the bream population that was present from the beginning of the sampling period (1997), the initial numbers marked and the estimated population size in November 1997 were used in this formula (for M_{t-1} and N_{t-1} respectively). In this way, the size of this resident population in January and April 1999, after clay-pit 1 and clay-pit 2 had been connected with the main channel twice, could be estimated. The difference between estimated Nt and Nres is an estimate of the number of immigrants.

To compare mean length of resident and immigrant bream after inundation, a linear model that explained variance in length, for each clay-pit and period (January and April 1999) was used. Because only migration and residency of bream >30 cm were observed, only lengths of this size category were analysed:

$$L_{ij} = M_L + P_i + e_{ij}. \tag{4}$$

Where: L = fork length (cm) of an individual bream (j), M_L = mean fork length of the bream population larger than 30 cm (cm), P = Bream population as could be distinguished from the marks (i=resident, immigrant) and e = error term (cm).

To compare the individual conditions of resident and immigrant bream, length weight (w) relationships of both populations were assessed and compared by a linear model using Log(L) as a covariate for each clay-pit and period. With this model, weight and 95% confidence limits of a bream of 40 cm, which was the mean length of the bream >30 cm population in all floodplain lakes were predicted and compared between the populations (P):

$$Log(w_{ij}) = M_w + P_i + B \times Log(L) + e_{ij}. \qquad (5)$$

Where: M_w = mean Log_{10} weight of the population and B = parameter.

Length weight relationships retrieved from model (5) were used to calculate the mean weight of bream >30 cm in order to convert estimated population size (numbers per hectare) into estimated standing stock (kilograms per hectare). Because few adult pikeperch were caught, all individuals caught were weighed and their mean weight was used to calculate standing stock. For all species, length-frequency distributions were converted into length-biomass distributions using length weight relationships calculated from winter samplings in lacustrine systems in the Netherlands (Organisation for the Improvement of Inland Fisheries, unpublished data).

The models were implemented using PROC GLM of the SAS software package. Residuals were checked by a Wilk-Shapiro test on normality (alpha =0.05) and non-significant terms (p>0.05) were removed from the models.

5.3 Results

Bream >30 cm dominated the fish communities in all the floodplain lakes and at all times (Figure 5.3, 5.4), whereas no medium-sized bream (10-30 cm) were present. In the two clay-pits, bream >30 cm made up to 99% of the total biomass and, apart from pikeperch, almost no other species were observed. Adult pikeperch never contributed more than about 2-6% to the total biomass with the exception of oxbow 2 in autumn 1997 when adult pikeperch contributed 16%. In all the floodplain lakes however, medium-sized pikeperch (15-35 cm) were present in low numbers, compared to adult and 0-group pikeperch.

In November 1997, the only occasion during which all the floodplain lakes were sampled in late autumn, in oxbows 2 and 3, where aquatic vegetation was abundant, roach and other cyprinids such as common carp *Cyprinus carpio*, rudd *Rutilus erythrophthalmus* and sunbleak *Leucaspius delineatus* were present (Table 5.3). In oxbow 3, limnophilic cyprinids contributed 8% to the total numbers of 0-group fish and 90% to the total number of 1+ fish. In November 1997, in all lakes without vegetation (the turbid clay-pits and oxbow 1), limnophilic species occurred in low numbers (Table 5.3), while large numbers of 0-group fish were observed only in clay-pit 1 and oxbows 2 and 3. In oxbow 1, the only lake that had been connected with the main channel in the preceding summer (Figure 5.2), 0-group fish were observed only in relatively low numbers compared to older fish.

In January and April 1999, after all the lakes had been connected with the main channel, the fish community structure in terms of biomass per size category, had hardly

changed when compared with the fish community before connection (Figure 5.3, 5.4).
Bream >30 cm still dominated the fish communities in all lakes.

Figure 5.3. Percentage biomass by length class for the fish communities in the two clay-pits sampled
and in the main channel (lengths are midpoints of 10 cm classes; C indicates total catch (kg); dashed
lines indicate size groups which are distinguished in the text: <10, 10-30 and >30 cm). Data for the
main channel from Wiegerink *et al.*, 1997; Hartgers *et al.*, 1998; Stam *et al.*, 1999.

Figure 5.4. Percentage biomass by length class for the fish communities in the three oxbow lakes sampled (lengths are midpoints of 10cm classes; C indicates total catch (kg); dashed lines indicate size groups which are distinguished in the text: <10, 10-30 and >30 cm).

Table 5.3. Numerical composition of fish communities (total numbers caught) in the five floodplain lakes in November 1997.

Guild	Species	Clay-pit 1		Clay-pit 2		Oxbow 1		Oxbow 2		Oxbow 3	
		0-group	1+	0-group	1+	0-group	1+	0-group	1+	0-group	1+
Eurytopic	*Abramis bjoerkna*	.	1	.	2	.	5	.	.	.	66
	Abramis brama	189410	1022	594	436	128	439	33380	106	11057	223
	Alburnus alburnus	.	11	1	.	.	.	19	30	.	18
	Anguilla anguilla	.	.	.	.	.	.	.	7	.	8
	Cyprinus carpio	.	.	.	.	.	.	.	3	.	8
	Esox lucius	5	10	.	7	2	1	130	8	72	15
	Gymnocephalus cernuus	30	1	6	.	13	1	19	.	9	.
	Perca fluviatilis	5	3	12	.	1	.	208	18	349	24
	Rutilus rutilus	277	17	37	11	29	15	121	173	112	204
	Stizostedion lucioperca	2	23	5	4	3	16	18	47	10	1
	Percentage eurytopic	**100**	**99**	**100**	**97**	**100**	**100**	**100**	**85**	**92**	**10**
Limnophilic	*Carassius carassius*	.	1	.	.	.	.	.	.	.	.
	Leucaspius delineatus	.	1	.	10	.	1	.	13	205	4771
	Scardinius erythrophthalmus	.	2	.	2	.	.	19	50	764	111
	Tinca tinca	.	1	.	.	.	.	.	3	5	6
	Percentage limnophilic	**0**	**1**	**0**	**3**	**0**	**0**	**0**	**14**	**8**	**90**
Rheophilic	*Aspius aspius*	.	1	.	.	.	.	.	.	.	.
	Lampetra fluviatilis	.	.	.	.	.	.	.	1	.	.
	Leuciscus idus	.	.	.	.	.	.	.	4	.	.
	Percentage rheophilic	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**
	Total numbers caught	**189729**	**1094**	**655**	**472**	**176**	**478**	**33914**	**463**	**12583**	**5455**

Fish community structure in the main channel differed strongly from that in the lakes (Figure 5.3, 5.4). Bream dominated in both types of water but bream of all length classes were abundant in the main channel while medium-sized bream were absent from the lakes. Bream >30 cm contributed about 25% to the total biomass in the main channel while these bream contributed more than 90% in the clay-pits and oxbow 1. Pikeperch in the lakes and in the main channel were mainly adult fish while medium-sized pikeperch were present in low numbers at all locations. Roach and white bream, which occurred in low numbers in the lakes, were present in the main channel in relatively high numbers, contributing 25-30% to the total biomass. In contrast, limnophilous species were almost absent from the main channel.

In November 1997, the standing stock of bream >30 cm was highest in oxbow 2 (589 kg ha^{-1}) and lowest in oxbow 3 (333 kg ha^{-1}) whereas the standing stock in both clay-pits was comparable (436 kg ha^{-1} in clay-pit 1 and 425 kg ha^{-1} in clay-pit 2). From November 1997 to March 1998, when all lakes remained isolated, instantaneous winter mortality of bream in clay-pit 2 (1.46 yr^{-1}) was higher than in clay-pit 1 (0.41 yr^{-1}) leading to a lower standing stock (243 kg ha^{-1}) than in the latter (388 kg ha^{-1}; Table 5.4; Figure 5.5).

Apparently, a significant part of the bream >30 cm population remained resident in the floodplain lakes throughout the sampling programme despite the opportunity to leave when the floodplain lakes were connected with the main channel (Figure 5.5, 5.6). By March 1998, nearly the whole bream population had been marked in the two clay-pits after four consecutive sampling campaigns in November 1997 and March 1998. After the clay-pits had been connected with the main channel in November 1998, half of the bream population that was present in January 1999 consisted of residents that were already present before the floodplain was inundated (Figure 5.6). However, the standing stock had decreased significantly after inundation in both cases and the population of resident bream had decreased by 80%, through either emigration or mortality (Table 5.4). After both lakes were connected with the main channel again in March 1999, a large part of the bream >30 cm population again remained resident. In clay-pit 2, the standing stock in April 1999 was not significantly different from January 1999 (Figure 5.5), but the estimated population of resident bream was higher than before the connection. This probably reflects the lower accuracy of the estimate, caused by the lower numbers of resident bream recaptured, but may reflect returning immigrants. During the last sampling, in December 1999, the population of bream >30 cm still formed 21% in clay-pit 1 and 15% in clay-pit 2 (Figure 5.6), after three and two inundations respectively since March 1997.

Figure 5.5. Estimated standing stock of bream >30 cm (±95% confidence limits) in clay-pit 1 (top panel) and clay-pit 2 (bottom panel), and estimated numbers of immigrants. Vertical arrows indicate periods when the lakes were connected with the main channel, X indicates that no estimate could be made.

Bream >30 cm that had moved into the two clay-pits in November 1998 and March 1999 were significantly smaller than the resident bream (Figure 5.7, p=0.0002). From March 1997 to December 1999, the mean size of the resident population increased by 4 and 5 cm in clay-pit 1 and clay-pit 2 respectively (Figure 5.7). The increase was restricted to the summer periods (March-November 1997, March 1998-January 1999 and April-December 1999). Bream that had moved in November 1998 grew 2 and 3.5 cm within one year in clay-pit 1 and 2, respectively.

The immigrant bream were not only smaller but their condition was significantly lower than the condition of resident bream in the two clay-pits in November 1998 (p=0.0001, Figure 5.8) but such a difference did not exist for the oxbow lakes.

Figure 5.6. Proportions of the catch of bream (top panels) and pikeperch (bottom panels) that were marked during subsequent marking campaigns and censuses in clay-pits 1 (left panels) and 2 (right panels) (figures on top of the bars are total numbers caught; arrows indicate moments when the clay-pits were connected to the main channel). Results of marks applied in January and April 1999 are omitted.

Table 5.4. Results of mark-recapture experiments for bream >30 cm. M: number of fish marked; C: number of fish caught during census; R: number of recaptured fish; L95: lower 95% confidence limit; N: estimated population; U95: upper 95% confidence limit; SS: standing stock; N_{RES}: number of resident bream (population present from before the connection phase in November 1998); D: decrease in resident population. Z: instanteneous rate of decrease of resident population; I: number of fish that had moved in.

Floodplain lake	Period	M (#)	C (#)	R (#)	L95 (#)	N (#)	U95 (#)	SS ($kg\ ha^{-1}$)	N_{RES} (#)	D (#)	Z_R (yr^{-1})	I (#)
Clay-pit 1	March 1997	107	102	0	.	.	.	.				
	November 1997*	1804	3341	2147	2692	2808	2930	436	2808	360	0.41	
	March 1998	1938	1403	1111	2309	2448	2597	388	2448	1949	1.91	364
	January 1999	270	225	70	685	863	1086	157	499			
	April 1999**	808	1826	184								
Clay-pit 2	March 1997	53	106	9	319	578	1010	425	578			
	November 1997	427	486	409	462	508	560	374	508	70	0.19	
	March 1998	142	156	71	248	312	392	243	312	196	1.46	
	January 1999	65	25	13	74	123	200	96	53	259	2.13	70
	April 1999	50	48	9	138	250	437	190	65	-12	-0.82	185
Oxbow 1	November 1997**	430										
	March 1998		360	20								
Oxbow 2	November 1997	79			3236	6230	13116	589				
	March 1998		622	7								
Oxbow 3	November 1997	130			899	1522	2504	333				
	March 1998		150	12								

*: Population estimate based on recapture in March 1998. For the population estimate, all fish marked during marking and census in November 1997 (1804) and all fish recaptured during marking and census in April 1998 (3341) were taken. Since in April 1998 numerous bream were recaptured twice, independently, the number of recaptured fish was higher than the number of marked fish.

**: No estimate because of connection with the main channel between marking and census.

Table 5.5. Results of mark-recapture experiments for pikeperch >30 cm. M: number of fish marked; C: number of fish caught during census; R: number of recaptured fish; L95: lower 95% confidence limit; N: estimated population; U95: upper 95% confidence limit; SS: standing stock; N_R: number of resident pikeperch (population present from before the connection phase in November 1998); D: decrease in resident population. Z: instantaneous rate of decrease of resident population; I: number of fish that had moved in.

Floodplain lake	Period	M (#)	C (#)	R (#)	L95 (#)	N (#)	U95 (#)	SS (kg ha^{-1})	N_R (#)	D (#)	Z (yr^{-1})	I (#)
Clay-pit 1	March 1997	4	1	0								
	November 1997	15	15	7	17	32	58	10	32			
	March 1998*	8	8	4	7	16	32	4	16	16	2.1	
	January 1999	4	3	2	2	7	13	1	7	9	1.0	0
	April 1999**	3	14									
Clay-pit 2	March 1997	1	4	1	2	5	9	6	5			
	November 1997	4	4	2	3	8	21	10	8	-3	-0.71	
	March 1998	4	4	3	3	6	16	7	6	2	0.86	
	January 1999	2	2	1	1	5	8	7	4	2	0.49	
	April 1999	2	1	0								1
Oxbow 1	November 1997**	16										
	March 1998		14	0								
Oxbow 2	November 1997	23			17	42	84	9				
	March 1998		6	3								
Oxbow 3	November 1997	1			1	4	7	1				
	March 1998		3	1								

*: Standing stock based on mean weight pikeperch in March 1997
**: No estimate because of connection with the main channel between marking and census.

The condition of immigrants in clay-pit 1 in April 1999 was not significantly different from that of the residents (p=0.88), but condition was significantly lower for immigrants in clay-pit 2 (p=0.0045). During all periods, the condition of the bream in the turbid clay-pits was significantly better than in the clear oxbow lakes 2 and 3 and also better than in water bodies with a permanent connection to the main channel (Figure 5.8). Condition also differed between the two clay-pits, always being better in clay-pit 2 than in clay-pit 1.

A significant part of the pikeperch >30 cm population also remained resident in the floodplain lakes throughout the sampling programme (Figure 5.6; Table 5.5). In December 1999, 36% of the population in clay-pit 1 still consisted of pikeperch that had resided there from March 1997 onwards but the population had decreased significantly since March 1997. In clay-pit 2, no decline in the population was observed, possibly a reflection of the low numbers marked. Standing stock of pikeperch was low (1-10 kg ha^{-1}) in all lakes.

5.4 Discussion

Because of the large proportion of the population that was marked, population estimates of adult bream were accurate. 95% confidence limits of the estimated population size varied between 4 and 74%. For pikeperch, however, population estimates were inaccurate and for roach and white bream no quantitative data could be collected at all. Accuracy of estimates, which depends on the proportion of the population caught and marked, was influenced by the opportunities for fish to avoid the sampling gear. These opportunities increased at higher water levels. At low water levels, as in late 1997 in clay-pit 2, up to 96% of the estimated population could be caught and marked. The marked and unmarked fish did mix randomly, which is one of the three assumptions of the Lincoln-Petersen mark-recapture method (Marten, 1970; Ricker, 1975; Pollock *et al.*, 1990), since the proportions in which fish with the different marks were caught, were stable throughout the sampling programme. Marking fish by injecting alcian blue proved to be a good method for estimating the population and migration of fish by mark-recapture. The mark can be applied quickly and remained clearly visible over several years.

The observed migration pattern of bream between the main channel and the floodplain lakes supports the findings of Molls (1999) that bream show ontogenetic changes in their use of rivers and oxbows. In a German stretch of the River Rhine, 20 km upstream of the Dutch border, adult bream, which mature at 30 cm fork length, enter oxbows in spring to reproduce while young fish emigrate from the oxbows and spend

Figure 5.7. Length-frequency distributions of resident and immigrant adult bream in clay-pit 1 (left) and 2 (right). Mean lengths of the populations are indicated (L_R: mean length of the resident population; L_{nov}: mean length of bream that moved in in November 1998; $L_{nov/mar}$: mean length of bream that moved in either in November 1998 or in March 1999).

their lives in the main channel (Molls, 1999). In our study, bream that moved into the floodplain lakes along the River Rhine in the Netherlands were larger than 30 cm and were most probably adult. Bream in the Netherlands mature after six years (Van Densen *et al.*, 1990) and in 1984 in the main channel of the River Rhine, bream of six years old were 27 cm (De Boer & Te Brinke, 1984). Molls (1999) concluded also that it should be investigated how long adult bream remain resident in the floodplain water bodies.

Figure 5.8. Predicted weight (with 95% confidence limits of the mean) of bream of 40 cm fork length based on model (5). M.C. refers to condition of fish in water bodies with a permanent connection to the main channel.

Our study showed that during the connection phase, a significant part of the adult bream population remains resident, most probably for the rest of its life. The other part of the population will probably migrate out of the floodplain lakes but we could not distinguish emigration from mortality. In the turbid clay-pits, environmental conditions seem to be optimal for adult bream: they reproduce successfully, probably have sufficient food and are safe from predation by fish and birds. Their growth rates were in general moderate and their condition was good, which probably reflects good food conditions (Cazemier, 1982). In turbid floodplain lakes (the two clay-pits and oxbow 1) condition was significantly better than in the two clear oxbow lakes and the

main channel. In the turbid lakes, with their poor habitat and fish species diversity, bream may prosper in the absence of other species. Bream >30 cm will be safe from predation by pikeperch (the only predatory fish species) since, due to gape limitation, adult pikeperch cannot take bream larger than 15 cm fork length (Van Densen, 1994). In general, cormorants *Phalacrocorax carbo*, which are the most abundant piscivorous bird species in the area, do not predate on bream larger than 30 cm fork length (Veldkamp, 1995). Mortality of adult bream in the clay-pits was, however, sometimes high with instantaneous mortality rates of up to 1.5 yr^{-1} during winter 1997/1998. When floodplain lakes are isolated from the main channel, changing environmental conditions can lead to mortality of fish species that are not adapted to these conditions (Lowe-McConnell, 1975; Welcomme, 1979). The high mortality rate of bream in clay-pit 2 in winter 1997/1998 was perhaps caused by a combination of low water levels (the surface area in November was almost half that in March) and a high standing stock (425 kg ha^{-1} in March 1997).

Our results also corroborate the finding of Molls (1999) that the absence of medium-sized bream of 10 to 30 cm can probably be explained by avoidance of shallow floodplain lakes by these fish, rather than by predation or year-class failures. Predation by cormorants, which are abundant in the River Rhine area, can have a severe impact on the size structure of fish populations (Kainz, 1994; Wißmath & Wunner, 1996; Schwevers & Adam, 1998) and the size range most vulnerable to their predation is 5 to 35 cm (Veldkamp, 1995). However, the complete absence of medium-sized bream in the lakes we sampled is not likely to be a result of depletion by cormorants or fish. On two occasions, the lakes were sampled within a few weeks of becoming connected but, even after such a short time, no bream of these lengths were observed. Absence of medium-sized bream in floodplain lakes cannot be attributed to a number of poor year-classes since these length-classes were present in the main channel. Moreover, in 1994, 18 floodplain lakes along the River Rhine in the Netherlands were sampled and no medium-sized bream were observed (De Laak *et al.*, 1994).

We only have indications but no proof of the emigration of 0-group bream from floodplain lakes as part of their age-dependent habitat shifts (Molls, 1999). In oxbow 1, that was inundated between each sampling period, 0-group bream were almost absent at all times. In the other lakes, that had remained isolated during the preceding summer, 0-group bream were abundant in November 1997. After winter or after an inundation, however, almost no 0-group bream occurred in these lakes. These results might indicate that 0-group bream take the opportunity to leave during inundation or otherwise encounter high mortality rates during winter. In that case, timing of inundation would be an important factor determining recruitment of 0-group bream to

the river. It is difficult to quantify the contribution of floodplain lakes to the recruitment of bream since their suitability, and hence the numbers of offspring being produced, will vary among the different riverine habitats. If the main channel, with a surface of 39 km^2, is assumed to be unsuitable for reproduction (Molls, 1999), reproduction of bream depends on permanently connected sand-pits and harbours (9 km^2), floodplain lakes (10 km^2) and inundated floodplains (82 km^2). Water bodies with a permanent connection to the main channel, mainly man-made sand-pits and harbours, constantly provide suitable spawning and nursery areas for bream that are always accessible. Connected gravel-pits along the lower River Rhine in Germany for example, have been shown to be important nursery areas for riverine species including bream (Staas & Neumann, 1994). The contribution of inundated floodplains to the recruitment of bream may be limited because floods are more likely to occur in late winter and spring than during summer. Moreover, they will only contribute in years with an unusual discharge pattern during which floodplains are inundated for extended periods. The periodic recruitment of bream from isolated floodplain lakes may nevertheless be important for maintaining the population in the lower River Rhine. In that case, as for fish in many other lowland rivers (Welcomme, 1979; De Mérona & Gascuel, 1993; Spindler, 1995; Winemiller *et al.*, 2000), stochasticity of discharge may strongly control population size of bream in the lower River Rhine.

No quantitative data could be obtained for white bream and roach but it was obvious that both species avoid the turbid clay-pits. Because these two species were not present shortly after inundation, it seems unlikely that they enter the lakes but do not survive. In contrast to the isolated floodplain lakes, 0-group white bream and roach were abundant in permanently connected secondary channels and oxbow lakes along the River Waal and they use these types of water body as nursery areas (Grift *et al.*, 2001). During spring, adult white bream and roach move into flooded meadows and oxbow lakes that are permanently connected with the main channel, but leave these lakes at the end of the spawning season (Reimer, 1991; Molls, 1999). It could be that adult white bream and roach avoid becoming isolated in floodplain water bodies. Molls (1999) suggests that for white bream and bream, food is more abundant in the main channel but we think that the fine substratum and the difficulty of feeding for white bream and roach as compared to bream, might also explain their absence from floodplain lakes. Adult bream, white bream and roach will predominantly feed on benthic macroinvertebrates such as chironomids which they sieve out of the substrate over the branchiospinal system (Lammens, 1984). However, white bream and roach have a coarser branchial sieve than bream (Lammens, 1982, 1984; Lammens *et al.*, 1987; Van den Berg, 1993) so, if the substrate particles are small, as in floodplain lakes with clay bottoms, feeding of bream might be more efficient than that of white

bream and roach. If substrate particles are large, as in the main channel with its sandy bottom, feeding of white bream and roach might be more efficient (Lammens, 1984).

Acknowledgements

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Photo 6.Large stands of Nymphaeids in a shallow oxbow lake (Kil van Hurwenen).

Photo 7. Limnophilic tench *Tinca tinca*.

Chapter 6

The present status of fish communities in floodplain lakes along the lower River Rhine

Abstract

The present study investigates the current status of fish communities in floodplain lakes along the lower River Rhine. Fish community structure was assessed in 20 lakes, and factors that govern the species richness and the presence of limnophilic species were investigated. To assess how these lakes contribute to fish species diversity in the river-floodplain system, fish communities were compared with those in the main channel and in various types of floodplain water body that are permanently connected to the main channel. Floodplain lakes with abundant vegetation have low fish species richness but they are the only type of water body along the lower Rhine, which provide suitable habitat for the reproduction of limnophilic species such as tench *Tinca tinca*, rudd *Rutilus erythrophthalmus* and crucian carp *Carassius carassius*. The proportion of limnophilic species in these lakes is, however, outnumbered by eurytopic species such as bream *Abramis brama*. Some limnophilic species such as weatherfish *Misgurnus fossilis* and ten-spined stickleback *Pungitius pungitius* were not found which suggests that remote and seldom flooded lakes have disappeared almost completely from the floodplains along the lower Rhine. Floodplain lakes with abundant vegetation should be carefully preserved because they represent aquatic components that have disappeared from the river landscape. Future flood protection management in retention areas may provide the opportunity for restoring remote floodplain lakes with a limnophilic fish community. In this way, improved safety can be combined with rehabilitation of floodplain water bodies.

6.1 Introduction

The Netherlands lost their natural floodplains when the embankments along the lower River Rhine were completed around 1450. Before that time, the area inundated during floods must have been tens of kilometres wide, bounded only by the ridges of hills formed in the ice age (Van Urk & Smit, 1989). The embankments confined the floodplain to a narrow zone fringing both sides of the river. To facilitate agriculture during the industrial revolution (1700-1800), minor or summer dykes were built between the remaining floodplain and the main channel to prevent the cultivated areas from flooding in summer. Due to the presence of the summer dykes, erosion of the river bed and siltation of the floodplains, the natural, gradual connection between the main channel and its floodplains, was lost. Natural water bodies with a permanent opening were disconnected and at present the floodplains are more rarely and abruptly inundated than before embankment. Moreover, the original riverbed, characterized by sand and gravel beds, has cut down and nowadays has steep shorelines and low habitat variability (Buijse & Vriese, 1996; Middelkoop, 1997; Cals *et al.*, 1998). The resulting landscape is a main channel with a fringe of floodplain with little variation in frequency and duration of flooding. Remote lakes and floodplains that were seldom flooded, were completely disconnected from the river by winter dykes, except for ground water flow.

Variability of hydrological connectivity across a floodplain in a lateral direction supports high faunistic diversity (Tockner *et al.*, 1999; Schiemer *et al.*, 1999). In natural floodplains, fish have adapted to the variability of connectivity and consequently there is a lateral zonation of fish reproduction in floodplain water bodies (Copp & Peñáz, 1988; Copp, 1989; Guti, 1996). From the lotic main channel to lentic zones within the floodplains, fish community composition shifts from rheophilic species such as barbel *Barbus barbus* and ide *Leuciscus idus*, through eurytopic species such as roach *Rutilus rutilus* and bream *Abramis brama*, to limnophilic species such as tench *Tinca tinca* and weatherfish *Misgurnus fossilis* (Regier *et al.*, 1989; Schiemer & Waidbacher, 1992; Quak, 1994).

During the 20th century, the total number of fish species in the lower Rhine has decreased due to this deterioration in physical habitat combined with decreased water quality. This was mainly due to the decline in numbers of anadromous, rheophilic and limnophilic species (Lelek, 1989; Van den Brink *et al.*, 1990). In the Netherlands, the fish community in the main channel of the Rhine is currently dominated by only four eurytopic species: pikeperch *Stizostedion lucioperca*, bream, white bream *Abramis bjoerkna* and roach (Klinge *et al.*, 1998; Winter *et al.*, 2000). Rheophilic species are present only in low numbers and most of them are endangered since suitable spawning

and nursery areas have disappeared. They are more common in secondary channels and reconnected oxbow lakes, that were newly created for the purposes of river restoration during the 1990s (Grift *et al.*, 2001) but currently there are only ten of these water bodies along the lower Rhine.

The limited knowledge about fish communities in floodplain lakes constrains decision making on the future management of these lakes. We do not know which limnophilic species are still present in the floodplain lakes along the lower Rhine or which factors determine their presence. National fish monitoring programmes are limited to the main channel and some deep sand-pits, and so far, floodplain fish communities have been investigated mainly in water bodies that are permanently connected to the river. So far, the presence of fish species in floodplain lakes has been assessed in only one small-scale pilot study (Buijse & Vriese, 1996). Van den Brink (1994) investigated ecosystems in lakes along the lower Rhine and presented preliminary data on the presence of fish. Based on phyto- and zooplankton, macro-invertebrates and macro- and helophytes, he concluded that with increasing frequency of inundation, the ecosystem in floodplain lakes shifted from a submerged aquatic macrophyte-dominated, clear water community towards a planktonic microphyte-dominated, turbid water community. The results of both Buijse & Vriese (1996) and Van den Brink (1994) suggest a species shift from limnophilic to rheophilic fish species along a similar gradient.

The present study assesses the fish species richness of 20 floodplain lakes along the lower River Rhine and investigates factors that influence the species richness and the presence of limnophilic species in these lakes. These fish communities are compared with those in the main channel and in four floodplain water bodies that are permanently connected to the main channel (Table 6.1). Consequently, fish community structure was assessed in 25 water bodies along a gradient of connectivity with the main channel.

6.2 Materials and methods

6.2.1 Study area

The River Rhine, from its source in Switzerland to the outflow to the North Sea is now 1320 km long and has a catchment area of 185,000 km^2 (Lelek, 1989) of which 25,000 km^2 are situated in the Netherlands, forming the delta area. Where the Rhine enters the Netherlands (at Lobith, Figure 6.1), the average discharge is 2200 m^3 s^{-1} (Middelkoop & Van Haselen, 1999). On average, there are two peaks in the discharge every year although floods can occur at any time of the year (Figure 6.2). High precipitation and

low evaporation in the catchment area cause a peak in winter. Melting ice and snow in the Alps cause a peak in spring (April-June). Just after crossing the border, the river splits into two branches, one of which (the River Waal), transports 66% of the water and is free flowing. The main channel of the River Waal has an average width of 380 m and the average width of its floodplains is 550 m. There are approximately 300 floodplain lakes along the three Rhine branches, of which 20 were sampled along the River Waal in the present study. The distance between the most upstream and most downstream of these lakes is 61 km along the Waal (river km 872-933).

Table 6.1. Characteristics of the floodplain water bodies sampled. Map numbers refer to Figure 6.1; connectivity is the long term (1900-1995) average number of days per year during which the water body has been connected with the main channel; locations: MC: main channel; GF: groyne fields; SC: secondary channel; COL: connected oxbow lake; SP: sand-pit; CP: clay-pit; OX: oxbow lake; gears used: F: fyke nets; T: trawl; S: seine net; E: electro-fishing.

Map (Nr.)	Water body	Surface (10^4 m^2)	Depth (Nov/Dec) (m)	Connectivity (days/year)	Submerse vegetation (% cover)	Floating vegetation (% cover)	Helo phytes (% cover)	Gears used
-	MC	3900.0	4.0	permanent	0	0	0	F
-	MC (GF)	4.0	2.0	permanent	0	0	0	S,T
1	SC1	13.6	1.5	permanent	0^*	0	0	S,T
2	SC2	26.9	1.5	permanent	0^*	0	0	S,T
3	SC3	8.4	1.0	permanent	0^*	0	0	S,T
4	COL	5.4	2.5	permanent	0^*	0	0	S,T
5	SP1	5.0	2.0	2-20	0	0	0	S,T
6	CP1	0.7	1.5	2-20	11	5	2	S,E
7	CP2	0.6	1.5	2-20	0	10	2	S,E
8	CP3	0.7	1.0	2-20	28	9	4	S,E
9	CP4	2.0	0.8	2-20	4	0	0	S
10	CP5	1.4	0.8	2-20	42	34	12	S,E
11	CP6	0.9	0.5	2-20	0	75	20	E
12	CP7	4.0	1.5	2-20	0	2	1	S
13	CP8	8.0	1.5	50-150	0	0	0	S
14	CP9	2.0	1.0	50-150	2	14	0	S
15	CP11	0.1	0.8	2-20	60	50	6	S,E
16	CP12	0.9	0.8	2-20	57	46	6	E
17	CP13	0.3	0.4	2-20	89	0	5	E
18	CP14	1.3	0.8	2-20	0	0	0	S
19	CP15	0.2	1.0	2-20	81	4	4	S,E
20	OX1	3.5	1.5	50-150	3	0	0	S
21	OX2	12.6	2.5	50-150	2	0	0	S,T
22	OX4	0.2	1.5	2-20	0	0	0	S
23	OX5	1.8	0.8	2-20	32	34	3	S,E
24	OX6	10.1	1.0	2-20	0.2	14	5	S,E
25	OX7	4.3	1.0	2-20	5	50	3	S,E

* Vegetation is present at higher water levels when terrestrial vegetation is inundated. This occurred in April/May, September, November and December 1998 and from January to July 1999 continuously.

Figure 6.1. Map of the River Waal in the Netherlands and sampling locations. Numbers refer to numbers in Table 6.1; arrows indicate direction of flow.

The 20 lakes differ in surface area, depth, frequency of inundation and presence of vegetation. They comprise man-made sand and clay-mining pits and natural oxbow lakes (Table 6.1). Lakes that lie between summer dykes and the main channel, are connected with the main channel for 50-150 days per year, on average (at water levels between 9.6 and 11.2 m above sea level (a.s.l.) at Lobith, Figure 6.2). From 1900-1999, these lakes were connected with the main channel at least once, and sometimes several times, a year. Lakes behind summer dykes are connected less frequently, on average 2-20 days per year (water levels between 12.4 and 14.7 m a.s.l.), usually in winter. From 1900-1999, these lakes remained isolated in only nine years.

Figure 6.2. Water levels of the River Rhine (1993-1999): Lower grey bar: lakes connected 50-150 days/year (9.6-11.2 m a.s.l. at Lobith); upper grey bar: lakes connected 2-20 days/year (12.4-14.7 m a.s.l. at Lobith); black arrow: 1999 sampling period. Whisker and box plots (lower right panel) present minimum and maximum water levels (whiskers) and the 0.10, 0.50 and 0.90 percentiles (boxes) per month (data from 1970-1999).

The sand-pits (SP), which are usually deep (>5 m) with steep (>45°) banks, were excavated some 15 to 60 years ago. Most sand-pits are situated near the main channel and, although their substrate is primarily sand, silt can occur in the shore zone. In the sand-pit sampled, vegetation was completely absent. The clay-pits (CP), that are shallow (<2 m deep) with steep (>45°) to nearly vertical banks, were excavated 40-120 years ago. They are generally situated further from the main channel than sand-pits, and their substrate consists of clay and sometimes silt. About half of the 14 clay-pits sampled lacked almost any aquatic vegetation while the vegetation in the other half

was well developed and consisted of large stands of Nymphaeids (*Nuphar lutea* and *Nymphoides peltata*), often accompanied by dense submerged vegetation consisting of *Potamogeton pectinatus, P. trichoides* or *P. lucens*. In some clay-pits, shore zones were covered with helophytes, mainly *Sparganium erectum*, *Typha angustifolia* and/ or large *Carex* species. Oxbow lakes (OX) are naturally formed and are the oldest floodplain lakes, aged 200 to 700 years. Due to net sedimentation in the floodplain, all the lakes are subject to succession from open water to dry land. Most oxbow lakes are shallow (<1.5 m), have gentle banks and sometimes, reed beds form extensive shallow (<0.5 m deep) areas. Their substrates consist of silt and organic material. Vegetation is absent from oxbow lakes that are inundated frequently (50-150 days per year on average) while in those that are inundated less frequently (2-20 days per year on average), vegetation can be abundant (Table 6.1). Their aquatic vegetation consists of Nymphaeid species, but, in contrast to vegetated clay-pits, submerged vegetation is usually absent or scarce.

The species composition of the fish communities in floodplain lakes was compared with the species composition in the main channel and its groyne fields and in three permanently connected secondary channels and one connected owbox lake (Table 6.1). The main channel (MC) and its groyne fields (GF) are dynamic and rather inhospitable sites. The main channel has a low habitat variability, flow velocities vary between 0.5 and 1.5 m s^{-1} and sand, apart from the boulders covering the groynes, is the dominant substrate. Groyne fields are hydrologically dynamic and inhospitable due to strong eddies caused by ships that pass on average every three minutes. The secondary channels (SC) and the connected oxbow lake (COL) were created for floodplain rehabilitation purposes in the 1990s. In the secondary channels, moderately flowing water (<0.3 m s^{-1}) is permanently present whereas in the reconnected oxbow lake, that is connected with the main channel only downstream, flow is almost absent. The groyne fields, secondary channels and the connected oxbow lake had moderate depths (<2.5 m) and fine substrates (sand, clay or silt). Aquatic vegetation was scarce or absent but on about 120 days per year in spring and summer, terrestrial vegetation was inundated. A more detailed description of these locations is given in Grift *et al*. (2001).

6.2.2 Data collection

In November and December 1999, the floodplain lakes were sampled with seine nets of 100x3 m and 200x4 m (bag mesh 14 mm stretched) at sites without vegetation. Seine hauls were made in a standardized manner and the area covered by each haul was circa 3000 m^2 and 9000 m^2 for the 100 and 200 m seines respectively. Beds of

aquatic vegetation and shore zones covered with helophytes were sampled by electro-fishing (approximately 150 V DC, 5 A). At deeper sites (>3 m) a 7x1 m bottom trawl (mesh size 17 mm stretched) was towed behind two boats for 5 minutes. In each lake, the three types of habitat (shallow open water, shallow sites with vegetation, deep open water) were sampled representatively according to their proportion of the total surface. The fish caught were sedated in a chloride-butanol solution, species were identified and fork length measured to the nearest centimetre. All fish were kept in 'life nets' and set free at the end of each sampling day.

Data on fish communities in the main channel of the River Waal and in the floodplain water bodies with a permanent connection to the river were all collected in 1999, except data on 1+ fish in the floodplains, for which data from 1998 were used. We counted all fish that were born before the year of sampling as 1+ fish, and fish that were born in the year of sampling as 0-group fish. Data on 1+ fish from the main channel were retrieved from Stam *et al.* (1999) and Winter *et al.* (2000). In the former study, the main channel was sampled with a 3 m bream trawl (stretched mesh 20 mm) in March and hence, no 0-group fish were sampled. In the latter study, catches from fyke nets (stretched mesh 18-20 mm) of professional fishermen were recorded from April through October (river km 865-869 and 906-912). Since fish were not measured, we could not distinguish the 0-group from older fish and we used the fyke catches only to indicate the presence or absence of species. 1+ fish in the floodplains were sampled in 1998 in two secondary channels (SC1, SC2) and the reconnected oxbow lake. Each water body was sampled seven times evenly spread over the period from March through December. The same trawl, 100 m seine net and electro-fishing gear were used as in the floodplain lakes in November/December 1999.

0-group fish were sampled twelve times from April to September 1999 with fine meshed seine nets and trawls (stretched mesh size <7.5 mm). Several groyne fields were sampled along the main channel and we assumed that these data represent the 0-group fish assemblage in the main channel. In the floodplains, 0-group fish were sampled in two secondary channels (SC1, SC3) and the reconnected oxbow lake. 0-group fish were preserved in 4% formalin and identified in the laboratory as described in Grift *et al.* (2001).

In all the lakes, presence of vegetation was recorded in July and August 1999. In each lake, the percentage area covered by submerged, floating and emergent vegetation was estimated at 8-20 representative sites. The number of sites depended on lake size and the complexity of the vegetation structure. The coverage of submerged and floating vegetation in the whole lake was calculated by multiplying the percentage of the lake in which vegetation was present with the average cover of plants at each site. The area covered by helophytes was estimated as a percentage of the surface area

relative to the surface area of water in the lake. The surfaces of the lakes were calculated from a GIS database and depth was recorded with a portable echosounder during the fish surveys.

6.2.3 Data analysis

Fish species were classified into reproductive guilds according to Schiemer & Waidbacher (1992) and Quak (1994). 0-group fish were distinguished from older fish by evaluating length-frequency distributions, which gave clear cut-off lengths for all species. Length was converted into weight using length-weight relationships retrieved from winter samplings in lacustrine systems in the Netherlands (OVB, unpublished data). Canonical correspondence analysis (Canoco software Version 4; Ter Braak & Šmilauer, 1998) was selected to explore the relationship between species and the characteristics (vegetation, depth, surface, inundation duration) of the lakes. In this analysis, total numbers caught were square root transformed and the statistical significance of the effect of each environmental variable was tested using a Monte Carlo permutation test (p<0.10; 1000 random permutations).

6.3 Results

6.3.1 Occurrence of species along a connectivity gradient

In the individual floodplain lakes, the total number of species varied from 1-8 for 0-group fish and from 2-13 for 1+ fish (Table 6.2, 6.3; Figure 6.3). In contrast, in the main channel and the permanently connected water bodies the total number of species varied from 16-18 for 0-group fish and from 19-33 for the 1+ fish . This larger number of species was mainly because of the high number of rheophilic species such as barbel, nase *Chondrostoma nasus* and chub *Leuciscus cephalus* that were absent from the lakes. Since most rheophilic and diadromous species are on the Netherlands red list of endangered species, they contribute to the higher number of red list species in the main channel and permanently connected water bodies (Figure 6.3). Some species occurred in the main channel which were absent from all other sites: limnophilic ten-spined stickleback *Pungitius pungitius*, eurytopic grass carp *Ctenopharyngodon idella*, pumpkinseed *Lepomis gibbosus* and wels *Silurus glanus*, and diadromous sea trout *Salmo trutta* and sea lamprey *Petromyzon marinus*. Grass carp and pumpkinseed are exotic species of which only one individual of each was observed in the fyke catches.

Along a gradient of decreasing connectivity from the main channel to the floodplain lakes, there was a clear gradient in the presence of fish species which was stronger for 0-group than for 1+ fish (Table 6.2, 6.3). In water bodies with a permanent

connection to the main channel, there were 0-group fish of all rheophilic species at almost all sites whereas 0-group limnophilic fish were completely absent (Table 6.3). In some lakes that are inundated for 50-150 days per year, 0-group rheophilic asp *Aspius aspius*, ide and a coregonid species were present. Most probably these fish had migrated into these lakes in the preceding summer when the lakes became connected with the main channel. Limnophilic 0-group fish were absent from these lakes, whereas they were present in lakes with abundant vegetation and the lowest connectivity. From these lakes however, 0-group rheophilic fish were almost absent. Eurytopic 0-group fish were present in almost any water body although 0-group bleak *Alburnus alburnus*, white bream, common carp *Cyprinus carpio*, stickleback *Gasterosteus aculeatus* and pikeperch were almost absent from the lakes.

Figure 6.3. Number of fish species per reproductive guild in the main channel and its groyne fields, secondary channels, a reconnected oxbow lake and 20 floodplain lakes. Data for 1+ fish in the main channel are from fyke and trawl catches combined (grey diamonds: numbers of red list species).

1+ eurytopic and limnophilic species occurred both in water bodies that were permanently connected with the main channel and in the floodplain lakes that were inundated 2-20 days per year, whereas, 1+ rheophilic fish were mainly limited to permanently connected floodplain water bodies.

The number of water bodies in which the individual fish species occurred, differed strongly among species. Within the limnophilic guild, sunbleak *Leucaspius*

delineatus and rudd *Rutilus erythrophthalmus* were more widely distributed than crucian carp and tench. Within the eurytopic guild, bream and roach were the most widely distributed species occurring in 23 out of 25 water bodies. White bream, stickleback and common carp occurred in much fewer water bodies.

6.3.2 Fish species composition in floodplain lakes

Among floodplain lakes, presence of vegetation, surface area and depth, plus the frequency and duration of inundation of the lake, had a significant influence on species composition of their fish communities (Figure 6.4).

Limnophilic species were associated with shallow lakes with abundant vegetation (Figure 6.4) where 0-group limnophilic fish contributed up to 64% of the total numbers of fish present (Table 6.2, 6.3). Limnophilic species such as rudd and sunbleak occurred frequently and made up large proportions of the fish community. Tench had a low numerical contribution, but 1+ tench were observed in all lakes with abundant vegetation, except in CP15 (Table 6.2). Crucian carp were only observed in two small (<1 ha) vegetated lakes (CP2, CP12). In lakes without vegetation, limnophilic species only contributed 0-3% to the fish communities that were dominated by eurytopic bream, roach, perch *Perca fluviatilis* and pike *Esox lucius* (Table 6.2, 6.4). Within the eurytopic species, perch and 0-group pike occurred most frequently in lakes with abundant vegetation, whereas most other eurytopic species showed no clear preference (Figure 6.3). Rheophilic species were associated with frequently inundated lakes without vegetation.

In terms of biomass, fish communities in most (16) lakes were dominated (>50%) by bream (Figure 6.5). Limnophilic species were only important in some smaller clay-pits (CP11, CP13). The proportion of limnophilic species to the total fish biomass increased with increasing abundance of aquatic vegetation, but never exceeded 37%. In lakes without vegetation, the proportion of limnophilic species to total biomass was always less than 1%. Predatory pike contributed a large proportion (>25%) of the total biomass in some smaller lakes with abundant vegetation (Figure 6.5). In the scarcely vegetated clay-pit 9, pike even contributed 95% to the total fish biomass. We were surprised by this and consider it as an outlier since we have no explanation. In general, in smaller lakes with vegetation, pike were the most important predatory species while in larger lakes without vegetation, pikeperch became more important (Figure 6.5).

Table 6.2. Total catch and relative proportion of 1+ fish assemblages in the main channel and 23 floodplain water bodies along the lower River Rhine. Lakes are ordered according to their connectivity and increasing abundance of aquatic vegetation (% covered). Occ.: the number of water bodies in which a species occurred (including the main channel); '+': species observed but % unknown; '.': species not observed; '0': proportion lower than 0.05%.

Connectivity (days/year): 365 (MC fyke – COL) | 50–150 (CP 8 – CP 10) | 2–20 (CP 16 – CP 11)

Species (red list, *)	Occ.	MC fyke (**)	MC trawl (***)	SC 1	SC 2	COL	CP 8	OX 2	OX 1	SP 1	CP 14	OX 4	CP 7	CP 2	CP 4	CP 10	CP 16	CP 3	OX 7	OX 5	OX 5	CP 15	CP 13	CP 6	CP 12	CP 11
Aquatic vegetation (%)		0	0	1	2	0	8	2	1	16	0	0	0	2	4	10	16	37	55	66	75	76	85	89	100	100
Total catch		2375	6108	2878	2326	2878	2005	260	86	79	12	379	35	1695	138	7721	204	295	427	232	200	194	61	232	54	221
Total number of species		27	23	25	22	19	11	9	6	2	5	10	5	11	6	10	10	8	13	13	7	4	8	5	7	4
Carassius carassius (V)	5	+	0.0	0.0	0.0	.	.	.	.	.	.	.	.	.	.	0.0	.	.	.	.	.	.	.	.	1.9	.
Leucaspius delineatus (V)	14	.	0.0	0.7	0.2	0.3	.	.	2.1	80.8	.	.	.	.	97.1	.	5.4	4.1	41.2	0.9	.	.	6.6	.	51.9	92.8
Pungitius pungitius	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rutilus erythrophthalmus	19	+	.	0.7	0.1	0.1	.	.	8.6	.	.	0.5	.	0.1	2.2	0.1	3.9	8.5	12.6	48.3	1.0	4.6	39.3	40.0	13.0	5.4
Tinca tinca	15	+	0.0	0.1	0.0	.	.	.	8.6	.	.	0.3	.	.	0.1	.	0.1	5.4	3.4	0.7	0.9	2.0	.	13.1	20.0	0.5
Percentage limnophilic		0.0	0.0	1.5	0.3	0.4	0.0	0.0	8.6	80.9	0.0	2.9	0.0	2.2	97.4	0.0	14.7	15.9	54.6	50.0	3.0	4.6	59.0	60.0	68.5	98.6
Limnophilic species		4	2	4	4	2	0	0	1	3	0	3	0	1	4	0	3	3	3	3	2	1	3	2	4	3
Abramis bjoerkna	10	+	25.0	4.8	3.1	8.5	.	1.5	.	.	.	.	.	4.0	.	0.1	.	0.3	5.2	2.2	.	.	.	.	.	.
Abramis brama	23	+	35.6	51.5	49.8	55.3	91.2	78.5	48.8	55.7	16.7	69.4	25.7	11.4	63.8	1.6	54.9	60.0	19.9	12.9	84.0	.	3.1	6.6	20.0	24.1
Alburnus alburnus	12	+	0.0	9.1	26.1	14.5	0.4	1.9	9.3	25.0	4.5	0.1	.	.	.	.	.	2.1	0.4	.	.	.	3.1	.	.	.
Anguilla anguilla (S)	9	+	0.1	1.4	0.9	3.4	0.0	.	.	.	.	.	.	.	.	0.5	0.5	.	.	1.0	.	.	.	3.3	6.7	.
Ctenopharyngodon idella	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cyprinus carpio	8	+	.	0.1	.	0.1	.	.	8.3	.	.	.	.	0.1	.	0.1	0.1	.	.	0.2	.	.	.	.	.	.
Esox lucius	22	+	0.0	0.1	0.4	0.1	0.9	1.2	15.1	44.3	1.1	42.9	.	0.3	1.4	0.1	3.9	4.7	2.1	2.6	1.0	.	8.2	13.3	5.6	1.4
Gasterosteus aculeatus	3	+	0.0	0.1	0.1	.	.	.	.	.	.	.	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnocephalus cernuus	12	+	8.7	1.4	0.6	1.4	0.1	.	.	.	.	.	.	0.1	5.8	.	7.4	.	.	6.5	.	.	.	.	.	.
Lepomis gibbosus	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Perca fluviatilis	14	+	1.3	1.4	0.3	0.5	0.0	.	.	.	.	.	.	0.5	0.2	.	3.9	4.1	2.6	5.6	4.5	.	3.6	19.7	.	.
Rutilus rutilus	21	+	19.5	19.8	11.2	5.4	1.4	9.2	24.4	.	41.7	8.6	.	6.5	22.5	0.5	9.8	14.9	11.9	16.4	6.0	88.7	.	.	.	1.9
Silurus glanis	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stizostedion lucioperca	13	+	2.8	2.6	5.2	9.1	0.7	3.8	1.2	.	8.3	.	.	4.4	2.9	.	.	.	0.9	.	.	.	.	.	.	1.9
Hybrid	4	.	0.5	0.2	0.1	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Connectivity (days/year)		365							50-150								2-20									
Species (red list, *)	Occ.	MC fyke (**)	MC trawl (***)	SC 1	SC 2	SC	COL	CP 8	OX 2	OX 1	OX	CP 9	SP 1	CP 14	OX 4	CP 7	CP 3	OX 7	OX 5	OX	CP 5	CP 15	CP 13	CP 6	CP 12	CP 11
Percentage eurytopic	.	.	**93.7**	**92.5**	**97.8**	**98.7**	**94.9**	**96.9**	**98.8**	**100.0**	**100.0**	**96.3**	**77.1**	**96.4**	**96.4**	**2.6**	**84.3**	**84.1**	**44.7**	**47.4**	**96.5**	**95.4**	**41.0**	**40.0**	**31.5**	**1.4**
Eurytopic species		**14**	**10**	**11**	**11**	**10**	**8**	**7**	**5**	**2**	**5**	**7**	**3**	**8**	**5**	**6**	**6**	**5**	**9**	**8**	**5**	**3**	**5**	**3**	**3**	**1**
Aspius aspius	9	+	0.1	0.5	0.8	0.3	4.9	1.5	.	.	.	.	.	.	.	.	0.5	0.5	0.5	1.7	.	.	.	.	.	.
Barbus barbus (E)	1	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chondrostoma nasus (E)	4	.	0.0	.	0.0	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cobitis taenia	2	.	0.1	.	.	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Coregonid	2	+	.	.	.	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cottus gobio	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gobio gobio	4	+	4.2	0.4	0.2	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lampetra fluviatilis (V)	2	.	0.7	0.0	.	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leuciscus cephalus (V)	5	+	0.1	3.5	0.6	0.1	.	.	.	.	.	.	.	.	.	.	.	.	.	0.4	.	.	.	.	.	.
Leuciscus idus (S)	7	.	0.3	1.2	0.1	0.3	0.1	1.2	.	.	.	.	14.3	.	.	.	.	.	.	.	.	.	.	.	.	.
Leuciscus leuciscus (V)	5	.	.	0.0	0.0	0.0	.	.	1.2	0.0	.	.	.	.	.	.	.	.	0.0	.	.	.	.	.	.	.
Osmerus eperlanus	1	.	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Petromyzon marinus (E)	1	+	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Platichthys flesus	4	+	0.1	0.2	0.1	0.0	0.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salmo trutta (V)	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Percentage rheophilic	.	.	**6.2**	**5.8**	**1.8**	**0.8**	**5.1**	**2.7**	**1.2**	**0.0**	**0.0**	**0.0**	**14.3**	**0.0**	**0.0**	**0.0**	**0.5**	**0.5**	**0.5**	**2.2**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Rheophilic species		**8**	**11**	**10**	**7**	**7**	**3**	**2**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**2**	**2**	**0**	**0**	**0**	**0**	**0**	**0**

(*):   Red list species (De Nie & Van Ommering, 1998): X: Extinct as viable population; E: Endangered; V: Vulnerable; S: Susceptible.

(**):   Data from fyke catches (Winter et al., 2000).

(***): Data from trawl surveys (Stam et al., 1999).

Table 6.3. Total catch and relative proportion of 0-group fish assemblages in the main channel and 23 floodplain water bodies along the lower River Rhine. Lakes are ordered according to their connectivity and increasing abundance of aquatic vegetation (% covered). Occ.: the number of water bodies in which a species occurred (including the main channel); '·': species was not observed; '0': proportion lower than 0.05%.

Connectivity (days/year)			365			50-150											2-20								
Species (red list, *)	Occ.	MC	SC 1	SC 3	COL	CP 8	OX 2	OX 1	CP 9	SP 1	CP 14	OX 4	CP 7	CP 4	CP 2	CP 1	CP 3	OX 7	OX 5	CP 5	CP 15	CP 13	CP 6	CP 12	CP 11
Aquatic vegetation (%)		**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2**	**4**	**10**	**16**	**37**	**55**	**66**	**75**	**76**	**85**	**89**	**100**	**100**
Total catch		**4182**	**122342**	**2354**	**116832**	**108531**	**601**	**128**	**508**	**150**	**593**	**83**	**4815**	**1768**	**99540**	**441**	**2754**	**260**	**83**	**35**	**83**	**97**	**14**	**137**	**168**
Total number of species		**16**	**18**	**16**	**16**	**8**	**6**	**7**	**5**	**4**	**1**	**7**	**3**	**4**	**6**	**5**	**6**	**7**	**7**	**3**	**4**	**5**	**3**	**5**	**5**
Leucaspius delineatus (V)	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0.8	·	·	·	·	·	·	·
Rutilus erythrophthalmus	8	·	·	·	·	·	·	·	·	·	·	·	13.1	·	·	0.4	·	24.6	2.4	·	·	4.1	42.9	1.5	14.9
Tinca tinca	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	21.4	·	·
Percentage limnophilic		**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**13.1**	**0.0**	**0.0**	**0.4**	**0.0**	**25.4**	**2.4**	**0.0**	**0.0**	**4.1**	**64.3**	**1.5**	**14.9**
Limnophilic species		**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**0**	**1**	**2**	**1**	**1**
Abramis bjoerkna	4	2.8	·	0.4	5.3	15.0	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Abramis brama	22	55.8	66.6	22.2	71.2	98.2	65.2	35.2	61.6	4.0	100	72.3	85.4	77.4	75.8	78.5	91.1	41.2	6.0	·	9.6	53.6	·	84.7	72.6
Alburnus alburnus	6	3.1	0.3	6.2	0.7	0.3	·	1.2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cyprinus carpio	4	0.1	0.0	0.3	0.0	0.0	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Esox lucius	16	·	·	0.3	0.3	0.0	·	·	·	0.7	·	2.4	·	0.0	·	4.5	0.9	2.3	19.3	57.1	·	21.7	21.6	35.7	7.7
Gasterosteus aculeatus	4	0.2	·	0.0	·	0.1	·	·	·	·	·	·	·	0.1	·	·	·	·	·	·	·	·	·	·	·
Gymnocephalus cernuus	16	0.5	0.4	0.3	0.2	0.2	3.7	43.0	1.4	·	·	1.2	·	·	1.9	·	0.5	0.8	19.3	·	·	·	10.9	·	·
Perca fluviatilis	18	0.8	0.3	3.7	0.3	3.5	3.5	7.0	5.5	·	·	18.1	·	·	6.5	12.2	3.5	3.5	13.3	40.0	56.6	13.4	1.8	6.6	·
Rutilus rutilus	22	5.1	24.8	11.5	3.5	1.4	22.1	2.3	30.1	93.3	·	·	3.7	20.6	4.3	7.5	·	26.9	8.4	2.9	12.0	7.2	4.4	·	·
Stizostedion lucioperca	6	8.0	1.2	5.8	5.5	0.0	·	·	·	·	·	·	0.0	·	·	·	·	·	·	·	·	·	·	·	·
Hybrid	6	0.0	0.0	0.0	0.1	·	2.5	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0.6	·	·
Unidentified	4	1.0	2.8	1.7	1.1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Percentage eurytopic		**77.4**	**96.7**	**57.3**	**97.6**	**100.0**	**97.2**	**87.5**	**98.6**	**100.0**	**100.0**	**95.2**	**86.9**	**100.0**	**99.6**	**100.0**	**100.0**	**74.6**	**66.3**	**100.0**	**100.0**	**95.9**	**35.7**	**98.5**	**84.5**
Eurytopic species		**9**	**10**	**9**	**9**	**6**	**5**	**4**	**4**	**4**	**1**	**5**	**5**	**3**	**5**	**5**	**5**	**5**	**5**	**3**	**4**	**4**	**1**	**4**	**4**
Aspius aspius	8	1.8	0.3	0.8	1.4	0.0	·	·	·	·	·	2.4	·	·	·	·	·	·	31.3	·	·	·	·	·	·
Barbus barbus (E)	4	6.5	0.6	17.0	0.6	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Chondrostoma nasus (E)	3	4.6	0.0	1.7	0.0	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

Connectivity (days/year)		365					50-150									2-20									
Species (red list, *)	Occ.	MC	SC 1	SC 3	COL	CP 8	OX 2	OX 1	CP 9	SP 1	CP 14	OX 4	CP 7	CP 4	CP 2	CP 1	CP 3	OX 7	OX 5	CP 5	CP 15	CP 13	CP 6	CP 12	CP 11
Coregonid	5	0.2	0.0	0.1	0.0	0.0	.	.	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gobio gobio	4	2.8	0.0	12.0	0.0	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leuciscus cephalus (V)	4	0.3	0.0	0.1	0.0	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leuciscus idus (S)	9	6.4	2.4	5.0	0.4	0.4	0.0	0.3	10.2	1.4	.	.	2.4	.	.	.	.	.	2.4	.	.	.	.	.	.
Leuciscus leuciscus (V)	4	0.3	0.0	5.9	0.0	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Osmerus eperlanus	2	.	0.0	.	.	0.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Percentage rheophilic		**22.9**	**3.3**	**42.6**	**2.4**	**0.0**	**0.0**	**0.3**	**11.9**	**1.4**	**0.0**	**0.0**	**4.8**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**31.3**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Rheophilic species		**7**	**8**	**7**	**7**	**2**	**1**	**1**	**3**	**1**	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**

(*):   Red list species (De Nie & Van Ommering, 1998): X: Extinct as viable population; E: Endangered; V: Vulnerable; S: Susceptible.

6.4 Discussion

Although we think that the fish communities were sampled representatively, conclusions from data presented in this study cannot be drawn without consideration of the sampling of the fish in these diverse water bodies. The variety of the environmental conditions in the water bodies sampled, necessitated the use of different types of gear but we think that the sampling effort per water body was so high, that occurrence of species and species composition was sampled representatively in each of the water bodies. We have, however, no further proof or statistical testing to support this assumption. The mesh sizes used in the lakes may have led to underestimation of 0-group fish of some species in the seine catches. Quantitative methods of fish sampling were not feasible within the current project. Mark-recapture studies for example, cost a lot of sampling effort and are only suitable for abundant species. Gillnetting and poisoning of fish were impossible because we aimed to keep the fish alive since all these floodplains are either situated in nature reserve areas or are important for recreational fisheries.

Vegetated floodplain lakes make an important contribution to the fish species diversity of the lower Rhine, because they are essential for limnophilic fish that cannot reproduce anywhere else. The limnophilic species contribute little to the total species richness, but they are characteristic of the less dynamic parts of floodplain rivers and, moreover, some of them are on the Netherlands Red list of endangered species. The average number of species decreased with decreasing connectivity, and species richness in vegetated floodplain lakes was considerably lower (5-8 species) than in permanently connected water bodies (up to 28 species). A similar gradient was observed along the River Danube where, with decreasing connectivity, the total number of fish species and the number of endangered species decreased. For other groups (macrozoobenthos, odonata, macrophytes), however, highest species richness occurred in water bodies with intermediate connectivities and for one group (amphibians) in water bodies with the lowest connectivity (Ward *et al.*, 1999; Tockner *et al.*, 2000). It is evident that the ecological value of water bodies should not be judged by the number of species of one ecological group alone.

The array of fish species that was observed along a lateral gradient of connectivity conformed to the classification of rheophilic, eurytopic and limnophilic species according to Schiemer & Waidbacher (1992) and confirms the results of the preliminary studies along the lower River Rhine (Van den Brink, 1994; Buijse & Vriese, 1996). A similar gradient from rheophilic to limnophilic species from lotic to lentic water bodies was also observed in the natural Szigetköz floodplains along the
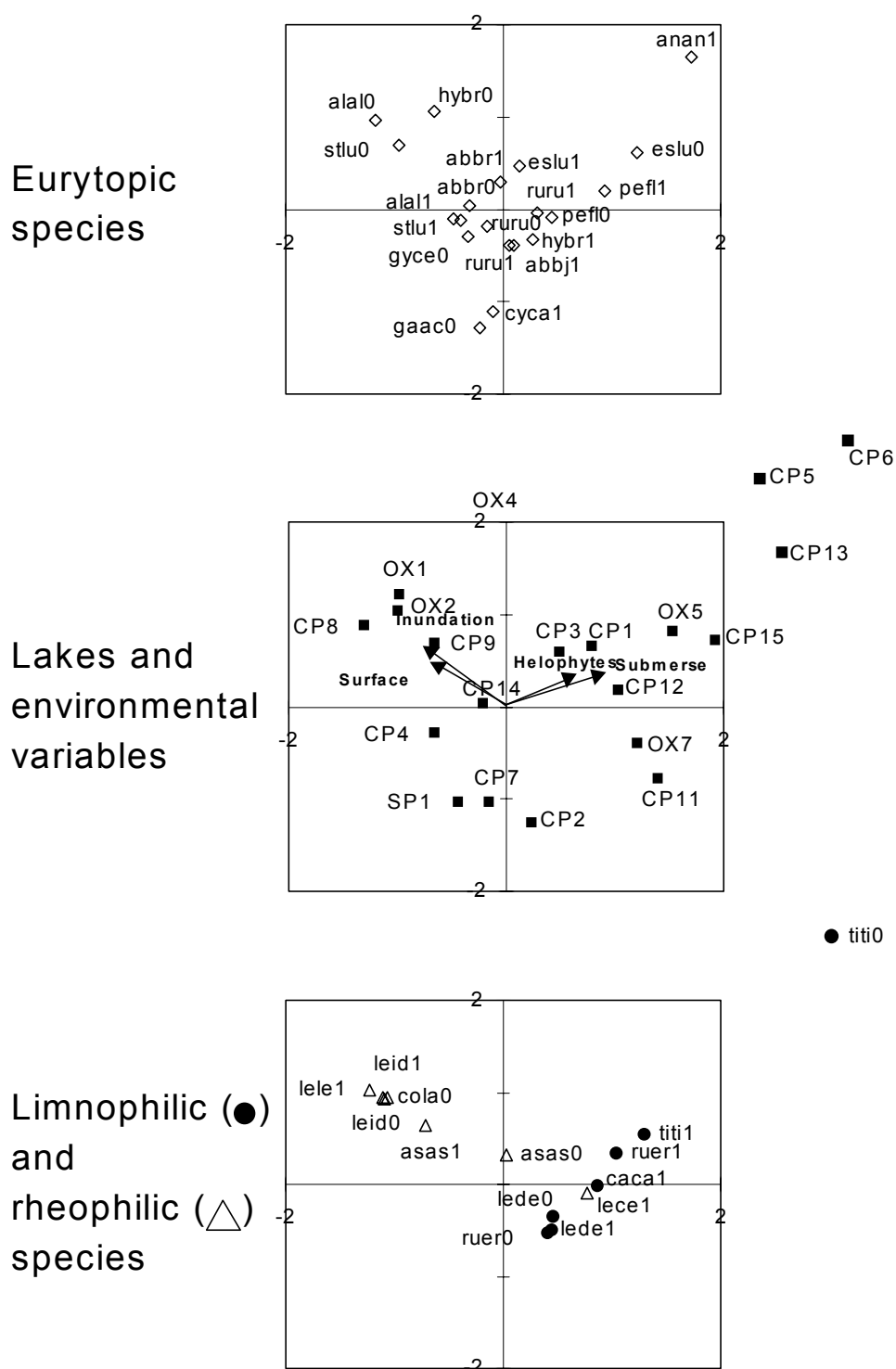
Figure 6.4. Distribution of fish in floodplain lakes along the River Rhine. Canonical correspondence analysis ordination diagram with fish species, floodplain lakes and environmental variables. Figures are the result of one analysis but eurytopic species (upper panel), lakes and environmental variables (middle panel) and limnophilic and rheophilic species (lower panel) are presented separately. First and horizontal axis explains 16.5%, the second axis 7.9%. Species are abbreviated with their first two letters of genus and species name and their stage (0: 0-group fish; 1: 1+ fish).

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River Danube (Guti, 1996) and floodplains along the Upper Rhône (Copp & Peñáz, 1988). In the most remote floodplain lakes of the Danube delta, limnophilic species (tench, crucian carp and pike) even dominated (>50% of total biomass) the fish communities (Navodaru *et al.*, 2000). This dominance of limnophilic species was explained by the intact river-floodplain interaction in the delta. In none of our floodplain lakes, however, did limnophilic species dominate in terms of biomass. It could be that the frequent inundation of the floodplain lakes favours eurytopic species such as the bream and is unfavourable for limnophilic species.

Figure 6.5. Biomass composition of fish communities in 20 floodplain lakes. The lakes are ordered first according their connectivity (arrows on top) and second according to increasing cover of aquatic vegetation (solid line; Table 6.1).

Frequent inundation of floodplain lakes may prevent them from succession into a stage where they are dominated by limnophilic species. In natural lowland rivers, floodplain lakes undergo succession during which they are colonized by riparian plants (Amoros & Roux, 1988) and the different stages imply a succession of spawning possibilities for different fish species. In a final stage, when the former meander becomes heavily silted and/or impeded with aquatic vegetation, fish reproduction is gradually reduced to limnophilic species only (Copp *et al.*, 1991). Crucian carp and weatherfish for example, are well adapted to withstand environmental conditions that may occur during longer periods of isolation (Holopainen *et al.*, 1997; Meyer & Hinrichs, 2000) but these conditions go beyond the tolerance limits of other, more sensitive species such as bream (Backiel & Zawiswa, 1968) and roach. In natural floodplain lakes, differential mortality of fish species with different life histories occurs (Lowe-McConnell, 1975; Welcomme, 1979; Merron *et al.*, 1993; Winemiller & Jepsen, 1998; Winemiller *et al.*, 2000), and may even determine species composition to

a greater extent than migration during connection (Halyk & Balon, 1983; Tejerina-Garro *et al.*, 1998). To date, along the lower River Rhine, almost all floodplain lakes are connected with the main channel almost every year, which frequently disturbs or resets the succession process of the lakes (Petts, 1994; Heiler *et al.*, 1995), and causes a decreasing species richness and abundance of aquatic macrophytes and helophytes (Van den Brink *et al.*, 1991). The absence of vegetation, and the absence of low water levels and low oxygen contents, is more favourable for eurytopic species such as the bream than for limnophilic species. In lakes without vegetation, bream contributed up to 98% of the fish biomass. Due to their benthivorous mode of feeding (Lammens, 1982, 1984), mature bream can resuspend bottom sediment, reduce transparency and prevent macrophytes from colonizing these lakes (Meijer *et al.*, 1990). Nowadays, remote lakes that were once seldom flooded and were in a final stage of succession, are completely disconnected from the river by winter dykes. Consequently, floodplain lakes in which limnophilic species would dominate seem to be lacking.

At present, the national policy concerning major rivers in the Netherlands may provide the opportunity to improve the environmental conditions for both rheophilic and limnophilic fish species. The policy aims at sustainable flood protection along the rivers that will be achieved through a combination of measures: strengthening the dykes, giving the rivers more room to expand and retaining the water (Ministry of Transport, Public Works and Water Management, 1998). The latter two are complementary measures from the viewpoint of fish, from which the various species may profit selectively. Rheophilic fish species profit from recently created secondary channels and reconnected oxbow lakes (Grift *et al.*, 2001) that were created to give rivers more room to expand as they did in the past (WWF, 1993; Buijse & Vriese, 1996; Cals *et al.*, 1998). The retention areas may provide the opportunity for restoring remote floodplain lakes that provide suitable habitats for the limnophilic species. These retention areas will only become connected with the main channel during calamities and consequently, they will seldom be inundated and will remain isolated for long periods (Ministry of Transport, Public Works and Water Management, 1998). If these retention areas are designed in such a way that aquatic vegetation can develop, they might compensate for the current scarcity of less dynamic floodplain lakes with abundant vegetation. In this way, improved safety can be combined with rehabilitation of floodplain water bodies. In our study, only abundance of aquatic vegetation explained fish community structures that did not differ between man-made clay-pits and natural oxbows. Therefore, we suppose that man-made lakes can provide suitable habitat for limnophilic fish. Frequently inundated floodplain lakes without vegetation had low species richness. They would be better permanently connected with the main channel, when development of aquatic vegetation is unlikely, since they will probably

then benefit rheophilic species. Vegetated man-made clay-pits and natural oxbow lakes should however be preserved and not be permanently connected to the main channel since they have an additional and unique value for the riverine fish community as 'islands' with remnants of limnophilic fish populations.

Acknowledgements

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Photo 8. Juvenile ide *Leuciscus idus* (upper fish) and nase *Chondrostoma nasus* (lower fish).

Photo 9. Adult ide *Leuciscus idus*.

Chapter 7

Synthesis:

How fish benefit from floodplain restoration

along the lower River Rhine

7.1 Introduction

The objectives of this study were to test the beneficial value of newly created secondary channels and reconnected oxbow lakes and to give advice on position, shape and character of future water bodies. These objectives were pursued by assessing the fish community structure in various types of floodplain water body and by assessing the function these water bodies fulfil as spawning, nursery and refuge areas during the life cycles of distinct fish species. This chapter integrates results of the previous Chapters 2-6. First, seven conclusions are drawn that summarize the results of the previous chapters. Next, the national policy concerning large rivers and their floodplains in the Netherlands is described. Thereafter, the life cycles of fish in the lower River Rhine are described and the functions floodplain water bodies fulfil are inferred. From these life cycles, the factors that determine the fish community in the lower Rhine are assessed. Finally, it is described how results of this study can be used within the national policy to improve environmental conditions to rehabilitate the populations of riverine fish. In this section, directions for future research are indicated.

7.2 Conclusions

1. Almost all fish species that are typical of the lower Rhine utilize floodplain water bodies during some stage of their lives.

    In total, throughout this study, 32 fish species were recorded of which for 25 species it could be demonstrated that they utilize the different types of floodplain water body along the lower Rhine during some stage of their lives. All species use the main channel mainly as a transport route to migrate among different habitats in the floodplains, which are essential for the life cycle of most fish species. Rheophilic species only utilize floodplain water bodies that are permanently connected to the main channel, such as secondary channels and connected oxbows (**Chapter 2, 6**). Some species, such as barbel *Barbus barbus* and nase *Chondrostoma nasus*, only use the floodplains along the lower Rhine during short periods of their lives (**Chapter 4**). Eurytopic species, however, complete their entire life cycle within the lowland stretch of the Rhine and utilize all types of floodplain water body. Some of these species utilize different types of floodplain water body during their lives as was demonstrated for bream *Abramis brama* (**Chapter 5**). Limnophilic species only utilize vegetated floodplain lakes, they are rare in the main channel and water bodies permanently connected to it (**Chapter 2, 3, 6**). Diadromous species do not utilize any of the floodplain water bodies.

2.   Fish rapidly colonize newly created floodplain water bodies.

Within three years after the creation of secondary channels, and within four years after reconnecting an oxbow lake to the main channel, 30 fish species (from the 47 species present in the lower Rhine) occurred in these water bodies and from 23 species, 0-group fish were observed (**Chapter 2**, **3**). Their species composition and their functioning resembled those of natural floodplain water bodies along other, less degraded rivers (**Chapter 3**, **4**).

3.   Floods are important to create and connect habitats.

Due to the poor habitat diversity in the main channel, fish reproduction depends on habitats that are created and connected during floods. Inundated terrestrial vegetation proved to be an important habitat for the larvae of barbel, ide *Leuciscus idus*, gudgeon *Gobio gobio*, asp *Aspius aspius*, bream, roach *Rutilus rutilus*, white bream *Abramis bjoerkna*, bleak *Alburnus alburnus* and pikeperch *Stizostedion lucioperca* (**Chapter 3**). Moreover, for juvenile rheophilic fish, shallow habitats that are formed during floods, are important as nursery areas. For many species, inundated terrestrial vegetation is important since in the main channel, the area of habitat that is suitable for reproduction is limited. Recruitment of bream from floodplain lakes, depends on floods in autumn during which they have to move out of the lakes to grow up in the main channel (**Chapter 5**).

4.   Newly created secondary channels and reconnected oxbow lakes do have a beneficial value for the riverine fish community.

Compared to the groyne fields and floodplain lakes that were already present before floodplain restoration, secondary channels and reconnected oxbow lakes provide habitats that are significantly better suitable for 0-group fish (**Chapter 2, 3**). Moreover, they form important spawning and nursery areas that currently curtail populations of rheophilic cyprinids (**Chapter 4**). They function as nursery areas for almost all rheophilic species of which densities of juveniles (3-5 cm) peak in summer. Secondary channels may also function as spawning areas for ide and gudgeon but this could not be demonstrated. For the lithophilic species (barbel, asp, nase, dace *Leuciscus leuciscus*) they do not function as spawning areas since suitable substrate lacks. Eurytopic species utilize the secondary channels and reconnected oxbow lakes as spawning and nursery areas. Some species remain present throughout the year (**Chapter 4**). Within the

strict conditions with regard to shipping and protection against flooding, water bodies can thus be created that contribute to the rehabilitation of the riverine fish community.

5. Remote lakes, in which limnophilic species dominate, have disappeared.

    Floodplain lakes with abundant vegetation are the only type of water body along the lower Rhine that provides suitable habitat for the reproduction of limnophilic species. In none of these lakes, however, limnophilic species dominate and some limnophilic species are absent. This indicates that these lakes get inundated too frequently for limnophilic species to become dominant over eurytopic species and that remote lakes, in which they dominate in natural floodplains, have disappeared (**Chapter 6**).

6. Habitat availability in floodplain water bodies determines the fish species composition. The beneficial value of newly created water bodies can thus be influenced by their design.

    Among water bodies, total fish density increased along a gradient of decreasing water movement whereas the proportion of rheophilic species decreased. Flow velocity and depth at a site determine the species assemblage at that site and consequently, the assemblage of sites in a water body determines the habitat suitability (**Chapter 3**). As a consequence, a gradient from rheophilic, via eurytopic to limnophilic species exists along a lateral gradient of connectivity, from lotic to lentic water bodies (**Chapter 2, 6**). The different types of water body clearly had complementary values: secondary channels with low shoreline complexity were most beneficial for barbel and gudgeon, secondary channels with higher shoreline complexity for ide and asp whereas reconnected oxbow lakes contributed most to the eurytopic community (**Chapter 2**, **3**).

7. Floodplain management should focus on increasing the number of secondary channels and on restoring the natural interaction between the river and its floodplains.

    The absence of secondary channels and the reduced area of dynamic floodplain caused the decline of populations of rheophilic fish. Since rheophilic fish are still present, and this study showed that they are able to colonize new habitats rapidly, further restoration of low-flow floodplain water bodies and of the

aquatic/terrestrial transition zone will further contribute to the rehabilitation of the endangered populations of rheophilic fish.

7.3 Current policy on river management

Above all, the current policy on river management aims at increased safety against floods, but recent insights in ways to increase safety, provide the opportunity to enhance environmental conditions for fish. "A safe and habitable country with healthy and sustainable water systems" is the aim of Dutch water management for the period of 1998-2006. With regard to the major rivers, policy focuses on maintaining flood protection in the face of larger design discharges, while at the same time conserving landscape, ecological and historical features, promoting navigational use and creating new wildlife areas. To achieve this objective, rivers will be given more room to expand as they did in the past, primarily by making their winter beds broader and deeper (Ministry of Transport, Public Works and Water Management, 1998). This policy aims at coupling safety to mining activities and to the development of nature areas. Mining activities would contribute significantly to financing this policy, and deep sand-mining pits can be used to deposit excavated soil that has no other use. Combining floodplain excavation with nature development serves two goals: increased safety can be payed for from different budgets and targets for nature development along the lower River Rhine can be achieved more easily and faster. Moreover, less land needs to be reclaimed from farmers that use floodplains for agricultural activities.

Current advice on increased safety against flooding is adjusted to the expected increase in water levels in the near future as a result of climate change and sea level rise. Although the overall yearly discharge will remain rather constant, extremely high and low flows will become more common. Flow in the lower River Rhine is forecast to drop 10 to 20 percent in the summer due to increased evaporation. In winter, however, floods will occur more frequently due to increased precipitation and greater likelihood of snow melting in the Alps shortly after precipitating. To maintain the current safety standards, discharge capacity of the Rhine needs to be increased. The highest water level that a dyke should be able to withstand is referred to as the design hydraulic load (DHL). From the DHL, requirements such as dyke height and stability are derived (Middelkoop & Van Haselen, 1999). Until 2000, the DHL was set at a discharge of 15,000 $m^3 s^{-1}$ at Lobith. From 2001 onwards, the DHL, which is assessed every five years, will probably be set at 16,000 $m^3 s^{-1}$.

A safe discharge of the DHL should go hand in hand with lowering the water levels in the river and adjacent floodplains during floods. Lowering water levels by increasing discharge capacity in the floodplains has highest priority. Increasing

discharge capacity in the main channel has lower priority and heightening dykes has lowest priority and will only happen if none of the above measures has effect. The proposed measures in the floodplains, ordered with decreasing preference, are to: 1) widen the floodplain by moving winter dykes, 2) excavate floodplains and link excavation to nature rehabilitation and 3) remove obstacles from floodplains (brick factories, bridges, summer dykes; Bestuurlijke Begeleidingsgroep Ruimte voor Rijntakken, 2000). In the main channel, water levels during floods can be lowered by lowering groynes and excavating the main channel. These measures are attuned to a DHL of 16,000 $m^3 s^{-1}$.

To deal with even higher peak discharges (>18,000 $m^3 s^{-1}$), retention areas (or calamity polders) outside the floodplains may be created to store large volumes of water (>10^8 m^3) temporarily during floods. Retention areas are not part of current policy yet, but locations for these areas need to be assigned and reserved.

Locations for the proposed measures vary among the three branches of the Rhine in the Netherlands because of their different morphological and hydrological characteristics. Owing to its dynamic characteristics, it was proposed that management of floodplains along the free flowing River Waal should focus on creating larger areas with dynamic wet nature. Along the River Nederrijn/Lek, that has a regulated discharge due to the presence of three weirs, it was proposed that management focuses on low dynamic nature. Because of its narrow floodplains, floodplain excavation poses a larger danger for instability of the dykes than along the Waal. Most dykes along the River IJssel are currently safe at a discharge of 16,000 $m^3 s^{-1}$. Consequently, present policy is not directed towards large scale measures along this branch. At stretches with dykes that are not safe yet, however, measures were proposed to develop nature areas along this branch for which the relatively broad floodplains are suitable (Bestuurlijke Begeleidingsgroep Ruimte voor Rijntakken, 2000).

At present, the surface of nature areas in floodplains along the Rhine is 80 km^2 of the total area of 290 km^2 of floodplain (including lakes). By 2018, a National Ecological Network of protected areas should be created. The target of this policy is to maintain 7000 km^2 of smaller and larger nature areas throughout the Netherlands, which are connected through ecological corridors. This network should comprise floodplains and the rivers should form wet corridors among nature areas. The plans aim at doubling the area of nature in the floodplains by which 160 km^2 of the total area floodplains should be nature areas (Bestuurlijke Begeleidingsgroep Ruimte voor Rijntakken, 1999).

7.4 Life cycles of fish in the lower Rhine

In total, throughout this study, 32 fish species were recorded of which for 25 species it could be demonstrated that they utilize the different types of floodplain water body along the lower Rhine during some stage of their lives (Table 7.1). These species can roughly be classified into four groups that mainly differ in the scale of their home range and the types of habitat they utilize during their life cycle. This scale varies from the hundreds of metres that limnophilic fish move within a single floodplain lake to the hundreds of kilometres that barbel travel between their spawning and nursery areas, using gravel banks, the main channel and nurseries in the floodplains. Of the 32 species recorded, coregonids, Rheophilic C species (smelt *Osmerus eperlanus*, flounder *Platichthys flesus*) and some exotic species (stone moroko *Pseudorasbora parva*, grass carp *Ctenopharyngodon idella*) do probably not utilize floodplains.

Table 7.1. Overview of the functioning of main channel and floodplain water bodies for different species of fish as could be demonstrated in this study. Species indicated are examples for the reproductive guilds. M: migration; S: spawning; N: nursing; -: no function; ?: function assumed but not demonstrated.

Reproductive guild	Species	Main channel	Secondary channel	Downstream connected oxbow	Floodplain Lake
Rheophilic A	Barbel	M	N	-	-
	Nase	M	N	-	-
	Coregonid		-	-	-
Rheophilic B	Ide	M?	S?,N	S?,N	-
	Gudgeon	M?	S?,N	S?,N	-
	Asp	M	N	N	-
Rheophilic C	Smelt	M?	-	-	-
	Flounder	M?	-	-	-
Eurytopic	Bleak	M?	S,N	S,N	-
	Bream	M?	S,N	S,N	S,N
	Pikeperch	M?	S,N	S,N	S,N
Limnophilic	Sunbleak	M?	-	-	S,N
	Tench	M?	-	-	S,N

The life cycle of lithophilic species (barbel, chub, asp and dace) covers an area larger than the Dutch part of the Rhine (Figure 7.1[a]). They cannot complete their life cycles within this stretch since it lacks gravel that they require as a spawning substrate. In the German part of the Rhine, all life stages of these species occur. Their larvae probably move passively downstream to the lowland floodplains that form suitable nursery areas. Juveniles also occur in the groyne fields. Larvae prefer shallow (<0.5 m) areas with inundated terrestrial vegetation and low to moderate flow velocities (0.05-0.20 m s^{-1}). With increasing length, they move to deeper areas (0.5-1.0 m) with higher flow velocities (up to 0.30 m s^{-1}) and inundated terrestrial vegetation becomes less
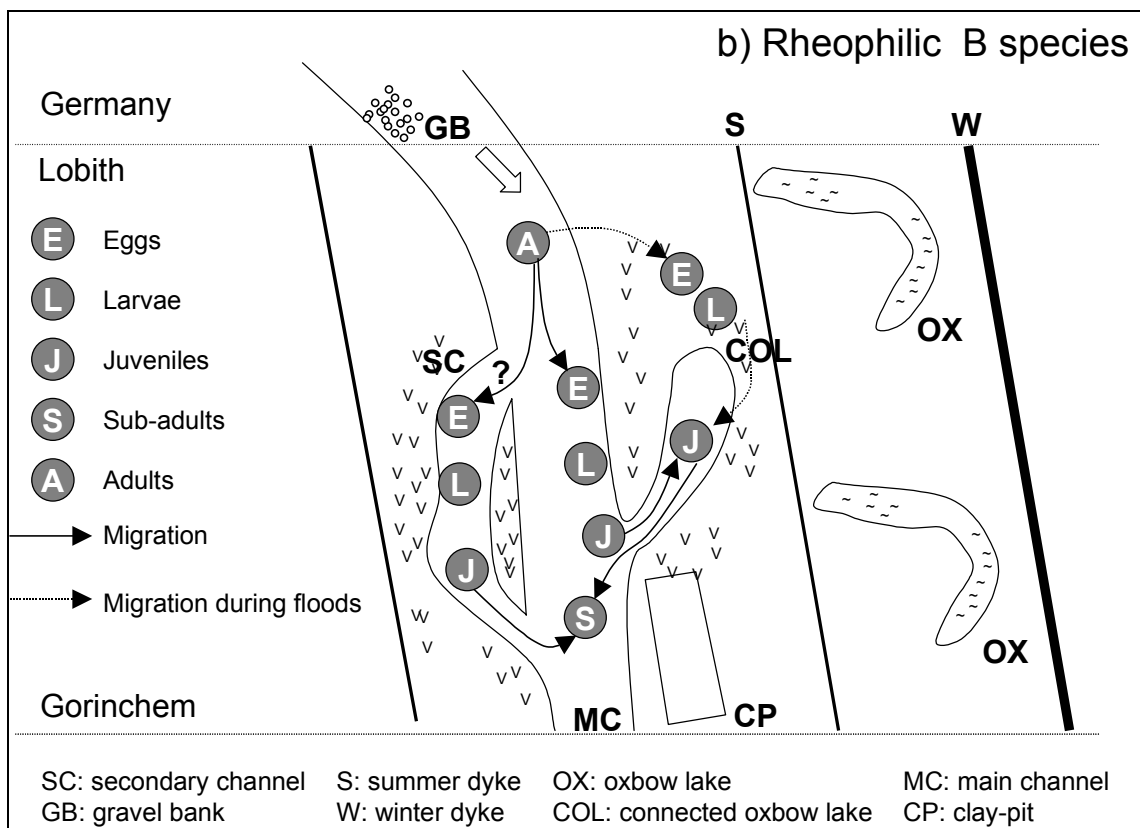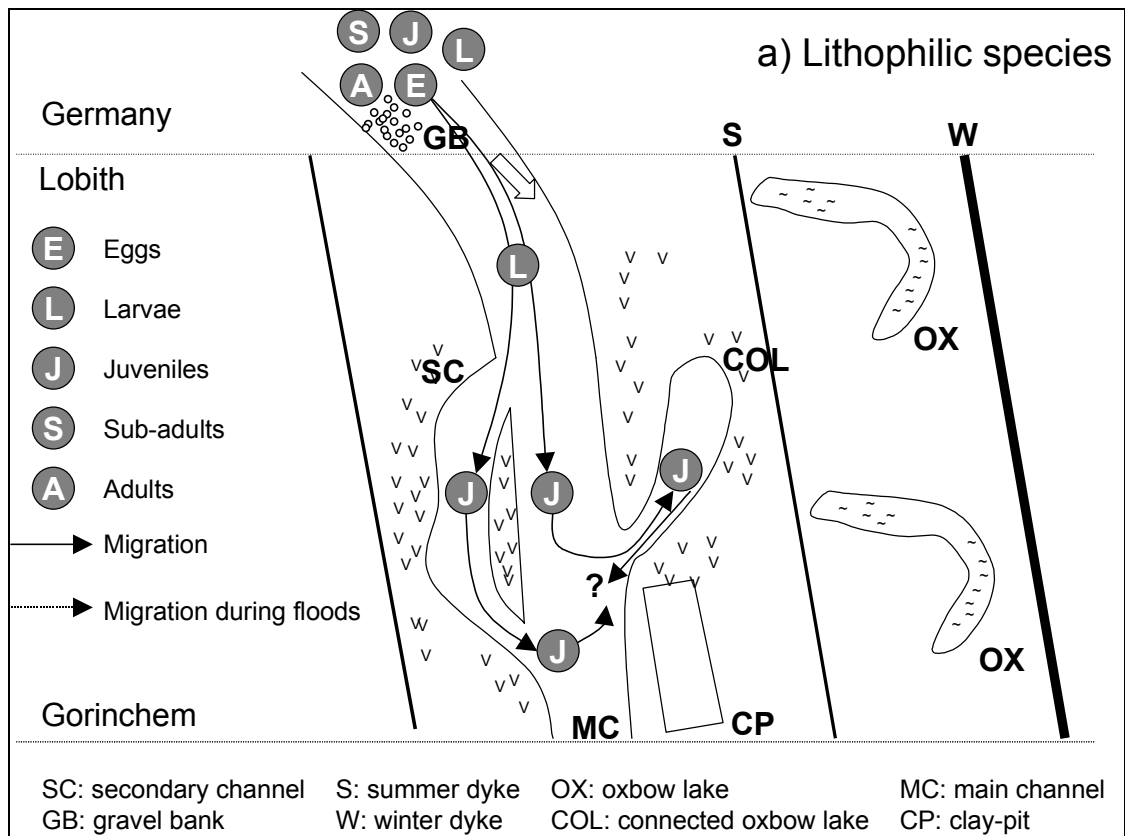
Figure 7.1a and 7.1b. Life cycle of lithophilic (as being represented by barbel) and of rheophilic B species (as being represented by ide) along the lower Rhine. The horizontal hatched line indicates the border of the study area (Lobith-Gorinchem).
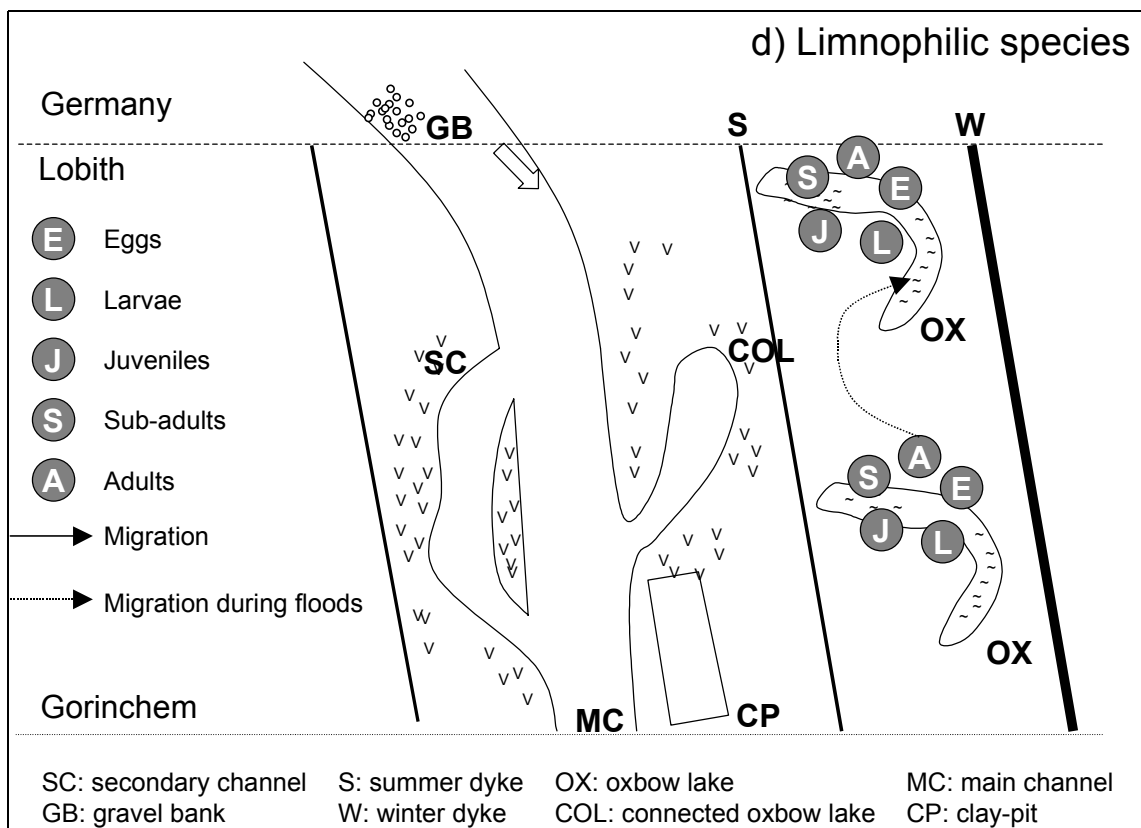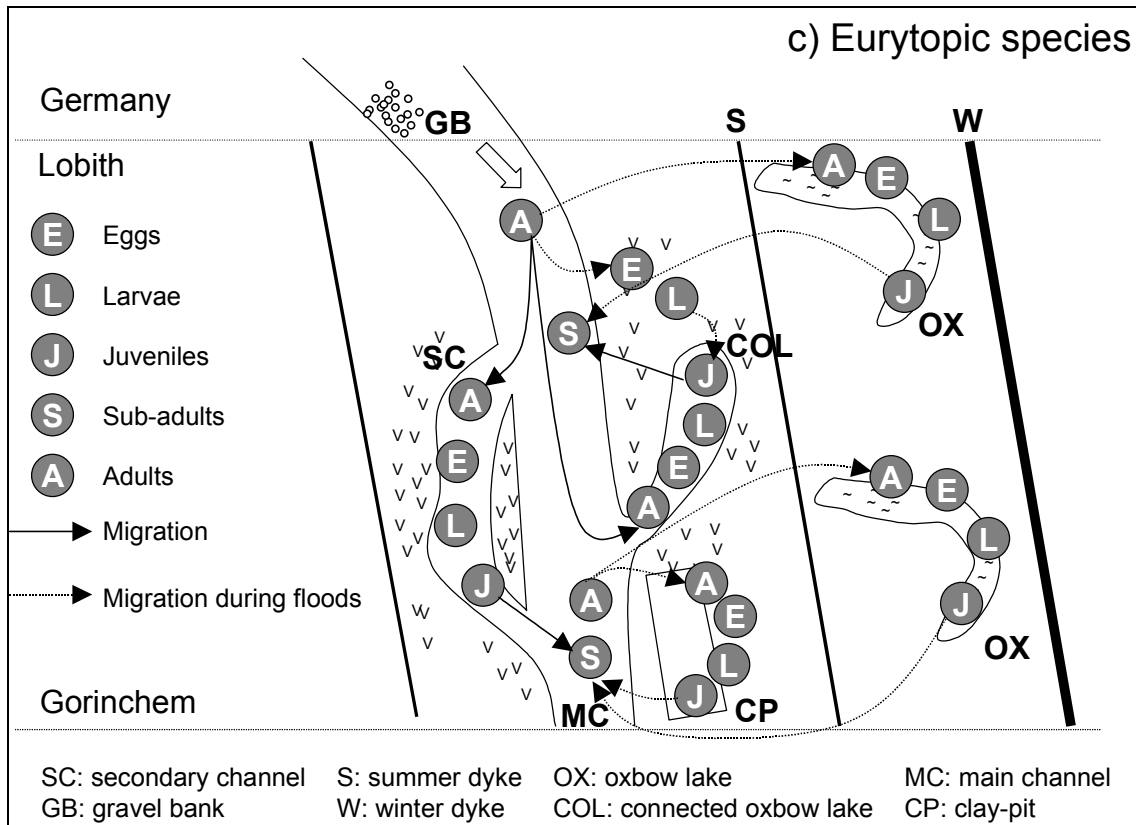
Figure 7.1c and 7.1d. Life cycle of eurytopic species (as being represented by bream) and of limnophilic species (as being represented by tench) along the lower Rhine. The horizontal hatched line indicates the border of the study area (Lobith-Gorinchem).

important. Barbel, chub and dace only use the floodplains for short periods of their lives (when they are 3-5 cm) and asp for a longer period (when they are 3-12 cm). In the main channel, almost all length classes of these species are present but their densities are low. The main channel is mainly used as a transport route between the spawning areas and the floodplains downstream. There is no difference in the functioning between secondary channels and reconnected oxbow lakes as nursery areas, but differences in densities of juveniles are significant and are caused by differences in hydrological conditions. The density of juvenile barbel is almost six times higher in a dynamic secondary channel than in a stagnant oxbow lake. On the contrary, densities of asp are highest in the stagnant oxbow lake (six to nine times those in the dynamic secondary channel). None of the lithophilic species utilize isolated floodplain lakes.

Rheophilic B species (ide and gudgeon) complete their life cycles most probably within the lower Rhine but only use inundated floodplains and water bodies that are permanently connected to the main channel (Figure 7.1[b]). They may utilize secondary channels and flowing parts in inundated floodplains as spawning areas but this could not be demonstrated. Spawning in connected oxbow lakes does probably not happen since flowing water is absent. Larvae of ide and gudgeon occur at sites with flow velocities up to 0.2 m s^{-1} that are mainly shallow (<1 m deep). Ide larvae prefer sites with a dense vegetation. Juvenile ide and gudgeon occur at deeper sites (up to 2 m deep) with flow velocities up to 0.5 m s^{-1}, gudgeon preferring higher flow velocities than ide. In the main channel, ide and gudgeon of all sizes occur but in low densities. As for the Rheophilic A species, there is no difference in the functioning between secondary channels and connected oxbow lakes as nursery areas, but differences in hydrological conditions cause significant differences in densities of juveniles. Densities of ide are highest in secondary channels with moderate flow whereas densities of gudgeon are highest in the more dynamic secondary channel (up to 30 times those in the stagnant oxbow lake). They also occur in the groyne fields but densities of ide are two to five times higher in the floodplains. Densities of gudgeon are six times higher in the groyne fields than in the connected oxbow lake but three to five times lower than in the most dynamic secondary channels.

Eurytopic species (bream, roach, white bream and pikeperch) migrate among habitats within the lower Rhine and complete their life cycles within this stretch (Figure 7.1[c]). During their life cycles, they utilize various types of floodplain water body as spawning and nursery areas. Groyne fields seem to have no function as spawning and nursery areas for them. All these species use permanently connected water bodies and bream also uses floodplain lakes to reproduce. During floods, adults migrate to floodplain lakes to spawn and juveniles leave the floodplain lakes at the first

opportunity to become resident in the main channel until maturity. A significant part of the adult bream remains resident in the floodplain lakes, probably for the rest of its life. In turbid clay-pits, bream dominate the 0-group fish assemblage, contributing up to 100%. In permanently connected water bodies, larvae of all species prefer moderate depths; bream and bleak sites <0.2 m that are stagnant and roach, white bream and pikeperch sites of 0.5-1.0 m with flowing conditions (up to 0.3 m s^{-1}). For larvae of almost all species, and bream in particular, is inundated terrestrial vegetation important. Roach, bream and white bream move to deeper sites with various flow velocities (up to 0.3 m s^{-1}) when they grow larger. All these species make up a large part of the fish community in the main channel where of each species, almost all size classes occur. This is in contrast to the floodplain lakes, from which sub-adult, medium sized bream (10-30 cm) and almost all size classes of white bream and roach are absent. There is no difference in the functioning as spawning and nursery areas among secondary channels and connected oxbow lakes, but differences in hydrological conditions cause significant differences in densities. In general, densities of juvenile eurytopic fish are highest in the less dynamic water bodies: the stagnant connected oxbow lake and secondary channel 2 (up to twelve times those in the dynamic secondary channel), which has abundant sites with stagnant water in connected clay-pits. Of all eurytopic species, densities are lowest in the groyne fields.

Limnophilic species (tench *Tinca tinca*, rudd *Rutilus erythrophthalmus* and crucian carp *Carassius carassius*) complete their life cycles within one floodplain lake and do not seasonally migrate among different habitats (Figure 7.1^d). They may, however, move to other lakes during floods which results in a prevention of inbreeding. For reproduction, they depend on submerse aquatic vegetation. Consequently, they are limited to isolated floodplain lakes with abundant vegetation and cannot reproduce in turbid floodplain lakes without vegetation. They do not utilize the main channel and water bodies permanently connected to it except may be for migration among different habitats.

7.5 Factors determining the fish community in the lower Rhine

The fish community in the lower Rhine

The riverine fish community is disturbed as a result of the regulation and normalization. The species composition of the fish community in the lower Rhine shows a remarkable difference between the 0-group and the 1+ fish assemblages (Figure 7.2). In the main channel (MC), Rheophilic A and B species contribute 23% to the total number of 0-group fish whereas they only contribute 6% to

the 1+ fish assemblage (Figure 7.2). This is not due to a habitat shift from the main channel to connected waters (SC1, SC2, COL) in this stretch of the Rhine, since in these water bodies, their contribution to the 0-group fish assemblage (4-41%) is also larger than that to the 1+ fish assemblage (1-4%). In turbid clay-pits, eurytopic species dominate and make up more than 99% of both the 0-group and 1+ fish assemblages whereas they are less important in vegetated floodplain lakes (OX3) where limnophilic species dominate numerically. The densities (numbers per 1000 m^2) of both rheophilic and eurytopic 0-group fish are high in the main channel and connected waters whereas densities of 1+ rheophilic fish are almost zero (Table 7.2).
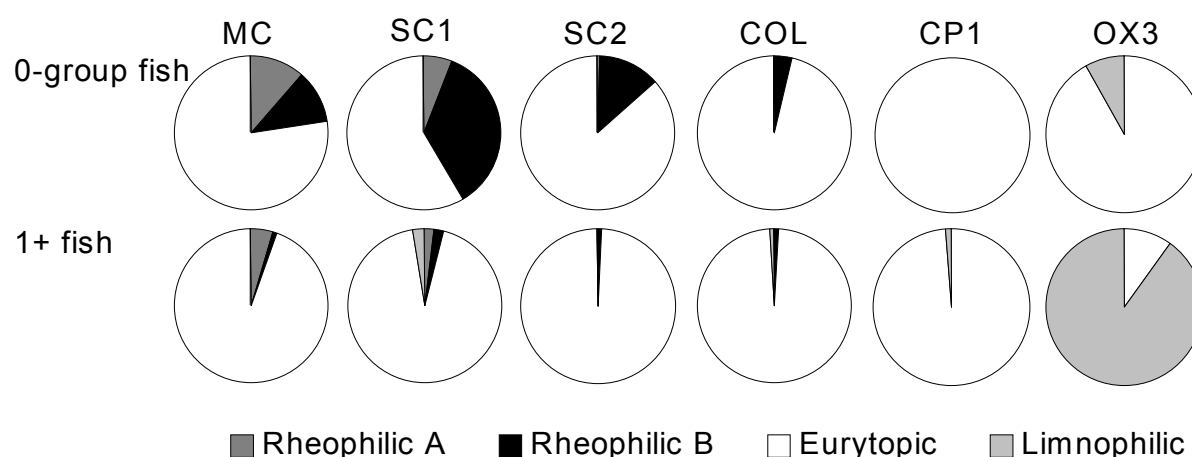

Figure 7.2. Numerical composition of fish communities in the main channel (MC) and floodplain water bodies (secondary channels (SC1, SC2); connected oxbow lake (COL); turbid clay-pit (CP1); vegetated oxbow lake (OX3). Data from SC1, SC2 and COL from 1997 and 1998 combined (Table 4.2) and from CP1 and OX3 from 1997 (Table 5.3), data from the main channel from 1999 (0-group fish from groyne fields this study (Table 3.2), 1+fish from a national monitoring programme with a 3 m beam trawl; Stam *et al*., 1999).

The differences in species composition among 0-group and 1+ fish assemblages in the main channel and connected waters may be caused by migration of 1+ rheophilic fish out of the study area and by a different recruitment of rheophilic and eurytopic fish, determined by the area of suitable spawning and nursery areas.

Migration of rheophilic cyprinids

Migration by cyprinid fishes is an important component of their life cycles and it may be possible that rheophilic cyprinid species move out of the research area after their first year either by a directed migration or by random dispersion. Longitudinal migration of juvenile cyprinids in rivers has often been observed. In the River Vecht, the most downstream tributary of the Rhine, both adult and juvenile roach, white bream and ide migrated upstream in spring (Winter, 2001). In an artificial secondary

channel along the Danube, 14% of the ascending fish were juveniles of which bleak, roach, gudgeon and rudd were the most abundant species (Schmutz & Jungwirth, 1999). Apart from juveniles, adult cyprinids may also migrate along the river. Lucas *et al*. (2000) observed that adult barbel, chub, dace and roach moved over distances up to 30 km within a year. The movements of barbel and chub followed a seasonal pattern with upstream movements in spring and downstream movements in summer and autumn (Lucas *et al.*, 2000). In the upper reaches of the Danube, barbel and nase frequently migrated distances of more than 30 km for both foraging and reproductive purposes (Steinmann *et al.*, 1937 in Waidbacher & Haidvogl, 1998) and in the same study, migration distances of 5 to 148 km have been demonstrated for bream, common carp *Cyprinus carpio*, chub, roach, rudd and tench (Steinmann *et al.*, 1937 in Schmutz & Jungwirth, 1999). Migration for cyprinids is thus common and may play an important role in determining the number of rheophilic cyprinids in the lower Rhine.

Table 7.2. Mean densities (numbers per 1000 m^2) of 0-group and 1+ fish in the main channel and floodplain water bodies of the four most abundant rheophilic and the five most abundant eurytopic species. '0': density <0.5 per 1000m^2; '.': absent.

N per 1000 m^2		0-group fish				1+ fish			
Guild	Spec	MC[*]	SC1[**]	SC2[**]	COL[**]	MC[***]	SC1[**]	SC2[**]	COL[**]
Rheophilic	Barbel	13	56	1	25	0	.	.	.
	Asp	3	37	71	40	0	0	0	0
	Ide	8	342	307	72	0	0	0	0
	Gudgeon	2	33	3	0	0	.	.	0
Eurytopic	Roach	9	1434	425	325	7	4	2	1
	Bream	69	3983	80	2843	34	11	6	8
	White bream	1	20	12	331	3	1	0	1
	Bleak	3	33	216	115	0	1	4	2
	Pikeperch	9	28	613	359	1	1	1	1

[*]: Data from this study (average over 1997-1999).
[**]: Data from this study (average over 1997-1998).
[***]: Beam trawl data from national monitoring programme, March 2000 (Winter *et al.*, 2000).

Recruitment

Recruitment of fish to the 1+ fish community is, among others, determined by the surface of suitable spawning and nursery areas along the lower Rhine. The availability of these areas depends on the assemblage of aquatic habitats that comprise the main channel and groyne fields, water bodies permanently connected to the main channel, isolated floodplain lakes and temporarily inundated floodplains or the aquatic/terrestrial transition zone.

Table 7.3. Surface area (km^2) of habitats along the River Waal (Jansen & Backx, 1998).

			km^2	%
Water	Permanently	Main channel	39.0	25.8
	Connected	Connected sand-pit	6.6	4.4
		Harbour	1.1	0.7
		Connected oxbow	1.6	1.1
		Secondary channel	0.1	0.1
	Isolated	Isolated sand/clay-pit	5.5	3.6
		Scour hole	0.3	0.2
		Oxbow lake	4.7	3.1
Total water			**58.9**	**39**
Floodplain	150-365		2.1	1.4
(days/year flooded)	50-150		8.2	5.4
	20-50		12.5	8.3
	2-20		58.7	38.8
	<2		11.0	7.3
Total floodplain			**92.5**	**61.2**
Total			**151.4**	**100.0**

The potential spawning and nursery habitat in the main channel and floodplains of the Waal, comprises 19.9 km^2 of permanent water apart from 82 km^2 of floodplain that can become inundated. The total surface area of groyne fields is about 9.3 km^2 (103 km x 45 m x 2) of which the sandy shallow shore zones (10 m) have an area of about 2 km^2. Of the water bodies permanently connected to the main channel, deep harbours and sand-pits have an area of 7.7 km^2 whereas shallow secondary channels and connected oxbows have an area of only 1.7 km^2 (Table 7.3). Within the floodplains, 10.5 km^2 of lakes that are permanently present occurs (sand-pits, clay-pits, scour holes and oxbow lakes). This comprises sand-pits and scour holes that are usually deep (>10 m) with steep shore faces, and shallow (<2 m) clay-pits and oxbow lakes. The part of the floodplain that inundates frequently is only small (Table 7.3) and larger parts only inundate seldom and abruptly. During the growing season, from March through September, 10 km^2 of floodplain is inundated 109 days, 23 km^2 of floodplain is inundated 33 days, and 82 km^2 is inundated only 12 days on average (1970-1999; Figure 7.3). Moreover, the variability in the area of inundated floodplain among years is high.

The present availability of aquatic habitats along the lower Rhine favours the recruitment of eurytopic over rheophilic species. This study demonstrated that hydrological and morphological conditions in a habitat determine the species assemblage in that habitat, and that the assemblage of habitats in a water body determines the fish density and species composition of the water body. When this result is scaled up to the entire river, species composition in the main channel would be determined by the assemblage of floodplain water bodies from which fish recruit (Figure 7.4).
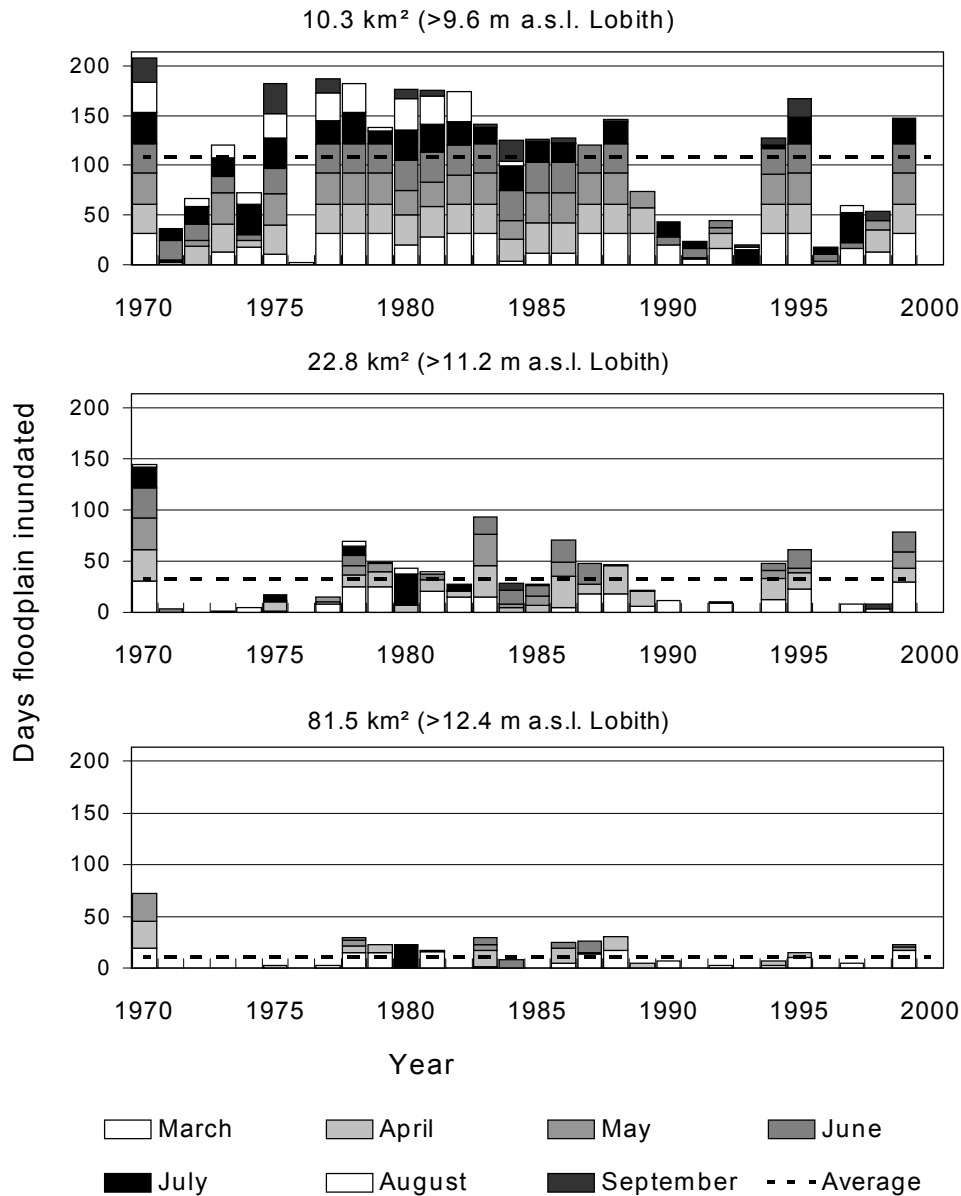
Figure 7.3. Number of days per month (1970-1999) during which different areas of the floodplain along the River Waal were inundated. Areas indicated are cumulative.

For rheophilic species, suitable nursery areas that are always available, are limited to the shore zones of groyne fields (2 km^2) and to the secondary channels and connected oxbows (1.7 km^2). In the groyne fields the proportion of rheophilic species to the 0-group fish assemblage is high (23%), but fish densities are low. Secondary channels and connected oxbow lakes have habitats in which the proportion and densities of rheophilic species are high (4-41%). The total recruitment of rheophilic fish is not substantial when compared to eurytopic species due to the limited area of suitable spawning and nursery areas (3.7 km^2), and the low densities of rheophilic fish in the groyne fields (Figure 7.4).

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Large numbers of eurytopic fish recruit from the floodplains to the riverine fish community (Figure 7.4) because the surface area of suitable spawning and nursery areas is large (20 km^2) and their proportion and densities in these water bodies are high. Eurytopic species utilize all types of shallow floodplain water body (12.2 km^2). The shore zones of the deep sand-pits and harbours (total surface 7.7 km^2) may also provide spawning areas for eurytopic fish whereas the deep open water may function as nursery areas. Neumann *et al.* (1994) conclude that deep connected sand-pits along the lower Rhine have a rich zooplankton production and offer suitable habitats for many fish species as nursery and refuge areas. Since juvenile rheophilic and eurytopic species are spatially separated by depth (eurytopic species occurring at deeper sites than rheophilic species), the open water zone of the deep sand-pits and harbours seems better suitable for eurytopic than for rheophilic species.

Obviously, the figures for the areas of suitable habitat in Figure 7.4 for the various species are only rough estimates and do not account for differences in morphology within types of water body nor for differences in the suitability as spawning and nursery areas. For deep water bodies, for example, the surface area may not be the optimal unit to use for the potential recruitment of fish. The area of shallow shore zones may be better to use. At present this type of data is, however, not available but the presented figures give an impression of the order of magnitude at which habitats are available.

Causes for the deteriorated fish community in the lower Rhine

The present degraded status of the lower Rhine enhances the life cycle of eurytopic species and constrains life cycles of rheophilic and limnophilic species. They face a lack of suitable habitat during some or all parts of their life cycles, which led to a dominance of eurytopic species, who may prosper in the absence of other species. In the main channel, gravel banks have disappeared and subsequently the spawning opportunities for lithophilic species. For all rheophilic species, the surface of suitable nursery areas has decreased due to the loss of connected backwaters and the declined aquatic/terrestrial transition zone. The fish community in the main channel of the lower Rhine is dominated by a few eurytopic species due to the large area of suitable spawning and nursery areas for these species relative to those of rheophilic species. Limnophilic species depend completely on vegetated floodplain lakes for their reproduction. They do not reproduce in lakes without vegetation and only in lakes with abundant vegetation, is their numerical contribution to the fish community large. In terms of biomass, however, almost all floodplain lakes are at present dominated by bream >30 cm. Apart from the loss of the dynamic component of floodplains, the low

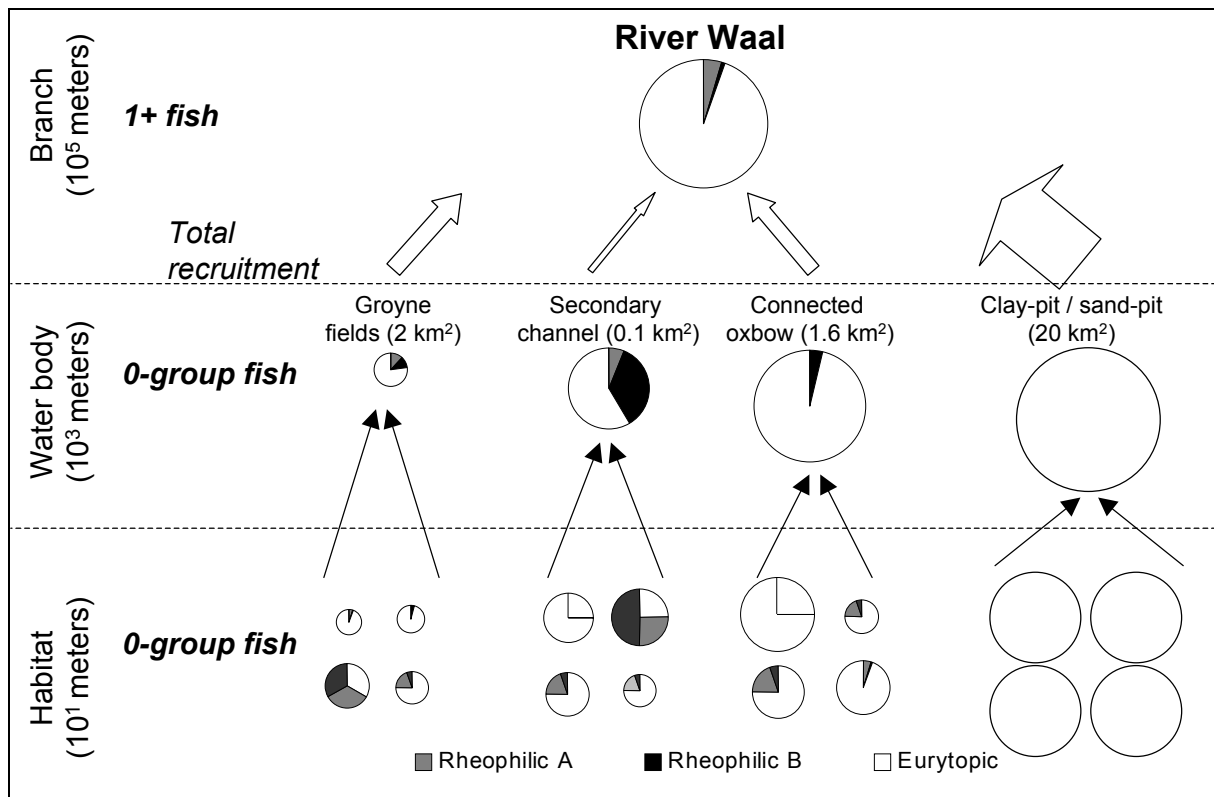dynamic parts, in which floodplain lakes undergo succession, have also disappeared from the lower Rhine.

Figure 7.4. Schematic presentation of the habitats from which fish recruit to the River Waal fish community (1+ fish). The sizes of the pies indicate fish densities (numbers of fish per square metre of habitat). The upper pie illustrates the species composition in the River Waal, that is determined from the recruitment of 0-group fish from the groyne fields and the different floodplain water bodies (all other pies). Fish density and species composition of the 0-group fish assemblage in these water bodies is determined by the assemblage of habitats present in each type of water body. In the secondary channels, for example, a large variability of habitats (the flowing channel, shallow shore zones, etc.) is present and each type of habitat has a specific fish species composition and fish density. On the contrary, in turbit clay-pits, habitat variability is almost zero and in each habitat, fish density is high and species composition is almost equal.

These causes for the different recruitment of fish species in the lower Rhine can be explained by the disturbed interaction between the river and its floodplains. The floodplain is an essential component of the system without which production is drastically reduced, and community composition and energy pathways are radically changed (Junk *et al.*, 1989; Bayley, 1991). In natural floodplain rivers, the aquatic/terrestrial transition zone provides environmental conditions combining high spatial heterogeneity, a large supply of organic matter and shallow habitats with few piscivores. Consequently, it is a critical part of the river, where most fish reproduction occurs (Schlosser, 1991). At present, as in other regulated rivers (Bayley, 1991), the aquatic/terrestrial transition zone is reduced in size and the flood pulse in the lower

Rhine may be too short and sudden for fish to respond to the increased production and the presence of new habitats. Consequently, strong year-classes of rheophilic species depend on erratic floods in spring and summer that nowadays have low probabilities to occur. It has been shown that, in lowland rivers, discharge stochasticity sometimes strongly controls population size (Grossman *et al.*, 1982; Schlosser, 1985; Winemiller, 1996) and this may apply for rheophilic fish in the lower Rhine also. The rather unpredictable discharge regime is, however, typical of the lower Rhine and is not caused by floodplain embankment. In temperate regions, precipitation in the catchment area is often stored as snow and ice during winter and in many cases, floods in summer result from temperature changes that sometimes occur abruptly and unpredictably (Junk, 1999). Before embankment, however, more favourable conditions occurred at various water levels.

The result of this study, that floodplain habitats are essential for the ecological functioning of the riverine ecosystem, is fully consistent with the Flood Pulse Concept (Junk *et al.*, 1989). Flood pulses control biota in three ways: directly by facilitating migration of animals and indirectly by enhancing primary production and by structuring of habitats. In this study, it was demonstrated that during a flood pulse, adult bream migrate to floodplain lakes whereas 0-group bream leave from these lakes. During a flood pulse, juveniles use inundated floodplains as nursery areas. Almost all species use floodplain habitats during some parts of their life cycles and use the main channel only as a transport route between these habitats (Table 7.1). This is also fully in line with Junk *et al*. (1989) who describe the river-floodplain system analogous to a highway network, with the vehicles corresponding to the fish. Due to the disturbed aquatic/terrestrial transition zone, new habitats in the floodplains are not formed naturally and the presence of secondary channels and connected oxbow lakes is fully dependent on man-made water bodies that result from river restoration projects.

7.6 Implications for management

The evaluation of the first few restoration projects shows that it is possible to create new habitats that are colonized by fish within a few years, and contribute to the rebuilding of the populations of rheophilic fish in the lower Rhine. Moreover, the morphological and hydrological characteristics of these water bodies determine the fish species colonizing them. However, to restore their populations on the scale of the entire river, the area of suitable spawning and nursery areas should be further increased. The proposed coupling of safety to mining activities and to the development of nature areas, provides an excellent opportunity to improve the environmental conditions for both rheophilic and limnophilic fish species.

Rehabilitation of the population rheophilic fish

The creation of low-flow connected backwaters fits very well in the proposed floodplain excavation and the proposed large areas with dynamic wet nature along the River Waal. These dynamic areas can be designed to match the habitat requirements of rheophilic fish optimally. In general, these water bodies should be shallow, have complex shorelines with a high variability of flow velocities, and have moderate slopes. The morphology and hydrology of floodplain water bodies can probably be designed to enhance specific groups of fish species. For example, to enhance species such as barbel and gudgeon, floodplain water bodies should have shallow (<1 m) areas with moderate flow velocities of 0.05-0.15 m s^{-1}. Shallow (<1 m) areas are also important for other species such as ide and asp, but for these species, flow velocities should be less than 0.10 m s^{-1}.

When floodplain water bodies are to be connected to the main channel permanently, secondary channels are preferable above downstream connected oxbow lakes. Ide and gudgeon probably spawn in secondary channels and do not spawn in downstream connected oxbow lakes. Between secondary channels and connected oxbow lakes, there is no difference in their functioning as nursery areas, but of all rheophilic species, densities are higher in secondary channels. On the contrary, densities of eurytopic species are higher in the connected oxbow lake. Moreover, the abundance of Rheophilic A species in the connected oxbow lakes is low. Many rheophilic fish move into the floodplain water bodies when they are larvae or juveniles. Therefore, the opportunities to move into these water bodies, either actively or passively, should be maximized. This opportunity is higher for flow-through secondary channels than for downstream connected oxbow lakes.

Restoration of the aquatic/terrestrial transition zone should have priority in all restoration projects since inundated floodplains proved to be important as spawning areas in spring and as refuge and foraging areas in summer. Therefore, the slopes of future connected water bodies should be moderate and balanced between too steep (terrestrial vegetation will develop but will seldom be submerged) and too shallow (the shore zone will be flooded too frequently and no terrestrial vegetation can develop). Apart from the shorelines along connected water bodies, the inundation of floodplains may also be restored along other stretches where no floodplain water bodies occur. Within the proposed removal of summer dykes, which are regarded as obstacles in the floodplains, the area with terrestrial vegetation that gets inundated frequently, can be increased as well. Removing summer dykes should result in extended floodplains with a high inundation frequency and duration. In groyne fields, the aquatic/terrestrial transition zone could be restored as well, and shoreline complexity could be increased.

Due to their large total surface, restoration measures in the groyne fields could significantly contribute to the rehabilitation of populations of rheophilic fish.

Rehabilitation of the population limnophilic fish

To enhance the population of limnophilic species, the area of floodplain lakes with a low inundation frequency and developed vegetation, should be increased. The present lakes can be preserved and new lakes can be restored naturally within the plans to widen the floodplain, and artificially by the plans for the creation of retention areas. The proposed widening of the floodplain by moving winter dykes along the River Nederrijn/Lek has a high potential for low dynamic floodplain lakes. The conditions in this weir-regulated river, will minimize the probability of these lakes getting inundated. Hence, vegetation has a higher probability to develop. Moreover, they may undergo succession, during which they are colonized by riparian plants (Amoros & Roux, 1988), into a final stage, when they become heavily silted and/or impeded with aquatic vegetation. In this stage in natural floodplain lakes, fish community is gradually altered into limnophilic species only (Copp *et al.*, 1991).

Vegetated lakes with abundant vegetation may also be restored man-made by means of the proposed retention areas. These areas, which will be situated behind the winter dykes, will only become connected with the main channel during calamities and consequently, they will seldom be inundated and will remain isolated for longer periods. If these areas are designed in such a way, that aquatic vegetation can develop, they may compensate for the current scarcity of low dynamic floodplain lakes with abundant vegetation. Only the abundance of aquatic vegetation explains the presence and reproduction of limnophilic species in floodplain lakes, which does not differ between man-made clay-pits and natural oxbows. Therefore, it is supposed that man-made lakes can provide suitable habitat for limnophilic fish. From an ecological point of view, however, a more frequent inundation than once or twice per century should be realized to facilitate exchange of fish.

Future research

This study was a first test on the functioning of newly created secondary channels and reconnected oxbow lakes and investigated fish communities in floodplains along the lower Rhine for the first time. There are, however, several questions that remain unanswered and several aspects that may be addressed in future studies.

The objective of this study was to assess the function of floodplain water bodies as spawning, nursery and refuge areas. Inferring the function of these water bodies as

spawning areas from the observed patterns in time, gave problems for some species (ide and gudgeon for example). Demonstrating the spawning of species in connected water bodies, such as secondary channels will always remain difficult. To assess this function from the pattern in time for rheophilic fish, the sampling frequency for adult fish during the spawning season should be increased to at least once per week. Apart from sampling spawning fish, their eggs (which are difficult to identify) could be collected. The function of floodplains as refuge areas during periods of high discharge, was also difficult to assess; the inundated floodplains could not be sampled with the active gear used in this study. Sampling with passive gear could solve this problem.

Due to the frequent sampling and the mark-recapture program in the larger floodplain lakes (>4 ha.), processes of recruitment and mortality in these lakes could be studied well. The hypothesized differential mortality between eurytopic and limnophilic species in the smaller, vegetated lakes (<1 ha.), however, could not be demonstrated since they were only sampled once. Future research could address this issue by sampling small lakes more frequently: immediately after a flood and again after a period of isolation.

The four types of life cycle demonstrate that most fish migrate between different habitats in the floodplain. For several species, it was demonstrated that they are absent from the floodplains during certain stages of their lives. It remains unknown, for example, where juvenile ide and barbel move to after they have left the secondary channels, and where adult eurytopic species remain during winter. Therefore, future research should include sampling deep sand-pits and harbours, which may be important overwintering areas. It should also study larger stretches of the Rhine to investigate migration in the longitudinal direction, both downstream and upstream. Apart from investigating larval drift between upstream gravel beds and our secondary channels, migration of fish between the secondary channels and the downstream estuaries should be addressed. During summer and winter, the estuaries may form important habitats for adult fish that were absent from the secondary channels and reconnected oxbow lake.

Finally, continued monitoring of the riverine fish community in the main channel is required to be able to evaluate the effect of river restoration for fish on the population level. Furthermore, this study investigated the functioning of secondary channels and a reconnected oxbow lake within a few years after they had been created. To be able to assess the sustainability of their functioning for fish, monitoring fish in these water bodies should also be continued.

Perspectives

At present, the area of spawning and nursery areas for rheophilic and eurytopic fish is unbalanced, and this can be restored within the present plans on floodplain restoration. The area of suitable nurseries along the River Waal for rheophilic fish was estimated at 3.7 km^2 (apart from inundated floodplains) and for eurytopic species more than five times higher (19.9 km^2; Table 7.3). The area of inundated floodplains, which is an important spawning and nursing habitat for many species, is small and during spring and summer, inundation seldomly occurs. Moreover, for lithophilic species, suitable spawning areas are completely absent. As a restoration goal, the relationship between these habitat types as they were 200 years ago could serve. At that time, the area of secondary channels along the Rhine was ten times higher and that of connected oxbow lakes more than three times higher than at present. The area of natural oxbow lakes was more than twice as high and the area of floodplain lakes 19 times lower than at present (Table 7.4). Moreover, the area of the floodplain that was dynamic and inundated frequently, was almost seven times higher than it is now.

Table 7.4. Historical and present percentage distribution of habitat types in the River Waal and its floodplains. Data from 1780 and 1830 from Maas *et al*. (1997), from 1998 from Jansen & Backx (1998).

	Habitat	1780[*]	1830[*]	1998[**]
Main channel	Main channel	29.2	32.5	25.6
	Gravel banks	0.5	0.0	0.0
	Sandbank	3.7	1.3	0.2
Floodplain	Secondary channel	1.0	3.5	0.1
(aquatic)	Connected oxbow	3.6	1.3	1.1
	Connected sand-pit/harbour	0.0	0.0	5.1
	Oxbow	7.0	9.8	3.1
	Floodplain lake (clay-pits)	0.2	1.0	3.8
Floodplain	Dynamic floodplain (inundated >50 days/ year)	46.7	20.1	6.8
(terrestrial)	Low dynamic floodplain (inundated <50 days/ year)	7.9	30.5	54.4
	Total	100.0	100.0	100.0

[*]: River Waal (based on river km 884.5-916.3; between cities of Nijmegen and Tiel; total area of main channel and floodplains 47 km^2).
[**]: River Waal (based on river km 857-960; between cities of Lobith and Gorinchem; total area of main channel and floodplains 151.2 km^2).

Decreasing the area of suitable habitat for eurytopic species goes hand in hand with increasing this area for rheophilic species by converting turbid clay-pits into secondary channels. These clay-pits had low species diversity and the species present were mostly eurytopic. Moreover, it was demonstrated that they are important source areas for bream. Due to the large standing stock of bream, and the frequent inundation,

aquatic vegetation will probably not develop and turbid clay-pits will never form suitable habitats for limnophilic species.

Whether vegetated floodplain lakes (man-made clay-pits and natural oxbow lakes) should be connected with the main channel permanently or should be preserved as they are now, depends on the restoration goal and how rheophilic species are valued in relation to limnophilic species. At present, these lakes have an additional and unique value for the riverine fish community as 'islands' with remnants of limnophilic fish populations. When floodplain restoration aims at restoring the riverine integrity, these water bodies should be preserved because of their additional value and because they were originally present. Schiemer (2000) defines riverine integrity as "functional entity with regard to its original state". Van den Brink (1994) also proposed to connect frequently flooded, turbid lakes to the main channel of the lower Rhine permanently, but to preserve vegetated lakes with low flood frequencies. He based this proposition on his results on algae, zooplankton, macro-invertebrates and macrophytes. In floodplains along the lower Rhine, species richness of these groups decreased with increasing connectivity with the main channel. Moreover, the species inhabiting frequently flooded lakes were also abundant in the main channel and comprised mainly non-riverine invaders from other aquatic systems (Van den Brink, 1994). A similar gradient was observed along the River Danube where, with decreasing connectivity, the total number of fish species and the number of endangered species decreased. For other groups (macrozoobenthos, odonata, macrophytes), however, highest species richness occurred in water bodies with intermediate connectivity and for one group (amphibians) in water bodies with the lowest connectivity (Tockner *et al.*, 1999). Tockner *et al.* (2000) propose that preservation of a high biodiversity is preferred above active management for a single species. The arguments against preserving these lakes, and changing them into dynamic secondary channels, can be found in the specificness of the riverine landscape for rheophilic species. Habitats for rheophilic species can only be found and preserved in and along rivers whereas habitats for limnophilic species also occur outside the riverine landscape. Since there are opportunities to restore floodplains in a way from which both groups of fish benefit, floodplain management should, however, not focus on increasing the area of dynamic nature only, and take into account the value that vegetated oxbow lakes have for limnophilic fish and other ecological groups.

Excavation of floodplains to restore habitats for rheophilic fish should be concentrated in the most dynamic part of the river. The habitat variability in the main channel, as it was in 1780, with sand and gravel banks, cannot be restored within the strict conditions with regard to shipping and protection against flooding, but these opportunities exist along the main channel and in the floodplains. Of the three

secondary channels that were investigated in this study, the two secondary channels (SC1, SC3; Figure 3.1) that were both situated in the most dynamic part of the floodplain, were the most successful for rheophilic fish. Within these types of secondary channels, sand banks can be restored on the islands between the secondary channel and the main channel. Flow velocities in the secondary channels will probably be too low for gravel banks to be restored and we better not have the illusion to restore the spawning conditions for lithophilic species. Concentrating floodplain restoration for rheophilic fish in the most dynamic part of the river, and utilizing the differences in hydrological characteristics among the three lower Rhine branches, leaves space for the preservation and restoration of vegetated floodplain lakes in the low dynamic parts of the lower Rhine.

Increasing discharge capacity should focus on excavation of the floodplain rather than on excavation of the main channel. At present, the incision of the river bed resulted in lowered groundwater tables in the floodplain and lower inundation frequencies of the floodplain. Since the flow in the River Rhine is forecast to drop 10 to 20 percent in the summer due to increased evaporation, connectivity between the main channel and the floodplains will even decrease further, especially in summer when availability of floodplains is essential for many fish species. From an ecological point of view, deepening of the main channel should thus have lowest priority in the current plans on river management. The present view on the River Rhine, however, does recognize both its ecological values and its importance for humans. Therefore, all opportunities should be taken to utilize the current flood protection plans to further restore the riverine fish community.

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Summary

With regard to the major rivers, Dutch policy focuses on maintaining flood protection in the face of larger design discharges, while at the same time conserving landscape, ecological and historical features, promoting navigational use and creating new wildlife areas. Within these plans, floodplains are excavated and ecologically restored. At several locations in the floodplains, secondary channels have been dug and isolated oxbows have been reconnected to the main channel by a downstream opening. These water bodies should compensate for the loss of low-flow zones and connected backwaters, and should provide living conditions for rare or endangered organisms that are still present in the lower River Rhine.

Poor habitat diversity, in combination with the poor water quality in the 1960s, led to a dramatic decline in the species diversity of the Rhine fish community. At present, the fish community is dominated by only four eurytopic species. Numbers of rheophilic species declined strongly and most are listed as vulnerable or endangered on the Netherlands red list of fresh water fish species. A potential stock of rheophilic cyprinid species is, however, currently present and ecological rehabilitation is no longer limited by water quality. Further expansion of their populations is thought to be curtailed by scarcity of suitable habitats. The restored floodplain habitats should provide suitable habitat as spawning and nursery areas and contribute to the rebuilding of the populations of rheophilic fish.

The objectives of this study were to test the beneficial value of newly created secondary channels and reconnected oxbow lakes along the lower Rhine for fish, and to give advice on position, shape and character of future water bodies. It was not yet known which fish species had colonized these new water bodies in the lower Rhine and utilize them as spawning and nursery areas. Moreover, the limited knowledge on the occurrence of fish in floodplains along the lower Rhine constrained the decision making on future management.

These objectives were pursued by assessing the fish community structure in various types of floodplain water body and by assessing the function these water bodies fulfil, as spawning, nursery and refuge areas, during the life cycles of fish. Fish communities in 25 water bodies (secondary channels, reconnected oxbows, clay-pits and oxbow lakes) were sampled from November 1996 to December 1999. The functions these water bodies fulfil, were inferred from the description of patterns of presence of fish in time and space.

Within four years after the creation of secondary channels and reconnecting an oxbow lake to the main channel, 30 fish species, most of the 47 species present in the lower Rhine, occur in these water bodies of which of 23 species, 0-group fish were

recorded. Their species composition and their functioning resembles that of natural floodplain water bodies along other, less degraded rivers. Within water bodies, flow velocity and depth determine the species assemblage. Densities of all rheophilic species are highest in secondary channels whereas densities of eurytopic species are highest in the reconnected oxbow lake.

Secondary channels and reconnected oxbow lakes function as nursery areas for rheophilic species (ide *Leuciscus idus*, gudgeon *Gobio gobio*, barbel *Barbus barbus* and asp *Aspius aspius*) of which densities of juveniles peak in summer. Secondary channels may also function as spawning areas for ide and gudgeon, but this could not be demonstrated. For lithophilic species (barbel and asp) they do not function as spawning areas since suitable substrate lacks. Their stock rehabilitation in the lower reaches of the Rhine may be constrained by lack of suitable upstream spawning areas and the opportunities for larvae to passively reach downstream nursery areas. Eurytopic species (bream *Abramis brama*, roach *Rutilus rutilus* and pikeperch *Stizostedion lucioperca*) use the water bodies as spawning and nursery areas.

Isolated floodplain lakes, which are only connected with the main channel during floods, are important source areas for bream. Small bream (<10 cm) leave the lakes during floods to become resident in the main channel until maturity. Once mature (at about 30 cm), they return to the lakes during the next inundation and stay there. Bream dominates fish communities in turbid lakes without vegetation. Floodplain lakes with abundant vegetation have low fish species richness, but they are the only type of water body which provide suitable habitat for the reproduction of limnophilic species such as tench *Tinca tinca* and rudd *Rutilus erythrophthalmus*. The abundance of these species along the lower Rhine is, however, low which may indicate that remote and seldom flooded lakes have disappeared almost completely.

At present, the area of spawning and nursery areas is more than five times larger for eurytopic than for rheophilic species. For limnophilic species, which depend on vegetated lakes, this area is also limited. The flood protection plans provide the opportunity to enlarge the area of suitable habitat for both rheophilic and limnophilic fish species. Within the proposed floodplain excavation, creation of secondary channels is preferable above reconnecting oxbow lakes. They should be shallow, have complex shorelines with a high variability of flow velocities and moderate slopes. Increasing the shoreline complexity in the groyne fields, that have a large surface area, could also significantly contribute to the rehabilitation of populations of rheophilic fish. The proposed retention areas, which store large volumes of water during floods, could compensate the low area of lakes with abundant vegetation. Within the strict conditions with regard to shipping and protection against flooding, water bodies can be created that contribute to the rehabilitation of the riverine fish community.

Samenvatting

Hoe vissen profiteren van natuurlijk herstel van de uiterwaarden langs de Rijn

Door menselijke ingrepen is het natuurlijke karakter van de Rijn sterk veranderd. Het oppervlak aan uiterwaarden is drastisch afgenomen. Bovendien overstromen ze minder vaak en veel abrupter dan voor de aanleg van dijken het geval was. Uiterwaardwateren die in permanente verbinding met de hoofdstroom staan, zoals nevengeulen en een-zijdig aangetakte strangen (voormalige rivierarmen), zijn bovendien verdwenen. Veel vissoorten benutten deze wateren als kinderkamers en zijn voor hun voortplanting juist van deze wateren afhankelijk. De stroming is hier minder sterk en er is meer voedsel dan in de hoofdstroom. Door kanalisatie en aanleg van kribben is de hoofdstroom ook niet meer geschikt als leefgebied voor vissen. Dit onderzoek toont aan dat het mogelijk is om natuurgebieden in de uiterwaarden van de Rijn te ontwikkelen die een bijdrage te leveren aan het herstel van de visgemeenschap.

Door het veranderde karakter en de slechte waterkwaliteit in de jaren '60, is de soortdiversiteit van de visgemeenschap in de Rijn achteruit gegaan. Momenteel domineren vissoorten die geen hoge eisen aan hun leefomgeving stellen; zogenaamde eurytope soorten. Dit zijn bijvoorbeeld brasem, blankvoorn, kolblei en snoekbaars. Typische riviervissen, zoals winde, barbeel en kopvoorn (stroomminnende of reofiele soorten), stellen wel hoge eisen aan hun omgeving. Zij zijn dan ook sterk in aantal achteruit gegaan. Veel stroomminnende vissen worden momenteel als bedreigd beschouwd. Ze hebben stromend water nodig om hun eieren in af te zetten. De jonge vissen hebben langzaam stromend water nodig om in op te groeien. Een derde groep vissen, limnofiele soorten zoals zeelt, kroeskarper en ruisvoorn, komt van nature voor in de geïsoleerde, stilstaande plassen in de uiterwaarden. Zij zijn afhankelijk van waterplanten om eieren op af te kunnen zetten. Doordat de waterkwaliteit van de Rijn vanaf de jaren '70 sterk is verbeterd, vormt deze geen belemmering meer voor natuur-lijk herstel van de visgemeenschap. Verondersteld wordt dat het herstel nu voorna-melijk nog door een tekort aan geschikte paai- en opgroeigebieden belemmerd wordt.

Recent zijn plannen ontwikkeld om het overstromingsgevaar van de grote rivieren te verkleinen. De plannen bieden kansen om het areaal geschikte paai- en opgroeigebieden voor stroomminnende soorten te vergroten. Ze zijn gericht op het uit-graven van uiterwaarden om de afvoercapaciteit van de rivier te vergroten. De uiterwaarden worden zo uitgegraven dat er natuurgebieden met nevengeulen en aan-getakte strangen ontstaan. Het mes snijdt aan twee kanten: via de uitgegraven uiter-waarden kan de rivier meer water afvoeren en voor vissen worden verdwenen leefgebieden hersteld. Momenteel is op tien plaatsen in de uiterwaarden van de Rijn de

natuur op deze manier hersteld (circa 300 ha.). Er zijn plannen om nog eens 8000 ha. natuur op dezelfde manier te ontwikkelen. In deze studie is onderzocht of de reeds aangelegde natuurgebieden een bijdrage leveren aan het herstel van de populatie stroomminnende vissen in de Rijn. In andere Europese rivieren blijkt namelijk dat deze vissen het soort wateren dat nieuw aangelegd is gebruiken als paai- en/of opgroeigebied. Het onderzoek beschrijft de samenstelling en de veranderingen door het jaar heen van de visgemeenschap in diverse uiterwaardwateren. Hieruit wordt afgeleid hoe vissen de diverse wateren in de uiterwaarden gebruiken. Met deze kennis worden adviezen gegeven voor de inrichting en het beheer van uiterwaarden.

Van 1997 tot en met 1999 is de visgemeenschap in 25 wateren in de uiterwaarden van de Waal, de grootste en vrij afstromende tak van de Rijn in Nederland, intensief bemonsterd. Hiertoe zijn vissen in zowel nieuw aangelegde nevengeulen en aangetakte strangen als in geïsoleerde rivierplassen (zoals kleiputten en strangen) bemonsterd. In nevengeulen en aangetakte strangen is tot veertien keer per jaar gevist om de dynamiek van de visgemeenschap door het jaar heen te kunnen beschrijven. De rivierplassen zijn een tot drie keer per jaar bemonsterd. Vissen zijn er met inkt gemerkt om te kunnen schatten hoeveel exemplaren de plassen in- en uitzwemmen tijdens een overstroming.

Nieuw aangelegde nevengeulen en aangetakte strangen leveren een belangrijke bijdrage aan het herstel van de populatie stroomminnende vissen. De manier waarop verschilt echter per water en per vissoort. Binnen drie tot vier jaar na de aanleg van deze wateren zijn er in totaal 30 vissoorten aangetroffen van de 47 die er in de Rijn waargenomen zijn. Van 23 van deze soorten zijn tevens jonge exemplaren aangetroffen. Globaal kunnen vier manieren onderscheiden worden waarop vissen de uiterwaarden langs de Rijn in Nederland benutten.

Stroomminnende soorten als barbeel, kopvoorn en serpeling komen alleen voor in uiterwaardwateren die in permanente verbinding met de hoofdstroom staan. Ze benutten de nevengeulen en aangetakte strangen uitsluitend als opgroeigebied en niet als paaigebied. Deze soorten hebben grindbanken nodig om hun eieren op af te zetten. Die ontbreken in Nederland. Ze paaien waarschijnlijk in Duitsland, waar nog wel grindbanken zijn. De larven zweven met de stroming naar de ondiepe nevengeulen. De jonge vissen gebruiken de uiterwaarden slechts gedurende een paar maanden in de zomer, wanneer ze 2-5 cm groot zijn. Voor het eind van de zomer verlaten ze de uiterwaarden weer. Andere stroomminnende soorten, zoals winde en riviergrondel, komen ook alleen in nevengeulen en aangetakte strangen voor. Ze kunnen waarschijnlijk wél in de nevengeulen paaien. Hierdoor kunnen ze hun hele leven in het Nederlandse deel van de Rijn doorbrengen. Ze paaien waarschijnlijk niet in de

eenzijdig aangetakte strangen omdat daar geen stroming is. Eurytope soorten benutten vrijwel alle wateren in de uiterwaarden als paai- en opgroeigebied. Zowel nieuw aangelegde nevengeulen en aangetakte strangen als geïsoleerde rivierplassen. In het voorjaar trekken volwassen brasems, blankvoorns en snoekbaarzen de nevengeulen en aangetakte strangen binnen om er te paaien. Na het paaiseizoen komen er grote aantallen larven voor. De jonge vissen brengen hier hun eerste jaar door. Voor brasem zijn bovendien troebele rivierplassen belangrijk als paai- en opgroeigebied. Volwassen vissen trekken deze wateren tijdens een overstroming in het voorjaar binnen. De jonge brasems verlaten de plassen tijdens een overstroming in het najaar om in de hoofdstroom volwassen te worden. Limnofiele soorten brengen hun hele leven in heldere rivierplassen met waterplanten door.

In nevengeulen en aangetakte strangen bepalen de vorm en diepte van het water en de aanwezigheid van stroming het aantal dat van een vissoort voorkomt en dus voor welke soort het water het meest geschikt is. Planten die tijdens hoogwater onderlopen vormen voor larven van bijna alle vissoorten een belangrijke leefomgeving. Nevengeulen met een matige stroming (5-15 cm s^{-1}) zijn het meest geschikt voor jonge barbeel en riviergrondel. Nevengeulen met een zwakke stroming (<5 cm s^{-1}) zijn juist voor winde en roofblei geschikt. Eurytope soorten hebben voorkeur voor stilstaand en dieper water en profiteren het meest van de eenzijdig aangetakte strangen. De aantallen reofiele vissen zijn hier juist laag. In de geïsoleerde rivierplassen bepaalt met name de aanwezigheid van waterplanten de samenstelling van de visgemeenschap. In troebele rivierplassen (kleiputten) zonder waterplanten domineert brasem, die soms meer dan 99% van de visbiomassa uit maakt. Alleen in heldere plassen waar volop waterplanten zijn, zijn limnofiele soorten talrijk. Dit soort plassen is echter zeldzaam.

Het toekomstig beleid met betrekking tot de grote rivieren biedt de mogelijkheid om de omstandigheden voor zowel stroomminnende als limnofiele vissen te verbeteren. Wanneer uiterwaarden uitgegraven worden, kunnen beter nevengeulen dan eenzijdig aangetakte strangen aangelegd worden. Bovendien is het herstel van de verbinding tussen de uiterwaarden en de hoofdstroom noodzakelijk. Ondergelopen uiterwaarden vormen immers een belangrijke leefomgeving voor jonge vissen. Nevengeulen moeten flauwe oevers hebben waarop planten kunnen groeien die een grote kans hebben om in de zomer onder water te lopen. Troebele rivierplassen, waarin waarschijnlijk geen waterplanten tot ontwikkeling komen, kunnen het beste in nevengeulen veranderd worden. Het areaal met een geschikte leefomgeving voor stroomminnende vissen wordt hierdoor vergroot, terwijl het areaal voor brasem hiermee afneemt. De voorgestelde retentiebekkens en de laag-dynamische natuur langs de Nederrijn/Lek bieden de mogelijkheid om heldere plassen, die geschikt zijn voor limnofiele soorten, te herstellen.

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Curriculum Vitae

Robert Ernst Grift is op 24 september 1972 geboren in Nunspeet. Na het voltooien van het Atheneum aan het Lambert Franckens College in Elburg begon hij in 1990 aan de studie zoötechniek aan de Landbouwuniversiteit Wageningen. In het 3^e jaar koos hij voor de specialisatie visteelt en visserij en deed afstudeervakken in de visserij en de theoretische productie ecologie. Hij liep stage op het Cornell Biological Field Station in de Verenigde Staten. Na zijn afstuderen in september 1996 begon hij in oktober van dat jaar als Assistent in Opleiding, in dienst van de Landbouwuniversiteit, aan het onderzoek 'Kansen Voor Stroomminnende Vissen'. Tijdens dit project werd het onderzoek uitgevoerd dat in dit proefschrift beschreven is. Sinds oktober 2000 werkt Rob Grift bij het RIVO Nederlands Instituut voor Visserijonderzoek als visserijbioloog. Hij doet onderzoek aan de visgemeenschap en de visserij in de Noordzee en het Nederlandse kustgebied.