

**Community patterns and recruitment of fish in  
a large temperate river floodplain**

-

**The significance of seasonally varying hydrological  
conditions and habitat availability**

In a u g u r a l - D i s s e r t a t i o n

zur

Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Universität zu Köln

vorgelegt von

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Köln

2009

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Tag der mündlichen Prüfung: 21.10.2009

„Das Prinzip aller Dinge ist das Wasser, denn Wasser ist alles und ins Wasser kehrt alles zurück.“

Thales von Milet (griechischer Philosoph ~ 625 - ~ 547 v.Chr.)



### **Mein Dank gilt:**

PD habil Dr. Jost Borchering für die Betreuung dieser Arbeit, für sein Engagement, für viele gute Ideen und Ratschläge, für seine Nachsicht und Unterstützung und die zahlreichen Wochenendschichten in der Schlussphase der Arbeit

Prof. Dr. Hartmut Arndt für die Übernahme des Koreferats, für seine Geduld und seinen Optimismus

Besonderer Dank gilt meiner Lebensgefährtin Bozena Hermasch für ihre Hilfe bei den Untersuchungen, ihren Beistand in allen Lebenslagen, für das Aufmuntern, die zahlreichen Entbehrungen, das leibliche Wohl, die mathematischen Diskussionen und für das Dasein

Den Protagonisten der „Jugend-forscht“ Truppe (Lisa Heermann, Werner Scharf, Ulrike König, Joscha Grodek, Peter Beeck, Andreas Zipperle, Patricia Murawski), ohne deren Hilfe im Freiland diese Arbeit nicht hätte durchgeführt werden können, für die angenehme Zeit in der Grietherbuscher WG und ihre Freundschaft

Armin Lorenz und Daniel Hering für zahlreiche Ratschläge und Hilfestellungen in Ordinationsbelangen

Ulrich Werneke für die Hilfe bei Freilanduntersuchungen, den Tiefenlotungen und GIS-Problemchen

Stefan Staas und Fabio Rochol für das Rückenfreihalten auch wenn im Büro die Hölle los war, die fachlichen Diskussionen und ihre Freundschaft

Christoph Schiawo für die Hilfe bei den Untersuchungen, auch nach Feierabend, das Instandhalten der Gerätschaften und seiner Frau Iris dafür, dass man sich in der Station immer wohl fühlen durfte

Heinrich Evers für seine Ortskenntnisse, und für die Zerstreuung bei den Kaffeepäuschen

Den Fischern Rudi Hell und Horst Liebsch für den Verzicht der Nutzung ihrer Pachtgewässer in der Zeit in der ich dort forschte und Hilfe bei Stellnetzbefischungen

Stellvertretend für die Flächeninhaber, -betreuer und Landwirte die mir den Zugang zu den Untersuchungsgewässern ermöglicht haben, möchte ich stellvertretend Herrn Gottschalk vom FORSTAMT WESEL, Herrn Schulze vom REGIONALVERBAND RUR,

der Firma PFEIFFER & LANGEN, sowie den Landwirten Reymers und Stockhorst danken

Heiko Geyer vom REGIONALVERBAND RUHR für den Zugang zu den Luftbildservern des RVR und Martina Erzner (BIOLOGISCHE STATION IM KREIS WESEL) für die nützlichen Hinweise hinsichtlich des Schreibens der OGC-files

Barbara Guhl und Herrn Ulkan (LANUV NRW) für das zur Verfügungstellen der Temperaturdaten des Rheins

Frau Rubart vom WSA Duisburg für die Zusendung der Abflussdaten des Rheins

Pavel Jurajda für die konstruktiven Anmerkungen hinsichtlich früherer Versionen einzelner Manuskripte dieser Arbeit

Meinen Eltern Siegfried und Christa weil sie mir die Durchführung des Studiums überhaupt erst ermöglicht haben, für ihre Rückendeckung in allen Phasen meiner Ontogenese und dafür dass sie meine Entscheidungen stets akzeptiert haben

Zoltan für die Frischluft- und Bewegungseinheiten, ohne die ich wahrscheinlich eingegangen wäre und seine Treue

Manuel Langkau und Egbert Franke für die Momente der profanen Annäherung an das Themenfeld der Fischökologie

und Diane für ihr immer offenes Ohr und ihr gutes Gedächtnis

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# **Introduction**

Most large alluvial temperate rivers all over the world have undergone drastic anthropogenically induced changes in the past centuries (Petts, Möller, and Roux 1989; Dynesius and Nilsson 1994; Kern 1994; Cowx and Welcomme 1998; Buijse *et al.* 2002). Due to the fertility of the alluvial deposits and despite the risk of seasonal flooding, river floodplain areas have been early reclaimed for colonisation, cultivation, and agricultural utilisation. In Europe deforestation of river basins has started in prehistoric times and was yet almost completed in some densely populated regions in the middle ages. In the following centuries many rivers were shortened, canalised, their beds deepened and reinforced. Levees were raised to protect the mostly densely populated areas of the river basins from seasonal floods. These modifications were often followed by deleterious direct and indirect impacts on the rivers hydrological characteristics, including strongly increasing flood peaks, however shortened flood durations and disturbed sediment loads (Buijse *et al.* 2002). Furthermore they led to a fragmentation of habitats, and headwater regions were often disconnected from downstream areas for migratory fish. As a consequence and in combination with intensive fishing, stocks of migratory fish and their fishing yield in many European rivers declined sharply (Böcking 1982; De Groot 2002). Although the relationship of threads for fish stocks arising from longitudinal river fragmentation has been addressed early, e.g. documented by the “Lachsvertrag” from 1885 (Iksr 1999), the consequences of the lateral dimensions of river modifications, by either losses of floodplain area or disturbed interactions between rivers and its wetlands have been overseen for a long time. The findings of Antipa (1910; 1923), who firstly addressed the recruitment and productivity of potamal fish species in the lower Danube to the extent and duration of floodplain inundation, are the earliest deliverances that stressed the significance of such interactions for riverine fish populations, what has been repeatedly confirmed for upstream sections of the Danube in the following decades (Balon 1963; Balon 1966; Stankovic and Jankovic 1971; Holcik and Bastl 1976). Numerous studies conducted in the last 30 years in temperate systems found similar relationships of productivity and the degree of connectivity to occur in further biota, e.g. peaking abundances of phytoplanktonic and zooplanktonic organisms in inundated stagnant floodplain waterbodies relative to the river channel (Amoros and Roux 1988; Admiraal *et al.* 1994; Hein *et al.* 1999; Baranyi *et al.* 2002; Keckeis *et al.* 2003), or even with respect to nutrient cycling, energy flow and food webs (Tockner *et al.* 1999; Woodward and Hildrew 2002;

Winemiller 2004). Many ecological theories and concepts arising from these relationships stress the four-dimensionality of processes in aquatic environments, which involve vertical (e.g. between the water column and the hyporheic zone, the groundwater table), longitudinal (along the tributaries and the river course) and lateral (between the river and its riparian zones, the floodplain) exchanges, however, particularly emphasise the role of the 4<sup>th</sup> dimension, the time (Junk, Bayley, and Sparks 1989; Ward 1989; Ward and Stanford 1995; Junk 1999; Tockner, Malard, and Ward 2000). By now, it has become a common perception that in lowland river systems most of the productivity derives from the lateral expansion into the floodplain, which however highly depends on the seasonal occurrence and predictability of the river-floodplain interaction (Junk *et al.* 1989; Sparks *et al.* 1990; Bayley 1991; Gutreuter *et al.* 1999). Since most species are expected to have adapted their life-cycle and behaviours to long term patterns of the environment, such as natural flow regimes and typical hydro-periods (Schlosser 1991; Winemiller and Rose 1992; Schlosser 1998; Lytle and Poff 2004), alterations from these patterns involve detriments of recruitment for adapted organisms (Bayley 1995; Freeman *et al.* 2007).

Natural and undisturbed river floodplains are characterised by a broad range of ecotones with different physical habitat conditions, which are differently affected by surface and groundwater exchanges and provide a high species diversity (Copp 1989; Schiemer and Zalewski 1992; Shiel, Green, and Nielsen 1998; Ward 1998; Tockner *et al.* 2000; Ward *et al.* 2002). Particularly fish require different habitats during their complex life-cycles (Schiemer *et al.* 1991; Schlosser 1991; Schiemer and Waidbacher 1992; Schiemer *et al.* 2001), thus, habitat loss, fragmentation and modification is considered as a major threat for many riverine fish species and declining biodiversity (Lelek 1987; Schiemer and Waidbacher 1992; Jungwirth, Muhar, and Schmutz 2000; Muhar *et al.* 2000; Rosenfeld and Hatfield 2006). However, in contrast to other temperate regions (Sparks, Nelson, and Yin 1998; Humphries, King, and Koehn 1999; King, Humphries, and Lake 2003; Zeug and Winemiller 2007), still little information exists on the adaptations of fish species towards flood patterns with regard to recruitment and determinants that shape communities within the floodplain and how these are influenced by altered hydrological and the related habitat conditions in European temperate river

floodplains. This knowledge is required for re-establishing ecological integrity of large rivers (Jungwirth, Muhar, and Schmutz 2002).

For the River Rhine, modifications and its implications apply to a particular degree, since the Rhine basin is actually one of the densest populated areas in Europe (290 inhabitants per km<sup>2</sup>). With a length of 1320 km from its source in the Swiss Alps to its mouth into the North Sea and a drainage area of 185,000 km<sup>2</sup>, the Rhine belongs to the largest European rivers. The Lower Rhine section reaches from the northern threshold of the low mountain range, downstream of the city of Cologne, where the river originally took the character of a broad alluvial lowland river, and the border to the Netherlands. A few kilometres downstream of the Dutch boarder the river splits into the branches of the delta Rhine. The mean discharge before entering the Netherlands is 2270 m<sup>3</sup> s<sup>-1</sup> ( $Q_{\min}$ : 790 m<sup>3</sup> s<sup>-1</sup>;  $Q_{\max}$ : 12000 m<sup>3</sup> s<sup>-1</sup>). The Lower Rhine receives the majority of its summer discharge from melting ice and snow in the Alps, however, winter discharge is mainly driven by rainfall in the river basin. These preconditions cause a characteristic pluvio-nivale discharge regime with elevated discharges during winter and lowest in late summer and autumn (Quick 2004) (Fig.1). Though single floods may occur at any time of the year, the highest probabilities are given in winter and spring when high precipitation coincides with low evapo-transpiration. Further discharge peaks often occur in early summer, when melting of snow in the Alps reaches its maximum. Under pristine situations single floods endured for several weeks and their amplitude was only a few meters (Nienhuis *et al.* 2002; Quick 2004).

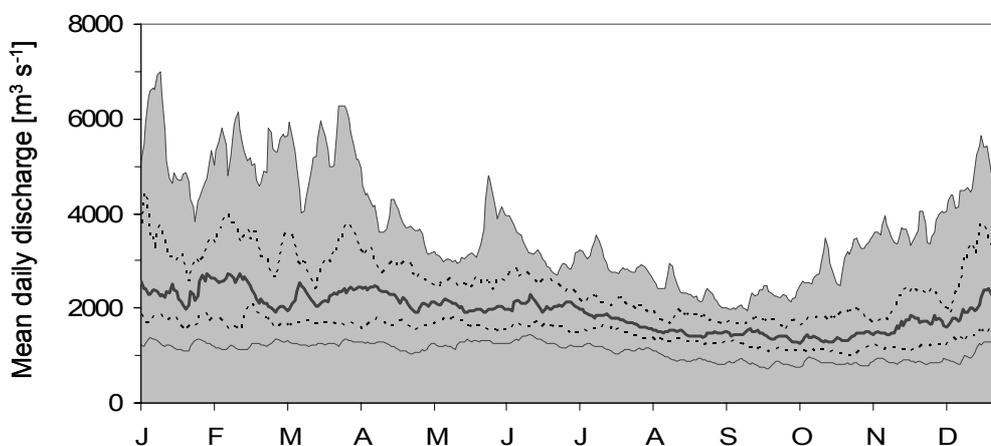


Fig. 1: Long-term (1955-2005) discharge pattern of the Lower Rhine. (bold solid line: median; dotted line: quartiles; grey area and thin lower solid line: 99% intervals).

From the 14<sup>th</sup> century onwards the Rhine was subject to intensive direct modifications: closed levees were constructed and hydrological engineering, in terms of meander cuttings, removal of isles situated in the channel and installation of groynes were conducted, in order to maintain the increasingly important becoming navigation even under low discharges (Gelinsky 1951; Hoppe 1970; Lelek 1989; Tittizer and Krebs 1996; Middelkoop and Van Haselen 1999). These measures led to a massive degradation of in-stream and bank structures and an almost complete loss of the floodplain, which actually accounts for approximately only 15% of its original in the Lower Rhine area (Neumann 2002). The shortening of the Lower Rhine section (approximately 23 km), led to an increase of flow velocity (today 1.0-2.2 m s<sup>-1</sup> in the channel (Engel, Menzel, and Wander 1988). In contrast to many other large temperate rivers (Petts *et al.* 1989; Buijse *et al.* 2002), to the Upper Rhine section and almost all of its tributaries, the Lower Rhine is free-flowing and not impounded or regulated by weirs. However, for the Lower Rhine this implies deficits of sediment load and disturbed erosion and sedimentation processes (Tittizer and Krebs 1996; Middelkoop and Van Haselen 1999). Due to the increased current velocity and a prevented lateral erosion, the river became increasingly forced to take material from its own bed, which led to an ongoing incision and deepening of the channel (averagely 1-2 cm year<sup>-1</sup> (Dröge, Engel, and Gölz 1992; Bundesministerium für Verkehr 1997). Alone in the period from 1828 to 1920 a lowering of the Rhine bed of 3 m occurred, and an increase of 7 m in recent years stands to expect (Nienhuis *et al.* 2002). Conversely an increased accretion of sediments occurs at the river banks and particularly in the floodplain, which successively becomes heightened relative to the mean water mark (Middelkoop and Van Haselen 1999; Neumann 2002). Although the general discharge pattern persisted, the canalisation and the loss of retention resulted in a reduced run-off buffering and rapidly rising peak discharges with high magnitudes, however, a shortening of duration of floods compared to the pristine situation (Fig. 1). The amplitude between high and low water mark has changed from 1.5-2.5 m a 1000 years ago to 7-10 m at present (Nienhuis *et al.* 2002). Today, the Lower Rhine has become the most important inland waterway in Europe with 500-600 ship passages per day and the river banks are exposed to artificial alternating currents and heavy waves (Pottgiesser *et al.* 2005). Moreover, parallel to the industrial revolution and population increase, the Rhine was subject to increasing amounts of untreated sewage effluents. The climax

of highest pollution was reached in the 1960 and 70 years, and the oxygen saturation fell far below the requirements of most aquatic organisms, resulting in a strong decline of fish and invertebrate species, which however recovered from the 1980ies onwards due to the exhaustive implementation of sewage plants. However, many of the invertebrate species currently occurring in the Rhine are immigrants which colonised the Rhine system via the Rhine-Main-Danube channel or have been spread by ships from various regions of the world (Kureck 1992; Bij de Vaate *et al.* 2002). Although some pollutants still reach critical levels, the water quality of the Rhine is commonly regarded not to preclude the recovery of the original biocoenosis, whereas the structural deficits resulting from the excessive river modification, by now remained widely untouched.

In addition, the modifications of the Lower Rhine not only imply a habitat degradation of the River channel, but also a disturbed hydrological interaction with its floodplain. Owing to river deepening and a corresponding drawdown of the groundwater table, many natural floodplain waterbodies (oxbows, flood channels, scour pools), are situated vertically far above the rivers recent channel and took a semi-permanent or ephemeral hydrological character due to a decrease of the ground water level. Many of them show a considerable decrease in water level in periods of low discharge or, if not sealed towards the groundwater table, even dry out completely. Almost all waterbodies have a strictly lentic character and current only occurs during extreme floods.

In order to estimate the number and area of waterbodies situated in the recent floodplain and their hydrological status a GIS-analysis based on aerial pictures from public OGC-files taken during high and low summer discharge conditions was conducted. At present a total of 168 permanent and 62 semi-permanent (strong decrease of lake area during summer, seldom complete desiccation) waterbodies is present in the area between the winter dykes (total area approximately 290 km<sup>2</sup>) in the Northrhine-Westphalian section of the Lower Rhine, from which 69 are permanently and 162 only temporarily connected with the river. Almost all permanently connected waterbodies are former or recent gravel pits (n = 23; area ~ 540 ha), former oxbows (n = 7; area ~ 105 ha, which have often been additionally subject to excavation), industrial harbours and marinas (n = 41, area ~ 650 ha). Most of these waterbodies are characterised by large depths (up to 25 m), steep banks and

a low shoreline diversity, and riparian or aquatic vegetation is either absent or due to extreme water-level fluctuations situated far above the average water mark (Neumann *et al.* 1996; Staas and Scharbert 2001; Borcharding and Staas 2008). In contrast, non-permanently connected waterbodies are natural floodplain waterbodies (oxbows, flood channels, scour pools; n = 29; area ~ 210 ha), former refilled or reconstructed gravel-pits (n = 53; area ~ 330 ha) or small, however, with respect to their origin, not clearly distinguishable waterbodies, which result either from geomorphological processes, coalmining-induced terrain lowering, gravel-mining or borrowing (n = 75; area ~ 31 ha). Categorically, non-permanently connected waterbodies are characterised by a lower average depth, greater shoreline diversity and often abundant riparian and aquatic vegetation (Staas and Scharbert 2001; Scharbert and Greven 2002).

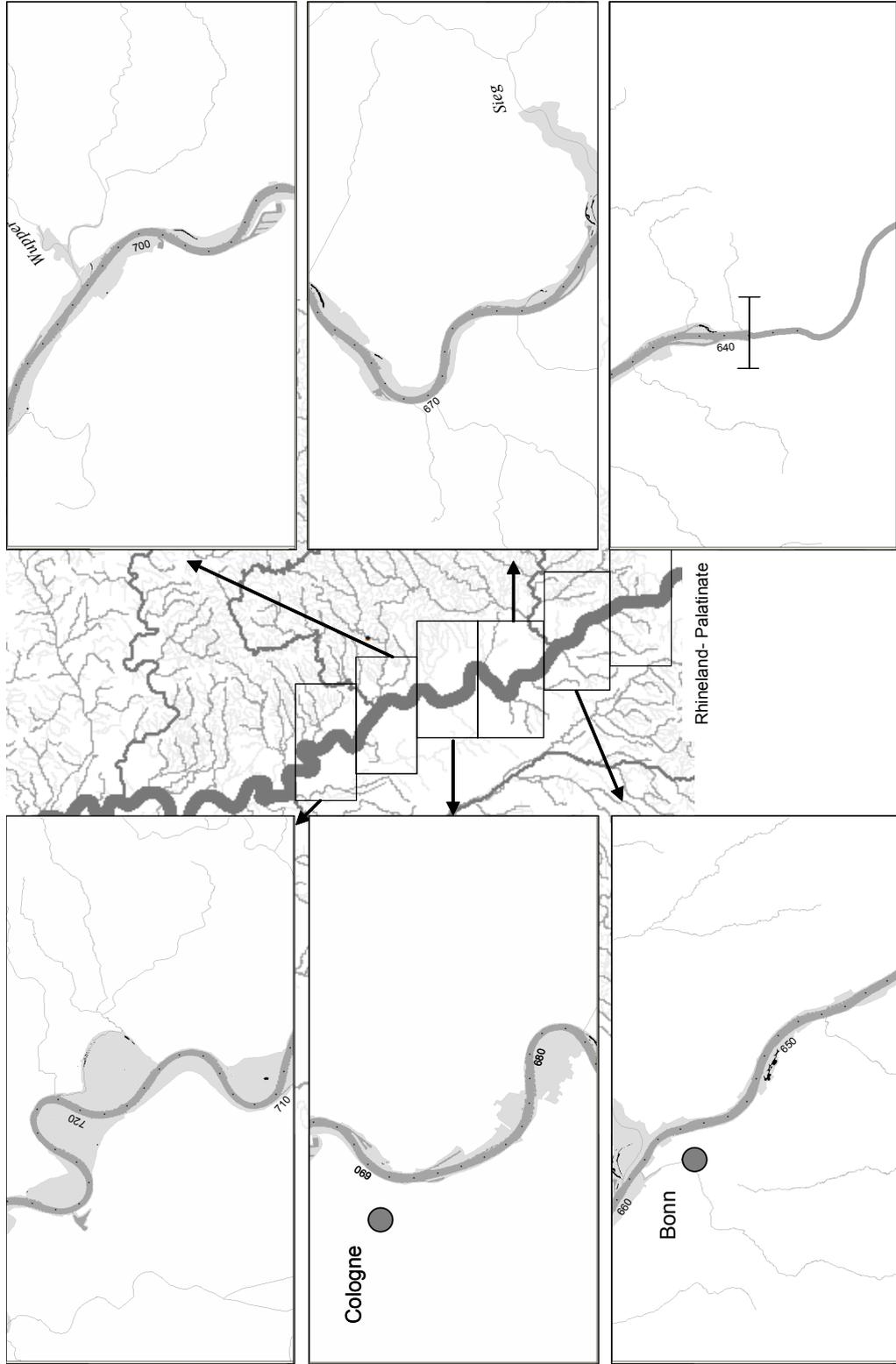


Fig.2a: Map of the Northrhine-Westphalian section of the Lower Rhine between the border to Rhineland-Palatinate (river km 640) and the upstream of Düsseldorf (river km 730). The maximally floodable are given in pale grey. Areas taken by the Rhine and permanently connected waterbodies are given in dark grey and these of non-permanently connected waterbodies in black. Hatched areas mark locations where regularly ephemeral waterbodies remain after floods. Waterbody areas refer to average summer discharge conditions.

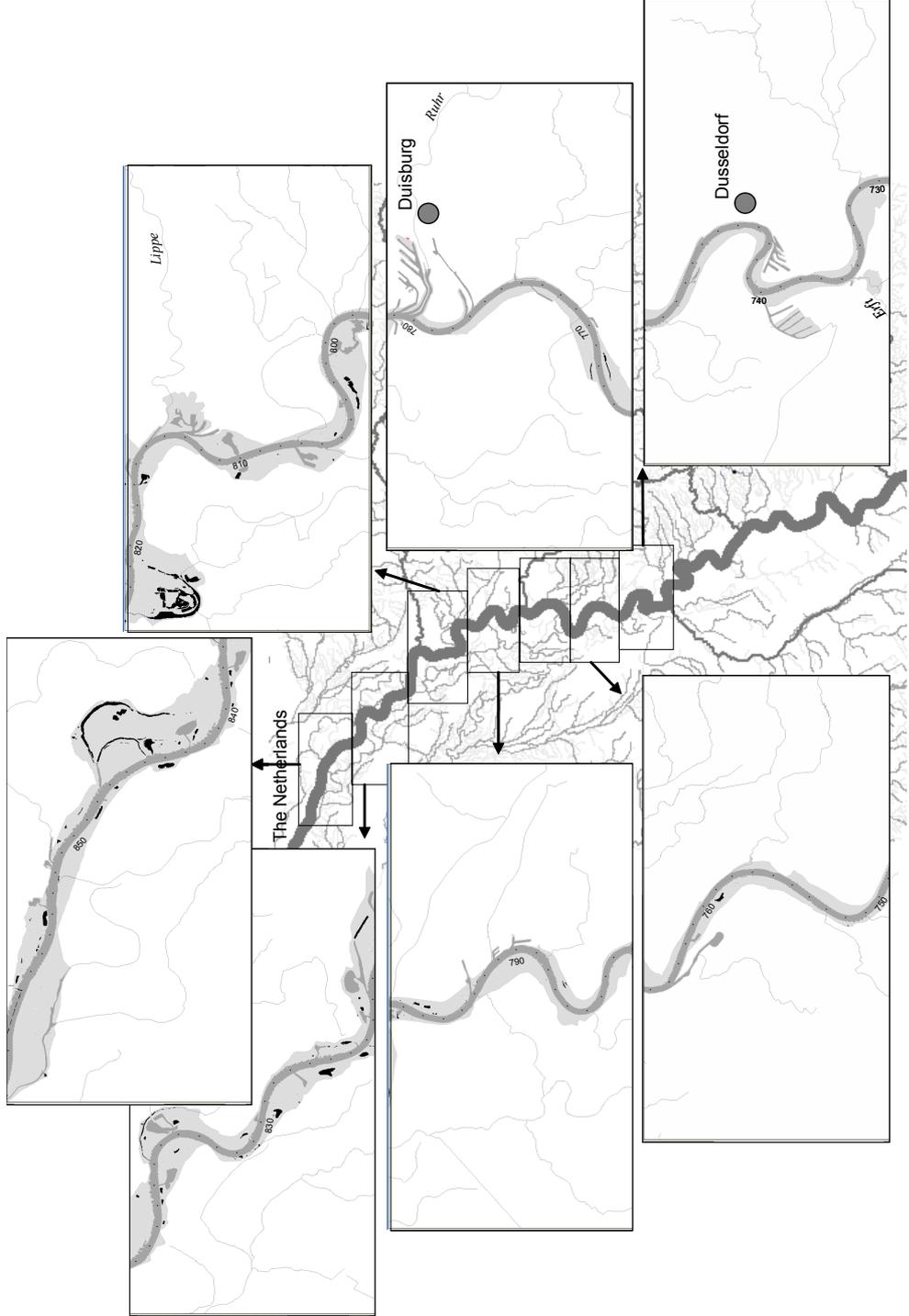


Fig.2b: Map of the Northrhine-Westphalian section of the Lower Rhine between river km 730 and the border to the Netherlands (river km 730). The maximally floodable area is given in pale grey. Areas taken by the Rhine and permanently connected waterbodies are given in dark grey and these of non-permanently connected waterbodies in black. Hatched areas mark locations where regularly ephemeral waterbodies remain after floods. Waterbody areas refer to average summer discharge conditions.

Furthermore there is a considerable number of ephemeral waterbodies situated in the floodplain, which originate from former flood-channels, scour pools or filled gravel-pits, however, their number and area could not be quantified representatively, since their occurrence depends on the strength of the floods and thus varies inter-annually and seasonally.

During average summer discharge conditions the ratio of the area taken by the channel and those of all non-ephemeral stagnant waterbodies is 4:1, and 12:1 regarding non-permanently connected waterbodies. When taking into account only non-ephemeral waterbodies, there is still a quasi-natural gradient of increasing numbers (spearman rank correlation:  $r_s = 0.868$ ,  $P < 0.001$ ) and areas of stagnant waterbodies ( $r_s = 0.873$ ,  $P < 0.001$ ) in longitudinal direction. This longitudinal pattern was initially, or would even be under potential conditions, determined by the width and the slope of the valley, the granulation of the deposits and the related geomorphological processes (Quick 2004). Today, this gradient is exclusively determined by the position of the major embankments, the degree of anthropogenic over-forming and the intensity of gravel mining, respectively.

Exploring fish communities in a such highly modified environment offers the opportunity not only to illuminate how these or either single species cope with the strongly altered conditions, but, by identifying patterns along seasonal, spatial and hydrological gradients and related habitat conditions, to determine fundamentals of recruitment and community organisation. The aim of the present thesis is to illuminate whether there are persistent adaptations of species to hydrological patterns and related habitat availability, and which factors influence recruitment patterns and habitat utilisation and, thus, shape fish communities in floodplain waterbodies. For this reason this study focuses mainly on non-permanently connected waterbodies, since these represent the respective gradients.

Chapter 1 explores the significance of seasonal floodplain inundations on recruitment patterns and spatio-temporal habitat utilisation of species. Hydrology in terms of seasonal inundations is considered as a crucial factor for fish communities in the floodplain, since it determines upon exchange mechanisms and involves an expansion of habitat area and an increase of productivity. Lateral migrations of adult fishes in order to spawn onto the floodplain probably represent the highest degree of

adaptation. Thus, such species are hypothesised to recruit most successfully when the requirements for placing the progeny under optimal conditions, and lowest recruitment should take place when unfavourable conditions occur. In contrast, reverse adaptations are to expect for species typically inhabiting stagnant and more remote waterbodies, for which inundations might be detrimental, since they involve disturbances. However, little knowledge exists with regard to such adaptations of species in European lowland rivers and, most important, whether these are related to life-history strategies. Furthermore, habitat requirements particularly in YOY fishes vary strongly and some species are characterised by only seasonal floodplain habitat utilisation, whereas other inhabit floodplain lakes more permanently. But again, only little is known about the seasonal aspects and the reasons for such spatio-temporal patterns. Consequently, this study aims on closing these gaps of knowledge, which are considered to be crucial for maintenance of biodiversity and for sustaining of fish populations in riverine wetlands, particularly in the light of ongoing river modifications and possible effects of climatic change.

Hydrology not only determines upon possible exchange patterns of fish between and within different zones of the floodplain, but also controls the availability of physical habitat in space and time. For instance, stagnant floodplain waterbodies situated adjacent to the river often experience excessive changes in habitat availability, e.g. area draw-downs from the flood peak to the moment of disconnection and seepage in the course of the isolation phase. In contrast, more stable conditions prevail in waterbodies less affected by fluctuations of river discharge. Consequently, different preconditions of recruitment for species exhibiting distinct reproductive strategies and habitat requirements are to expect. Particularly YOY fish are considered to exhibit very narrow habitat preferences, which vary between different species and are often attributed to ontogenetic steps, swimming and feeding capabilities. Thus, site characteristics in space and time might control survival of YOY fishes with different requirements. Therefore, this second part of the study (Chapter 2) aims on illuminating the significance of seasonally varying habitat availability in front of species-specific habitat requirements and other determinants of survival in YOY fish, like predator abundance, growth performance and size, as well as density-dependent implications.

Species-specific temperature requirements for spawning in fishes and their reproductive adaptation towards predictable discharge patterns are expected to provide their progeny with benefits associated to optimal energy gain and related growth performance. It is commonly argued that early spawning species are advantaged over later spawners, since they attain a relative larger size, higher motility and forage more efficiently. This particularly applies to piscivorous species, however, the onset of piscivory in YOY fish is known to depend on further determinants, such as prey availability to maintain a size advantage over extended periods in the first year of life. Both abundant planktonic organisms serving as initial prey as well as small fish larvae being available for extended periods should enhance YOY piscivory. However, little is known about the determinants and the implications of early piscivory in European river floodplains. Consequently, the third part of this study (Chapter 3) aims on the identification of the causes for early piscivory in two functionally different piscivorous fish species, as well as its consequences for their potential prey fish populations in front of hydrological and habitat parameters.

Since all topics of the present work deal with differences of abundance of species in space and time, a modified sampling approach was used to compare data gathered over several habitat scales, which is documented in appendix chapter 1.

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**Relationships of hydrology and life-history strategies on spatio-temporal habitat utilisation of fish in European temperate river floodplains**

**Abstract**

Floodplain inundation is considered as crucial for recruitment of fish in lowland rivers, by either providing suitable spawning areas as well as breeding habitats for young-of-the-year fish (YOY), or supporting species that exhibit different life history-strategies to be differently adapted to long term discharge patterns. Fish communities in a set of 38 waterbodies in the Lower Rhine floodplain, representing different long-term frequencies of inundation and differently affected by seasonal inundations, were sampled with electrofishing (Point abundance sampling, total n = 42,701 points) over a four-year period in order to identify species-specific and life-history strategy related patterns of spatio-temporal floodplain habitat utilisation. For 18 species (total catch: n = 107,150), typically occurring in European lowland rivers and representing different ecological guilds, different responses towards seasonal inundations were found. YOY of most species closely associated to the periodic strategy (e.g., *Abramis brama*, *Aspius aspius*, *Blicca bjoerkna*) were highly abundant in frequently inundated waterbodies, as long as these were subject to inundations occurring in spring and early summer and coincided with required temperatures for spawning. However, recruitment in these species was impaired or even failed when no inundations in this time frame occurred, although adults were present. In contrast, most species associated to the opportunistic strategy (e.g., *Gasterosteus aculeatus*, *Pseudorasbora parva*, *Leucaspis delineatus*) had highest recruitment in waterbodies unaffected by inundations in this time frame, which had detrimental effects on these predominantly small sized species. Spatio-temporal floodplain habitat utilisation of YOY fish (most rheophilic species as well as eurytopics like *Abramis brama*, *Cyprinus carpio* and *Sander lucioperca*) is suggested to be size-related, since most fast growing periodic strategists left the floodplain at given connectivity at latest in winter and were then absent in the subsequent year. Smaller YOY fishes and all opportunistic species remained in more isolated waterbodies, from which they dispersed across the floodplain to some degree during extensive winter floods. These findings suggest adaptations to the long-term hydrograph of large river systems, with flood-related recruitment patterns predominantly occurring in periodic strategists and low-flow recruitment strategies in opportunistic strategists and stagnophilic species. The results of this study point to the significance of hydrological transversal floodplain gradients for providing diverse communities and population maintenance of different life-history strategies under a variety of hydrograph scenarios.

## Introduction

The significance of floodplain inundation for fish production in temperate lowland rivers as well as seasonally differing species compositions between the river channel and floodplain lakes have been early recognized (Antipa 1923; Balon 1963; Holcik 1988) and similar relationships have been demonstrated to occur in further biota (Hein and Heiler 1999; Baranyi *et al.* 2002; Van Geest *et al.* 2003). Though originally conceived to tropic systems, the ecological implications of seasonal floodplain inundation are well displayed in the conceptual framework of the flood-pulse-concept (FPC) (Junk, Bayley, and Sparks 1989), pronouncing that flood events in lowland rivers act as disturbances, by facilitating aquatic organisms access to different habitats, by nutrient and matter exchange and by structuring the habitats within the aquatic-terrestrial transition zone. The interactions of these factors are addressed to cause the high overall productivity and diversity of floodplain systems. The periodicity of inundations implies a transition from more physically (flow, temperature, water quality, habitat complexity) driven systems during the connection phase to more biologically (competition, predation) driven systems during the isolation phase (Bayley 1991; Ward and Stanford 1995; Junk 1999).

In rivers with predictable flow regimes, individual fish species are believed to have evolved different strategies to maintain their populations, e.g. by synchronizing their reproduction with flood events that coincide with optimum temperatures for spawning in order to place their offspring in the floodplain, where it can benefit from the high productivity associated with the aquatic-terrestrial transition zone (Junk *et al.* 1989). This synchronisation might either function by stimulating spawning of adults within the floodplain directly, or by spawning outside the floodplain but providing larvae and juvenile access to the flooded habitats (Schiemer *et al.* 2001). However, with regard to temperate systems, it is suggested that recruitment of species that are highly adapted to reproduction within the floodplain is impaired, when floods fail to appear, retreat too quickly or do not coincide with appropriate temperatures (Bayley 1991). In contrast, recruitment of species that exhibit alternative reproductive strategies might be supported under low flow conditions (Humphries, King, and Koehn 1999).

Hence annual hydrological conditions are expected to affect reproduction and recruitment of species with different life-history strategies differently. Winemiller and Rose (1992) demonstrated that these adaptations are strongly correlated with

other species-specific life-history traits, such as longevity, age and size at maturity and growth performance and proposed species to be arranged within a triangular continuum, which endpoints represent the three major life-history strategies. When linking the tenets of the FPC with that of life-history theory, species that synchronize their reproduction with optimal discharge and temperature conditions should predominantly belong to the group of periodic strategists, which delay maturity until they are large enough to produce large numbers of small eggs which are placed under appropriate, but often short-lasting conditions (Winemiller and Rose 1992). Species that are less adapted towards predictable flow regimes are often characterised by an attainment of maturity at small lengths and young age, protracted spawning periods with multiple spawning bouts, which enables them to maintain their population even under unfavourable conditions and to compensate an increased adult mortality, which are typical features of opportunistic strategists and favours these species to colonize new habitats quickly (Winemiller and Rose 1992). Though this scheme was initially conceived to the North American fishfauna, it has been extended to a range of species typically inhabiting European freshwaters (Vila-Gispert and Moreno-Amich 2002; Blanck, Tedesco, and Lamouroux 2007). However, until now no attempts have been undertaken to investigate the relationships of species exhibiting different life-history strategies and their habitat utilization in European temperate river floodplains.

Taking into account the four-dimensional nature of alluvial floodplain rivers and the instability of habitat conditions in space and time (Ward 1998; Junk 1999), it is hypothesized that the community organisation within the different patches of the floodplain results from different species-, stage- and life-history strategy-specific adaptations towards a) the disturbances caused by inundations, b) the changing habitat conditions and c) the interactions of biota (food availability, predation). Depending on the seasonality of inundations and the connectivity of habitats within the floodplain, species life-stages are thus considered to form spatially and temporarily distinct communities in patches. With respect to young-of-the-year (YOY) fish assemblages it has indeed been demonstrated that communities change along a lateral, i.e. hydrological gradient as a consequence of spatially distinct reproduction and nursery zones (Copp 1989).

Schiemer and Waidbacher (1992) classified European fish species into ecological guilds according to the presence of their life-stages in characteristic assemblages in

channel and differently connected floodplain habitats of the Danube River. However, only little information exists with regard to the seasonal aspects and the causes of laterally directed exchange processes and their significance for population maintenance. Hence, our knowledge of spatio-temporal dynamics and the species- and stage-related adaptation towards seasonal floodplain inundation in temperate European rivers remains limited. Furthermore, today most of the temperate lowland rivers are heavily altered by human activities, including massive losses of floodplain area and reduced habitat diversity, as well as modified hydroperiods (Buijse *et al.* 2002) and it is not sufficiently known how the different species cope with these changed conditions.

In this study we analyse data gathered in a four-year study from a large set of floodplain waterbodies of different degree of connectivity, origin, hydrological character and spatial distance to the river in front of inter-annually and seasonally varying inundation patterns, in order to estimate the relative importance of seasonal inundations on fish communities and recruitment patterns of species representing different life-history strategies. We aim to determine which species typically inhabiting large European river floodplains have adapted their life-cycle to long-term discharge patterns and how they are affected by deviations from this scheme. We analyse how seasonal floodplain habitat utilisation of species life-time stages in a modified river floodplain responds to seasonal inundations and whether these patterns could be related to life-history strategies. This knowledge is of importance for sustaining population maintenance in the light of still proceeding modifications of river-floodplain interactions or probably occurring in the course of climate change.

## Methods

### Study site

With a length of 1320 km from its source in the Swiss Alps to its mouth into the North Sea and a drainage area of 185,000 km<sup>2</sup>, the Rhine is one of the largest rivers in Europe. In contrast to all of his tributaries and most other large temperate rivers in the world, the longest part of the Rhine is free flowing and not regulated by dams. The present study was conducted at the Lower Rhine area within the borders of the German federal state North Rhine-Westphalia. The river section reaches from the northern threshold of the low mountain range downstream of the city of Cologne and the border to the Netherlands. The mean discharge before entering the Netherlands is 2270 m<sup>3</sup> s<sup>-1</sup> (mean low-water discharge: 1030 m<sup>3</sup> s<sup>-1</sup>; mean-high water discharge: 6550 m<sup>3</sup> s<sup>-1</sup>). The Lower Rhine receives the majority of its summer discharge from melting ice and snow in the Alps, however, winter discharge is mainly driven by rainfall in the river basin. In the pristine situation these preconditions caused a characteristic temperate-seasonal discharge regime with often long enduring floods occurring from late winter until the beginning of summer and lowest discharges in late summer and autumn (Quick 2004).

Straightening and reinforcement in order to protect the densely populated hinterland and agricultural areas from floods caused a massive loss of the floodplain area initially available. Since the Lower Rhine has become the most important inland waterway in Europe with 500-600 ship passages day<sup>-1</sup>, groynes have been constructed, in order to maintain navigation even under low discharges. Owing to these modifications, the flow velocity within the channel increased considerably (mean 1.5 m s<sup>-1</sup>) which led to an irreversible and still preceding erosive incision of the river channel (mean 2 cm year<sup>-1</sup>). Furthermore, the canalization and the loss of retention area in the whole basin causes rapidly rising peak discharges with high magnitudes, but a reduced duration of floods and strongly fluctuating water levels even at moderate discharges.

Most of the waterbodies within the active floodplain (in terms of the maximum floodable area between the winter-dykes) of the German stretch originate from gravel mining, of which the majority was partly refilled with allochthonous material and disconnected from the river after excavation.

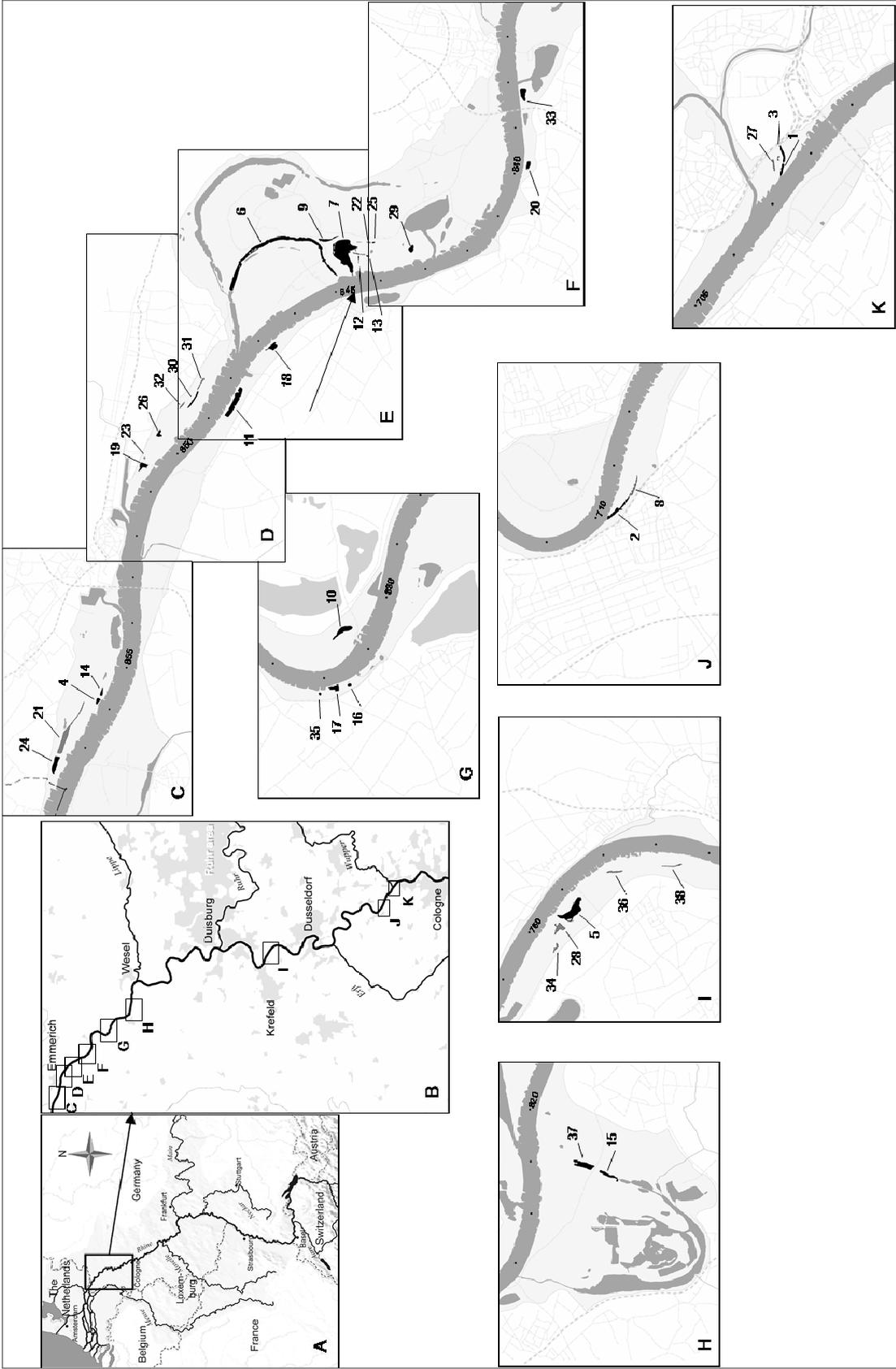


Fig. 1 (previous page): Map with location of the area of investigation and the sampled waterbodies (black) in the Lower River Rhines floodplain (pale grey area). Arrow in Figure 1e denotes the location of the anchored stow-net. Numbers of waterbodies increase with descending long-term degree of connectivity (see Table 1).

Table 1: Characteristics of the waterbodies situated the Lower Rhine's floodplain and the sampling scheme in the annual cycles between the May of 2002 and the November of 2005. Waterbodies are sorted after their degree of connectivity. Numbers refer to whether sampling was conducted in the first (1) and/or the second (2) half of the respective period (S = spawning, G = growth, W = winter; compare Figure 1 for definitions). Asterisks denote more than one sampling date per sub-period. † = waterbody was initially permanently connected to the channel and disconnected in August 2003 after sampling was conducted. The total of sampled waterbodies and the sampling effort (sum of point-samples) per period are given below.

No. of waterbody	origin	distance from river (km)	days inundated (50 year mean)	area (ha)	hydrological character	2002/03			2003/04			2004/05			2005/06		
						S	G	W	S	G	W	S	G	W	S	G	W
1	oxbow	0	365	0.54	perennial			1/2		1	1/2	1*/2	1/2*	2	1/2	1/2	
2	oxbow	0	365	1.90	perennial	2		2	2	1	2	1/2*	1*/2	1/2	1/2	1/2*	
3	oxbow	0.21	237	0.77	semi-perennial	2			2		2	1/2*	2		1	2	
4	scour pool	0.01	190	0.79	perennial			2	2	2	2	2	1/2			2	
5	former gravel-pit	0.03	186	6.89	perennial				2	2	2	1/2	1/2		2	1/2*	
6	oxbow	0.05	154	18.77	perennial			2	1/2	2	2	1/2	1/2*	1	1/2	1/2	
7	former gravel-pit	0.09	132	18.90	perennial					1†	1	2	1/2*		1	1	
8	oxbow	0.61	131	0.74	ephemeral			2			2	1*/2			1*		
9	oxbow	1.15	114	1.18	semi-perennial		2				2	2	1/2	1/2	1/2	1/2	
10	former gravel-pit	0.09	111	2.67	perennial			2		1	1/2	2*	1/2*	1/2	1/2	1/2	
11	former gravel-pit	0.03	108	6.50	perennial			2		1	1/2	2	1/2	1	2	1/2	
12	former gravel-pit	0.71	103	0.21	perennial					2		1/2*	2		1		
13	former gravel-pit	0.95	98	0.12	perennial			2			1/2	2*			1		
14	scour pool	0.09	82	1.74	perennial			2			2	2					
15	former gravel-pit	6.00	67	1.61	perennial					1*	2	2	1*/2	1/2		1/2	
16	flood channel	0.03	67	0.23	semi-perennial			2		2	2	2			2		
17	closed groynefield	0.03	67	1.42	perennial			2		2	2	2	1/2		2	1/2	
18	former gravel-pit	0.16	59	1.84	semi-perennial			2		2	2	2	1/2	1/2	2	1/2	
19	scour pool	0.14	55	1.85	semi-perennial	2		2		1	2	1	1/2	2	2	2	
20	former gravel-pit	0.06	55	1.18	perennial			2		2	2	2	1/2		2	1/2	
21	flood channel	0.19	51	6.50	ephemeral	2		2			2			2			
22	flood channel	2.17	48	0.17	semi-perennial	1/2	2	1/2			2			2			
23	scour pool	0.25	45	0.56	ephemeral			2			2			2			
24	flood channel	0.20	43	3.17	perennial	2		2		2	1/2	2				2	
25	flood channel	2.32	43	0.12	semi-perennial	1	2	1/2		1	2			2	2		
26	flood channel	0.34	36	0.91	semi-perennial	1/2		2		1	2			2	2		
27	scour pool	0.58	35	0.44	ephemeral			2			2			2			
28	filled gravel-pit	0.11	34	1.91	ephemeral	1		2			1/2			2			
29	filled gravel-pit	3.14	34	1.18	perennial	2		1/2		2	2	2	1/2	1/2	2	1/2	
30	flood channel	1.29	33	1.07	semi-perennial	1		1/2		1	2			2	2		
31	flood channel	1.69	33	0.55	ephemeral	2		2			2			2			
32	flood channel	1.14	30	0.35	ephemeral			2			2			2			
33	filled gravel-pit	0.04	23	2.55	perennial			2		2	2	2	1/2	1/2		1	
34	scour pool	0.57	20	0.87	ephemeral						1/2			2			
35	scour pool	0.04	12	0.17	perennial			2		2	2	2	1/2		2	1/2	
36	flood channel	0.17	11	0.95	ephemeral	1		2			2			2			
37	former gravel-pit	6.80	6	3.34	perennial					2	1/2	2	1/2	2		2	
38	flood channel	0.30	5	0.14	semi-perennial	1		2			2			2			
No. waterbodies sampled						12	4	31	2	22	38	21	23	26	19	22	1
No. inundated per period						10	2	31	1	0	38	13	5	24	14	7	0
No. samples						1565	570	5547	427	3137	9262	4340	6438	4755	1868	4482	310

Owing to river deepening and a corresponding drawdown of the groundwater table, many of the original floodplain water bodies (oxbows, flood channels, scour pools), are situated vertically far above the rivers recent mean discharge channel and took a semi-permanent or ephemeral hydrological character (Neumann 1994; Borcharding and Staas 2008). Many of them show a considerable decrease in water level in periods of low discharge or, if not sealed towards the groundwater table, even dry completely. The majority of permanently connected backwaters are recently excavated gravel-pits or harbours, which characterized by large depths and surfaces, but predominantly extremely steep banks (Neumann *et al.* 1996; Borcharding and Staas 2008).

### Sampling design

The present study comprised 38 floodplain waterbodies, which were sampled over a 4 year period lasting from the beginning of May 2002 to the end of November 2005, (see Table 1 for the sampling scheme). Only two of the waterbodies are permanently connected to the river. All non-permanently connected waterbodies differ in respect to frequency of inundations, origin, area, depth, hydrological character, and distance to the channel (Table 1, Fig. 1) and are regarded to display the different types of floodplain habitats present in the area of investigation. The connected waterbodies are characterised by comparable depths and areas like the majority of infrequently inundated waterbodies. A total of 19 non-perennial waterbodies were taken into account that drought down for at least once in the study period. These are considered to allow drawbacks about immigration and reproductive strategies during inundations more clearly than in perennial waterbodies, where abundance might be influenced by resident stocks and processes occurring during the isolation phase (reproduction, competition, predation).

Except when water temperatures were  $< 5^{\circ}\text{C}$ , sampling was conducted year-round by means of point abundance sampling by electrofishing (PAS) (Persat and Copp 1989). Samples (distance between particular units  $\geq 5$  m) were taken randomly across the whole area of the waterbody, except in two deeper gravel-pits, where the mean depth exceeded 2 m and sampling was restricted to the shallow areas. A generator powered DC DEKA 5000 electrofishing unit (300 V, 6.6 A, DEKA Gerätebau, Marsberg, Germany) transported by a boat and a ring anode with an inserted landing net (diameter 0.4 m, mesh size 4 mm) was used at all sampling occasions. For sampling

between April and August, when high numbers of larval and small juvenile stages were to expect, additional sampling with a pulsed DC device (DEKA 3000; 12 V, 5 A, DEKA DEKA Gerätebau, Marsberg, Germany) and a separate dip-net (mesh size 0.5 mm) was conducted (at least 30 samples per waterbody), which was modified with a small ring anode (diameter 0.1 m) to enhance the selectivity for small fishes (Copp and Garner 1995). The activated anode was immersed quickly as near to the bottom as possible and lifted slowly in a strictly vertical position for approximately 5 sec.. All stunned fish were harvested, determined, measured to the nearest millimetre (total length, TL) and released afterwards, except larvae and early juvenile stages, which were fixed in 5% formalin solution and determined in the laboratory using keys of Koblickaya (1981) and Pinder (2001). To take into account the effects of fish size, current density, water temperature and conductivity, which are the main determinants of accurate abundance estimation in PAS (see Scholten 2003), the proper distance reaction of differently sized fish towards the activated anode was scrutinised in the field for the different sampling devices and abiotic conditions, and plotted against the total length of the galvo-narcotized fishes. Non-linear regressions were then used to calculate the effective range of the electrical field on a fish at a given size for each sample (see Appendix) and transformed into abundance (including null-samples), expressed as individuals per m<sup>-2</sup>. The number of samples depended on the area of the water body and ranged from at least 50 to many hundred samples per waterbody (total effort 42,701 point samples in the four-year period, see Table 1)

To explore whether decreases in abundance of particular species and age groups within the floodplain after inundations are related to emigrations from the floodplain, the by-catch of an anchored framed stow-net was analysed. The gear is fixed on a vessel which is stationed in the river channel (approximate water depth and distance from the bank 5 and 15m, at mean water level, respectively) at the lower boundary of the area of investigation (river km 845, see Fig.1). The gear resembles a giant fyke-net (height: 5m, upstream opening-width: 10m, length: 30m) and reaches vertically from the bottom till close beneath the surface (for detailed description see Klust 1970). Mesh sizes decrease from 200 mm at the upstream end approximately every 3 m to 15 mm at the downstream end. Since the intention of this gear is to monitor the downstream migration of silver-eels, we only dispose over data gathered between the beginning of August and mid-December (main period of eel downstream migration),

of the years 2005 and 2006. Sampling was conducted from Monday to Friday of each week in this period, except in full moon phases or when no eel were caught for a number of successive days. Each morning the by-catch of a 12 h sampling effort was determined and measured (to the nearest cm) and abundance of ecospecies treated as CPUE (individuals per day).

#### Life history traits of species

We used life-history trait parameters (Table 2) that are considered to allow discriminations between different life-history strategies and are comparable to those proposed by Winemiller and Rose (1992). Trait data and assignment to strategies were obtained from literature sources (Vila-Gispert and Moreno-Amich 2002; Blanck *et al.* 2007; Blanck and Lamouroux 2007). Traits of species or additional parameters not taken into account in these studies were gathered from FishBase or additional papers and species assigned to the possible strategies after their traits. Since several traits of particular species vary largely over their latitudinal ranges (Blanck and Lamouroux 2007), we used data gathered in the present thesis, from other findings in the area of investigation (Molls 1997), or indications from similar latitudes, which were transformed into trait categories. Besides trait data, we additionally considered variables regarding specialisations of species in terms of feeding characteristics (trophic guild membership of adults, occurrence of ontogenetic diet shifts), that might even influence patterns of habitat utilization. Qualitative categories were defined in ascending order, e.g. diet categories after their energetic content.

Table 2 (next page): Species codes, life-history trait and ecological variables (categorical variables without units, mean values in case of non-categorical variables) of the eighteen species used to explore relationships of habitat utilisation and their assignment to life-history strategies. Entries left blank when no reliable values were found.

Legend to Table 2:

- 1.) Maximum length (mm) in the area of investigation (Molls 1997; Staas 1999; Scharbert, unpublished data)
- 2.) Growth coefficient ( $K \text{ year}^{-1}$ ) of females as a parameter of the Von-Bertalanffy growth function,
- 3.) Longevity as the maximum age reported (year)
- 4.) Length (TL mm) at maturity (50% maturation of females),
- 5.) Age at 50% maturation of females (age): 1 = 1+, 2 = 1+-2+, 3 = 2+-3+, 4 = 3+-4+, 5 = 4+-5+),
- 6.) Fecundity (mean number of eggs per female in a single spawning season categorized as 1  $\leq$  500, 2 = 500-5,000, 3 = 5,000-10,000, 4 = 10,000-50,000, 5 = 50,000-100,000, 6 = > 100,000),
- 7.) Egg size (mean diameter of mature oocytes (mm)),
- 8.) Spawning temperature (as the lower threshold) ( $^{\circ}\text{C}$ )
- 9.) Spawning mode (categorized as 1 = single spawning per year, 2 = from 2 to 4 spawning per year, 3 = more than 4 spawning per year),
- 10.) Spawning season (first occurrence of early larvae; after Pinder 2001) in our dataset, categorized as: 1 = 1<sup>st</sup> half of April, 2 = 2<sup>nd</sup> half of April; 3 = 1<sup>st</sup> half of May; 4 = 2<sup>nd</sup> half of May; 5 = 1<sup>st</sup> half of June; 6 = 2<sup>nd</sup> half of June,
- 11.) Length of spawning season (number of weeks in which early larvae occurred)
- 12.) Parental care: 0 = no special spawning substrate selection (phyto-lithophilic after Balon 1975) and no guarding by adults; 1 = special spawning substrate selection (lithophilic, phytophilic after Balon 1975) but no guarding by adults; 2 = special spawning substrate selection (lithophilic, or phytophilic, nest-building, after Balon 1975) and guarding by adults or broodhiding in mussels,
- 13.) Final YOY size as the mean total length (mm) at the end of the growing season (September, October) in our dataset
- 14.) Adult trophic guild classification after Noble *et al.* (2007): 1 = omnivorous (not specialized), 2 = herbivorous, 3 = invertivorous, 4 = inverti-piscivorous, 5 = piscivorous
- 15.) Ontogenetic diet shifts from the initial prey category (zooplankton/microbenthos) (Nunn, Harvey, and Cowx 2007) towards another prey category during the first year of life: 0 = no abrupt diet shift reported, 1 = herbivory (Reckendorfer *et al.* 2001), 2 = invertivory (Vilizzi 1998; Bischoff and Freyhof 1999; Persson and Bronmark 2002a), 3 = invertivory /piscivory (Persson and Greenberg 1990; Beek *et al.* 2002), 4 = piscivory (Korte 1999; Persson and Bronmark 2002b)
- 16.) Trait-related assignment to endpoint strategies after the classification of Winemiller and Rose (1992). Species previously assigned (Vila-Gispert and Moreno-Amich 2002; Blanck *et al.* 2007) are denoted with asterisks.

Species	Species code	maximum length (mm)	$K$ ( $\text{year}^{-1}$ )	longevity (years)	length at maturity (mm)	age at maturity	fecundity	egg size (mm)	spawning temperature ( $^{\circ}\text{C}$ )	spawning mode	spawning season	length of spawning season (weeks)	parental care	final YOY size (mm)	trophic guild	ontogenetic diet shifts	life-history strategy
<i>Alburnus alburnus</i>	Aa	197	0.18	6.9	80	2	3	1.6	17	2	4	9	0	58.0	1	0	opportunistic*
<i>Aspius aspius</i>	Aas	808	0.08	11	384	5	6	1.7	8	1	1	3	1	94.9	5	4	periodic
<i>Abramis brama</i>	Ab	611	0.14	10.8	244	5	6	1.33	12	1	2	8	1	77.8	3	2	periodic*
<i>Barbus barbus</i>	Bb	817	0.43	6.3	175	3	4	2.17	16	2	3	8	1	62.8	3	2	periodic*
<i>Blicca bjoerkna</i>	Bbj	442	0.18	9.7	100	3	4	1.47	16	2	4	13	1	47.1	1	0	periodic*
<i>Cyprinus carpio</i>	Cc	873	0.23	10.7	366	4	6	1.42	16	1	3	11	1	86.4	3	0	periodic*
<i>Chondrostoma nasus</i>	Cn	545	0.13	9.1	340	3	4	2.2	8	1	1	2	1	77.0	2	1	periodic*
<i>Cobitis taenia</i>	Ct	113	0.29	5	76	2	1	1.88	16	2	5	5	1	60.7	3	0	opportunistic
<i>Gasterosteus aculeatus</i>	Ga	79		2.6	42	1	1	1.52	12	3	3	10	3	39.7	1	0	opportunistic
<i>Leuciscus cephalus</i>	Lc	523	0.15	10.8	172	4	4	1.55	16	2	4	14	1	60.7	1	0	periodic*
<i>Leucaspis delineatus</i>	Ld	72	0.39	3	61	1	2	1.38	16	2	5	13	2	41.8	1	0	opportunistic
<i>Leuciscus idus</i>	Li	554	0.11	14	341	5	5	1.7	10	1	1	2	0	101.0	1	0	periodic
<i>Perca fluviatilis</i>	Pf	486	0.11	12.7	190	3	3	1.8	8	1	1	2	0	90.2	4	3	periodic*
<i>Pseudorasbora parva</i>	Pp	93	0.39	3.3	77	1	2	1.18	15	3	4	16	2	31.7	1	0	opportunistic
<i>Rhodeus amarus</i>	Ra	78	0.32	7	51	1	1	2.1		2	4	16	2	39.8	1	0	opportunistic*
<i>Rutilus rutilus</i>	Rr	410	0.16	10.5	181	3	4	1.13	8	1	2	6	0	85.0	1	0	periodic*
<i>Sander lucioperca</i>	Sl	859	0.19	7.2	367	4	6	0.95	8	1	1	2	2	110.7	5	4	periodic*
<i>Tinca tinca</i>	Tt	504	0.35	7.7	280	4	6	1.03	16	2	5	6	1	35.8	1	0	periodic*

## Data analysis

Sampling dates were pooled to predefined periods, which are considered to represent major ecological and physiological definable seasons in the annual-cycle and to be constrained by underlying temperature conditions (spawning: April-June; growth: July-October; over-wintering: November-March). Each period was subdivided into two sub-periods in order to adjust abundance values and to enhance the comparability of pre- and post inundation situations (Fig. 2). Sampling effort differed between the annual cycles and periods, particularly due to annual and seasonal differences in the number of inundated ephemeral waterbodies (Table 1). However, many waterbodies were subject to repeated sampling occasions per sub-period.

The average sampling effort was 194 samples per waterbody and period (spawning: 162; growth: 192; winter: 229). Lifetime-stages (YOY, juveniles  $\geq 1+$ , adults; henceforth ecospecies) were discriminated by length-frequency distributions (LFD). The YOY stage was considered to end at the beginning of the subsequent spawning period. Species known to mature at the end of the first growing season or in which no clear cut-off value between YOY and older year-classes were discernable in the LFD, were only discriminated into the YOY and the adult stage, using a cut-off value of TL 45 mm.

Inundation thresholds of the particular waterbodies were determined by repeated field observations during flood events (estimated accuracy  $\pm 0.05$  m), related to the hydrograph of the nearest gauging station and transformed into discharge data. The occurrence and duration of inundations at different periods were derived from the hydrograph of the respective year. Waterbodies were categorized after the mean of days per year inundated in the past 50 years (1 = 365; 2 = <365-100; 3 = < 100-50; 4 = <50-25; 5 = <25 days year<sup>-1</sup>). The surface area of the waterbodies and their distance to the channel (measured as the inundation pathway at floods of different intensity) were estimated from GIS-Maps. Depths and the estimated cover percentage of submerged and flooded riparian (helophytes, willows) vegetation in a radius of approximately one meter around the anode were determined at each sampling point. Temperature data of the River Rhine were received from a bilateral measuring station situated at the border to the Netherlands (Bimmen-Lobith). The hydrological character was categorized as 0) ephemeral (water bodies desiccate in almost every year a few weeks or months after inundation), 1) semi-perennial (water

bodies with a shrinkage in area of >30% during the isolation phase; fish kills and/or drought in particular summers) or 2) perennial (water bodies that exhibit a minor shrinkage in area during the isolation phase).

18 species (total 107,150 specimens) in the four-year dataset were present in each annual cycle and occurred in at least 5 different waterbodies, and were thus taken into account for statistical analysis of spatio-temporal floodplain habitat utilization (Table 2). All other (20 species and two cyprinid hybrids) species which does not match the criteria, as well as rare lifetime-stages that have to be expected to act as outliers in multivariate statistical analysis, were eliminated from the dataset.

In preparation to all statistical procedures the dependent (abundance and CPUE-data) and independent non-categorical variables, were  $\log_{10}(n+1)$  or arcsine-square root (in case of proportional data) transformed to approximate normal distributions. For multivariate procedures, a samples-by-species and a samples-by-variables matrix was generated. The first matrix contained the mean of the ecospecies abundance values per site (waterbody\*sampling date) and the second matrix the respective site-specific variables (see Table 3). The environmental variables were subjected to a Principal Component Analysis (PCA) using a correlation matrix, in order to explore correlations among variables and directions of gradients.

After creating a Bray-Curtis-similarity matrix of the ecospecies abundance data, non metric multidimensional scaling (NMS) was used to identify a) relationships between hydrological scenarios and communities and b) patterns in spatio-temporal habitat utilization of ecospecies. NMS is an ordination method that is well suited to data that are on non-normal scales and heterogeneous datasets (Legendre and Legendre 1998). Since NMS is based on ranked distances, it tends to linearise the relation between environmental and sociological distance. We used random starting coordinates and 250 runs on the original data-matrix and 250 iterations of the randomised data in order to search for a ranking and optimal placement of samples in multidimensional space until the stress was lowest (in terms of departure from monotonicity in the relationships between the dissimilarity in the original configuration of samples and in the reduced-dimensional ordination space) (McCune, Grace, and Urban 2002). The solution with the lowest stress was used for the configuration of samples and weighted averaging was then used to project the position of the ecospecies in ordination space. The scores of species represented by more than one stage were determined by calculating its gravity centres in the multi-dimensional ordination

space. Pearson correlations of the environmental variables with NMS-Axes were used to explore hydrological and environmental gradients, which were considered to explain ecospecies ordination significantly, when  $r^2$  was  $> 0.1$ . The relationship of species coordinates on NMS-axes to life-history strategies was tested by means of two-sample  $t$ -tests. Bivariate relationships of species scores on NMS-axes with species life-history traits and feeding characteristics were analysed using Pearson correlations ( $r_p$ ) if life-history variables were on a interval scale or by Spearman's rank correlation ( $r_s$ ) in case of categorical variables, respectively.

Table 3: Descriptions and units of the thirteen independent variables used to explore relationships of species habitat utilisation.

Variable	factor/unit	Comments
Annual cycle	1	1 <sup>st</sup> May 2002 - 31 <sup>st</sup> March 2003
	2	1 <sup>st</sup> April 2003 - 31 <sup>st</sup> March 2004
	3	1 <sup>st</sup> April 2004 - 31 <sup>st</sup> March 2005
	4	1 <sup>st</sup> April 2005 - 31 <sup>st</sup> November 2006
period	1	spawning (1 <sup>st</sup> April - 30 <sup>th</sup> June)
	2	growth (1 <sup>st</sup> July - 31 <sup>st</sup> October)
	3	winter (1 <sup>st</sup> November - 31 <sup>st</sup> March)
hydrological Character	0	ephemeral
	1	semi-perennial
	2	perennial
droulnun	0/1	drought prior to last inundation
indirectly inundated	0/1	inundated via other waterbodies; no immediate contact with the river
_days	log (days)	Days inundated per period-specific inundation
isolation days	log (days)	number of days from sampling since the last inundation
distance	log (m)	Distance to river
area	log (ha)	waterbody surface area
helophyte cover	arcsinesqrt (Proportion)	Proportion of waterbody area covered by flooded Helophytes (mean of sample records)
submerged vegetation cover	arcsinesqrt (Proportion)	Proportion of waterbody area covered by submerged vegetation (mean of sample records)
mean depth	log (m)	mean of samples records

The relationship of seasonal differences in ecospecies abundance to period-specific inundation events was tested by one-way-ANOVA. Data were designated to inundation categories (1 = not inundated perennial waterbodies, 2 = inundated perennial waterbodies; 3 = inundated ephemeral waterbodies (drought prior to the

respective inundation), 4 = permanently connected waterbodies) and sub-periods were used for the adjustment of weighted least squares per period-specific comparison. Due to expected differences caused by inundations during the spawning period from waterbodies that remained isolated since winter, an additional category (inundated during the spawning period) was defined for the period-specific comparisons following the first spawning sub-period. Since inundations after the spawning period occurred almost exclusively in the second sub-periods, only one comparison was made for the growth and winter period. Due to heteroscedasticity caused by the high number of null-samples in the datasets post-hoc-comparisons were confirmed by Dunnett-T3 test statistics after applying a *Bonferroni* correction.

The differences of the estimated marginal means (reference category: permanently connected) of the period-specific comparisons of abundance for each species lifetime-stage were used to create a categorical matrix (1 = significant positive differences; 0 = no significant differences; -1 significant negative differences; -2 = ecospecies absent in the respective category). A Euclidian-distance matrix was generated from this matrix and afterwards submitted to a cluster analysis using complete linkages in order to identify groups of species with similar responses to period-specific inundations. Pearson correlations of mean YOY and adult abundance within non-permanently connected waterbodies during the spawning period were calculated in order to estimate whether recruitment occurs within the floodplain.

Seasonal differences in the CPUE of ecospecies in the anchored stow-net in the river channel were analysed by multiple linear regressions. We only used ecospecies that were present in floodplain waterbodies, which occurred in at least 1% of the total by-catch and had a frequency of occurrence of at least 0.2 in one of both years, respectively. Besides mean daily discharge ( $\text{m}^3 \text{s}^{-1}$ ), discharge trend (deviation from previous day), sampling-date, water temperature, and the proportion of inundated floodplain waterbodies (based on inundation thresholds and the hydrograph of the respective years) were used as predictors, since the latter are expected to allow drawbacks about floodplain emigration. Since we only dispose over information on inundation thresholds of waterbodies in this study, we used the proportion of the total non-ephemeral waterbodies as an estimate of the total floodplain. All statistical analyses were performed with PC-Ord (version 5.12) and SPSS for Windows (Version 14.0).

## Results

### Hydrological parameters

Discharge of the River Rhine and inundation patterns differed considerably amongst annual cycles with above-average discharges only in the first annual cycle, and below-average discharges in the subsequent annual cycles (mean discharge  $\pm$  standard deviation per annual cycle 2002/03:  $2422 \pm 1155$ ; 2003/04:  $1348 \pm 771$ ; 2004/05:  $1637 \pm 559$ ; 2005/06:  $1553 \pm 709$ , Fig. 2). Winter floods caused inundations to all floodplain waterbodies studied, except in annual cycles 2003/04 and 2004/05, when only the most isolated waterbodies were not inundated. Moreover, only strong winter floods cause lotic conditions within the floodplain, however, in the study period this only applied to waterbodies of the categories  $\leq 4$  ( $<50$ -25 days year<sup>-1</sup>). Floods occurring during the spawning period were generally less excessive and affected only waterbodies of the categories 2 ( $<365$ -100 days year<sup>-1</sup>) and 3, ( $<100$ -50 days year<sup>-1</sup>) except in annual cycle 2002/03, when even waterbodies of the category 4 became inundated, whereas waterbodies of the category 5 ( $<25$  days year<sup>-1</sup>) remained isolated outside of the winter period in all annual cycles. Discharge peaks occurring in the 2<sup>nd</sup> spawning sub-period and the growing period in all annual cycles affected only some waterbodies of the category 2, which have been previously affected by inundations during the first spawning sub-period. (compare Table 3 and Fig. 2 for discrimination of periods).

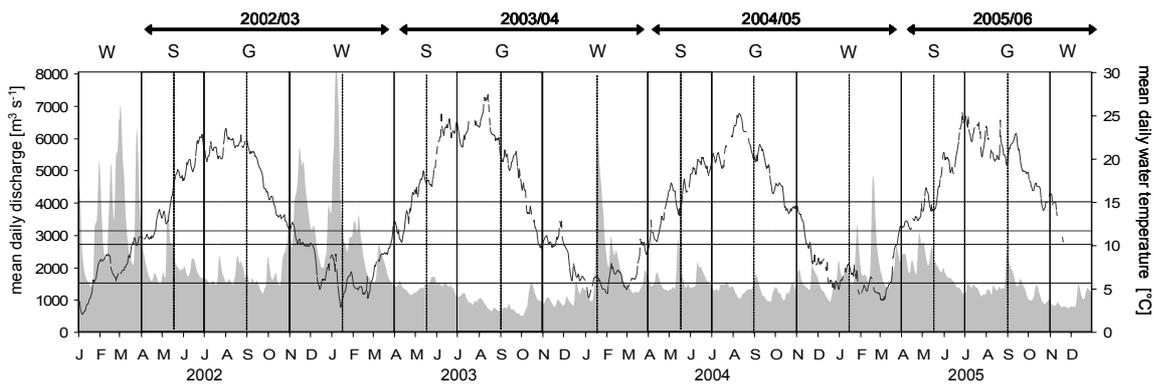


Figure 2: Hydrograph (grey area) and water temperature (dotted graph) of the River Rhine in the four annual cycles and inundation thresholds (horizontal lines) of waterbodies of different long-term inundation categories ( $<25$ ;  $>25$ -50;  $>50$ -100;  $>100$ -364 days year<sup>-1</sup>, respectively). Boxes indicate periods (S = spawning; G = growth; W = winter) of the annual cycle (horizontal double-arrows). Vertical broken lines discriminate sub-periods.

The annual cycle 2003/04 was characterized by far above average temperatures and an exceptionally low discharge of the River Rhine during the spawning and growth period, in which, with one exception none of the non-permanently connected waterbodies became inundated and all ephemeral and most semi-perennial waterbodies dried out completely. River temperatures during inundations of non-permanently connected waterbodies in either spawning sub-periods differed between the annual cycles (SP1: 2002/03: 12.3 (10.8-15.7); 2003/04: 11.7 (10.7-11.0); 2004/05: 12.5 (10.5-15.4); 2005/06: 13.7 (11.9-16.7); SP2: 2002/03: 19.5 (15.8-22.9); 2003/04: -; 2004/05: 18.5 (13.8-20.2); 2005/06: 18.2 (14.1-20.8); mean (range) °C, respectively). River temperatures during winter floods, which occurred regularly in the second half of winter, were in all years < 7°C, with lowest minima (2.9°C during the flood peak) in 2002/03.

In 2006 (analysis of anchored stow-net by-catch only) discharge peaks during the 1<sup>st</sup> spawning sub-period affected nearly all waterbodies studied in the previous annual cycles and a flood during the 2<sup>nd</sup> spawning sub-period affected even waterbodies of the 4<sup>th</sup> inundation category. The latter were subject to inundations occurring in the first half of the subsequent winter period.

#### Abundances and stage composition

In our dataset the three most abundant species *A. brama* (n = 41,324), *R. rutilus* (n = 12,803) and *B. bjoerkna* (n = 12,429) were more than fifty-fold more frequent than the least abundant *C. nasus* (n = 220) and *C. taenia* (n = 563), however inter-annual differences in abundance and stage-ratios were most pronounced in the most frequent species, in which three life-time stages could be discriminated in length frequency distributions (YOY, juveniles  $\geq 1+$ , adults, see Table 4). *C. nasus* and *Barbus barbus* occurred exclusively as YOY in the floodplain. *Aspius. aspius*, *Leuciscus cephalus*, and *L. idus* occurred in three stages, however, stage-ratios were considerably wide, due to the relative rareness of juveniles compared to YOY, as well as of adults to juveniles. In four species (*B. bjoerkna*, *Perca fluviatilis*, *R. rutilus*, *Tinca tinca*) all three lifetime-stages were present, with successively decreasing numbers from the YOY to the juvenile, and from the juvenile to the adult stage.

Table 4: Species abundance (mean  $\pm$  standard error; as numbers  $m^{-2}$ ) and stage-ratios (YOY:juvenile:adult; in numbers) per period and total numbers in the four-year dataset. In species in which only YOY and adults were discernible, stage-ratios refer to these. Asterisks denote that occurrence was restricted to connected waterbodies.

Species	2002/03			2003/04			2004/05			2005/06			total number
	S	G	W	S	G	W	S	G	W	S	G	W	
<i>Alburnus alburnus</i>	0.03±0.01 (0:1)	0.14±0.12 (1:1)	0.14±0.02 (2:1)	0.01±0.01* (10:1)	0.20±0.09* (1:1)	0.13±0.02 (2:1)	1.82±0.35 (4:1)	0.37±0.06 (10:1)	0.06±0.02 (3:1)	0.48±0.18 (1:3)	0.42±0.10 (26:1)	•	2,883 (3:1)
<i>Aspius aspius</i>	0.07±0.03 (1:0)	0.05±0.03 (1:0)	<0.01±0.00 (1:0)	<0.01±0.00* (1:0)	0.07±0.02* (26:1)	•	0.42±0.08 (28:0.3)	0.04±0.01 (13:0.8)	<0.01±0.00 (1:0)	7.47±1.27 (1:0)	0.74±0.06 (16:0.04)	•	3,698 (12:0.1)
<i>Abramis brama</i>	144.56±20.87 (16:0.01)	0.73±0.23 (8:0:1)	0.27±0.03 (9:0:1)	0.05±0.03* (1:0:1)	0.02±0.00* (1:1:1)	0.02±0.01 (1:0:5)	21.45±4.27 (95:0.1)	0.63±0.08 (21:0.1)	0.02±0.01 (1:0:2)	121.22±23.71 (13:0:0)	1.10±0.12 (22:0.1)	<0.01±0.00 (0:0:1)	41,324 (57:0.1)
<i>Barbus barbus</i>	0.01±0.01 (1:0)	0.02±0.02 (1:0)	•	<0.01±0.00* (1:0)	0.34±0.15* (1:0)	<0.01±0.00* (1:0)	3.18±1.20 (1:0)	0.19±0.11 (1:0)	•	•	0.11±0.07 (1:0)	•	2,092 (1:0)
<i>Blacca hyporkna</i>	0.55±0.15 (44:70)	3.48±1.05 (12:0.1)	0.34±0.05 (13:0.4)	<0.01±0.00* (0:1)	0.13±0.08* (75:4)	0.01±0.00 (0:1)	9.15±2.13 (29:0.2)	5.68±0.74 (20:0.1)	0.48±0.12 (42:0.1)	3.08±1.49 (35:2)	0.94±0.15 (42:3)	0.04±0.04 (1:0)	12,492 (35:1)
<i>Cyprinus carpio</i>	5.84±2.04 (47:0:1)	0.03±0.03 (1:0)	0.04±0.02 (5:0:1)	0.12±0.07 (1:0)	0.27±0.03 (75:0.1)	<0.01±0.00 (9:1)	9.31±1.62 (15:0.01)	0.73±0.08 (81:0:1)	0.11±0.02 (24:0:1)	5.68±1.47 (62:0:1)	0.16±0.03 (23:0.1)	•	6,826 (13:0.01)
<i>Chondrostoma nasus</i>	•	•	<0.01±0.00 (1:0)	<0.01±0.00* (1:0)	<0.01±0.00* (1:0)	<0.01±0.00* (1:0)	0.29±0.10 (1:0)	0.01±0.00 (1:0)	•	0.04±0.02 (1:0)	•	•	220 (1:0)
<i>Cobitis taenia</i>	<0.01±0.00 (0:1)	0.05±0.03 (1:2)	0.01±0.00 (2:1)	0.05±0.02 (1:4)	0.05±0.01 (2:1)	0.02±0.00 (1:1)	0.04±0.01 (1:1)	0.09±0.01 (3:1)	<0.01±0.00 (1:1)	0.02±0.01 (1:1)	0.10±0.01 (2:1)	0.01±0.01 (1:0)	563 (2:1)
<i>Gasterosteus aculeatus</i>	0.28±0.07 (3:1)	0.03±0.03 (1:1)	0.04±0.01 (1:1)	0.07±0.04 (3:1)	0.10±0.02 (23:1)	0.03±0.00 (1:1)	0.32±0.06 (8:1)	0.38±0.05 (20:1)	0.04±0.01 (2:1)	0.47±0.13 (50:1)	0.40±0.07 (62:1)	•	1,492 (9:1)
<i>Leuciscus delinca</i>	0.34±0.14 (1:1)	0.18±0.14 (7:1)	0.05±0.02 (7:1)	•	0.44±0.12 (8:1)	0.04±0.02 (8:1)	0.31±0.09 (7:1)	0.55±0.08 (14:1)	0.05±0.02 (2:1)	0.31±0.14 (10:1)	0.44±0.08 (15:1)	•	1,766 (9:1)
<i>Leuciscus cephalus</i>	<0.01±0.00 (0:1)	0.30±0.17 (1:0)	0.03±0.01 (82:8)	0.01±0.01* (14:1)	0.29±0.12* (14:1)	0.03±0.01 (15:1)	0.51±0.09 (10:1)	0.29±0.04 (11:1)	0.01±0.00 (12:1)	0.03±0.01 (1:0)	0.25±0.05 (82:1)	•	1,271 (12:0.9)
<i>Leuciscus idus</i>	0.06±0.02 (12:0)	0.03±0.02 (1:0)	<0.01±0.00 (3:1)	<0.01±0.00* (1:0)	0.02±0.01* (1:0)	<0.01±0.00 (1:3)	0.14±0.02 (12:0)	0.03±0.01 (44:1)	<0.01±0.00 (1:0)	1.39±0.34 (1:0)	0.41±0.05 (88:0.1)	0.15±0.13 (1:0)	1,437 (71:0.5)
<i>Perca fluviatilis</i>	0.37±0.20 (2:1)	0.53±0.17 (1:0)	0.08±0.01 (26:1)	0.79±0.17 (3:1)	0.42±0.04 (17:1)	0.02±0.00 (1:0)	0.90±0.19 (94:6)	0.25±0.03 (22:0.5)	0.06±0.01 (11:0)	1.84±0.36 (12:0.2)	0.84±0.06 (23:0.3)	0.14±0.06 (1:0)	6,033 (11:0.5)
<i>Pseudorasbora parva</i>	0.16±0.09 (1:1)	•	0.02±0.01 (2:1)	0.05±0.03 (0:1)	0.07±0.02 (3:1)	0.03±0.01 (19:1)	0.88±0.19 (8:1)	1.29±0.15 (10:1)	0.51±0.07 (10:1)	4.00±1.03 (27:1)	1.93±0.23 (20:1)	•	3,684 (12:1)
<i>Rutilus rutilus</i>	1.21±0.18 (13:18)	0.50±0.15 (1:1)	0.49±0.05 (12:2)	0.34±0.07 (82:12)	0.29±0.04 (45:2)	0.08±0.01 (20:1)	5.83±0.73 (71:2)	0.79±0.07 (36:1)	0.04±0.01 (27:5)	21.54±4.71 (9:1)	0.77±0.06 (11:0.4)	0.16±0.09 (10:1)	12,807 (14:1)
<i>Rhodeus amarus</i>	0.43±0.14 (1:1)	1.29±0.54 (14:1)	0.08±0.01 (3:1)	0.17±0.12 (1:1)	0.37±0.05 (8:1)	0.08±0.03 (8:1)	0.86±0.19 (7:1)	1.61±0.19 (44:1)	0.06±0.01 (25:1)	2.89±1.07 (4:1)	1.99±0.23 (15:1)	0.03±0.03 (0:1)	5,787 (12:1)
<i>Sander lucioperca</i>	0.01±0.01 (1:0)	0.07±0.03 (1:0)	<0.01±0.00 (3:1)	0.04±0.02 (4:1)	0.31±0.02 (32:0.1)	0.01±0.00 (2:0)	0.26±0.07 (53:0.5)	0.10±0.01 (14:0)	0.02±0.00 (18:0)	0.79±0.16 (59:0)	0.06±0.01 (55:1)	•	2,113 (11:0)
<i>Tinca tinca</i>	0.01±0.01 (1:1)	0.25±0.14 (4:0)	0.02±0.00 (12:2)	1.01±0.35 (28:1)	0.13±0.02 (59:2)	0.05±0.01 (62:1)	0.06±0.01 (1:17)	0.06±0.01 (6:6)	<0.01±0.00 (1:0)	0.04±0.02 (1:7)	0.09±0.02 (16:6)	0.03±0.03 (1:0)	662 (15:5)

In *A. brama*, *Cyprinus carpio* and *Sander lucioperca* wide ratios between the YOY to the juvenile stage existed, in contrast to a narrower ratio between the YOY to the adult stage, indicating low abundances of the juvenile stage. *Alburnus alburnus*, *C. taenia*, *Gasterosteus aculeatus*, *Leucaspius delineatus*, *Pseudorasbora parva* and *Rhodeus amarus* were only present in two discernible stages (YOY, adult).

Due to high numbers of larvae and early juveniles, highest abundance and widest stage-ratios occurred in the spawning periods of most annual cycles. Both parameters decreased successively during the growing and winter period, with exception of some species being only present in the YOY and adult stage. The strongest deviations from multiple-year abundance and stage-ratio patterns were observed in the annual cycle 2003/04, when abundances of many species were significantly lower and stage-ratios were narrower than in the other annual cycles. Though in this year only few waterbodies have been sampled in the spawning period, the far below recruitment (in terms of abundance and YOY to adult ratio) in most species was even apparent in the growing period. This was most pronounced in *A. brama*, and *B. bjoerkna*, whereas recruitment of other species was less negatively affected. Positive deviations from the long-term mean were only observed in *C. taenia*, and *T. tinca*. Highest recruitment in almost all species was encountered in the annual cycle 2005/06.

#### Spatio-temporal habitat utilization and life-history strategies

Samples containing similar communities (Fig. 3a) and patterns of species habitat utilisation in space and time (Fig. 3b) are considered to be displayed by different scores in ordination space. The two-dimensional solution of the non-metric dimensional scaling (NMS) explains 53.8% (Axis 1 = 23.5, Axis 2 = 30.3%) of the total variability of ecospecies abundance (final stress: 15.3). From the environmental variables matrix, only two variables were significantly and both negatively correlated ( $r_p < -0.6$ ) with Axis 1 (period:  $r^2 = 0.37$ ; days inundated in winter:  $r^2 = 0.32$ ). Negative ( $r_p < -0.4$ ) significant relationships with Axis 2 were found for the variables distance ( $r^2 = 0.14$ ), isolation days ( $r^2 = 0.34$ ) and submerged vegetation cover ( $r^2 = 0.29$ ), whereas positive ( $r_p > 0.4$ ) correlations are indicated for the number of inundation days during the first ( $r^2 = 0.31$ ) and second half ( $r^2 = 0.11$ ) of the spawning period. All other variables explained less than 10% of the variability or were correlated with axes of lower order.

The relationships amongst these after the PCA results are displayed in Fig. 3c. The duration of inundations during either sub periods of the spawning period and the growing period have similar eigenvectors on Axis 1 (34.7% explained variability). The opposite applies to the degree of isolation, the distance to the channel, the degree of interconnectivity with other waterbodies during floods and the submerged vegetation, which are hence strongly correlated with each other. Besides seasonal aspects (annual cycle, periods) Axis 2 (28.3% explained variability) displays mainly information on the waterbody characteristics.

Consequently, positions of ecospecies in NMS ordination space (Fig. 3b) are largely related to the seasonality of floodplain habitat utilization (in terms of seasonal differences in abundance) and to a gradient of connectivity. The latter is, besides spatial distance of the waterbodies to the channel, highly attributed to the occurrence and duration of inundations during the spawning period. Species lifetime-stages scores on Axis 2 increase with their relatedness to the duration of inundations during the spawning period (most positive scores indicate permanent connection). This effect is pronounced by very similar scores of samples gathered in connected waterbodies throughout the annual cycle (Fig 3a). In contrast, communities altered strongly in non-permanently connected waterbodies, depending on seasonal inundations, particularly during the spawning period and resulted in either high or low scores along axis 2, regardless their long-term frequencies of inundation. Scores along axis 1 increase with increasing differences in abundance between the periods.

Stage-scores of most species that occurred in three lifetime-stages are characterised by larger distances from each other in ordination space, which indicates more complex spatio-temporal habitat utilisation patterns of this group of species. With regard to life-history traits, these species are characterised by slow growth (i.e. low  $K$ -values), high lifetime expectation, large and late maturing, however highly fecund adults, which spawn early in the season at comparably low water temperatures and produce only one to few spawning bouts (periodic strategists, see Table 2). Their species gravity centre (SGC) scores are (with exception of *T. tinca*) significantly discriminated only along NMS-Axis 2 (two sample  $t$ -test:  $t = 2.877$ ;  $P = 0.012$ , Axis 1:  $t = 1.798$ ,  $P = 0.094$ ) from those of predominantly fast growing and less fecund species, which mature early and at small size, and produce many, but considerably smaller spawning bouts over an extended reproductive season (opportunistic strategists, Table 2).

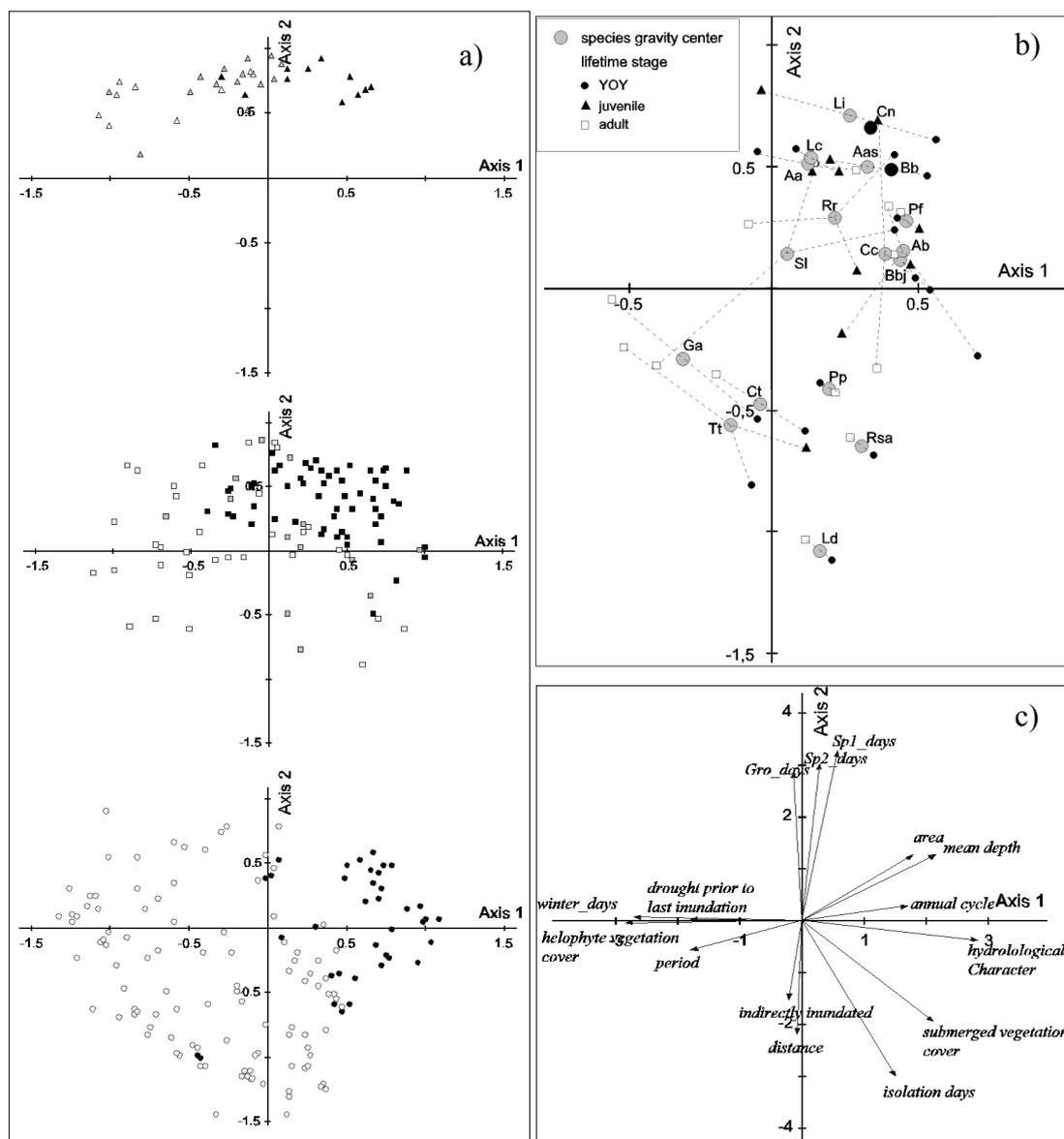


Figure 3: Ordination plots for a) NMS sample scores based on community (log-transformed abundance of species life-time stages) similarities for waterbodies of different long-term inundation categories (upper: triangles = permanently connected; centre: squares >100 days year<sup>-1</sup>; lower: circles < 100 days year<sup>-1</sup>) in the four-year dataset. Symbols filled after the last inundation occurring prior to sampling (black: in spawning period; grey: in growth period; white: in winter). b) NMS scores of species gravity-centres (SGC) and the different life-time stages calculated by weighted averaging. Broken lines indicate relationships of SGC and life-time stages. SGC scores in black refer to species only present as YOY. In species with extremely rare adult abundance (Aas, Li; see Table 2 for abbreviations) this stage has not been taken into account. c) PCA bi-plot of the environmental variables correlation matrix (see Table 3 for variables abbreviations).



Only two of the trait variables explain the position of SGC-scores along Axis 1 (longevity positively, spawning mode negatively correlated). With exception of the variables length of the spawning season, spawning temperature, egg size, trophic guild membership and the occurrence of ontogenetic diet shifts, in all further variables significant gradients occur along Axis 2 (Table 5). Furthermore, correlations among trait-variable pairs indicate the general relationship of traits associated to the extremes of the triangular life-history strategy model, e.g. positive correlations between maximum length, age and size at maturity, fecundity and final YOY size, however negative relationships with  $K$ , spawning temperature and mode, and the onset and duration of the spawning season. Although no significant relationship of the exertion of parental care with most of the variables was found, this variable was significantly correlated with NMS-Axis 2, indicating an increasing degree of parental care with decreasing connectivity.

#### Stage-specific responses towards seasonal inundations

The discrimination of species after the responses of their life-time stages (in terms of changes in abundance) towards the different inundations occurring throughout the annual cycle corresponded well to the modelled patterns of spatio-temporal habitat utilisation and life-history strategies. We identified three main groups (Fig. 4), which are identical with the commonly used habitat guilds (rheophilic, eurytopic, stagnophilic) and are further discriminated by their response on the occurrence of inundations during the spawning period and the presence of the different life-time stages in floodplain waterbodies affected by subsequent inundations.

The first main group contains exclusively species (regularly attributed as rheophilic) exhibiting features closely associated to the periodic life-history strategy, and in which YOY exclusively occurred in waterbodies affected by inundations in the spawning period. This group can be sub-discriminated into two sub-groups after the presence or absence of single life-time stages in the floodplain or to their responses to particular period-specific inundations. These sub-groups are named after their most prominent members.

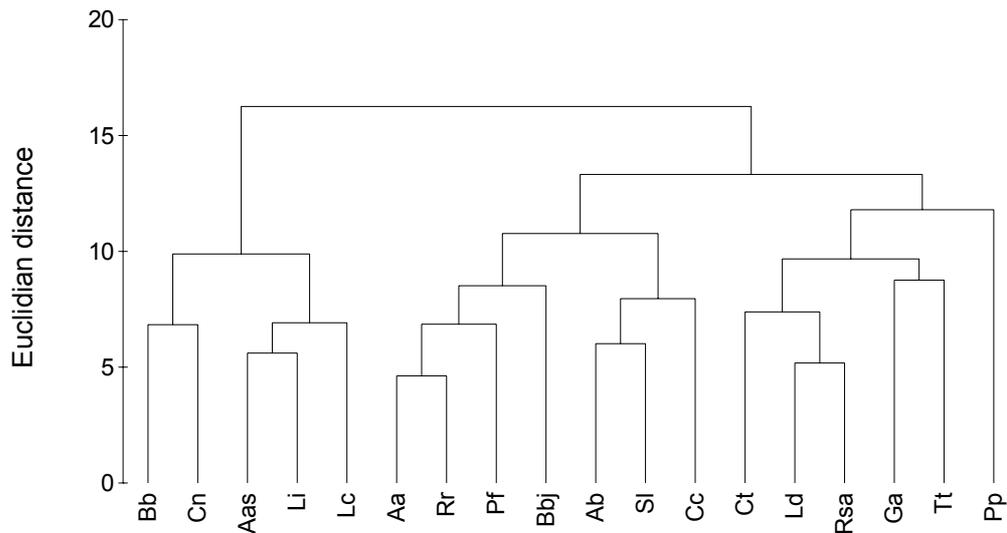


Figure 4: Dendrogram of a cluster analysis on species similarities in response to changes in abundance with regard to period-specific inundations (Table 2 for species abbreviations, see Methods for details)

- A. The *Barbus barbus*-group (also containing *C. nasus*). This group is characterised by a temporary floodplain habitat utilisation. YOY were the only life-time stage found in the floodplain.

YOY were most abundant in connected waterbodies and those inundated in either sub-periods of the spawning period. Their abundance diminished in connected waterbodies in the course of the annual cycle and with subsequent inundations in non-permanently connected waterbodies. YOY were almost absent from the floodplain in winter.

The *Aspius aspius*-group (also containing *L. cephalus*, *L. idus*). This group is discriminated from the previous by the more continuous habitat utilisation of YOY during their first year of life and the presence of juvenile stages, however, only sporadically occurring adults.

YOY abundance peaked in connected waterbodies and all kinds of waterbodies inundated during the first (*A. aspius*, *L. idus*) or second (*L. cephalus*) spawning sub-period. With exception of the latter, subsequent inundations in the growth period did not result in a further increasing YOY abundance or in significant differences to connected waterbodies. Their abundance decreased sharply during winter in all kinds of inundated waterbodies and their juveniles only infrequently occurred in non-permanently connected waterbodies in the subsequent annual cycle.

The second sub-group contains exclusively species that exhibit features closely associated to the periodic life-history strategy (with exception of *A. alburnus*) and in which YOY exclusively occurred or their abundance at latest increased significantly in waterbodies affected by inundations in the spawning period. These species are commonly designated as eurytopics. Two sub-groups can be discriminated, which differ with regard to the seasonality of habitat utilisation of particular stages.

B. The *Rutilus rutilus*-group (also containing *A. alburnus*, *P. fluviatilis*, *B. bjoerkna*). This group is characterised by a relatively constant habitat utilisation of YOY exterior of the spawning period and the presence of juvenile stages in connected more than subsequently inundated non-permanently connected waterbodies.

*R. rutilus* and *P. fluviatilis* recruit in waterbodies that remain isolated during the first half of the annual cycle, though being significantly more abundant in waterbodies affected by inundations in the first spawning sub-period. In contrast, YOY abundance of *A. alburnus* and *B. bjoerkna* peaked in waterbodies inundated in the second spawning sub-period (between mid-May and the beginning of July) and the growth period. YOY abundance of *R. rutilus* and *A. alburnus* was significantly higher in connected and ephemeral waterbodies. Inundations during the winter and growth period had no significant effect on YOY abundance within the floodplain in none of these species. Abundance of older stages decreased in non-permanently connected waterbodies with repeated inundations and was categorically highest in the connected waterbodies. Simultaneous peaks of YOY and adult abundance in non-permanently connected waterbodies during the spawning periods were observed in *P. fluviatilis* ( $r_p = 0.298$ ,  $P = 0.037$ ) and *B. bjoerkna* ( $r_p = 0.445$ ,  $P = 0.001$ ) but not in *A. alburnus* ( $r_p = -0.050$ ,  $P = 0.726$ ) and *R. rutilus* ( $r_p = 0.043$ ,  $P = 0.766$ ). The latter indicates that spawning even or predominantly occurred outside non-permanently connected waterbodies.

C. The *Abramis brama*-group (also containing *C. carpio* and *S. lucioperca*). This group is discriminated from the previous by a more temporary habitat utilisation of YOY in non-permanently connected waterbodies, where juveniles are rare, but resident adult stocks occur even in more isolated waterbodies.

YOY and adults of these species were significantly more abundant in the non-permanently connected waterbodies and their abundance increased significantly with inundations occurring in the first (*A. brama*, *S. lucioperca*) and/or second spawning sub-period (*C. carpio*) and, with exception of *S. lucioperca*, particularly in ephemeral waterbodies. Adults of these species had resident stocks and recruitment even occurred in waterbodies, which remain isolated in the spawning period (except *A. brama*). YOY abundance in non-permanently connected waterbodies during the spawning period was significantly related to the abundance of adults and simultaneous peaks of both stages were found to occur during inundations in the spawning period (*A. brama*:  $r_p = 0.478$ ,  $P < 0.0001$ ; *C. carpio*:  $r_p = 0.489$ ,  $P < 0.0001$ ; *S. lucioperca*:  $r_p = 0.389$ ,  $P = 0.005$ ). However, inundations during the growth and winter period caused significant decreases of YOY abundance and their juveniles are regularly absent from the floodplain after winter floods.

The third main-group almost exclusively contained species exhibiting features most closely associated to the opportunistic life-history strategy, which are commonly referred to be stagnophilic species. Although adults even occurred in more frequently inundated waterbodies, recruitment is widely restricted to waterbodies which remain isolated during the first half of the annual cycle and YOY abundance increased significantly with the degree of isolation.

Regularly their lifetime-stages were in all periods significantly higher abundant in waterbodies that have not been subject to inundations during either spawning sub-periods (exceptions *C. taenia*, *G. aculeatus*, *R. amarus*). Furthermore, their abundance decreased significantly the more frequently the waterbodies became inundated and rarely occurred in ephemeral or connected waterbodies, except after winter floods. The abundance of YOY during the spawning period was positively related to the abundance of adults (*G. aculeatus*:  $r_p = 0.694$ ,  $P < 0.0001$ ; *P. parva*:  $r_p = 0.983$ ,  $P < 0.0001$ ; *C. taenia*:  $r_p = 0.966$ ,  $P < 0.0001$ ; *R. amarus*:  $r_p = 0.852$ ,  $P < 0.0001$ ; *L. delineatus*:  $r_p = 0.898$ ,  $P < 0.0001$ , *T. tinca*:  $r_p = 0.352$ ,  $P = 0.011$ ). Adults of *P. parva* more frequently occurred in ephemeral waterbodies inundated in the first half of the annual cycle, and the species is therefore discriminated from the other species of this group. However, no successful recruitment was observed outside remote perennial waterbodies.

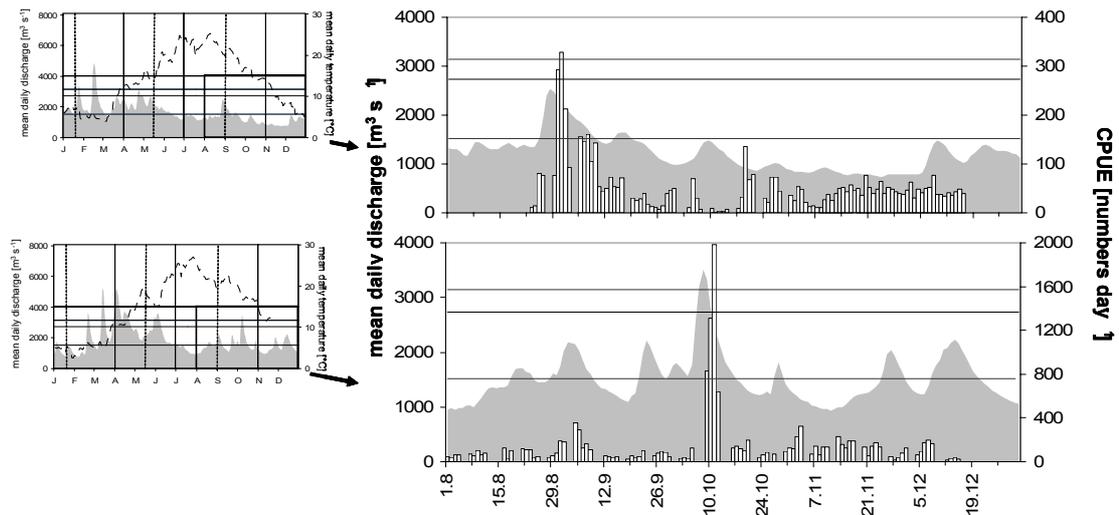


Figure 5: Hydrograph (grey area) and temperatures (dotted graph) of the River Rhine (left) and relationships of YOY fish CPUE values (columns) and the hydrograph in autumn and winter of the years 2005 and 2006 (right). Vertical lines indicate the inundation thresholds of inundation categories 2 till 4. CPUE values refer to the sum of the seven species given in Table 6

Only seven species present in the floodplain, occurred in the by-catch of the anchored stow-net in the river channel in sufficient numbers to explore relationships between CPUE and floodplain inundations occurring in autumn and winter. In 2005 and 2006, 91.8 and 93.4% of the total by-catch, respectively, accounts for these ecospecies, which were exclusively YOY stages (Table 6). CPUE in both years peaked with retreating floods from the floodplain. Nevertheless, CPUE peaks in 2006 were 6-fold higher than in 2005 and occurred after waterbodies of the inundation category 4 became inundated for the first time after the spawning period. However, multiple linear regressions indicate positive significant relationships of CPUE and the proportion of inundated waterbodies only for *A. brama*, *C. carpio* and *S. lucioperca*, whereas river discharge was the strongest predictor in *A. Aspius*, *L. idus*, *P. fluviatilis* and *R. rutilus*. Sampling date and water temperature were the only further variables that explained the variation in CPUE data, however, not significantly in all species.

Table 6: CPUE (mean  $\pm$  standard deviation) percentage in the by-catch of the anchored stow-net in the River Rhine between the beginning of August and the end of December in the years 2005 and 2006 and linear regressions results of CPUE data (log-transformed) of seven YOY species versus five independent variables.

				linear regression						
CPUE		Percentage of total by-catch		variable	$\beta$	$t$	$P$	Model		
2005	2006	2005	2006					$r^2$	$F$	$P$
<i>Abramis brama</i>										
43.6 $\pm$ 43.3	123.5 $\pm$ 245.6	74.7	76.6	sampling date	-0.0001	-0.252	0.852	0.955	536.235	< 0.0001
				temperature	-0.011	-1.163	0.247			
				discharge	0.482	1.128	0.261			
				discharge trend	-0.0001	-0.957	0.340			
				proportion of waterbodies inundated	3.225	3.831	< 0.0001			
<i>Aspius aspius</i>										
2.5 $\pm$ 5.1	1.3 $\pm$ 1.7	4.3	0.8	sampling date	-0.0001	-7.127	< 0.0001	0.517	26.727	< 0.0001
				temperature	-0.027	-3.300	0.001			
				discharge	2.191	6.814	< 0.0001			
				discharge trend	0.0001	0.024	0.981			
				proportion of waterbodies inundated	-1.438	-2.272	0.025			
<i>Cyprinus carpio</i>										
0.8 $\pm$ 2.5	1.7 $\pm$ 4.3	1.5	1.0	sampling date	-0.0001	-6.262	< 0.0001	0.814	109.532	< 0.0001
				temperature	-0.006	-1.385	0.168			
				discharge	0.877	4.668	< 0.0001			
				discharge trend	-0.001	-7.068	< 0.0001			
				proportion of waterbodies inundated	2.675	7.236	< 0.0001			
<i>Leuciscus idus</i>										
0.01 $\pm$ 0.1	5.0 $\pm$ 8.0	0.1	3.0	sampling date	-0.0001	-4.696	< 0.0001	0.533	29.206	< 0.0001
				temperature	-0.012	-1.404	0.162			
				discharge	1.470	4.021	< 0.0001			
				discharge trend	-0.0001	-1.234	0.219			
				proportion of waterbodies inundated	1.272	1.768	0.076			
<i>Perca fluviatilis</i>										
2.6 $\pm$ 4.0	7.0 $\pm$ 9.1	4.5	4.4	sampling date	-0.0001	-5.282	< 0.0001	0.712	61.904	< 0.0001
				temperature	-0.027	-2.719	0.007			
				discharge	2.265	5.172	< 0.0001			
				discharge trend	0.0001	0.060	0.952			
				proportion of waterbodies inundated	-0.388	-0.450	0.654			
<i>Rutilus rutilus</i>										
2.5 $\pm$ 3.4	8.5 $\pm$ 18.0	4.4	5.2	sampling date	-0.0001	-3.898	< 0.0001	0.589	35.754	< 0.0001
				temperature	-0.062	-6.054	< 0.0001			
				discharge	2.035	4.521	< 0.0001			
				discharge trend	0.0001	0.560	0.576			
				proportion of waterbodies inundated	-1.691	-1.909	0.058			
<i>Sander lucioperca</i>										
1.3 $\pm$ 2.8	2.4 $\pm$ 2.3	2.3	2.4	sampling date	-0.0001	-3.075	0.003	0.717	63.246	< 0.0001
				temperature	0.034	4.892	< 0.0001			
				discharge	0.743	2.466	0.016			
				discharge trend	0.0001	0.448	0.655			
				proportion of waterbodies inundated	0.899	2.586	< 0.0001			

## Discussion

For floodplain rivers with predictable flood regimes, the flood-pulse-concept (FPC, Junk *et al.* 1989) is considered to allow predictions upon recruitment of species, as long as floods are coupled with increases in water temperature, or typical photoperiods and reproductive adaptations of species towards the discharge regime are to expect. Zeug and Winemiller (2007) demonstrated that reproductive activities in terms of increases of the gonadosomatic index in species inhabiting temperate floodplain rivers are related to the long-term hydrograph, providing hints for differential reproductive adaptations of species towards the seasonality of high and low flow conditions.

### The significance of seasonal inundations for recruitment

In our study, flood events occurring during the spawning period had the strongest influence on the recruitment of species and community organisation within the floodplain. We identified patterns of recruitment being significantly related to the occurrence of inundations between the beginning of April and the end of June, i.e. when water temperatures exceeded a temperature threshold of at least 10°C, which is considered to be at least required for most potamal species to spawn (Alabaster and Lloyd 1982; Mann 1996; Pinder 2001). The significance of the coincidence of inundations and species-specific optimum temperature conditions for spawning is stressed, when comparing the effects on recruitment of inundations occurring later in the season that resulted in significantly higher numbers of YOY in a range of species spawning at higher temperatures (e.g., *A. alburnus*, *B. bjoerkna*, *L. cephalus*). Only in these species, inundations occurring during the summer months, (the growth period after our definition), caused a protracted occurrences of early larvae in the floodplain, however they were absent when inundations occurred at lower temperatures than required. Repeated inundations at higher temperatures than required for spawning, did not cause significant increases in YOY abundance in most earlier spawners (e.g. *A. brama*, *S. lucioperca*,) or had negligible effects (*A. aspius*, *P. fluviatilis*). In contrast, YOY of *R. rutilus* increased after almost all period-specific inundations, an observation which is clearly decoupled from spawning activity. The seasonal sequence of species spawning activities within the Rhine's floodplain has been previously described by Molls (1999) and Korte (1999), who documented temperature-dependent lateral spawning migrations from the river into oxbows

during several flood-events occurring between April and June and subsequent spawning for *R. rutilus*, *A. brama*, *C. carpio* and *B. bjoerka* (in this sequence). With exception of *R. rutilus*, our data suggests immigrations of adults and spawning within the floodplain for the same species, as derived from synchronous peaks in abundance of adults and YOY, what was particularly pronounced in ephemeral waterbodies, which most likely represent the “aquatic-terrestrial transition zone” (Junk *et al.* 1989).

YOY abundance of further species in the floodplain was promoted by inundations occurring during their spawning seasons, however, was apparently decoupled from lateral spawning migrations of adults and spawning within the floodplain. Spawning of rheophilic species, like *B. barbatus* and *A. aspius* is restricted to lotic habitats (gravel beds exposed to swift currents) (Balon 1975; Mann 1996; Winter and Fredrich 2003; Fredrich 2003). After hatching or emergence larvae drift with the current in order to reach their shallow lentic nursery areas close to the bank (Bardonnnet 2001). Accordingly early developmental stages have been found to be abundant in drift-studies carried out in large Rivers (e.g., Zitek, Schmutz, and Ploner 2004). Thus, massive larval peaks of these rheophilic species in inundated floodplain waterbodies are most probably attributed to a displacement from channel-habitats with intruding floods. Our data suggests the same for YOY of *A. alburnus* and *R. rutilus*. YOY of those and rheophilic species have been demonstrated to be highly abundant in channel habitats of the Lower Rhine, regardless the discharge conditions during the spawning period (Staas 2000). In contrast YOY of e.g. *A. brama*, *B. bjoerkna* and *C. carpio* infrequently occur along the banks of the river (Staas 1997; Staas 2000), which underlines the relative importance of floodplain inundation for population maintenance for these species.

When there were no inundations in the spawning period (e.g., 2003), recruitment within non-permanently connected waterbodies either failed completely (*A. brama*, *B. bjoerkna*, *A. alburnus*, *A. aspius*, *B. barbatus*, *C. nasus*, *L. cephalus*, *L. leuciscus*) or was heavily impaired (*R. rutilus*). Nevertheless, this does not apply to connected waterbodies, in which probably spawning might take place, but also permanent exchanges of fish with the channel are to expect (Penczak *et al.* 2003; Hohausova, Copp, and Jankovsky 2003). Though being significantly more abundant in temporarily inundated rather than in connected waterbodies, recruitment of *C. carpio*, *P. fluviatilis* and *S. lucioperca* in the isolated waterbodies in 2003 was not

significantly different from the other years in our study, which indicates that these species exhibit more flexible recruitment strategies, e.g., by either immigrating into the floodplain and spawning on freshly flooded vegetation or recruiting from resident adult stocks in isolated waterbodies with dense aquatic vegetation, as found for *C. carpio*. The latter strategy was exhibited by almost all small sized species (*C. taenia*, *G. aculeatus*, *L. delineatus*, *P. parva*, *R. amarus*) and *T. tinca* and supported high recruitment even in 2003. For these species inundations during the spawning period have obvious detrimental effects on recruitment and YOY are furthermore entirely absent from channel habitats (Staas 1997; Staas 2000)

#### Life-history strategy-related patterns of recruitment

The observed patterns of recruitment and inter-annual variance were closely related to different life-history strategies identified after the trait characteristics of the species in our study. Slow growing species, with predominantly large size and late maturing, however highly fecund adults, early spawning seasons and only few spawning bouts per season, are most closely associated to the periodic life-history strategy (Winemiller and Rose 1992). Although, some of our species exhibited intermediate characteristics, e.g. prolonged reproductive seasons, multiple spawning bouts and small sized YOY at the end of the first growing period (e.g. *B. bjoerkna*, *L. cephalus*), YOY abundance in the floodplain was significantly related to inundations occurring synchronously or immediately after the required temperatures for spawning have been fulfilled. This observation is in accordance to the predictions of the life-history theory after Winemiller and Rose (1992) and even reflects those of the FPC (Junk et al 1989, Bayley 1991, Junk 1999). One central prediction of the life-history theory is that periodic strategists delay maturity until they are large enough to produce large numbers of small eggs to place them directly in most favourable habitats in order to enhance growth and survival of the offspring (floodplain spawners) or at least to synchronise spawning with favourable periods within the temporal cycle of the environment (riverine spawners). Their early spawning seasons provide their offspring, when entering the floodplain, with the opportunity to exploit the onset of high primary and secondary production within freshly inundated waterbodies and to yield substantial higher growth rates, which is supported by higher final abundances and lengths attained by YOY at the end of the growing season. However, our findings also point clearly to the disadvantages

associated with the periodic strategy, particularly in species that have strongly adapted their spawning activity to the long-term hydrograph and particularly when undertaking lateral spawning migrations in order to spawn on flooded vegetation within the floodplain. We could demonstrate that recruitment failed, when these conditions were not fulfilled. Moreover, this behaviour may result in massive mortalities and potential detriments to the population, i.e. losses of eggs and larvae due to a rapidly declining hydrograph (Scharbert and Greven 2002), or when fish immigrate into ephemeral waterbodies that become immediately disconnected from the river and desiccate soon afterwards. In the pristine situation the magnitude of floods at the lower Rhine was appreciably lower, however their duration prolonged (Quick 2004). Thus, the placement of eggs in recently flooded habitats with dense helophyte cover probably involved high recruitment success, which is, however, no longer the case after river correction took place and hydroperiods became shortened (Buijse *et al.* 2002). Deviations from the long-term flood patterns, as occurring in 2003, on one hand hampered adults to enter the floodplain and moreover caused that the riparian vegetation along the shorelines remained unflooded, which is, despite they accommodated resident adult stocks, the most probable cause for failing recruitment in all of our waterbodies in 2003.

On the contrary, fast growing species that mature early and at small size, with a later but prolonged spawning season and many spawning bouts (most typical characteristics of the opportunistic life-history strategy after Winemiller and Rose 1992), had the highest recruitment in waterbodies remaining unaffected by inundations during the first half of the annual cycle. Consequently, these species have adopted their recruitment to low flow periods and a higher probability of the floodplain to remain isolated (Humphries *et al.* 1999), which have been demonstrated to favour particularly recruitment of equilibrium strategists (Zeug and Winemiller 2007). Indeed, the species found to predominantly recruit in most isolated waterbodies that become only inundated in winter, exhibit intermediate characteristics of opportunistic and equilibrium strategists, particularly due to a comparably high degree of parental care. However, none of the species in our study exhibits further features typically for the equilibrium life-history strategy (small or medium sized species, low fecundity, late maturation, prolonged length of breeding season, producing large eggs (Winemiller and Rose 1992). This confirms that

European freshwater species exhibit a more restricted range of styles within life-history compared to North American fish (Blanck *et al.* 2007).

In contrast to winter floods, inundations during spring and summer, are associated to a massive increase of adult and larval abundance, which is frequently accompanied by an increase of eutrophication and turbidity caused by benthivorous and planktivorous fish (Breukelaar *et al.* 1994; Jeppesen *et al.* 1996) and involves detrimental conditions for the stocks of aquatic plants (Van Geest *et al.* 2003; Roozen *et al.* 2003). Consequently, inundations during the first half of the annual cycle imply possible direct and indirect disadvantages to the small sized and, with regard to their diet, less specialised (see Table 2) opportunistic species: by either competition for food and an increased risk of becoming predated by larger fish (Winemiller and Rose 1992) and an impairment of habitat requirements. Most of these species strictly require aquatic plants for the deposition of their eggs or nest building (phytophilous and ariadnophilous spawners, after Balon 1975), which provide shelter even for older stages.

These preconditions might explain the observed inter-annual shifts of communities dominated by extremes of either endpoint strategies, particularly in waterbodies with intermediate to low long-term frequencies of inundations, and depending on whether inundations during the spawning period occurred and thus deciding upon which strategists prevails upon the opposite. In the first case, YOY communities were dominated by *A. brama* and adult communities by adults of this species. In the same waterbodies, when not inundated in the consecutive annual cycle and, even more pronounced when the resident adult stock suffered mortalities during the previous year, communities were dominated by YOY and adults of *L. delineatus*, *G. aculeatus*, or *P. parva*. However, their stocks became almost extinct, when inundations occurred in the spawning period of the subsequent year and were substituted by species found to depend on inundations during the spawning period. Consequently, at least species most closely associated to endpoints of the opportunistic strategy, yielded highest recruitment in the most isolated waterbodies, particularly when these remained isolated throughout the winter (e.g., in the winter 2004/05). However, we also found less extreme responses towards spring and summer inundations in other opportunistic strategists, e.g. *R. amarus*. Their recruitment has been demonstrated to be, besides habitat characteristics and abundance of predators, strongly related to the abundance of unionids (Smith,

Reynolds, and Sutherland 2000), as adults of this species place their eggs in the gill chamber of unionid mussels, from which the larvae emerge at a size and developmental stage at which they are less susceptible to predation and being more able to compete with other species. A more balanced co-existence of both extremes of the endpoint strategies was only observed in remote and not directly inundated waterbodies, in which, though being inundated in spring, YOY abundance of periodic strategists was appreciably lower than in waterbodies situated closer to the river, and the sizes of YOY were similar to those of opportunistic species.

#### Patterns of spatio-temporal habitat utilisation

We identified large differences in terms of the seasonality of floodplain habitat utilisation, on one hand amongst life-history strategies, and on the other hand amongst species of the same habitat guilds (Schiemer and Waidbacher 1992), particularly in YOY. Obviously, the observed patterns seem to be size-related. Almost all species most closely associated with the opportunistic life-history strategy (exception *A. alburnus*) and additionally *T. tinca* have been bound to almost identical and most remote waterbodies. This behaviour is identical with what Schiemer and Waidbacher (1992) proposed for stagnophilic species. However, their early life-time stages more frequently occurred in all types of floodplain waters after winter floods (particularly ephemeral waterbodies). Since this pattern consistently occurred during the course of our study and was most pronounced after years in which strong year-classes were produced (e.g. *T. tinca* in 2003), it most likely serves their dispersion across the floodplain and probably aims on the colonisation of new habitats appropriate for recruitment. It can be argued that their dispersion during winter floods might have accidental causes. Due to their small size they are considered to have disadvantages to maintain their position in the current compared to larger specimens. This is expected to be much more pronounced during winter floods, which involve higher currents and considerably lower temperatures. Such conditions additionally reduce swimming capabilities (see Wolter and Arlinghaus 2003). However, no comparable pattern of dispersion was evident for floods occurring in the first half of the annual cycle, providing hints that the observed behaviour aims on the avoidance of competition with faster growing species, which are more associated to a higher degree of connectivity.

A positive relationship between the size attained at the end of the growing season and the duration of floodplain habitat utilisation was evident in YOY of further species. Most species which remained relatively small after their first summer (e.g. *B. bjoerkna*, *L. cephalus*, *A. alburnus*) inhabited the floodplain at least until or throughout the first winter. Although attaining considerable larger sizes, a significantly decreasing abundance occurred not until inundations in winter (rheophilics like *A. aspius* and *L. idus*) or in the consecutive year (eurytopics like *P. fluviatilis* and *R. rutilus*), although swimming capabilities have to be expected to be yet well developed to cope with lotic conditions (Wolter and Arlinghaus 2003). However, it can not be excluded that possible emigrants at former inundations are overbalanced by immigrants from the river (Penczak *et al.* 2003; Hohausova *et al.* 2003).

Some rheophilic and eurytopic YOY, particularly species in which ontogenetic diet shifts occur, emigrated from the floodplain at given connectivity during the first summer or at least until winter. With exception of the rheophilic species, which left the floodplain earlier and at smaller size, they attained comparably high total lengths (see Table 2) at the end of the first growing season. For rheophilic species (e.g. *B. barbuis* and *C. nasus*) ontogenetic habitat shifts have been demonstrated to be related to feeding and swimming capabilities and to expire stepwise from lentic to more lotic habitats with increasing size of the YOY (Bischoff and Freyhof 1999; Reckendorfer *et al.* 2001). Our results also indicate large-scale habitat shifts in the eurytopic species *A. brama*, *C. carpio* and *S. lucioperca*, which are displayed by sharply decreasing abundances in inundated floodplain waterbodies and synchronously increasing abundances in the channel from the end of summer onwards. Similar shifts of YOY of the same species from river banks to mid-channel habitats have been found in other lowland rivers (Wolter and Bischoff 2001). These findings are in good accordance to those of Molls (1999), who first described such complex life-cycle adaptations exemplarily for *A. brama* and addressed the ontogenetic habitat shift of YOY and juvenile to the river channel to a decrease of prey in the oxbows and to aim on the exploitation of greater resources of benthic invertebrates in the channel. Since juveniles were entirely absent from the floodplain, this behaviour probably reduces the competition with YOY in the nursery habitats and might imply benefits for population maintenance (Molls 1999; Grift 2001).

Although it is commonly argued, that floodplain lakes serve as important winter refuges for fish (Schlosser 1991), we only found slight increases of YOY abundance in ephemeral waterbodies, which had the highest structural complexity and should therefore provide suitable shelter from floods, whereas sharply decreasing abundances, were observed in most perennial waterbodies. This might be due to increasing mortalities caused by low food availability during winter, which should however mainly affect small fish with fewer lipid storages (Borcherding, Hermasch, and Murawski 2007). However, larger YOY are considered to be more appropriately sized to meet the preferences of avian predators, which frequently infest river floodplains in late autumn and winter and cause high mortalities in wintering fish (Santoul *et al.* 2004). Previous investigation carried out in the Lower Rhine area, however confirmed that juvenile and adult fish during winter were highly abundant in deep connected gravel-pits and harbours (Lelek and Köhler 1993; Molls and Neumann 1994), which were not subject to our study. These lakes are, however, apparently more suitable wintering habitats for many species than shallow waterbodies, in which mortality risks might be increased, and probably explains, why older juveniles rarely occurred in non-permanently connected waterbodies.

In conclusion, our findings demonstrate (1) how seasonal inundations affect recruitment patterns of fish communities in floodplain lakes and (2) how the complex life-cycle adaptations of a range of species that occur widespread in temperate lowland Rivers in Europe are related to seasonal inundations. Despite our study provides similar results to classifications based on ecological guilds (Schiemer and Waidbacher 1992), we found notable differences in the seasonality of floodplain habitat utilisation amongst eurytopic species, with a sub-group of species which recruitment is strongly tied to inundated floodplain habitats, and in which YOY exhibit ontogenetic habitat shifts from the floodplain to river channel. Furthermore our data on the relationship of inundations and life-history strategies gives further evidence for long-term adaptations of floodplain fishes to the long-term hydrograph (Junk *et al.* 1989; Zeug and Winemiller 2007), since we found the lateral zonation of fish communities to be highly related to the degree of connectivity during the spawning season and to favour different life-history strategies. In species most closely associated to the periodic life-history strategy, recruitment patterns follow the predictions of the FPC, whereas almost all opportunistic strategists recruit under low flow conditions. Finally, our findings point to the significance of hydrological

transversal floodplain gradients for providing diverse communities and population maintenance of different life-history strategies under a variety of hydrograph scenarios, and to possible detriments for highly adapted species in case of severe deviations from the natural hydrograph.

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**Determinants of recruitment and mortality of YOY-fish cohorts  
within floodplain lakes during the isolation phase**

**Abstract**

Young of the year (YOY) fish often require specific habitats and habitat availability is regarded as essential for the recruitment of riverine fish. River floodplain lakes provide a broad range of different habitat types, however, lake surfaces and their riparian zones may undergo marked changes within short time-frames after becoming disconnected from the river. The effects of seasonal changing habitat availability on the survival of nine YOY fishes were analysed in front of their habitat preferences, predator abundance as well as size and density related parameters. In correlation to spawning activities of the adults, larval densities of most periodic strategists (rheophilic/lithophilic and eurytopic/phytolithophilic guilds) were highest in large waterbodies inundated during spring and early summer, however only in bream (*Abramis brama*) a positive relationship to the amount of flooded vegetation was identified. Mortality rates of all species significantly increased with increased YOY fish densities, suggesting extensive competition after the disconnection from the river, and even increased with increasing predator abundance. In correspondence to weak habitat preferences of juvenile YOY, habitat availability explained only a low percentage of the mortality during the isolation phase, and only in YOY pikeperch (*Sander lucioperca*) and perch (*Perca fluviatilis*), cohort mortalities increased in presence of high proportional vegetation cover. Though in most species no direct relationship between mortality and growth was evident, a larger relative size of a YOY species cohort increased survival. Species that spawned later in the season and which YOY are smaller in comparison to the mean size of all YOY cohorts within the juvenile fish community (all opportunistic strategists: *Gasterosteus aculeatus*, *Rhodeus amarus*; members of phytophilic/eurytopic group: *Cyprinus carpio*, white bream, *Blicca bjoerkna*) exhibited high preferences for dense vegetation; their mortalities increased with decreasing availability of vegetation stands. In these species (exception: white bream), highest larval densities and recruitment occurred in small and remote lakes, unaffected by inundations in spring or summer. These findings suggest that morphological and structural waterbody characteristics and their degree of seasonal connectivity to the river decide upon reproductive success, recruitment and community patterns and the results may thus provide a useful tool for floodplain habitat rehabilitation.

## Introduction

During the life-cycle of fish mortality is highest within the first year of life and survival of young-of-the-year (YOY) fish is therefore most crucial for recruitment and population maintenance. Highest mortality rates usually occur during early ontogeny (Houde 1997; Balon 1999), however, accelerated growth, which depends on elevated ambient temperatures, sufficient food availability and density-dependent processes, lessens mortality in YOY fish (Mooij, Lammens, and Van Densen 1994; Mooij 1996; Cowan, Rose, and DeVries 2000). Consequently, the formation of strong year-classes in river systems, as a result of high survival of YOY fish, have been found to be advanced by above average ambient river temperatures and below average discharges during the growing phase (Grenouillet *et al.* 2001; Nunn *et al.* 2003; Nunn *et al.* 2007). However, these studies did only point to channel populations and did not take into account the effects of interactions with the floodplain.

From freshwater systems, river floodplains are considered as the most productive, sustaining high biomass production and biodiversity of fish (Welcomme 1985; Junk, Bayley, and Sparks 1989; Winemiller 2004), which has been confirmed for several climatic regions (Copp 1989; Bayley 1991; Fernandes 1997; Arthington *et al.* 2005; Zeug and Winemiller 2007). This is attributed to a broad range of different habitat types and the seasonal impact by flood events, which cause increases of flooded areas and a high primary and secondary production (Gebhardt 1990; Bayley 1995; Amoros and Bornette 2002; Ward *et al.* 2002; Winemiller 2004). These circumstances provide optimal conditions for reproduction, habitat availability, growth, and, thus, recruitment for numerous fish species.

YOY fish communities are considered to develop in interaction with their surrounding environment, and the influence of habitat characteristics on YOY fish assemblages has been demonstrated to act on different landscape units. Many studies have identified habitat associations of YOY fish in European Rivers on the microhabitat (Copp 1992; Copp 1997; Watkins, Doherty, and Copp 1997; Gozlan *et al.* 1998), mesohabitat (Schiemer *et al.* 1991; Staas 1997; Jurajda *et al.* 2001; Bischoff 2002) and macrohabitat scale (Copp 1989; Poizat and Pont 1996; Berrebi, Boet, and Tales 2001; Pont and Nicolas 2001; Tales and Berrebi 2007), and habitat characteristics to support communities of similar requirements and ecological guilds, respectively. Moreover, habitats of high structural complexity reduce the risk of

becoming predated, to which small fish are highly vulnerable (Stalnaker, Bovee, and Waddle 1996; Copp and Jurajda 1999; Grenouillet, Pont, and Seip 2002). However, little information exists on how habitat availability affects survival of YOY fish during their first year of life and if YOY mortality can be addressed to variations of preferred or even required habitats.

Only few studies traced the fate of YOY cohorts over longer periods of a year (Staas 1997; Grift 2001; Bischoff 2002), which is complicated due to problems of accurate density estimation and changing patterns of habitat utilisations, particularly when these occur on intermediate to large scales. Consequently, the causes for changes of abundance in YOY cohorts in open systems, which imply shifts between different habitat scales (Copp 1990; Schiemer *et al.* 1991; Gaudin 2001; Wolter and Bischoff 2001), do not allow discrimination between colonisation-extinction processes and mortality. However, habitat availability is considered to be a key factor for recruitment of YOY fish (Schiemer 1999) and particularly early life-stages are commonly regarded to be most vulnerable to small-scale habitat limitations (Stalnaker *et al.* 1996; Rosenfeld and Hatfield 2006).

The available habitats to YOY fish, may change notably within short time intervals (Amoros and Bornette 2002; Ward *et al.* 2002), due to (1) an intrusion of river water during inundations, (2) its retrieve with decreasing river discharge and seepage, as well as (3) to groundwater exchanges after disconnection from the river. Repeated quantification of both, YOY fish densities and availability of different habitat parameters may thus provide a good opportunity to identify relationships between survival and changing habitat conditions in defined time-intervals.

In this study we explore how habitat availability during different phases of the first year of life affects recruitment in YOY fish cohorts in front of community- and growth-related parameters, using data gathered in a two year study in the Lower Rhine floodplain, with special attention to processes occurring during the isolation phase. Since it stands to expect that recruitment of species with different ecological requirements and life-history characteristics are differently affected by these parameters, we used nine species, representing different types of reproduction and ecological guilds, and life history strategies, respectively, which all occur frequently in European temperate rivers and their floodplains. Illuminating the determinants of recruitment in the context of habitat requirements as well as the interactions between YOY cohorts, might provide ideas for future rehabilitation of impaired lowland river

floodplains and attempts to sustain biodiversity and productivity of YOY fish communities.

## **Methods**

### **Study area**

The study area is located in the active floodplain, in terms of the potentially flooded area situated between major embankments of the free flowing section of the lower River Rhine (Northrhine-Westphalia, Germany), which is one of the largest rivers in Europe (length: 1320 km, catchment area: 185,000 km<sup>2</sup>, mean discharge before entering the Netherlands: 2,300 m<sup>3</sup> s<sup>-1</sup>). The floodplain of the Lower Rhine originally was many kilometres broad, however, today it is restricted to a narrow fringe comprising only approximately 15% of the original floodplain area (Neumann 2002) along the river banks, in which only few natural floodplain (oxbows, scour pools) waterbodies remained (Borcherding and Staas 2008, Chapter I). Most of the waterbodies originate from gravel-mining and many of them have been disconnected from the river and partly refilled. Depending on their lateral distance to the channel and the topography of the floodplain they are differently affected by surface water exchanges with the river during phases of increased discharge. For the same reasons, areas and volumes of the lakes and the amount of shallow and vegetated areas vary considerably. Highest discharges of the Lower Rhine usually occur in winter and the majority of waterbodies becomes regularly inundated during winter-floods. Minor flood peaks often occur in spring and early summer, which coincides with the spawning season of many fish species, however, these floods affect only waterbodies situated at lower latitude in the floodplain (see Chapter I). Besides exchange of fish between the floodplain and the channel, the magnitude of floods directly determines the flooded area and the habitat availability for fish within the waterbodies during inundations. Lowest discharge of the Lower Rhine occurs during summer and autumn and most non-permanently connected waterbodies remain isolated from June onwards, which is often accompanied by a decrease of lake area and volume during this phase (henceforth isolation phase). However, the degree varies depending on lake morphology and the extent of water exchange with the ground water table.

From approximately 165 non-permanently connected waterbodies of permanent and semi-permanent hydrological character (see chapter 1 for classification) present in the study area, we pre-selected 13 waterbodies which differed with regard to inundation threshold, origin, morphology and vegetated area, in order to estimate the relative importance of habitat availability during the spawning season and the isolation phase on recruitment of YOY fish.

### Sampling

In 2004 and 2005, fish in all 13 waterbodies were sampled at least three to five times between the end of May and the beginning of September, approximately every four to six weeks (except WB No 4 and 33, only in 2004). In both years, this interval represented the isolation phase in which the majority of waterbodies was not affected by surface water exchange with the adjacent river and immigration and emigration of fish were disabled. Additional samplings in a subset of the waterbodies were carried out before first inundations occurred (end of April and mid-May, in 2005 and 2004, respectively) between September and the end of December, when the waterbodies were not subject to inundations in the meantime and before the occurrence of winter floods. Fish were collected by means of point abundance sampling by electrofishing, a sampling approach considered to be very suitable and frequently used for abundance estimation in YOY fish. Samples (distance between particular units  $\geq 5$  m) were taken randomly across the whole area of the waterbody, except in WB No 5, where mean depth exceeded 2 m and sampling was restricted to the shallow areas. The sampling effort (number of samples) varied with lake area and was at least 50 in small and maximally 400 in large lakes. For all sampling occasions until September a pulsed DC device (DEKA 3000; 12 V, 5 A, DEKA Gerätebau, Marsberg, Germany) was used, which was modified with a small ring anode (diameter 0.1 m) to enhance the selectivity for small fishes (Copp and Garner 1995). From the beginning of July onwards, a generator powered DC DEKA 5000 electrofishing unit with a ring anode with an inserted landing net (diameter 0.4 m, mesh size 4 mm) (300 V, 6.6 A, DEKA Gerätebau, Marsberg, Germany) was used that was transported by a boat, in order to reduce bias caused by increasing escape distances of larger YOY. All stunned fish were harvested, determined, measured to the nearest millimetre (total length, TL) and released afterwards, except larvae and early juvenile stages, which were fixed in 5% formalin solution and determined in the laboratory. Since we expected

ontogenetically caused differences in habitat utilisation and mortality, threshold values of TL at which >50% of YOY of the different species had lost larval characteristics (e.g. fin fold, notochord) and entered the juvenile stage (sensu Balon 1999) were determined, in order to discriminate between major stages. Non-linear regressions of fish TL and proper reaction distance towards the activated anode, which were estimated for both types of gear separately, were then used to calculate species abundance for each sample as individuals  $m^{-2}$  and means per waterbody (including null-samples).

A set of microhabitat variables was recorded at each sampling point. We distinguished between three major and six sub-types of vegetation, which were considered to provide a different degree of habitat complexity: 1 aquatic vegetation 1a) aquatic plants (entirely submerged higher plants with whorled or branched shoots and leaves, e.g. *Ceratophyllum*, *Elodea*, *Potamogeton*), 1b) Nymphids (mostly inflated emergent, sometimes submerged floating leaf blades, e.g. *Nuphar*, *Nymphoides*); 1c) filamentous algae (e.g. *Cladophora*); 2 riparian vegetation 2a) grasses (monocotylous herbaceous plants with linear, mostly flat leaves, e.g. *Agrostis*, *Carex*, *Phalaris*), 2b) flooded helophytes (dicotylous herbaceous plants with mostly branched shoots and broad leaves, e.g. *Lythrum*, *Rorippa*, *Myosotis*), 2c) ligneous structures (trees and bushes, e.g. *Salix*, *Alnus*, *Populus*, and their roots, woody debris). Proportional cover of each vegetation sub-type and proportions of substrate grain sizes (boulders, pebbles, gravel, sand, silt, clay, in descending order) and organic matter (coarse and fine particulate) within the sampled area (approximated as one  $m^2$  around the centre of the anode) of each subtype were estimated by visual observation at each sampling point. Depth and distance to the bank were measured to the nearest 0.05 m at each sampling point using a yard-stick when these were  $\leq 2m$  and estimated to 0.5 m above this value.

### Determination of habitat availability and variability

Three-dimensional topographic models of each waterbody were used to model water level dependent changes in habitat availability. Input data (Gauss-Krüger coordinates, depths) were derived from GPS (Leica GS 50 using Beacon data correction; accuracy 0.6 m) and depth measures during phases of highest observed water-levels (predominantly during inundations), approximately every 5 meters, using a yard-stick in shallow (maximum depth < 2m) and an GPS-coupled echo beam sounder (Navitronic Navisound 10; accuracy 0.05 m) in deeper waterbodies. The spatial distribution of aquatic and riparian plant stands (> 30% cover) and areas of similar substrate composition (cover % of the different grain sizes and particulate organic matter) were charted during inundations and at each consecutive sampling survey, digitalized and clipped with topographic data in a GIS-project. Changes in water-level were read from marked poles placed in each waterbody during flood peaks, from the moment of disconnection and at each subsequent sampling survey. ArcView GIS (Version 3.3, ESRI) and the programme extensions Spatial-analyst, 3D-analyst and Tika (developed by the biological station of the Northrhine-Westphalian district Kleve) were used to create the topographic models and to simulate water level-related changes in lake volumes and surface areas. Related effects upon vegetated areas were calculated by means of the intersect function of the XTools-Extension. The mean depth was determined via the volume-surface ratio.

### Cohort and community parameters

From a total of 31 YOY species recorded in this study, we focussed on nine species representing different ecological guilds and life-history strategies, which all occurred in both years in a) sufficiently high numbers to estimate changes in abundance and to derive cohort parameters properly, and b) in most of the sampled waterbodies in varying densities, which allows us to estimate the relative importance of community characteristics and habitat conditions on recruitment and changes in abundance in these species. Following the classifications of Balon's (1975) reproductive guilds, Schiemer's and Waidbacher's (1992) ecological guild concept and the life-history-strategy discrimination of Winemiller and Rose (1992) these species represent six reproductive guilds (lithophilic: Asp (*Aspius aspius*); phyto-lithophilic: perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), bream (*Abramis brama*); phytophilic: carp (*Cyprinus carpio*), white bream (*Blicca bjoerkna*); phytophilic/nestgarder: pikeperch

(*Sander lucioperca*); ariadnophilic: threespined stickleback (henceforth stickleback, *Gasterosteus aculeatus*); ostracophilic: bitterling (*Rhodeus amarus*)), three ecological guilds (rheophilic: asp; eurytopic: bream, carp, perch, pikeperch, roach, white bream, stagnophilic: bitterling, stickleback), and two life-history strategies (with exception of bitterling and stickleback, which represent the group of opportunistic strategists, all other species belong to the group of periodic strategists, see chapter 1).

Mean values of density (individuals  $m^{-2}$ ) and total length of YOY species cohorts within the several waterbodies were used to estimate mortality (in terms of rate of change of abundance:  $\text{density}_{t-1} - \text{density}_t / t - t_{-1}$ ) and growth rate ( $(TL_t - TL_{t-1}) / t - t_{-1}$ ). The relative size of a species YOY-cohort was determined by the deviation of its mean TL from the mean TL of all YOY species cohorts per lake and sampling date, in order to estimate the importance of differential sizes on a cohort's survival.

Abundance of piscivores (pike, *Esox lucius*,  $\geq$  age 0+; asp, perch, sander  $\geq$  age 1+) was determined by means of gill netting at least once per sampling period (at the end of summer) and at all supplementary sampling surveys carried out during autumn and winter. We used multi-mesh gill nets (length and height 30 and 1.5 m; mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm, respectively) and in lakes  $>3$  ha additional gill nets (mesh size 38, 45, 60 mm, only in autumn), which were set in the littoral area after sunset for short time intervals (90 to 240 minutes), in order to minimize sampling-induced mortality. The sampling effort varied with lake area (approximately 1 gill net per 0.5 ha). All fish were measured (TL mm) and released afterwards. Biomass was determined using length-weight relationships gathered in the area of investigation (Molls 1997) and expressed as standardized piscivore biomass (catch per unit effort (CPUE), calculated per  $100 m^2$  net panel (selective mesh sizes) and exposure time ( $\text{weight} \cdot (\text{h} \cdot 100 m^2)^{-1}$ ) per lake and season, respectively).

## Data analysis

Prior to all analyses, predictor variables were tested for co-linearity using Spearman's rank correlation. From variable pairs with significant relationships one of both was omitted from further analysis when  $r_s$  was  $> 0.7$ . Canonical correspondence analysis (CCA) were used to identify 1) the relative importance of macrohabitat characteristics during the spawning and early breeding season on initial densities (i.e. larval peaks) and 2) the microhabitat preferences of YOY during major phases of ontogeny. In the first case log-transformed initial densities and a set of predictor variables were submitted to the analysis, which were considered to display the availability of different habitat parameters and their variability during the time-frame when spawning occurs. As long as no larvae were recorded earlier, we expected the first inundations from the beginning of April to the end of June as the period of major spawning activity. In case of variables regarding rates of change ( $\delta$ : area change per time interval) in waterbodies that have been subject to inundations during the spawning season, we used the sum of rate of change from maximum water level (flood peak) observed in the respective lake to the moment of disconnection and the rate of change from the moment of disconnection to the occurrence of species larval peaks, whereas the rate of change in the reference situation (flood peak) was used for lakes that remained isolated during the spawning season.

Microhabitat preferences of YOY were determined for each one PAS dataset containing the abundance data for larval and juvenile stages and the respective matrix containing the microhabitat variables. The habitat parameters were transformed to categorical variables (cover proportions: 0 = absent, 1  $\leq$  0.30; 2  $\leq$  0.60; 3  $>$  0.60; depth: 0  $\leq$  0.2; 1  $\leq$  0.5; 2  $\leq$  1.0; 3  $>$  1.0 m; distance to bank: 0  $\leq$  1.0; 1  $\leq$  3.0; 2  $\leq$  6.0; 3  $>$  6.0 m) in order to reduce deviations from normal distributions. Since the abundance of the different species varied largely within the different lakes, the proportional catch per point sample, species and lake and sampling date, respectively, was calculated and submitted as the dependent variable to the CCA (instead of absolute abundance) after applying an arcsine square-root transformation and eliminating all null-samples from both matrices.

Multiple linear regression analysis was used to identify factors which affect the mortality of a species YOY cohort from the larval stage until winter, or at least as long as the lake became inundated, since biases due to exchange processes with the river were to expect. We only took into account data when the abundance of a

species had decreased relative to the previous sampling date and when larval stages did no longer occur, in order to prevent bias caused by prolonged spawning activities and apparently increased survival. Consequently, in species in which elongated spawning periods were found to occur (bitterling, carp, stickleback, white bream) datasets were smaller. A set of variables indicating cohort-, community- and habitat characteristics, as well as their variability ( $\delta$ ) during the isolation phase were submitted to the analysis as predictors. Lake volume and cover proportions of substrate types, and their rates of change were omitted from the analysis, since these were significantly correlated with either lake or vegetated areas and their rates of change. We only used main types of vegetation, due to significant positive correlations of the area of sub- with those of main types. All variables were tested for normal distribution using Kolmogorow-Smirnov test and log- or arcsine-square-root transformed, when they deviated from normality. In a first step, an analysis including all non-significantly correlated variables (see above) was run in order to identify any factors which most significantly explained mortality rates of the single species. Since the density of the respective species at the previous date was found to explain mortality rates most significantly ( $P < 0.0001$ , in all species), this variable was used for the adjustment of weighted least squares in the following analysis in order to prevent an over-estimation of density on mortality. A stepwise backward procedure initially including all remaining variables (include criteria:  $P < 0.05$ ; exclude criteria  $P \geq 0.10$ ) was then used to find the maximum fit by reducing the model to significant predictors.

## Results

### Habitat variability

In 2004, the isolation phase reached from mid-May till November in the waterbodies No 9 to No 17, from mid-June till November in No 4 to No 6, and from February 2004 to February 2005 in all other waterbodies. In 2005, it reached from the beginning of June till the beginning of September for the waterbodies No 5 and No 6, from mid-May to September in the waterbodies No 9 to No 12, from Mid-April till January 2006 in the No 17 to No 20 and from February 2005 to February 2006 in the No 29 to No 35.

Mean lake areas, volumes and depths in the sampled waterbodies ranged from 21.4 ha, 357,000 m<sup>3</sup> and 3.3 m in the largest, to 0.2 ha, 800 m<sup>3</sup> and 0.4 m in smallest lakes (Table 1). Variations of these parameters from the spawning period (maximum) in the course of the isolation phase (minimum in September ) were categorically stronger in inundated waterbodies (percentage of area decrease: mean = 41.3, SD = 15.5, min = 23.7, max = 67.8; percentage of volume decrease: mean = 64.0, SD = 23.2, min = 19.3, max = 87.5; percentage of mean depth decrease: mean = 45.6, SD = 22.7, min = 14.7, max = 74.8) than in non-inundated waterbodies (percentage of area decrease: mean = 23.8, SD = 14.7, min = 2.4, max = 44.7; percentage of volume decrease: mean = 40.7, SD = 20.0, min = 4.0, max = 64.4; percentage of mean depth decrease: mean = 24.1, SD = 11.6, min = 2.2, max = 35.7). Though the maximum proportional areas of riparian vegetation to the whole surface area were higher in inundated ( $40.4 \pm 22.7$  %) than in non-inundated ( $15.4 \pm 0.8$  %) waterbodies, the degree of variation until autumn was in a similar range ( $82.4 \pm 2.5$  and  $73.3 \pm 33.8$  % decrease, respectively). The strongest decrease in inundated waterbodies occurred from the flood peak to the onset of the isolation phase (owing to a higher flood peak, variations were higher in 2005), however, was similar to the observed values in non-inundated waterbodies during the isolation phase and categorically lowest between September and December. Aquatic vegetation was present in all non-inundated waterbodies and its proportional area was considerably higher (percentage of surface area: mean = 66.6, SD = 13.7, min = 6.0, max = 97.4) than in inundated waterbodies (percentage of surface area: mean = 9.1, SD = 16.7, min = 0, max = 47.0). In contrast to the cover proportions of riparian vegetation, those of aquatic vegetation mostly increased in non-inundated, whereas it mostly decreased or completely collapsed in inundated waterbodies in some cases in the course of summer.

Table 1: Properties (area, volume, mean depth), cover proportions of vegetated areas (RV: flooded riparian vegetation; AV: aquatic vegetation), water clarity (sechi depth), standardised piscivore biomass and total YOY densities, species richness and numbers of the nine relevant YOY species taken into account for derivation of mortality rates in the sampled waterbodies in 2004 and 2005 (for WB No 4 and 33 only data for 2004) and their range during the sampled interval. Waterbodies in descending order after their long-term frequencies of inundation (compare Table 1 and Fig. 1 in Chapter I for location). Maximum properties refer to the situation during the spawning season (at inundation) or at the reference situation in non-inundated waterbodies (\*) in this time frame. Waterbody origins are: clGF= closed groyne field, fGP = former gravel-pit, recGP = reconstructed gravel-pit, Ox = oxbow, SP = scour pool. Relevant species are a = asp, b = bitterling, c = bream, d = carp, e = perch, f = pikeperch, g = roach, h = stickleback and i = white bream. The symbol † denotes that water clarity exceeded maximum lake depths.

Waterbody code	origin	Year	surface area (ha)		volume (10 <sup>3</sup> m <sup>3</sup> )		mean depth (m)		RV cover*lake area <sup>-1</sup>		AV cover*lake area <sup>-1</sup>		water clarity (m)		piscivore biomass (CPUJE)		total YOY density (Ind m <sup>-2</sup> )		YOY species richness (N)		relevant YOY species (N)
			mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	
WB No 4	SP	2004	0.9	(0.5 - 1.5)	6.8	(2.5 - 12.8)	0.7	(0.5 - 0.9)	0.27	(0.0 - 0.5)	0.00	(0.0 - 0.0)	0.90	(0.6 - 1.1)	0.00	(0.0 - 0.0)	22.30	(2.5 - 53.9)	11	(10 - 12)	6 (a,c,e,f,g,h)
WB No 5	recGP	2004	7.8	(7.1 - 9.7)	252.9	(215.9 - 376.0)	3.2	(3.0 - 3.9)	0.05	(0.0 - 0.2)	0.01	(0.0 - 0.0)	2.68	(2.0 - 3.4)	2.34	(0.0 - 0.0)	8.11	(0.7 - 26.6)	14	(4 - 19)	9
		2005	7.9	(7.1 - 9.9)	266.4	(221.4 - 395.2)	3.3	(3.1 - 4.0)	0.06	(0.0 - 0.2)	0.13	(0.1 - 0.1)	3.53	(3.5 - 3.6)	1.98	(0.0 - 0.0)	1.31	(0.9 - 1.8)	9	(7 - 10)	5 (a,c,f,g,h)
WB No 6	Ox	2004	19.4	(15.2 - 25.0)	260.3	(131.1 - 564.6)	1.3	(0.9 - 2.3)	0.13	(0.0 - 0.3)	0.00	(0.0 - 0.0)	0.74	(0.3 - 1.6)	2.11	(0.0 - 0.0)	72.72	(28.9 - 95.5)	16	(11 - 18)	9
		2005	21.4	(16.2 - 25.4)	356.7	(151.4 - 602.0)	1.6	(0.9 - 2.4)	0.18	(0.1 - 0.3)	0.00	(0.0 - 0.0)	0.98	(0.4 - 1.7)	1.19	(0.0 - 0.0)	55.08	(12.1 - 107.4)	13	(11 - 14)	9
WB No 9	Ox	2004	1.3	(0.7 - 2.1)	10.9	(4.3 - 29.4)	0.7	(0.5 - 1.4)	0.26	(0.1 - 0.9)	0.25	(0.0 - 0.4)	1.27	(0.7 - 1.8)	0.77	(0.0 - 0.0)	44.56	(1.3 - 76.9)	7	(4 - 10)	6 (b,c,d,e,f,i)
		2005	1.7	(1.2 - 2.2)	17.5	(6.9 - 32.6)	1.0	(0.6 - 1.5)	0.53	(0.1 - 0.9)	0.41	(0.4 - 0.5)	1.31	(0.7 - 1.7)	1.55	(0.0 - 0.0)	75.71	(22.7 - 164.0)	10	(7 - 12)	9
WB No 10	fGP	2004	2.7	(1.9 - 4.0)	27.2	(9.1 - 73.1)	0.9	(0.5 - 1.8)	0.17	(0.0 - 0.4)	0.00	(0.0 - 0.0)	0.63	(0.2 - 1.4)	2.89	(0.0 - 0.0)	20.86	(0.3 - 87.2)	8	(6 - 9)	8 (a,b,c,d,e,f,g,h)
		2005	3.1	(1.9 - 4.1)	36.3	(10.1 - 79.1)	1.1	(0.5 - 1.9)	0.21	(0.0 - 0.4)	0.00	(0.0 - 0.0)	0.89	(0.2 - 1.9)	2.66	(0.0 - 0.0)	45.46	(4.0 - 146.5)	9	(7 - 11)	6 (a,c,e,f,g,h)
WB No 11	fGP	2004	6.3	(5.6 - 7.4)	100.7	(75.8 - 145.9)	1.6	(1.4 - 2.0)	0.06	(0.0 - 0.2)	0.00	(0.0 - 0.0)	0.83	(0.5 - 1.1)	2.35	(0.0 - 0.0)	8.33	(0.3 - 23.8)	12	(7 - 15)	8 (a,b,c,e,f,g,h,a)
		2005	6.6	(5.8 - 7.6)	116.7	(85.5 - 156.7)	1.7	(1.5 - 2.1)	0.10	(0.0 - 0.2)	0.00	(0.0 - 0.0)	1.19	(0.8 - 1.6)	2.68	(0.0 - 0.0)	21.23	(4.7 - 37.8)	11	(10 - 12)	8 (a,b,c,e,f,g,h,a)
WB No 15	recGP	2004	1.8	(1.7 - 2.4)	17.9	(17.0 - 21.0)	1.0	(0.9 - 1.0)	0.18	(0.1 - 0.3)	0.20	(0.2 - 0.2)	1.44	(1.3 - 1.7)	2.68	(0.0 - 0.0)	38.40	(13.9 - 56.6)	12	(10 - 13)	7 (b,c,d,e,f,h,i)
		2005	2.1	(1.7 - 2.9)	19.8	(17.0 - 24.4)	1.0	(0.8 - 1.0)	0.25	(0.1 - 0.4)	0.32	(0.3 - 0.3)	1.63	(1.4 - 1.8)	1.37	(0.0 - 0.0)	31.19	(6.5 - 71.1)	15	(14 - 15)	9
WB No 17	clGF	2004	2.0	(1.4 - 2.6)	22.1	(7.4 - 53.2)	1.0	(0.5 - 2.1)	0.17	(0.0 - 0.3)	0.00	(0.0 - 0.0)	0.46	(0.1 - 0.9)	2.58	(0.0 - 0.0)	31.60	(25.8 - 37.4)	13	(13 - 13)	7 (a,c,e,f,g,h,i)
		2005	2.2	(1.9 - 2.6)	25.7	(10.7 - 58.3)	1.1	(0.6 - 2.2)	0.20	(0.1 - 0.3)	0.00	(0.0 - 0.0)	0.59	(0.1 - 1.1)	2.11	(0.0 - 0.0)	22.69	(6.8 - 53.4)	9	(8 - 9)	5 (a,c,e,f,g)
WB No 18	fGP	2004*	0.8	(0.7 - 0.8)	4.8	(3.6 - 6.3)	0.6	(0.5 - 0.7)	0.02	(0.0 - 0.1)	0.48	(0.2 - 0.7)	2.37	(2.2 - 2.5)	0.00	(0.0 - 0.0)	2.44	(1.7 - 3.6)	3	(2 - 3)	2 (b,h)
		2005	1.3	(0.6 - 2.0)	9.6	(2.9 - 15.4)	0.7	(0.5 - 0.8)	0.36	(0.0 - 0.6)	0.23	(0.1 - 0.4)	1.31	(0.5 - 2.5)	0.00	(0.0 - 0.0)	31.04	(15.4 - 61.3)	6	(5 - 8)	4 (a,c,g,h,i)
WB No 20	fGP	2004*	1.2	(1.2 - 1.2)	15.9	(15.4 - 16.1)	1.3	(1.3 - 1.3)	0.01	(0.0 - 0.0)	0.59	(0.5 - 0.7)	3.00†	(2.6 - 3.3†)	1.37	(0.0 - 0.0)	10.34	(5.7 - 13.3)	5	(5 - 5)	3 (b,h)
		2005	1.3	(1.2 - 1.6)	18.3	(15.0 - 24.6)	1.4	(1.3 - 1.5)	0.13	(0.1 - 0.3)	0.00	(0.0 - 0.0)	0.45	(0.1 - 0.9)	0.11	(0.0 - 0.0)	44.27	(16.9 - 95.1)	6	(6 - 7)	5 (a,b,c,e,h)
WB No 29	fGP	2004*	0.8	(0.6 - 1.2)	2.7	(1.7 - 4.8)	0.3	(0.3 - 0.4)	0.08	(0.0 - 0.2)	0.51	(0.1 - 0.8)	0.45	(0.4 - 0.6)	0.00	(0.0 - 0.0)	56.78	(25.0 - 81.3)	3	(3 - 3)	2 (b,d)
		2005*	0.9	(0.7 - 1.2)	3.0	(1.8 - 4.9)	0.3	(0.3 - 0.4)	0.10	(0.0 - 0.2)	0.97	(1.0 - 1.0)	0.49	(0.4 - 0.6)	0.00	(0.0 - 0.0)	59.51	(43.7 - 87.5)	3	(3 - 4)	3 (b,d,h)
WB No 33	fGP	2004*	2.8	(2.4 - 3.2)	34.0	(26.9 - 42.5)	1.2	(1.1 - 1.3)	0.03	(0.0 - 0.1)	0.66	(0.3 - 0.8)	0.67	(0.2 - 1.1)	0.00	(0.0 - 0.0)	8.59	(0.6 - 12.1)	4	(3 - 5)	2 (d,h)
WB No 35	SP	2004*	0.2	(0.2 - 0.2)	0.8	(0.6 - 1.0)	0.4	(0.4 - 0.5)	0.17	(0.1 - 0.2)	0.73	(0.7 - 0.8)	1.52†	(1.4 - 1.7)†	0.00	(0.0 - 0.0)	19.02	(16.6 - 21.1)	3	(3 - 3)	1 (b)
		2005*	0.2	(0.2 - 0.2)	0.8	(0.6 - 1.0)	0.4	(0.3 - 0.5)	0.16	(0.1 - 0.3)	0.76	(0.6 - 0.8)	1.52†	(1.4 - 1.7)†	0.00	(0.0 - 0.0)	22.44	(21.4 - 23.2)	4	(4 - 4)	2 (b,h)

In all cases aquatic vegetation became almost absent until December. Water clarity only slightly differed between inundated (mean = 1.23, SD = 0.80, min = 0.08, max = 3.60 m) and non-inundated which was higher (mean = 1.43, SD = 0.98, min = 0.19, max = 3.30 m, note that in some cases secchi depth exceeded maximum lake depth) and remained rather stable in non-inundated, by contrast, in most cases strongly decreased in inundated waterbodies in the course of summer. Piscivore abundance, YOY species richness and maximum YOY densities were categorically higher in inundated waterbodies.

#### Initial fish densities and habitat associations

Although all of the nine species co-occurred with each other, four (asp, bream, pikeperch, white bream) were only present in waterbodies inundated in the spawning season. In both years highest (initial) densities in most species were reached at the middle/end of May, though larval peaks of some species occurred either earlier (perch and pikeperch: beginning of May) or later (white bream: late June). Highest and lowest mean values of larval density per lake ranged from  $40.0 \pm 41.5$  to  $0.81 \pm 0.91$  individuals  $m^{-2}$  in bream and pikeperch, respectively. On the species level, significant differences between years of sampling occurred only in asp and bream (one-way ANOVA<sub>asp</sub>:  $F_{1, 25} = 35.417$ ,  $P < 0.0001$ ; one-way ANOVA<sub>bream</sub>:  $F_{1, 25} = 5.970$ ,  $P = 0.022$ ). Five species (carp, threespined stickleback, perch, bitterling and pikeperch) showed significant differences of initial densities between the lakes (one-way ANOVA<sub>carp</sub>:  $F_{12, 25} = 3.568$ ,  $P = 0.017$ ; one-way ANOVA<sub>stickleback</sub>:  $F_{12, 25} = 4.030$ ,  $P = 0.011$ ; one-way ANOVA<sub>perch</sub>:  $F_{12, 25} = 2.737$ ,  $P = 0.045$ ; one-way ANOVA<sub>bitterling</sub>:  $F_{12, 25} = 12.045$ ,  $P < 0.0001$ ; one-way ANOVA<sub>pikeperch</sub>:  $F_{12, 25} = 4.252$ ,  $P = 0.009$ ). In white bream and roach, no significant effects of year of sampling or lake upon larval densities occurred.

Initial densities of the different species were significantly attributed to macrohabitat characteristics during the spawning season. After the CCA, two groups of species are clearly separated along Axis 1 (explained variance 44.7%), which mainly displays information about the effects of inundations (maximum lake area, mean depth, maximum temperature at last inundation,  $\delta$  lake area,  $\delta$  flooded riparian and  $\delta$  aquatic vegetation). The 2<sup>nd</sup> Axis (explained variance 14.2%) additionally displays information regarding the proportional areas of riparian and aquatic vegetation stands, and their degree of variability, respectively (Fig 1a).

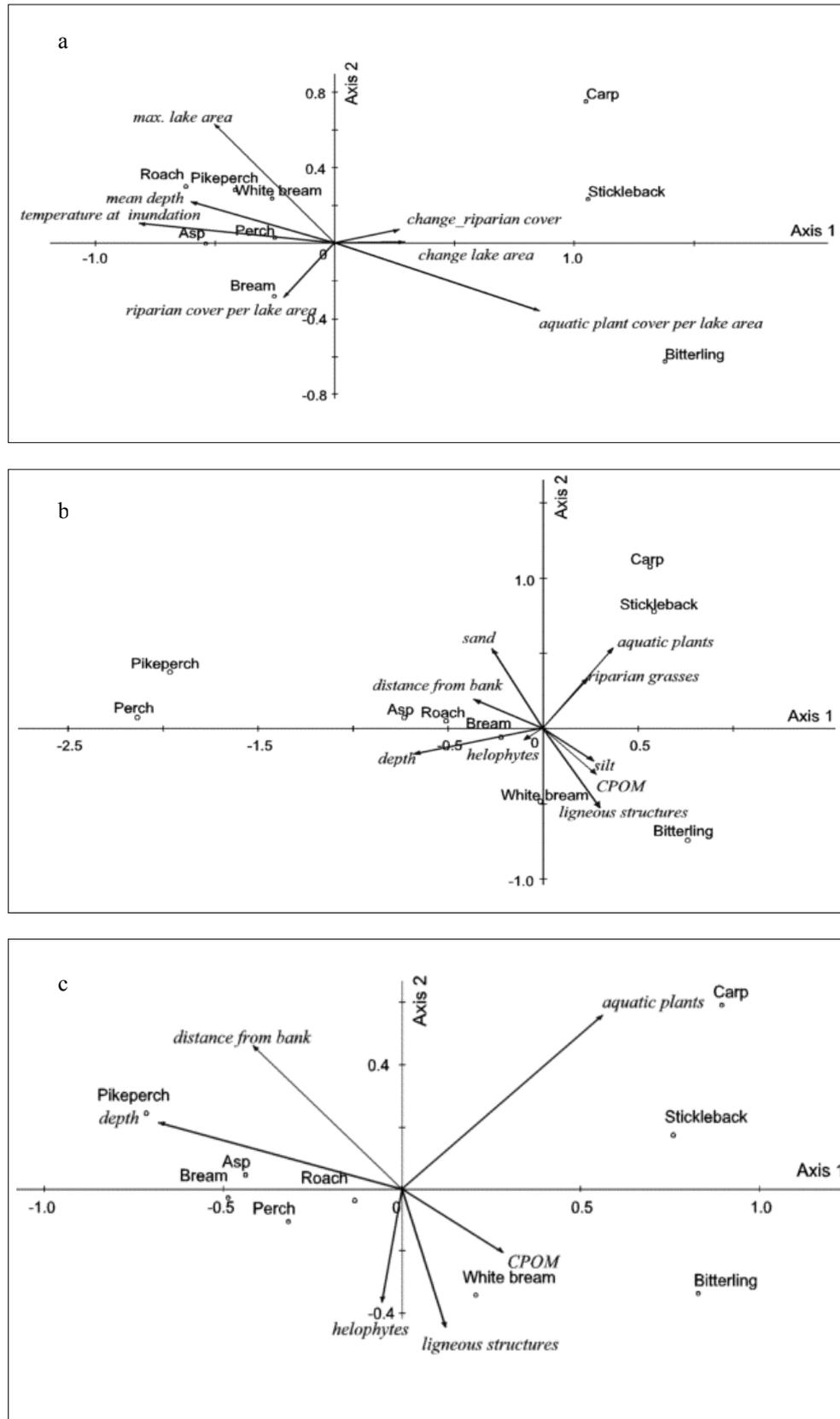


Fig 1: Canonical correspondence analysis biplots on a) relationships of initial densities of YOY and macrohabitat characteristics during the spawning season, and microhabitat associations of b) larvae and c) juveniles in the sampled waterbodies. Only habitat variables (in italic letters) are displayed when  $R^2$  is  $> 0.1$ . Note that rates of change in Fig. 1a) take mostly negative values and positive correlations with Axis 1 indicate weak changes.

In species with positive scores along Axis 1 (carp, stickleback, bitterling) highest initial densities occurred in lakes that were predominantly small and shallow and had not been subject to inundations during the spawning season, and which were characterised by minor decreases of lake area and flooded riparian vegetation, and yet well established stands of aquatic vegetation. Species with negative scores along axis 1 had highest initial densities, or exclusively occurred in lakes inundated in the spawning season. With exception of bream larvae, in none of these species close relationships of initial density and the amount of flooded vegetated areas during the spawning season are indicated.

The CCA results of microhabitat preferences of larvae (explained variability 32.9% and 22.5% for Axis 1 and 2, respectively) provide similar results (Fig. 1b), compared to the distribution of species initial densities. Larvae of carp and stickleback exhibited high preferences for shallow areas with dense cover proportions of aquatic plants or flooded grasses, whereas larvae of bitterling were predominantly associated with dense ligneous structures and organically enriched fine substrates close to the bank. White bream and bream preferred habitats of moderate depth and helophyte or ligneous cover, whereas larvae of roach and asp exhibited minor preferences for shallow and vegetated habitats. Larvae of perch and pikeperch highly preferred unstructured open water habitats.

In most species microhabitat preferences became less distinct after entering the juvenile stage, which is indicated by a considerably lower explained variability of the CCA results (19.1% and 3.3% for Axis 1 and 2, respectively) and increasing distances of the species scores to the environmental vectors in ordination space (Fig. 1c). The preferred habitats of bitterling, carp, stickleback and white bream rather resembled those occupied as larvae, whereas all other species showed, with few exceptions (roach moderate depth and aquatic plant cover), less preference for any habitat parameter, however, increasingly tended to occupy habitats of larger depth and distance to the bank. Compared to the larval stage most pronounced shifts are indicated for bream and perch, since they either exhibited a stronger preference for open water habitats or areas situated closer to the bank, respectively, whereas the smallest differences between larval and juvenile habitat selection occurred in pikeperch.

## Growth and mortality

In only two species (bitterling, stickleback) narrow relationships between initial density and remaining densities at the end of summer (final densities) occurred, whereas these were considerably smaller in asp and roach, and rather weak in bream, carp, pikeperch and white bream (Fig. 2). This indicates different degrees of and seasonally varying mortalities in the different species. The highest mortality rates (Fig. 3a) occurred in bream and white bream, which differed significantly (ANOVA  $F_{8, 282} = 10.567$ ,  $P < 0.0001$ ) from those of the other species (Dunnett T3-Test:  $P < 0.0001$ ), except of carp and roach (Dunnett T3-Test  $P > 0.05$ ). However, no significant differences occurred between carp and roach and amongst all other species (Dunnett T3-Test  $P > 0.05$ ).

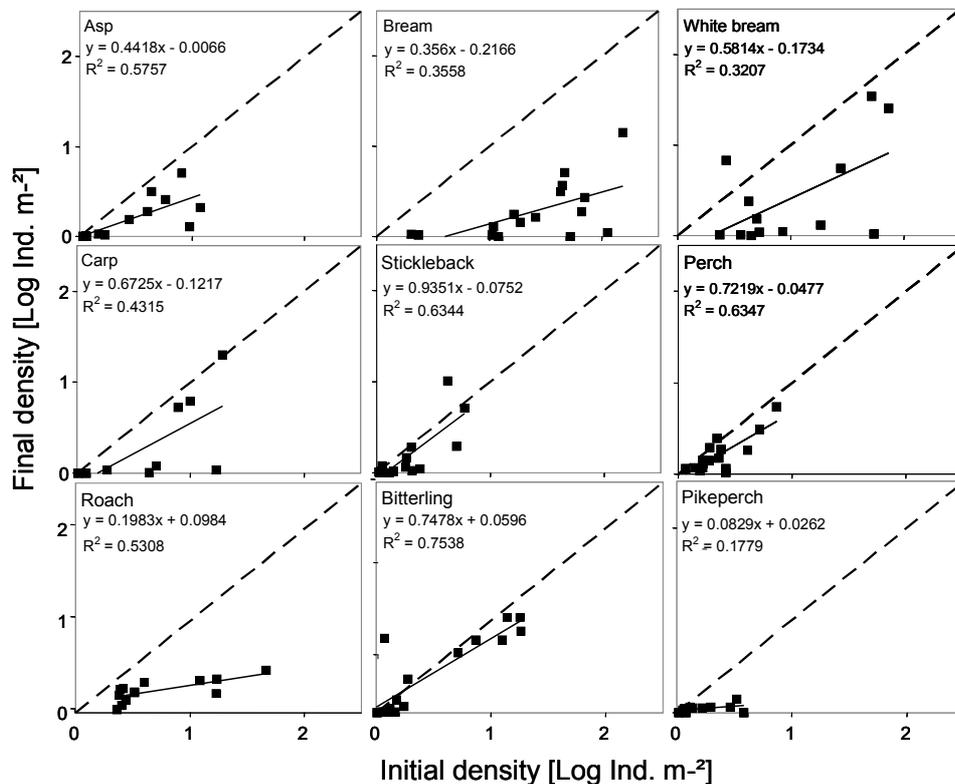


Fig 2: Relationships between initial densities and final densities (beginning of September) in the sampled lakes.

Cohort growth rates of bitterling, stickleback and white bream were significantly lower (ANOVA  $F_{8, 282} = 10.671$ ,  $P < 0.0001$ ) than in the other species, whilst no significant differences occurred between these, as well as between all other species (Fig. 3b). The cohorts of the slowly growing species were thus sub-averagely sized, those of bream and roach averagely, and those of asp, carp, perch and pikeperch above averagely sized during the entire YOY stage (Fig. 3c).

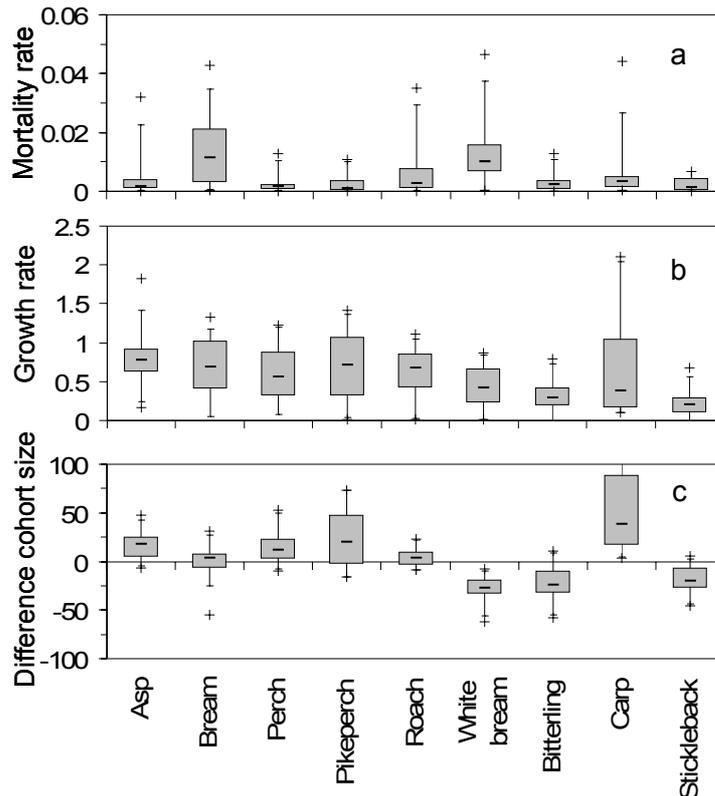


Fig 3: Box-Whisker Plots (median, quartiles, 99%-intervals, max, min) of a) cohort mortality rates [ $\text{mean density}_{t-1} - \text{mean density}_t / t - t_{-1}$ ], b) growth rates [ $\text{mean TL}_t - \text{mean TL}_{t-1} / t - t_{-1}$ ] and c) the difference of mean species cohort size from total YOY cohort size [ $\text{mean TL}_{\text{cohort}} - \text{mean TL}_{\Sigma\text{cohort}}$ ]. Species ordered after their position along Axis 1 in Figure 1a).

The multiple linear regression analysis significantly explained mortality rates in all species.  $P$ -values and explained variance ( $R^2$ ) were lower in the models of perch, pikeperch and white bream, whereas best model fits are indicated for asp, bream and carp. Maximum fits were reached after 6 to maximum 11 steps (Tab. 2). From the thirteen variables submitted to the analysis, each explained mortality rates significantly in at least one species. In all cases variables associated to either habitat availability or variability, significantly explained species mortality rates and contributed to more than the half of explained variance in perch, pikeperch, bitterling

and carp, whereas mortality rates in asp, bream, roach, white bream and stickleback were stronger attributed to community or cohort characteristics.

Table 2: Model statistics (No of steps after which maximum fits were reached,  $R^2$  and ANOVA results) and results of the stepwise multiple linear regression results (coefficients, significance) of community- and cohort and habitat parameters and their rate of change ( $\delta = x_t - x_{t-1} / t_t - t_{t-1}$ ) on mortality rate of the nine YOY species. Only variables displayed which were included in the model after the final step of the backward procedure. Note, for coefficients in case of habitat variability that these variables usually took negative values and coefficients have to be inversely interpreted.

Asterisks indicate significance (ns =  $P \geq 0.05$ ; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ).

		Asp	Bream	Perch	Pikeperch	Roach	White bream	Bitterling	Carp	Stickleback
Model	No of steps	10	6	8	11	9	11	6	8	9
	$R^2$	0.77	0.85	0.45	0.3	0.59	0.59	0.69	0.93	0.643
ANOVA	d.f.	4, 29	8, 38	6, 46	3, 31	5, 35	3, 22	8, 33	6, 22	5, 26
	F	19.49	29.04	5.02	5.66	10.38	5.77	6.78	29.51	10.31
	P	< 0.001	< 0.001	0.001	0.024	< 0.001	0.011	< 0.001	< 0.001	0.001
Variables										
	constant	- 0.111 **	0.029 ns	0.048 ns	0.029 **	- 0.018 ns	- 0.034 ns	- 0.020 ns	- 0.204 **	- 0.005 ns
	community									
	total YOY density $t_{-1}$	0.035 ***	0.043 ***	.	.	0.024 *	.	0.012 ns	0.036 **	0.013 ns
	YOY species richness $t_{-1}$	.	- 0.035 ***	.	.	- 0.062 **	.	.	- 0.053 ***	.
	piscivore biomass	0.044 *	0.022 ns	0.044 *	.	0.045 ns	0.060 *	.	.	0.061 **
	cohort									
	$\delta$ growth rate $t$	.	0.051 ***	.	.	.	.	.	0.081 ***	.
	size deviation $t$	- 0.001 **	- 0.001 ***	.	- 0.010 **	.	- 0.022 **	- 0.001 **	.	0.001 ns
	habitat availability									
	lake area $t$	0.030 ***	.	- 0.021 **	.	0.039 ***	.	0.016 *	0.060 **	.
	mean depth $t$	.	0.041 *	- 0.129 ***	.	.	.	0.140 **	.	.
	water clarity $t$	.	0.035 *	- 0.031 ns	.	.	.	- 0.039 ns	.	.
	proportional area RV $t$	.	.	0.098 **	0.065 *	.	- 0.143 *	- 0.079 **	.	- 0.037 *
	proportional area AV $t$	.	0.017 *	0.024 ns	.	.	.	- 0.022 *	.	0.024 ns
	habitat variability									
	$\delta$ lake area $t_{t+1}$	.	.	.	.	- 4.004 ns	.	7.277 **	.	.
	$\delta$ area RV $t_{t+1}$	.	.	- 0.692 ***	- 0.488 ns	.	.	.	1.318 **	.
	$\delta$ area AV $t_{t+1}$	.	.	.	.	.	.	.	- 1.519 ***	.

From the community parameters, total YOY density was found to increase mortality rates in all species except white bream and perch. On the contrary, in three of these species negative relationships of mortality rates and the diversity (species richness) of the YOY community are indicated. In more than the half of the species (asp, bream, perch, white bream, stickleback) mortality rates increased significantly with the increased abundance of piscivorous species. From the cohort parameters growth rates explained mortality in only two species (bream, carp), which increased with the cohort's growth rate in both cases. On the contrary, mortalities decreased with the relative size of the cohorts in asp, bream, stickleback and most pronounced in white bream and pikeperch.

From the habitat characteristics, lake area significantly affected mortalities of most species, which either increased (in asp, roach, bitterling and carp) or decreased

(perch) with lake size. In the latter, mortality rates analogously strongly decreased with increasing lake depth, whereas opposite tendencies are indicated for bream and bitterling. Bream was the only species which mortality increased with increasing water clarity. The mortality rates either decreased (of bitterling, stickleback, white bream) or increased (of perch and pikeperch) in presence of high proportions of densely vegetated areas, however, in only two species significant effects of rates of change of sheltered areas and the corresponding mortality rates were found. In perch, mortality rates strongly decreased with the loss rate of riparian vegetation. Though a similar effect occurred in pikeperch it was not significant. On the contrary, mortalities strongly increased with the decrease of areas of riparian vegetation, however decreased parallel to aquatic vegetation cover. The most pronounced increase of mortality occurred in bitterling, though the model results do not attribute this to a decrease of sheltered areas, but a general decrease of lake area.

## **Discussion**

### Habitat availability and reproduction

Although it is widely accepted, that YOY fish communities are shaped by macrohabitat conditions (Lamouroux *et al.* 1999; Berrebi *et al.* 2001; Tales and Berrebi 2007), by now only few studies linked the effects of habitat availability at different scales (Poizat and Pont 1996), or related recruitment to habitat availability from the moment of reproduction onwards. Our findings demonstrate that the initial distribution of YOY fish was mainly determined by the degree of interaction with the river in the time-frame of spawning and early ontogeny (Welcomme 1985; Junk *et al.* 1989) (see also chapter 1), however, mortality and recruitment largely varied depending on several parameters, including habitat availability.

Inundations of the river in spring and summer involve immigrations of fish as well as an increase of habitat area in terms of total lake area and of flooded vegetation stands along the banks, what Junk *et al.* (1989) denominated as the aquatic-terrestrial-transition zone (ATTC). The amount of the ATTC is considered to explain the high productivity and diversity of floodplain communities (Ward and Stanford 1995; Bayley 1995; Ward *et al.* 2002), which is reflected well by considerably higher total YOY densities and numbers of species in inundated compared to non-inundated lakes in our study. In six of the nine species, we found larval densities at the beginning of the isolation phase to be significantly related to river temperatures at

previous inundations and/or to inundation-related increases of lake area per se or that of flooded terrestrial vegetation. In some of these species (e.g. bream, carp, roach, white bream) immigrations of adults into floodplain lakes at increased water-levels and adequate temperatures and spawning on freshly flooded vegetation has been repeatedly confirmed (Spindler 1995; Molls 1997; Molls 1999; Korte 1999; Scharbert and Greven 2002), whereas lithophilic species, like asp, incubate their eggs at coarse substratum at lotic sites outside the floodplain (Fredrich 2003). However, larvae of lithophilic species are known to migrate to lentic areas soon after hatching (Schiemer *et al.* 1991; Baras and Nindaba 1999a; b) and larval occurrence of asp and other lithophilic species within stagnant floodplain waterbodies is attributed to either passive displacement or immigrations from channel habitats during flood events (see Chapter 1).

Only in case of bream, initial densities were directly related to the amount of flooded vegetation, although it is commonly considered to exhibit little preferences for certain spawning substrata (Balon 1975). Nevertheless, some authors suggest bream to highly select flooded vegetation for spawning (Diamond 1985; Mann 1996), which is in accordance to observations made in the field (Scharbert, unpublished data). Moreover, strongest spawning activity of bream in floodplains occurs at the peaks of spring and early summer floods, when the available area of flooded vegetation reaches its maximum (Molls 1997; Scharbert and Greven 2002). In contrast, though initial densities were significantly related to inundations during their spawning season, no relationship to the increase of the ATTC were obvious for the other species, which is most probably attributed to their low spawning substrate preferences, e.g. in perch and roach (Diamond 1985; Mann 1996; Wolter and Vilcinskas 1997), or nest-building (pikeperch), as well as in-drift of larvae from spawning locations outside the floodplain (asp), or later gravities of spawning activity.

White bream spawns at higher temperatures later in the season than the previous species, and moreover repeatedly (Mann 1996; Molls 1999), and similar to the statements made for bream, high densities of YOY white bream have been found to occur when floods in late spring and early summer lead to sustained flooding of vegetation stands (Spindler 1995; Pont and Nicolas 2001). However, in the Rhine area, summer floods are mostly less extreme (see chapter 1) and do not cause a large expansion of inundated lakes over their banks, thus, the increase of flooded area is

probably underestimated in the CCA results. Furthermore, spawning at higher temperatures involves a faster embryonic development and a shorter time-span for the embryos to hatch from their eggs (Herzig and Winkler 1986; Kucharczyk *et al.* 1997). Successful breeding in later spawning species might thus be less reliant to large areas of continuously flooded vegetation. Although carp is known to exhibit a similar spawning behaviour and high larval densities in floodplains often occur analogously to inundations and increases of the ATTC (Gebhardt 1990; King, Humphries, and Lake 2003) (see also chapter 1), in our study highest initial densities occurred in non-inundated and densely vegetated waterbodies with low habitat variability (since no ephemeral waterbodies have been subject to the topic of this study). The same applies to bitterling and stickleback, which both exhibit highly adaptive reproductive tactics, by either incubating their eggs in mussels and nest-building from plant materials, respectively, and elongated spawning periods.

Such adaptations are typical for opportunistic life-history strategists and involve, in contrast to the previous species, an independency from periodical suitable conditions for reproduction (Winemiller and Rose 1992; Welcomme, Winemiller, and Cowx 2005; Zeug and Winemiller 2007). This explains highest initial densities in waterbodies unaffected from floods during the spawning season. Furthermore, small and less frequently inundated floodplain lakes tend to develop stands of aquatic vegetation more than larger and frequently inundated lakes (Van den Brink *et al.* 1991; Van Geest *et al.* 2003) and, thus, probably provide more suitable conditions for recruitment of species requiring aquatic plants for spawning or as a habitat for YOY fishes.

#### Habitat-independent determinants of mortality

Mortality rates were highly density-dependent. As stated above, mortality rates of a species YOY cohort increased with its density, wherefore we used this parameter for the adjustment of mortality rates, instead of using it as an explaining variable in the analysis, in order to identify further determinants of mortality. However, even the total YOY density explained much of the mortality in our species, which indicates that resource limitation plays a major role for recruitment in most of our species. Though we did not estimate food availability, it is well known that high densities of YOY fish lead to food deprivation, low growth performances and increased mortalities (Mooij 1996; Houde 1997; Cowan *et al.* 2000; Grenouillet *et al.* 2001).

However, in only two species, in bream and carp, we identified significant relationships of cohort growth rates and mortalities, which were both positive. Bream and carp were the most abundant species and occurred in extraordinary high initial densities in either, lakes inundated during the spawning season or lakes remaining isolated. The most possible explanation for the positive relationship between growth and mortality is that high consumption and rapid growth rates of certain individuals, lead to food shortages for smaller individuals of the same cohort, which might have lead to reduced survival. Such intra-cohort relationships have been demonstrated for differently sized sub-cohorts in YOY fish cohorts (Mikheev and Wanzenböck 1999; Vilizzi and Walker 1999; Cowan *et al.* 2000). Similar relationships might have occurred in other species, however, these implications may be probably masked, since we did not discriminate between size related mortalities and thus underestimate the importance of such implications. In front of this background it seems reasonably that mortalities of the same species decreased with an increase of YOY species diversity, which possibly reduced intra-cohort competition. In contrast, an increased relative size of the different cohorts significantly reduced mortality in the majority of our species, which indicates that growth in fact reduced mortality, by either competitive advantages towards smaller species cohorts or a decreasing risk of becoming preyed upon by predators (Werner *et al.* 1983; Copp and Jurajda 1999). Indeed piscivore abundance explained much of the mortality in most species.

In accordance to the predictions of life-history theory (Winemiller and Rose 1992), our findings demonstrate that the progeny of periodic strategists, which adults produce many eggs that are incubated under optimal, but often short lasting conditions (e.g. inundations in spring or early summer), suffer higher mortalities than those of opportunistic strategists, which produce fewer eggs and spawn over elongated periods. In the former we identified only weak relationships between initial densities and densities at the end of summer. By the example of pikeperch, who was characterised by the lowest initial densities, it can be concluded, that the potential output decreases with the numbers of YOY present at the beginning of summer.

### Habitat-dependent determinants of mortality

Water depth and current are known to be crucial factors that explain habitat utilisation in YOY fish (Schlosser 1991; Gaudin 2001; Schiemer *et al.* 2001; Lamouroux and Souchon 2002) and indeed water depth explained much of the variability in the microhabitat preferences in our study. However, in contrast to many other studies regarding microhabitat associations of YOY fish (Copp *et al.* 1991; Copp *et al.* 1994; Watkins *et al.* 1997; Gozlan *et al.* 1998), current does not occur in the stagnant waterbodies in our study. Thus, the identified habitat preferences might point to further habitat requirements, despite current, since several habitat parameters are often closely correlated to lotic-lentic gradients in riverine landscapes, i.e. bottom substrate composition, oxygen and temperature regimes (Gozlan *et al.* 1998; Amoros and Bornette 2002; Ward *et al.* 2002). In our study, besides depth and distance to the bank, particularly the cover proportions of riparian vegetation and aquatic plants explained most of the variability in a) microhabitat preferences of YOY fish, and b) mortality rates of particular species. Larvae of bitterling, carp and stickleback exhibited high preferences for dense stands of aquatic plants and riparian vegetation, which were either absent or became rapidly scarce in inundated waterbodies when the flood retreated, whereas these habitats remained more stable in non-inundated lakes. Larvae of phytophilic species, such as carp remain attached to aquatic plants after hatching (Balon 1975), which might explain the high preferences for vegetated habitats of early larvae.

In all cohorts of sub-averagely sized and slow growing species (bitterling, stickleback, white bream), the preferred habitats of larvae and juveniles were similar and categorically situated close to the bank and further characterised by low water depths and dense vegetation cover. Similar habitat association patterns are described for the same species in other systems (Copp *et al.* 1994; Gozlan *et al.* 1998; Copp, Kovac, and Blacker 2002; Reichard *et al.* 2002). Such behaviours has often been interpreted to serve the avoidance of predators, towards small fish are more vulnerable (Copp and Jurajda 1999), and habitat complexity is known to reduce attack efficiency of predators (Bean and Winfield 1995). However, in our study the described habitat preferences consistently occurred in waterbodies from which fish predators were absent. Grenouillet *et al.* (2002) explained the high preferences of juvenile fish for vegetation stands besides their shelter function towards predators, particularly with higher densities of zooplanktonic organisms in macrophyte stands,

serving as prey for YOY fishes. Nevertheless, these benefits were highest at stands of intermediate complexity, however decreased at high cover proportions (Grenouillet *et al.* 2002), which might explain the increased mortality of carp and stickleback with increasing areas of aquatic vegetation. Although both species highly preferred stands of aquatic vegetation, some waterbodies became completely overgrown (see Table 1) so that hypoxic conditions during the night-time are to expect. With exception of extreme expansions of aquatic plants, mortality rates in all of the mentioned species decreased in presence of high cover proportions or increased with negative rates of change. Moreover, at least in carp and bitterling, mortality rates increased with size of the waterbodies, which had a lower structural complexity, however, supported higher overall YOY fish densities, thus competitive disadvantages for small and specialised species are to expect. Negative relationships between phytophilic YOY species density and lake-size and positive relationships to the degree of isolation have also been found in other European river floodplains (Gozlan *et al.* 1998; Berrebi *et al.* 2001; Pont and Nicolas 2001; Tales and Berrebi 2007).

We found no significant positive relationships between mortality rates and the availability or variability of vegetation cover in faster growing and larger-sized YOY-cohorts, which all belonged to the lithophilic/rheophilic and phytolithophilic/eurytopic guild, respectively. Nevertheless, mortality rates of bream significantly increased at high cover proportions of aquatic vegetation, an observation which was repeatedly made during this study. YOY bream often suffered extreme mortality rates in shallow waterbodies (maximum depth < 1m) when these were highly covered with e.g. *Elodea nutallii*, whereas no similar observations were made for other YOY fish. In contrast, YOY bream were most abundant and had higher survival in turbid lakes, which are often phytoplankton-dominated environments with low presence of aquatic vegetation (Van den Brink, Van Katwijk, and Van der Velde 1994; Van Geest *et al.* 2003; Roozen *et al.* 2003), although the reason for the positive relationship of aquatic plant cover and mortality of YOY bream remains unclear.

Larvae of asp and roach were weakly associated to shallow and vegetated habitats along the banks, which were on the contrary strictly avoided by perch and pikeperch. In most of these species habitat preferences diminished further after entering the juvenile stages, and shifts in microhabitat utilisation were identifiable in perch, roach and bream. Juvenile perch apparently shifted from their larval open-water habitats to

areas situated closer to the bank, which is in well agreement to findings from larger lake systems, since larvae of some percid species are known to utilise pelagic areas (Ali and Ryder 1977; Urho 1996; Scharf *et al.* 2009). According to our findings, Copp (1990) described juvenile roach to exhibit more complex habitat associations, particularly high preferences for aquatic and riparian plants than their larvae, though this is only weakly displayed in the CCA results. Juvenile bream showed a complementary behaviour and shifted also to open water habitats, a process which became increasingly significant with increasing size of the YOY bream. Despite such observations have by now not been described for YOY bream in stagnant waterbodies, comparable size-related shifts to off-shore areas frequently occur in YOY fish (Schiemer *et al.* 1991; Gaudin 2001; Wolter and Bischoff 2001; Reichard *et al.* 2002), although these descriptions are restricted to fluvial systems and were interpreted as a consequence of increasing swimming performance and a lower predation risk. In our case, these shifts probably underline an increasing independency from shelter structures and might explain the weak relationships of habitat availability and mortality in these species.

Mortality of perch and pikeperch strongly increased in presence of high proportions of vegetated areas. At least pikeperch is a typical YOY piscivore, which starts to feed on smaller YOY in the first weeks after hatching and has been demonstrated to suffer elevated mortalities when not shifting to piscivorous feeding during its first year of life (Buijse and Houthuijzen 1992). Since this foraging strategy is accompanied by accelerated growth, and the cohorts of YOY pikeperch were indeed above-averagely sized that in turn was found to reduce pikeperch mortality rates, it seems rather probable that high structural complexity acts as shelter for potential prey fish and, thus, reduces foraging efficiency of pikeperch. Mortality of perch significantly decreased in the larger, deeper and less turbid waterbodies with low structural complexity, which are typical attributes of gravel-pits. Such types of waterbodies are suspected to sustain an onset of early piscivory even in perch (Beeck *et al.* 2002). However, it has to be taken into account that amongst all models of mortality, those of perch and pikeperch had the smallest explained variability.

To conclude, our findings attest how habitat availability in floodplain lakes affects recruitment of YOY cohorts and that life-history trait-related parameters, particularly the size of the YOY decides upon the determinants of recruitment. Initial densities,

as a consequence of reproductive success, were clearly attributed to the degree of interaction with the river during the spawning season (Chapter 1) and inundations in this time-frame favoured high larval densities of periodic life-history strategists, which almost exclusively belonged to the phyto-lithophilic/eurytopic and lithophilic/rheophilic guild. Although inundation related increases of habitat availability are important for reproduction, and mortality rates were rather high, habitat availability plays only a minor role for recruitment after entering the juvenile stage. In contrast, species with less distinct spawning seasons, which mostly belonged to the phytophilic guild or exhibit more advanced reproductive traits, exhibited high habitat preferences during the entire season and had highest recruitment under stable conditions during the spawning season and the following months. Mortality rates in these predominantly small-sized species significantly increased with losses of preferred habitats. Finally, we suggest, that morphological and structural waterbody characteristics and their degree of seasonal connectivity to the river decides upon reproductive success, recruitment and community patterns: large and frequently inundated waterbodies with a high temporal variability of riparian habitats favour the recruitment of species of the phyto-lithophilic/eurytopic and lithophilic/rheophilic guild, and periodic life-history strategists, respectively, whereas small and less frequently inundated waterbodies with a low temporal variability favour recruitment of phytophilic/stagnophilic dominated communities, and opportunistic strategists, respectively. In front of the knowledge of local discharge regimes these findings might provide a useful tool for floodplain habitat rehabilitation in order to maintain diverse fish communities.

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**Causes and consequences of piscivory in young-of-the-year  
pikeperch and perch in floodplain lakes of a large temperate  
lowland river**

**Abstract**

Although seasonal floodplain inundation has been demonstrated to be beneficial to the recruitment of many species, less is known about the growth and predator-prey interactions of young-of-the-year fishes within temperate river floodplains. We explored the diet-dependent growth and recruitment of two functionally different piscivorous percids (young-of-the-year pikeperch and perch) in nine floodplain waterbodies of the Lower Rhine. Piscivory led to accelerated growth and was enhanced by an earlier hatching (in April) and a size advantage over their fish prey. Small juvenile cyprinids, which were the most frequently consumed prey, were highly abundant in waterbodies inundated in the middle of May. Pikeperch selected smaller, shallow-bodied prey more strongly than perch did. Piscivory in perch was related to relative predator size and habitat conditions. The proportion of piscivores (pikeperch 47.1%, perch 13.6%) in the population increased from June onwards, but decreased at the end of summer due to a shortage of suitably sized prey (body depth of prey < gape width of predator), except in waterbodies that had been repeatedly inundated or in which multiple-spawning prey species were present.

## Introduction

Floodplain inundation plays a crucial role with respect to total productivity and diversity in lowland rivers. The flood pulse concept (FPC; Junk, Bayley, and Sparks 1989) postulates that the production of plant and animal biomass increases with the duration of floodplain inundation; this concept has been confirmed for several climatic regions (Bayley 1991; Van den Brink and Van der Velde 1994; Sparks, Nelson, and Yin 1998). In temperate regions, the benefits of flooding on the recruitment of riverine fish species depend on the seasonal coincidence of rising water levels and temperatures and consequently on the timing of inundations that provide suitable spawning and nursery areas (Copp 1989; Bayley 1991; Ward and Stanford 1995). Although the FPC stresses the importance of floodplain inundation on the recruitment of fish, little information on diet selection and accelerated growth of young-of-the-year (YOY) fish in floodplains exists (Gutreuter *et al.* 1999). The progeny of immigrating fish as well as those of resident fish are hypothesized to provide large numbers of suitable prey, a fact which should enhance the probability of fish switching to piscivory during early ontogeny and thus increasing growth, survival and recruitment (Buijse and Houthuijzen 1992; Olson 1996; Persson and Bronmark 2002).

A size advantage over and a sufficient availability of prey are considered to be the most important preconditions for the onset and maintenance of piscivory in YOY piscivores (Mittelbach and Persson 1998). The availability of prey for a predator is mainly determined by the predator's gape size as well as the size and morphological constraints of their fish prey (Hambright 1991; Christensen 1996; Dörner and Wagner 2003). In addition, physical habitat structure, e.g. in terms of turbidity and aquatic plant cover, have been demonstrated to develop heterogeneously within floodplain lakes of different frequency of inundation (Van Geest *et al.* 2003; Roozen *et al.* 2003), suggesting differential effects on optically orientated predators (Ali and Ryder 1977; Greenberg, Paszkowski, and Tonn 1995; Snickars, Sandstrom, and Mattila 2004).

The piscivores pikeperch (*Sander lucioperca*) and perch (*Perca fluviatilis*) occur in many European rivers. Both display typical features of piscivores (Mittelbach and Persson 1998), e.g. spawn in early spring, providing a potential size advantage over their prey (Thorpe 1977; Lappalainen, Dörner, and Wysujack 2003), and have large gapes (Dörner and Wagner 2003; Dörner *et al.* 2007). According to the classification

of Keast (1985), the pikeperch is designated as a specialist piscivore, which turns piscivorous within the first weeks after hatching, actively selecting fish over alternative prey. The onset of piscivory in pikeperch is thereby related to environmental factors (Buijse and Houthuijzen 1992; Persson and Bronmark 2002). In contrast, perch are reported to be facultative piscivores; starting to feed on fish in a less specialized manner when they are at least 150 mm (Willemsen 1977; Van Densen, Ligtoet, and Roozen 1996). Nevertheless, there are also indications that perch might start to feed on fish within their first year of life (Popova and Sytina 1977; Mehner, Dörner, and Schultz 1998; Beeck *et al.* 2002; Borcharding, Hermasch, and Murawski 2007).

In this study, we used YOY pikeperch and perch to investigate whether differences in diet, growth and the timing of the shift to piscivory in floodplain lakes of a large temperate river could be related to environmental parameters and differences in individual prey availability, as predicted by the FPC. In addition, this study aims to explore predator-specific differences with regard to the species and size-related selectivity of the prey, and finally, how early piscivory of pikeperch and perch influences the YOY fish community structure in floodplain lakes. We hypothesized that both the availability and the vulnerability of the different prey species vary on a spatial (i.e. within different zones the floodplain) as well as on a seasonal scale, depending on the growth of the predator and prey species as well as on the species composition and the habitat characteristics.

## Material and Methods

### Study sites

The study was conducted in the floodplain in the German section of the lower River Rhine, a large temperate lowland river with a mean discharge of  $2,270 \text{ m}^3 \text{ s}^{-1}$ . Due to the climate in the drainage basin area ( $185,000 \text{ km}^2$ ), the maximum discharge occurs during winter and spring and the lowest in late summer and autumn (temperate seasonal discharge regime). Over the last few centuries, canalization of the River Rhine and all of its major tributaries, together with a significant loss in the original floodplain area, have led to an irreversible deepening of the river channel and therefore to a drastic disturbance of the river-floodplain-interaction. This generally leads to reduced frequency and duration of inundations. Today, most of the waterbodies in the River Rhine's floodplain are recent or former gravel-pits, whereas only few oxbows remain (Borcherding and Staas 2008).

The present study comprised nine different floodplain waterbodies. Besides surface area and maximum depth, in particular the frequency of inundation, the stability of water levels after disconnection from the river and the trophic situation differ considerably between the study sites (Table 1). In 2004, all waterbodies except GP3 were inundated in early May, and two of them (Ox1, GP1) again in early June. Two of the water bodies (GP2, Ox2) are not inundated by the River Rhine directly, but via adjacent oxbows. The water level of some of the water bodies decreased dramatically during the isolation phase, resulting in a reduction of lake surface area, mean and maximum depths, and the proportion of riparian cover relative to the lake surface. This was most pronounced in shallow lakes with predominantly coarse-grained sediment (Ox1 and 2, GP3, CGF), and was caused by a decrease in the ground water table.

Riparian cover (willows, woody debris, helophytes) was present in all lakes, but was considerably reduced in lakes that experienced a drop in water level over the course of the summer. Aquatic vegetation (mainly *Elodea nuttallii*, *Potamogeton pectinatus*) was present in Ox2, GP2 and GP4. Water clarity in terms of secchi depth was highest in the infrequently inundated and lowest in the more frequently connected water bodies. It progressively decreased in most of the water bodies starting in June, with the lowest values (0.2 m) in September

Table 1: Location, characteristics and inundation patterns of the sampled floodplain waterbodies (GP = gravel-pit; Ox = oxbow; CGF = closed groyne field). All waterbodies remained isolated from June onwards. % cover refers to riparian and aquatic vegetation.

waterbody <sup>†</sup>	location	surface (ha)	vegetation (% cover)	depth		secchi depth (m)	surface temperature (°C)	duration of inundation (days)	river		prevailing sediment
				June					temperature during inundation (°C)		
				September	June					May (mean; range)	
	E			mean	max		mean (range)	total 2004 (May/June)	May (mean; range)	June (mean; range)	
	N										
GP1	6°43.08'	7.2	6.3	3.1	6.1	4.3	22.4 (19.5 - 24.5)	69 (8/12)	(14.2; 13.4-15.0)	(19.7; 18.5-20.2)	gravel-sand
GP2	51°19.70'	6.9	0.8	2.9	5.7	2.0	22.3 (19.2 - 29.3)	19	(14.0; 13.6-14.3)	(14.0; 13.6-14.3)	gravel-sand
GP3	6°30.58'	1.6	36.6	1.0	2.9	2.5	22.0 (18.3 - 28.8)	(2/-)	-	-	sand-silt
	51°39.02'	1.6	36.2	1.0	2.9	1.5	20.6 (19.6 - 21.2)	33	(13.9; 13.4-14.3)	(13.9; 13.4-14.3)	sand-silt
	6°25.34'	3.5	27.5	1.1	2.2	2.0	20.7 (18.3 - 23.8)	(5/-)	-	-	silt-clay
	51°43.06'	2.0	0	0.6	1.2	0.2	22.2 (18.4 - 25.2)	13	-	-	silt-clay
GP4	6°21.67'	1.2	71.0	1.3	2.6	2.6*	20.6 (19.8 - 21.9)	37	(14.0; 13.4-14.3)	(14.0; 13.4-14.3)	gravel-sand
	51°45.13'	1.2	71.0	1.3	2.6	2.6*	20.7 (18.3 - 23.8)	(-/-)	-	-	silt-clay
GP5	6°20.12'	18.9	2.3	4.2	8.4	5.4	20.6 (19.8 - 21.9)	31	(14.0; 13.4-14.3)	(14.0; 13.4-14.3)	gravel-sand
	51°47.29'	18.8	2.2	4.2	8.3	3.4	21.9 (18.6 - 26.9)	(6/-)	-	-	silt-clay
GP6	6°17.24'	6.5	13.6	1.6	3.5	1.8	20.8 (17.9 - 24.3)	31	(14.0; 13.4-14.3)	(14.0; 13.4-14.3)	silt-clay
CGF	51°48.56'	6.4	13.3	1.5	3.4	0.5	20.6 (17.9 - 24.3)	(5/-)	-	-	gravel-sand
	6°42.41'	2.3	19.3	0.8	1.7	1.4	21.9 (18.6 - 26.9)	19	(13.9; 13.6-14.1)	(13.9; 13.6-14.1)	gravel-sand
	51°43.16'	1.4	0	0.5	1.1	0.2	20.8 (17.9 - 24.3)	(2/-)	-	-	sand-gravel
Ox1	6°20.33'	19.5	21.6	1.1	3.1	1.6	20.8 (17.9 - 24.3)	65	(14.1; 13.6-14.7)	(14.1; 13.6-14.7)	sand-gravel
	51°47.97'	14.7	5.1	0.9	2.6	0.2	20.8 (17.9 - 24.3)	(8/9)	(19.8; 19.4-20.2)	(19.8; 19.4-20.2)	sand-CPM
Ox2	6°20.28'	1.2	87.2	0.7	1.8	1.8*	20.8 (17.9 - 24.3)	33	(13.9; 13.6-14.1)	(13.9; 13.6-14.1)	sand-CPM
	51°47.50'	0.7	76.6	0.5	1.3	1.3*		(5/-)	-	-	

\*secchi-depth > maximum lake depth

<sup>†</sup> compare waterbody codes: Table 1 and Fig.1 in Chapter 1: GP1 = No 5; GP2 = No 15; GP3 = No 10; GP4 = No 20; GP5 = No 7; GP6 = No 11; CGF = No 17; Ox1 = No 6; Ox2 = No 9

## Sampling

Fish were sampled on at least three sampling dates between June and September by means of point abundance sampling by electrofishing in a stratified random manner (Persat and Copp 1989). A battery-powered DEKA 3000 portable electrofishing unit (pulsed DC, 600 V, DEKA Gerätebau, Marsberg, Germany) with a ring shaped anode (diameter 0.1 m) and a separate dip-net (mesh size 0.5 mm) was used on all sampling dates. Some of the lakes were already sampled in mid-April in the same manner. From July onwards, when most YOY fish had attained a larger size and might hence escape the electrical field of the pulsed DC unit more easily, additional sampling with a generator powered DC DEKA 5000 electrofishing unit (300 V, 6.6 A, DEKA Gerätebau, Marsberg, Germany) and a ring anode with an inserted landing net (diameter 0.4 m, mesh size 4 mm) was undertaken. In the shallow lakes, sampling was extended across the whole lake surface, whereas it was restricted to the shallow areas close to the bank in the deeper gravel-pit lakes (GP1, GP5). The number of point samples varied with surface area and was at least 90 in small and at most 400 in large water bodies. In order to quantify abundance (as individuals per m<sup>2</sup>) and to enhance comparability of sampling devices, we used regression equations of observed galvanonarkosis and total length, which were estimated for both devices separately (see appendix chapter 1). Mean densities were calculated for each single species and point sample, including samples with no specimens caught (null points). Sampling was conducted once per month; when this was not possible, or when sampling dates were close to the next month, these were pooled in order to compare data from waterbodies (Table 2).

Smaller fish (e.g. larvae, early juveniles) which couldn't be determined directly in the field were preserved in 4% formalin solution for analysis in the laboratory, whereas larger fish were measured to the nearest millimetre and then released. If available, at least ten randomly selected YOY perch and pikeperch per lake and sampling date were preserved in 4% formalin solution for diet analysis. Length frequency distributions and additional measurements of the opercular bones were used to differentiate between age groups.

## Diet analysis

Preserved fish were measured (nearest mm) and weighed (nearest mg) in the laboratory. Invertebrates found in their stomachs were determined at least to the family level; consumed fish were identified to species level. If available, at least 15 individuals of each taxa were measured and their wet mass determined using length-mass relationships for zooplankton and invertebrates (Bottrell *et al.* 1976; Mehner, Schultz, and Herbst 1995; Benke *et al.* 1999; Borcharding, Murawski, and Arndt 2006). Fish larvae were identified using keys of (Koblikiaya 1981; Pinder 2001).

Stomach contents were assigned to one of four categories: 1) zooplankton (copepods, daphnids, bosminids, ceriodaphnids, *Leptodora*), 2) benthic invertebrates, henceforth MZB (insect larvae and pupae, isopods, amphipods), 3) mysids (*Limnomysis benedeni*, *Hemimysis anomala*) and 4) fish. Assignment of total stomach content to the respective category was determined by the prevailing proportion (> 50 % wet mass) in the diet. For statistical purposes, empty stomachs were designated as a 5<sup>th</sup> category.

The index of stomach fullness (ISF, Hyslop 1980) was calculated as the proportion of prey wet mass relative to predator wet mass.

$$ISF[\%] = \frac{WM_{Prey}}{WM_{Predator}} \cdot 100$$

To compare growth of fish utilizing different prey categories, the daily growth coefficient (DGC, (Iwama and Tautz 1981)) was calculated.

$$DGC = \frac{W_t^{(1/3)} - W_i^{(1/3)}}{\Delta t} \cdot 100$$

for which  $W_t$  is the weight at time  $t$ ,  $W_i$  is the initial weight, and  $\Delta t$  is the intermediate time interval (days).

### Availability and selectivity of fish prey

The specific availability of prey species for each predator was determined by means of A) relationship between total length and gape width of perch and pikeperch, the values for which were obtained from the literature (Mehner *et al.* 1998; Dörner and Wagner 2003; Dörner *et al.* 2007), and B) the relationship between total length and maximum body depth (BD) of prey species identified in the stomachs of YOY perch and pikeperch. The latter was determined by measuring maximum body depth of different-sized YOY using a digital calliper rule (nearest 0.01 mm) and then plotting these values against the total length (nearest 0.5 mm). The abundance of suitably sized prey available to each predator fish was obtained by filtering the PAS-Dataset (restrictions:  $BD_{\text{Prey}} \leq \text{gape width}_{\text{Predator}}$ ;  $PPR < 0.6$ ) of the respective water bodies and sampling date.

### Statistics

We applied logarithmic (n+1) transformations to the data prior to all statistical procedures except to proportional data (cover, ISF), which were arcsine-square root transformed (Sokal and Rohlf 1995) to approximate normality. Differences in growth (DGC) and stomach fullness (ISF) between species and between prey categories were tested by means of a hierarchical ANOVA. The dependent variables were tested for normal distribution principally using the Kolmogorov-Smirnov Test and for equal variances using Levene's Test. A Bonferroni adjustment was applied prior to multiple comparisons. We used Tukey-HSD for equal variances and a Dunnett-T3 post hoc-test for unequal variances.

In order to quantify the effects of an individual predator's size, the position of an individual in the size distribution of the respective YOY-cohort (total catch) and the percentiles of the size distribution were determined for each species, (per lake and sampling date), and individual fish assigned to one of the resulting six size categories ( $\leq 5\%$ ;  $>5-25\%$ ;  $>25-50\%$ ;  $>50-75\%$ ;  $>75-95\%$ ;  $>95\%$ ).

Mean mortality rates (for each species and water body) were estimated in terms of the change in mean abundance of a species between sampling dates, divided by the number days between sampling. Multiple linear regressions were used to test for differences in log-transformed (ln+1) mortality rates and to analyse the influence of prey selection and the proportion of piscivorous YOY-pikeperch and perch in the cohort on mortality of prey species.

In order to determine whether or not the onset and extent of early piscivory in YOY-pikeperch and perch is related to certain environmental or biotic variables, logistic regression analysis was used. Fish with empty stomachs were excluded from the analysis. All environmental variables (lake area, mean and maximum depth, transparency, proportion of aquatic and terrestrial vegetation relative to the lake area) entered the model on an interval or ratio scale as presented in Table 1. Predator-specific variables such as specific available abundance of prey fish and estimated cohort-strength of the respective predatory species entered the model as numbers  $m^{-2}$ . The categorical variables month, frequency of inundation and size category (as described above) were deviation-coded with the smallest category as the reference. To test for seasonal and size-related effects on available prey abundance, interaction terms of the respective variables were constructed. A stepwise backward procedure using LR statistics was used to select variables that significantly improved the fit of the model. The overall fit of the models was tested by means of chi-squared test and Hosmer-Lemeshow statistics.

Underlying gradients in prey species selection of piscivorous YOY pikeperch and perch were identified by means of principal component analysis (PCA), using a correlation matrix of a set of variables that we expected to influence prey selection. We used prey morphology (BD-TL-ratio), relative predator size (percentiles of size distribution, see above), predator-prey relationships (PPR, difference between predator GW and Prey BD) and total and relative (proportion of all available prey species) specific available abundance of respective prey items and the month of consumption to explore seasonal patterns in prey selection.

## Results

### Species composition and abundance

Spawning of pikeperch and perch was observed in late March and their larvae (pikeperch:  $11.0 \pm 1.6$  mm TL; perch:  $11.5 \pm 1.5$  mm TL) were already present in some of the lakes (Ox1, GP1, GP3, GP6), which had already been sampled in mid-April. At this time, roach and pike were the only other YOY fish. From June onwards YOY perch were present in each lake studied, whereas occurrence of YOY pikeperch was restricted to only six of the water bodies (Table 2). Point abundance sampling and additional sampling with multi-mesh-gillnets revealed that older juvenile specimens of both species were either absent or occurred in very low numbers. Densities of the YOY of perch and pikeperch differed slightly between waterbodies, with highest values in GP3 in both species. With exception of the latter, densities of perch were higher than that of pikeperch. Due to the randomized sampling design and the formation of large shoals of YOY perch in early summer, no perch were caught in GP5 in July. The composition of the YOY fish community varied between water bodies, with higher densities of the rheophilic cyprinids barbel (*Barbus barbus*), chub (*Leuciscus cephalus*), asp (*Aspius aspius*), ide (*Leuciscus idus*), dace (*Leuciscus leuciscus*), gudgeons (*Gobio gobio*, *Romanogobio belingii*) and eurytopic bleak (*Alburnus alburnus*) and roach (*Rutilus rutilus*) in the more frequently inundated water bodies, and stagnophilic species, e.g. bitterling (*Rhodeus amarus*) and sunbleak (*Leucaspius delineatus*) in the infrequently inundated and remote lakes (Table 2). With exception of GP4, which has not been inundated since winter, eurytopic bream (*Abramis brama*) and white bream (*Blicca bjoerkna*) were the most abundant YOY in all water bodies studied. The densities of most species decreased from June to September. However, larval stages and early juveniles of multiple spawning species were still present in July; thus densities remained stable or increased due to repeated spawning of adults within the floodplain lakes (bitterling, sunbleak, white bream) or immigration of larvae from the river during phases of connection (bleak, chub).

Table 2: Abundance (numbers  $m^{-2}$ , mean  $\pm$  SD) of YOY pikeperch and perch and their prey fish in the sampled floodplain lakes. Predator-prey interactions are denoted by symbols: † pikeperch, ‡ perch.

water-body	date	pooled month	prey														
			perch	pikeperch	barbel	bitterling	bleak	breem	carp	chub	gudgeons	pumpkinseed	roach	spined loach	sunbleak	tubenose goby	white bream
GP1	03.06.2004	June	0.2 $\pm$ 1.0	0.1 $\pm$ 1.0	20.5 $\pm$ 244.9	•	0.5 $\pm$ 6.8†	1.0 $\pm$ 10.2†	•	0.2 $\pm$ 2.0	0.2 $\pm$ 1.9	•	1.4 $\pm$ 12.8	•	•	•	0.0 $\pm$ 0.9
	20.07.2004	July	0.1 $\pm$ 1.2	0.1 $\pm$ 0.9	0.1 $\pm$ 1.4	0.0 $\pm$ 0.3	1.0 $\pm$ 4.5††	0.6 $\pm$ 7.6	0.0 $\pm$ 0.2	1.1 $\pm$ 6.0†	0.0 $\pm$ 0.4	•	1.2 $\pm$ 9.3	•	•	•	2.6 $\pm$ 15.4††
	15.08.2004	August	0.1 $\pm$ 0.7	0.1 $\pm$ 0.6	0.0 $\pm$ 0.4	0.0 $\pm$ 0.2	0.2 $\pm$ 1.0††	0.2 $\pm$ 1.8	0.0 $\pm$ 0.2	0.6 $\pm$ 3.2†	0.0 $\pm$ 0.4	•	0.7 $\pm$ 2.9	•	•	•	0.4 $\pm$ 3.6‡
	05.09.2004	September	0.2 $\pm$ 0.6	0.1 $\pm$ 0.5	•	•	0.0 $\pm$ 0.1‡	0.0 $\pm$ 0.1	0.0 $\pm$ 0.1	0.2 $\pm$ 1.1†	0.0 $\pm$ 0.1	•	0.1 $\pm$ 0.3	•	•	•	0.0 $\pm$ 0.2‡
GP2	02.06.2004	June	0.4 $\pm$ 3.7	0.4 $\pm$ 2.8	•	17.2 $\pm$ 55.3	•	18.2 $\pm$ 59.1†	4.0 $\pm$ 22.0	•	•	0.4 $\pm$ 2.1†	0.5 $\pm$ 4.8†	•	•	•	1.3 $\pm$ 13.3
	16.07.2004	July	0.2 $\pm$ 1.8	0.2 $\pm$ 1.3	•	23.4 $\pm$ 72.2	•	1.1 $\pm$ 4.0	0.5 $\pm$ 2.5	•	•	0.0 $\pm$ 0.4	0.8 $\pm$ 2.6†	1.7 $\pm$ 11.3††	•	•	26.7 $\pm$ 108.8††
	09.08.2004	August	0.2 $\pm$ 1.3	0.2 $\pm$ 1.0	•	13.9 $\pm$ 51.9	•	0.5 $\pm$ 2.2	0.3 $\pm$ 0.9	•	•	•	0.9 $\pm$ 3.4‡	1.3 $\pm$ 10.4††	•	•	15.8 $\pm$ 53.1††
	01.09.2004	September	0.2 $\pm$ 1.0	0.2 $\pm$ 0.8	•	6.6 $\pm$ 24.3	•	0.5 $\pm$ 2.3	0.2 $\pm$ 0.9	•	•	•	0.0 $\pm$ 0.2	0.5 $\pm$ 1.8††	0.0 $\pm$ 0.4	•	•
GP3	07.06.2004	June	1.6 $\pm$ 11.5	2.0 $\pm$ 9.2	•	0.3 $\pm$ 1.9	•	9.5 $\pm$ 26.2†	15.9 $\pm$ 63.5†	•	•	•	1.5 $\pm$ 5.8	•	•	•	53.1 $\pm$ 116.5††
	24.06.2004	July	0.6 $\pm$ 1.7	0.9 $\pm$ 2.6	•	0.1 $\pm$ 1.0	•	3.8 $\pm$ 15.4	0.8 $\pm$ 4.7	•	•	•	0.6 $\pm$ 2.5	•	•	•	5.9 $\pm$ 27.8††
	05.08.2004	August	0.5 $\pm$ 1.6	0.9 $\pm$ 2.1	•	•	•	0.1 $\pm$ 0.9	0.3 $\pm$ 0.8	•	•	•	0.3 $\pm$ 1.4	•	•	•	0.0 $\pm$ 0.3‡
	29.08.2004	September	0.1 $\pm$ 0.6	0.3 $\pm$ 0.9	•	0.0 $\pm$ 0.2	•	0.0 $\pm$ 0.2	0.1 $\pm$ 0.4	•	•	•	0.2 $\pm$ 0.7	•	•	•	0.0 $\pm$ 0.4
GP4	07.06.2004	June	6.1 $\pm$ 40.6	•	•	11.5 $\pm$ 56.9	•	•	•	•	•	•	•	•	•	•	•
	15.07.2004	July	5.7 $\pm$ 24.0	•	•	10.9 $\pm$ 33.2†	•	•	•	•	•	•	•	•	•	•	•
	30.08.2004	September	2.8 $\pm$ 14.1	•	•	5.2 $\pm$ 19.7	•	•	•	•	•	•	•	•	•	•	•
	01.06.2004	June	1.5 $\pm$ 18.3	•	2.2 $\pm$ 15.7	0.3 $\pm$ 4.3	1.4 $\pm$ 13.3	11.0 $\pm$ 91.4	•	0.2 $\pm$ 3.2	0.1 $\pm$ 2.0	•	16.3 $\pm$ 59.3	•	•	•	4.0 $\pm$ 36.2
GP5	12.07.2004	July	•	•	0.2 $\pm$ 1.3	0.2 $\pm$ 2.2	1.3 $\pm$ 16.9	2.5 $\pm$ 23.9	•	0.0 $\pm$ 0.4	•	4.1 $\pm$ 14.2	•	•	•	•	0.0 $\pm$ 0.4
	16.08.2004	August	0.1 $\pm$ 1.1	•	0.1 $\pm$ 0.8	0.3 $\pm$ 2.2	0.1 $\pm$ 1.1	0.4 $\pm$ 2.9	•	0.3 $\pm$ 1.4	•	0.7 $\pm$ 3.1	•	•	•	•	1.8 $\pm$ 10.4
	09.09.2004	September	0.0 $\pm$ 0.2	•	•	0.1 $\pm$ 0.6	0.0 $\pm$ 0.1	0.0 $\pm$ 0.1	•	0.2 $\pm$ 1.6	•	0.1 $\pm$ 0.9	•	•	•	•	0.0 $\pm$ 0.1
	07.06.2004	June	3.1 $\pm$ 31.9	1.6 $\pm$ 22.6	1.0 $\pm$ 9.0	•	•	9.8 $\pm$ 66.1†	•	0.2 $\pm$ 2.2†	•	•	1.4 $\pm$ 8.7	•	•	•	7.5 $\pm$ 64.2††
GP6	13.07.2004	July	0.8 $\pm$ 6.0	0.5 $\pm$ 4.3	0.3 $\pm$ 2.9†	0.4 $\pm$ 6.8	•	0.9 $\pm$ 7.0	•	0.2 $\pm$ 2.6†	0.0 $\pm$ 0.2	0.9 $\pm$ 6.0	•	•	•	•	7.4 $\pm$ 73.7††
	03.09.2004	September	0.8 $\pm$ 3.1	0.5 $\pm$ 2.2	0.0 $\pm$ 0.1	•	•	0.3 $\pm$ 0.7	•	0.0 $\pm$ 0.1†	•	1.0 $\pm$ 2.9	•	•	•	•	0.1 $\pm$ 0.5
	01.06.2004	June	1.2 $\pm$ 9.1	0.9 $\pm$ 6.7	3.5 $\pm$ 25.0	•	14.7 $\pm$ 54.6†	45.3 $\pm$ 128.7†	•	•	0.7 $\pm$ 6.9	•	3.0 $\pm$ 9.1	•	•	•	•
	13.07.2004	July	0.7 $\pm$ 2.7	0.5 $\pm$ 2.0	0.6 $\pm$ 3.3	•	1.0 $\pm$ 3.6†	6.7 $\pm$ 10.6†	•	•	0.5 $\pm$ 3.6	•	1.2 $\pm$ 3.9	•	•	•	4.3 $\pm$ 40.8†
ClGF	26.08.2004	September	0.5 $\pm$ 1.3	0.3 $\pm$ 1.0	0.1 $\pm$ 0.4	•	0.0 $\pm$ 0.2†	4.2 $\pm$ 6.7	•	•	0.1 $\pm$ 0.3†	•	1.2 $\pm$ 5.8	•	•	•	0.1 $\pm$ 0.5†
	29.05.2004	June	1.2 $\pm$ 7.8	0.7 $\pm$ 5.6	5.3 $\pm$ 37.1	•	•	65.5 $\pm$ 365.5	1.2 $\pm$ 7.0	0.4 $\pm$ 3.4	0.1 $\pm$ 1.4	•	1.8 $\pm$ 8.1†	•	•	•	•
	26.06.2004	July	1.3 $\pm$ 7.9	0.8 $\pm$ 5.7	1.0 $\pm$ 8.2	0.9 $\pm$ 4.5	0.7 $\pm$ 5.8†	8.7 $\pm$ 37.0†	3.3 $\pm$ 14.7	0.3 $\pm$ 1.8	0.3 $\pm$ 3.3†	•	1.0 $\pm$ 5.3	0.0 $\pm$ 0.5	•	•	71.9 $\pm$ 420.5††
	30.07.2004	August	1.2 $\pm$ 4.4	0.7 $\pm$ 3.2	0.1 $\pm$ 1.0	2.2 $\pm$ 8.3	0.2 $\pm$ 1.6†	1.4 $\pm$ 4.0	0.2 $\pm$ 1.5	0.5 $\pm$ 2.8	0.1 $\pm$ 1.1	•	0.6 $\pm$ 2.4	0.2 $\pm$ 1.2	•	•	87.8 $\pm$ 279.5††
Ox2	06.09.2004	September	1.5 $\pm$ 3.0	0.8 $\pm$ 2.2	•	1.3 $\pm$ 9.1	0.0 $\pm$ 0.3	0.9 $\pm$ 2.7	0.0 $\pm$ 0.2	0.3 $\pm$ 1.3	•	0.5 $\pm$ 1.5	0.0 $\pm$ 0.4	•	•	•	24.2 $\pm$ 88.9††
	06.06.2004	June	12.6 $\pm$ 45.7	•	•	0.7 $\pm$ 6.4	•	24.7 $\pm$ 62.3	•	•	•	•	•	•	•	•	50.9 $\pm$ 204.3
	29.07.2004	August	0.2 $\pm$ 1.6	•	•	0.1 $\pm$ 1.2	•	6.2 $\pm$ 14.9	1.2 $\pm$ 6.6	•	•	•	0.1 $\pm$ 0.8	•	•	•	56.3 $\pm$ 145.5†
	25.08.2004	September	0.3 $\pm$ 1.6	•	•	0.1 $\pm$ 2.0	•	0.5 $\pm$ 2.3	0.0 $\pm$ 0.1	•	•	•	•	•	•	•	28.1 $\pm$ 178.4†

### Diet composition

The proportions of prey categories differed between YOY perch and YOY pikeperch and also varied over the course of the sampling period in most waterbodies (Fig. 1). In general, the proportion of zooplankton and MZB in the diet was significantly higher in YOY perch. In some water bodies mysids contributed to a large amount to the diet of perch, whereas pikeperch utilized this prey resource exclusively in June. The proportion of fish in the diet of pikeperch increased progressively from June to August in most of the lakes, decreasing again in September. At this time the only exceptions were in GP1 and G2, where all pikeperch with non-empty stomachs had fed exclusively on fish. The total proportion of piscivores was 57.1% (June: 50.0%; July: 53.1%; August: 53.7%; September: 35.2%). Fish were nearly absent in the diet of perch in June, after which time they became increasingly important until August, but decreased again in September (June: 2.1%; July: 13.6%; August: 34.5%; September: 12.4%; total 13.6%).

No significant differences were found in respect to stomach fullness between perch and pikeperch (ANOVA,  $F_{1, 482} = 2.492$ ,  $P = 0.115$ ). Although ISF values were generally highest for piscivorous individuals of both species (Fig. 2), differences between prey categories were significant at the  $P < 0.0001$  level, except between zooplankton and mysids (Dunnett-T3 test,  $P = 0.734$ ). No empty stomachs were found in June, but the proportion of pikeperch with empty stomachs increased significantly from 4.7 % in July, to 9.8% in August and 28.4% in September ( $r = 0.813$ ,  $P < 0.0001$ ). A similar change was also seen for perch (3%, 5.2% and 14.3%, respectively;  $r = 0.687$ ,  $P < 0.0001$ ).

### Growth

The mean total length (TL mm  $\pm$  standard deviation) attained in late August/early September ranged from 76.9 ( $\pm 6.4$ ) and 122.4 ( $\pm 8.3$ ) mm in perch, and from 86.7 ( $\pm 5.4$ ) to 147.6 ( $\pm 16.5$ ) mm in pikeperch in the different water bodies (Table 3). Growth in terms of DGC (Fig. 2) was neither significantly different between the two species (ANOVA,  $F_{1, 85} = 0.280$ ,  $P = 0.598$ ) nor between differently inundated water bodies (ANOVA,  $F_{8, 85} = 0.369$ ,  $P = 0.947$ ), but were highly significant between prey categories (ANOVA<sub>pikeperch</sub>,  $F_{4, 57} = 5.522$ ,  $P = 0.003$ ; ANOVA<sub>perch</sub>,  $F_{4, 83} = 4.714$ ,  $P = 0.002$ ). YOY of both species which had consumed fish or mysids grew significantly better than those which had fed on MZB or

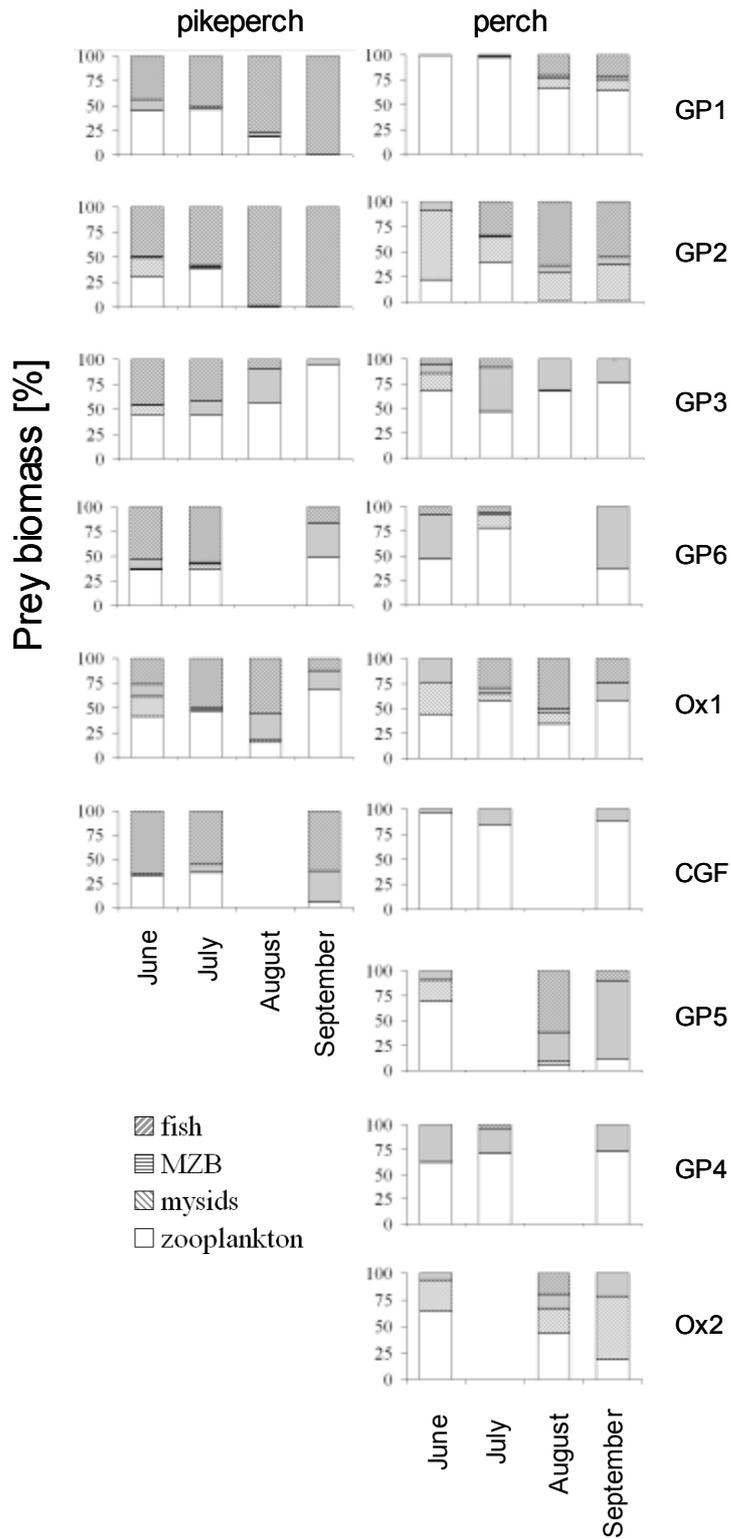


Fig. 1: Relative diet composition (% wet mass of fish with non-empty stomachs) of YOY pikeperch (left) and perch (right) in the sampled floodplain water bodies. Missing columns = not sampled.

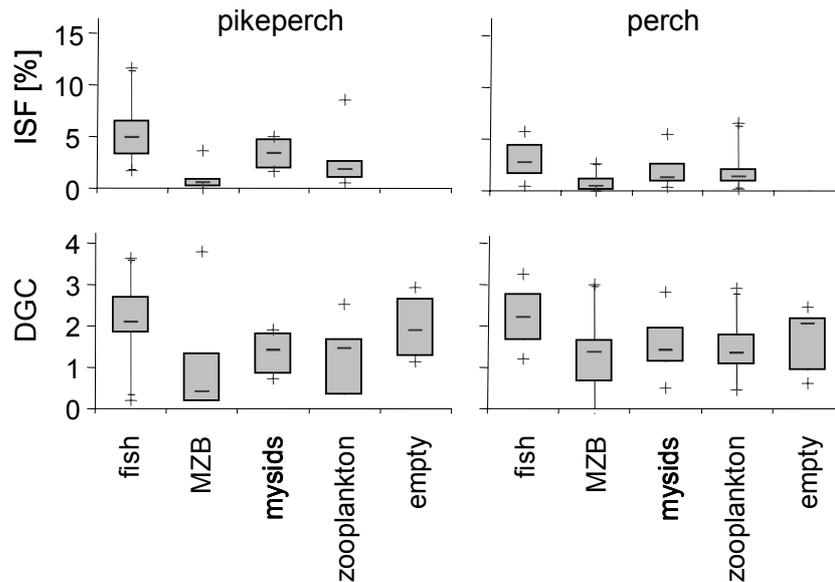


Fig. 2: Box and Whisker Plots (horizontal line represents median, boxes upper and lower 25%-confidence limits, error bars 95% limits, crosses minima and maxima) of index of stomach fullness (ISF in %, upper panel) and daily growth coefficient (DGC, lower panel) of YOY pikeperch (left) and perch (right) utilizing different prey categories.

zooplankton (Tukey HSD-Test<sub>pikeperch</sub>, fish versus MZB:  $P = 0.012$ ; fish versus mysids:  $P = 0.441$ ; fish versus zooplankton:  $P = 0.008$ ; Tukey HSD-Test<sub>perch</sub>, fish versus MZB:  $P = 0.003$ ; fish versus mysids:  $P = 0.035$ ; fish versus zooplankton:  $P = 0.004$ ). No significant differences were found between piscivores and fish with empty stomach (Tukey HSD-Test<sub>pikeperch</sub>, fish versus empty:  $P = 0.839$ ; Tukey HSD-Test<sub>perch</sub>, fish versus empty:  $P = 0.303$ ), nor amongst the remaining categories (Tukey HSD-Test<sub>pikeperch</sub>, zooplankton versus MZB:  $P = 0.985$ ; zooplankton versus mysids:  $P = 0.997$ ; zooplankton versus empty:  $P = 0.361$ ; Tukey HSD-Test<sub>perch</sub>, zooplankton versus MZB:  $P = 0.953$ ; zooplankton versus mysids:  $P = 0.995$ ; zooplankton versus empty:  $P = 0.891$ ).

#### Predator-prey interactions

A total of 13 prey fish species was identified in the stomachs of pikeperch (ten species) and perch (eight species). Prey species differed appreciably in terms of their body depth-body length ratios (Table 4). With the exception of spined loach, stagnophilic and eurytopic YOY fishes were deeper bodied than the more slender rheophilic species. Although many appropriately sized potential prey were

Table 3: Total length (mm, mean  $\pm$  SD) of YOY pikeperch and perch and their prey fish in the sampled floodplain lakes. Standard deviation is only given if  $n > 3$ . Predator-prey interactions are denoted by symbols: † pikeperch, ‡ perch

water-body	date	pooled month	prey														
			perch	pikeperch	barbel	bitterling	bleak	bream	carp	chub	gudgeons	pumpkinseed	roach	spined loach	sunbleak	tuberose goby	white bream
GP1	03.06.2004	June	34.6 $\pm$ 4.3	35.0 $\pm$ 4.7	22.0 $\pm$ 2.0	•	13.4 $\pm$ 0.9†	13.6 $\pm$ 2.5†	•	13.3 $\pm$ 1.2	24.9 $\pm$ 2.7	•	19.7 $\pm$ 1.9	•	•	•	8.0
	20.07.2004	July	87.9 $\pm$ 9.4	79.3 $\pm$ 16.5	50.8 $\pm$ 12.7	36.0	30.9 $\pm$ 8.9††	54.7 $\pm$ 7.0	•	33.7 $\pm$ 7.1†	57.3 $\pm$ 16.8	•	54.4 $\pm$ 5.8	•	•	•	25.8 $\pm$ 4.2††
	15.08.2004	August	101.3 $\pm$ 6.6	106.4 $\pm$ 14.1	70.3 $\pm$ 6.8	42.0	40.4 $\pm$ 8.5	81.1 $\pm$ 7.1	107.3 $\pm$ 6.1	51.5 $\pm$ 8.9†	70.8 $\pm$ 8.8	•	74.1 $\pm$ 7.6	•	•	•	37.4 $\pm$ 6.5†
GP2	05.09.2004	September	117.9 $\pm$ 9.6	119.9 $\pm$ 25.9	•	•	62.0	102.0 $\pm$ 21.2	41.0	69.3 $\pm$ 7.6†	76.0 $\pm$ 0.0	•	99.3 $\pm$ 14.0	•	•	•	40.0 $\pm$ 8.5†
	02.06.2004	June	31.8 $\pm$ 2.9	44.9 $\pm$ 5.4	•	10.3 $\pm$ 4.4	•	11.6 $\pm$ 1.5†	15.3 $\pm$ 3.0	•	•	•	•	18.8 $\pm$ 1.5†	12.0 $\pm$ 0.0†	•	7.1 $\pm$ 0.4
	16.07.2004	July	84.8 $\pm$ 6.4	99.5 $\pm$ 14.5	•	25.9 $\pm$ 6.9	•	48.4 $\pm$ 6.2	68.3 $\pm$ 19.4	•	•	•	39.0	36.5 $\pm$ 6.8†	28.9 $\pm$ 6.8††	•	21.9 $\pm$ 4.2††
GP3	09.08.2004	August	108.6 $\pm$ 8.4	129.6 $\pm$ 11.4	•	33.1 $\pm$ 6.4	•	73.3 $\pm$ 7.5	91.8 $\pm$ 12.4	•	•	•	•	41.1 $\pm$ 8.4†	35.4 $\pm$ 6.5††	•	40.2 $\pm$ 8.7††
	01.09.2004	September	122.4 $\pm$ 8.3	147.6 $\pm$ 16.5	•	41.0 $\pm$ 4.7	•	70.6 $\pm$ 5.8	99.2 $\pm$ 18.4	•	•	•	57.0	51.8 $\pm$ 8.1††	40.5 $\pm$ 4.9	•	50.2 $\pm$ 7.7††
	07.06.2004	June	42.8 $\pm$ 2.6	44.3 $\pm$ 4.9	•	12.5 $\pm$ 4.9	•	22.0 $\pm$ 6.0††	18.3 $\pm$ 4.6†	•	•	•	26.0 $\pm$ 6.3	•	•	•	10.6 $\pm$ 1.5††
GP4	24.06.2004	July	60.1 $\pm$ 7.7	65.7 $\pm$ 8.6	•	14.0	•	31.3 $\pm$ 6.9	46.1 $\pm$ 13.7	•	•	•	40.2 $\pm$ 7.2	•	•	•	15.6 $\pm$ 2.5††
	05.08.2004	August	82.3 $\pm$ 6.1	80.0 $\pm$ 5.0	•	•	•	82.6 $\pm$ 7.3	102.6 $\pm$ 11.4	•	•	•	75.8 $\pm$ 7.0	•	•	•	48.0
	29.08.2004	September	86.7 $\pm$ 5.9	86.7 $\pm$ 5.4	•	45.0	•	104.0 $\pm$ 19.9	135.3 $\pm$ 17.7	•	•	•	93.7 $\pm$ 5.5	•	•	•	66.5 $\pm$ 3.5
GP5	07.06.2004	June	38.8 $\pm$ 4.8	•	•	12.5 $\pm$ 2.2	•	•	•	•	•	•	•	•	•	•	•
	15.07.2004	July	79.7 $\pm$ 8.4	•	•	30.7 $\pm$ 6.6†	•	•	•	•	•	•	•	•	•	•	•
	30.08.2004	September	104.2 $\pm$ 4.1	•	•	40.8 $\pm$ 8.7	•	•	•	•	•	•	•	•	•	•	•
GP6	01.06.2004	June	33.3 $\pm$ 2.9	•	21.4 $\pm$ 2.3	9.8 $\pm$ 1.0	10.8 $\pm$ 0.9	13.1 $\pm$ 1.7	•	9.7 $\pm$ 0.6	16.7 $\pm$ 2.1	•	20.7 $\pm$ 1.9	•	•	•	7.6 $\pm$ 0.6
	12.07.2004	July	•	•	35.4 $\pm$ 7.6	19.3 $\pm$ 8.1	38.7 $\pm$ 3.9	41.0 $\pm$ 6.4	•	39.7 $\pm$ 3.2	•	14.0	49.3 $\pm$ 6.2	•	•	•	24.6 $\pm$ 6.8
	16.08.2004	August	98.9 $\pm$ 6.2	•	78.1 $\pm$ 7.6	30.1 $\pm$ 7.5	60.0 $\pm$ 6.3	82.1 $\pm$ 5.1	•	43.5 $\pm$ 4.1	21.1 $\pm$ 4.6†	•	82.0 $\pm$ 4.4	•	•	•	33.3 $\pm$ 4.8
GP6	09.09.2004	September	115.4 $\pm$ 13.8	•	•	46.8 $\pm$ 6.2	71.0	98.0	•	62.7 $\pm$ 5.6	•	19.8 $\pm$ 3.5	94.3 $\pm$ 8.8	•	•	•	58.5 $\pm$ 13.4
	07.06.2004	June	37.2 $\pm$ 4.1	47.9 $\pm$ 6.9	23.4 $\pm$ 2.2	•	•	13.8 $\pm$ 3.1†	•	14.0 $\pm$ 1.6†	•	•	22.5 $\pm$ 2.4	•	•	•	11.9 $\pm$ 1.3††
	13.07.2004	July	81.2 $\pm$ 7.4	95.6 $\pm$ 15.8	40.2 $\pm$ 7.5†	15.9 $\pm$ 4.0	•	52.8 $\pm$ 8.8	•	28.3 $\pm$ 9.4†	56.0	•	58.2 $\pm$ 7.1	•	•	•	19.3 $\pm$ 5.2††
ClGF	03.09.2004	September	94.6 $\pm$ 7.2	124.9 $\pm$ 29.2	86.0	•	•	86.6 $\pm$ 13.5	•	51.0	†	56.0	89.0 $\pm$ 5.0	•	•	•	51.0 $\pm$ 2.8
	01.06.2004	June	30.4 $\pm$ 3.8	45.9 $\pm$ 7.5	21.5 $\pm$ 2.3	•	11.1 $\pm$ 1.1†	11.2 $\pm$ 1.3†	•	•	21.3 $\pm$ 3.4	•	22.1 $\pm$ 2.2	•	•	•	18.7 $\pm$ 2.5†
	13.07.2004	July	69.5 $\pm$ 7.4	104.6 $\pm$ 12.8	48.7 $\pm$ 9.0	•	36.0 $\pm$ 4.0†	46.4 $\pm$ 8.2†	•	•	46.5 $\pm$ 6.7	•	57.1 $\pm$ 3.5	•	•	•	52.0 $\pm$ 3.2†
Ox1	26.08.2004	September	91.1 $\pm$ 6.8	133.9 $\pm$ 21.0	91.2 $\pm$ 7.5	•	71.0 $\pm$ 4.2†	72.2 $\pm$ 4.5	•	•	62.7 $\pm$ 13.8†	•	82.6 $\pm$ 5.1	•	•	•	•
	29.05.2004	June	28.0 $\pm$ 4.4	37.8 $\pm$ 2.5	17.2 $\pm$ 3.1	•	•	9.5 $\pm$ 1.5†	9.3 $\pm$ 0.8	8.5 $\pm$ 0.7	11.0	•	18.7 $\pm$ 2.2†	•	•	•	•
	26.06.2004	July	61.6 $\pm$ 10.0	77.2 $\pm$ 11.0	18.3 $\pm$ 2.1	12.6 $\pm$ 6.0	21.2 $\pm$ 6.3†	27.0 $\pm$ 5.8†	14.2 $\pm$ 8.7	14.0 $\pm$ 0.0	24.8 $\pm$ 4.0	•	43.5 $\pm$ 3.3	•	•	•	9.5 $\pm$ 1.3††
Ox2	30.07.2004	August	76.3 $\pm$ 10.2	107.0 $\pm$ 16.3	56.7 $\pm$ 7.8	30.1 $\pm$ 6.8	38.8 $\pm$ 3.4†	65.5 $\pm$ 6.9	89.3 $\pm$ 9.4	43.8 $\pm$ 9.4	53.0 $\pm$ 8.5†	•	68.2 $\pm$ 4.9	•	•	•	22.6 $\pm$ 5.1††
	06.09.2004	September	85.4 $\pm$ 7.4	130.5 $\pm$ 28.3	•	38.9 $\pm$ 7.4	64.3 $\pm$ 4.5	79.7 $\pm$ 11.0	103.7 $\pm$ 6.7	59.0 $\pm$ 5.5	•	•	87.3 $\pm$ 7.0	•	•	•	44.8 $\pm$ 6.9††
	06.06.2004	June	33.0 $\pm$ 2.7	•	•	10.3 $\pm$ 1.0	•	12.9 $\pm$ 1.3	•	•	•	•	•	•	•	•	8.0 $\pm$ 0.6
Ox2	29.07.2004	August	67.3 $\pm$ 6.7	•	•	31.5 $\pm$ 0.7	•	26.9 $\pm$ 4.6	12.4 $\pm$ 0.7	•	•	•	•	•	•	•	14.1 $\pm$ 2.9†
	25.08.2004	September	76.9 $\pm$ 6.4	•	•	29.6 $\pm$ 4.4	•	43.2 $\pm$ 5.5	74.0	•	•	•	•	•	•	•	20.6 $\pm$ 7.3†

abundant in most waterbodies, only seven species were present in the stomachs of at least one of the two predators, with an overall frequency of occurrence of 0.01 (referring to all inspected specimens of the respective percid species), namely white bream (0.25 pikeperch; 0.1 perch), bream (0.09; < 0.01), bleak (0.08; 0.03), chub (0.05; 0), sunbleak (0.03; 0.01) spined loach (0.01; 0.02) and gudgeons (0.01; 0). Although piscivorous YOY pikeperch and perch utilized a comparable range of prey species, some prey species consumed by pikeperch were not utilized by perch and vice versa (e.g. in case of chub or tubenose goby), even when sampled from the same lake. Most individual piscivores preyed exclusively on one prey species; in a very few cases more than one species was present in the stomachs.

Table 4: Regression parameters of the relationship  $BD = a * TL^b$  between YOY prey fish total length (TL, in mm) and body depth (BD, in mm). Species in ascending order after their mean BD-TL-ratio after reaching the juvenile stage.

Prey species	Size range (TL mm)	N	Parameters		R <sup>2</sup>	P	BD-TL-ratio	
			a	b			mean	SD
spined loach	17 - 63	41	0.09	1.09	0.99	<0.0001	0.12	0.01
gudgeons	11 - 78	54	0.14	0.98	0.98	<0.0001	0.13	0.01
bleak	8 - 66	51	0.08	1.17	0.99	<0.0001	0.15	0.01
barbel	14 - 66	58	0.20	0.96	0.95	<0.0001	0.17	0.01
chub	8 - 67	47	0.08	1.23	0.98	<0.0001	0.17	0.02
sunbleak	8 - 58	44	0.06	1.30	0.99	<0.0001	0.18	0.01
tubenose goby	20 - 65	27	0.14	1.10	0.98	<0.0001	0.20	0.01
roach	7 - 78	53	0.06	1.34	0.98	<0.0001	0.20	0.01
white bream	7 - 64	112	0.07	1.32	0.98	<0.0001	0.22	0.02
bream	6 - 102	75	0.05	1.40	0.99	<0.0001	0.22	0.02
bitterling	8 - 58	58	0.08	1.33	0.98	<0.0001	0.26	0.03
pumpkinseed	9 - 66	16	0.07	1.37	0.99	<0.0001	0.27	0.05
carp	7 - 100	72	0.11	1.25	0.99	<0.0001	0.28	0.03

Body depth of prey fish was linearly related to gape width (GW) in both predators (linear regression  $GW_{\text{pikeperch}}$  vs. log-transformed  $BD_{\text{prey}}$ :  $r = 0.889$ ,  $r^2 = 0.789$ ,  $F_{1, 219} = 766.493$ ,  $P < 0.0001$ ; linear regression  $GW_{\text{perch}}$  vs. log-transformed  $BD_{\text{prey}}$ :  $r = 0.835$ ,  $r^2 = 0.969$ ,  $F_{1, 87} = 167.465$ ,  $P < 0.0001$ ), and was, with one exception, always lower than gape width (Fig. 3). BD of prey was larger in pikeperch in individuals < 90 mm TL. In contrast, perch preyed on deeper-bodied prey above this threshold. Prey-predator-size-ratio (PPR) increased in both species over the course of the season (ANOVA  $F_{1, 306} = 14,783$ ,  $P < 0.0001$ ), although differences were only significant between September and the previous months (Dunnett-T3 Test,  $P < 0.0001$ ). BD of prey and PPR in pikeperch were lower when prey was abundant, but

increased with decreasing prey abundance (multiple linear regression BD:  $B = -0.867$ ,  $T = -4.834$ ,  $P < 0.0001$ , PPR:  $B = -0.064$ ,  $T = -9.248$ ,  $P < 0.0001$ ). Specific prey abundance had no significant effect on BD (multiple linear regression:  $B = 0.313$ ,  $T = 0.832$ ,  $P = 0.413$ ) but on PPR of prey eaten by perch ( $B = -0.038$ ,  $T = -2.556$ ,  $P = 0.013$ ).

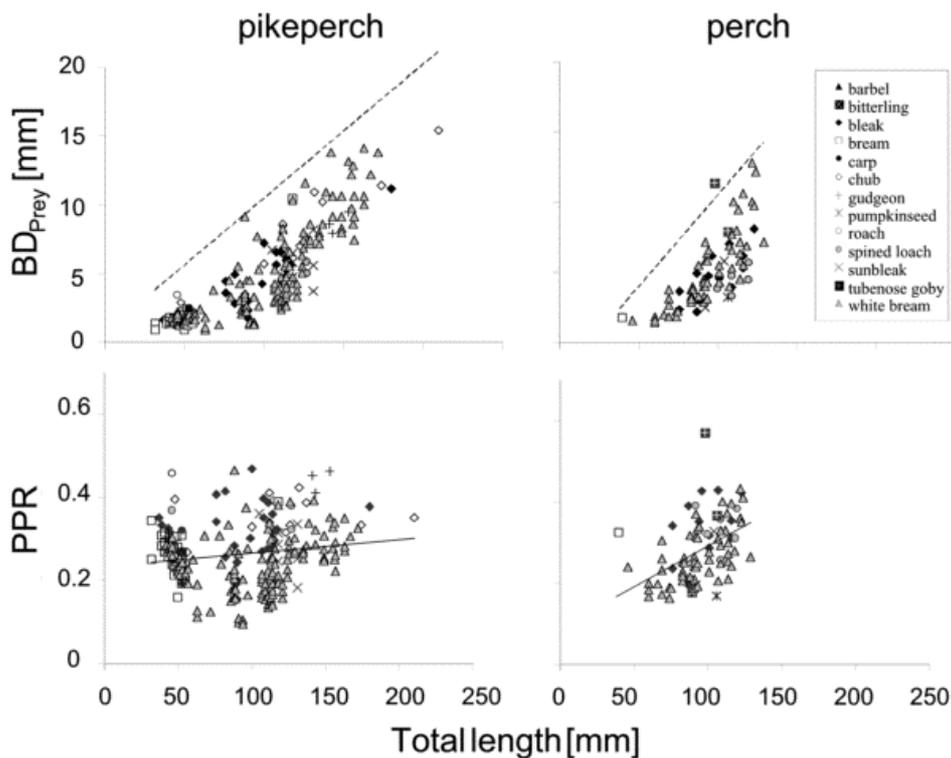


Fig. 3: Relationships of body depth (BD, upper panel) and predator-prey size ratio (PPR, lower panel) of prey fish plotted against total length of piscivorous YOY pikeperch (left) and perch (right). Dashed line: maximum gape width (after indications of Mehner et al. 1998; Dörner and Wagner 2003; Dörner et al. 2007).

#### Size-specific availability and selectivity of prey

Referring to the seven most common prey species exemplarily, gape-width-dependent availability of prey fish differed between the size categories of both predatory species (ANOVA log-transformed abundance,  $F_{4, 61085} = 18.765$ ,  $P < 0.0001$ ). Large pikeperch ( $\geq 75\%$  CL of the size-cohorts) were capable of utilizing the majority of the actually present prey fish (Dunnet-T3 test, total prey abundance versus available prey abundance large pikeperch:  $P = 0.973$ ). In contrast, large perch, small pikeperch and perch ( $\leq 25\%$  CL of the size-cohorts) could only use a small number of the available prey fish size classes (Dunnet-T3 test, total abundance

versus available prey abundance large perch:  $P = 0.045$ ; small pikeperch:  $P = 0.035$ ; small perch:  $P < 0.001$ ). The proportion of piscivores in the cohorts of pikeperch was positively correlated to the availability of suitably sized prey ( $r = 0.285$ ,  $P < 0.0001$ ), however an inverse relationship occurred with respect to the proportion of fish with empty stomachs ( $r = -0.568$ ,  $P < 0.0001$ ). No such significant correlations were found in perch, neither with respect to the proportion of piscivores ( $r = 0.091$ ,  $P = 0.431$ ) nor to the proportion of fish with empty stomachs ( $r = -0.137$ ,  $P = 0.235$ ).

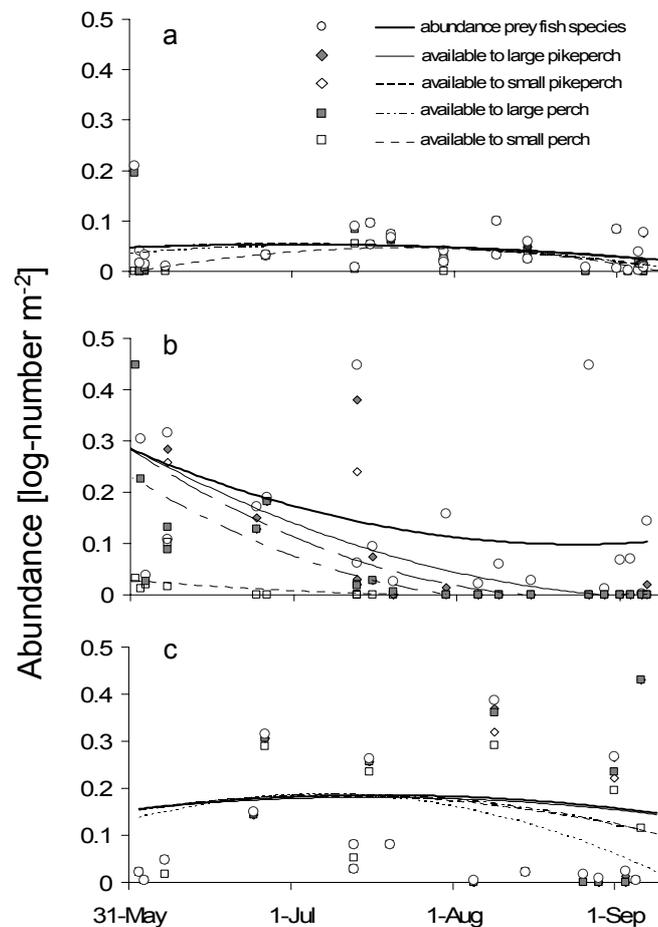


Fig. 4: Seasonally available abundance (as log-numbers  $m^{-2}$ ) of main prey fish species to differentially sized members (large 75% CL; small 25% CL) of the YOY cohorts of pikeperch and perch, based on relationships of BD of prey and maximum gape width of predators: a) shallow-bodied species (gudgeons, spined loach, bleak, chub, sunbleak), b) early spawning, moderately deep-bodied species (bream), c) repeatedly spawning, moderately deep-bodied species (white bream). Data refer only to the six lakes in which both percid occurred.

Availability of the different prey species decreased over the course of the season, but to differing degrees for large and small specimens of the respective size-cohorts. This was most pronounced in fast-growing and deep-bodied species, e.g. bream, which completely outgrew the risk of being preyed upon by YOY percids in all lakes in August (Fig. 4b). Only larger perch were capable of preying upon bream in early summer; smaller perch could only utilize a vanishing portion of the YOY bream cohort due to gape-width restrictions. In contrast, the progeny of the later, repeatedly spawning white bream were available to all YOY pikeperch and perch cohorts in early summer, although the available number decreased over the course of the season for smaller individuals of both percids. The more shallow-bodied YOY fishes (gudgeons, spined loach, bleak, sunbleak, chub) were completely available to all size classes of pikeperch and perch during the whole season (Fig. 4a). Consequently, the time frame for becoming piscivorous was markedly narrower for smaller individuals, particularly in perch.

The first two axes of the PCA on prey species selectivity explained 33.4% and 26.7% of total variability in piscivorous pikeperch, and 33.0% and 24.8% in piscivorous perch, respectively (Fig. 5). Information on total available prey abundance (AA), seasonal aspects of consumption (Month), relative predator size (RPS) and predator-prey size ratios are displayed on axis 1 for both datasets. In accordance with prey availability (Fig. 4), AA and Month were negatively correlated, AA and RPS positively correlated. In both species, a decrease in prey availability over the course of the summer led to an increase in PPR and relative BD of consumed prey (BD-TL-ratio). At the beginning of summer, pikeperch predominantly preyed upon the most abundant prey species, particularly bream; however, such prey were no longer consumed by the end of the summer due to their increase in BD. Both predators avoided preying upon the more deep-bodied species (e.g. bitterling, carp), although these were highly abundant (Table A2). In contrast, at least a part of the pikeperch populations chose predominantly slender prey species (bleak, spined loach, gudgeons, chub) of relative large size, despite their lower availability, whereas the majority selected the most abundant, but smaller prey. A similar behaviour, though less pronounced, was found for perch, which obviously selected prey more opportunistically, as expressed by the closer relationship of RAA and AA. No clear seasonal patterns were obvious with regard to the consumption of the moderately deep-bodied and most available progeny of white bream.

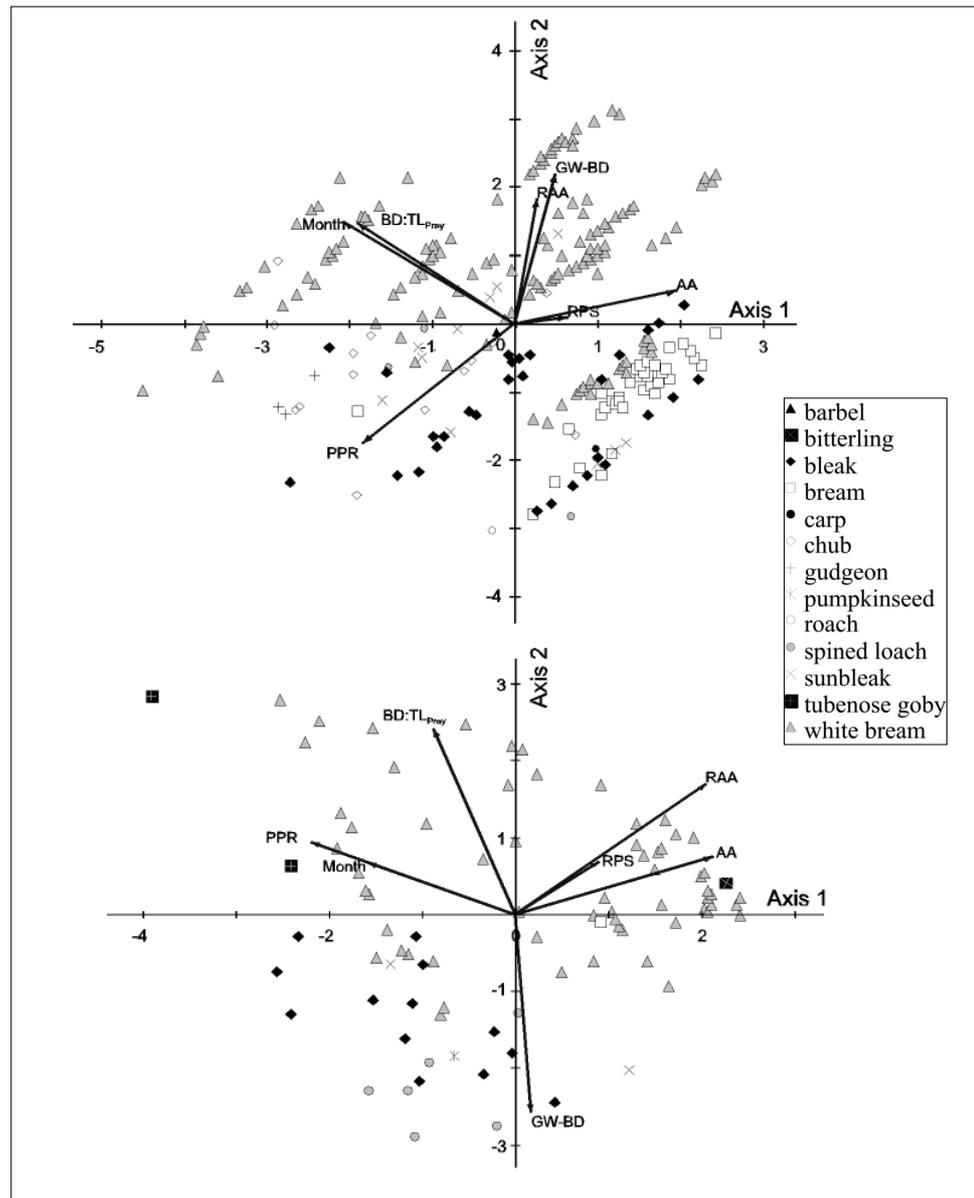


Fig. 5: Principal component analysis of prey species selection in piscivorous YOY pikeperch (upper) and perch (lower). The gradients are: total available prey abundance (AA), relative available prey abundance (RAA – as the proportion of the consumed prey species abundance of the AA), body depth to size ratio of consumed prey (BD:TLPrey), relative predator size (RPS – as the membership to confidence intervals of the respective size cohort), the difference between the predators' gape width and the body depth of the consumed prey (GW-BD), the predator-prey size ratio (PPR) and the month of consumption (Month). Plot symbols indicate the consumed prey species.

### Mortality of prey

Species preyed upon by YOY pikeperch and/or perch suffered significantly higher mortalities than those not consumed (ANOVA,  $F_{1, 100} = 9.593$ ,  $P < 0.0001$ ). Taking only the 13 prey species into account, mortality rates did not differ between the months (ANOVA,  $F_{2, 62} = 0.568$ ,  $P = 0.569$ ), indicating that mortalities are not attributed to ontogeny. The multiple linear regression ( $r^2 = 0.509$ ,  $F_{13, 57} = 4.544$ ,  $P < 0.0001$ ) of the mortality rates with the “proportion of piscivores in the cohort” and the “abundance of pikeperch” used as predictors revealed that predation by pikeperch had a strong impact on mortality rates of prey species. The variables “prey selection of pikeperch in the previous month” ( $B = 2.860$ ,  $T = 2.899$ ,  $P = 0.005$ ), “abundance of pikeperch in the previous month” ( $B = 2.424$ ,  $T = 1.811$ ,  $P = 0.075$ ), “proportion of piscivores in the cohort of pikeperch” ( $B = 2.533$ ,  $T = 1.425$ ,  $P = 0,160$ ) improved the fit of the model substantially. With respect to variables related to perch, only “prey selection of perch in the previous month” ( $B = 1.848$ ,  $T = 2.631$ ,  $P = 0.011$ ) and “abundance of perch in the previous month” ( $B = -1.918$ ,  $T = -2.061$ ,  $P = 0.044$ ) contributed significantly to the fit of the model. The impact of “prey selection by perch” is suspected to have been underestimated, since this variable was significantly correlated to “prey selection of pikeperch” ( $r = 0.420$ ,  $P < 0.0001$ ).

### Determinants of piscivory

Taking only specimens with non-empty stomachs into account, the datasets analysed with logistic regression contained 213 cases for pikeperch (55.4% piscivores) and 293 cases for perch (17.1% piscivores). The models were able to predict piscivory in YOY pikeperch (model chi-square:  $\chi^2 = 132.914$ , d.f. = 19,  $P < 0.0001$ ; Hosmer-Lemeshow test:  $\chi^2 = 13.103$ , d.f. = 8,  $P = 0.108$ , -2-Log-Likelihood: 159.878) and YOY perch (model chi-square:  $\chi^2 = 168.601$ , d.f. = 16,  $P < 0.0001$ ; Hosmer-Lemeshow test:  $\chi^2 = 6.737$ , d.f. = 8,  $P = 0.565$ , -2-Log-Likelihood: 98.775; Table. 5) quite precisely. 86.4% of piscivorous and 79.9% of non-piscivorous pikeperch were predicted correctly; the explainable variance of the model for pikeperch (Nagelkerke  $R^2 = 0.62$ ) was lower than that for perch (Nagelkerke  $R^2 = 0.73$ ). Here, 70% piscivores and 97.5% non-piscivores were predicted correctly, indicating that the onset of piscivory in the specialist piscivore pikeperch is not as strongly related to environmental factors as in perch,

Table 5: Parameters and statistics of the logistic regression models to predict piscivory in YOY pikeperch and perch in floodplain lakes of the Lower River Rhine.

Variable	pikeperch					perch								
	$\beta$	Wald	d.f.	P	odds ratio	95% CL lower	95% CL upper	$\beta$	Wald	d.f.	P	odds ratio	95% CL lower	95% CL upper
lake area	-0.201	12.778	1	**	0.818	0.732	0.913	-0.546	11.754	1	**	0.569	0.412	0.785
mean depth		0.507	1	ns				-11.953	19.881	1	***	0.000	0.000	0.001
max depth		0.990	1	ns				8.151	21.616	1	***	3467.465	111.605	10773.131
Transparency		1.437	1	ns				1.553	10.368	1	**	4.726	1.836	12.164
% riparian cover		1.785	1	ns				0.467	15.066	1	***	1.595	1.260	2.019
% cover aquatic vegetation		1.853	1	ns					0.055	1	ns			
Frequency of inundation		0.662	1	ns					15.550	2	***			
May								-3.518	12.126	1	***	0.030	0.004	0.215
May and June								2.370	6.440	1	*	10.694	1.715	66.680
cohort strength									0.092	1	ns			
month	-4.243	18.852	1	***	0.014	0.002	0.097		14.128	3	**			
July	1.003	4.138	1	*	2.726	1.037	7.615	1.372	3.526	1	ns	3.943	0.942	16.510
August	1.403	6.041	1	*	4.068	1.329	7.165	2.822	12.196	1	***	16.815	3.450	81.960
September	-2.733	8.250	1	*	0.065	0.100	0.420	-0.886	1.540	1	ns	0.412	0.102	1.670
availability of prey		6.597	1	**	732.676	9.774	54921.095		0.024	1	ns			
availability of prey by month									11.343	3	*			
July	-6.556	8.876	1	*	0.001	0.000	0.106	-0.072	5.384	1	*	0.931	0.876	0.989
August	-6.549	8.856	1	*	0.001	0.000	0.107	-0.036	2.638	1	ns	0.964	0.923	1.007
September	19.652	8.859	1	*	3E+08	821.606	1.43E+14	0.209	10.891	1	**	1.233	1.089	1.396
size category		29.268	5	***					29.271	5	***			
>5-25%	-1.943	14.808	1	***	0.143	0.053	0.385	-4.181	19.527	1	***	0.015	0.002	0.980
>25-50%	-0.636	2.381	1	ns	0.530	0.236	1.187	-1.311	3.221	1	ns	0.270	0.064	1.128
>50-75%	0.981	4.644	1	*	2.667	1.093	6.507	-0.745	1.002	1	ns	0.475	0.111	2.041
>75-95%	1.606	13.585	1	***	4.985	2.122	11.714	1.751	6.289	1	*	5.758	1.466	22.614
>95%	2.586	12.350	1	***	132.282	3.139	56.197	8.057	9.981	1	**	3155.443	21.297	467519.273
availability of prey by size		6.217	5	ns					3.273	5	ns			

Asterisks indicate significance (\* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001, ns: not significant)

or that there might have been additional variables not taken into account. Lake area was the only habitat-specific variable influencing piscivory in pikeperch significantly: Piscivory increased with a decrease in lake area. The number of piscivores decreased with increasing numbers of conspecifics in the water body. The probability of becoming piscivorous was highest in midsummer, decreasing significantly towards the end of summer. Piscivory was significantly enhanced in the presence of large numbers of available prey fish, a fact which became increasingly important towards the end of the growing season. In general, the largest individuals in the cohort had the highest chance of being or becoming piscivorous, whereas the model indicates the opposite to be true for the smaller half of the size-cohort. No general or significant interactions were found between the availability of prey and the size of the predator (Table. 5).

In contrast to pikeperch, environmental conditions strongly affect piscivory in perch, which increased with decreasing lake area and mean depth but was generally enhanced in the deeper (gravel-pit) lakes, in the more frequently inundated lakes and under conditions of low turbidity. As also the case for pikeperch, the probability of perch being piscivorous was highest in midsummer. No general influence of prey availability is indicated by the model, whereas this factor significantly promoted the chance of being piscivorous in late summer, when prey became less available. Size was one of the most prominent factors leading to piscivory in perch, with a considerably steeper gradient between the lower and the upper limits of the size cohort than found for pikeperch. Related to the smallest individuals in any given cohort, the probability of being piscivorous was more than 3000-fold higher for the largest YOY perch, however no conspicuous interaction with respect to the number of available prey was identified (Tab. 5).

## Discussion

Recruitment and diet dependent growth of YOY pikeperch and perch within the floodplain

Floodplain lakes are important habitats for the recruitment of YOY perch and pikeperch, an observation supported by the high densities estimated in our study, as well as by comparisons of abundances between the main channel of the river Rhine and floodplain lakes carried out in the same river section (Staas 1997; Grift 2001). To our knowledge, no information on differential growth of the two species between rivers and floodplain habitats exists. However, the growth rates of YOY percids and the total lengths attained at the end of first summer were extraordinarily high compared to published data for several freshwater systems. Although we found no general relationship between growth and the frequency of inundations, as proposed by the FPC to exist (Junk *et al.* 1989; Gutreuter *et al.* 1999), we identified a high degree of diet specialisation and a rapid growth in both species, particularly in specimens shifting to piscivory during summer. Similar or even higher growth, with total lengths of appreciably above 100 mm at the end of the growing season, were found for YOY perch feeding predominantly on mysids in brackish waters in the Netherlands (Houthuijzen, Backx, and Buijse 1993; Van Densen *et al.* 1996). The same applied to perch that utilized a mixture of mysids and fish prey in a flood plain lake of the Lower River Rhine (Borcherding *et al.* 2007) or fed exclusively on fish in a gravel-pit lake (Beeck *et al.* 2002). Total lengths of pikeperch at the end of the first growing season in our study were of a similar (or even slightly higher) range as found for other waters in the same geographic region (Willemsen 1977; Buijse and Houthuijzen 1992; Van Densen *et al.* 1996).

The role of floodplain inundation upon the onset and maintenance of piscivory

Our findings indicate that the rapid growth and, in interaction, the large proportions of piscivorous YOY were favoured by the seasonal occurrences of inundations and the related amount of prey during summer. The size advantage the two studied species had over their later prey species, which enabled them to consume other YOY fishes, was apparently promoted by an earlier hatching and rapid growth in the following weeks (Mittelbach and Persson 1998). Owing to spring warming, the lower temperature threshold of approximately 8°C required by both species for spawning (Thorpe 1977; Lappalainen *et al.* 2003) was already attained in the floodplain lakes

in late March, whereas the major prey species bream, chub, bleak, sunbleak, spined loach, sunbleak and white bream require water temperatures of at least 12°C for spawning (Mann 1996; Pinder 2001). In accordance to the predictions of the FPC, it has been demonstrated for European temperate rivers that the reproduction of many species depends on the coincidence of rising water levels and species-specific temperature thresholds, which enable spawners of many species (e.g., bream and white bream) to immigrate into and to spawn on the floodplain (Spindler 1995; Molls 1999; Grift 2001) and enables larvae of riverine-spawning species (e.g., bleak, chub, barbel) to colonize the floodplain. Although we did not measure this parameter, it has been demonstrated that inundations cause parallel high densities of zooplanktonic organisms in floodplain lakes (Baranyi *et al.* 2002), serving as prey for YOY fish and providing benefits to their recruitment (Junk *et al.* 1989).

Most of the floodplain lakes became inundated in the middle of May. Water temperatures were appropriate for spawning of most species at this time, resulting in a peak in abundance of cyprinid larvae in the following weeks, providing large numbers of small prey fish for the larger YOY perch and pikeperch. It is suggested that the size advantage of YOY percids and, in interdependency, the availability of prey and consequently the probability of becoming piscivorous decreases if the time frame between the hatching of percids and their potential future prey is narrow. Furthermore, if the hatching dates of the percids and the cyprinids are too close together, interspecific competition for planktonic prey probably occurs, implicating disadvantages for perch and pikeperch (Persson and Greenberg 1990; Persson and Bronmark 2002). However, high densities of zooplankton and the associated rapid initial growth of YOY piscivores have been demonstrated to favour an early switch to fish diet (Persson and Bronmark 2002). Particularly perch normally utilize invertebrate prey before utilizing fish prey from age 1+ onwards. This transitional benthivorous feeding stage is explained by competitive disadvantages due to cyprinid species feeding more efficiently on planktonic prey (Persson 1988) and may last several years. In our study, this ontogenetic shift occurred quickly within the first weeks or months after hatching and might indeed have been triggered by an increasing competition for zooplankton, which is suggested by a continuous decrease in water clarity in all lakes where specialist planktivores occurred in high abundance, owing to an increased predatory pressure on grazing zooplankton organisms (Jeppesen *et al.* 1996).

In addition to benthic invertebrates, both percids (in particular perch) already preyed upon the energetically more beneficial mysids (Van Densen *et al.* 1996) in June, which have been demonstrated to promote very rapid growth (Houthuijzen *et al.* 1993; Borcharding *et al.* 2007). Although the growth rates attained by specimens specifically preying upon mysids were lower than in piscivorous fish, we hypothesize that the intensive consumption of mysids favours an earlier shift to piscivory in perch. This hypothesis is supported by the fact that the number of piscivorous, most rapidly growing perch increased in lakes where mysids had accounted for a large proportion of the diet of perch in June (inasmuch as fish prey was available). This may seem at first glance to be in disagreement with the findings of the authors cited above, which showed that perch continued to prey on mysids at least throughout the first growing season; however, the abundance of potentially available prey fish was markedly lower in the waterbodies in which these studies were conducted.

Besides the high densities of small YOY fish in general, we consider the prey species composition in the different floodplain lakes to be an important parameter, since the adults of most of the YOY prey fish spawn repeatedly (Nunn, Harvey, and Cowx 2007), thus providing suitably sized prey for piscivorous YOY fish over an extended period of the first growing season. This was found in particular for lakes inundated for a second time in the middle of June, causing an increase in abundance of early life stages of white bream, chub and bleak. These species are considered to effectuate a revitalisation of the spectrum of available prey, thus giving the YOY percids in such lakes an advantage over piscivorous individuals in lakes where this is not the case, or giving smaller and previously non-piscivorous individuals in the cohort the opportunity to switch to piscivory. In most of the lakes not inundated repeatedly, or in which no adults of multiple spawning species were present, the availability of prey decreased continuously due to predation or due to an increase in size and/or body depth of the prey fish.

#### Seasonal and species-specific implications of predator-prey relationships

Differences in morphological development during ontogeny of several fishes occurring in the floodplain caused a differential vulnerability towards gape-width restricted predators, since more deep-bodied species have been shown to reach a size-refuge at a smaller size and were thus selected less often by predators than

shallower-bodied species of similar size (Nilsson and Bronmark 2000). This is clearly reflected by the seasonal prey selection and by seasonal patterns of predator-induced mortality in our study. In late summer, fast-growing and more deep-bodied species suffered much lower mortalities, whereas many shallow-bodied species completely vanished in lakes where piscivorous YOY percids were present. This demonstrates the structuring role of piscivorous YOY fish upon the YOY fish community in floodplain lakes and might favour the predominance of more deep-bodied YOY fishes in such habitats. In contrast, shallow-bodied species have been shown to dominate the fish community in predator-free environments (Hambright 1991).

Although the size of an individual within any given cohort was the most prominent factor in determining the individual was piscivorous or not for both species, there were still discernible differences between perch and pikeperch. Intermediate or even small-sized pikeperch frequently became piscivorous in late summer as long as appropriately sized prey was available; however, this applied only to individuals in the upper size range of the YOY perch cohort. This is not satisfactorily explained by lower gape-width-dependent prey availability, since the differences between the smallest and largest individuals in the cohorts of both species diminished in early summer, indicating that only largest (and presumably earlier piscivorous) perch maintained piscivory. In pikeperch, a reduction in the availability of fish prey yielded an increasing and higher number of individuals with empty stomachs, indicating a stronger specialisation towards this food resource (Keast 1985). An early occurring shortage of fish prey forced pikeperch to remain in the planktivorous or benthivorous niche, which resulted in retarded growth (e.g. GP3), compared to the lakes in which prey was available for a longer period. However, we cannot exclude the possibility that formerly piscivorous pikeperch switched back to a diet of lower trophic levels.

The size advantage of larger individuals in a cohort over smaller individuals, which might have been caused by earlier hatching or an earlier specialisation to the energetically beneficial fish prey (Post 2003), resulted in a higher availability of prey in late summer, in particular in the lakes in which prey became scarce. The capture success in gape-limited piscivores has been shown to decrease with increasing prey size (Lundvall *et al.* 1999), enabling only the largest individuals to sustain piscivory by preying upon large or deep-bodied prey. This might explain the increasing number of pikeperch and perch with empty stomachs in the lakes in which the prey

availability had sharply decreased. The high growth rates estimated for specimens of both species with empty stomachs suggest that such individuals had indeed originally been piscivorous. Besides the advantage of larger gape widths, the maintenance of piscivory was probably additionally favoured in individuals which had switched to fish diet earlier and were thus better adapted for the capturing and handling of prey (Galarowicz and Wahl 2005). Furthermore, we found differences in prey species selection between pikeperch and perch: Pikeperch actively selected more slender prey species despite their lower availability, an observation which is in agreement with the results of previous studies (Willemsen 1977; Buijse and Houthuijzen 1992) and is probably attributed to advantages with respect to handling of prey. However, pikeperch selected the smallest prey at high prey densities, which indicates active prey selection in order to maximise energy intake per unit time (Turesson, Persson, and Bronmark 2002). On the contrary, perch preyed more opportunistically and predominantly selected the most abundant species, which might be attributed to a lower degree of specialisation, and a different hunting strategy in combination with shoaling behaviour of prey (Turesson and Brönmark 2004).

Differential adaptation of YOY pikeperch and perch towards the environmental conditions in the floodplain lakes

At least a part of the YOY-cohort of pikeperch became piscivorous in all lakes; this fact did not apply to perch and can be partially addressed to certain environmental factors. Perch only infrequently preyed upon fish in lakes that had become turbid over the course of the summer, which is in agreement to the findings of Persson *et al.* (1991). The authors found the proportion of piscivorous perch to decrease with increasing eutrophication (Persson *et al.* 1991), which is most often accompanied by intensive phytoplankton primary production and additionally enhanced in the presence of high densities of planktivorous fish (Jeppesen *et al.* 1996). Besides high densities of planktivores, resuspension of sediments and increased nutrient cycling through benthivorous cyprinids (Breukelaar *et al.* 1994) have also been demonstrated to promote the turbidity of floodplain lakes (Roozen *et al.* 2003). The resulting decrease in water transparency apparently impairs the capture success of the visually feeding perch (Radke and Gaupisch 2005; Pekcan-Hekim and Lappalainen 2006). In contrast, we found higher proportions of piscivorous YOY perch in the deep gravel-pit lakes, which are less turbid and provide little shelter for the prey fish, enabling

perch to detect and capture prey more efficiently (Eklöv and Diehl 1994). In comparison to perch, pikeperch are well adapted towards turbidity and scattered light conditions (Ali and Ryder 1977) and are considered to be able to detect prey even in turbid environments, which might explain the higher proportion of piscivorous YOY pikeperch in the more turbid floodplain lakes.

Pikeperch have even been shown to prey more efficiently in environments of low structural complexity (Greenberg *et al.* 1995), however, this circumstance was negligible in our study. Nevertheless, the number of piscivores of both species increased with a decrease in water level in the lakes (as indicated by the negative regression coefficients concerning lake area and mean depth in Table 1), which is probably attributed to the associated decrease in riparian shelter structures for their fish prey. The available abundance of white bream, the most frequently taken prey, was markedly higher in late summer in lakes with denser vegetation cover, and outweighs (in our opinion) the effect of more shelter for the prey provided by vegetation.

Even though accelerated growth is known to be beneficial at the individual as well as at the population level (Buijse and Houthuijzen 1992; Lappalainen *et al.* 2000), we cannot prove whether or not piscivores had higher survival rates than non-piscivorous during winter since juveniles of both species are either absent or only marginally abundant in the floodplain in the subsequent spring (see chapter 1). This is probably due to an emigration to the river during flood events. Similar ontogenetic patterns of habitat utilization, e.g. juveniles emigrating from the floodplain, have been documented in other potamal species (Molls 1999; Grift 2001), however these shifts have yet to be fully explained. They might have evolved to overcome an increased risk of predation by wintering cormorants (Santoul *et al.* 2004) or to exploit alternative food resources, since the availability of food in the isolated floodplain waterbodies decreases with the duration of the isolation phase and the number of competitors. In case of gape-limited YOY piscivores, the shift to the river is hypothesized to provide a broader spectrum of appropriately sized prey fish, in particular the preferred slow-growing and shallow-bodied fish prey (e.g., bleak or chub), which are much more abundant in river habitats than in floodplain habitats (Copp 1989; Staas 1997).

In conclusion, our findings not only indicate the significance of seasonal flooding events on recruitment, but the indirect effects caused by the flood-dependent

availability of prey on the first-year growth of two functionally different predatory species in a temperate river floodplain. Although we have no experimental data on diet relatedness, we found considerable first-year growth differences in both percid species. Retarded growth and a poor recruitment of both YOY percids, and in contrast, an enhanced recruitment of their potential prey species was observed in years when inundations were coupled with a sudden increase in water temperature (to levels required for cyprinid species to spawn) which occurred too soon after the temperature requirements for spawning of pikeperch and perch had been met. These disadvantages for the percid species were also observed, when no inundations occurred in the time frame when cyprinid spawning usually takes place. This underlines the significance of simultaneous spring warming and seasonal floodplain inundations and might point to their benefits for any particular species. Further work is required to be able to extrapolate our observations to apply to other temperate floodplain rivers, to explore whether comparable relationships exist in other YOY piscivores, and finally, to investigate whether or not year class strength in river populations can be attributed to appropriate conditions for the onset of piscivory in the respective YOY cohort.

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### **Point abundance sampling by electrofishing and density estimation in floodplain lakes**

The sampling method used in the present thesis had to meet several constraints: It should 1) require a low man power, 2) provide accurate abundance estimates for all size- and age-classes of fish present and over several habitat scales to make data comparable in space and time, 3) allow to sample habitats of high structural complexity (e.g. dense vegetation or woody debris), and 4) should keep the impact of sampling on the fish community as low as possible, since some topics of this work required repeated measurements of species densities over an extended time scale, which precludes the use of sampling techniques implying an increased risk of violation or death to the fish. This is most important, since many waterbodies studied were rather small and comprised a manageable number of inhabiting fish, thus, sampling induced mortalities had to be strictly avoided. On these constraints several techniques frequently used for abundance estimates, such as seining or gillnetting, could not be exerted. The same applies to electrofishing procedures in the way they are commonly used (permanent exertion of current), since these does not allow replicated samples, as required for analysis of microhabitat associations and probably bear the problem of inaccurate quantification due to a “fright bias” caused by the perception of the current field by fish (Halsband 1980; Heggenes, Brabrand, and Saltveit 1990; Reynolds 1990).

In contrast, fractional sampling techniques, in which numerous small samples instead of few large samples are taken, are considered to estimate the spatial structure of assemblages or even populations more representatively and make data statistically more reliable, since fish are often patchily distributed (Chessel 1978; Copp and Penaz 1988; Garner 1997). Stealthy approaching to the sampling point reduces the probability of disturbance prior to sampling and minimizes fright bias and, thus, leads to higher catch efficiency (Persat and Copp 1989; Copp and Garner 1995; Perrow, Jowitt, and Gonzales 1996).

For those reasons point abundance sampling by electrofishing (PAS) has become a frequently used and well established technique for sampling of juvenile fish in many European rivers and their floodplains (e.g., Copp 1989; Copp *et al.* 1994; Poizat and Pont 1996; Copp 1997; Freyhof 1998; Jurajda 1999; Grenouillet, Pont, and Olivier 2001; Pont and Nicolas 2001; Bischoff 2002), and was recently even applied for sampling of adult fish (e.g., Fladung, Scholten, and Thiel 2003). In the present thesis,

a PAS method for the sampling of YOY fish was applied from April till September using a battery-powered pulsed DC unit (6 A, 600 V, Deka 3000; DEKA Gerätebau, Marsberg) with a small ring-shaped anode (diameter 0.1). Sampling was conducted by approaching the sampling point carefully and immersing the activated anode swiftly to maximally one meter depth, keeping it motionless for approximately five seconds, after which all narcotised fish were harvested with a separate dip-net (mesh-size 0.5 mm). Despite some authors proposed PAS in general and the described gear modification to be particularly suitable to catch differently sized YOY and older juveniles quite representatively (e.g., Copp 1990; Copp and Garner 1995; Perrow *et al.* 1996; Garner 1997), other authors suggested the method to be highly selective for small larvae and juveniles and to underestimate density of larger YOY fish (Cox, Nunn, and Harvey 2001; Oesmann and Scholten 2002). To overcome this problem, additionally a generator-powered DC unit (300 V, 6.6 A, Deka 5000; DEKA Gerätebau, Marsberg, Germany) and a ring anode with an inserted landing net (diameter 0.4 m, mesh size 4 mm) was used, which exerts a stronger attraction of fish towards the activated anode and, thus, was considered to reduce the effects of size-related bias, when used in combination with the equipment modified for small fishes. The sampling technique with the DC unit differed to some degree from the previously described. After approaching the sampling point, the generator was started simultaneously to the immersion of the anode, which was dipped as close to the bottom as possible and slowly pulled to the surface in a strictly vertical position and all attracted fish were harvested after deactivating the anode (under help of an assistant with a second landing net in case of numerous narcotised fish).

In most published studies, density estimated by PAS were calculated by assuming the effective range of the current field in which the fish are narcotised as a static area, e.g. by determining the threshold values of current density being strong enough to narcotise fish (e.g., Copp and Garner 1995; Fladung *et al.* 2003; Lewin, Okun, and Mehner 2004). However, this procedure does not take into account the size of fishes, which is an important determinant of its reaction to the current field (Reynolds 1990). Freyhof (1998) determined correction factors for different size-classes of fish and Bischof (2002) plotted observed reaction distances of stunned fish towards the activated anode versus their total length, in order to obtain equations to quantify the sampled area for differently sized fishes. Scholten (2003) developed regression equations on this topic, which additionally take the effects of conductivity and

differently grained bottom substrata into account. Conductivity during this study was always quite similar ( $748.2 \pm 83.6 \mu\text{S cm}^{-1}$ ) as was the prevailing substrate (silt) at most sampling occasions and waterbodies. However, because different gears were used over a wide range of temperatures ( $5.3\text{-}27.9^\circ\text{C}$ ), size-specific regressions of observed reaction distances were determined in a similar way as described by Bischof (2002). We only took into account observations of two persons, when these did not deviate for more than 0.05 m. The experiments were conducted by approaching espied schools and immersing the anode in their proximity and determining the total length (mm) and the distance of the most remote fish stunned fish relative to the point where the anode was immersed. Data were estimated for the pulsed DC and the DC unit separately, however, for the latter, which was the only system used in winter ( $<10^\circ\text{C}$ ), separate regressions were obtained for temperatures above and below  $10^\circ\text{C}$ . In all cases power functions explained most of the variability in the data. Using the obtained equations (Fig. 1), density (individuals  $\text{m}^{-2}$ ) was calculated implying that the sampled area was approximately circular ( $\pi r^2$ ).

The length-distributions obtained with different gears (Fig. 1) show that predominantly YOY fish were caught, which, particularly applied to the pulsed DC unit modified for small fish. Length-distributions derived from the pulsed DC unit were significantly different from those of the parallel used DC unit (Mann-Whitney-Test  $\text{DC}_{\text{summer vs pulsed DC}}$ :  $U = 1716 : 885$ ;  $P = 0.005$ ), which also applied when taking into account fish  $> \text{TL } 100$  (Mann-Whitney-Test  $\text{DC}_{\text{summer vs pulsed DC}}$ :  $U = 939 : 1662$ ;  $P = 0.015$ ), indicating that the combination of methods is reasonable to obtain an estimate of size-classes present.

Densities were then calculated for each species and gear and averaged (including 0-samples) for spatial or seasonal comparisons. To overcome bias caused by schooling behaviour of fish (Persat and Copp 1989; Garner 1997), this problem was encountered by taking many samples in order to sample a representative area of the total lake surface (at least 50 in waterbodies  $< 0.5$  ha and up to 1,000 in waterbodies  $> 10$  ha). Although it remains unknown if the applied sampling technique and the way of abundance estimation reflect the real situation, it makes at least the estimated values comparable over several spatial and seasonal scales.

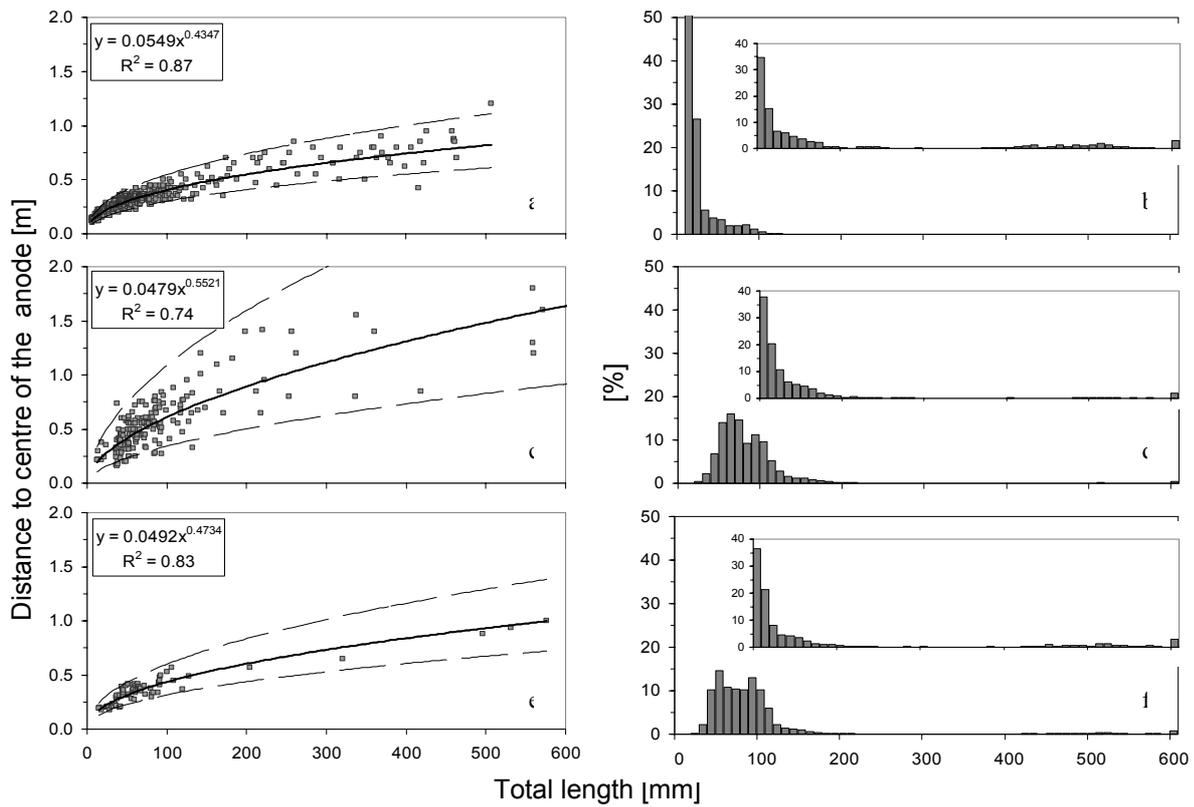


Fig. A1: Plots of reaction distance of differently sized fish towards the activated anode (a, c, e) and the relative length-frequency distribution (b, d, f) for a modified pulsed DC unit with small ring-shaped anode ( $d = 0.1$  m) (a, b), DC unit with anode ( $d = 0.4$  m) at water temperatures  $> 10^\circ\text{C}$  (c, d) and at water temperatures  $< 10^\circ\text{C}$  (e, f). Solid lines and parameters in a, c, e give regressions and equations used for density estimates (broken lines upper and lower 95% interval), insets in b, d, f refer to relative abundance of individuals  $> \text{TL } 100$  mm.

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Table A1: List of all species encountered by point abundance sampling by electrofishing in the present thesis, their ecological classification, vulnerability (after Red List for the FRG and the federal state Northrhine-Westphalia: 0 = extinct; 1 = critical; 2 = endangered; 3 = vulnerable) and their numbers and relative abundance in the total catch

Family	Species	English name	Ecological classification		Vulnerability			Number	%
			Reproductive guild <sup>1</sup>	Ecological guild <sup>2</sup>	RD FRG	RD NW	FFH-status		
Anguillidae	<i>Anguilla anguilla</i> (L.)	Eel	pelagophilic	eurytopic	3	.	.	65	0.06
Centrarchidae	<i>Lepomis gibbosus</i> (L.)	Pumpkinseed	nestguarder		.	.	.	42	0.04
Cobitidae	<i>Cobitis taenia</i> (L.)	Spined loach	phytophilic	rheophilic B	2	2	II	563	0.52
Coregonidae	<i>Coregonus lavaretus</i> (L.)	Whitefish	pelagophilic		3	.	.	4	<0.01
Coregonidae	<i>Coregonus oxyrinchus</i> (L.) <sup>†</sup>	Houting	pelagophilic	rheophilic B	0	0	II	1	<0.01
Cottidae	<i>Cottus rhenanus</i> (Freyhof, Kottelat & Nolte)	Bullhead	speleophilic	rheophilic A	.	.	.	1	<0.01
Cyprinidae	<i>Abramis brama</i> (L.)	Bream	phyto-lithophilic	eurytopic	.	.	.	41,324	37.85
	<i>Alburnus alburnus</i> (L.)	Bleak	phyto-lithophilic	eurytopic	.	.	.	2,883	2.64
	<i>Aspius aspius</i> (L.)	Asp	lithophilic	rheophilic B	3	.	II	3,698	3.39
	<i>Barbus barbus</i> (L.)	Barbel	lithophilic	rheophilic A	2	3	.	2,092	1.92
	<i>Blicca bjoerkna</i> (L.)	White bream	phytophilic	eurytopic	.	.	.	12,492	11.44
	<i>Carassius gibelio</i> (Bloch)	Prussian carp	phyto-lithophilic	eurytopic	.	.	.	207	0.19
	<i>Chondrostoma nasus</i> (L.)	Nase	lithophilic	rheophilic A	2	3	.	220	0.20
	<i>Cyprinus carpio</i> (L.)	Carp	phytophilic	eurytopic	.	.	.	6,826	6.25
	<i>Gobio gobio</i> (L.)	Gudgeon	psammophilic	rheophilic B	.	.	.	280 <sup>‡</sup>	0.26
	<i>Romanogobio belingi</i> (Slavenenko)	Whitefin gudgeon	psammophilic	rheophilic B	2	.	II		
	<i>Leucaspius delineatus</i> (Heckel)	Sunbleak	phytophilic	stagnophilic	3	3	.	1,766	1.62
	<i>Leuciscus cephalus</i> (L.)	Chub	lithophilic	rheophilic A	.	.	.	1,271	1.16
	<i>Leuciscus idus</i> (L.)	Ide	phyto-lithophilic	rheophilic B	3	.	.	1,437	1.32
	<i>Leuciscus leuciscus</i> (L.)	Dace	phyto-lithophilic	rheophilic A	3	.	.	429	0.39
	<i>Phoxinus phoxinus</i> (L.)	Minnow	lithophilic	rheophilic A	3	3	.	3	<0.01
	<i>Pseudorasbora parva</i> (Temnick & Schlegel)	Japanese minnow	phytophilic		.	.	.	3,684	3.37
	<i>Rhodeus amarus</i> (Bloch)	Bitterling	ostracophilic	stagnophilic	2	1	II	5,787	5.30
	<i>Rutilus rutilus</i> (L.)	Roach	phyto-lithophilic	eurytopic	.	.	.	12,807	11.73
	<i>Scardinius erythrophthalmus</i> (L.)	Rudd	phytophilic	stagnophilic	.	3	.	62	0.06
	<i>Tinca tinca</i> (L.)	Tench	phytophilic	stagnophilic	.	3	.	662	0.61
	<i>Vimba vimba</i> (L.)	Vimba bream	lithophilic	rheophilic A	2	.	.	9	0.01
	<i>Alburnus alburnus</i> x <i>Leuciscus cephalus</i>	hybrid			.	.	.	2	<0.01
	<i>Abramis brama</i> x <i>Rutilus rutilus</i>	hybrid			.	.	.	41	0.04
Esocidae	<i>Esox lucius</i> (L.)	Pike	phytophilic	eurytopic	3	3	.	190	0.17
Gasterosteidae	<i>Gasterosteus aculeatus</i> (L.)	Threespined stickleback	ariadnophilic	stagnophilic	.	.	.	1,492	1.37
	<i>Pungitius pungitius</i> (L.)	Tenspined stickleback	ariadnophilic	stagnophilic	.	.	.	179	0.16
Gobiidae	<i>Proterorhinus marmoratus</i> (Pallas)	Tube-nose goby	speleophilic	eurytopic	.	.	.	169	0.15
Ictaluridae	<i>Ameiurus melas</i> (Rafinesque)	Black bullhead	nestguarder		.	.	.	1	<0.01
Percidae	<i>Gymnocephalus cernuus</i> (L.)	Ruffe	phyto-lithophilic	eurytopic	.	.	.	300	0.27
	<i>Perca fluviatilis</i> (L.)	Perch	phyto-lithophilic	eurytopic	.	.	.	6,033	5.53
	<i>Sander lucioperca</i> (L.)	Pikeperch	nestguarder	eurytopic	.	.	.	2,113	1.94
Petromyzontidae	<i>Lampetra fluviatilis</i> (L.)	River lamprey	lithophilic	rheophilic A	2	2	II	18	0.02
	<i>Petromyzon marinus</i> (L.)	Sea lamprey	lithophilic	rheophilic A	2	2	II	4	<0.01
Pleuronectidae	<i>Platichthys flesus</i> (L.)	Flounder	pelagophilic	eurytopic	.	.	.	10	0.01
Siluridae	<i>Silurus glanis</i> (L.)	Catfish	nestguarder	eurytopic	2	1	.	9	0.01

<sup>†</sup> species is subject to a reintroduction programme and was stocked in a tributary of the Lower Rhine

<sup>‡</sup> *Gobio gobio* and *Romanogobio belingi* were present as adults, however YOY could not be discriminated below TL 60 mm

<sup>1</sup> Reproductive guild after Balon (1975)

<sup>2</sup> Ecological guild after Schiemer & Waidbacher (1992). Not specified species left blank.



**Abstract**

The seasonal occurrence of river temperatures in correlation to flood events is a key factor for lateral migrations, the recruitment dynamics and the related organisation of communities within different ecotones of the floodplain. The interaction of species-specific temperature requirements for spawning and reproductive strategies suggest adaptations to the long-term hydrograph, since the presence of species life-time stages within waterbodies are differently affected by seasonal inundations and recruitment patterns that occur along a hydrological gradient, thus, favouring different life-history strategies. Floodplain recruitment of most large species that mature late, with high fecundity and spawn comparably early in the season, is highly attributed to inundations occurring in this time-frame and resulted in massive larval peaks in all waterbodies affected by the connection to the main river. For some of these species, which predominantly exhibit typical trait features associated with the periodic life-history strategy, e.g. in bream (*Abramis brama*), this adaptation to long-term discharge patterns is evident by lateral spawning migrations of adults and spawning on freshly flooded vegetation. In contrast, the progeny of riverine spawning species, such as the asp (*Aspius aspius*), enters the floodplain by either passive in-drift or immigrations during flood events. Recruitment in some of these species in non-permanently connected floodplain waterbodies was drastically reduced (e.g. in the roach, *Rutilus rutilus*) or failed completely (e.g. in the bream), when no inundations occurred in the time-frame when their spawning takes place, confirming the strong adaptation to the long-term hydrograph.

The young-of-the-year (YOY) of these periodic strategists are mostly characterised by fast growth, which is favoured by the early spawning and is often accompanied by a diet specialisation. The relative large size of the YOY apparently influences habitat utilisation on different scales, since larvae and juveniles exhibit low preferences for vegetated microhabitats that provide shelter from predators, and emigrate from the floodplain at given connectivity in the course of the summer or at latest during inundations occurring in winter. This behaviour was apparent by sharp decreases of abundance in waterbodies that became inundated for the first time after spring inundations and parallel increases of YOY in the river channel. However, the timing of this shift differed between species belonging to different ecological guilds and was most pronounced in some rheophilic (e.g., barbel, *Barbus barbus*; nase, *Chondrostoma nasus*) and eurytopic species (e.g. bream; carp, *Cyprinus carpio*;

pikeperch, *Sander lucioperca*), which YOY and older juvenile stages were entirely absent from the floodplain in the subsequent spring.

In contrast, inverse adaptations to the long term hydrograph occur in predominantly small-sized species, which mature at young age, are less fecund and spawn at higher temperatures and over elongated periods of the summer. The YOY of these species attain only small sizes at the end of their first year of life. These features are closely associated to the opportunistic life-history strategy and imply competitive disadvantages towards faster growing species, which is expressed by a strong preference of YOY for densely vegetated microhabitats, increased mortalities and low recruitment when such habitats are lacking. Categorically small sized YOY exhibited more pronounced habitat requirements compared to larger and faster growing YOY. Accordingly most species associated to the opportunistic strategy (e.g., Threespined stickleback, *Gasterosteus aculeatus*, Japanese minnow, *Pseudorasbora parva*; Sunbleak, *Leucaspius delineatus*) had highest recruitment in waterbodies unaffected by inundations in the time frame when spawning of periodic strategists occurs. This relationship is attributable to the lateral zonation of communities in the floodplain and suggests that remote and less frequently inundated waterbodies within the floodplain, which experience low disturbances and provide relatively constant habitat conditions (low water-level changes, abundant vegetation) throughout the year, are predominantly inhabited by opportunistic strategists.

The temperature-dependent sequence of spawning in relation to inundation patterns and the habitat availability strongly influences the composition of the fish communities, however, also predator-prey interactions within the floodplain. At the example of two functionally different piscivores, which spawn in independency of inundations, it could be demonstrated that the onset of early piscivory is favoured by the earlier hatching and the faster initial growth compared to later spawning species. The maintenance of early piscivory depends on the size advantage over and the availability of smaller YOY fish prey. Due to prolonged spawning periods of multiple spawning species and high abundance of their small progeny (e.g. White bream, *Blicca bjoerkna*), early piscivory of Pikeperch (*Sander lucioperca*) and perch (*Perca fluviatilis*) was favoured in lakes that were subject to repeated inundations, particularly when the required habitats of the potential prey species were lacking or became scarce during early summer. Therefore early piscivory was even enhanced in the less specialised *P. fluviatilis*, particularly in waterbodies of low structural

complexity like gravel pits, and YOY piscivores caused high mortalities in the small sized prey species. In contrast the occurrence and maintenance of early piscivory was impaired, when the size-advantage towards other members of the YOY community decreases, as well as in lakes with high structural complexity.

In conclusion, the findings of this thesis suggest that the affectation by seasonal inundations and waterbody characteristics (morphology, hydrology) determine upon recruitment, the interactions of biota and shape the communities therein. When taking into account the long-term hydrograph this knowledge provides further hints for floodplain rehabilitation in order to maintain diverse communities even under heavily altered conditions.



## Zusammenfassung

Die Veränderungen der Wassertemperatur in Verbindung mit saisonalen Hochwasserereignissen ist einer der Schlüsselfaktoren für laterale Fischwanderungen in der Flussaue, die die Rekrutierungsdynamik und die daraus folgende Ausdifferenzierung der Artengemeinschaften in unterschiedlichen Ökotonen der Aue beeinflussen. Dabei lässt die Temperaturabhängigkeit der artspezifischen Laichzeiträume und die unterschiedlichen Reproduktionsstrategien der Arten vermuten, dass eine Anpassung an das langjährige Abflussmuster des Stroms besteht. Diese Vermutung wird durch das Vorkommen der verschiedenen Alters- und Entwicklungsstadien und deren starke Abhängigkeit von den saisonalen Anbindungsverhältnissen gestützt und zeigt, dass die Rekrutierungsmuster der Arten in der Aue einem hydrologischen Gradienten folgen, der unterschiedliche *life-history* Strategien begünstigt.

Großwüchsige und hoch fekunde Arten in der Aue, die sich gemeinhin durch eine spät einsetzende Geschlechtsreife und einen saisonal frühen Ablaichtermin auszeichnen hatten einen Rekrutierungserfolg, der stark von den Anbindungsverhältnissen der Gewässer an den Strom abhing. Dieser Rekrutierungserfolg manifestierte sich in Massenvorkommen von Larven, solange die Gewässer zur Laichzeit der jeweiligen Arten inundiert wurden. Bei einigen dieser Arten äußerte sich die Anpassung an den langjährigen Pegelgang durch laterale Laichwanderungen vom Strom in die Aue und das Ablaichen auf überfluteter Vegetation (z.B. beim Brachsen, *Abramis brama*), wohingegen bei im Strom laichenden Arten, wie dem Rapfen (*Aspius aspius*), das Vorkommen von Jungfischen in der Aue auf deren Einwanderung während Hochwässern zurückzuführen ist.

Ungeachtet dessen, ob das Laichgeschehen in der Aue oder im Strom erfolgt, tritt dessen zeitliche Anpassung vornehmlich in Kombination mit den oben genannten Lebenszyklusanpassungen auf, die als typisch für die periodische *life-history* Strategie zu erachten sind. Das Ausbleiben von Hochwässern in den relevanten Zeitfenstern hatte hingegen eine verminderte (z.B. beim Rotaugen, *Rutilus rutilus*) oder gänzlich ausbleibende Rekrutierung (z.B. beim Brachsen) in der Aue zur Folge, was die starke Abhängigkeit dieser Arten an den langjährigen Pegelgang unterstreicht.

Die Jungfische von Arten der periodischen Strategie zeichnen sich überwiegend durch ein rasches Wachstum aus, was durch die frühen Laichtermine, aber oftmals auch durch eine Nahrungsspezialisierung begünstigt wird. Dieser Größenvorteil ging mit einer vergleichsweise geringen Habitatbindung einher, da sowohl Larven als auch juvenile Stadien gering ausgeprägte Mikrohabitatpräferenzen zeigten. Dies betrifft insbesondere die geringe Bindung an pflanzliche Deckungsstrukturen, die im allgemeinen Schutz vor Prädatoren bieten könnten. Zudem verließen die Jungfische bei gegebener Anbindung bereits während ihres ersten Sommers, jedoch spätestens im Winter die Auengewässer und wanderten zum Strom hin ab, was durch eine rapide Abnahme der Individuendichten in den Auengewässern und eine parallele Zunahme im Strom gezeigt werden konnte. Der Zeitpunkt dieses Habitat *shifts* ist artabhängig. Einige rheophile (z.B. Barbe, *Barbus barbus*; Nase, *Chondrostoma nasus*) aber auch eurytope Arten (z.B. Brachsen; Karpfen, *Cyprinus carpio*; Zander, *Sander lucioperca*) wanderten vollständig aus den Auengewässern ab und ihre juvenilen Stadien konnten im folgenden Frühjahr nicht mehr in der Aue nachgewiesen werden.

Kleinwüchsige Arten, mit früh einsetzender Geschlechtsreife und geringer Fekundität, deren Laichgeschehen an höhere Temperaturen gebunden ist und sich über einen längeren Zeitraum des Sommers erstreckt, zeigten eine gegensätzliche Anpassung an das langjährige Abflussgeschehen. Diese Arten (z.B. Dreistachliger Stichling, *Gasterosteus aculeatus*; Blaubandbärbling, *Pseudorasbora parva*; Moderlieschen, *Leucaspius delineatus*), die gemäß ihrer Lebenszyklusanpassungen als opportunistische *life-history* Strategen anzusprechen sind, hatten die besten Rekrutierungserfolge in Gewässern, die nicht in dem Zeitraum an den Strom angebunden waren, in dem das Laichgeschäft der periodischen *life-history* Strategen erfolgte. Da ihre Jungfische langsam wachsen und zudem sehr enge Bindungen an spezifische Mikrohabitate, insbesondere Vegetationsstrukturen zeigten, dient diese Anpassung offensichtlich der Konkurrenzvermeidung. So wiesen langsamwüchsige Jungfische spät laichender Arten generell eine stärkere Habitatbindung auf, und ein unzureichendes Angebot entsprechender Habitate war mit einer erhöhten Mortalität und einem verringerten Rekrutierungserfolg verbunden.

Diese Anpassungen dürften die laterale Zonierung der Artengemeinschaften in der Aue erklären, wonach abgelegene und selten angebundene Gewässer, die über das gesamte Jahr betrachtet, geringeren Störungen und relativ konstanten

Habitatbedingungen unterliegen (geringe Wasserspiegelschwankungen, dichte Vegetation), überwiegend von opportunistischen *life-history* Strategen besiedelt wurden.

Die temperaturabhängige Abfolge der artspezifischen Laichzeiten in Verbindung mit dem zeitlichen Auftreten von Hochwasserereignissen und der Verfügbarkeit von Habitaten beeinflusst jedoch nicht nur die Ausprägung von Artengemeinschaften, sondern hat auch erheblichen Einfluss auf Räuber-Beute-Beziehungen in der Aue. Am Beispiel zweier funktional unterschiedlicher Raubfischarten, deren Laichgeschehen von Hochwasserereignissen unabhängig ist, konnte gezeigt werden, dass eine frühe Piscivorie bereits in den ersten Lebensmonaten durch den früheren Schlupf und ein beschleunigtes Wachstum in der ersten Lebensphase begünstigt wird. Die Aufrechterhaltung der piscivoren Lebensweise hing dabei von dem Größenvorteil gegenüber kleineren Jungfischen und deren Verfügbarkeit ab.

Diese frühe Piscivorie von Zander (*Sander lucioperca*) und Flussbarsch (*Perca fluviatilis*) trat vor allem in Auengewässern auf, die während der Sommermonate inundiert wurden und in denen, bedingt durch die sich lang erstreckende Laichzeit von portionslaichenden Arten, wie dem Güster (*Blicca bjoerkna*), über einen längeren Zeitraum des Sommers kleine Jungfische als Nahrung zur Verfügung standen. Dies geschah vor allem in Verbindung mit einer fehlenden Verfügbarkeit von Deckungsstrukturen, also vor allem in gering strukturierten Baggerseen, und begünstigte die frühe Piscivorie auch bei dem wenig spezialisierten Flussbarsch. Im Gegensatz dazu trat eine frühere Piscivorie nicht auf oder konnte nicht über einen längeren Zeitraum aufrecht erhalten werden, wenn die Größenunterschiede innerhalb der Jungfischgemeinschaft gering waren oder ein hohes Angebot an Deckungsstrukturen vorhanden war, was in beiden Fällen mit einer geringeren Anbindungshäufigkeit in Verbindung steht.

Die im Rahmen dieser Arbeit gewonnenen Ergebnisse belegen eindeutig, dass die Rekrutierung einzelner Arten, die Interaktionen zwischen Organismen und die Prägung der Artengemeinschaften innerhalb der Aue, maßgeblich von den saisonalen Anbindungsverhältnissen und den Habitatbedingungen in den jeweiligen Gewässern abhängen. Unter Berücksichtigung der langjährigen Abflussmuster der Ströme, lassen sich aus diesen Befunden Rückschlüsse für die Rehabilitierung von Auen auch in anthropogen modifizierten Flusslandschaften ableiten, anhand derer Artengemeinschaften mit einer hohen Diversität gefördert werden können.



## ERKLÄRUNG

Meerbusch, den 24.08.2009

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Abbildungen und Tabellen - die anderen Werken im Wortlaut oder dem Sinn nach entnommen habe, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie - abgesehen von den auf der folgenden Seite angegebenen Teilpublikationen - noch nicht veröffentlicht worden ist sowie, dass ich solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde.

Die Bestimmungen dieser Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von PD Dr. habil Jost Borchering betreut worden.

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