

On the importance of longitudinal river connectivity for fishes

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Denise Anne Weibel

von Zürich, ZH

Leiter der Arbeit:

Dr. A. Peter

Eawag Swiss Federal Institute of Aquatic Science and Technology

Prof. Dr. O. Seehausen

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Von der Philosophisch-naturwissenschaftlichen Fakultät angenommen.

Bern, 13. Mai 2014

Der Dekan:

Prof. Dr. Silvio Decurtins

Meinen Grosseltern

und dem Wal

gewidmet

„Nicht wahr, o Freund, der Fluss hat so viele Stimmen, sehr viele Stimmen? Hat er nicht die Stimme eines Königs, und eines Kriegers, und eines Stieres, und eines Nachtvogels, und einer Gebärenden, und eines Seufzenden, und noch tausend andere Stimmen?“

TABLE OF CONTENTS

SUMMARY	3
ZUSAMMENFASSUNG	5
CHAPTER 1: General introduction	7
CHAPTER 2: Effectiveness of different types of block ramps for fish upstream movement	15
CHAPTER 3: Longitudinal patterns of fish diversity and abundance along river gradients	27
CHAPTER 4: Home ranges and space use of freshwater fish in streams and rivers – a literature review	57
CHAPTER 5: Synopsis	91
DANK	98
APPENDIX 1: Merkblatt: Durchgängigkeit von Blockrampen	101
APPENDIX 2: Lebensraumverbund Fliessgewässer: Die Bedeutung der Vernetzung	109
ERKLÄRUNG	123
CURRICULUM VITAE	125

SUMMARY

Longitudinal habitat connectivity within streams and rivers plays a key role for fish in freshwater systems because they migrate between different habitats used for spawning, feeding, or sheltering in alternating cycles during different life-history stages. The worldwide fragmentation of rivers due to human impacts has a negative effect on fish movement and dispersal. Many artificial barriers such as river bed sills and small weirs are nowadays replaced by block ramps in order to reestablish longitudinal connectivity for fish in rivers and streams. We studied the upstream passage of several fish species on eight different types of block ramps with slopes between 3.6 and 13.4 %. We conducted translocation experiments in the field based on mark-recapture and on the use of PIT-tags. Temporal movement patterns were observed by an instream antenna. Hydraulic and morphological characteristics of block ramps were measured and compared with fish passage efficiency. Our results clearly showed that upstream passage efficiency differs between fish species, size classes and block ramps.

In order to grasp the effect of river fragmentation and its consequences on fish diversity and abundance, it is necessary to understand the factors structuring fish communities. Hence, we characterized longitudinal patterns along a downstream-upstream gradient and quantified spatial variation in local species richness and abundance. Two streams and a river (including one floodplain) in the prealpine region north and south of the Alps of Switzerland were investigated. For that purpose, electro-fishing was conducted at 37 study sites and environmental parameters regarding fish habitat and water quality were sampled. We evaluated whether assemblage changes happen gradually or abruptly and whether habitat fragmentation influences spatial distribution patterns. The contribution of local, environmental habitat factors and of spatial factors in explaining longitudinal variation of abundance were evaluated.

Knowledge about the individual space use of fish is fundamental in order to understand the impact of river fragmentation. Hence, a literature review about home ranges of fish in stream and rivers of the northern hemisphere was conducted. Home range sizes were compiled in detail for a taxonomic overview. The various meanings of the term home range as applied by different authors were introduced and the problem of defining a home range was discussed. Selected methodical approaches to estimate home range sizes were compared with particular attention to the temporal aspect. Additional aspects relating to mobility of fish as well as factors influencing home range size were discussed. Finally, the findings of the present thesis were discussed in view of future river management and restoration strategies.

ZUSAMMENFASSUNG

Die Längsvernetzung in Fließgewässern spielt für Fische eine entscheidende Rolle. Im Verlauf ihres Lebenszyklus suchen Fische unterschiedliche Habitate auf, die sich zum Laichen, für die Nahrungsaufnahme oder als Zufluchtsort eignen. Die durch den Menschen verursachte, weltweite Fragmentierung der Gewässer hat negative Konsequenzen für die Wanderungen und Ausbreitung der Fische. Viele künstliche Wanderbarrieren wie Querbauwerke und Sohlschwellen werden heutzutage durch Blockrampen ersetzt, um das Gewässerlängskontinuum für Fische wiederherzustellen. Wir führten Erfolgskontrollen auf acht verschiedenen Blockrampentypen mit Gefällen zwischen 3.6 und 13.4 % durch. In einer Feldstudie wurden mittels Fang-Wiederfang-Versuchen und PIT-tags Translokationsexperimente durchgeführt. Zeitliche Bewegungsmuster wurden mit einer am Gewässer installierten Antenne verfolgt. Hydraulische und morphologische Blockrampenparameter wurden gemessen und mit dem Aufstiegserfolg der Fische verglichen. Unsere Resultate zeigen klar, dass der Aufstiegserfolg abhängig ist von der Fischart, der Größenklasse der Fische und dem Blockrampentyp.

Um die Folgen von Gewässerfragmentierung auf Fischdiversität und –abundanz zu begreifen, muss man verstehen, welche Faktoren die Fischgemeinschaften strukturieren. Dafür wurden longitudinale Verteilungsmuster entlang von Gewässergradienten quantifiziert und die räumliche Variation der lokalen Artenzahl und Abundanz bestimmt. Es wurden zwei Bäche und ein Fluss (inkl. Flussaue) nördlich und südlich der Schweizer Alpen untersucht. An 37 Untersuchungsstellen wurden Elektroabfischungen durchgeführt und Umweltparameter im Bezug auf Fischhabitat und Wasserqualität erhoben. Es wurde beurteilt, ob es zu graduellen oder abrupten Änderungen in der Fischartengemeinschaft kommt und ob Wanderbarrieren die räumlichen Verteilungsmuster beeinflussen. Der Zusammenhang zwischen Veränderungen der Abundanz und lokalen Habitatsfaktoren oder räumlichen Faktoren wurde evaluiert.

Das Wissen um die individuellen Raumansprüche der Fische ist nötig, um die Auswirkungen von Fragmentierung überhaupt zu verstehen. Deshalb wurde eine Literaturarbeit zum Thema Home ranges (Aktionsräume) der Fische in Fließgewässern der nördlichen Hemisphäre durchgeführt. Die unterschiedliche Bedeutung des Begriffs Home range und die Schwierigkeit, eine Home range zu definieren, wurden erörtert. Ausgewählte methodische Ansätze zur Größeneinschätzung der individuellen Home ranges wurden miteinander verglichen mit Fokus auf den zeitlichen Aspekt. Wir analysierten weitere Aspekte im Bezug auf Fischbewegungen und Faktoren, welche die Größe von Home ranges beeinflussen. Zum Schluss wurden die Erkenntnisse der vorliegenden Doktorarbeit im Hinblick auf zukünftiges Fließgewässermanagement besprochen.

CHAPTER 1

General introduction

The importance of connectivity in fluvial systems

Lotic ecosystems are characterized by a four-dimensional, spatio-temporal framework (Ward, 1989). Accordingly, the river system interacts in a longitudinal, lateral and vertical pathway on a temporal scale. The longitudinal dimension connects downstream with upstream habitat within the river corridor in both directions of flow as well as between the main stem and its tributaries. The lateral exchange takes place between the aquatic and the terrestrial or alluvial ecosystem. It includes interactions between the instream habitat and the riparian, floodplain or island habitat. The vertical exchange occurs between the river bed surface and the saturated sediments, called hyporheic interstitial. It is important for the infiltration of the groundwater (Fig. 1).

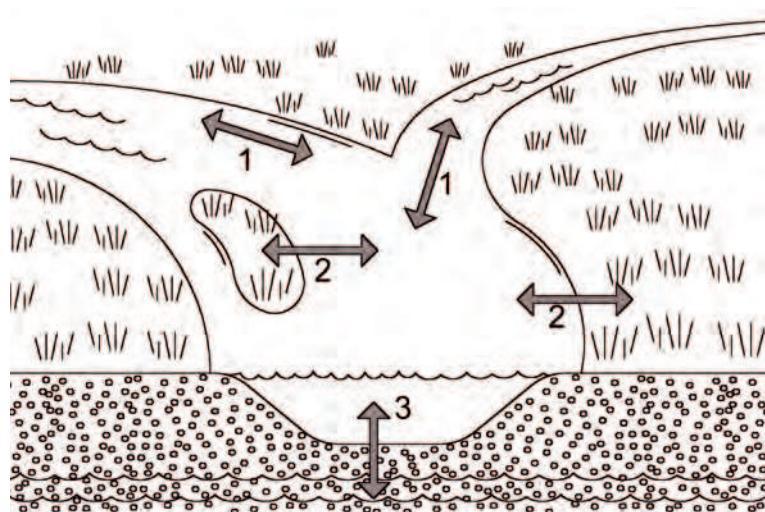


Figure 1.The three spatial dimensions of connectivity within a river corridor. 1) longitudinal connectivity between up- and downstream sites or main stem and tributaries; 2) lateral connectivity between instream and riparian, floodplain or island habitat; 3) vertical connectivity between the river bed surface and the hyporheic interstitial. According to Ward (1989) and Malmqvist (2002).

Apart from these three spatial dimensions of interactions, there is a temporal scale (the fourth dimension). Hence, processes along these spatial dimensions naturally follow a highly dynamic pattern and temporally fluctuate. Longitudinal, lateral and vertical connectivity guarantee the intact exchange between habitats through active or passive dispersal of organisms or the transport of water, bed load, energy, nutrients and organic matter (Woolsey

et al., 2005). Occasionally, ecologists differentiate between structural and functional connectivity. Structural connections simply describe the physical characteristics of the catchment, whereas functional connections between communities are assessed by organisms that actually use available corridors for dispersal and migration. The level of functional habitat connections within heterogenous riverscapes can be altered by short-term hydrological and geomorphologic changes (e.g. floods).

Connections of the branching fluvial networks are predominantly longitudinal in headwaters and become increasingly lateral in lower rivers (Fullerton et al., 2010; Fig. 2, top panel). Lateral and longitudinal habitat connectivity plays a key role for fish in freshwater systems. Freshwater fish exhibit complex life histories and they migrate between different habitats used for spawning, feeding, or sheltering in alternating cycles during different life-history stages (Northcote, 1998). Thus, the access to headwater tributaries is particularly important in order to reach remote spawning sites (e.g. Kanno et al., 2014). Further, prey availability and temperature conditions in main-stem rivers provide more optimal growing conditions for salmonids as individuals increase in size. Hence, the connectivity between small spawning and rearing tributary streams and main-stem river habitats is crucial (Leeseberg & Keeley, 2014).

The problem of fragmentation

Longitudinal connectivity within rivers and streams is often disrupted by natural or anthropogenic barriers. For example, a high cascade poses an abrupt natural barrier, whereas the climatic gradient represents a gradual natural barrier (Banarescu, 1990). Likewise, altered hydrologic conditions can limit connectivity either naturally or by human-induced water abstraction. Weirs, dams, hydropower facilities, river bed sills of little height and culverts fragment fluvial systems and constitute anthropogenic barriers to fish migration and dispersal. Barriers in head water systems disconnect the longitudinal corridor to tributaries, whereas in lower rivers, barriers often eliminate lateral connections with side channels (Fullerton et al., 2010; Fig. 2, bottom panel). Since watershed connectivity can vary with barrier assessment methods, the choice of method is crucial for the connectivity assessment (Bourne et al., 2011). Europe contains the smallest number of completely unfragmented large river systems (Nilsson et al., 2005). In Switzerland, approximately 101,000 anthropogenic barriers with a minimal height of 0.5 m have been assessed within the river network of 65,000 km, resulting in a mean distance between barriers of 650 m; 7 % of the Swiss river network is piped to culverts (Zeh-Weissmann et al., 2009). The consequences of fragmentation for fish are severe and it can lead to the loss of species and

to a reduced local abundance in above-barrier sites (Peter, 1998; Nislow et al., 2011). In Switzerland, 15 % of native fish species are extinct, whereof most are diadromous, long-distance migrating species (Kirchhofer et al., 2007). Apart from fragmentation and habitat destruction due to channel straightening, there are other anthropogenic impacts such as chemical pollution, water abstraction or temperature and oxygen that are implicated causes of changes in fish assemblages, fish diversity and abundance (Lucas & Baras, 2001). In Switzerland, the intensive production of hydropower has serious negative consequences for fish due to hydropeaks caused by short-term changes in hydropower operation. In the river Rhone, there is a trend towards smaller weights of individuals of brown trout (*Salmo trutta*) in stretches with higher intensity of hydropeaking compared to stretches with natural flow (Fette et al., 2007).

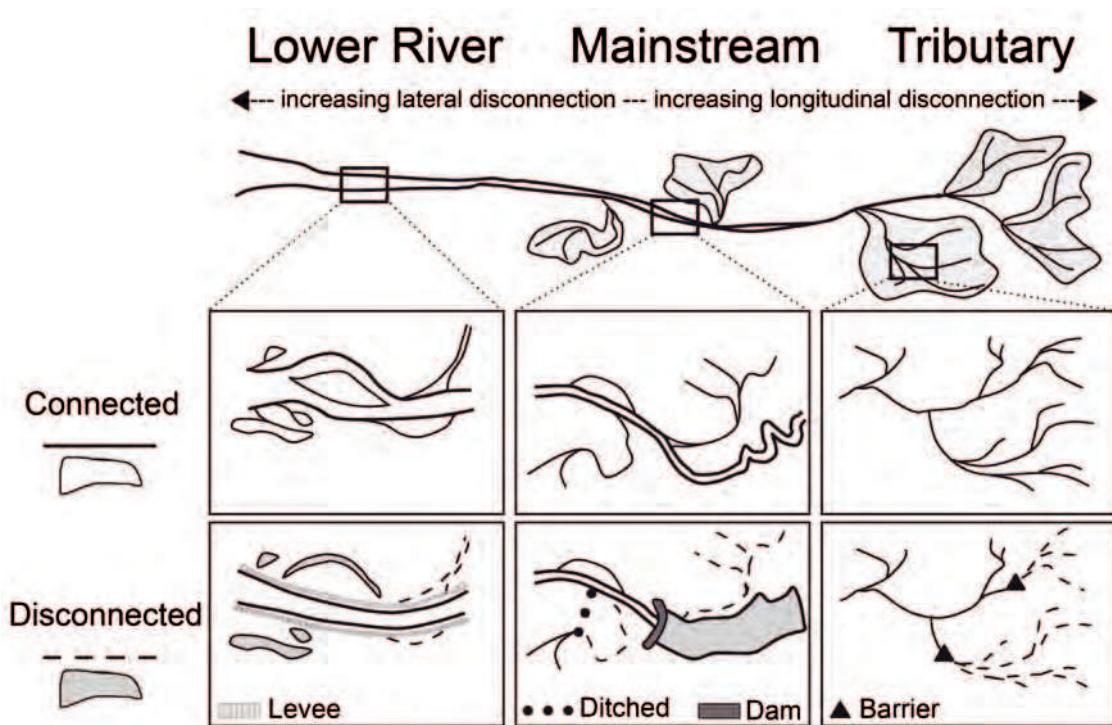


Figure 2. Schematic connections and disconnections along a typical river. Top panels: connections naturally present. Bottom panels: potential disconnections caused by anthropogenic actions. Owing to channel width and gradient, disconnections among habitats in tributaries are often longitudinal; whereas disconnections among habitats in lower rivers are often lateral (between main channel and off-channel habitats). (Fullerton et al. 2010, modified).

The effect of connectivity on fish communities

In general, stream fish assemblages are temporally and spatially heterogeneous and controlled by various factors. Local species diversity reflects disturbance history, resource partitioning, habitat fragmentation and successional phenomena across river systems (Ward & Tockner, 2001). Likewise, population processes such as meta-population dynamics, population persistence, immigration or colonization are highly influenced by spatial processes, for example limited connectivity of watersheds or the distance to species pools and to source-populations. It has been postulated that research about connectivity among riverine habitats should clearly identify how spatial processes structure fish communities (Fullerton et al., 2010). For instance, the location of natural barriers (i.e. waterfalls) (Hein et al., 2011) or the longitudinal position within streams (Mullen et al., 2011) are among the most important variables to explain fish community structure. Recent findings demonstrate the ecological significance of obstacles like weirs and dams, and reveal that they constitute the most relevant predictor of young-of-the-year fish community structure (Musil et al., 2012). However, when evaluating the regional effects of obstacles on fish assemblages, it is necessary to incorporate environmental factors, which potentially are co-influential (Wang et al., 2011). Temporally dynamic systems like floodplains have stochastic physical conditions and a varying degree of longitudinal and lateral habitat connectivity. Hence, the relative contribution of environmental factors and of spatial processes in structuring the fish-metacommunity of a floodplain varies through time (Fernandes et al., 2013). A reduction of frequency and duration of floodplain inundation due to managed flow regimes has consequences on connectivity and hence, is likely to reduce stream fish recruitment (Dutterer et al., 2013). Similar to floodplains, junctions of tributaries into main-stem rivers are temporally dynamic nodal points within the riverine channel network. At tributary junctions, thermal and productivity regimes are discontinuous and instream habitat heterogeneity is increased due to effects of stochastic watershed disturbances (e.g. floods) and sediment transport (Benda et al., 2004). Such physically heterogeneous habitat sets the stage for a diverse fish fauna.

Key questions of the present thesis

In recent years, the restoration of longitudinal connectivity has become a major goal in river rehabilitation. In Switzerland, fish ladders were built and migration barriers such as small weirs had been removed and were replaced by bed-stabilizing block ramps. Block ramps are engineering measures built of boulders, they prevent channel erosion and are supposed to

allow for fish upstream movement. Are blockramps efficient restoration measures? In **chapter two** of this thesis, the efficiency of block ramps for fish upstream passage is tested. Anthropogenic barriers disrupt the longitudinal connectivity within river corridors. What is the influence of anthropogenic alterations to connectivity on fish communities? And to what extent determine spatial as well as habitat factors the abundance of fish species? In **chapter three**, longitudinal patterns in fish diversity and abundance are examined in relation to spatial factors and various environmental parameters.

In view of recent river restoration projects that comprise the restoration of longitudinal connectivity, one crucial question arises: how much space do individual fish need to successfully complete their life cycle? What is the size of their so-called home ranges? Are there any differences in the use and size of home ranges between fish species and families of freshwater fish of the northern hemisphere? In **chapter four**, existing literature about fish home ranges is reviewed and available data about home range sizes is compiled for an overview.

The results of the present studies are combined to a synopsis in **chapter five**, and perspectives on future rivermanagement are discussed. The present thesis was part of the interdisciplinary project “Integrated River Management”, supported by the Swiss Federal Office for the Environment (FOEN). Both appendices are outputs of the project “Integrated River Management”. **Appendix 1** is an information sheet about block ramps that was developed based on the findings of the present thesis. It provides advice for practitioners and river engineers involved in the construction of block ramps. **Appendix 2** is an article about connectivity in river landscapes and constitutes one part of the interdisciplinary synthesis of the project. It was written in cooperation with other scientists.

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CHAPTER 2

Effectiveness of different types of block ramps for fish upstream movement

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Effectiveness of different types of block ramps for fish upstream movement

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Abstract Rivers are worldwide highly fragmented due to human impacts. This fragmentation has a negative effect on fish movement and dispersal. Many artificial barriers such as river bed sills and small weirs are nowadays replaced by block ramps in order to reestablish longitudinal connectivity for fish in rivers and streams. We studied the upstream passage of several fish species on different types of block ramps with slopes between 3.6 and 13.4 %. We conducted translocation experiments in the field based on mark-recapture and on the use of PIT-tags. Temporal movement patterns were observed by an instream antenna. Hydraulic and morphological characteristics of block ramps were measured and compared with fish passage efficiency. Our results clearly showed that upstream passage efficiency differs between fish species, size classes and block ramps. We observed that brown trout (*Salmo trutta fario*) performed better than bullhead (*Cottus gobio*) and several cyprinid species on the same block ramps. Passage efficiency of brown trout and chub (*Leuciscus cephalus*) was size-selective, with small-sized individuals being less successful. For brown trout, size-selectivity became more relevant with increasing slope of ramp. We conclude that block ramps with slopes of >5 % are ineffective for the small-sized cyprinid species and that vertical drops within step-pool ramps can hinder successful upstream passage of bullhead.

Keywords Passage efficiency · Block ramp · Rock ramp · Fish ramp · PIT-tag · Longitudinal connectivity

Introduction

The fragmentation of the longitudinal river corridor by weirs, dams, hydropower facilities and culverts represents a major global human impact on running waters (Jungwirth 1998). In Switzerland, the extensive straightening of lowland rivers has led to a long-term increase in channel incision, which was usually counteracted by building river bed sills (Lange 2007). As a consequence, especially small rivers and streams are nowadays highly fragmented. Approximately 101,000 anthropogenic barriers with a minimal height of 0.5 m have been assessed within the Swiss river network of 65,000 km, resulting in a mean distance between barriers of 650 m (Zeh Weissmann et al. 2009).

In river systems, connectivity between downstream and upstream habitats is essential for short-term movements of fish within home ranges and directional, periodic long-distance migration. Fish usually migrate in alternating cycles between feeding, spawning and wintering habitat during different life-history stages over distances that may vary from a few metres to thousands of kilometres (Northcote 1998). Barrier-free confluences into main rivers are important linkages and provide access to spawning sites and refuges. It has been shown that dams, weirs and even small obstacles often constitute significant migration barriers to fish (Ovidio and Philippart 2002) and hence, intercept longitudinal connectivity.

The consequences of fragmentation for fish are severe. Artificial barriers can cause a loss of suitable spawning habitat in headwaters where accessibility is blocked (Sheer

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and Steel 2006). Particularly, long-distance migrants such as salmon (*Salmo salar*) are susceptible to fragmentation. Thus, migration barriers triggered the loss of all diadromous species and populations in Switzerland, except the European eel *Anguilla anguilla*. Even instream structures of low height such as river bed drops of 0.2 m can represent a major threat to small-sized species like bullhead (*Cottus gobio*) or spirlin (*Alburnoides bipunctatus*) because they can separate populations (Bless 1990; Breitenstein and Kirchhofer 1999; Utzinger et al. 1998). The disruption of the longitudinal continuum can cause abrupt changes in fish communities and reduce species richness in the above-weir sites to less than half of the original richness (Peter 1998). Furthermore, it has been shown that fragmentation of the riverine system by dams has effects on the genetic composition of fish populations and leads to the loss of genetic diversity in the above-dam sites (Yamamoto et al. 2004).

The restoration of longitudinal connectivity has become a major goal in river rehabilitation. In recent years, many migration barriers such as weirs and bed-stabilizing drop structures have been removed in Switzerland and have been replaced under notable costs by block ramps, also called rock ramps, fish ramps or bottom ramps (DVWK 1996). Block ramps span the entire stream or river width and are built of boulders. They stabilize the river bed and prevent channel erosion. Since block ramps are supposed to allow for fish upstream movement and, hence, reestablish connectivity, their construction has become a popular as well as a promising approach in river engineering and management. Block ramps differ by their bed material as well as by their size and arrangement of boulders. The two main types of common block ramps consist of the classical, uniform ramp with closely embedded boulders (Type block carpet) and of the dispersed ramp (Type block clusters) that can be either structured (e.g. by rocky sills) or unstructured (Lange 2007; Tamagni et al. 2010). Roughness condition of river bed and slope are important factors that influence hydraulics and energy dissipation on block ramps (Pagliara and Chiavacini 2006). Other characteristics of block ramps include water depth, current velocity, water temperature as well as length of ramp. A laboratory study showed that uniform block ramps can rarely satisfy the hydraulic criteria for fish migration, whereas structured block ramps are more efficient (Studer and Schleiss 2011). Fish passage can become critical with increasing discharge and steep slopes. Like in fishways, where successful upstream movement can be highly species-selective according to their design and hydraulic regime (Knaepkens et al. 2006), fish ideally benefit from repeated resting pools that reduce long reaches of strong current. There are significant differences in fish swimming capacities between species and life-stages. Since, particularly, juveniles and non-salmonids exhibit

weak swimming capabilities, some hydraulic conditions—especially high velocities and critical water depths—could become problematic on block ramps. As there still is a lack of knowledge about the suitability of block ramps to benefit fish passage, the assessment of the efficiency of fish passage on block ramps is crucial.

Here, we study the upstream movement of several fish species on different types of block ramps in Switzerland. We focus on field experiments that investigate short-distance movement behavior and temporal movement patterns. We perform translocation experiments based on mark-recapture and on the use of PIT-tags. The goal of the present study was to gain information about the success of fish upstream movement on block ramps and to identify potential barrier effects for different species and size classes. We hypothesize that fish species exhibiting pronounced swimming capacities will pass steep block ramps more likely than species exhibiting weaker swimming capacities. We complement our analyses by measuring hydraulic and morphological characteristics of the block ramps. Our results may provide helpful tools for ecological evaluation of future engineering measures that effectively restore longitudinal connectivity in river networks.

Materials and methods

Block ramp characteristics

We chose eight block ramps situated in seven running waters in Central and Northern Switzerland (Table 1; Fig. 1). We classified their construction type and measured the following morphologic and hydraulic parameters: slope, length, wetted width, water depths and flow velocity. Measuring points for the latter three parameters were either regularly distributed on iterative transects within the sill-pool structure along the block ramps or situated within a grid of $1 \times 0.5\text{--}1$ m. We used an electro-magnetic flowmeter (Flow-Mate 2000, Marsh-McBirney) to determine flow velocity at $0.6 \times$ water-depth and a gauge to measure water levels and bed topographies. If there was an obvious overfall at the measuring point, we determined the water level difference. We additionally measured the minimal water level difference at the sills of ramp ST because several sills caused overfalls that spanned the entire stream width and potentially posed a barrier to fish. Last, we roughly defined the granulometry of the building material of each block ramp by sizing 10 randomly selected boulders.

Translocation experiments

We based our experiments on the concept of homing behavior of fishes, which describes the tendency of fish to

Table 1 Details of the eight block ramps studied in Central and Northern Switzerland

Ramp-label	Name of the river/stream	Fish zone	Constructional subtype	Method applied	Slope (%)	Length (m)	Vertical height ^a (m)	Mean wetted width (m; SD)	Mean water depth (m; SD)	Mean flow velocity (m/s; SD)	Maximum flow velocity (m/s)
WY1	Wyna	Lower trout zone	Block carpet	Mark-recapture	13.4	13	1.7	6.0 (0.6)	0.18 (0.18)	0.54 (0.52)	1.95
WY2	Wyna	Lower trout zone	Unstructured	Mark-recapture	7.7	17	1.3	5.7 (1.0)	0.27 (0.18)	0.25 (0.32)	1.44
OF	Oftringen	Lower trout zone	Block carpet	PIT-tag logging, recapture	9.4	16	1.6	2.5 (0.4)	0.20 (0.12)	0.23 (0.24)	0.92
SI	Sissle	Lower trout zone	Structured by transversal sills	Mark-recapture	3.6	41	1.4	11.0 (1.5)	0.26 (0.14)	0.27 (0.25)	0.98
ST	Staffellegg	Lower trout zone	Structured by transversal sills	Mark-recapture	6.1	39	2.4	4.2 (0.4)	0.20 (0.11)	0.28 (0.26)	1.03
KA	Kaegiswil	Lower trout zone	Unstructured	PIT-tag logging	11.4	4	0.5	2.3 (0.6)	0.20 (0.05)	0.74 (0.45)	1.50
SU	Suhre	Grayling zone	Structured by transversal sills	Mark-recapture	5.2	40	2.1	14.0 (1.4)	n.d.	n.d.	0.70 ^b
GL	Glatt	Grayling zone	Block carpet	Mark-recapture	8.9	14	1.2	14.8 (1.0)	n.d.	n.d.	3.12 ^b

n.d. not determined due to exceedingly high flow velocities^a In reference to water surface^b Maximal velocity refers only to measurement at the margin of the block ramp

swim back to their home site after translocation. Armstrong and Herbert (1997) observed that experimentally displaced brown trout rapidly headed in both up- and downstream directions to the area from which they were captured. The same behavior has been described for other species, e.g. juvenile salmon, minnow (*Phoxinus phoxinus*), longear sunfish (*Lepomis megalotis*) or river blackfish (*Gadopsis marmoratus*) (Gerking 1959; Kennedy and Pitcher 1975; Huntingford et al. 1998; Khan et al. 2004). These homing movements occurred at distances of a few meters to 3.5 km. Hence, we assumed that the recaptured proportion of individuals, which we translocated, was an appropriate estimator of the passage efficiency of the block ramp investigated.

We conducted our translocation experiments at eight block ramps, two of which (SU, GL) were situated within the grayling zone and the other six (WY1, WY2, OF, SI, ST, KA) within the lower trout zone (Huet 1959). We included the grayling zone in our study because it is characterized by a broad diversity of cyprinids. In all experiments, fish were sampled by electro-fishing (electroshocker EFKO, 8 kW, 150–300/300–600 V) within a stretch of 50–200 m length located directly upstream of the block ramp. The captured fish were kept in oxygenated water tanks and were anaesthetized with clove oil before handling (Hänseler AG, Herisau, Switzerland; 0.5 ml diluted in 9.5 ml alcohol added to 20 l water). We determined the fish species, measured their total body length (± 1 mm) and marked individuals subcutaneously with blue dye (Alcian Blue, Fluka, Buchs). When fish had recovered from handling, they were transferred downstream to the bottom of the block ramp and released back into the river at high densities in order to trigger active dispersal. We then gave the fish a time interval of 7–34 days to migrate back to their home sites, before we re-sampled the identical river stretches above the block ramps with electro-fishing. The recaptured individuals were carefully checked for color-marks. To test for consecutive upstream movements, translocation experiments were replicated up to three times by applying color-marks at different parts of the body to discriminate each run.

To study individual temporal movement patterns in more detail, we supplied all fish at two block ramps OF and KA with half-duplex passive integrated transponders (PIT-tag; 23 mm \times 3.9 mm, 0.6 g, Texas Instruments, Dallas). We injected PIT-tags into the peritoneal cavity with a hypodermic needle on individuals with a body length >100 mm. To detect PIT-tagged fish, we installed a radio frequency identification (RFID) system and placed an instream low-frequency antenna at the upstream edges of both block ramps. We constructed the antenna with three loops of litz wire that were spanned in a single string over the stream resulting in an antenna width of approximately 3 m. The antenna was tuned to resonate at the frequency of 134.2 kHz and was connected to a RFID data-logger

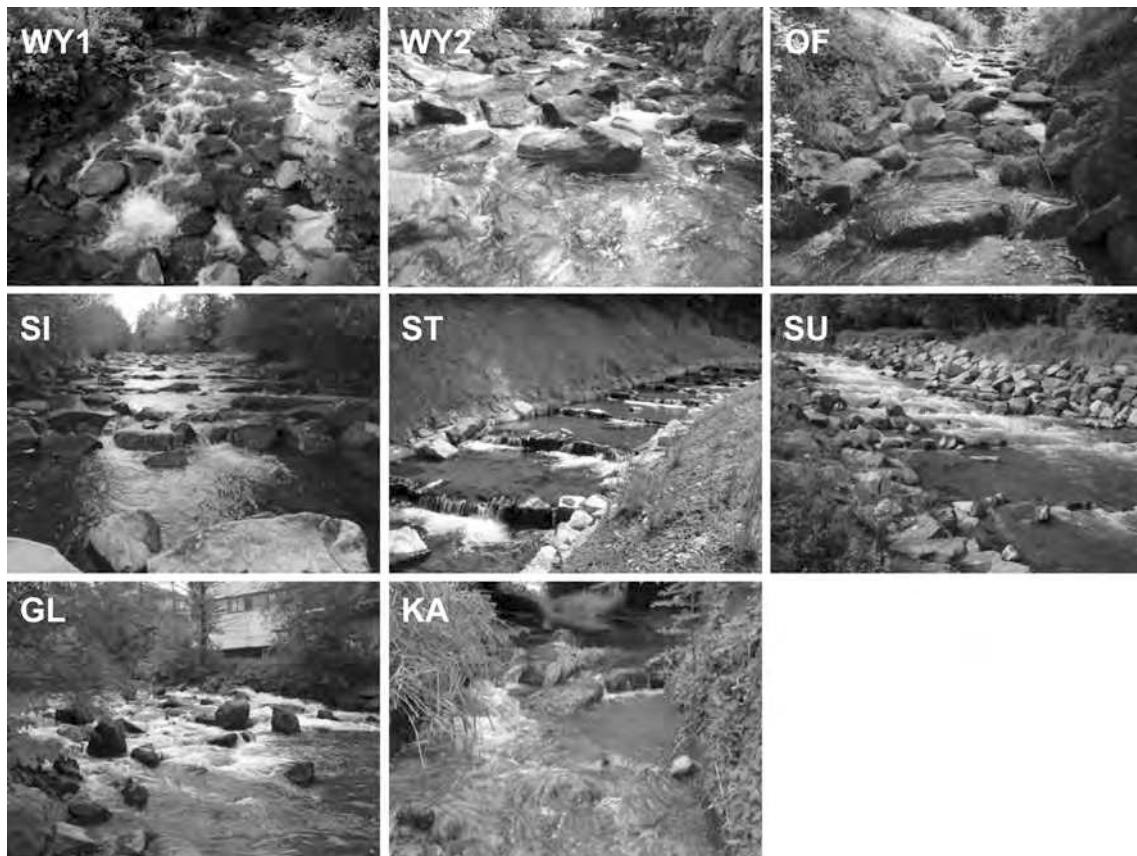


Fig. 1 Photographs taken during the field study of the block ramps WY1, WY2, OF, SI, ST, SU, GL and KA studied in Central and Northern Switzerland. See Table 1 for details

(Oregon RFID, Portland). Two interconnected batteries supplied the system with power of 18 V DC. The data-logger recorded exact date, time and individual PIT-tag identity numbers of fish passing the loop-antenna. To control for the operational efficiency of the data-logging system, we performed a recapture survey (as described above) at block ramp OF at the end of the experiment and compared logged data to the actual recapture data.

Field investigations for both block ramp characterization and translocation experiments were carried out during summer/fall (July–November) 2008 and spring (May–June) 2009.

Data analysis

We calculated mean water levels and mean flow velocities of five systematically measured block ramps (WY1, WY2, OF, SI, ST). On two occasions (SU and GL), strong water current allowed measuring only at marginal zones of the block ramps (0.3 m apart from river banks).

We calculated passage efficiency (i.e. the proportion of total fish moved) of each block ramp by dividing the number of recaptured or logged migrants by the total number of color-marked or tagged individuals. We derived passage

efficiencies for different fish species and size-classes. The effects of fish body length and ramp slope on passage success were statistically analyzed on block ramps WY1, WY2, OF and SI for brown trout, the most abundant species. For this, we used two different logistic regression models (SPSS Statistics 17.0). We omitted block ramps from the grayling zone, SU and GL, from the logistic regression analysis because of a comparatively small sample size of brown trout on these ramps. Both logistic regression models (1) and (2) included as categorical outcome, i.e. dependent variable, the individual recapture above the block ramps (yes/no). Model (1) included fish body size as a single predictor (independent variable). Model (2) included fish body size, slope of block ramp as well as their interaction as predictors (stepwise forward method).

Results

Block ramp characteristics

Of the eight block ramps investigated, bed slopes ranged from 3.6 to 13.4 %, with WY1 and KA having the steepest

slopes (Table 1; Fig. 1). Note that block ramps have different characteristics. Block ramps with slopes below 6.5 % were more than twice as long as steeper ramps. Usually, maximum flow velocity increased with slope, except for the outlier ramp OF (Table 1). Water levels were not critical for fish under discharge conditions during the experiment. The most critical velocity for fish was recorded at the ramp GL having a maximal flow velocity of 3.12 m/s on marginal zones. Comparatively, the presence of calm marginal areas turned out to be relevant on ramp SU because boulders on beds formed zones with a maxima of 0.7 m/s. Mean flow velocity of other block ramps was distributed between 0.23 and 0.28 m/s (Table 1) with maximal velocity of 0.9–1.5 m/s, but was higher on the steepest block ramp WY1, which had a mean velocity of 0.54 m/s and a maximum of 1.95 m/s. Occasionally, we recorded a minimum water level difference at vertical drops of 0.1–0.23 m between sills at block ramp ST.

Upstream passage efficiency

Table 2 provides an overview of all species captured, as well as the number of marked or tagged individuals at each block ramp. We marked more than 3,000 individual fish belonging to 16 different fish species, with body lengths ranging from 35 to 540 mm. Passage efficiencies are listed in Table 2 expressed as either recapture or detection rates for each block ramp and fish species.

Lower trout zone

We caught 666 brown trout at block ramps WY1, WY2, OF and SI with a mean body length of 144 mm. The corresponding passage efficiencies of these four block ramps are depicted in Table 2. Note that the second recapture rates were slightly lower than the rates of the first recapture. Our results clearly show major and consistent differences in passage efficiency between size classes within species and block ramps. Figure 2 depicts the strong difference between the two size classes <200 mm and ≥200 mm of brown trout on each of these four block ramps. The logistic regression model (1), which compared recaptures of OF, WY1, WY2 and SI altogether, revealed that body size as a single factor makes a significant contribution to predicting the passage rate of brown trout (Table 3). With increasing body length, the odds for a brown trout of getting recaptured upstream of the ramp increased by a factor 1.02 [95 % CI (1.016; 1.023)]. The stepwise forward logistic regression model (2) revealed a significant interaction between the factors slope and fish size (Table 3), whereas slope did not fulfill the significance criterion and was excluded from the model. The model (2) showed that the difference between small- and large-sized brown trout in passing the block ramp

increased with the steepness of the ramp slope. This means the influence of fish size on passage success was more prominent on a steep than on a smooth ramp. Surprisingly, total passage efficiency independent of size-class for brown trout was highest on the steepest block ramp WY1 and lowest on the block ramp SI, which had the smallest slope. Furthermore, it is noteworthy that a relatively high proportion of twice-translocated brown trout passed the block ramps a second time (72.4 % on block ramp WY1, 47.2 % on WY2 and 50.0 % on SI, respectively, relative to the total of double-marked individuals).

In contrast to brown trout, we encountered an extremely poor upstream passage efficiency of bullheads on block ramps WY1, WY2 and ST (Table 2). Of the total 477 marked bullheads, none was recaptured after 7 or 14 days upstream of block ramps WY1 and WY2, nor after 11 days, 20 days or 34 days upstream of block ramp ST. Block ramp ST consists of a step-pool-step system with 13 sills in total. Several marked individuals had moved up to pool numbers 1–5 during the first (7.6 %; N = 17), second (7.7 %; N = 24) and third (3.2 %; N = 10) recapture. Nevertheless, none crossed the sixth sill, which had a height of 15 cm under the conditions that were met during the experiment.

At block ramp SI, we encountered a large minnow population. Of the total 1,104 marked and translocated minnows, however, none were recaptured after 7 or 14 days, respectively.

Grayling zone

At block ramp KA, passage efficiency of large sized chub (≥ 200 mm) was relatively high: almost a third of this size class had passed the ramp after 4.5 days (Table 2).

The two study sites SU and GL were characterized by high, yet different species diversities. At block ramp SU, the highest efficiency was seen by the size class of large brown trout (Table 2). Sample sizes were small for small-sized fish like gudgeon, grayling, minnow, dace and spirlin and we did not recapture any individuals of these species after 6 or 29 days. Sample sizes of chub and barbel at block ramp SU were quite high, yet passage efficiency was surprisingly low (Table 2). We did not observe any consecutive upstream passages at ramp SU for neither of these species. At block ramp GL, upstream passage in reasonable numbers was restricted to large-sized chub and brown trout. A strikingly unsuccessful upstream passage was revealed for gudgeon, barbel, roach and small-sized chub (<200 mm) after 22 days.

Temporal movement patterns

The PIT-tag reading-system operated during 16 days at block ramp OF and during 4.5 days at block ramp KA with

Table 2 Fish recapture rates upstream of ramps WY1, WY2, OF, SI, ST, SU, GL and KA for the 16 species encountered

Fish species	Size class	WY1				WY2				OF			SI			ST				KA			SU			GL							
		N ₁	N _{tot}	RC ₁	RC ₂	N ₁	N _{tot}	RC ₁	RC ₂	N _{tot}	DT	RC	N ₁	N _{tot}	RC ₁	RC ₂	N ₁	N _{tot}	RC ₁	RC ₂	RC ₃	N _{tot}	DT	N ₁	N _{tot}	RC ₁	RC ₂	N _{tot}	RC				
Brown trout <i>Salmo trutta fario</i>	<200 mm	140	206	33.6	33.5	141	218	26.2	18.3	80	35.0	25.0	33	48	9.1	6.3	—	—	—	—	—	—	—	23	52	4.3	1.9	9	11.1				
	≥200 mm	35	47	82.9	80.9	28	44	57.1	47.7	9	77.8	44.4	12	14	41.7	35.7	—	—	—	—	—	—	—	6	13	33.3	23.1	3	100				
Bullhead <i>Cottus gobio</i>		78	107	0	0	46	57	0	0	—	—	—	—	—	—	—	223	313	0	0	0	—	—	—	—	—	—	—	—	—			
Chub <i>Leuciscus cephalus</i>	<200 mm	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0	46	57	8.7	0	67	0		
	≥200 mm	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	29.2	58	90	6.9	3.3	7	14.3		
Barbel <i>Barbus barbus</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	56	105	7.1	1.9	74	2.7				
Gudgeon <i>Gobio gobio</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	12	0	0	0	225	1.3			
Grayling <i>Thymallus thymallus</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	10	0	0	0	—	—			
Minnow <i>Phoxinus phoxinus</i>		—	—	—	—	—	—	—	—	—	—	—	472	1,104	0	0	—	—	—	—	—	—	—	9	11	0	0	0	—	—			
Dace <i>Leuciscus leuciscus</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	5	0	0	0	—	—			
Spirlin <i>Alburnoides bipunctatus</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	23	0	0	0	—	—			
Roach <i>Rutilus rutilus</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	0		
Tench <i>Tinca tinca</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0		
Stone loach <i>Barbatula barbatula</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0		
Pike <i>Esox lucius</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0	—	—	—	—	—	1	0	
Eel <i>Anguilla anguilla</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0		
Perch <i>Perca fluviatilis</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	100	—	—	—	—	—	4	0	
Sunfish <i>Lepomis gibbosus</i>		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	0		

Recapture rates for brown trout and chub are listed for two size classes separately (>200, <200 mm)

RC_X Xth recapture event, DT detection rate by PIT-tag reader, N₁ number of marked and translocated individuals before 1st recapture, N_{tot} cumulative number of marked and translocated individuals before 2nd (or 3rd) recapture

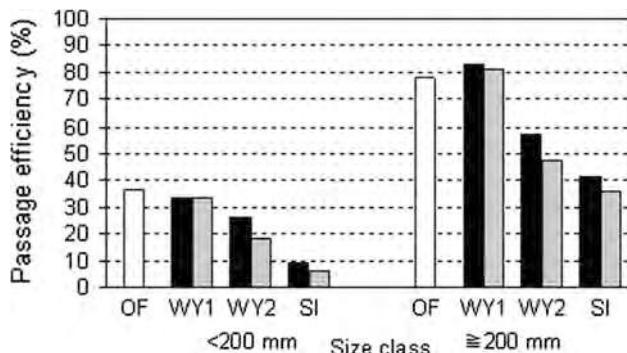


Fig. 2 Passage efficiency according to Table 2 of brown trout (*Salmo trutta fario*) for small-sized and large-sized individuals. Passage efficiency at ramps WY1, WY2 and SI corresponds to 1st and 2nd recapture rate. Passage efficiency of block ramp OF is pooled data from recaptured as well as reader-detected individuals. Black bar 1st recapture rate. Gray bar 2nd recapture rate. White bar recapture pooled with detecting rate

short interruptions to accommodate battery changes and data transfer. At block ramp KA, 26.9 % of chub had passed after 4.5 days, whereas in total 40.5 % of trout had passed after 16 days (pooled with recapture data) at block ramp OF.

Upstream movements of chub were concentrated in the evening, whereas the movement activity of trout started in the afternoon and ceased in the morning, reaching a peak before midnight (Fig. 3). On block ramp OF, two peaks of movement activity of brown trout became evident during the course of observation. The first peak consisted in a clear preference for upstream movement during the first night and day after translocation (40 % of movements; Fig. 4). The second peak (28.6 % of movements) followed during and after a heavy rainfall that caused an increase in discharge and turbidity combined with a drop in water temperature.

Comparing passage efficiencies of mark-recapture and reader-system at block ramp OF, we found that the control catch indicated an efficiency of brown trout of 26.9 %, with only one individual not being detected by the antenna. In contrast, efficiency according to reader-system was

higher and accounted for 39.3 % of the brown trout. Additionally, the advantage of the reader-system was the recording of four individuals, which had passed the ramp successfully but moved downstream again and were recaptured at the ramp bottom.

Discussion

The main objective of the present study was to assess the effectiveness of block ramps for fish upstream movement. We studied brown trout, bullhead and several species of cyprinids and found that upstream passage differs between species. Brown trout performed better than bullhead and any cyprinid species on the same block ramps. Successful passage in reasonable numbers for the nonsalmonid, comparatively small-bodied species bullhead, minnow and gudgeon was not observed. Our results clearly show that upstream passage efficiency differs between size classes within species and block ramps. Passage efficiency of brown trout and chub is size-selective, with small-sized individuals being far less successful. For brown trout, this effect becomes more important with increasing slope of ramp. However, we do not know whether the differences between small- and large-sized individuals are caused by efficiency per se or by differing motivation. Furthermore, we showed that environmental factors can influence behavior and that with elevated discharge, upstream swimming activity of brown trout is stimulated. Generally, swimming and leaping performances as well as physiological condition of fish limit their passage efficiency across obstacles. The distance a fish can swim in upstream direction with constant effort declines with increasing water velocity. Velocity barriers that exceed the physiological or behavioral capabilities of fishes define the distributional limits of their populations (Haro et al. 2004). Agreeing with our study, large-sized trout cope well with slopes of 26, 16.5 and 10 % on relatively short obstacles of 2.98, 5.13 and 8 m in length, respectively (Ovidio et al. 2007). However, the repeated recovery in resting pools is necessary for fish in order to prevent total exhaustion

Table 3 Logistic regression models (1) and (2) calculated for passage of brown trout on block ramps WY1, WY2, OF and SI

Model	Variables	B	SE	Wald	df	Sig.	Exp (B)	95 % CI for Exp (B)	
								Lower	Upper
Model (1)	Fish size	0.019	0.002	112.716	1	0.000	1.019	1.016	1.023
	Constant	-3.782	0.303	156.273	1	0.000	0.023		
Model (2)	Fish size	0.008	0.002	11.407	1	0.001	1.008	1.003	1.013
	Fish size × slope	0.001	0.000	36.639	1	0.000	1.001	1.001	1.002
	Constant	-3.950	0.317	155.377	1	0.000	0.019		

Model (1): Cox & Snell R² 0.202, Nagelkerke R² 0.287. Model (2): Cox & Snell R² 0.249, Nagelkerke R² 0.353

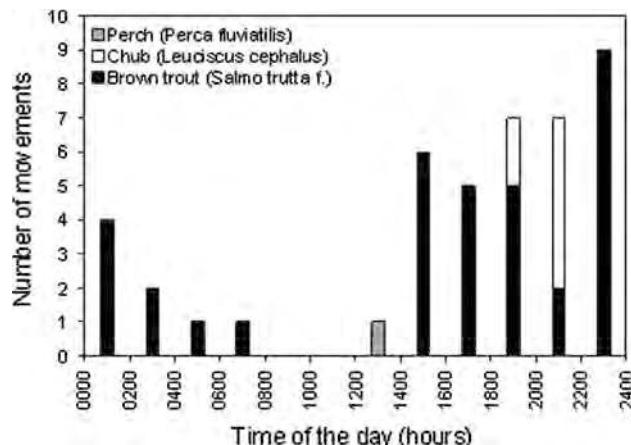


Fig. 3 Temporal movement activity expressed as number of upstream movements obtained from PIT-tagged individuals on ramps OF and KA related to time of the day. Pooled number of upstream movements over a period of 16 days at ramp OF and of 4.5 days at ramp KA (ramp KA: perch N = 1, chub N = 7; ramp OF: brown trout N = 35; translocated fish were released in each case between 1100–1200 hours)

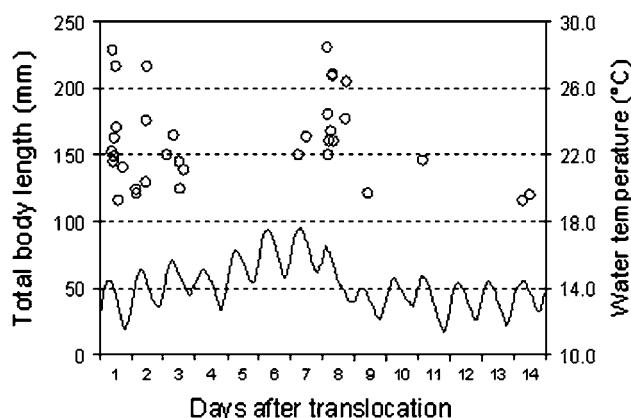


Fig. 4 Temporal progress of upstream movement of PIT-tagged brown trout on ramp OF. White circles indicate individuals in respect of their body size. The curve below depicts the water temperature. Start of temporal axis at 12 a.m. after release of fish. Interruption of detection on day number 5 due to battery failure. Increase in discharge on the evening of day 7

because burst swimming is anaerobic and can only be maintained for a few seconds. A number of studies have shown that physical swimming capabilities are influenced by water temperature (Hammer 1995). Holthe et al. (2005) document leaping heights of 0.18–0.27 m for minnow depending on size-class at water temperatures of 14.0–16.5 °C, but recorded no leaping behavior at low temperatures outside of spawning season. We conclude that swimming performance of small species is often not sufficient to cope with flow velocities measured on the block ramps we studied.

In European minnow, a general motivation for active homing under laboratory conditions has been reported (Kennedy and Pitcher 1975). However, the cause for the missing passage of minnows across the block ramp SI in our study is unclear. Whereas adult brown trout are usually highly mobile and also migrate outside the spawning period (Ovidio and Philippart 2002), this may not be the case for the minnow. Even though the low passage rate of the migratory species barbel in our data is likewise surprising, it nevertheless corresponds to previous findings that showed that obstacles systematically blocked migration of barbel, whereas trout could clear obstacles with slopes of more than 30 % (Ovidio and Philippart 2002). Unsuccessful passage of roach has been described in a different study, in which upstream movement of roach was limited by physical barriers as they do not frequently clear obstacles even during reproduction migration (Geeraerts et al. 2007). Passage failure of downstream transferred bullhead has also been observed at a fish pass, most likely due to excessive water velocities (Knaepkens et al. 2006). Like our findings at step-pool-step ramp ST, there was a general tendency of a few individuals to move upstream several pools, but they never fully ascended. High bidirectional mobility for a closely related *Cottus* species has been demonstrated in a continuous stream during a 1-year period using longitudinal home ranges of up to 435 m (Ovidio et al. 2009). Hence, we suppose that bullhead had failed to pass the block ramps during our experiments due to limiting swimming and leaping capabilities rather than to a lack in motivation for micro-homing. We conclude that sills of 0.15 m hinder upstream movement of bullhead upon structured block ramps.

Evidence on species-specific responses to habitat fragmentation by weirs is provided by Blanchet et al. (2010) comparing chub, dace, gudgeon and minnow. Contradictory to our results, their genetic study showed that the smallest-sized species minnow was the least affected by fragmentation, and the authors therefore suggest that dispersal behavior rather than dispersal ability per se could explain species sensitivity to weirs. However, we note that differences in effective population size could also explain these results if smaller species had larger effective population sizes. Recent findings indicate that chub as well as brown trout are likely to perform micro-homing after translocation and that with increasing body length of trout the probability of micro-homing increases (A. Peter, unpublished data). It is possible that individual behavior such as timing of migration and motivation for micro-homing could have influenced our experiments. Under the assumption that all species that we studied tend to return to the capture-site, our data reveal a strong lack of connectivity across block ramps. However, given the uncertainties regarding homing behavior in cyprinid species, our results

should not be considered as a definite indicator of effectiveness for cyprinids. We stress the need for comparative studies on micro-homing behavior outside spawning season, notably for small-sized species.

Comparing antenna-detection with mark-recapture, we cannot exclude an underestimation of actual upstream movements in the mark-recapture experiments. Hence, the antenna-detection of PIT-tagged fish is a qualified method to evaluate the effectiveness of block ramps and out-performs the conventional method of mark-recapture to detect movement patterns. Our temporal observation showed that upstream passage of brown trout and chub happens within a short time period. Contrary to a study on sea lamprey (Quintella et al. 2004), we found fish to be particularly active not only during darkness, but also in the afternoon. The response of fish to movement during a heavy rainfall suggests the close dependence on discharge conditions or turbidity. Likewise, clearance of obstacles and fishways in an upstream direction can be triggered under elevated discharge and within a certain range of temperature (Laine et al. 2002; Ovidio and Philippart 2002), whereas diurnal movement of the cyprinid species *Leuciscus idus* was found to be influenced by turbidity per se independent of discharge (Kulíšková et al. 2009). Our temporal data on brown trout indicates that the testing of block ramps during summer should be avoided because physical stress due to elevated water temperatures may affect upstream passage. If fish are unable to pass an obstacle, they wait downstream, sometimes several weeks, for environmental conditions to improve (Ovidio and Philippart 2002), which consequentially delays the arrival at spawning grounds. The hydraulic measurements, which we took during low flow condition on each block ramp, only revealed excessive current velocities of ramps in the grayling zone. Nevertheless, these measurements reflect the snap-shot conditions and it is recommended that passage for fish should be assured during approximately 300 days per year (Friedrich et al. 2005).

We conclude that steep block ramps with a slope $>6\%$ can reestablish longitudinal connectivity and fish migration corridors in the trout zone only for large-sized brown trout. Although passage rates for brown trout indicate less success for juveniles, large-sized individuals pass these block ramps successfully. The comparably long, step-pool-like block ramp comes with low current velocities and has the advantage of providing resting pools. However, there is a risk at low discharge for having vertical drops of sills that fish can only clear by leaping. In view of our results and of previous findings of Utzinger et al. (1998), such drops have a serious negative effect on small-sized species with low leaping potential like bullhead. Block ramps should be constructed in such a way that sills do not feature vertical drops. Our results indicate that block ramps with slopes of

$>5\%$ in the grayling zone are insufficient for the small-sized cyprinid species. Block ramps within the grayling zone can be improved by rip-rap structures along the shoreline that provide calm areas underneath boulders.

Our study is a first attempt to assess the effectiveness of block ramps for different fish species. We point out that the results are subject to potential constraints caused by the behavioral experiments. We emphasize the necessity of monitoring block ramps during the pre- and post-construction phase to determine species as well as genetic diversity down- and upstream of the obstacle and to quantify effects of the block ramp construction on fish assemblage structure. If block ramps were more effective at interconnecting downstream with upstream fish habitat they could considerably contribute to goals of river restoration and conservation. However, more research is needed to improve the design of block ramps to achieve this.

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CHAPTER 3

Longitudinal patterns of fish diversity and abundance along river gradients

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Abstract

In order to grasp the effect of river fragmentation and its consequences on fish diversity and abundance, it is necessary to understand the factors structuring fish communities. The aim of this study is to characterize longitudinal patterns along a downstream-upstream gradient and to quantify spatial variation in local species richness and abundance. We investigated two streams and a river (including one floodplain) in the prealpine region north and south of the Alps of Switzerland. For that purpose, electro-fishing was conducted at 37 study sites and environmental parameters regarding fish habitat and water quality were sampled. We evaluated whether assemblage changes happen gradually or abruptly and whether habitat fragmentation influences spatial distribution patterns. We applied a neutral model and found that fish species are not randomly distributed and that dispersal distance per se does not appropriately explain variation in abundance patterns. For the two most abundant species brown trout and bullhead, the contribution of local environmental habitat parameters and spatial factors (e.g. dispersal distance, dispersal barriers) in explaining longitudinal variation of abundance was evaluated. Information on predictive factors that control local distribution of fish species are of particular interest for developing effective river basin management and restoration plans to counteract river impoundment.

Introduction

In river ecosystems, the gradual change of aquatic communities is described by the theoretical framework of the River continuum concept. The River continuum concept predicts a continuous gradient from headwater streams to large rivers of energy input, of nutrient availability and of associated biological processes like productivity and respiration in natural and undisturbed lotic systems (Vannote et al., 1980). For aquatic macroinvertebrates, the River continuum concept describes a continuous transition in the structural composition and functional characteristics of their biotic community in response to the abiotic environment. Comparably, the succession of characteristic fish communities in streams and rivers is proposed in the zonation concept by discrete biogeographic zones. In accordance to this, species zonation of fish communities results from differences in water temperature, flow velocity, width and slope of the river (Rahel & Hubert, 1991; Torgersen et al., 2006; Huet, 1959). Species composition can be predicted by other local geomorphic variables and bed characteristics (Walters et al., 2003). Naturally, the importance of limnophilic species versus rheophilic ones increases from upstream to downstream reaches (Belliard et al., 1997). However, Ibarra et al. (2005) suggest that fish assemblages are too complex to be identified with a single species as in the zonation model and they found the replacement and succession of species along a gradient without defined boundaries. There is a difference in fish community function among stream size categories and it becomes evident in the variations in trophic ecology, reproductive behavior, and preferences for substrate and geomorphic habitat types (Goldstein & Meador, 2004). Santoul et al. (2005) observed that a few biological traits related to life-history attributes significantly influenced fish distribution in a french river system. They had demonstrated that fecundity, potential size and maximum age increased from headwater to plain reaches.

The reasons for longitudinal variation and the determinants for the structure of fish assemblages have concerned many fish biologists. A couple of studies have investigated the response of fish assemblages to the fluvial environment and landscape features. Fish diversity and species richness often depend on watershed area (Walters et al., 2003; Grubbs et al., 2007) and progressively increase from upstream to downstream sites with increasing stream order, distance from the source, river size and decreasing elevation (Belliard et al., 1997; Robinson & Rand, 2005; Rahel & Hubert, 1991; Oberdorff et al., 1993; Hutchison, 1993; Ibanez et al., 2007; Reyjol et al., 2003; Santoul et al., 2005; Ibarra et al., 2005). Landscape factors, such as human land use, occurs to influence fish habitat directly, whereas the habitat directly influences fish assemblages (Rowe et al., 2009). The type of land use along the river can change fish assemblages, but do not always disrupt the dominant longitudinal assemblage patterns (Rahel & Hubert, 1991). For example, relative

abundance of flathead catfish (*Pylodictis olivaris*) was observed to be higher in more agricultural areas (Paukert & Makinster, 2009) whereas fish species diversity was found to decrease with higher levels of urban land use (Slawski et al., 2008; Long & Schorr, 2005). Similarly, increasing urbanization followed by hydrologic alteration can cause a shift in fish assemblages towards generalist species and a loss of fluvial specialists (Roy et al., 2005). In addition to landscape features, differences in assemblage structure correspond with local habitat gradients such as depth, water velocity, channel gradient and water temperature (Torgersen et al., 2006). These physical and geomorphologic habitat gradients are responsible for species addition and replacement along the river course. Hence, fish assemblage composition relates to environmental variables such as variation in land use, mesohabitat structure, water quality, stream volume, substrate size, riparian condition (Hitt & Angermeier, 2008), pH or water conductance (Ibanez et al., 2007).

One of the most influential factor determining fish assemblage composition was found to be hydrological connectivity (Lasne et al., 2007). For instance, geologic barriers to fish movement influence the distribution of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) (Kruse et al., 1997). Additionally, anthropogenic barriers such as dams, weirs and road-crossing culverts highly fragment the river corridor and disrupt longitudinal habitat connectivity. The distance-dependent effect of dams on lotic systems has been described by the Serial discontinuity concept. The Serial discontinuity concept addresses the river ecosystem responses such as upstream-downstream shifts or discontinuities in abiotic variables and processes that have a serious effect on the biota if the river's geomorphologic continuum is disrupted (Ward & Stanford, 1983). Hence, fish assemblage structures are influenced by the discontinuities caused by dams along the river course (Araujo et al., 2009). Due to a change of hydrology, dams were found to reduce microhabitat diversity and consequently have an effect on the dominance structure of fish assemblages (Gozlan et al., 1999). Apart from river-bed structures that act as barriers, monotonous and channelized river sections are likely to hinder fish movement and to constitute dispersal barriers, too.

It was recently demanded that research about connectivity in rivers should enhance the understanding of how spatial processes structure fish communities (Fullerton et al., 2010). The disruption of longitudinal connectivity through a presumptive barrier is supposed to be reflected in an abrupt change of the assemblage composition, i.e. in species richness and relative as well as absolute abundance of species. In order to grasp the effect of river fragmentation and its consequences on fish diversity and abundance, we need to understand the underlying longitudinal patterns of fish assemblages. It is further important to understand the role of species pools such as lakes or large rivers that can potentially influence distant assemblages in streams or tributaries through colonization. We further need to recognize

whether local key factors that are relevant predictors can explain variation in fish assemblages.

The aim of this study is to characterize longitudinal patterns of fish assemblages along a downstream-upstream gradient of environmental parameters. We investigate species abundance patterns in three selected stream or river systems (including one floodplain) north and south of the Alps of Switzerland. Our main objective is to quantify local species richness and spatial abundance. Further, we intent to determine their associations to selected habitat and spatial factors that structure assemblages. For that purpose, we examine the influence of environmental parameters, dispersal barriers and the distance from the river mouth that constitutes a colonization factor. We attempt to identify among-site variations and similarities between different watercourses. This study evaluates whether assemblage changes happen gradually or abruptly and whether habitat fragmentation influences spatial distribution patterns (i.e. barrier-effect). We expect that variation in abundance can be explained by local environmental factors as well as spatial factors (i.e. distance from the mouth, dispersal barriers). Information on predictive factors that control local distribution of fish species are of particular interest for developing effective river basin management and restoration plans to counteract river impoundment. It is equally essential when focussing on the long-term effect of climate change.

Materials and methods

Study sites

The study was conducted in two prealpine streams of Central Switzerland and in the middle and lower reaches of an alpine-prealpine river of Southern Switzerland. The stream Muelibach partly is an urban, modified and channelized stream that has a small restored section and that runs into Lake Lucerne. The Chlausenbach is mostly a near-natural and partly a forest stream that flows through a rural area and feeds Lake Lauerz. The Brenno river is located to the south of the Alps. This large river is a tributary of Ticino river and is characterized by three natural floodplains. The lowest, prealpine floodplain of Brenno river, which is situated near the village Loderio, was included in our study. Study sites were selected beforehand along the stream or river principally at a regular interval starting from the mouth. The distance between study sites had to be adapted if it was impossible to access the stream or river due to the terrain. Standardized sampling was performed during September to October 2009 (stream Muelibach), in November 2009 (stream Chlausenbach) and during March to April 2010 (Brenno river).

Electro-fishing

We conducted electro-fishing at each study site along a predefined stretch using a semiquantitative approach. This approach included one single-pass survey (no block nets, except from upstream endings of the stretches of stream Chlausenbach), which provides a representative index of species diversity (Reid et al., 2009). Electro-fishing was conducted using a backpack electroshocker (EFKO, 1.5 kW, 150-300/300-600 V). Sampled stretches had a length of 100 m. In three cases, the study stretch was slightly shorter than 100 m because of the terrain. Both streams Chlausenbach and Muelibach were fished the entire stream width. Surveys of the Brenno river was carried out on strips of 3 m width. Each sampling stretch of the Brenno river was fished along two parallel strips. One strip was preferably situated in the middle of the channel if the water depth was not too deep, whereas an additional strip was randomly either on the left or on the right bank. In addition to the regular sampling along the Brenno river, the lowest floodplain was sampled in different floodplain habitats. We herefore fished different backwater channels (in one case connected to a backwater pool), the main channel (middle of the channel and bankside) as well as a groundwater-fed tributary. The number of study sites for both streams, the river and its floodplain are listed with further details in Table 1.

Captured fish were kept in oxygenated water tanks and anaesthetized with clove oil before handling (Hänseler AG, Herisau, Switzerland; 0.5 ml diluted in 9.5 ml alcohol added to 20 l water). We visually determined fish species and measured their total body length (± 1 mm). Extremely rare, nonnative individuals were excluded from our analyses (*Lepomis gibbosus* and two salmonid species that were most likely escaped from a nearby fish farm). When measured individuals had recovered from handling, they were released into the sampled stretch.

Table 1. Details of the study streams and study river.

Name of the stream or river	Number of study sites	Length of river or stream section that included study sites (m)	Mean longitudinal distance between study sites (m; SD)	Mean stream or river width at study sites (m)	Mean stream or river depth of study sites (m)
Stream Muelibach	10	3022	405 (152)	1.4 - 5.0	0.3 – 0.6
Stream Chlausenbach	8	2569	354 (114)	2.4 - 3.5	0.1 – 0.5
Brenno river	River: 11 Floodplain: 8	14457	River: 1423 (1083)	Floodplain: 2.5 - 15	n.d.

SD: Standard deviation.

n.d.: not determined because water depth was often too deep to conduct measuring transects.

Environmental parameters

At each sampling site, we recorded different environmental parameters regarding fish habitat and water quality. Therefore, we conducted measuring transects at intervals of 10 meters and measured on each transect the maximum depth and wetted stream width. In the river Brenno, we measured the maximum depth across the 3 m-strip only. In the equally-spaced segments of 10 meter length we determined several habitat variables. We identified the availability of different types of fish cover and determined its proportion relative to the sampled area. Categories of fish cover included vegetation, turbulence, pool, stones, scoured banks, wood and, finally, total cover availability. In addition, we visually estimated the relative proportions of different aquatic habitat types in each segment. These mesohabitats were classified into riffle, glide, run, cascade, pool and trench pool (Bisson et al., 1982). Further, we analyzed the relative substrate composition for every study stretch. For this, at least 140 substrat particles along a randomly placed stick were assigned into one of the following coarseness classes: gravel (1-2 cm), pebble (2-6 cm), cobble (6-25 cm) or boulder (25-40 cm) following (Bain & Stevenson, 1999). Immediately before the electro-fishing, we took a water sample and measured the temperature ($^{\circ}\text{C}$) as well as conductivity ($\mu\text{S}/\text{cm}$) of the water. The water sample was cooled, filtered and later analyzed in the laboratory according to standard protocols. We determined for each study site pH, O_2 (mg/l), $\text{o-PO}_4\text{-P}$ ($\mu\text{g/l}$), $\text{NO}_2\text{-N}$ ($\mu\text{g/l}$), $\text{NO}_3\text{-N}$ ($\mu\text{g/l}$) and $\text{NH}_4\text{-N}$ ($\mu\text{g/l}$).

Data analysis

At stream sites and floodplain channels, the size of the sampled area was defined by stretch length multiplied by stream width. At the river sites, the two 3 m-strips defined the survey area. For each of the 37 study sites, we calculated the following fish parameters: total fish density (individuals per hectare), species richness (number of species) and type I Brillouin's Diversity Index H (Bits per Ind) (Krebs, 1989). In addition, we determined the relative abundance (%) of each species as well as the absolute abundance (ind/ha) of each species at all sites. We then conducted complimentary approaches.

The neutral model (nullmodel): In general, the neutral model is a popular tool used in landscape ecology for understanding patterns in spatial data. It is particularly useful in investigating the relationships between fragmentation on biological diversity and tests whether a particular hypothesized mechanism is needed to explain an observed pattern (Pearson & Gardner, 1997). We used a neutral model in order to understand which major processes (i.e. spatial dependencies) has an effect on the observed fish abundance and diversity pattern within a river system. In other words, from the basis of our observational data, which are limited to a single observation, we hoped to find a causal correlation between parameters of the river system (*spatial correlation, barrier*) and the observed fish

assemblage pattern. The neutral model tries to show that observed patterns happen in the absence of a causal correlation. Hence, when observed data differ from model predictions, then there is a strong evidence for the importance of the process (e.g. environmental and spatial dependencies) (Pearson & Gardner, 1997).

Simple nullmodel (1): Our nullmodel (1) simulated fish distribution patterns (abundance) along the river or stream without any potential causal correlation (i.e. distance from the mouth as spatial dependency). The model repeated the randomization 10,000 times (without changing any system characteristics). The obtained distribution of fish abundance for each species among study sites was then compared to the field observation data. A poor fit and significant deviation of the model from the observed data ($p<0.01$; $p>0.99$) would indicate a potential correlation with other factors and ask for further investigation.

The principle is the following: each species (S_i) occurs with a specific probability (P_i) at a specific site i (according to their observed abundances). We create one single (global) pool of all the probabilities altogether of the species from all the sites. We then redistribute all individuals according to this probability to all sites *without any spatial limitation* (global dispersal). We expect that all species can freely colonize without any limits in space. This results in a matrix with each cell indicating the presence or absence of species S_i at site i and its assigned probability P_i (proportional abundance). Finally, we plot the observed abundance ($\log x$) against the mean as well as the minimum and maximum confidence interval of the expected value from the model. Through the non-parametric, pairwise comparison of the observed value x with the model distribution, bounded by the confidence interval, we get a p-value for each species in each site (each cell of the matrix). The p-value informs about the significant deviation of the observed data from the expected distribution according to the model. If $p<0.01$ or $p>0.99$, the model failed to predict observed values correctly.

Nullmodell (2): To improve the predictive power of our nullmodel, we included as an additional predictor the “distance from mouth” to test whether assemblage distributions are constrained by the spatial distance. Hence, contrary to the nullmodel (1), the nullmodel (2) assumes a local pool for each randomly picked site i from which one individual locally disperses as a function of distance. The distribution of species S_i is, hence, a function of distance and its probability decreases with increasing distance.

The linear regression analysis was used as an additional approach and the following procedure was applied (*SPSS Statistics 20.0*). In total, we derived 25 environmental parameters belonging to one of the four groups (i) fish cover, (ii) type of mesohabitat, (iii) substrate and (iv) water chemistry. All environmental data was transformed using arcsin-square-root-transformation for proportional data (%) and $\log_{10}(x+1)$ -transformation for water chemistry data. We then applied factorial analysis in order to reduce these numerous potentially intercorrelated variables to a subset of uncorrelated factors (i.e. to overcome

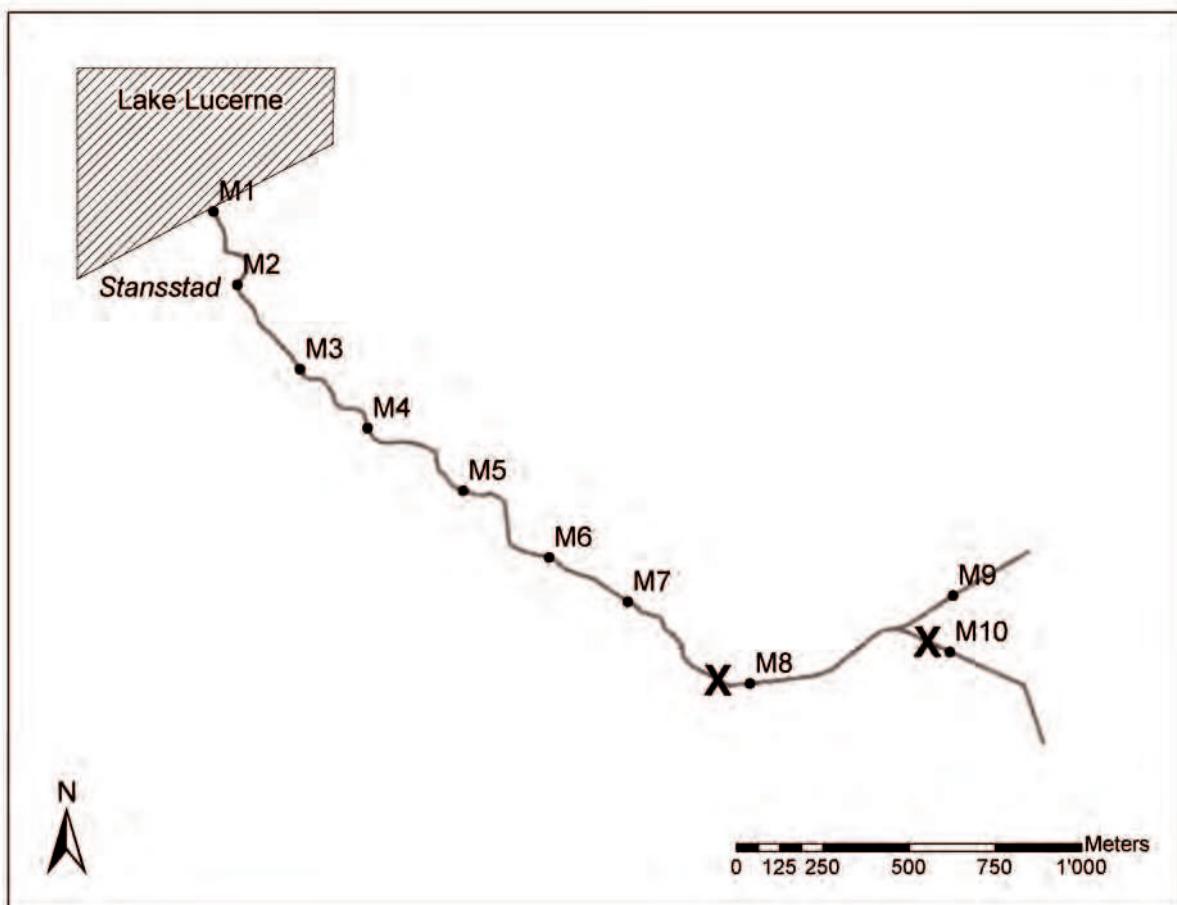
multicollinearity), which adequately summarize the original information. Therefore, we conducted Principal Component Analyses (PCA) with the five different categories stream Muelibach, stream Chlausenbach, Brenno river, Brenno floodplain and the three river systems altogether (excluding floodplain) with their associated environmental parameters. Factors with eigenvalue >1 were retained from matrices of associations. The extracted principle components that explained at least 10% of variance between sites were used for the regression models. By means of linear regression, we tested the relationship between the most abundant species and the habitat factor as well as spatial factor (i.e. environmental parameters and river distance from mouth). Hence, the relative abundance of brown trout and bullhead were put as dependent variables into separate models. The distance from mouth of the individual study sites together with the factor scores of extracted components defined by PCA constituted the independent variables. Abundance and distance from mouth were $\log(x+1)$ -transformed beforehand in order to comply with the assumption of normality.

Results

Electro-fishing was conducted at 37 study sites in total (Table 1). Both streams were studied upon a total distance of 2.6 or 3.0 km from the lake upwards (Fig. 1a, 2a). River Brenno was sampled in regular intervals upwards to kilometer 7.3, whereas two additional sites were included at 11.0 and 14.2 km distance from the confluence into Ticino river (Fig. 3a). The number of native fish species varied between one to four species depending on site (Fig. 4a,b). In both streams Muelibach and Chlausenbach, species richness was highest close to the lake and rapidly declined with increasing distance from mouth. Species richness of Brenno river was fairly constant over a comparably long river distance. It increased at the river mouth and right below the floodplain, whereas it reached a maximum at floodplain sites. Heterogeneity of species richness was highest among the different floodplain habitats (Fig. 4b). Brown trout (*Salmo trutta*) was the only species that was abundant at all sites of both streams, of Brenno river and floodplain, with the exception of one site (Fig. 1b, 2b, 3b, 3c). As it is typical for Swiss prealpine rivers and streams, either brown trout or bullhead (*Cottus gobio*) dominated the fish communities along the three watercourses, apart from two sites.

Figure 1

a) Locations of the study sites along the stream Muelibach. Each point indicates the downstream end of the study stretch (M1 to M10). Crosses symbolize a culvert between M7 and M8 and an artificial overfall (<1 m) right downstream of M10.



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b) Relative fish species abundances in each study site of stream Muelibach (M1-M10). Crosses: see above.

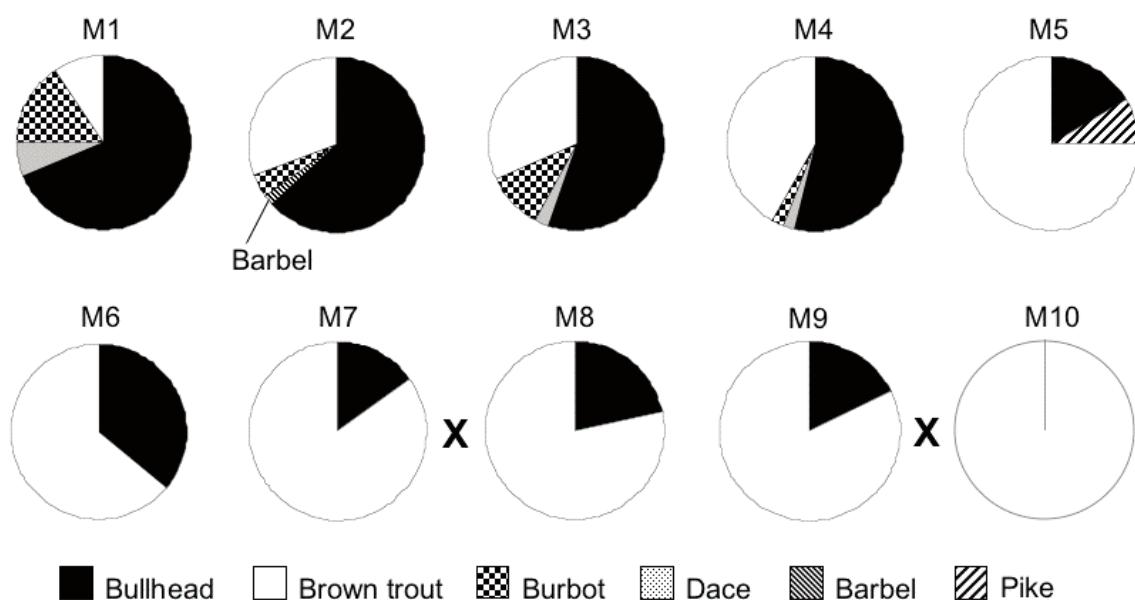
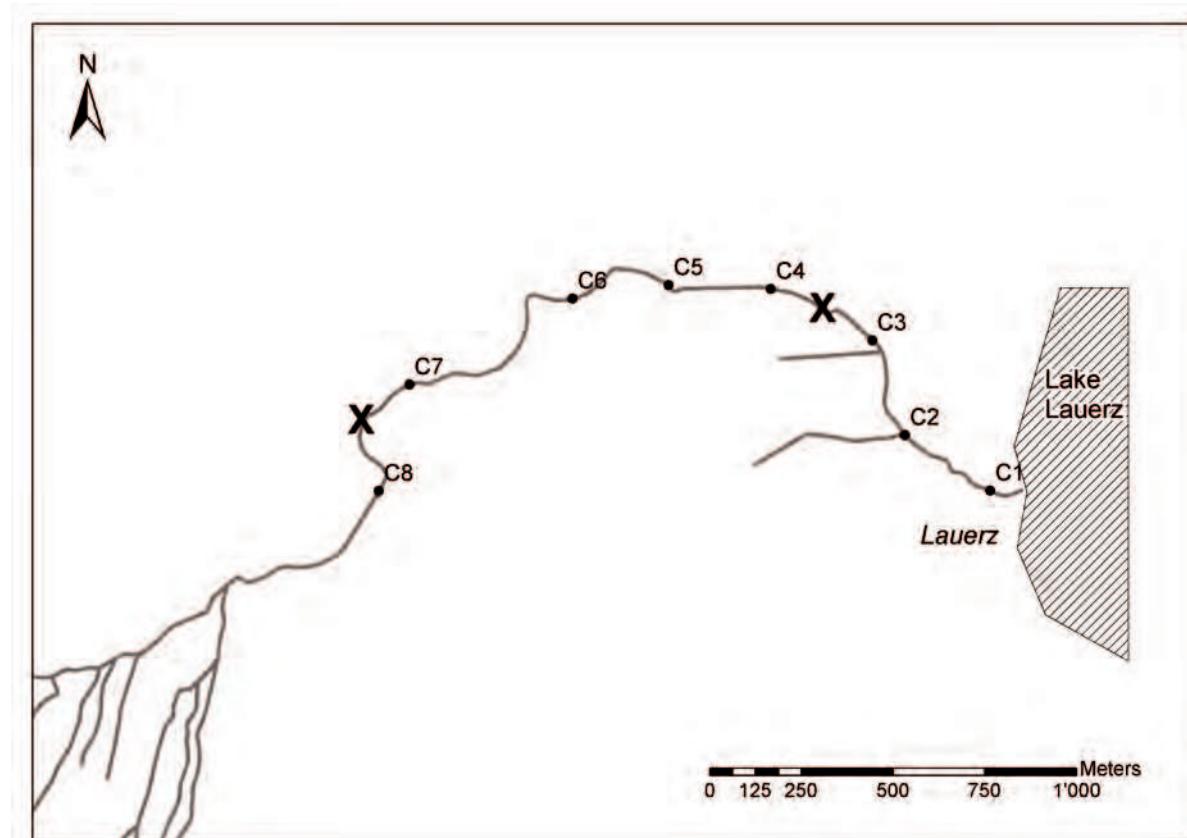


Figure 2

a) Locations of the study sites along the stream Chlausenbach. Each point indicates the downstream end of the study stretch (C1 to C8). Crosses symbolize road-crossing culvert between C3 and C4 and between C7 and C8.



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b) Relative fish species abundances in each study site of stream Chlausenbach (C1-C8). Crosses: see above.

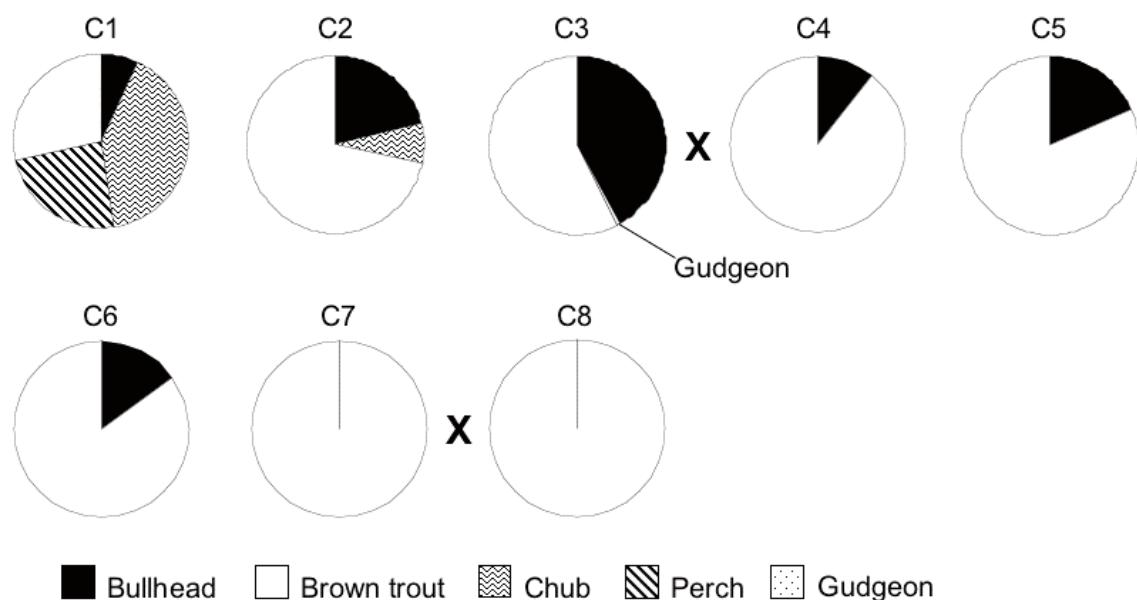
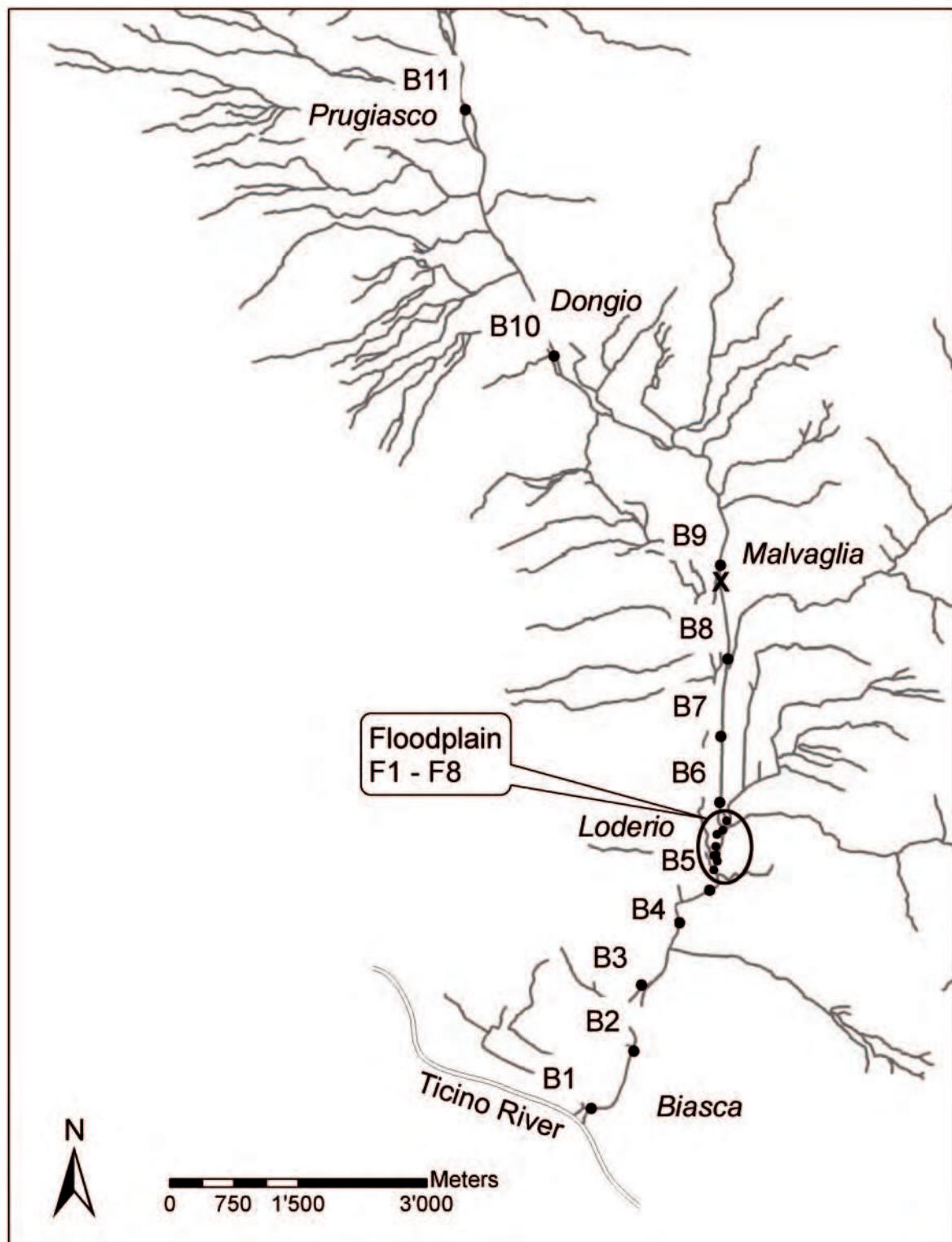


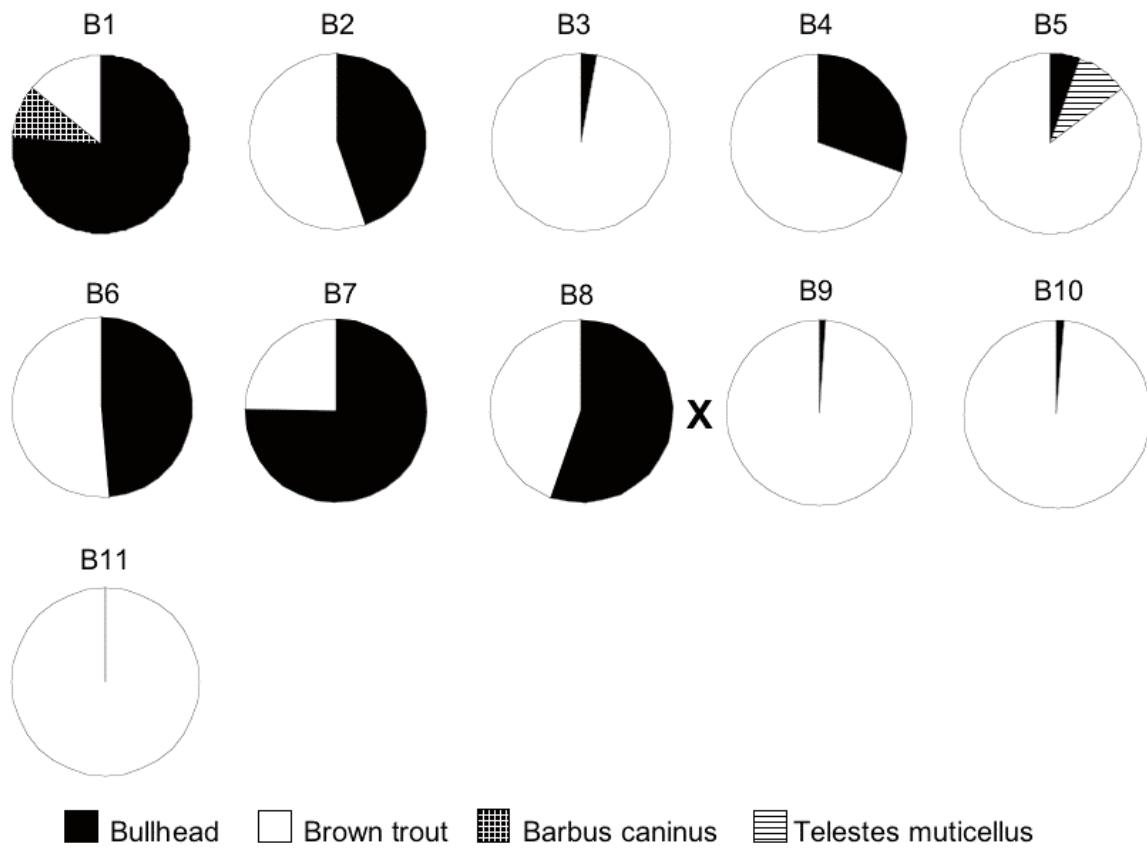
Figure 3

a) Locations of the study sites along the Brenno river (B1 to B11) and within the lowest floodplain next to Loderio (F1 to F8). Each point indicates the downstream end of the study stretch. Cross symbolizes an artificial overfall (1.35 meters) right downstream of B9.



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b) Relative fish species abundances in each study site of Brenno river (B1-B11). Cross: see above.



c) Relative fish species abundances in each study site within Brenno Floodplain (F1, F2 and F3: backwater channel; F4 and F7: main channel bankside; F5: main channel middle of river; F6: groundwater-fed tributary; F8: backwater channel with a backwater pool).

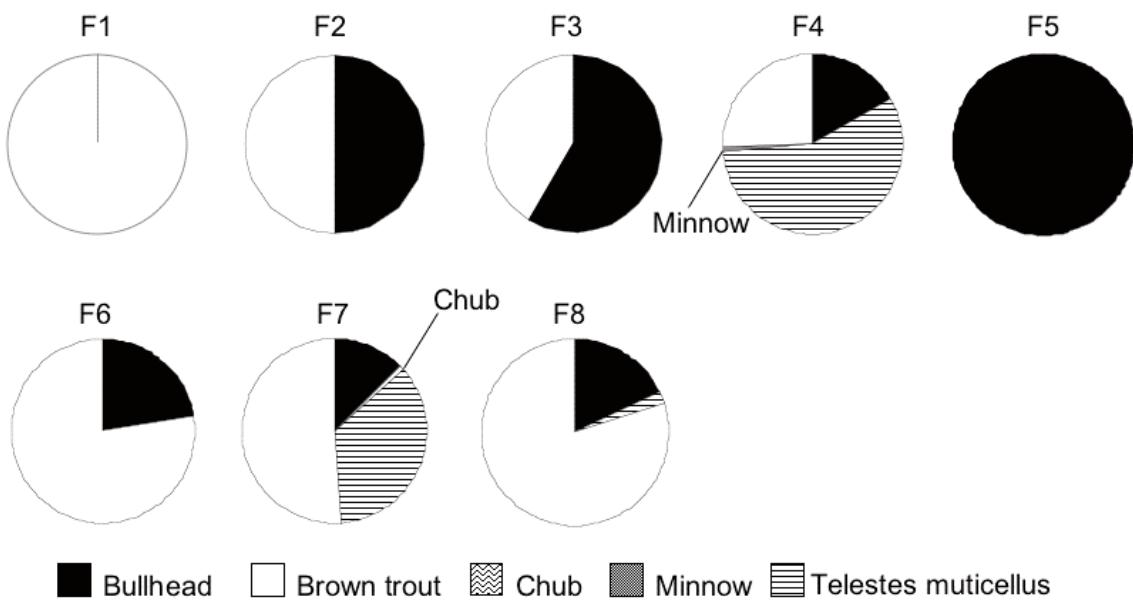
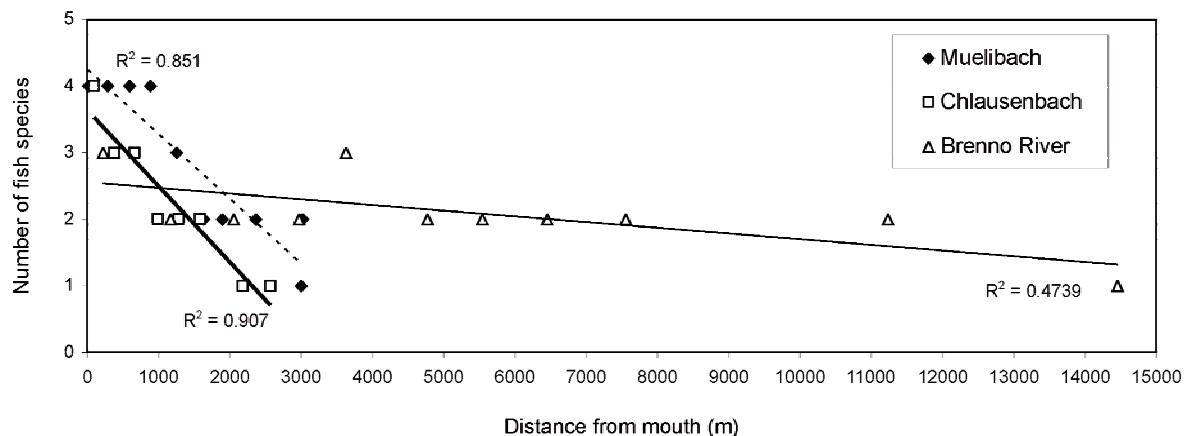
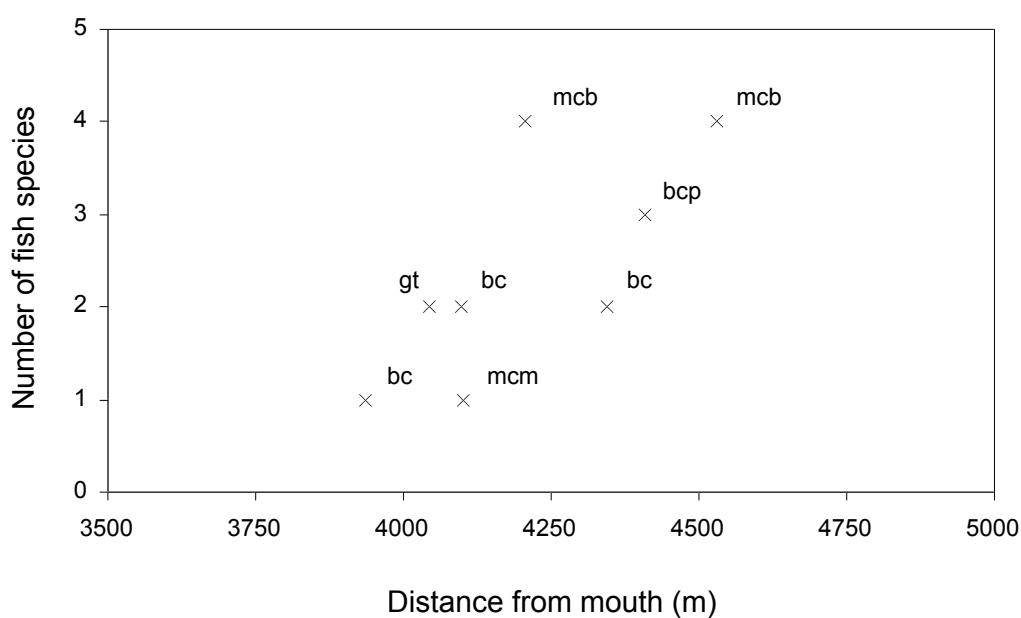


Figure 4

a) Number of fish species along the watercourses of both streams Muelibach and Chlausenbach and of Brenno river excluding the floodplain. Each symbol mark represents a study site. The regression lines indicate the individual trends.



b) Number of fish species at individual study sites within the Brenno floodplain (cross symbols). Labels depict the different channel types of study sites. bc: backwater channel; mcb: main channel bankside; mcm: main channel middle of river; gt: groundwater-fed tributary; bcp: backwater channel with backwater pool.



Stream Muelibach

The lower sites M1 to M4 of stream Muelibach were characterized by a relatively high species richness and the dominance of bullhead (Fig. 1b). Apart from brown trout, typical lake-species like burbot (*Lota lota*) and dace (*Leuciscus leuciscus*) were present. The barbel (*Barbus barbus*) uniquely occurred. With increasing distance from mouth, brown trout gradually became the dominating species. At site M5, which is a morphologically restored section, pike (*Esox lucius*) was caught. In contrast, the sites further upstreams (M6 to M10) are characterized by a poor species richness. A culvert of more than 100 m length between M7 and M8 did not distinctively influence the relative portions of the present species brown trout and bullhead. However, a small overfall of <1 m height just downstream of site M10 obviously hindered bullhead to successfully colonize this contributing arm of the stream. Surprisingly, bullhead were abundant at the parallel site M9, which is characterized by an artificial, impervious river-bed.

Stream Chlausenbach

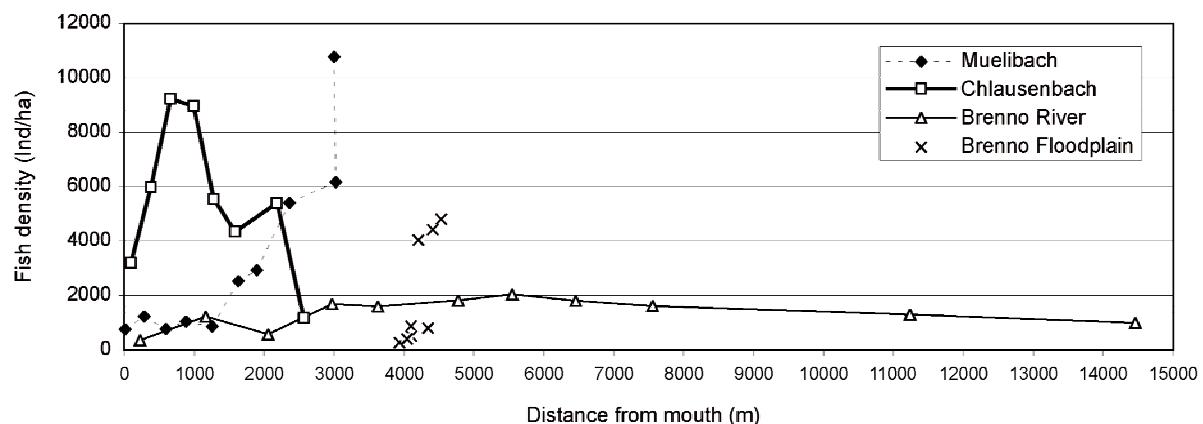
In stream Chlausenbach, the near-lake site C1 exhibited highest species richness and was dominated by chub (*Leuciscus cephalus*) (Fig. 2b). It was further characterized by perch (*Perca fluviatilis*), brown trout and bullhead. Brown trout dominated all other sites (C2 to C8). A small proportion of chub occurred at site C2, whereas a single individual of gudgeon (*Gobio gobio*) was present at site C3. Relative abundance of bullhead became noticeably reduced from site C3 to C4, after a road-crossing culvert. Brown trout was the only abundant species above a sequence of natural, rocky overfalls of >1m height upstream of site C6. At site C8, which is segregated by an impervious road-crossing culvert from site C7, brown trout were abundant.

Brenno river and floodplain

Apart from the floodplain, the fish fauna of Brenno river was mainly characterized by bullhead and brown trout (Fig. 3b). The unrestricted connection to Ticino river positively influenced the number of species at the site close to the confluence (site B1). There, the barbel *Barbus caninus* occurred, which is endemic to rivers south of the Alps in the north-italian catchments (Zaugg et al., 2003). In addition, brown trout and bullhead, which was the dominating species, were present at this site. The sites between the confluence and the floodplain (B1 to B5) were characterized by bullhead and dominating brown trout. Directly downstream of the floodplain (B5) the rare and vulnerable species *Telestes muticellus* (in italian: strigione) occurred, which is known to be native to rivers south of the Alps as well as to northern and central italy (Zaugg et al., 2003). The floodplain itself was characterized by a heterogeneous, well-connected habitat that supported a diversity-hotspot (Fig. 3c). Species richness within

the floodplain varied between sites and was highest in the bankside main channel (sites F4 and F7). At those sites, there was a relatively high abundance of *Telestes muticellus*, among brown trout, bullhead and individuals of minnow (*Phoxinus phoxinus*) and of chub. *Telestes muticellus* also occurred at the site with the backwater pool (F8) together with brown trout and bullhead. The three backwater channels (F1 to F3) and the groundwater-fed tributary (F6) were either exclusively inhabited by brown trout or by both species, brown trout and bullhead. In the middle of the main channel only bullhead were captured (F5). With the beginning of the monotonous, channelized river section directly upstream of the floodplain (site B6; Fig. 3b), species richness dropped abruptly and all cyprinid species disappeared. The site B9, which is located directly above an overfall structure of 1.35 m height, does not differ from B8 with regard to species composition. However, there is a significant decline in the abundance of bullhead above the overfall. Bullhead became then minimally represented and were fully absent at the most upstream site, 14 km from the confluence.

Figure 5. Fish density (individuals per hectare) along the watercourses of stream Muelibach, of stream Chlausenbach, of Brenno river and within Brenno floodplain . Each symbol-mark represents a study site.



Fish density (individuals per hectare) highly varied between both streams, the river and the floodplain (Fig. 5). Fish density of stream Muelibach was relatively low and constant in the lower section M1 to M5 (754 to 1222 ind/ha), that is characterized by a mostly urban, channelized section and that also included a restored site. Density then almost exponentially rises with increasing distance from the lake and peaks at the upper most site M10. The exceedingly high density (10773 ind/ha) of brown trouts (mean body size 126 mm) directly above the overfall can be ascribed to stocking efforts. Fish density at the mouth of stream Chlausenbach was higher than at the corresponding sites of Brenno river and stream Muelibach. Fish density of stream Chlausenbach increased and peaked at site C3 (9217

ind/ha) and C4. The lowest density was found at the uppermost site C8. However, the small size of individuals at site C8 (mean body size 92 mm) clearly indicates that this site has lately been subject to stocking of 0+ brown trout. Comparatively, fish density of Brenno river excluding the floodplain was relatively constant and low (< 2034 ind/ha). Density reached a minimum and maximum within the floodplain sites. Highest density (4033 to 4800 ind/ha) was found in the backwater channel with the pool as well as in the bankside main channel, though it was much lower than peaks of both streams.

Nullmodel 1

Significance values for all species across sites are indicated in Table 2. Overall, the model poorly predicts the distribution of the two most common species, brown trout and bullhead in all three river systems including the floodplain. With very few exceptions, the model predicts a rather inhomogenous distribution across the different sampling sites, and it deviates significantly from observed abundance of brown trout and bullhead in almost all sites. This result suggests that dispersal is limited and fish are not randomly distributed. Other environmental and/or spatial factors must be important to predict the presence and abundance of the two most common species.

Bullhead: In the site of stream Muelibach and Brenno river that are close to the mouth, the model predicts a significantly lower abundance of bullhead than it was actually observed. This pattern is not consistent with the stream Chlausenbach, where the model prediction was higher than the observed abundance (Table 2).

Brown trout: The model predicts a significantly higher abundance of brown trout at the sites of both streams that are near the lake, compared to the actual observation. With increasing distance from the lake, there is a shift in the pattern along both streams. For the upper section of both streams, we observed a higher abundance of brown trout than the model had predicted. A possible explanation for the underestimation of the model in the two most upstream sections M10 and C8 might be the fact that in those sections stocking took place. Similarly to both streams, brown trout abundance of Brenno river close to the confluence into Ticino river was below the model prediction. In the most upstream sections of the river, observed trout abundance was higher than the predicted abundance by the model. However, in the longitudinal course of Brenno river and floodplain, the predictions are inconsistent and it is hard to detect a clear pattern for brown trout. Model predictions for the backwater channels and the main course of the floodplain are either significantly lower or higher than the actual trout abundances, with a high predictive power in only a few cases.

In both streams, there is a pattern that reflects the influence of the lake on the species assemblage. Close to the mouth, there were more individuals of chub, perch, dace and

burbot than the model had predicted. Those species are not truly rheophil and hence, not constrained to riverine habitat. In fact, the burbot is a species that typically occurs in lakes. With increasing distance from the lake, there is a shift in this pattern and the model prediction is higher than the observed abundances. Contrary to sites near the mouth, model expectations of abundance are then significantly higher for chub, perch, dace and burbot, which were in fact absent.

It appears that species that occurred in very low numbers, i.e. gudgeon, barbel, dace, pike, *barbus caninus* and minnow are the species that were best predicted by the model. However, the validity of the model in these cases is strongly limited because these species were extremely rare and absent in most sites. This is why the model predictions do not significantly deviate from observed abundance. Although there is no significant deviation from the expectations, we assume that the model has a low predictive power on these species.

Nullmodel 2

Strong deviations between the model expectations and the actual observations, as well as the limitation with the rare species forced us to extend our model 1 to a model 2 that took into account the spatial dependence. Hence, we included *river distance between each pair of sampled sites* in addition to the observed abundance of each species within each site. We thus generated expectations for a dispersal-limited community given local abundance and pairwise river distances. The predictions of model 2 for each species within each site are listed in Table 3.

Bullhead: the predictive power of model 2 for both streams and the river is even lower than it was for model 1. With one exception, the observed abundance of bullhead significantly deviates from the model's expectation. The model 2 predicts a higher abundance than we had actually found in the three most upstream sites of both streams and the river, whereas it accurately predicts the abundance in two backwater channels of the floodplain.

Brown trout: model 2 poorly predicts abundance of brown trout in all watercourses. There is a similar pattern to model 1 with a lower abundance in the sites near the mouth than model 2 had predicted as well as a shift to an underestimation of the model 2 with increasing distance from mouth. In stream Muelibach, this shift is not associated to the culvert section between sites 7 and 8 nor to the artificial overfall downstream of site 10. There is no significant deviation from model 2 at site 4 of stream Chlausenbach, which is situated upstream from a road crossing culvert. Model predictions for Brenno floodplain are very inconsistent and inaccurate.

The model predictions of chub, gudgeon, burbot and *barbus caninus* do not at all, or not remarkably, differ from model 1. Interestingly, there is an improve of the predictive power for

perch in model 2. Our model 2 does not significantly deviate from observed values in all the sites where perch was absent. The accuracy of model 2 for *barbus caninus*, dace and pike is weaker than it was in model 1. Especially at sites where they were absent, model 2 predicts a higher abundance. The model 2 slightly improved predictions for a few sites where *Telestes muticellus* and minnow were absent.

To conclude, it seems that our model 2 does not correctly explain the occurrence of species by only including dispersal distance as a determining factor. There must be other explaining determinants, for example the influence of a species pool such as a lake, the different habitat parameters or migration barriers.

p-values of nullmodel 1 (ABUNDANCES)	Muelibach										Chlausenbach							Brenno River											Brenno Floodplain								
Species / Sites	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7	8
Brown trout	***	***	***	***	*	***	**	*	**	**	***	***	***	**	**	**	**	**	*	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	
Bullhead	**	**	**	**	*	**	***	**	*	***	***	***	***	***	***	***	***	***	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	
Chub																																					
Perch																																					
Gudgeon																																					
Barbel	*	**	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*																			
Dace	**	*	**	*	**	*	*	*	*	***	***	***	***																								
Pike	*	*	*	*	**	*	*	*	***	***	***	***																									
Burbot	**	**	**	**	*	***	***	***	***	***	***	***																									
<i>Leuciscus s. muticellus</i>																																					
<i>Barbus caninus</i>																																					
Minnow																																					

Table 2. Listing of the significant deviation from the nullmodel (1). For each site and fish species the observed abundance (ind/ha) is pairwise compared to the confidence interval (CI) of the model. Significant deviation from model if observed value is below CI ($p<0.01$: ***) or above CI ($p>0.99$: **). No significant deviation from model if observed value is within CI ($0.01 < p < 0.99$: *).

p-values of nullmodel 2 (ABUNDANCES; DISTANCES)											Muelibach										Chlausenbach										Brenno River											Brenno Floodplain							
Species / Sites	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7	8												
	***	***	***	***	**	*	**	**	**	**	***	***	***	*	***	**	**	**	***	***	***	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***						
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Minnow																																																	

Table 3. Listing of the significant deviation from the nullmodel (2). For each site and fish species the observed term abundance and distance is pairwise compared to the confidence interval of the modell. Significant deviation from modell if observed value is below CI ($p<0.01$: **) or above CI ($p>0.99$: **). No significant deviation from model if observed value is within CI ($0.01 < p < 0.99$: *).

Linear regression models

The Principal Component Analyses (PCA) reduced the environmental parameters in each study system to 6 or 7 extracted components explaining cumulatively 82.7 to 100.0% of the total variance within the original data. Thereof either 3 or 4 extracted components explained at least 10% of variance, respectively, and became part of the regression models.

Table 4 lists the results (overall fit) of the model testing (p-values of ANOVA). Note that a few variables did not fulfill the assumption of non-normality even after transformation, probably due to the small number of sampling sites. However, we still tried the regression analysis. Hence, the results of bullhead in stream Muelibach, Brenno floodplain and in three river systems altogether as well as trout abundance in Brenno floodplain should be handled with care. Overall, distance from mouth together with habitat factors significantly accounted for the variation in absolute abundance of brown trout within each and over all river systems outside the Brenno floodplain. It is the opposite case for bullhead. Variation in bullhead abundance was poorly explained by the combination of river distance and habitat factors outside the Brenno floodplain. In the floodplain, however, habitat factors either with or without the influence of river distance significantly contributed to the variation of bullhead abundance. These results suggest that habitat and spatial factors together (i.e. environmental parameters, distance from mouth) are important and common predictors for variation in trout abundance. These findings support our previous conclusions from nullmodels 1 and 2. For bullhead however, such a prevalent effect could not be proved.

Table 4. Overall fit of linear regression models (p-values of ANOVA). The models tested the relationship between brown trout or bullhead abundance with the explaining variables distance from mouth and extracted principal components (explaining at least 10% of variance). Significant p-values are in bold. *For the category floodplain, additional regression models were conducted excluding distance from mouth as predictor variable because these study sites were clustered compared to the other Brenno sites.

	All 3 river systems together (excl. floodplain)	Stream Muelibach	Stream Chlausenbach	Brenno River	Brenno Floodplain	
Brown trout abundance (ind/ha)	p=0.000 F=11.337 $R^2=0.654$	p=0.001 F=51.460 $R^2=0.985$	p=0.018 F=55.701 $R^2=0.993$	p=0.032 F=5.594 $R^2=0.789$	0.740	*0.887
Bullhead abundance (ind/ha)	0.414	0.607	0.059	0.173	p=0.018 F=19.429 $R^2=0.963$	*p=0.017 *F=12.241 * $R^2=0.902$

Discussion

Our main objective was to quantify spatial variation in fish assemblages of three different river systems and to evaluate the contribution of spatial and habitat factors in explaining longitudinal patterns of fish distribution. Species richness overall decreased with increasing distance from the mouth in both streams as well as the river (except the floodplain), and assemblage changes in an upstream-downstream gradient mainly occurred through the addition of species rather than replacement. This effect has previously been observed in river systems (Hutchison, 1993). Our findings supports Matthews (1998), who anticipates a continuum of gradual longitudinal changes in fish distributions in North American streams instead of abrupt transitions from one distinct faunal “zone” to another. The faunistic differences between our three studied systems are remarkable. The longitudinal assemblage pattern of stream Chlausenbach features a shift into a brown trout dominated assemblage not far from the confluence, whereas stream Muelibach supports the cyprinid, esocid and lotid families over a relatively long section. The longitudinal pattern of Brenno river indicates a distinct structural change at the floodplain and punctually features the presence of the species *Barbus caninus* and *Telestes muticellus*. Both of these species are vulnerable according to the red list and pristine for river systems south of the Alps. Apart from the floodplain and the confluence into Ticino river, the fish fauna of Brenno river showed an overall low species diversity. In general, trophic progression in fish guilds along the longitudinal gradient is common from invertivores (benthivores, insectivores) upstreams to omnivores, detritivores, herbivores and piscivores downstreams (Hugueny et al., 2010). In our study, the fauna predominantly consisted of invertivorous species with the exception of dace and chub (omnivorous) as well as burbot and pike (piscivorous). Of course, trophic patterns in fish assemblages are likely to be related to food availability (Oberdorff et al., 1993). Most of our species belonged to the lithophilous guild (relating to the preferred spawning substrat), with the exception of bullhead (speleophilous) and pike (phytophilous). We found meso-eurythermal species close to the confluences and within the floodplain (*Barbus caninus*, dace, pike, chub), though oligo-stenothermal species dominated. Apart from burbot and pike, that typically occur in lakes too, all species were rheophilic.

Diversity hotspots

Our results highlight the importance of connectivity to potential species pools in lakes, at tributary junctions or floodplains. The network dynamics hypothesis by Benda et al. (2004) predicts an increased species diversity at tributary confluences due to abrupt changes in water flux as well as punctuated inputs of sediment and organic material that triggers changes in channel morphology and enhances physical habitat heterogeneity. Our findings,

which demonstrate an increased species number at the confluence to Ticino river, support this hypothesis and provide evidence that river junctions promote biological diversity within a river network. Further, the relevance of Brenno floodplain as diversity hotspot and its heterogeneous assemblage structure is impressive. The distribution of *Telestes muticellus*, minnow and chub was limited to the floodplain and the site directly below. At the floodplain, some species were observed in main channel habitats only, whereas others were found all over in the main channel, side channel and backwater pool habitats. Our findings highlight the importance of the spatio-temporal habitat heterogeneity of floodplains for a high fish species richness. This is consistent with other studies that attribute high species diversity of fish to habitat diversity (Kaemingk et al., 2007). The connection of calm back water pools and side channels with the active channel plays a key role during disturbances like floods, when fish exhibit sheltering movements in order to access refuge areas (Allouche et al., 1999). Similarly, heterogeneous off-channel environments of floodplains are driving forces to benthic macroinvertebrate assemblage diversity by providing numerous refugia (Arscott et al., 2005; Burgherr et al., 2002). But floodplains do not only account for high species diversity. They are due to their flood pulse characteristics and lateral exchange highly important for nutrient storage, nutrient recycling and productivity of the river system (Junk et al., 1989). The peak in fish density that we had encountered in Brenno floodplain supports this hypothesis. However, despite of legislative protection, the Brenno floodplain is endangered by an altered flow regime due to water abstraction (Brunke, 2002). Hydrologic alterations have a severe impact on the fish fauna. In fact, it was discovered that the timing and magnitude of low flow influence the diversity of fish communities and the total fish abundance, respectively (Yang et al., 2008).

Dispersal barriers

Local fish communities present within a river reach depend on the river basin species pool, and dispersal along the river network plays a major role for community structure and dynamics (Hugueny et al., 2010). Connectivity between populations supports colonization processes such as immigration, which is important after stochastic events or river restoration activities. Previous findings suggest that fish communities in relatively close reaches are more similar to each other than reaches separated by larger distances (Chick et al., 2006). Above all, potential dispersal capacities affect how fish species respond to their local environment (Grenouillet et al., 2008). We argue that in stream Muelibach, an artificial riverbed sill of almost 1 m height highly affected dispersal of bullhead and caused their abrupt absence above the obstacle. In Brenno river, it is likely that a similar barrier is the reason for an abrupt decrease of local bullhead abundance in above-barrier sites. This is not surprising, considering the fact that bullhead have a low leaping potential and are hampered

to clear vertical obstacles of 0.15 m (Weibel & Peter, 2013). Other findings support our results, which demonstrate that small barriers impassable to upstream movement have a negative effect on diversity and upstream abundance of at least some species (Nislow et al., 2011). Longitudinal patterns of fish assemblages can be strongly influenced by the presence of dams resulting in low species richness above dams (Brenkman et al., 2012). We found a positive floodplain-effect on species richness patterns with *Telestes muticellus* appearing not only within, but also at the site below the Brenno floodplain, though this effect was not far-ranging. Further, the abrupt decrease in the channelized reach above the floodplain is striking. This fact illustrates that deficits in channel morphology resulting in a highly monotonous habitat are presumptive dispersal barriers that evidently reduce local species richness. The findings are comparable to hydrodynamic barriers that limit fish diversity, caused by the inability of immigrants to pass sections of fast flow velocities (Grossman et al., 2010). Furthermore, there is an apparent effect of brown trout stocking on the abundance patterns in both streams. In fact, we assume that such high densities accompanied by an unnatural age distribution of individuals can be found in many river systems because stocking is massively applied across Switzerland (Droz et al., 2006). However, abrupt shifts in community structure can also happen through trophic interactions (Lujan et al., 2013). Based on our observations of abiotic and spatial factors, we cannot exclude a causal relation of species abundance with biotic interactions (e.g. resource competition or predation) at those sites where abrupt shifts occur. Biotic factors are major and complex determinants that control assemblage structures of riverine fish communities, too.

Spatial and habitat factors

The predictive neutral models clearly demonstrate that the two most prevalent species brown trout and bullhead are not randomly distributed and, additionally, that dispersal distance is not the exclusive determining factor for their longitudinal abundance pattern. This is consistent with findings that describe a higher association of fish assemblage composition with the local environment than with position along the river (Winemiller et al., 2008). We conformed with common approaches to incorporate environmental factors when evaluating regional effects of potential dispersal barriers on fish distribution (Wang et al., 2011) because fish assemblage patterns can be strongly associated to abiotic habitat variables (Balcombe et al., 2011; Humpl & Pivnicka, 2006). Longitudinal variations in fish abundance can reflect species-specific habitat requirements and are related to the preferred habitat type (Inoue & Nunokawa, 2002). Often, density of species increases with fish cover area, for example of fluvial sculpin *Cottus nozawae* (Yagami & Goto, 2000). Poff (1997) integrates the various conditions (so-called filters) that predict local distribution and abundance of species in stream communities into a heuristic hierarchical framework. This framework considers abiotic and

biotic filters at different hierarchical landscape scales ranging from basin and reach scale to channel unit and microhabitat patch. Accordingly, species in a regional pool must possess appropriate functional attributes (selective species traits) to “pass” through the multiple, nested filters. Our results suggest that spatial as well as habitat factors together explain longitudinal variation of brown trout abundance. There is evidence from other studies demonstrating that distance from the ocean is a good predictor of fish distribution patterns in coastal rivers (Lyons & Schneider, 1990) and that river distance or distance from the mouth correlates with variation in fish assemblages (Pyron & Lauer, 2004) and variability over time (Schaefer & Kerfoot, 2004).

Outlook

It must be pointed out that the spatial resolution and extent of predictive models can influence the perceived importance of different environmental predictor variables on community variation and the perceived importance can change from one region to another (Troia & Gido, 2013) or between headwater tributaries and mainstem tributaries (Hitt & Angermeier, 2008). Furthermore, fluvial habitats are temporally highly dynamic due to environmental disturbances and seasonal hydrologic variability. Species composition and structure of fish communities are under constant change because most fish species seasonally migrate in order to avoid abiotic stress (Zalewski et al., 1990). Hence, for a holistic perspective of fish communities, it is necessary to study the variation of riverine systems over time. Analyzing the level of gene flow among populations can be a helpful tool to measure dispersal and the influence of human-induced landscape alterations (Crispo et al., 2011), whereas historical biogeographical effects within the branching river network should be considered. Longitudinal connectivity is particularly important facing the expected climate change and the associated increase in water temperature of Alpine rivers. Under the expected conditions, temperature-sensitive species (e.g. brown trout) will need to access adequate sites at higher elevations in order to avoid critical temperatures. Consequently, the local extinction of some coldwater species is probable in the near future and the diversity and distribution patterns are supposed to change depending on the position along the river course (Matulla et al., 2007). We stress the importance of longitudinal connectivity in river and stream corridors for dispersal and species diversity. We further claim that management implications should acknowledge the importance of heterogeneous floodplain habitats as diversity hotspots and guarantee a natural flow and bedload regime in order to sustain heterogeneity and hydrologic connectivity of fish habitat.

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CHAPTER 4

Home ranges and space use of freshwater fish in streams and rivers - a literature review

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Abstract

Home ranges of freshwater fish have drawn the attention of many researchers. In view of recent river restoration projects that comprise the restoration of longitudinal connectivity, one crucial question arises: how much space do individual fish need to successfully complete their life cycle, and how much space do populations need to stably persist? In this article, studies about home ranges of fish in stream and rivers of the northern hemisphere are reviewed to address the first of these questions. First, the various meanings of the term home range as applied by different authors are introduced and the problem of defining a home range is discussed. Further, selected methodical approaches to estimate home range sizes are compared with particular attention to the temporal aspect. Home range sizes are compiled in detail for a taxonomic overview. Additional aspects regarding mobility of fish as well as factors influencing home range size can be specified. The review stresses that knowledge about the space use of fish is fundamental in order to understand the impact of river fragmentation and hence, to develop appropriate future river management and restoration strategies.

Introduction

When we try to understand the role of connectivity for fish within river corridors, one major question arises: how much space do individual fish use for successful completion of their life cycle, and how much space do populations need to stably persist? In order to assess the ecological effects caused by anthropogenic fragmentation in river systems and the influence of migration barriers, it is essential to comprehend the spatial requirements, i.e. home ranges of individuals, for different fish species. Moreover, it is difficult to predict the effect of exotic invaders that have become a potential threat to a specific river system, without additional knowledge on home ranges apart from spatial niche overlap (Curry et al., 2007). So far, little work has been done about spatial requirements with the focus on more than just one fish species. Knowledge about the specific use of home ranges in different species of fish, and possible differences between larger taxonomic units, such as families is very limited. Analyzing the movement and home ranges of potamodromous fish gives us an idea about their use of space and hence, about their spatial requirements. Such knowledge is necessary when developing action plans for reestablishing connectivity in rivers and management strategies to safeguard and restore fish diversity.

The importance of movement

The migratory strategy of freshwater fishes and their movement behavior in longitudinal or lateral direction has evolved as an adaptation to seasonal cycles as well as to alternating environmental conditions, and it illustrates the need for fishes to access different habitats to complete their life cycles (Baras & Lucas, 2001). Such rapid and frequent environmental changes are caused by either abiotic (e.g. temperature, light, flow regime) or biotic factors (predation and competition) (Heggenes et al., 2007).

Literature about fish movement mostly focuses on diadromous species performing spawning migration and neglects nonmigratory species and nonmigratory ecotypes of diadromous lineages. Accordingly, the impact of migration barriers is often studied with the focus on diadromous, long-distance (100+ km) swimmers only, because fish species that complete their entire life cycle in freshwater are frequently considered as “resident” (Baras & Lucas, 2001). However, apart from spawning behavior, the unhindered movement of fish is crucial in population processes such as source-sink and metapopulation dynamics. Long-distance movement even occurs in sedentary fish, and can be important in recolonization processes after stochastic events (Hudy & Shiflet, 2009). Movement within a small range, however, usually occurs daily, for example when fish shift their habitat from cover to open water or deeper areas at night (Perkin et al., 2010; Slavik et al., 2005). In contrast, the concept of restricted movement of fish populations by (Gerking, 1959) represented the conventional assumption for many years, namely that fish normally are sedentary and remain in a restricted area: they actively return to this area if they are displaced. The concept of the restricted movement of fish was later broadened by the perspective of a restricted home range, within which a fish is highly mobile. Under laboratory conditions, European minnow (*Phoxinus phoxinus*) take up a restricted home range during acclimatization and rapidly perform homing after an artificial transfer (Kennedy & Pitcher, 1975; Kennedy, 1981). It is generally thought that the attachment to a specific familiar site, i.e. home range,

and the astonishing behavior of accurately homing to a formerly occupied location brings some key benefits.

The aim of this study

Here we present a review on the research that characterizes daily and seasonal movements within a home range for different fish species. Major aims of this review were to compile a summary on current literature and to give an overview on the conducted studies and the fish species that have been investigated. Our objectives were to, first, identify the different definitions of the term home range or movement range used by various authors. We then compile available data about home range sizes and address the specific question what the differences and communalities are between fish species and higher taxonomic units. Further, we focus on the key aspects of fish movement and spatial activity within home ranges, such as dependencies on fish body size or other factors. We do not intend to provide an overview on movement distances of fish, especially during long-distance spawning migration (see Baras & Lucas (2001) for a review), but rather focus specifically on the term home range and its corresponding aspects. Thereby, it is vital to recognize the dynamic space use of riverine fish and to explain the demand of connected habitat within river networks. The present review is not meant to be an exhaustive synopsis on this topic, it rather indicates ways that future research should take. We hope that this review will also be useful as a basis that would be consulted when recommendations are made for conservation management and river restoration.

Literature search and evaluation

A literature search was conducted by means of the Web of Science. There is an excessive amount of literature about fish movement and it was not possible to include all of this work about movement in the present review on home ranges. We therefore used the key terms "home range" combined with "fish" and looked for literature published by February 2011. From about 800 published papers, 160 were usable based on title or abstract, and were read. Of these 160 read articles, 84 dealt with the expression "home range" or "movement range" of freshwater fish and contained original data according to the general criteria listed below. Those 84 articles were then compiled for detailed analysis of home range sizes. Additional literature was occasionally obtained by following key references in papers. We confined the review to freshwater fish of lotic systems of the northern hemisphere. Any research conducted in lentic systems such as lakes or reservoirs, coastal deltas and transition zones like estuaries, brackish tributaries, marsh habitat or tidal streams were excluded from the study. The analysis focused on behavioral field studies, thus studies from artificial ponds or experimental aquaria were not considered. For each evaluated article, fish species was listed according to its taxonomic family and the following key features were noted if available: year of publication, country of study, study system (the term "river" or "stream" used by the author), tracking interval, duration of study, field observation method, body size of individuals, home range size estimation method, home range size (total longitudinal or areal movement range), daily home range size (daily movement range or daily activity area) as well as factors influencing home range size.

Results

Table 1 presents an overview of the 84 out of 160 reviewed publications that contain data on movement range or home range sizes (Table 1). More than 70 additional reviewed articles could not be used for the detailed analysis, but still contained useful information about home ranges and fish movement in general. The first literature about fish home ranges that is available online dates back to the seventies. Work done before that time is most probably not uploaded to common online-database systems. Only few studies were found from the seventies and eighties (Fig. 1). A sudden increase in the publication process during the nineties reflects on the one hand a rising interest in fish movement behavior in the context of river ecosystems. On the other hand, the ongoing improvement of tracking technology in the nineties (e.g. telemetry) has made enhanced research in this field possible. However, the rise of publications in the nineties is partly a general trend and an outcome of more people publishing papers in research.

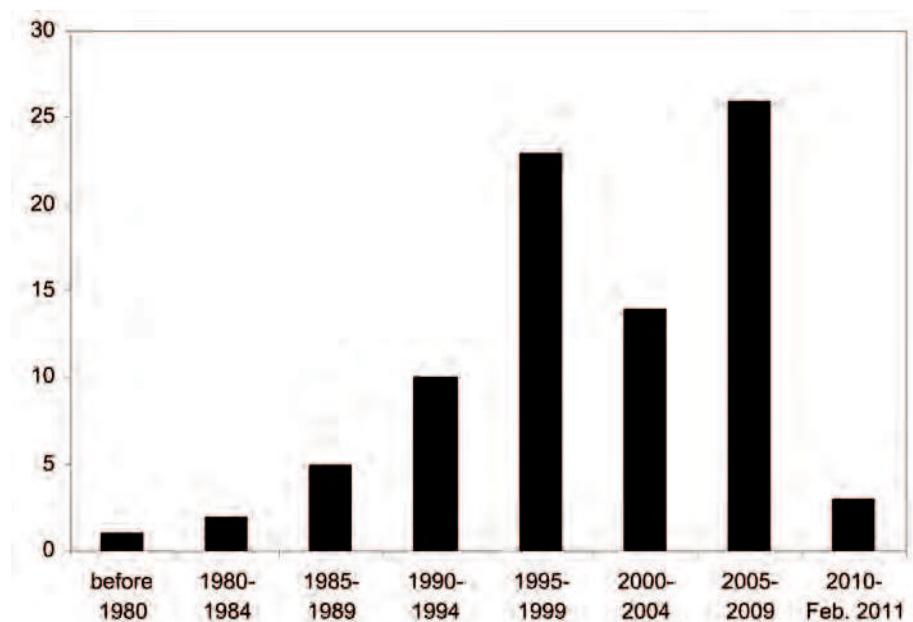


Figure 1. Number of publications in the last decades that comprise data about fish home range sizes (movement ranges).

Radio-telemetry is the most popular method when observing fish movement ranges and it has been used in almost two thirds of the studies (Fig. 2). The traditional mark-recapture survey was applied in one fourth of the studies. Usually, these methods were applied in the field by a non-standardized approach. The mark-recapture method measures the displacement distance between a capture and a successive recapture event, which corresponds to the minimum distance that an individual has moved within this time span. The use of radio-tracking allows a finer scale of detection. Repeated localization of fish and the use of multiple stationary receivers enable to study space use and direction of movement more precisely. Due to the influence of the size of the sampling-area on the recaptured proportion of fish in mark-recapture studies, the use of telemetry is preferable (Gerking, 1959; Gowan

et al., 1994). Surprisingly, the compared to telemetry more cost-effective use of PIT-tags has not been established well in fish home range studies so far. The use of hydro-acoustic telemetry and visual observation is minimal, too. Only a few authors combined radio-telemetry with either hydro-acoustic telemetry or mark-recapture. In the majority of studies (60 %), fish were observed in rivers, whereas 40 % of study systems were defined as streams. Unfortunately, it was not common practice to indicate width of river or stream.

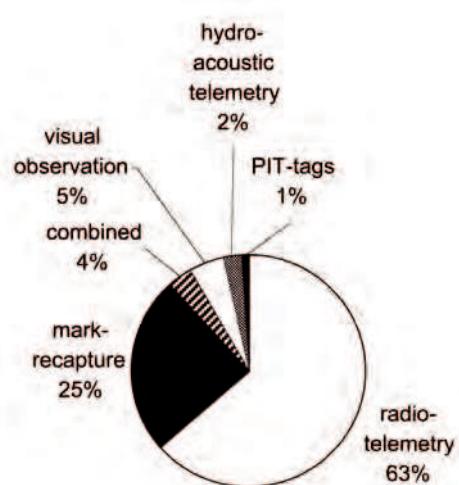


Figure 2. Relative frequency of observation methods used in the studies.

Information on home ranges came from studies conducted in the USA, Canada, Mongolia, Japan and several European countries (Fig. 3). The highest number of publications about fish home range were carried out in the USA. Quite a few studies originate from Belgium, mostly by the same authors.

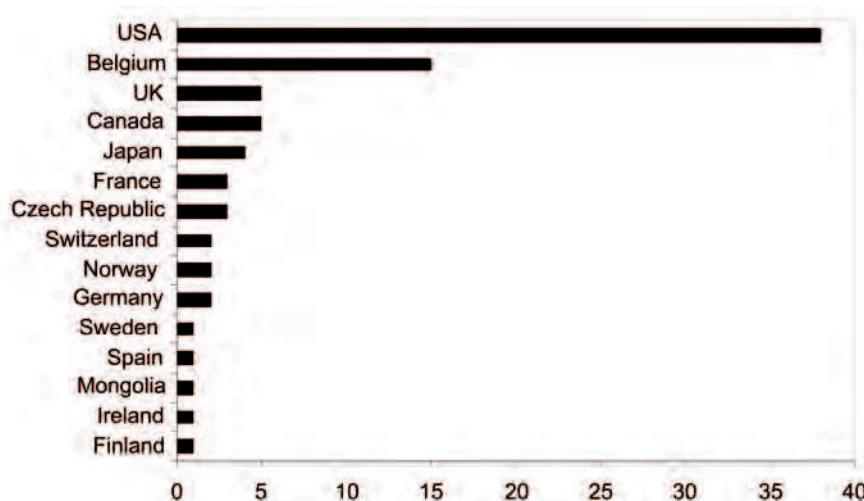


Figure 3. Number of publications per country (referring to table 1).

Home range sizes have been studied for many species from several different families. Salmonids and Cyprinids dominated in literature and accounted together for approximately half of the studies (Fig. 4). The number of studies with Cottidae and Centrarchidae add up to about a fourth. Percidae, Esocidae and Catostomidae were less frequently studied. For many families, only one or two publications exist, namely for Acipenseridae, Anguillidae, Ictaluridae, Siluridae, Polyodontidae, Lotidae and Lepisosteidae.

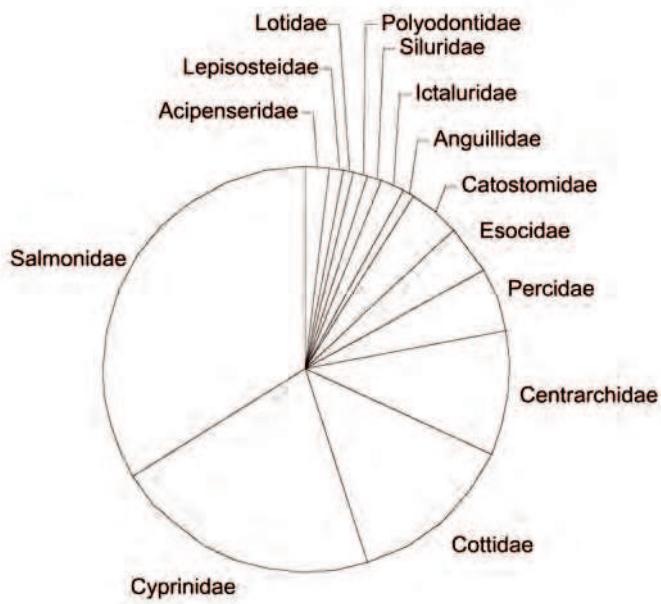


Figure 4. Distribution of studies over families of fish.

Although there are many studies about Salmonidae, they have been conducted on only a few species (Fig. 5). Cyprinidae exhibited the highest number of studied species.

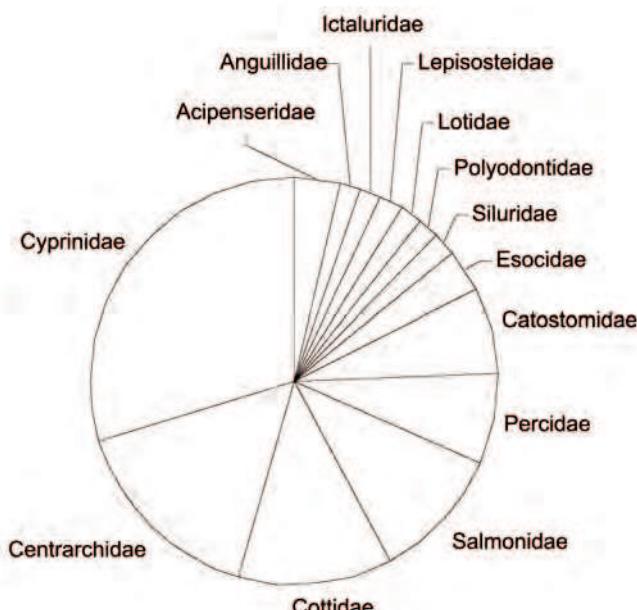


Figure 5. Distribution of counts of species over families of fish.

Author(s)	Index of publication	Title (abbreviated)	Year	Country	System	Name of species
Allouche, S. et al.	1	Habitat use by chub (<i>Leuciscus cephalus</i> L. 1766) in a large river	1999	France	river	chub (<i>Leuciscus cephalus</i>)
Aparicio, E. & De Sostoa, A.	2	Pattern of movements of adult <i>Barbus haasi</i>	1999	Spain	stream	<i>Barbus haasi</i>
Armstrong J. D. & Herbert, N. A.	3	Homing movements of displaced stream-dwelling brown trout	1997	UK	river	brown trout (<i>Salmo trutta</i>)
Baade, U. & Fredrich, F.	4	Movement and pattern of activity of the roach in the River Spree	1998	Germany	river	roach (<i>Rutilus rutilus</i>)
Bachman, R. A.	5	Foraging behavior of free-ranging wild and hatchery brown trout	1984	USA	stream	brown trout (<i>Salmo trutta</i>)
Baras, E.	6	Environmental determinants of residence area selection	1997	Belgium	river	barbel (<i>Barbus barbus</i>)
Baras, E. & Cherry, B.	7	Seasonal activities of female barbel <i>Barbus barbus</i> (L.)	1990	Belgium	river	barbel (<i>Barbus barbus</i>)
Baras, E. et al.	8	Seasonal variations in time and space utilization by radio-tagged	1998	Belgium	stream	European eel (<i>Anguilla anguilla</i>)
Berra, T. M. & Gunning, G. E.	9	Seasonal movement and home range of the longear sunfish	1972	USA	stream	lepisomis megalotis (Longear sunfish)
Breen, M. J. et al.	10	Movements of mottled sculpins (<i>Cottus bairdii</i>) in a Michigan	2009	USA	stream	mottled sculpin (<i>Cottus bairdii</i>)
Bridcut, E. E. & Giller, P. S.	11	Movement and site fidelity in young brown trout <i>Salmo trutta</i>	1993	Ireland	stream	brown trout (<i>Salmo trutta</i>)
Braylants, B. et al.	12	The movement pattern and density distribution of perch	1986	Belgium	river	perch (<i>Perca fluviatilis</i>)
Bunnel, D. B. et al.	13	Diel movement of brown trout in a Southern Appalachian River	1998	USA	river	brown trout (<i>Salmo trutta</i>)
Burrel, K. H. et al.	14	Seasonal movement of Brown trout in a Southern Appalachian	2000	USA	river	brown trout (<i>Salmo trutta</i>)
Cavalli, L. et al.	15	Twenty-four hours in the life of Zingel asper	2009	France	river	Zingel asper
Chart, T. E. & Bergersen, E. P.	16	Impact of mainstream impoundment on the distribution	1992	USA	river	flannelmouth sucker (<i>Catostomus latipinnis</i>)
Clapp, D. F. et al.	17	Range, activity, and habitat of large, free-ranging brown trout	1990	USA	river	brown trout (<i>Salmo trutta</i>)
Clough, S. & Beaumont, W. R. C.	18	Use of miniature radio-transmitters to track the movements	1998	UK	river	dace (<i>Leuciscus leuciscus</i>)
Colyer, W. T. et al.	19	Movements of fluvial bonneville cutthroat trout in the Thomas	2005	USA	stream	Bonneville cutthroat trout (<i>Oncorhynchus clarkii utah</i>)
Curry, R. A. et al.	20	Using movements and diet analyses to assess effects	2007	Canada	river	muskellunge (<i>Esox masquinongy</i>)
Daugherty, D. J. & Sutton, T. M.	21	Seasonal movement patterns, habitat use, and home range	2005	USA	river	flathead catfish (<i>Pylodictis olivaris</i>)
DePhilip, M. M. et al.	22	Movement of walleye in an impounded reach of the Au Sable	2005	USA	river	walleye (<i>Stizostedion vitreum</i>)
Diana, J. S. et al.	23	Movement patterns of large brown trout in the mainstream Au	2004	USA	stream	brown trout (<i>Salmo trutta</i>)
Doherty, C. A. et al.	24	Spatial and temporal movements of white sucker: implications	2010	Canada	river	white sucker (<i>Catostomus commersonii</i>)
Downhower, J. F. et al.	25	Movements of the chabot (<i>Cottus gobio</i>) in a small stream	1990	France	stream	bullhead (<i>Cottus gobio</i>)
Fredrich, F.	26	Long-term investigations of migratory behaviour of asp	2003	Germany	river	asp (<i>Aspius aspius</i>)
Gatz, A. J. & Adams, S. M.	27	Patterns of movement of centrarchids in two warmwater streams	1994	USA	stream	1) redbreast sunfish (<i>Lepomis auritus</i>) 2) bluegill (<i>Lepomis macrochirus</i>) 3) rock bass (<i>Ambloplites rupestris</i>) 4) largemouth bass (<i>Micropterus salmoides</i>) 5) warmouth (<i>Lepomis</i> roach (<i>Rutilus rutilus</i>)
Geeraerts et al.	28	Mobility of individual roach <i>Rutilus rutilus</i> in three weir-fragmented	2007	Belgium	river	1) pallid sturgeon (<i>Scaphirhynchus albus</i>) 2) shovelnose sturgeon (<i>Scaphirhynchus platorynchus</i>)
Gerrity, P. C. et al.	29	Habitat use of juvenile pallid sturgeon and shovelnose sturgeon	2008	USA	river	taien (<i>Hucho taimen</i>)
Gilroy, D. J. et al.	30	Home range and seasonal movement of taimen, <i>Hucho taimen</i>	2010	Mongolia	river	brown trout (<i>Salmo trutta</i>)
Giroux, F. et al.	31	Relationship between the drift of macroinvertebrates and the	2000	Belgium	stream	yellowfin shiner (<i>Notropis lutipinnis</i>)
Goforth, R. R. & Foltz, J. W.	32	Movements of the yellowfin shiner, <i>Notropis lutipinnis</i>	1998	USA	stream	1) hardhead (<i>Mylopharodon conocephalus</i>) 2) Sacramento squawfish (<i>Ptychocheilus grandis</i>)
Grant, G. C. & Maslin, P. E.	33	Movements and reproduction of hardhead and Sacramento	1999	USA	stream	banded sculpin (<i>Cottus carolinus</i>)
Greenberg, L. A. & Holtzman, D. A.	34	Microhabitat utilization, feeding periodicity, home range and	1987	USA	river	cuttert trout (<i>Oncorhynchus clarkii</i>)
Heggenes, J. et al.	35	Spatial stability of cutthroat trout (<i>Oncorhynchus clarkii</i>)	1991	Canada	stream	brown trout (<i>Salmo trutta</i>)
Heggenes, J. et al.	36	Movements by wild brown trout in a boreal river: response to	2007	Norway	river	1) Atlantic salmon (<i>Salmo salar</i>) 2) brown trout (<i>Salmo trutta</i>)
Hesthagen, T.	37	Home range of juvenile Atlantic salmon, <i>Salmo salar</i> , and brown	1990	Norway	stream	1) mottled sculpin (<i>Cottus bairdii</i>) 2) longnose dace (<i>Rhinichthys cataractae</i>) 3) rosaside dace (<i>Clinostomus funduloides</i>)
Hill, J. & Grossman, G. D.	38	Home range estimates for three North American stream fishes	1987	USA	stream	pike (<i>Esox lucius</i>)
Hodder, K. H. et al.	39	Techniques for evaluating the spatial behaviour of river fish	2007	UK	river	brown trout (<i>Salmo trutta</i>)
Höjesjö, J. et al.	40	Movement and home range in relation to dominance; a telemetry	2007	Sweden	stream	nase (<i>Chondrostoma nasus</i>)
Huber, M. & Kirchofer, A.	41	Radio telemetry as a tool to study habitat use of nase	1998	Switzerland	river	potomac sculpin (<i>Cottus girardi</i>)
Hudy, M. & Shiflet, J.	42	Movement and Recolonization of potomac sculpin in a Virginia	2009	USA	stream	Colorado pikeminnow (<i>Ptychocheilus lucius</i>)
Irving, D. B. & Modde, T.	43	Home-range fidelity and use of historic habitat by adult Colorado	2000	USA	river	dark chub (<i>Zacco temmincki</i>)
Katano, O.	44	Foraging tactics and home range of dark chub in a Japanese	1996	Japan	river	Atlantic salmon (<i>Salmo salar</i>)
Keeley, E. R. & Grant, J. W. A.	45	Allometric and environmental correlates of territory size in	1995	Canada	stream	bullhead (<i>Cottus gobio</i>)
Knaepkens, G. et al.	46	Assessment of residency and movement of the endangered	2004	Belgium	stream	bullhead (<i>Cottus gobio</i>)
Knaepkens, G. et al.	47	Assessment of the movement behaviour of the bullhead	2005	Belgium	river	ide (<i>Leuciscus idus</i>)
Kuliksova, P. et al.	48	Factors influencing movement behaviour and home range size in	2009	Czech Republic	river	barbel (<i>Barbus barbus</i>)
Lucas, M. C. & Battley, E.	49	Seasonal movements and behaviour of adult barbel <i>Barbus</i>	1996	UK	river	bream (<i>Abramis brama</i>)
Lyons, J. & Lucas, M. C.	50	The combined use of acoustic tracking and echosounding to	2002	UK	river	northern hog suckers (<i>Hypentelium nigricans</i>)
Mattheney, M. P. & Rabeni, C. F.	51	Patterns of movement and habitat use by northern hog suckers	1995	USA	river	California golden trout (<i>Oncorhynchus mykiss aquabonita</i>)
Matthews, K. R.	52	Diel movement and habitat use of California golden trout in the	1996	USA	river	1) rainbow trout (<i>Oncorhynchus mykiss</i>) 2) brown trout (<i>Salmo trutta</i>)
Matthews, K. R. et al.	53	Cool water formation and trout habitat use in a deep pool in the	1994	USA	river	redband trout (<i>Oncorhynchus mykiss gairdneri</i>)
Muhlfeld, C. C. et al.	54	Fall and winter habitat use and movement by Columbia River	2001	USA	stream	central stoneroller (<i>Campostoma anomalum</i>)
Mundahl, N. D. & Ingersoll, C. G.	55	Home range, movements, and density of the central stoneroller	1989	USA	stream	Japanese fluvial sculpin (<i>Cottus pollux</i>)
Natsumeda, T.	56	Space use by the fluvial sculpin, <i>Cottus pollux</i> , related to	2001	Japan	river	Japanese fluvial sculpin (<i>Cottus pollux</i>)
Natsumeda, T.	57	Home range of the Japanese fluvial sculpin, <i>Cottus pollux</i> , in	2007	Japan	river	Japanese fluvial sculpin (<i>Cottus pollux</i>)
Natsumeda, T.	58	Estimates of nocturnal home-range size of the adult Japanese	2007	Japan	river	blue sucker (<i>Cyclopterus elongatus</i>)
Neely, B. C. et al.	59	Seasonal use distributions and migrations of blue sucker	2009	USA	river	nase (<i>Chondrostoma nasus</i>)
Ovidio, M. & Philippart, J. C.	60	Movement patterns and spawning activity of individual nase	2008	Belgium	river	brown trout (<i>Salmo trutta</i>)
Ovidio, M. et al.	61	Seasonal variation of activity pattern of brown trout (<i>Salmo trutta</i>)	2002	Belgium	stream	

Ovidio, M. et al.	62	Environmental unpredictability rules the autumn migration of	1998	Belgium	stream	brown trout (<i>Salmo trutta</i>)
Ovidio, M. et al.	63	Spawning movements of European grayling <i>Thymallus thymallus</i>	2004	Belgium	river	grayling (<i>Thymallus thymallus</i>)
Ovidio, M. et al.	64	Mobility and home-range use of Atlantic salmon parr over short	2007	Canada	river	Atlantic salmon (<i>Salmo salar</i>)
Ovidio, M. et al.	65	Methodological bias in home range and mobility estimates when	2000	Belgium	stream	brown trout (<i>Salmo trutta</i>)
Ovidio, M. et al.	66	Movement behaviour of the small benthic Rhine sculpin <i>Cottus</i>	2009	Belgium	stream	Rhine sculpin (<i>Cottus rhenanus</i>)
Parkinson, D. et al.	67	A preliminary investigation of spawning migrations of grayling	1999	Belgium	stream	grayling (<i>Thymallus thymallus</i>)
Perkin, J. S. et al.	68	Movement and microhabitat associations of guadalupe bass in	2010	USA	river	Guadalupe bass (<i>Micropterus treculii</i>)
Peter, A.	69	Interruption of the river continuum by barriers and the consequences	1998	Switzerland	river	1) brown trout (<i>Salmo trutta</i>) 2) rainbow trout (<i>Oncorhynchus mykiss</i>)
Petty, J. T. & Grossman, G. D.	70	Size-dependent territoriality of Mottled Sculpin in a Southern	2007	USA	stream	mottled sculpin (<i>Cottus bairdii</i>)
Ross, M. J. & Winter, J. D.	71	Winter movements of four fish species near a thermal plume	1981	USA	river	1) yellow perch (<i>Perca flavescens</i>) 2) pike (<i>Esox lucius</i>) 3) walleye (<i>Stizostedion vitreum</i>) 4) largemouth bass (<i>Micropterus salmoides</i>)
Schmetterling, D. A. & Adams, S. B.	72	Summer movements within the fish community of a small	2004	USA	stream	1) westslope cutthroat trout (<i>Oncorhynchus clarkii lewisi</i>) 2) slimy sculpin (<i>Cottus cognatus</i>)
Slavík, O. et al.	73	Diurnal and seasonal behaviour of adult and juvenile European	2007	Czech Republic	river	catfish (<i>Sturisoma glanis</i>)
Slavík, O. et al.	74	Does stream morphology predict the home range size in burbot?	2005	Czech Republic	river	burbot (<i>Lota lota</i>)
Snedden, G. A. et al.	75	Diel and seasonal patterns of spotted gar movement and habitat	1999	USA	river	spotted gar (<i>Lepisosteus oculatus</i>)
Stormer, D. G. & Maceina, M. J.	76	Habitat use, home range, and movement of shoal bass in	2009	USA	stream	shoal bass (<i>Micropterus cataractae</i>)
Todd, B. L. & Rabeni, C. F.	77	Movement and habitat use by stream-dwelling smallmouth bass	1989	USA	river	smallmouth bass (<i>Micropterus dolomieu</i>)
Vehanen, T. et al.	78	Patterns of movement of adult northern pike (<i>Esox lucius</i> L.)	2006	Finland	river	pike (<i>Esox lucius</i>)
Vokoun, J. C. et Rabeni, C. F.	79	Home range and space use patterns of flathead catfish during	2005	USA	stream	flathead catfish (<i>Pylodictis olivaris</i>)
Young, M. K.	80	Summer movements and habitat use by Colorado River	1996	USA	river	Colorado River cutthroat trout (<i>Oncorhynchus clarkii pleuriticus</i>)
Young, M. K.	81	Summer diel activity and movement of adult brown trout in	1999	USA	stream	brown trout (<i>Salmo trutta</i>)
Young, M. K.	82	Mobility of brown trout in south-central Wyoming streams	1994	USA	stream	brown trout (<i>Salmo trutta</i>)
Young, M. K. et al.	83	Contrasting movement and activity of large brown trout and	1997	USA	stream	1) rainbow trout (<i>Oncorhynchus mykiss</i>) 2) brown trout (<i>Salmo trutta</i>)
Zigler, S. J. et al.	84	Movement and habitat use by radio-tagged paddlefish in the	2003	USA	river	paddlefish (<i>Polyodon spathula</i>)

Table 1 Overview of the analyzed articles that contain data on fish movement ranges (usually referred to as home range). Columns comprise authors (alphabetically ordered), index of publication, abbreviated title of article, year of publication, country of study, study system (river or stream) and fish species (common and scientific name).

Terminology and the problem of defining a home range

There are nearly as many definitions for the term “home range” as studies about this topic exist. In general, a home range is defined as the area where daily feeding and refuge movements take place. The problem for a clear definition is the unclear threshold of the spatial and temporal aspect. A lot of publications handle the term home range rather arbitrary. For example, the author defines “a home range to have been established if a fish was repeatedly found within a limited area (less than 1 km) for at least two weeks” (Simpson & Mapleston, 2002) or the author excludes “obvious wandering” from a home range (Baras & Cherry, 1990). Some authors explicitly exclude spawning places from the home range, whereas others add seasonal migrations to a fish’s home range. In the latter case, a small home range for any migratory fish suggests that foraging habitat for adults is available near the spawning ground and that they use the same grounds during spawning and nonspawning (Godinho & Kynard, 2006). Unfortunately, most of the reviewed literature does not make a clear distinction between seasonal spawning movement and everyday movement that can be measured over several months. For example in a study about fluvial sculpin, half of the females did not have any nests in their home ranges and spawned out of their home ranges, followed by homing after spawning (Natsumeda, 2001). Therefore, we include also those studies to this review that refer to movements that potentially are recorded during the reproduction period (which is in the majority of cases not clearly stated!). However, we are aware that those movements are beyond what one might call a “home” range. Nevertheless, we are convinced that this kind of data is still helpful in order to determine spatial requirements of fish in stream and rivers. Here we provide an overview about the most commonly used definitions in literature relating to fish home range and the distinctive meanings.

1) Entire area: The term home range is used for “the entire area within which an individual fish is observed during the period of the study” (Gilroy et al., 2010). It is the undefended area used by an individual during its normal activities, such as foraging or mating (Natsumeda, 2007a; Hayne, 1949). In particular, it can be standardized to *daily activity area* or *daily home range*, which describes the overall surface of the river occupied by an individual during a 24-hours cycle. It encompasses a resting place, an activity center, where the fish demonstrates feeding activity, and routes in between (Allouche et al., 1999; Baras, 1997).

2) Longitudinal distance: Most authors use the term home range for the longitudinal distance between the most upstream and most downstream location (i.e. total linear distance) of a fish during the study period or during a daily cycle. Correspondingly, the daily linear home range is the distance between an individual’s most upstream and the most downstream daily locations along the river channel (Diana et al., 2004; Crook, 2004a; Ovidio et al., 2002; Curry et al., 2007; Young, 1996). Accordingly, the seasonal linear home range encompasses the distance between the most upstream and the most downstream location within a season (Burrell et al., 2000; Daugherty & Sutton, 2005), usually without large-scale unidirectional movements associated with spawning. In most cases, the linear home range is defined by the most extreme up- and downstream locations within the entire study period (Ovidio et al., 2009; Khan et al., 2004). It should not be confounded with mobility or the “distance travelled”, which is the sum of distances overall travelled between subsequent locations during an observation cycle (Ovidio et al., 2002; Ovidio et al., 2000; Baras, 1998).

3) Core range: Some species exhibit a high site fidelity to relatively small core areas of intensive use within home ranges (Crook, 2004a). The core range is the place, where most activity takes place and which is not necessarily defended nor centrally located (Richard, 1970). It is defined by the mobility pattern over time (Woolnough et al., 2009). For example, pike were observed to spend about 90% of time in a core range within their home range, from where they occasionally undertook excursion (Hodder et al., 2007). Similarly, Baras (1997) uses the term residence area for a single or several neighboring resting places within the same habitat type (e.g. boulders). Hence, the net daily journey results from the distance between the residence areas occupied during a 24-h cycle. Barbels (*Barbus barbus*) can have up to four residence areas within a defined home range of 1.6 km (Baras & Cherry, 1990).

Site fidelity and homing

Moreover, literature concerning fish movement and home range is often about the terms site fidelity, home site or homing. Fidelity to a familiar site or area is the prerequisite to using a home range. Site fidelity is the tendency of an animal to return to an area previously occupied or to remain within this area for an extended period of time. Common carp (*Cyprinus carpio*) displayed site fidelity to within 20 m of river or floodplain habitat (Jones & Stuart, 2009). Crook (2004a) considers that if a fish is recaptured after a year in the same pool where it was originally collected, the existence of site fidelity to a home range that encompasses the pool is clear, but it is less clear if the individual was recaptured several hundred meters away. Hence, the distinction between the simple extent of movement and the fidelity to a home range is necessary, though not always possible. Attachment to a specific site was described for many species. Redbreast sunfish (*Lepomis auritus*) mainly moved within river sections of 50 m for more than 6 months, and only a few extreme movements involved distances up to 17 km (Gatz & Adams, 1994). Similarly, murray cod (*Maccullochella peelii peelii*) exhibited fidelity to home sites, where an individual was recorded on four or more successive tracking within a 50-m river reach and then undertook seasonal large scale movement up to 130 km (Koehn et al., 2009).

Individual fish can have multiple home sites that are separated from each other (Diana et al., 2004). Some brown trout rotated among up to four home sites, which resulted in unexpectedly large travels of up to 1.5 km upstream, and downstream again, in one night (Clapp et al., 1990). Individuals of nase (*Chondrostoma nasus*) were found to regularly move between two resting places separated by 2 km (Ovidio & Philippart, 2008). Many studies describe fidelity to a particular habitat site, i.e. shoal bass (*Micropterus cataractae*) or sunfish that stick to the exact same habitat structure such as a pool over a period from several months to consecutive years (Stormer & Maceina, 2009; Gerking, 1959). Bass (*Micropterus dolomieu*) were found to stay within home pools, but still sometimes migrated several kilometers (Todd & Rabeni, 1989). Often, juvenile Salmonids are associated to 'home' boulders or stones (Bridcut & Giller, 1993; Gatz, 2007; Cunjak, 1988), to a home pool or specific riffles (Burrell et al., 2000). Different eel species (*Anguilla*) exhibited considerable fidelity to a particular bank (Jellyman & Sykes, 2003).

The return of a fish to a familiar home site is called homing. (Gerking, 1959) refers to homing as "the choice that a fish makes between returning to a place formerly occupied instead of going to other equally probable places". The fidelity in repeatedly returning to natal sites or historical spawning sites

is an adaptive strategy for reproduction (Baras & Lucas, 2001). In white sucker (*Catostomus commersonii*) and river sculpin (*Cottus hangiongensis*) homing happens after spawning migration (Doherty et al., 2010; Goto, 1988). However, homing does not necessarily have to be linked to spawning behavior. Homing can happen to a segment or even a particular cover structure, such as woody debris, to which a fish returns after an extended absence (Clapp et al., 1990; Daugherty & Sutton, 2005). Homing sometimes happen to the precise pool-riffle sequence in grayling (*Thymallus thymallus*) (Parkinson et al., 1999) and to within 0.5-2 km of their starting position in ide (*Leuciscus idus*) (Kulí_ková et al., 2009). Homing of trout cod (*Maccullochella macquariensis*) takes place after movements from a few meters to more than 1 km (Koehn et al., 2008). Golden perch (*Macquaria ambigua*) were capable of homing after movements of up to 80 km from their home site (O'Connor et al., 2005). Similarly, paddlefish (*Polyodon spathula*) returned to the specific area that it previously inhabited after having moved upstream more than 61 km (Zigler et al., 2003). Postreproductive homing sometimes is completed within a short time frame of 24 hours in grayling (Parkinson et al., 1999; Ovidio et al., 2004) and within a few days in brown trout (Burrell et al., 2000).

The fidelity to a home site or home range in fish was tested by experimental displacement of individuals. Salmonids (Huntingford et al., 1998), golden perch (*Macquaria ambigua*) and carp (*Cyprinus carpio*) (Crook, 2004a) return to the area from which they were originally captured. Even under laboratory conditions, the European minnow establishes a home range and does perform homing after artificial displacement (Kennedy & Pitcher, 1975). Homing after experimental displacement is usually directed and rapid (Armstrong & Herbert, 1997) and can happen within relatively short period of time. It happens within minutes in barbel (Baras, 1997), within 48 hours in river blackfish (*Gadopsis marmoratus*) (Khan et al., 2004) and within three days in green sunfish (*Lepomis cyanellus*) in both up- and downstream direction (Gatz, 2007). Brown trout relocate their home range by directed movements using specific orientation cues, rather than by accident or a random search pattern (Armstrong & Herbert, 1997). They are able to perform homing by a positive as well as negative rheotactic response, which is likely to be affected by olfaction (Halvorsen & Stabell, 1990). However, the sensory cue used for homing still remains unclear and the behavioral mechanisms are speculative. Homing may be beneficial because of returning to qualitatively good habitat regarding food, cover, spawning or mating (Gatz, 2007). When homing, fish return to an environment that has been experienced already which in turn reduces the energetic costs needed to explore a new area (Baras & Cherry, 1990).

The movement defines the home range.

Variations in mobility patterns

It has turned out that a lot of authors try to specify fish home range through the categorization of movement. Riverine fish are characterized by a high variety of mobility patterns. In brown trout (*Salmo trutta*) two categories of movement were observed: (i) long-range travel (active displacement) from one part of the range to another or between winter and summer ranges, (ii) short-range movements (foraging) that might occur when searching for food (Clapp et al., 1990). These two movement types are similarly described for Mary River cod (*Maccullochella peelii mariensis*): (i) rapid, relatively unpredictable and directional, long-distance movements when home range was abandoned and

individuals dispersed to other habitats, (ii) localized, non-directional activity within the well-defined home range throughout the year, with one to three core areas of most frequent use (Simpson & Mapleston, 2002). Similarly, Baade and Fredrich (1998) distinguish between close range, wide range and long-distance migration in roach (*Rutilus rutilus*). A more precise definition of different mobility patterns is given in a mark-recapture study of Japanese fluvial sculpin (*Cottus pollux*): (i) one-way, unidirectional movement, (ii) round-trip and homing with subsequent recapture in the original unit, (iii) haphazard movement, bi-directionally without returning to original unit (Natsumeda, 2007b). Likewise, three distinct movement strategies were found in Atlantic salmon parrs: (i) restricted mobility in a single area, (ii) movements between two distinct areas, which means that parr are able to recognize and take advantage of particular river sectors, (iii) progressive upstream movement using a river section of up to 1800 m (Ovidio et al., 2007b). Gilroy et al. (2010) further describe four distinct utilization strategies for home ranges observed in taimen (*Hucho taimen*): (i) restricted core home range where individual fish are most commonly found, (ii) core range with seasonal departures (e.g. for spawning) to multiple other locations followed by a return to their core range, (iii) core range with seasonal movements to a single alternate location where they were observed multiple times, indicating some site fidelity, (iv) home range transfer (often over long distances), shifting to a new region for multiple seasons. Summing up the reviewed literature, there are two to three common patterns of home range utilization: (i) the long-range, often unidirectional movement either from one part of the range to another, between home ranges or when abandoning a home range, (ii) the seasonal roundtrip-movement with homing, (iii) the short, haphazard and local movement within a restricted range. However, when considering this classification in literature, a precise and common definition of the term home range remains difficult and different authors will probably continue to use it differently.

Ways to estimate home range size- selected methodical approaches

There are different estimation methods for linear as well as polygon home range analysis and much literature that compares different approaches (see Hodder et al. (2007) for a review). Hayne (1949) discusses methods for calculating home range size in mammals, which can be determined by trapping an area to define the “center of activity” and which in consequence includes information on the intensity of use. Information on fish home range size in streams and rivers includes the longitudinal and lateral dimension, whereas a vertical extent is not taken into account. Most commonly, fish movement range in river and streams is limited to one dimension and quantified as the net linear distance. As mentioned previously, this longitudinal extent of movement or linear home range is measured as the distance between the most upstream and most downstream location. It can be extended laterally, e.g. by the distance between the furthest locations onto floodplains. This way, areal home range is then calculated from the mathematical term “(downstream distance+upstream distance)*(left side distance+right side distance)” (Slavik et al., 2005). However, linear range multiplied by mean river width often oversimplifies spatial use (Hodder et al., 2007). Alternatively, a simple estimation of spatial range includes a proportion of location data, i.e. all sites where an individual was located. Advantageously, it excludes great individual variations, spawning migration and longer spontaneous movements (Baade & Fredrich, 1998). It is common to indicate the 95% home range

from which the 5% of the most distant, unusual locations is excluded in order to avoid an artificial inflation (Matheney & Rabeni, 1995). Further, areal home range for an individual can be assessed using the maximum convex-, the minimum convex- or the restricted-polygon method (Steingrimsson & Grant, 2008; Natsumeda, 1998; Ross & Winter, 1981; Allouche et al., 1999; Petty & Grossman, 2007). The maximum convex polygon method is defined by a polygon around the outermost locations, however, the disadvantage of this method is the sensitivity to sample size (Keeley & Grant, 1995). Some authors prefer the use of kernel density estimation. Kernel density reveals the internal structure of the home range by outlining “portions of the range that was used a specified percentage of the time” (Vokoun & Rabeni, 2005). It estimates the utilization distribution (i.e. the intensity of use) of an individual fish from a set of location data and describes the home range in terms of a continuous probabilistic model distribution (Worton, 1989). The utilization distribution comprises information about the amount of time spent at a given location within the home range (Vokoun, 2003). This way, Kernel density estimates can be employed to identify the number and size of core areas of most frequent use within a linear home range along the river channel (Gilroy et al., 2010). In general, density distributions are calculated for different use levels, with contours containing e.g. 95% of the estimated density distribution. The 50% kernel range is often regarded as the core home range of a fish, whereas the 95% or 90% estimates identify the total area utilized (Gilroy et al., 2010; Stormer & Maceina, 2009). Traditional use distribution estimators are considered to be imprecise with a sinuous river morphology because used area is overestimated by including terrestrial areas not available to fish (Neely et al., 2009). Thus, some authors consider the cluster analysis to be the best home range estimator because it keeps- contrary to kernel density estimator- within the river channel and follows the pattern of fish location data (Cavalli et al., 2009). Comparing different home range estimators, Knight et al. (2009) concludes that kernel analyses better reflects excursive activity, whereas cluster analyses better defines core ranges and range fragmentation.

The temporal aspect of home range studies

When studying fish movement and home range size, the temporal aspect is as important as it is tricky. If individual fish are repeatedly found within the same river segment, this should not be taken to imply that they remained stationary throughout the year, they may rather have occupied different river stretches as home-ranges for certain periods (Huber & Kirchhofer, 1998). For example, dace (*Leuciscus leuciscus*) was observed to spend several days in selected areas before periodically and rapidly relocating several kilometers up- and downstream (Clough & Beaumont, 1998). It is for this reason that studies can come to different conclusions depending on their temporal resolution (Koster & Crook, 2008). In some studies, range area increased with extended data sampling over a longer period (Hodder et al., 2007), whereas in others, there was no significant relationship between range size and number of tracking days or number of observations (Clapp et al., 1990; Katano, 1996). Home range measurements conducted over a long tracking period (i.e. a year) might include several shift events and would suggest a very large home range (Crook, 2004a). Conversely, the annual size of home ranges is underestimated if the spawning season is excluded from the study period (Allouche et al., 1999).

Börger et al. (2006) analyzed how the precision of estimation methods vary with sampling regime. The authors emphasize that the number of individuals and study areas monitored should be maximized because inter-individual variation contributes most to the total variance in home range size. It is further necessary to include both diurnal and nocturnal observations because some species have specific diel or nocturnal activity patterns (Snedden et al., 1999) and to incorporate all seasons of the year because habitat requirements may change (Daugherty & Sutton, 2005). The loss of information on estimated home range of Barbel (*Barbus barbus*) was found to be proportional to the positioning frequency (Baras, 1998). With an increasing time interval of more than a day between consecutive locations, a substantial reduction of accuracy and underestimation of home range size was found in brown trout (Ovidio et al., 2000). Similarly, the interval between recaptures influences the size of movement range of Cottus species (Natsumeda, 2007b; Downhower et al., 1990). In contrast, the length of intervals between recaptures (1 week to 6 months) did not seem to have an influence on the distances travelled by centrarchids (Gatz & Adams, 1994).

In order to eliminate effects of the observation interval, movement data can be standardized as activity rate or movement rate, such as daily distance travelled or daily home range (Hodder et al., 2007; Natsumeda, 2007b). It is calculated from the total distance travelled by an individual fish divided by the length of the tracking period (Baras & Cherry, 1990). Though, for this review, it was impossible to temporally standardize home range sizes because observation periods and data resolution was, unfortunately, often imprecisely indicated in the literature.

Home range sizes

Table 2 lists movement ranges for selected species and corresponding home range estimation method. In literature, mean home range size for a species was generally calculated based on several tracked individuals. In the following, home range is defined as the overall space used during the whole study period if not mentioned differently. The comparison between home ranges of linear and areal estimates is not possible because authors did not specify stream or river width. “Maximum” values refer to unusual movements, such as a single long-distance movement that often resulted in an obvious change of residence or spawning migration. Unfortunately, authors often neither indicate whether this movement happens in upstream or downstream direction nor whether the study includes a spawning period. Below, range sizes of table 2 are briefly summarized for each taxonomic family. The explicit daily home range and fish body size for a taxonomic family is listed, too, whenever authors had them provided. Further, I indicate the lengths of studies referring to short term (less than one month), mid term (one to several months) and long term (one year or longer) observations.

Taxonomic family	Name of species	Longitudinal movement range	Areal movement range	Daily movement range	Estimation method	Index of publication
Acipenseridae	palid sturgeon (<i>Scaphirhynchus albus</i>)	mean 15000 m (1100-73900 m)			TLD	29
Acipenseridae	shovelnose sturgeon (<i>Scaphirhynchus platycephalus</i>)	mean 16500 m (700-41500 m)			TLD	29
Anquillidae	European eel (<i>Anchova anguilla</i>)	max. 285 m	0.1 ha	10-15 m (=40 sqm)	TLD x width	8
Catostomidae	flannelmouth sucker (<i>Catostomus latipinnis</i>)	1340-14950 m			TLD	16
Catostomidae	white sucker (<i>Catostomus commersonii</i>)	mean 9200 m (SD 11000), max. 40000 m	winter-spring 812 m (SD 731), summer-fall 426 m (SD 450)	winter-spring 4.19 ha, summer-fall 1.98 ha	95% linear range	51
Catostomidae	northern hog suckers (<i>Hypentelium nigricans</i>)	blue sucker (<i>Cyclopterus elongatus</i>)	summer 8100 m, fall 78600 m, spring 174900 m		90% use distribution	59
Centrarchidae	leporinus megalotis (Longear sunfish)	mean 42 m			TLD	9
Centrarchidae	redbreast sunfish (<i>Lepomis auritus</i>)	<100 m between captures; max. 17600 m			TLD	27
Centrarchidae	bluegill (<i>Lepomis macrochirus</i>)	<100 m between captures; max. 17600 m			TLD	27
Centrarchidae	rock bass (<i>Ambloplites rupestris</i>)	<100 m between captures			TLD	27
Centrarchidae	largemouth bass (<i>Micropterus salmoides</i>)	<100 m between captures; max. 17600 m			TLD	27
Centrarchidae	largemouth bass (<i>Micropterus salmoides</i>)	<100 m between captures	4 ha (0.3-7.0)		minimum-area polygon	71
Centrarchidae	warmouth (<i>Lepomis gulosus</i>)	0-3420 m			TLD	27
Centrarchidae	Guadalupe bass (<i>Micropterus treculii</i>)				TLD	68
Centrarchidae	shoal bass (<i>Micropterus cataractae</i>)				KDE	76
Centrarchidae	smallmouth bass (<i>Micropterus dolomieu</i>)				minimum-area polygon	77
Cottidae	mottled sculpin (<i>Cottus bairdii</i>)	max. 511 m			i) MCP ii) TLD	10
Cottidae	mottled sculpin (<i>Cottus bairdii</i>)				MCP	70
Cottidae	mottled sculpin (<i>Cottus bairdii</i>)	mean 13 m (max. 55 m)			TLD	38
Cottidae	bullhead (<i>Cottus gobio</i>)	4-50 m			TLD	25
Cottidae	bullhead (<i>Cottus gobio</i>)	10-260 m			TLD	46
Cottidae	bullhead (<i>Cottus gobio</i>)	20-270 m			TLD	47
Cottidae	banded sculpin (<i>Cottus carolinus</i>)	6 m	47 sqm		TLD x width	34
Cottidae	potomac sculpin (<i>Cottus girardi</i>)	mean upstream 1575 m (SD 917, 386-3140 m), downstream 1596 m (SD 918, 30-2792 m)			TLD	42
Cottidae	Japanese fluvial sculpin (<i>Cottus pollux</i>)			males 78 sqm (SD 46.5) females 16 sqm (SD 17.4)	convex polygon	56
Cottidae	Japanese fluvial sculpin (<i>Cottus pollux</i>)			day 7 sqm (SD 17.2), night 68 sqm (SD 35.7)	convex polygon	57
Cottidae	Japanese fluvial sculpin (<i>Cottus pollux</i>)			with nests 15.2 sqm (SD 21.9), without 10 sqm (SD 17.2, 0.3-79.9 sqm)	MCP	58
Cottidae	Rhine sculpin (<i>Cottus rhenanus</i>)	short-term tracking 7-46 m; recapture mean 50 m (5-435 m)			TLD	66
Cottidae	slimy sculpin (<i>Cottus cognatus</i>)	median 18 m (16-209 m)			TLD	72
Cyprinidae	Barbus haasi	34 m (SD 55.8)	54 sqm		TLD x width	2
Cyprinidae	barbel (<i>Barbus barbus</i>)	200-2400 m			homing after translocation	6
Cyprinidae	barbel (<i>Barbus barbus</i>)	1600 m (max. 9600 m)			TLD	7
Cyprinidae	barbel (<i>Barbus barbus</i>)	2000-20000 m			TLD	49
Cyprinidae	nase (<i>Chondrostoma nasus</i>)	625-11250 m			mean 121 m (25-425 m)	41
Cyprinidae	nase (<i>Chondrostoma nasus</i>)	max. 4000 m			TLD	60
Cyprinidae	dace (<i>Leuciscus leuciscus</i>)	max. 9100 m			TLD	18
Cyprinidae	ide (<i>Leuciscus idus</i>)	summer 220-1215 m, winter <150 m	19496 sqm (SD 13891)		MCP	48
Cyprinidae	chub (<i>Leuciscus cephalus</i>)		0.5-5.8 ha		i) MCP ii) restricted polygon iii) TLD	1
Cyprinidae	dark chub (<i>Zacco temminckii</i>)		2-165 sqm		max. convex polygon	44
Cyprinidae	asp (<i>Aspius aspius</i>)	1000-40000 m (max. 166000 spawning)			TLD	26
Cyprinidae	roach (<i>Rutilus rutilus</i>)	max. 12700 m			TLD	28
Cyprinidae	roach (<i>Rutilus rutilus</i>)	mean 1006 m (75-3820 m)			90% linear range	4
Cyprinidae	bream (<i>Abramis brama</i>)	350-5400 m			TLD	50
Cyprinidae	Colorado pikeminnow (<i>Ptychocheilus lucius</i>)	1100-40600 m			TLD	43
Cyprinidae	yellowfin shiner (<i>Notropis lutipinnis</i>)	43 m (max. upstream 481 m, max. downstream 521 m)			TLD	32
Cyprinidae	hardhead (<i>Mylopharodon conocephalus</i>)	289 m (max. 1023 m)			TLD	33
Cyprinidae	Sacramento squawfish (<i>Ptychocheilus grandis</i>)	199 m (max. 1217 m)			TLD	33
Cyprinidae	central stoneroller (<i>Campostoma anomalum</i>)	mean 35 m (8-135 m)			TLD	55
Cyprinidae	longnose dace (<i>Rhinichthys cataractae</i>)	14 m (max. 40 m)			TLD	38
Cyprinidae	rosy-side dace (<i>Clinostomus funduloides</i>)	19 m (max. 98 m)			TLD	38
Esocidae	muskellunge (<i>Esox masquinongy</i>)	mean 28800 m (2500-90000 m)			TLD	20
Esocidae	pike (<i>Esox lucius</i>)	median 205 m (15-899 m)	median 2580 sqm (171-11231 sqm)		i) KDE ii) cluster polygon iii)	39
Esocidae	pike (<i>Esox lucius</i>)		157 sqm (18-582 sqm)		TLD	21
Esocidae	pike (<i>Esox lucius</i>)		19 ha (11.4-30.8 ha)		KDE	78
Ictaluridae	flathead catfish (<i>Pylodictis olivaris</i>)	mean spring 1513 m (214-2950 m), fall 1296 m (0-3601), summer 596 m (0-2477), winter no movement			minimum-area polygon	71
Ictaluridae	flathead catfish (<i>Pylodictis olivaris</i>)	i) median 3510 m (150-50400 m) ii) median 1085 m (70-69090 m)			TLD	21
Ictaluridae	flathead catfish (<i>Pylodictis olivaris</i>)				i) TLD ii) KDE	79
Lepisosteidae	spotted gar (<i>Lepisosteus oculatus</i>)	max. 9100 m		median spring 265 ha, summer 11 ha, fall-winter 6 ha	MCP	75
Lotidae	burbot (<i>Lota lota</i>)	mobile 68 m, stationary 4 m (SD 68.6)			TLD	74
Percidae	perch (<i>Perca fluviatilis</i>)	mean 74 m (SD 57.5)			TLD	12
Percidae	Zingel asper				95% cluster analysis	15

Percidae	walleye (<i>Stizostedion vitreum</i>)	100-46700 m			TLD	22
Percidae	walleye (<i>Stizostedion vitreum</i>)		2 ha		minimum-area polygon	71
Percidae	yellow perch (<i>Perca flavescens</i>)		13 ha (8.5-22 ha)		minimum-area polygon	71
Polyodontidae	paddlefish (<i>Polyodon spathula</i>)	median summer-winter 200-900 m, spring 13300-34600 m 675-1848 m			TLD	84
Salmonidae	brown trout (<i>Salmo trutta</i>)				homing after translocation	3
Salmonidae	brown trout (<i>Salmo trutta</i>)		16 sqm		i) MCP ii) ellipse (parametric)	5
Salmonidae	brown trout (<i>Salmo trutta</i>)	mean mobile 610 m (max. 2240 m), stationary max. 20 m			TLD	11
Salmonidae	brown trout (<i>Salmo trutta</i>)	5-270 m (max. 7650 m)		<80 m (max. 357 m)	TLD	13
Salmonidae	brown trout (<i>Salmo trutta</i>)	370-33420 m (spring-summer 4935 m, autumn-winter 11902 m)			TLD	14
Salmonidae	brown trout (<i>Salmo trutta</i>)				TLD	17
Salmonidae	brown trout (<i>Salmo trutta</i>)			150-2000 m	TLD	23
Salmonidae	brown trout (<i>Salmo trutta</i>)			9-80 m	TLD	31
Salmonidae	brown trout (<i>Salmo trutta</i>)	295-7014 m	median 3669 sqm (924-39229 sqm)		i) max. convex polygon	36
Salmonidae	brown trout (<i>Salmo trutta</i>)		40-50 sqm		ii) KDE	
Salmonidae	brown trout (<i>Salmo trutta</i>)	mean daytime 217 m, night 23 m (spawning 282 m)	30-123 sqm (depending on period of day)	mean 48 m (6-480 m)	TLD x width	37
Salmonidae	brown trout (<i>Salmo trutta</i>)	5600-22950 m			TLD	40
Salmonidae	brown trout (<i>Salmo trutta</i>)	13-354 m			KDE	53
Salmonidae	brown trout (<i>Salmo trutta</i>)	mean summer 1063 m, winter 510 m (spawning max. 50000 m)			TLD	61
Salmonidae	brown trout (<i>Salmo trutta</i>)	mean 41 m			TLD	62
Salmonidae	brown trout (<i>Salmo trutta</i>)	mean (depending on site and size) >340mm: 410-834 m (51-96000 m), <340mm: 28-95 m (1-1528 m)			TLD	65
Salmonidae	brown trout (<i>Salmo trutta</i>)	median 1158 m			TLD	69
Salmonidae	brown trout (<i>Salmo trutta</i>)		40-50 sqm		TLD	81
Salmonidae	Atlantic salmon (<i>Salmo salar</i>)		0.6 sqm (0.02-7.46)		TLD	82
Salmonidae	Atlantic salmon (<i>Salmo salar</i>)	max. 2000 m	123-5602 sqm		TLD	83
Salmonidae	Atlantic salmon (<i>Salmo salar</i>)	median 941 m			TLD x width	37
Salmonidae	rainbow trout (<i>Oncorhynchus mykiss</i>)		37-158 sqm		max. convex polygon	45
Salmonidae	rainbow trout (<i>Oncorhynchus mykiss</i>)				KDE	64
Salmonidae	redband trout (<i>Oncorhynchus mykiss gairdneri</i>)	mean summer 1176 m, winter 33 m (spawning max. 6500 m)			TLD	83
Salmonidae	California golden trout (<i>Oncorhynchus mykiss aquabonita</i>)	67 m (SD 99; 5-377 m)			KDE	53
Salmonidae	cutthroat trout (<i>Oncorhynchus clarki</i>)	mean 37-69 m			TLD	69
Salmonidae	westslope cutthroat trout (<i>Oncorhynchus clarkii lewisi</i>)	4 m			TLD	54
Salmonidae	Bonneville cutthroat trout (<i>Oncorhynchus clarkii utah</i>)	median 91 m (14-1581 m)	stationary <22 sqm, mobile 53 sqm		90% linear range	52
Salmonidae	Colorado River cutthroat trout (<i>Oncorhynchus clarki pleuriticus</i>)	50-18500 m (max. 86000 m spawning)			TLD x width	35
Salmonidae	taimen (<i>Hucho taimen</i>)	median 233 m (0-1792 m)			TLD	72
Salmonidae	grayling (<i>Thymallus thymallus</i>)	mean 23000 m (500-93200 m)			TLD	19
Salmonidae	grayling (<i>Thymallus thymallus</i>)	mean pre-spawning 258 m (SD 65; 10-950 m)			TLD	80
Salmonidae	grayling (<i>Thymallus thymallus</i>)	spawning 1234 m (SD 328, 70-4980 m)			TLD	30
Siluridae	catfish (<i>Silurus glanis</i>)	mean pre-spawning 29 m (SD 13) spawning 2727 m (SD 1619) postspawning 73 m (SD 21)	mean juvenile 5604 sqm (1171-14580 sqm), adult 15702 sqm (9519-47136 sqm)	MCP	TLD	63
Siluridae	catfish (<i>Silurus glanis</i>)				TLD	67
Siluridae	catfish (<i>Silurus glanis</i>)				MCP	73

Table 2 Movement ranges of different fish species assorted to taxonomic family. Columns comprise taxonomic family, fish species (common and scientific name), longitudinal movement range (occasionally with important remarks), areal movement range, daily movement range, estimation method and index of publication (referring to table 1). Abbreviations: SD=Standard deviation, max.=maximum, TLD=total linear distance, MCP=minimum convex polygon, KDE=Kernel density estimation.

Lepisosteidae:

The only representative, spotted gar (*Lepisosteus oculatus*; body size 584-738 mm), had in this mid term study (7 mths) median home ranges of 6-265 ha, depending on season.

Acipenserids:

Studied juveniles were comparatively large (body size >295 mm) and accordingly, they used large scale home ranges (>15 km) over a long term period (2 yrs).

Polyodontidae:

A long term study (3 yrs) with individuals of 600-1205 mm body size documented differences in movement ranges between season and study reach. Ranges were 200-900 m in summer and winter and peaked during spring (13.3-34.6 km).

Anguillidae:

They are large sized fish (>572 mm) with maximal movement of 285 m over a mid term period (4 mths) and a mean daily home range of 10-15 m.

Catostomidae:

Depending on species, body size (230-839 mm) and season, they moved from several hundred meters up to 175 km during spawning and post-spawning migrations over long term periods (1-3 yrs).

Cyprinidae:

In many of these studies about cyprinids, authors mention well defined home ranges that are distinct from the seasonal spawning or post-spawning movement. Short to long term studies (1 mth-3 yrs) documented a high variability in body size with small and large cyprinid species (40-743 mm). The small barbel species (*Barbus haasi*) had a home range of 34 m whereas the large *Barbus barbus* made overall movements from 200 m to 20 km during spawning or when homing after translocation. Nase (*Chondrostoma nasus*) used a mean daily home range of 121 m and made movements up to 112.5 km during the study. *Leuciscus* species moved within areas up to 5.8 ha or covered distances up to 9.1 km depending on season and species. Movement ranges of relatively large individuals of dark chub (*Zacko temmincki*), asp (*Aspius aspius*), roach (*Rutilus rutilus*), bream (*Aramis brama*) and Colorado pikeminnow (*Ptychocheilus lucius*) are highly complex and vary between species from several hundred meters to more than 40 kilometers, which makes it difficult to specify a home range. Other cyprinid species used small home ranges of 14 m-289 m with movement distances up to 1217 m.

Siluridae:

Catfish (*Silurus glanis*; 490-1450 mm) had different home range sizes during a long term study (2yrs) depending on life-stage. Mean area used by juveniles was 0.56 ha (max. 1.46 ha) whereas it was 1.57 ha (max. 4.71 ha) for adults.

Ictaluridae:

For the flathead catfish (*Pylodictis olivaris*; body sizes 439-1210 mm), home ranges were highly variable between individuals and ranged from zero movement to 69.09 km depending on season, estimation method and mid or long term study (3-14 mths). However, mean or median sizes were usually between 596 m to 3.51 km.

Esocidae:

There are large differences within literature documenting mid to long term studies (5 mths-2 yrs; body sizes 520-922 mm). Muskellunge (*Esox masquinongy*) used a mean home range of 28.8 km. Values of pike (*Esox lucius*) highly vary between restricted home ranges of 157 sqm of rather sedentary pikes to range areas of 19 ha.

Salmonidae:

In the reviewed literature, salmonidae was the most represented taxonomic family. Many short, mid and long term studies (10 d-3 yrs) describe home range sizes of brown trout and other members of the salmonid family (body sizes of 29-1250 mm). There is a wide spectrum of home range sizes in brown trout that highly varies depending on author, period of the day, fish body size or season. Due to this fact, it is impossible to explicitly specify a typical brown trout range. Stationary individuals used ranges around 20-40 m or up to 123 sqm. More mobile individuals used several hundred meters to a couple of kilometers (or 4 ha). Large individuals were observed to undertake extensive spawning movements up to 96 km. Five authors report on a specific daily home range for brown trout, which was in most cases below 80 m, ranging from 6-480 m. However, there is one study with a daily home range of brown trout of 150-2000 m. Brown trout were observed to have multiple, separated home sites and differed between nocturnal and diel activity. Literature about Atlantic salmon (*Salmo salar*) dealt with juvenile individuals. Young salmon used small defended territories of 0.6 sqm, that expand with increasing body size to ranges up to 5602 sqm or 2 km. Home range sizes of members from the genus *Oncorhynchus* vary in a similar way like brown trout. They are, depending on season and period of the day, confined to a few meters in stationary individuals, whereas they can range from several hundred meters to a few kilometers. During spawning, movement ranges of *Oncorhynchus* had a size of up to 86 km. For taimen (*Hucho taimen*), home ranges of 500 m to 93.2 km are documented. They seasonally departed from core home ranges and their movement peaked during spawning. Home ranges of grayling (*Thymallus thymallus*) substantially varied between season. Mean ranges during pre-spawning were smallest, either 29 or 258 m, depending on study. Home range of post-spawning was about the same as observed during pre-spawning. Though, spawning home ranges extended as far as 5 km.

Percidae:

Individuals of percids (100-680 mm) were studied on a short- to longterm basis (10 d-1.5 yrs). Perch (*Perca fluviatilis*) and *Zingel asper* used home ranges between 4-74 m with high inter-individual differences (high standard deviations). Ranges of walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) are much larger. Yellow perch occupied areas up to 22 ha whereas walley used 2 ha with movements up to 46.7 km.

Centrarchidae:

In mid term to long term studies (4 mths-3 yrs) body size varied between species (96-503 mm). Some species remained sedentary within a restricted home range of <100 m between successive captures with only few individuals undertaking movements up to 17.6 km. While other species were observed to use areas between 0.05-4 ha, depending on season.

Cottidae:

Several publications report about resident and mobile individuals in the cottus populations. The majority of individuals were relative stationary whereas a small proportion was highly mobile. With one

exception, species of this small-sized fish (<130 mm) altogether used home ranges between 4-511 m or 0.3-123 sqm depending on species, sex, day- or night-time, spawning and on availability of nests in short to long term studies (3 weeks-3 yrs). However, great dispersal capability was found in potomac sculpin (*Cottus girardi*) that moved 3.14 km in upstream and 2.792 km in downstream direction.

Lotidae:

A single long term study (16 mths) documented maximum movement ranges of 9.1 km in burbot (*Lota lota*; 375-660 mm).

Residency versus mobility

Many authors have recognized that only some individuals of a population move while the rest remains resident. Whereas a majority of stream fishes may stay in home pools, some individuals- independent of body size- regularly move (Smithson & Johnston, 1999). This behavioral variation within a population has been described as the concept of partial migration and it occurs in a variety of habitats and at several different spatial scales (Chapman et al., 2012; Shaw & Levin, 2011). The concept of sedentary versus mobile fractions in population of Salmonids has been widely reviewed in Gowan et al. (1994). Diana et al. (2004) discovered in large brown trout two general categories of daily movement behavior, either a mobile (i.e. individuals moved frequently) or a stationary category (i.e. individuals did not move further than 150 m away from home site and spent 94 % of time at this site). The stationary and mobile component of a population was also observed in 1+ and 2+ juvenile brown trout (Bridcut & Giller, 1993) and in other Salmonids, like redband trout (*Oncorhynchus mykiss gairdneri*) (Muhrfeld et al., 2001) and cutthroat trout (*Oncorhynchus clarki*) (Heggenes et al., 1991). Different groups of resident and mobile individuals within populations were observed for Cyprinids, too. For example in *Barbus haasi* (Aparicio & De Sostoa, 1999) and chub (*Leuciscus cephalus*), whose sedentary component remained in a restricted zone while a mobile component undertook movements between different zones (Nicolas et al., 1994). Asp was found to maintain stationary behavior for 12 months occupying home ranges of up to 10 km, whereas non-stationary individuals moved longer distances during spawning and lived in areas of 10-40 km (Fredrich, 2003). Similarly, most common carp stay within ranges of up to 100 m occupying up to five sites whereas some individuals move up to 238 km (Jones & Stuart, 2009). This dualistic movement behavior is also exhibited by perch, that were observed to belong to either a stationary group that displaced 4 m (+/- 69 m) or to the mobile group that moved much larger distances than 69 m (Bruylants et al., 1986). The use of either a stationary or mobile strategy is also common in the small-sized Cottids such as fluvial sculpin (*Cottus pollux*) (Natsumeda, 2007b) or mottled sculpin (*Cottus bairdii*) (Breen et al., 2009). Individuals of bullhead (*Cottus gobio*) were found to be either always resident or mobile, or to switch between both behaviors. However, the majority of bullhead observed (up to 72%) stayed at or near (<10m) their initial site (Knaepkens et al., 2004; Knaepkens et al., 2005). The challenge of home range studies is to capture the movement of individuals in a population which encompasses both, mobile and sedentary fish.

Home range shift

It has been reported for brown trout to establish their home range mostly in the first or second year of life and to change it little thereafter (Bachman, 1984). In contrast to this study, brown trout were observed to move up to 10 km between spatially separate winter and summer ranges, while during the spring-summer period, they had up to four home sites between which they rotated every 2-3 days (Clapp et al., 1990). Indeed, some authors observed the abandonment of a home range and the shift and fidelity to a new home range. The reestablishment of a new home range seems to be common in some species, like cutthroat trout, golden perch and carp (Heggenes et al., 1991; Crook, 2004a). The process of a home range shift has been discussed in detail by Crook (2004a). It includes an emigration phase, a mobile phase and a home range establishment phase. This behavior of moving away from an original home range and the settlement in an unfamiliar area may be a mechanism to respond to changes of spatially and temporally dynamic resources (Crook, 2004b), and it is particularly important for the recolonization process in restored habitats (Riley et al., 1992).

Home range overlap

In many species, individual fish share a substantial area of their home range with other individuals (Hendriks et al., 2009). No home range overlap between individuals would imply either low densities or dominance hierarchies with territories from where intruders are expelled. It is important to clearly distinguish between a home range and a territory. A territory is a spatially restricted zone which is commonly occupied by one dominant fish that aggressively defends these favored reproduction or feeding resources against intruders. Whereas territory size can be defined by interactions with intruders (Keeley & Grant, 1995), a home range does not necessarily have to be defended (Gerking, 1959). The relative degree of territoriality can indirectly be measured through calculating the percentage area that overlaps between individuals. A home range overlap of 25% was set as a threshold for nonterritorial organisms, and less than 15% overlap for strongly territorial organisms (Petty & Grossman, 2007). Typically, young-of-the-year Atlantic salmon are territorial and alternate among several exclusive central-place foraging stations (Steingrimsson & Grant, 2011; Steingrimsson & Grant, 2008). There are species that develop strong territoriality only at adult stage, but have highly overlapping ranges between juveniles, i.e. mottled sculpin (*Cottus bairdii*) (Petty & Grossman, 2007). In the reviewed literature, home range overlapped widely in many species, for example in fluvial sculpin (*Cottus pollux*) (Natsumeda, 2001), brown trout (Heggenes et al., 2007; Bachman, 1984), smallmouth bass (*Micropterus dolomieu*) (Todd & Rabeni, 1989), dark chub (Katano, 1996) and burbot (Slavik et al., 2005). Barbel seem to benefit from social interaction and occupy residence areas through shoals of more than 10 fish (Baras, 1997). There are fish species that share the same area but temporally segregated, e.g. flathead catfish (*Pylodictis olivaris*) (Vokoun & Rabeni, 2005). Some species only overlap in preferred areas but still use distinct core areas, e.g. pike or Mary River cod (*Maccullochella peelii mariensis*) (Vehanen et al., 2006; Simpson & Mapleston, 2002). No home range overlap was found in river blackfish (*Gadopsis marmoratus*) (Koster & Crook, 2008) and between juveniles and adults of catfish (*Siluris glanis*) (Slavik et al., 2007). Seasonal variation of spatial overlap occurs in brown trout, with an increase of common space use during spawning (Höjesjö et al., 2007).

However, the degree of overlap between individuals is probably underestimated because of the presence of non-monitored individuals (Hodder et al., 2007).

Factors influencing home range size

There is considerable variation in movement behavior between individuals, which makes it difficult to detect a significant influence of predictive factors such as body size or sex on home range size (Allouche et al., 1999; Heggenes et al., 2007; Ovidio et al., 2007a). Even within a single shoal, some individuals prefer distinct day and night habitats whereas others do not (Huber & Kirchhofer, 1998). Individual differences of home range size may reflect local variation of prey abundance or differences in foraging tactics (Ovidio et al., 2002; Katano, 1996), social interactions (e.g. time taken to establish a position within a dominance hierarchy) or different motivations to explore and assess habitats (Crook, 2004b).

Sex: space use patterns can be different among sexes. Especially during spawning period, movement distances of *Zingel asper* were found to be longer in males than in females (Danancher et al., 2004). Home ranges of female fluvial sculpin were not only much smaller than the male home range but they also were located within male home ranges (Natsumeda, 2001). In other taxa, there are no differences between male and females in home range sizes, such as in dark chub (Katano, 1996) or in annual movement distances of murray cod (Koehn et al., 2009).

Body size and age: the potential effect of body size on space use has been investigated in several different species. Generally, there are reports about a positive correlation of fish body size and home range size (Woolnough et al., 2009; Minns, 1995), although mobility can decrease with increasing age of individuals (Bruylants et al., 1986; Bachman, 1984). Body size had a positive effect on home range size of fluvial sculpin (Natsumeda, 2001) and mottled sculpin (Petty & Grossman, 2007), on territory size of juvenile Atlantic salmon (Keeley & Grant, 1995), on movement rates of pike (Vehanen et al., 2006) and on movement distances of murray cod, which was probably related to spawning behavior (Koehn et al., 2009). Although a higher activity was detected in large brown trout (>340 mm) compared to small individuals, home range of brown trout did not relate to body size (Ovidio et al., 2002; Young, 1994). No significant relationship between home range size and fish body mass or body size has been detected for burbot (Slavik et al., 2005), dark chub (Katano, 1996), river blackfish (Koster & Crook, 2008) and taimen (*Hucho taimen*) (Gilroy et al., 2010).

Dominance: the home range of old and dominant individuals is smaller compared to the range of young and smaller individuals probably because they force the subordinates to move more (Bachman, 1984). From this perspective, dominance would be beneficial because it allows a less energy-consuming home range. However, it was observed that dominant brown trout generally moved more and that they had, contrary to the studies mentioned above, a larger home range than subordinate individuals (Höjesjö et al., 2007). Those findings agree with the behavior of giant kokopu (*Galaxias argenteus*), a drift feeding stream fish, whose dominant individuals increased home range size compared to subordinates during constraints of food supply (Hansen & Closs, 2005). In contrast,

juveniles and sexually immature individuals establish larger home ranges than large, sexually mature adults of mottled sculpin and flannelmouth sucker (Petty & Grossman, 2007; Chart & Bergersen, 1992).

Foraging and competition: space use patterns of fish in streams and rivers are subject to the foraging strategy and energetic constraints of fish. With movement and homing behavior fish are likely to optimize the use of food, space and shelter (Simpson & Mapleston, 2002). It provides benefits such as familiarity with the locations of food sources, shelter, potential mates, and predators (Crook, 2004b). Cruising foragers tend to have overall larger home ranges than individuals that use a different tactic, such as sit-and-wait (Katano, 1996). Potentially, home range size is a function of actual fish density as well as intraspecific competition, and it decreases under increasing fish densities (Hesthagen, 1990). According to the current literature, the enlargement of home range size due to limited prey availability remains a hypothesis. However, food availability affects movement behavior. Drift rate correlated with the activity of brown trout especially at night (Giroux et al., 2000). Hence, brown trout forage at night and stay in cover at specific home sites during the day (Clapp et al., 1990).

Period of the day: often, home ranges are distinct on each period of the day. Japanese fluvial sculpin was observed to use day and night home ranges in three different ways: i) most commonly, the nocturnal range encompassed entirely the diurnal range, ii) the diurnal and nocturnal home range overlapped only partially, iii) the diurnal and nocturnal home ranges never overlapped (Natsumeda, 1998). Home ranges in salmon parr only partially overlapped between the four periods of the day (day, dusk, night, dawn) (Ovidio et al., 2007b). In many fish species, nocturnal or crepuscular mobile activity is common and either peaks at dusk, night or dawn, whereas activity is reduced during the day. This was shown for river blackfish (Koster & Crook, 2008), pike (Hodder et al., 2007), brown trout (Diana et al., 2004) or nase (Huber & Kirchhofer, 1998). An actual increase in nocturnal home range size compared to the diurnal range has been observed in spotted gar, sculpin and brown trout (Snedden et al., 1999; Natsumeda, 1998; Matthews et al., 1994; Parkinson et al., 1999). In contrast, two authors found larger home ranges during daytime than at night in brown trout and *zingel asper*, which was explained by reduced food availability during the day and reduced sensory capacity at night (Höjesjö et al., 2007; Cavalli et al., 2009).

Seasonality: within the same family, there was considerable variation between species regarding seasonality of home range sizes. Some members of Centrarchidae showed no variation in home range size among seasons (Stormer & Maceina, 2009), whereas others displayed seasonality (Todd & Rabeni, 1989). Seasonal differences in home range size are most probably caused by a change of habitat requirements during the year, reproductive movement and the temperature-related metabolism of fish that controls activity. Brown trout were observed to have separate winter and summer ranges (Clapp et al., 1990). Hence, the largest movement distances often occur during spring and fall when fish transit between summer and winter habitats, while in summer and winter, they use relatively small home ranges or are inactive (Daugherty & Sutton, 2005). A reduced mobility and home range size from spring or summer to winter is explained by a decrease in water temperature and is reported for

many species from across a wide range of taxa, for example brown trout, barbel, bass, chub, nase, sculpin, golden perch and ide (Ovidio et al., 2002; Lucas & Batley, 1996; Todd & Rabeni, 1989; Allouche et al., 1999; Ovidio et al., 2009; Kulísková et al., 2009; Huber & Kirchhofer, 1998; O'Connor et al., 2005). Outside spawning season, daily home range of brown trout was observed to be proportionally related to water temperature, and they travelled longer distances with temperatures above 12°C (Ovidio et al., 2002). However, some studies report that brown trout had larger home ranges in winter than in other seasons (Burrell et al., 2000). Similarly, northern hog sucker had a larger home range in winter compared to summer (Matheney & Rabeni, 1995). Daily home ranges and movement distances of brown trout and bullhead, respectively, increase during spawning season (Ovidio et al., 2002; Knaepkens et al., 2004). However, it is sometimes impossible to determine whether high movement rates observed during spawning season relate to spawning behavior or to other seasonal cues (Gilroy et al., 2010).

Environmental variables: Kulísková et al. (2009) investigated effects of multiple environmental variables like water temperature, dissolved oxygen, conductivity, pH, atmospheric pressure, moon phase and light intensity on home range size but found no significant effects. Reports about movement and home range size in relation to river discharge and temperature are contradictory. Many studies found an increase in the mobility of fish that was related to water temperature or river discharge (Baras & Cherry, 1990; Natsumeda, 2003; Clapp et al., 1990; Heggenes et al., 2007; Baras et al., 1998; Neely et al., 2009; O'Connor et al., 2005). Similarly, downstream movements in spring typically start when reaching a threshold temperature or when discharge increase (Zigler et al., 2003) or, in contrast, decrease (Ovidio et al., 2004). Thermal stress such as high and low water temperatures in summer and winter, respectively, decrease movement rate of certain species (Bunnell Jr et al., 1998; Vehanen et al., 2006). It has been reported that smallest home ranges occurred at low temperatures and high flows (Slavik et al., 2007), whereas extensive flooding caused a greater movement range (Hodder et al., 2007). Sometimes discharge positively correlated with movement distances for some species (Simpson & Mapleston, 2002) but not for all species (Matheney & Rabeni, 1995; Heggenes et al., 2007). Scruton et al. (2008) found a positive response of moving distances in juvenile Atlantic salmon to experimental hydropeaking. An increase of home range size relating to turbidity independently of discharge was most likely due to reduced foraging success in turbid water (Kulí_ková et al., 2009).

Habitat: due to varying spatial availability of habitat, that provide space for feeding, reproduction or shelter, home range sizes for a species can contrast between different river sections or in different river systems (Hill & Grossman, 1987; Snedden et al., 1999; Vokoun & Rabeni, 2005; Zigler et al., 2003). This contributes to between-population variance in home range size beside individual variation. One study found that river slope, which of course relates to other parameters like flow velocity, substrate, or depth, influenced home range size positively. This can potentially be explained by lower food availability in such an area that force fish to move to feeding areas (Slavik et al., 2005). Further, the availability of a specific habitat, like stagnant backwaters or instream cover such as undercut banks, woody debris or riffle is important for species that specifically select a structure and are

strongly associated to it (Daugherty & Sutton, 2005; Khan et al., 2004; Allouche et al., 1999; Baade & Fredrich, 1998). For example, river blackfish (*Gadopsis marmoratus*) were often located within pools (Koster & Crook, 2008), whereas home range of Japanese fluvial sculpin were located around several rocks (Natsumeda, 2007a). The requirement for different habitat can change on a seasonal basis (e.g. overwintering) (Vehanen et al., 2006) or during a daily cycle (e.g. the change from calm sections at night to the main channel during the day) (Baade & Fredrich, 1998). Habitat quality is a relevant factor controlling home range size of fish. In sections with homogenous habitat, which was considered to be poor habitat, individuals were not attached to a particular home site and stayed mobile. In heterogeneous sections, however, almost a third of studied fish stayed within a home range (Bruylants et al., 1986). Accordingly, in habitat with low suitability, as suggested by low estimates of population density, fish extent their home range by crossing these zones (Baras et al., 1998). Hence, home range become significantly larger in channelized river sections compared to natural sections (Heggenes et al., 2007). Fragmentation of the river corridor by barriers such as weirs and dams inhibits free long-distance movement of fish and blocks access to potential spawning grounds (Ovidio & Philippart, 2008; Young, 1996). Additionally, in fragmented river sections, the range of movement of fish is restricted to the distance separating two dam impoundments or other kind of barriers (Geeraerts et al., 2007; Lucas & Batley, 1996; DePhilip et al., 2005).

To summarize, apart from body size and season, there are many other factors that influence spatial behavior of fish and, hence, the use and size of a home range. Among them are also anthropogenic alterations in impounded river systems.

Conclusion and perspectives

This literature review provides insight into the often very spacious home ranges of riverine fish. We find that the nature, size and stability of home ranges in riverine fish is complex and currently not enough data for sufficiently many taxa is available to make strong predictions. There is considerable variation in home range sizes among and within families and we could not arrive at robust generalizations concerning either families or fish size. One important lesson that has been learned in recent studies is that there is very considerable inter-individual variation in behavioral strategies related to home range use even within populations, and this relates to the concept of partial migration (Chapman et al., 2012). There are many examples that documented sedentary fish with fidelity to a relatively small home range, whereas some other individuals in the same population were seen undertaking movements over very long distances (see for instance Jones & Stuart (2009)). Many studies found home ranges that were restricted to a few meters a day, but movement over many kilometers was not uncommonly found when seasonal migration was included. This challenges the validity of determining daily home range sizes if one tries to answer the question posed at the beginning, "how much space do fish need". To this end, the information content of home range studies that had no data on spawning activities is limited. Estimating the space needs of fish from daily activity around a home site, such as daily feeding and refuge movements, will inevitably often result in underestimates. To understand space use of fish, it is essential to observe movement on a long term

basis including several seasons as well as the spawning period. For this, a temporally standardized repeated sampling or tracking design as well as a clear definition of the “home range” are requisite in order to retrieve data that is comparable between studies. The large intra-population variation among individuals, falling into mobile and sedentary fractions in many populations, makes large sample sizes inevitable when studying movement and home ranges sizes in river fish. Additionally, one should be aware that in rivers impacted by hydro-peaking, research about mobility is affected due to the changing discharge. Study rivers should further not be impounded by anthropogenic migration barriers. Though, this becomes highly problematic considering the fact that very few barrier-free rivers and streams still exist. To our surprise, we found very few publications only that addressed effects of pollution, hydro-peaking, river channelization or fragmentation on home range sizes and utilization. Future research should explicitly examine the influence of these major anthropogenic stressors on fish home ranges.

Our review strongly supports the statement of Gilroy et al. (2010), that knowledge about the core home range is important for understanding habitat use whereas knowledge of occasional extreme movements away from the core range is necessary to understand population connectivity. It is important to note that home range size or movement distance is different from dispersal distance. In this review we dealt with the former, but the latter is important too to predict long term population sustainability. Only through the understanding of extreme movements is it possible to identify potential barriers to long distance dispersal. Dispersive behavior can also happen in a passive way (e.g. drifting larvae), through which colonization potential especially in downstream direction of flow is high. High mobility in both up- and downstream directions in many different fish species belonging to a wide range of different families underscores the necessity of longitudinal connectivity within river corridors during all seasons. A fish population can only be sustained on the short term if access to remote spawning grounds is provided, even if home ranges of fish are small. In addition, their seasonal non-spawning migration is an important behavior in response to seasonally fluctuating trade-offs between predator avoidance and foraging gains (Brönmark et al., 2008). River fragmentation is likely to have very significant consequences for river fish assemblages. It is crucial for some species to have access to specific habitats such as a floodplain and floodplain side-channels, that can serve as important spawning and nursery habitat (Koehn et al., 2008; Snedden et al., 1999). Fish with small home ranges, on the other hand, may be especially vulnerable to degradation of habitat or exposure to local pollution because of the extended residence time at a specific site (Erickson et al., 2002). We are in complete agreement with the suggestion that recovery plans for riverine habitat should focus on resources (e.g. nutritional, reproductive, but also refuge from predation), which are usually present within home ranges and which are needed by individuals of different species to successfully complete their life cycle (Woolnough et al., 2009). However, efforts in river restoration should not only focus on habitat quality improvement. Preferably, conservation strategies also focus on area size and habitat quantity by restoring longitudinal connectivity on a large scale and by removing migration barriers in order to allow fish to shift between and explore home ranges and to ensure long-distance dispersal. Habitat restoration should also consider the effects of proximity to sites that still harbor source populations for facilitating re- colonization by populations the members of which may occupy a limited

home range with only a few individuals moving larger distances (Koehn et al., 2008; Irving & Modde, 2000).

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CHAPTER 5

Synopsis

Achievements

The present thesis provides some insight into the importance of longitudinal connectivity of streams and rivers for fish populations. My data speak to the impacts of fragmentation of the river corridor by anthropogenic barriers and the associated consequences for the fish fauna. Restoring longitudinal connectivity has become a major aim for river rehabilitation. The thesis focuses on the current situation in Switzerland and sheds light on the success of specific restoration measures that are supposed to re-establish longitudinal connectivity for fish movement. The most important findings from my thesis are the following:

- Block ramps are helpful engineering measures to replace artificial barriers such as river bed sills, small dams and weirs. The usefulness for fish upstream movement depends strongly on the type of construction and the appropriate hydraulic and morphological characteristics. Block ramps with slopes of >5 % are ineffective for small-sized cyprinid species and vertical drops within step-pool ramps prevent upstream passage of bullhead. Upstream passage efficiency differs between fish species and size classes.
- The use of PIT-tags in connection with an instream antenna proved to be a recommendable method to study effective fish passage and temporal movement behavior. Applying this method, functional connectivity between fish habitat can accurately be evaluated. However, floods can limit the application of instream antennas.
- Riverine fish communities are non-randomly assembled and dispersal distance per se does not appropriately explain variation in abundance pattern of different fish species. In the rivers I studied, habitat factors (environmental parameters) together with spatial factors (river distance from the mouth) have significant effect on the abundance of the most dominant species brown trout. Abrupt shifts in longitudinal patterns and a drop in fish abundance and species richness of fish occur above anthropogenic dispersal barriers (river bed sills) and in highly modified, channelized sections. Floodplains and junctions to the river mouth or lake are characterized by an increased species richness. They constitute important species pools, from where potential colonization of rivers can happen provided sufficient longitudinal connectivity.

- There are several different definitions of the concept of fish home range. Various approaches exist to estimate the daily and seasonal home ranges of freshwater fish within lotic systems. Radio-telemetry is the most popular method used to observe mobility patterns of fish. There is considerable variation in home range sizes among and within families and it is not possible to make generalizations concerning either families or fish size. Even within a population, individuals can have different behavioral strategies and can be either resident or mobile. Often, home ranges are restricted to a few meters a day, but movements occur over many kilometers during seasonal migration. Hence, estimating the space needs of fish from daily activity around a home site will inevitably result in underestimates. Apart from body size and season, there are a lot of additional factors that influence mobility patterns of fish and hence, the use and size of a home range.

When evaluating connectivity, behavior is an important component and it should be empirically monitored (Fullerton et al., 2010). This does not only apply to the passage efficiency of block ramps, but also holds for the evaluation of river corridor restoration in general. Individual movements of fish offer valuable clues to habitat connectivity, habitat use and hence, habitat quality for fish. One should be aware of the constraints of observational studies based on behavior. Behavioral studies often require large sample sizes because of large intra- and inter-individual variance. In addition, behavioral field studies are laborious, time-consuming and costly. However, some researchers argue that behavior will provide a better index of the quality of a site after restoration efforts than the documentation of species presence or absence, and it will indicate resources that are important to species (Lindell, 2008).

In Switzerland, almost a quarter of the entire river and stream system is nowadays heavily impacted, regulated or piped to culverts (Zeh-Weissmann et al., 2009). Main stressors affecting fish populations in Swiss rivers comprise fragmentation of the river corridor (artificial barriers, hydropower plants), water pollution (e.g. biocides, micropollution caused by pharmaceuticals), water abstraction and hydro-peaking due to hydropower production, rising temperatures caused by climatic changes, impairment of bedload regime, and habitat loss, especially of dynamic floodplain habitats, due to channel straightening. There are only few studies that have tried to quantify the ecological effects of connectivity alterations on riverine fish. Fragmentation in river systems is a complex environmental disturbance and a thorough understanding of life-history and dispersal ecology of fish is needed to predict its

consequences (Rolls et al., 2013). For example, the negative impact on young of the year fish caused by poor connectivity in watersheds aggravates with increasing number of obstacles and decreasing distance between two consecutive obstacles (Musil et al., 2012). Efforts to restore or conserve ecological integrity of rivers may focus on different aims. Ecological integrity of rivers comprise elements of hydrological connectivity, flux of nutrients and organic matter, habitat availability, connectivity for fish and biodiversity (Schiemer, 2000). One should be aware that threats to riverine systems are mediated along river corridors, which means that the condition of the entire catchment influences river biodiversity downstream (Hermoso et al., 2011). Hence, in the course of river restoration, it should be considered that the effectiveness of local, reach-scale rehabilitation efforts may be comprised by negative effects of disturbances at larger scale, i.e. regional scale (Howson et al., 2009; Vehanen et al., 2010). It has been postulated that the re-establishement of functional processes (e.g. hydrologic or successional processes) within the river corridor would restore habitat heterogeneity, followed by an increase of aquatic species diversity (Ward & Tockner, 2001). However, the improvement of habitat heterogeneity *per se* does not necessarily lead to an increase of macroinvertebrate diversity because many other factors such as disturbance regime, food resources and regional species pools influence diversity (reviewed by Palmer et al., 2010). Further, the installation of a fish ramp and spoiler baffles in order to enhance fish upstream movement has in some cases proved to increase species richness and total fish density upstream of a culvert (e.g. Franklin & Bartels, 2012). Nevertheless, river restoration by improvement of habitat quality and by removal of migration barriers can only lead to a potential increase of fish abundance and species diversity if the connection to a source-population and a species pool exist that foster (re-)colonization processes. Using our study system Brenno river as an example, this would mean the following: removing the one prominent dispersal barrier itself would probably not improve the current state of the fish fauna in above-barrier sites if the channelized, impounded habitat section just downstream of the barrier was not simultaneously amended, because this section constitutes the connecting corridor to the species-rich floodplain further downstream. On the other hand, a mere improvement of the habitat quality and heterogeneity in the impacted, channelized section right upstream of the floodplain would not considerably increase habitat area followed by a large-scale effect on the fish fauna if the barrier was not removed, which fully disconnects the upper part of the river system. Concurrently, the heterogeneous, laterally well-connected habitat of the floodplain and its role as a potential species pool are likely to cease in the long term without the maintenance of a catchment-wide, natural, dynamic discharge regime. Since 1960, movements of the Brenno channel through floods have ceased to occur (Brunke, 2002). Heterogeneity and productivity of floodplain habitats strongly depend upon a certain level of disturbances through flood pulses

with regard to amplitude, duration, frequency and regularity (Junk et al., 1989). For an integrated river management, the maximization of fish habitat quality, quantity and connectivity through morphological improvements or barrier removal should be simultaneously fostered along with efforts that guarantee a natural, unregulated flow regime.

Outlook

There are still substantial gaps in the scientific knowledge concerning restoration of longitudinal connectivity and hence, ecological integrity of rivers. There are contradictive studies that evaluate the success of restoration activities enhancing structural habitat heterogeneity. Often, species diversity of macroinvertebrates did not significantly increase after channel complexity had been improved (Palmer et al., 2010). Furthermore, some authors claim that the importance of connectivity as favored option for conservation in the face of climate change is being overemphasized (Hodgson et al., 2009). It is argued that uncertainties in the estimation and effects of connectivity is generally higher than uncertainties about habitat area and quality, and threatening processes like habitat destruction. Here, I present three major, instant challenges for river management and conservation and explain why they should remain focal points of freshwater fish research in the near future.

- i) How do budget-constrained managers set the priorities for the restoration of river systems? The priority setting in restoration projects is a complex action and needs a holistic approach. The decision making in view of restoration measures should be based on a procedure that first accurately evaluates the deficits of ecosystem processes based on analyzed criteria (e.g. fragmentation, discharge regime, habitat quality and dynamics) (Baumgartner et al., 2013). It is further necessary to identify sections within the river system of high conservation value (e.g. the existence of endemic or endangered species, proximity to species pools). Further, mitigation measures have to be prioritized (e.g. morphological or hydrological improvements, barrier-removal) that maximize the improvement of the natural functions of the river system and that foster potential site-specific species diversity. It has to be clarified at first through which measures major success for the natural fish fauna can be achieved.
- ii) In view of the ongoing efforts to restore upstream migration possibilities for fish, passage problems encountered by fish during downstream migration should be

considered, too. Several studies document negative effects of different obstacles on fish downstream migration. Downstream passage efficiency of fishes can be seriously affected by pumping stations (Buyssse et al., 2014) or by dams and hydroelectric plants (Norrgard et al., 2013). In particular, the bypassing of hydroelectric turbines at power plants can be critical for fish. Further, low-level weirs do not only impede upstream passage but may also inhibit downstream fish movement and prevent fish from reaching their downstream home range areas (O'Connor et al., 2006). Future research should keep an eye on the problems of down- as well as upstream passage of fishes at various obstacles and investigate the success of mitigation measures for down- and upstream migration simultaneously.

- iii) Anthropogenic activities alter connectivity for freshwater fish in fluvial systems through either the disruption or the enhancements to natural connectivity (reviewed by Fullerton et al. (2010)). The former actions cause habitat fragmentation, whereas the latter actions (e.g. barrier removal) are major goals for river restoration. However, Fullerton et al. (2010) report that enhancements to connectivity can also negatively impact fish populations of fluvial systems. Increased connectivity can have unintended consequences on the local fish fauna through the spread of pathogens or non-indigenous species (e.g. *Lepomis gibbosus* in Switzerland). It is necessary to recognize such occasional negative consequences of longitudinal connectivity enhancements in order to prevent them by appropriate actions.

The present thesis adds to the growing knowledge about the importance and the restoration of longitudinal habitat connectivity for different riverine fish species. It further demonstrates the contribution of connectivity to the spatial structuring of fish communities. It is my hope that this thesis will make a contribution to the public awareness of the significance of an intact longitudinal connectivity in streams and rivers.

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APPENDIX 1

Merkblatt: Durchgängigkeit von Blockrampen

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6 > Durchgängigkeit von Blockrampen

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Blockrampen sind Fliessgewässerabschnitte mit erhöhtem Gefälle, die mit Steinblöcken befestigt werden. Sie dienen als Ersatz für künstliche Abstürze und Wehre zur Stabilisierung der Gewässersohle und verbessern die longitudinale Vernetzung für aquatische Organismen. Das vorliegende Merkblatt stellt die verschiedenen Blockrampentypen vor und diskutiert, welche Typen sich für welche Arten und Situationen eignen.

Fragmentierte Fliessgewässer

Durch die Melioration der Fliessgewässer wurde ihr Lauf begradigt und kanalisiert. Als Folge davon kam es vielerorts zu Gerinne-Erosion und Eintiefungen der Gewässersohle (z. B. Kander, BE). Künstliche Abstürze und Schwellen (Abb. 1) wurden gebaut, um die Gewässersohle zu stabilisieren und der Erosion entgegenzuwirken (Flussrevitalisierungen: eine Übersicht). Diese Bauwerke stellen für viele aquatische Organismen Hindernisse dar, welche die Wanderung flussaufwärts behindern und die Fliessgewässer zerschneiden (MB 4, Vernetzung von Fliessgewässern). Weitere Hindernisse sind: künstliche Wehre zur Ausleitung von Wasser bei Kraftwerken oder zur Bewässerung, eingedolte Bäche sowie ver-

baute, sehr schnell fliessende Gewässerabschnitte mit glatter betonierter oder gepflasterter Sohle. Fische und andere aquatische Organismen wie Krebse sind darauf angewiesen, dass sie in Fliessgewässern ungehindert wandern können. Barrieren be- oder verhindern ihre natürliche Ausbreitung und verunmöglichen die Laichwanderungen von Fischen. Wirbellose Tiere mit geflügelten Adultstadien hingegen können solche künstliche Hindernisse überfliegen. Auch für Wirbeltiere wie Biber und Spitzmäuse, welche die Hindernisse auf dem Landweg umgehen können, stellen solche Bauwerke keine Barrieren dar.



Blockrampe am Aabach in Wildegg (AG).

Foto: Thomas Schläppi

Blockrampen fördern Vernetzung

Im Wasserbau wird die Gerinne-Erosion häufig mit dem Bau von Blockrampen verhindert. Eine Blockrampe ist eine mit Steinblöcken befestigte Fliessgewässerstrecke mit erhöhtem Gefälle (Lange 2007). Im Vergleich zu Schwellen und Abstürzen erleichtert sie den Fischaufstieg erheblich. In fragmentierten Fliessgewässern werden deshalb zur Wiederherstellung der longitudinalen Vernetzung Querbauwerke entfernt und durch Blockrampen ersetzt. Blockrampen müssen gewisse hydraulische Kriterien erfüllen, damit sie die Durchgängigkeit von Fliessgewässern für aquatische Organismen und insbesondere für Fische tatsächlich erhöhen.

Es gibt verschiedene Typen von Blockrampen: klassische und aufgelöste (Abb. 2). Die klassischen Blockrampen erfüllen oft die Durchgängigkeitskriterien für Fische nicht. Als Kriterien für den Fischaufstieg gelten in der Literatur eine maximale Abflussgeschwindigkeit von 2 m/s und eine minimale Abflusstiefe von 20 cm (DVWK 1996). Bei strukturierten Rampen ist die Geschwindigkeitsverteilung ungleichmäßig, was den Fischaufstieg erleichtert. Beim Bau von Blockrampen spielen mehrere Faktoren eine wichtige Rolle (Box 1). Zudem muss der Blockrampentyp auf die bereits vorkommenden oder die potenziell vorkommenden Fischarten und ihre Schwimmkapazität abgestimmt sein.

Erfolgskontrolle

Beim Bau einer Blockrampe sollte eine Erfolgskontrolle durchgeführt werden, um zu überprüfen, ob die Blockrampe die Durchgängigkeit für die gewünschten Fische tatsächlich verbessert. Vor dem Bau wird dafür die Fischregion gemäss Fliessgewässerzonierung bestimmt. Aufgrund des Gefälles, der Gewässerbreite und der Wassertemperatur wird auf die potenzielle Fischfauna geschlossen (Abb. 3). Deren tatsächliche Zusammensetzung kann mittels Elektroabfischung erhoben werden. Nach dem Bau der Rampe wird die Durchgängigkeit des Gewässerabschnittes für bestimmte Fischarten und Grössenklassen untersucht, indem Fische versetzt werden. Für Bäche bzw. kleine Flüsse eignen sich Fang-Wiederfang-Versuche mit Farbmarkierung an flussabwärts versetzten Fischen. Genauere Beobachtungsresultate erzielt man mit individuellen passiven Sendern, sogenannten PIT-tags. Diese werden den Fischen in die Bauchhöhle gespritzt. Die markierten Fische werden bei ihrem Aufstieg entweder mit einer fest installierten Antenne direkt oberhalb der Rampe oder mit einer Handantenne erfasst. Bei mittleren und grossen Fliessgewässern (z. B. Glatt ZH, Aare BE) ist der Einsatz von Radiotelemetrie (aktive Sender mit weitreichendem Radius) von Vorteil.



Abb. 1 Sohlstufen und künstliche Abstürze bilden Wanderhindernisse für Fische. Querbauwerke an der Sissle (AG) (oben) und Suhre (AG) (unten). Fotos: Denise Weibel

> Box 1: Wichtige Faktoren beim Bau von Blockrampen

- > Rampengefälle
- > Länge der Rampe
- > Rampentyp (Art, Struktur der Rampe)
- > Bereits und potenziell vorkommende Fischarten
- > Stabilität bei Hochwasser, insbesondere des Rampenfusses
- > Durchgängigkeit für Fischarten mit unterschiedlichen Schwimmleistungen

Durchgängigkeit von Blockrampen

Die Durchgängigkeit von Rampen unterscheidet sich je nach Fischart, Fischgrösse und Blockkrampentyp. So hängt die Aufstiegsrate bei Bachforellen und Alet von der Körpergrösse ab und ist bei Jungfischen (<200 mm) eingeschränkt. Blockrampen mit einem Gefälle von mehr als 6 % verbessern die Vernetzung der Fließgewässer nur für grosse Bachforellen (>200 mm). Für juvenile Tiere hingegen sind solche Blockrampen nur beschränkt überwindbar, und für Gruppen sind sie sogar unüberwindbar. Auch die schwimmschwächeren Karpfenartigen (Cypriniden) haben Schwierigkeiten, Blockrampen mit einem Gefälle von mehr als 5 % zu überwinden.

Für viele Karpfenartige, etwa für Kleinfische wie Gründling und Strömer, ist die für den Fischaufstieg als zulässig geltende Abflussgeschwindigkeit von maximal 2 m/s (DVWK 1996) zu hoch bemessen. Die relativ langen Blockrampen mit Becken- und Querriegelstruktur weisen geringe Abflussgeschwindigkeiten auf und gewährleisten Erholungszonen. Bei Niedrigwasser besteht allerdings die Gefahr, dass sich bei diesen Blockrampen vertikale Abstürze auf den Querriegeln bilden (Abb. 4). Für die schwimmschwachen Gruppen stellen bereits Abstürze von 15 cm ein Wanderhindernis dar.

Versuche mit Rampenmodellen

Im Projekt «Integrales Flussgebietsmanagement» wurden in Laborversuchen Messungen auf Rampenmodellen durchgeführt. Diese zeigten, dass klassisch gesetzte Blockrampen bei Neigungen von 6 und 10 % auch bei kleinen spezifischen Abflüssen die Durchgängigkeitskriterien ($v_{max} = 2 \text{ m/s}$; $h_{max} = 20 \text{ cm}$) nicht erfüllen. Blockrampen mit regelmässigen Querriegeln erfüllen bei einer Neigung von 6 % die Durchgängigkeitskriterien bis zu einem spezifischen Abfluss von $2 \text{ m}^3/\text{s/m}$. Falls die Querriegel unregelmässig angeordnet sind, werden die Durchgängigkeitskriterien bis zu einem spezifischen Abfluss von $1 \text{ m}^3/\text{s/m}$ erfüllt. Als Alternative zur klassisch gesetzten Blockrampe wurde die mäanderförmige Blockrampe entwickelt (Studer und Schleiss 2011). Die hügelartige Oberfläche erzeugt eine breite Geschwindigkeitsverteilung und erleichtert den Fischen den Aufstieg. Bei diesem Blockkrampentyp werden deshalb die Durchgängigkeitskriterien bei einer Neigung von 10 % bis zu einem spezifischen Abfluss von $1 \text{ m}^3/\text{s/m}$ und bei einer Neigung von 6 % bis zu einem spezifischen Abfluss von $1,5 \text{ m}^3/\text{s/m}$ erfüllt (Abb. 5). Gleichmässige Blockrampen werden den Durchgängigkeitskriterien kaum gerecht. Strukturierte Blockrampen sind für den Forellenaufstieg wesentlich besser, weil sie bei Neigungen bis 6 % für spezifische Abflüsse bis zu $2 \text{ m}^3/\text{s/m}$ und bei Neigungen bis 10 % für spezifische Abflüsse bis $1 \text{ m}^3/\text{s/m}$ optimale Verhältnisse gewährleisten.



Abb. 2 Unterschiedliche Bauweisen von Blockrampen.
Oben: klassisch gesetzte Rampe an der Emme in Burgdorf (BE) (Foto: Thomas Berchtold). Mitte: aufgelöst strukturierte Rampe mit Becken- und Riegelstruktur am Staffeleggbach (AG). Unten: aufgelöste unstrukturierte Rampe am Aabach in Seengen (AG). Fotos: Denise Weibel

Empfehlungen für die Praxis

- > Strukturierte Blockrampen sind den klassischen Rampen vorzuziehen, da sie aufgrund einer breiteren Geschwindigkeitsverteilung bessere Verhältnisse für den Fischaufstieg bieten.
- > In der Forellenregion können Blockrampen mit einem Gefälle von mehr als 6 % gebaut werden, wenn die Bachforelle die einzige Fischart ist, die dort vorkommt. Kleine Bachforellen werden jedoch bei der Aufwanderung benachteiligt. Wenn andere Fischarten vorkommen können (z. B. Groppe), sollte das Rampengefälle kleiner sein.
- > In der Äschenregion sind Blockrampen mit einem Gefälle von mehr als 5 % für kleinere Cypriniden ungeeignet. Bei einem Vorkommen von schwimmschwachen Fischen (z. B. kleine Karpfenartige, Groppe) sollte das Gefälle 3 % nicht übersteigen (DVWK 1996). Strukturen mit losen Blöcken im Uferbereich können am Rand grösserer Rampen strömungsberuhigte Bereiche (Abb. 6) mit geringer Abflussgeschwindigkeit bilden, die von Fischen durchschwommen werden können.



Abb. 4 Vertikale Abstürze bei Querriegeln am Staffeleggbach (AG). In Fließgewässern, in denen die Groppe vorkommt, sollten solche Abstürze vermieden werden. Foto: Denise Weibel

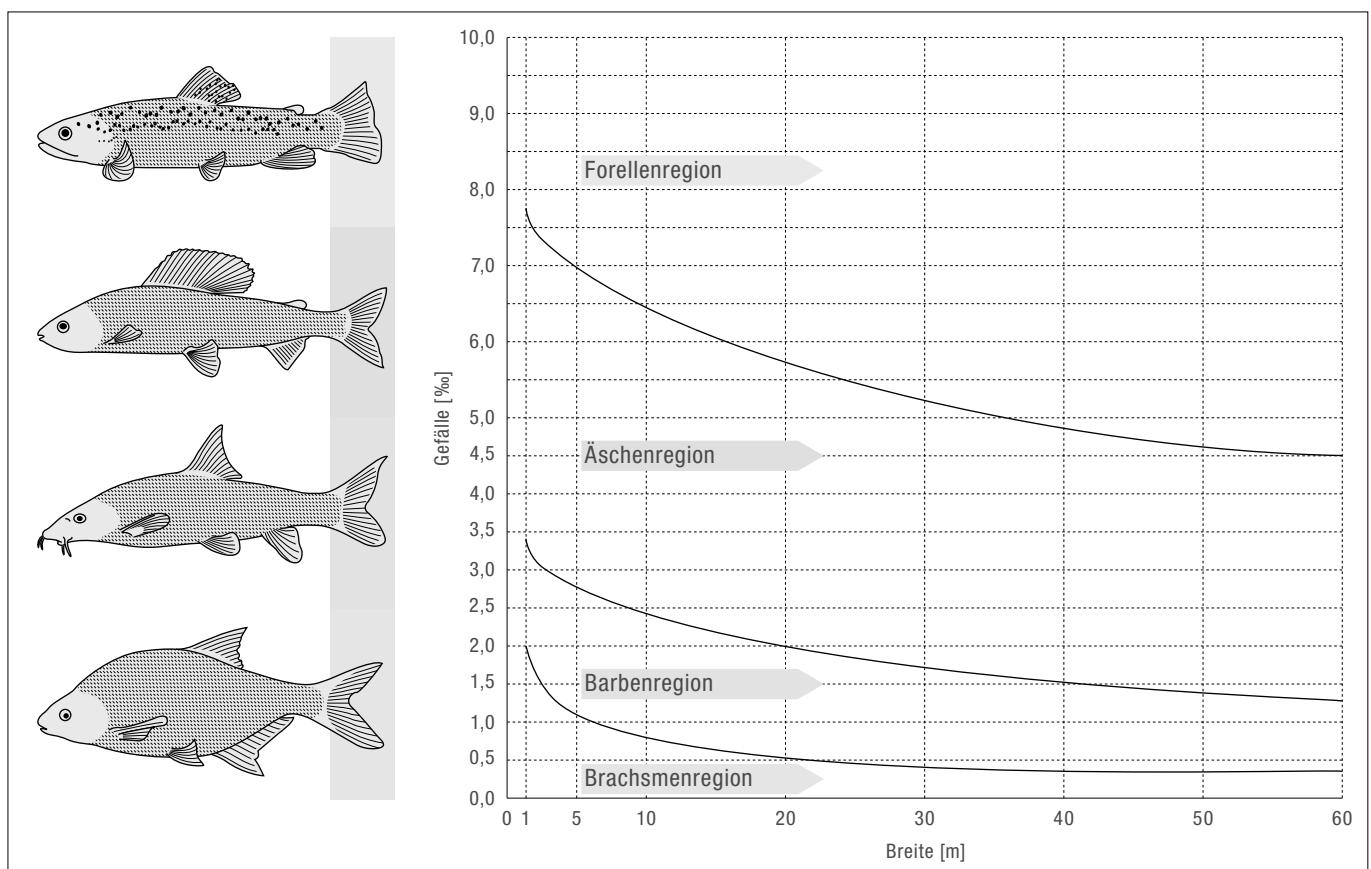


Abb. 3 Fischregion als Funktion von Gefälle und Breite des Fließgewässers.
Illustration nach Modul Fische Stufe F (Schager und Peter 2004, nach Huet 1949)

- > Vertikale Überfälle bei Rampen mit Querriegeln sollten vermieden werden, damit die Durchgängigkeit während mindestens 300 Tagen im Jahr gewährleistet ist (Abfluss $Q_{30} - Q_{330}$, Friedrich *et al.* 2005).
- > Ein Monitoring vor und nach dem Bau der Blockrampe ist empfehlenswert, um die Zielfischarten zu bestimmen, die ökologische Funktionsfähigkeit zu überprüfen und Lehren für die Konstruktion künftiger Blockrampen zu ziehen.

Für praktische Empfehlungen zur Wahl, Dimensionierung und konstruktiven Gestaltung von Blockrampen wird auf die Publikation *Blockrampen Normalien* (Hunziker *et al.* 2008) verwiesen.



Abb. 6 Randbereiche mit stark reduzierten Fliessgeschwindigkeiten an der Suhre (AG). Foto: Denise Weibel

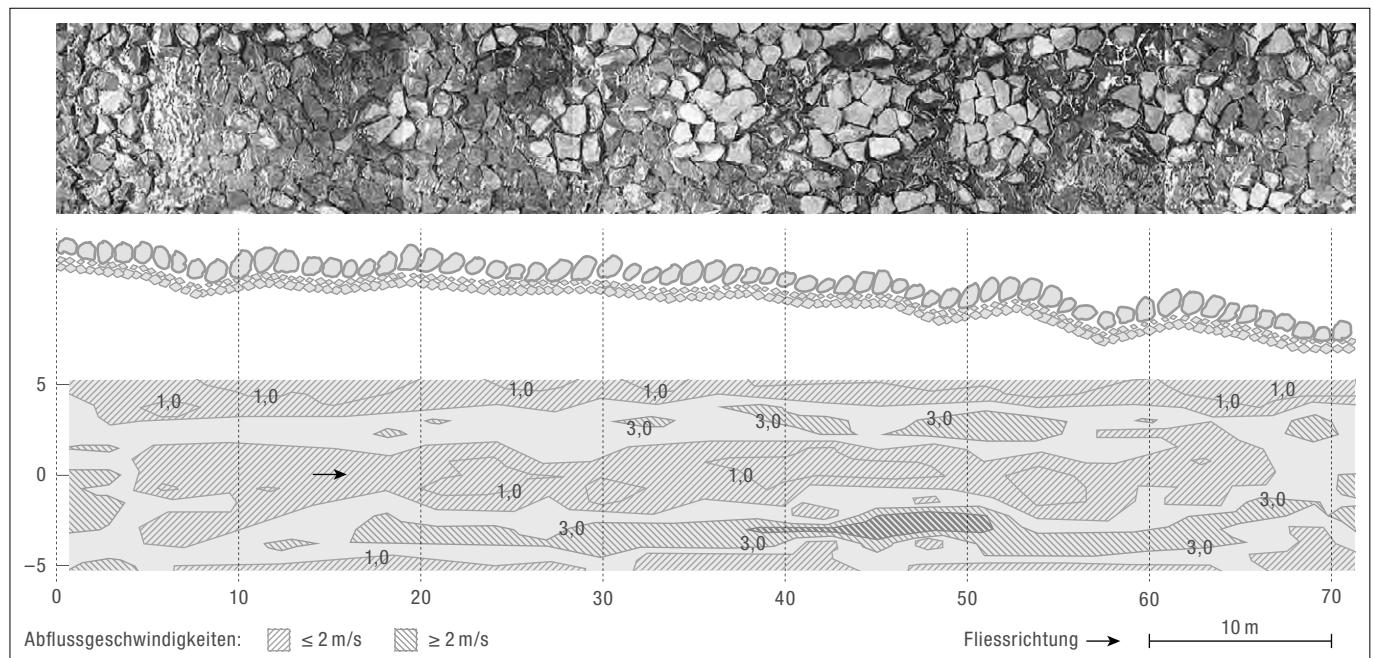


Abb. 5 Mäanderförmige Blockrampe (oben; Typ IV, 6%). Fliessgeschwindigkeiten in m/s für den spezifischen Abfluss von $1,5 \text{ m}^3/\text{s}/\text{m}$ (unten). Die orangen Bereiche umrunden Abflussgeschwindigkeiten $\leq 2 \text{ m/s}$. Graue Bereiche weisen Abflussgeschwindigkeiten $\geq 2 \text{ m/s}$ auf. Illustration nach Markus Studer

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APPENDIX 2

Lebensraumverbund Fliessgewässer: Die Bedeutung der Vernetzung

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Lebensraumverbund Fließgewässer: Die Bedeutung der Vernetzung

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Zusammenfassung

Die funktionelle Vernetzung von Flussgebieten spielt eine wichtige Rolle für aquatische und terrestrische Lebensgemeinschaften. Sie erlaubt eine Besiedlung der Habitate, den genetischen Austausch zwischen Populationen und führt zu einer zeitlichen Verknüpfung der Lebensräume zu unterschiedlichen Jahreszeiten, Tageszeiten oder Lebensphasen. Die strukturelle Vernetzung von Lebensräumen kann mit Erhebungen zur Ökomorphologie des Fließgewässers und einer Analyse des Vorhandenseins von künstlichen Barrieren erhoben werden. Der Grad der funktionellen Vernetzung kann mit drei Methoden quantifiziert werden – Fang markierter Individuen, Radiotelemetrie, oder mit Daten von genetischen Markern. Verschiedene Populationsmodelle beschreiben die Populationsstruktur und den genetischen Austausch zwischen Populationen am Fließgewässer. Insbesondere bei Metapopulationen und räumlich strukturierten Populationen muss darauf geachtet werden, dass die einzelnen Flussabschnitte gut vernetzt sind, denn das Ausbleiben von Ausbreitungsergebnissen würde räumlich fragmentierte Populationen voneinander isolieren und bei Metapopulationen langfristig zum lokalen Aussterben führen. Bei Arten, die in isolierten Einzelpopulationen vorkommen, ist vornehmlich darauf zu achten, diese Populationen lokal durch lebensraumverbessernde Massnahmen zu halten und zu fördern. Unsere Flusslandschaften sind weitgehend durch Barrieren unterbrochen. Es kommt ganz auf die Organismengruppe an, welche Strukturen effektiv als Barrieren fungieren. Künstliche Abstürze wirken als Barrieren für schwimm- und springschwache Fischarten und für kleine Größenklassen von Fischen, jedoch nicht notwendigerweise für aquatische Invertebraten. Künstliche Abstürze können durch den Bau von Blockkrampen für die Fischfauna durchgängig gemacht werden. Auch eine Entfernung von Eindolungen führt zur erhöhten Durchgängigkeit für Fische und andere aquatische Organismen. Bei Revitalisierungsprojekten ist insbesondere auf die Anbindung der Seiteneinmündungen zu achten, denn diese kann für den Erfolg von Revitalisierungsmassnahmen für verschiedene Organismengruppen ausschlaggebend sein. Für die Arten der Kiesbänke und der Auenstandorte ist es entscheidend, dass ihr Raumbedarf bei Revitalisierungsprojekten abgedeckt wird, und dass die revitalisierten Standorte vernetzt werden. Bei Revitalisierungsprojekten werden gute Erfolge erzielt, wenn die Vernetzung der zu revitalisierenden Standorte untereinander berücksichtigt wird, sowie deren Vernetzung mit naturnahen Standorten.

1. Was ist Vernetzung?

Flusssysteme bilden Netzwerke, in denen sich die Flussabschnitte gegenseitig beeinflussen (Poole, 2010). Kenntnis über die Vernetzung der Flusssysteme ist eine der Voraussetzungen, um lokale und regionale

Prozesse verstehen und voraussagen zu können.

Der Begriff Vernetzung beschreibt die Austauschprozesse und Interaktionen zwischen Habitaten; dazu zählen der Transport von Wasser, Geschiebe,

Energie, Nährstoffen, sowie der aktive oder passive Transport von Organismen (Woolsey et al., 2005; Kondolf et al., 2006). Wir verwenden diesen Begriff in Bezug auf Fließgewässer hier enger gefasst als Mass für den Transport bzw. die Wanderungsbewegungen aquatischer und terrestrischer, flussbegleitender Organismen.

Die vertikale Vernetzung beschreibt die Interaktionen zwischen dem Fluss und dem hyporheischen Interstitial, der kiesführenden Schicht unterhalb der Flusssohle (Malmqvist, 2002; Woolsey et al., 2005; Kondolf et al., 2006; Cote et al., 2009).

Unter lateraler Vernetzung bzw. Seitenvernetzung versteht man die Anbindung eines Fließgewässers via Ökoton, der Übergangszone zwischen Ökosystemen, an seine Auenhabitante und andere terrestrische Lebensräume (Bild 1). Die laterale Vernetzung von Flüssen mit dem Uferbereich und mit terrestrischen Habitaten spielt eine wichtige Rolle für den Austausch zwischen diesen Systemen (Baxter et al., 2005) sowie für einzelne Lebensphasen bestimmter Organismengruppen (z.B. Amphibien, aquatische Insekten). Eine Un-

Bild 1. Schematische Darstellung der Vernetzung in einer Flusslandschaft. 1. Longitudinale Vernetzung zwischen Abschnitten am Hauptfluss und zwischen Hauptfluss und Zuflüssen. 2. Laterale Vernetzung zwischen terrestrischen und aquatischen Ökosystemen. 3. Vertikale Vernetzung des Flusses mit dem Interstitial, dem Hohlräumsystem in den vom Fluss abgelagerten Sedimenten dicht unterhalb des Oberflächenwassers. Nach Malmqvist (2002).

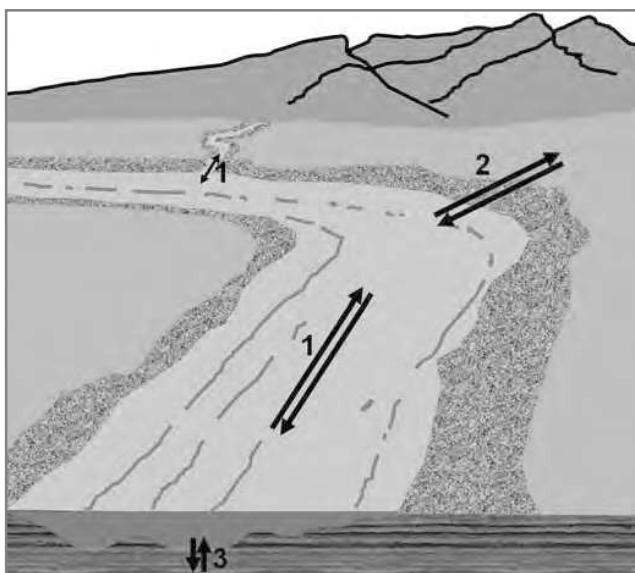




Bild 2. Beispiele für Habitatbeeinträchtigung in Flussökosystemen. A. Die stark verbaute Mündung des Lochrütibachs (Nidwalden) vor der Revitalisierung: der Bach fliesst über eine steil abfallende, betonierte Sohle in die Engelberger Aa – ein Beispiel für schlechte Vernetzung. B. Die gut vernetzte Brennoaue bei Loderio (Tessin). Gefangene Fischarten im April 2010: Bachforelle, Groppe, Alet, Südströmer, Elritze. C. Ein an die Brennoaue angrenzender, kanalisierte Flussabschnitt oberhalb mit den nachgewiesenen Fischarten Bachforelle und Groppe. Einher mit der Habitatdegradierung durch die Kanalisierung geht ein Verlust von Fischarten. Fotos: A: Armin Peter, B-C: Denise Weibel.

terbrechung der lateralen Vernetzung hat insbesondere negative Auswirkungen auf den Bestand von Fischen und Wirbellosen, deren Entwicklung vom seichten Flachufer (Fischlarven) mit grösseren Steinen (Eiablage von vielen aquatischen Insekten) abhängig ist (Woolsey et al., 2005; Bright et al., 2010).

Die longitudinale Vernetzung oder Längsvernetzung bezeichnet den Austausch mit den Lebensräumen flussaufwärts und flussabwärts innerhalb desselben Einzugsgebiets und zwischen Hauptfluss und Zuflüssen (Woolsey et al., 2005). Längsvernetzte Flusssysteme sind durchgängig für verschiedene Organismengruppen, ermöglichen die Wanderungsbewegungen von Tieren wie etwa der Bachforelle und die Samenausbreitung von Pflanzen. Die Längsvernetzung von Flusshabitaten ermöglicht eine Neugründung von Populationen und genetischen Austausch entlang von Flüssen, und ist somit entscheidend für die Populationsentwicklung vieler Organismen.

In Bezug auf die Vernetzung ist es wichtig, zwischen struktureller und funktioneller Vernetzung zu differenzieren. Habitate können rein strukturell miteinander vernetzt sein, etwa durch Korridore – Landschaftsstrukturen, die in der Theorie die Bewegung von Organismen von einem Habitat zum nächsten ermöglichen sollen. Die Habitate sind aber erst dann funktionell vernetzt, wenn diese Korridore tatsächlich von den Zielorganismen als Migrationsrouten angenommen werden. Für aquatische Organismen dient der Fluss selber mit seinen Haupt-, Neben- und Altarmen als Korridor, für terrestrische Arten hingegen die Alluvialzone – die Schwemmebene, in der Sediment abgelagert wird – sowie die Auenbereiche. Der Grad der funktionellen Vernetzung kann dabei in Abhängigkeit

von saisonalen Abflussschwankungen während des Jahres variieren.

2. Weshalb ist die funktionelle Vernetzung wichtig?

Die funktionelle Vernetzung von Flussökosystemen ist für die aquatischen und terrestrischen Lebewesen und Lebensgemeinschaften aus mehreren Gründen entscheidend. Die funktionelle Vernetzung ist einerseits die Voraussetzung für die Ausbreitung von Organismen in Flussgebieten. Besonders wichtig ist die funktionelle Vernetzung für Organismen mit schlechtem Ausbreitungspotenzial, wie aquatische Makroinvertebraten, die keine geflügelten Imaginalstadien bilden, oder für den kiesbankbewohnenden, kurzflügeligen Kiesbankgrashüpfer (*Chorthippus pullus*). So ist der Bachflohkrebs (*Gammaurus fossarum*) auf kleine Seitenzuflüsse mit viel Laubstreu angewiesen, die jedoch nur dann besiedelt werden können, wenn sie mit dem Hauptfluss vernetzt sind. Zum anderen spielt die funktionelle Vernetzung eine wichtige Rolle für die Verknüpfung von Habitaten, die zu unterschiedlichen Lebensphasen oder Jahreszeiten (bzw. Tageszeiten) von Organismen gebraucht werden (siehe Alp et al., diese Ausgabe).

So ist die Durchgängigkeit der aquatischen Lebensräume für Fische wichtig, die einen durchgängigen Wanderkorridor benötigen, weil sich ihre Lebensraumansprüche im Laufe ihres Lebenszyklus verändern (Northcote, 1998). Je nach Altersstadium suchen Fische unterschiedliche Habitate auf, um geeignete Nahrungsangebote oder Laichplätze zu finden. Zudem sind Fische auf kurzfristige Standortveränderungen angewiesen, um Schutz vor Fressfeinden und Konkurrenz zu suchen oder um ungünstigen Umweltbedingungen wie hohen Temperaturen

ausweichen zu können. Insbesondere an der Einmündung von Seitenzuflüssen ist eine intakte Vernetzung von Bedeutung. Nicht für Fische durchgängige Mündungen beeinträchtigen die saisonalen Fischwanderungen zu den flussaufwärts gelegenen Laichgebieten und verhindern die Besiedlung der Seitengewässer aus dem Hauptfluss (Bild 2a).

Die funktionelle Vernetzung liegt auch dem Konzept der Strahlwirkung zugrunde. Dieses besagt, dass naturnahe, ökologisch intakte Flussabschnitte positive Auswirkungen auf den ökologischen Zustand angrenzender, strukturell degraderter Flussabschnitte haben, denn die ökologisch weniger intakten Abschnitte können durch Migration von Pflanzen und Tieren aus dem naturnahen Gewässerabschnitt (»Strahlursprung«) besiedelt werden (Deutscher Rat für Landespflege, 2008). Ohne funktionelle Vernetzung sind solche positiven Beeinflussungen zwischen Flussabschnitten nicht möglich.

Viele Arten der Aue haben einen hohen Raumbedarf, und für die vollständige Durchführung ihres Lebenszyklus benötigen sie verschiedene Habitate oft in räumlicher Nähe, die miteinander vernetzt sein müssen. Amphibien benötigen etwa nicht nur Standorte wie Altarme zur Eiablage und Juvenilentwicklung, sondern auch solche, wo sie sich außerhalb der Reproduktionssaison aufhalten, wie etwa Hecken und Gebüsche beim Laubfrosch (Angelone et al., 2010).

Innerhalb von Auen bildet der Hauptfluss mit zahlreichen Neben- und Altarmen je nach Abflusssituation ein Netzwerk mit zeitlicher Dynamik. Eine Variabilität der Habitatstrukturen kann zur wiederkehrenden Besiedlung durch ein breites Artenspektrum führen. Umso wichtiger ist es, dass Auen als soge-

nannte Diversitäts-Hotspots gut mit den flussauf- und flussabwärtsgelegenen Gewässerabschnitten vernetzt sind und als Quellpopulationen funktionieren können. Kanalisierte Flussabschnitte können eine partiell durchlässige Barriere (»soft barrier«) für aquatische Arten darstellen. Sind Flussabschnitte durch kanalisierte Abschnitte isoliert, kann es in den direkt angrenzenden Abschnitten zu einer abrupten Verringerung der Artenzahl kommen. So wurden zum Beispiel in der untersten Aue des Brenno (Tessin) im April 2010 insgesamt fünf Fischarten gefangen (Bachforelle, Groppe, Alet, Südströmer, Elritze). Im monoton verbauten Abschnitt oberhalb der Aue wurden nur noch gerade zwei Arten nachgewiesen, nämlich Bachforelle und Groppe (Bild 2b,c).

3. Laterale Vernetzung: die trophische Verbindung zwischen Wasser und Land

Es ist aus vielen Studien bekannt, dass die Seitenvernetzung von aquatischen Habitaten mit dem Uferbereich eine wichtige Rolle für aquatische sowie terrestrische Organismen spielt und unter anderem trophische (d.h. Nahrungs-) Zusammenhänge zwischen verschiedenen Habitaten ermöglicht (Baxter et al., 2005). Viele Makroinvertebraten sind für ihre Nahrung auf Laubenträger durch die terrestrische Vegetation angewiesen. So sind etwa ins Wasser gefallene, terrestrische Insekten ein wichtiger Bestandteil der Nahrung der Bachforelle. Andererseits werden die geschlüpften Imagines der aquatischen Insekten von Vögeln, Eidechsen, Fledermäusen sowie anderen Prädatoren verzehrt. In ihrer Diplomarbeit an der Bünz hat Christina Baumgartner (2008) solche trophische Zusammenhänge untersucht und festgestellt, dass die Dichte der prädatorischen Uferarthropoden (Spinnen, Kurzflügler- und Laufkäfer) mit der Dichte der geschlüpften Imagines der aquatischen Insekten korreliert. Diese Zusammenhänge wurden ausserdem durch die Beschaffenheit des Uferbereichs beeinflusst. So konnte diese Arbeit auch zeigen, dass die Dichte bestimmter Prädatoren unter anderem durch die Vielfalt der Vegetation und die Länge der Uferlinie beeinflusst wird. Somit kann eine vom Menschen verursachte Unterbrechung der Seitenvernetzung negative Auswirkungen sowohl auf aquatische als auch terrestrische Lebensgemeinschaften haben und potenziell diejenigen Arten beeinträchtigen, die von der Vernetzung der Lebensräume abhängen; diese Ergebnisse bestätigen die Resultate einer früheren Studie (Iwata et al., 2003).

4. Migration, Genfluss und Populationsmodelle

Die Vernetzung zwischen Populationen der aquatischen und flussbegleitenden, terrestrischen Lebewesen beeinflusst auch den genetischen Austausch (den sogenannten Genfluss) zwischen Populationen. Genfluss findet statt, wenn Individuen sich in einer Population fortpflanzen, in welche sie eingewandert sind, und so zum Genpool beitragen, also zur Gesamtheit der Allele und Genotypen in einer Population. Andererseits hinterlassen viele Migrationsereignisse keine Spuren im Genpool, beispielsweise wenn die Migranten abwandern oder sterben, bevor sie sich fortgepflanzt haben. Da Arten unterschiedliche Ausbreitungskapazitäten haben und mehr oder weniger spezifisch in ihrer Habitatwahl sind, wurden mehrere theoretische Mo-

delle formuliert, um die Vernetzung einer Landschaft für Populationen zu beschreiben (Tab. 1) (Tero et al., 2003; Pollux et al., 2009). Abhängig von den lokalen Verhältnissen können verschiedene Populationsmodelle an unterschiedlichen Standorten für dieselbe Art gelten. So können manche Arten in einem Teil ihres Verbreitungsgebiets kontinuierliche Populationen bilden, in einem anderen Teil jedoch kleine, isolierte Bestände oder Metapopulationen aufweisen.

4.1 Isolierte Populationen

Entlang eines Flussabschnitts können die Populationen einer Art genetisch völlig isoliert sein; genetischer Austausch findet nicht statt. Dieses Populationsmodell gilt für extrem seltene Arten, die an Flussläufen in kleinen Beständen anzutreffen sind.

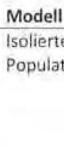
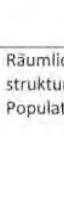
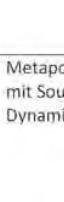
Modell	Schema	Beispiele	Priorisierung von Massnahmen
Isolierte Populationen		<ul style="list-style-type: none"> Tamariske im Schweizer Mittelland Kiesbankgrashüpfer am Inn in der Schweiz 	<ul style="list-style-type: none"> Förderung der Arten, dort wo sie noch vorkommen. Bei Pflanzen evtl. Erhaltungskulturen und Wiederansiedlungen, aber nur falls geeignetes Habitat vorhanden ist.
Räumlich strukturierte Population		<ul style="list-style-type: none"> Bachflohkrebs an der Sense Groppe an der Sense Schwarzpappel im Schweizer Mittelland 	<ul style="list-style-type: none"> Bestände müssen entlang der gesamten Länge des Flusses erhalten bleiben, damit keine Fragmentierung in isolierte Einzelbestände erfolgt. Longitudinale Vernetzung beachten
Metapopulation		<ul style="list-style-type: none"> Deutsche Tamariske am Vorder- und Alpenrhein (Graubünden, Sankt Gallen) Alpen-Knorpelsalat (<i>Chondrilla chondrilloides</i>) Kleiner Rohrkolben im Rheindelta (Österreich) Kiesbankgrashüpfer 	<ul style="list-style-type: none"> Soviele grosse Bestände einer Art wie möglich im Einzugsgebiet erhalten. Wenn immer möglich, Revitalisierungsmassnahmen nah bei existierenden Beständen durchführen, so dass neu zu besiedelnde Flächen geschaffen werden. Longitudinale Vernetzung beachten, evtl. Massnahmen zur Verbesserung Dynamik beachten
Metapopulation mit Source-Sink Dynamik		<ul style="list-style-type: none"> Tamariske am Ticino: Große Quellpopulationen im Oberlauf speisen kleine, flussabwärts gelegene Populationen. 	<ul style="list-style-type: none"> Bei Arten mit gerichteter Ausbreitung Quellpopulationen im Oberlauf erhalten und fördern Ansonsten dieselben Massnahmen wie bei Metapopulationen ohne Source-Sink Dynamik.
Kontinuierliche Population		<ul style="list-style-type: none"> Purpurweide Silberweide Eintagsfliege <i>Baetis rhodani</i> an der Sense (Bern, Fribourg) Schwarzpappel <i>Populus nigra</i> an der Rhone (Wallis) Tamariske im Einzugsgebiet des Schweizer Inn (Graubünden) 	<ul style="list-style-type: none"> Solange die Lebensräume weitgehend intakt sind, sind keine Massnahmen nötig. Ansonsten Massnahmen, die eine allgemeine Verbesserung der Lebensräume nach sich ziehen.

Tabelle 1. Populationsmodelle für terrestrische und aquatische Organismen der Flusslandschaften. Die Abbildungen folgen Tero et al. (2003) und Pollux et al. (2009).

4.2 Räumlich strukturierte Populationen

Wenn Gene und Individuen sich vornehmlich zwischen räumlich benachbarten Beständen bewegen, so spricht man von einem Austausch über Trittsteine (bzw. sogenannte «Stepping stones»). Diese Arten sind also keine guten Ausbreiter. Weil nur geringe Distanzen überwunden werden, haben die Arten, die diesem Muster folgen, meist räumlich strukturierte Populationen. Das heisst, an verschiedenen Flussabschnitten weisen diese Arten genetisch unterschiedliche Bestände auf.

4.3 Metapopulationsmodell

Wenn die Bestandsentwicklung einer Art von häufigem Erlöschen von lokalen Beständen und von Populationsneugründungen gekennzeichnet ist, spricht man von einer Metapopulation (Hanski, Zhang, 1993; Hanski, 1998; Hanski, Gaggiotti, 2004). Mehrere Arten der terrestrischen, flussbegleitenden Pflanzen bilden Metapopulationen (Tero et al., 2003; Jacquemyn et al., 2006; Honnay

et al., 2009). Bei Metapopulationen muss für das langfristige Überleben einer Art in einem Einzugsgebiet die Zahl der Neugründungen von Beständen das lokale Erlöschen von Beständen übersteigen. Dazu muss die longitudinale Vernetzung zwischen Habitaten gewährleistet sein. Altbestände und Flächen, auf denen sich neue Vorkommen etablieren können, sollten nicht zu weit voneinander entfernt liegen (innerhalb der mittleren Ausbreitungsdistanz der Art).

4.4 Metapopulation mit Source-Sink-Dynamik

Am Fluss ist es bei wasserverbreiteten Arten auch möglich, dass die Ausbreitung vermehrt flussab erfolgt. In diesem Fall stellen die Populationen flussaufwärts die einzige Quelle für die Gründung neuer Populationen dar. Wenn bestimmte Populationen vermehrt Migranten aussenden, und andere Migranten empfangen aber keine aussenden, so spricht man von einem «Source-Sink-Metapopulationsmodell» (Pulliam, 1988; Pulliam, Danielson, 1991).

Das Source-Sink-Modell stellt einen Spezialfall eines Metapopulationsmodells dar, mit Quellpopulationen, die Individuen aussenden und für die Besiedlung neuer Standorte verantwortlich sind, sowie Empfängerpopulationen, die Individuen empfangen, aber selbst nicht zur Gründung neuer Vorkommen beitragen. Dieses Populationsmodell ist für die Praxis höchst relevant, denn die Zerstörung der Quellpopulationen führt langfristig zum lokalen Aussterben von Arten innerhalb eines Einzugsgebiets. Andererseits kann man in diesem Fall Arten fördern, indem man sehr gezielt Ressourcen einsetzt, um das Bestehen der Quellpopulationen zu sichern und gleichzeitig die Vernetzung mit flussabwärts gelegenen Standorten sicher zu stellen.

4.5 Kontinuierliche Population

Wenn Bestände kontinuierliche Populationen mit räumlich ausgedehntem genetischem Austausch bilden, besteht für die Praxis kein Handlungsbedarf in Bezug auf Artenförderungsmassnahmen. Die Arten, die diesem Populationsmodell folgen, sind gute Ausbreiter, die neue Standorte über grosse Distanzen hinweg kolonisieren können. Viele dieser häufigen Arten können in der Regel auch dann von Revitalisierungsmassnahmen profitieren, wenn diese weit entfernt von anderen Beständen durchgeführt werden.

5. Welche Faktoren beeinflussen die Durchgängigkeit von Fließgewässern?

Die Vernetzung von Flusshabitaten aus Sicht der im und am Fluss lebenden Organismen wird durch natürliche und menschgemachte Barrieren beeinträchtigt. Ein Wasserfall stellt beispielsweise eine abrupte, ein klimatischer Gradient eine graduelle natürliche Barriere dar (Banarescu, 1990). Menschgemachte Barrieren sind vielfältig. Künstliche Abstürze und Schwellen zur Sohlenstabilisierung, Wehre, Staumäme oder Eindolungen fragmentieren den Gewässerverlauf und können Wanderhindernisse darstellen (Bild 3). Insbesondere eine Abschneidung der Seitenbäche durch künstliche Barrieren kann gravierende Auswirkungen auf die Artenzahl bei Fischen haben, denn die schwimm- und sprungschwachen Fischarten und kleine Individuen sind in nicht der Lage, Abstürze zu überqueren. An durch Barrieren abgetrennten Zuflüssen der Suhre wurde nur die Bachforelle nachgewiesen, an Bächen mit gut vernetzten Seiteneinmündungen hingegen drei oder mehr Fischarten (Am-

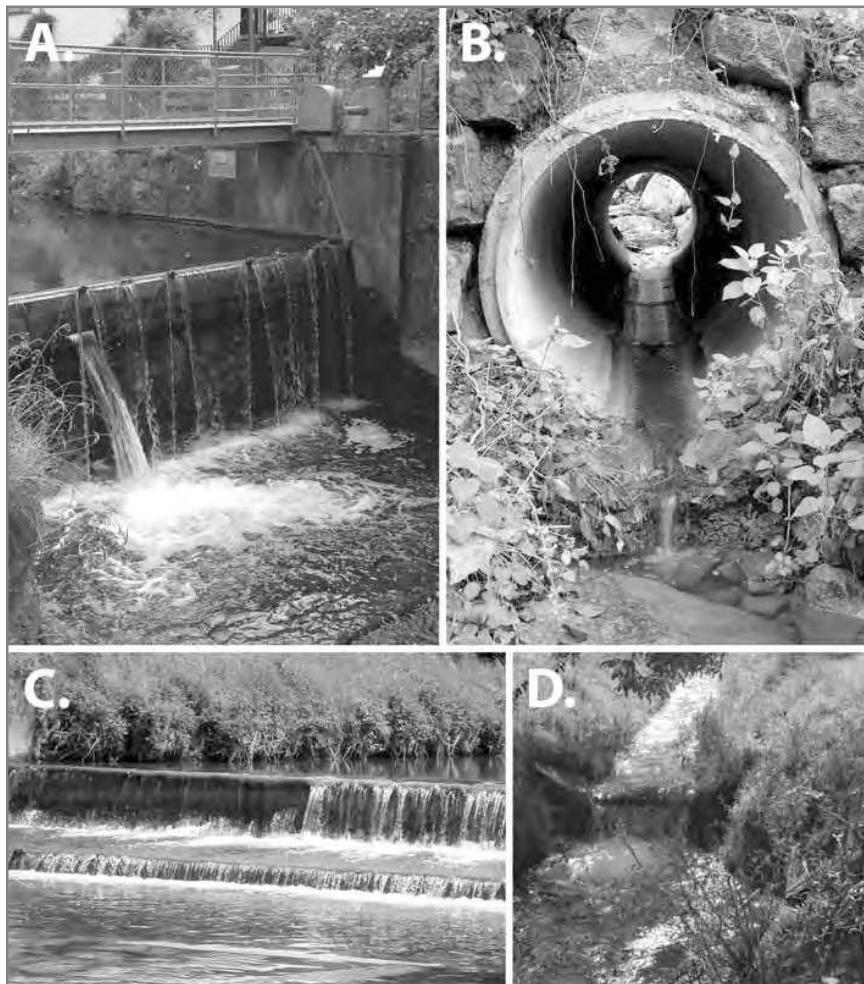


Bild 3. Die Durchgängigkeit in Fließgewässern wird durch künstliche Barrieren beeinträchtigt. A. Wehr. B. Eindolung. C. Absturz bei Sohlschwelle. D. Eine für Gruppen unüberwindbare Sohlstufe im Mülibach (Nidwalden). Fotos: Denise Weibel.

mann, 2006). Bei Fischen stellt somit die Mündung den wichtigsten Bereich für die Artenvielfalt im Gewässer dar.

Monoton verbaute, sehr schnell fliessende Flussabschnitte, sogenannte Schussrinnen, können ebenso als Barrieren («soft barriers») wirken wie punktuelle physikalische oder chemische Veränderung des Wassers aufgrund von Zuleitungen (z.B. Temperaturveränderung). Als Konsequenz einer Barriere wird die Wanderung von Fischen und aquatischen Invertebraten flussaufwärts behindert und ihre natürliche Ausbreitung begrenzt. Dabei kommt es auf die Organismengruppe an, welche Struktur eine Barriere darstellt. Ein mehrere Meter hohes Querbauwerk mag von Makroinvertebraten mit geflügelten Imagines problemlos überwunden werden, während sie die flussaufwärts gerichtete Migration der Fische sowie der flügellosen aquatischen Makroinvertebraten verunmöglich. Am Mülibach (Nidwalden) zeigte sich, dass sich eine kleine Sohlstufe von <1 m negativ auf den Gruppenbestand auswirken kann. Die Groppe als Fisch mit kleiner Springleistung fehlt im Streckenabschnitt oberhalb dieser Sohlstufe vollständig, während sie im gesamten übrigen Bach abundant war (*Bild 3d*).

6. Wie kann man die Durchgängigkeit messen und bewerten?

Es gibt eine Reihe Methoden, die es erlauben, die Durchgängigkeit von Flüssen für verschiedene Organismengruppen zu quantifizieren und Ausbreitungsdistanzen zu bestimmen. Fang- und Wiederfang markierter Individuen, Feldbeobachtungen der Organismenbewegung sowie populationsgenetische Analysen sind unter den wichtigsten Ansätzen für solche Untersuchungen.

Anhand von Versetzungsexperimenten lässt sich die Durchgängigkeit von potenziellen Wanderbarrieren für verschiedene Fischarten und Individuengrößen bestimmen. Hierfür werden oberhalb des Hindernisses lebende, markierte Fische unter das Hindernis versetzt, um anschliessend ihr Aufstiegsverhalten zu beobachten. Dafür eignen sich sowohl Reusen, die Fang-Wiederfang-Methode mit Markierung (z.B. Farbe) oder die Beobachtung mit individuellen, aktiven (Radiotelemetrie) oder passiven Sendern (PIT-tag). Auch bei grösseren Invertebraten wie Libellen können frisch geschlüpfte Imagines farblich markiert werden, um zu untersuchen, wie weit sie sich ausbreiten. Bei einer Studie der Zierlichen Moosjung-

Gruppe	Art	Distanz	Referenz
Insekten	Zierliche Moosjungfer (<i>Leucorrhinia caudalis</i>)	5 km	Keller et al. (2010)
Insekten	Kiesbankgrashüpfer (<i>Charthippus pullus</i>)	1 km	Ingrisch, Köhler (1998)
Mollusken	Schnecken	0,9-3 km	Kappes, Haase (2011)
Mollusken	Muscheln	10 km	Kappes, Haase (2011)
Amphibien	Kreuzkröte (<i>Bufo calamita</i>)	4 km	Mermod et al. (2010a)
Amphibien	Gelbbauchunke (<i>Bombina variegata</i>)	2 km	Mermod et al. (2011)
Amphibien	Laubfrosch (<i>Hyla arborea</i>)	0.75-1 km	Angelone, Holderegger (2009)
		1.5 km	Vos et al. (2000)
Amphibien	Geburtshelferkröte (<i>Alytes obstetricans</i>)	1.5 km	Mermod et al. (2010b)
Amphibien	Springfrosch (<i>Rana dalmatina</i>)	1 km	Lippuner et al. (2010)
Amphibien	Teichmolch (<i>Triturus vulgaris</i>)	1 km	Mermod et al. (2010c)
Amphibien	Kammolch (<i>Triturus cristatus, Triturus carnifex</i>)	1 km	Mermod et al. (2010c)
Amphibien	Fadenmolch (<i>Lissotriton helveticus</i>)	0.5 km	Meier (2003)
Fische	Nase (<i>Chondrostoma nasus</i>)	*140-*446 km	Steinmann et al. (1937)
Fische	Barbe (<i>Barbus barbus</i>)	318 km	Steinmann et al. (1937)
		22 km	Ovidio et al. (2007)
		20 km	Lucas, Frear (1997)
		9-10 km	Baras (1992)
Fische	Alet (<i>Leuciscus cephalus</i>)	*139-148 km	Steinmann et al. (1937)
Fische	Schleie (<i>Tinca tinca</i>)	*126 km	Steinmann et al. (1937)
Fische	Seeforelle (<i>Salmo trutta lacustris</i>)	126 km	Caviezel und Peter (2006)
Fische	Trüsche (<i>Lota lota</i>)	68-84 km	Breeser et al. (1988)
Fische	Rotauge (<i>Rutilus rutilus</i>)	*72 km	Steinmann et al. (1937)
Fische	Rotfeder (<i>Scardinius erythrophthalmus</i>)	*66 km	Steinmann et al. (1937)
Fische	Brachse (<i>Abrams brama</i>)	*58 km	Steinmann et al. (1937)
Fische	Hecht (<i>Esax lucius</i>)	*> 5 km	Steinmann et al. (1937)
Fische	Groppe (<i>Cottus gobio</i>)	12-48 m	Stahlberg-Meinhardt (1994), Downhower et al. (1990)
		318 m	Fischer (1999)
Pflanzen	Wasserverbreitung an grossen Fließgewässern	5-10 km	Müller (1955)
Pflanzen	Tamariske (<i>Myricaria germanica</i>)	*8-15 km	Werth, Scheidegger, unpubl. Daten
Pflanzen	Kleiner Rohrkolben (<i>Typha minima</i>)	50 km	Till-Botraud et al. (2010)

Tabelle 2. Ausbreitungsdistanzen verschiedener Arten und Artengruppen; *flussabwärts, †flussaufwärts.

fer (*Leucorrhinia caudalis*), einer Libellenart, wurde festgestellt, dass sich nur wenige Tiere über grössere Distanzen von mehreren Kilometern ausbreiten, die meisten Tiere jedoch in dem Bereich verweilen, wo sie bereits geschlüpft sind (Keller et al., 2010). Eine auf Fang- und Wiederfang markierter Tiere beruhende Studie zeigte Ausbreitungsdistanzen von bis zu 1.5 km für den Laubfrosch (Vos et al., 2000), und eine auf molekulargenetischen Untersuchungen beruhende Studie dokumentierte Wiederfänge in Distanzen von 0.75 km und 1 km (Angelone, Holderegger, 2009). Andere Amphibienarten haben eine ähnliche Reichweite. Fische hingegen können sich über sehr weite Distanzen bewegen, dokumentiert durch Fang- und Wiederfang und Radiotelemetrie. Im Einzugsgebiet des Alpenrheins wandert die Bodenseeforelle bis 126 km flussaufwärts, um sich im Vorderrhein fortzupflanzen (Caviezel, Peter, 2006). Auch andere Fischarten legen grosse Distanzen zurück, wie beispielsweise die Barbe und die Nase, doch es gibt auch standorttreue Arten wie die Groppe (*Tabelle 2*).

Auch mit populationsgenetischen Methoden ist es möglich, Aussagen über die Migration von Individuen und somit die Vernetzung zwischen Populationen zu machen. Wenn Populationen in einem Gebiet sich stark genetisch unterscheiden und wenn keine räumlich intermediären Popu-

lationen bei der Beprobung ausgelassen wurden, können einzelne Migranten detektiert und verschiedenen Populationen zugeordnet werden (Pritchard et al., 2000; Falush et al., 2003). Wasserverbreitete Pflanzenarten können oft grosse Distanzen überbrücken. Für die Tamariske wiesen wir mit molekulargenetischen Methoden eine klonale Ausbreitung über 15 km nach, und eine Ausbreitung derselben Art durch Samen über 8 km (*Tabelle 2*).

7. Vernetzung und Genfluss

Barrieren beeinflussen sowohl die Artenzahl im Fließgewässer als auch die Abundanz und den Genfluss einer Art; sie können sich stark auf die Genflussmuster der aquatischen und der terrestrischen, flussbegleitenden Arten auswirken. Wird der Genfluss für mehrere Generationen unterbunden, kann es vor allem bei in kleinen Populationen auftretenden Arten zu einer genetischen Differenzierung zwischen Teilpopulationen kommen. Bei grossen Populationen dauert es hingegen viele Generationen, bis eine genetische Differenzierung nachzuweisen ist (Hartl, Clark, 1997). Die Genflussmuster können mit verschiedenen genetischen Markern untersucht werden. Für solche Untersuchungen sind Mikrosatelliten besonders gut geeignet aufgrund ihrer hohen Mutationsrate, so dass oft gegenwärtiger Genfluss untersucht werden kann (*Box 1*). Im

Rahmen des Projekts «Integrales Flussgebietsmanagement» wurde die genetische Struktur von drei aquatischen und zwei terrestrischen Arten untersucht.

7.1 Populationsgenetische Struktur benthischer Makroinvertebraten an der Sense

An der Sense haben wir zwei benthische Makroinvertebraten mit unterschiedlichen Ausbreitungsstrategien untersucht. Eine dieser Arten war der Bachflohkrebs (*Gammarus fossarum*), der kleine Distanzen durch kriechen (flussabwärts und flussaufwärts) oder driften (nur flussabwärts) zurücklegt; diese Art wurde mit neun Mikrosatellitenmarkern untersucht (Alp et al., eingereicht). Die zweite untersuchte Art war die Eintagsfliege (*Baetis rhodani*), die sich als Larve wie der Bachflohkrebs ausbreitet, aber auch eine imaginalen fliegende Phase hat und somit Barrieren im Fluss überwinden kann; für diese Art wurden fünf Mikrosatelliten untersucht (Alp et al., eingereicht). Der ausschließlich aquatische Bachflohkrebs (Bild 4) zeigte viel weniger genetischen Austausch zwischen Populationen als die Eintagsfliege (Tabelle 3) und ist möglicherweise nicht nur in seiner Ausbreitung limitiert, sondern könnte auch an lokale Bedingungen angepasst sein. Das würde bedeuten, dass lokale Populationen des Bachflohkrebses einen zusätzlichen Wert für die Erhaltung der Biodiversität haben.

Dagegen scheint die Eintagsfliege in ihrer Ausbreitung im Sensegebiet nicht limitiert zu sein, sie bildet dort eine einzige, kontinuierliche Population. Die Barrieren im Fluss manifestieren sich bei beiden Arten nicht in der genetischen Struktur (Bild 5a, c).

7.2 Populationsgenetische Struktur der Groppe an der Sense

Die Groppe (*Cottus gobio*) hat eine durchschnittliche Grösse von 15 cm und lebt bodenorientiert. Sie hat eine reduzierte Schwimmblase und gilt als standorttreue oder eben rezidente Fischart. Je residenter eine Art ist, umso weniger Migration gibt es zwischen den einzelnen Populationen, was eine genetische Differenzierung zwischen diesen Populationen begünstigt. Als schwimmschwache Fischart kann die Groppe selbst kleinere Barrieren im Fluss nicht überwinden, so dass die Wanderung der Tiere flussaufwärts durch Barrieren verunmöglich wird.

Wir haben die populationsgenetische Struktur dieser Art in der Sense in den Kantonen Bern und Fribourg basierend auf zehn Mikrosatellitenmarkern

Mikrosatelliten, Allele, Loci, genetische Differenzierung

Mikrosatelliten sind kurze mehrfach wiederholte Motive auf der DNA, die sich in der Zahl der Wiederholungen und somit in ihrer Länge unterscheiden (Goldstein, Pollock, 1997). So kann beispielsweise ein Individuum eine genetische Variante (Allel) mit drei Wiederholungen der Basenpaare «CATG» tragen, (*CATG*)₃, und ein anderes Individuum kann auf derselben Stelle der DNA (Locus) ein anderes Allel besitzen, das fünf Wiederholungen besitzt, also (*CATG*)₅. Diese Längenunterschiede können entstehen, wenn bei der Replikation der DNA z.B. während der Zellteilung Wiederholungseinheiten übersprungen bzw. angehängt werden. Bei den meisten Mutationen ist eine einzige Wiederholungseinheit betroffen; sehr selten kann es passieren, dass gleich mehrere Wiederholungseinheiten angehängt oder entfernt werden (Weber, Wong, 1993; Goldstein, Pollock, 1997).

Für aussagekräftige genetische Studien werden meist mehrere Loci (sogenannte «Marker») untersucht. Wenn genügend Mikrosatellitenmarker untersucht werden, können genetisch unterschiedliche Individuen voneinander unterschieden werden, und beispielsweise die räumliche Ausdehnung von Klonen bei Pflanzen kann bestimmt werden. Selbst wenn man nicht vollständig zwischen Individuen unterscheiden kann, ist es vielfach möglich, einzelne Individuen anhand ihrer Kombination von Mikrosatellitenallelen einer bestimmten Population zuordnen. So können Migranten identifiziert werden. Die genetische Differenzierung zwischen Populationen wird mit dem Fixierungsindex F_{ST} angegeben. Ein Wert von 0 besagt, dass Populationen nicht differenziert sind, ein Wert von 1 gibt eine völlige genetische Isolation an (Hartl, Clark, 1997).

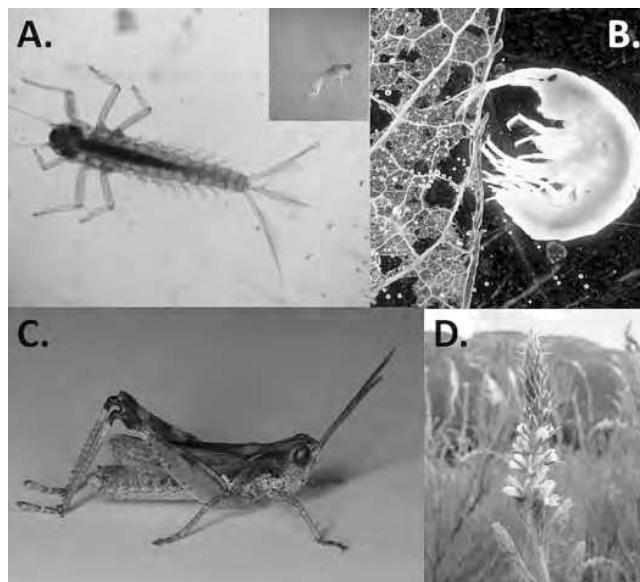


Bild 4. In den genetischen Studien untersuchte Arten.
A. Eintagsfliege (*Baetis rhodani*), Larve und geflügeltes adultes Tier (Foto: Maria Alp). **B.** Bachflohkrebs (*Gammarus fossarum*) (Foto: Maria Alp). **C.** Kiesbankgrashüpfer (*Chorthippus parallelus*) (Foto: Theresa Karpati). **D.** Tamarike (*Myricaria germanica*) (Foto: Silke Werth).

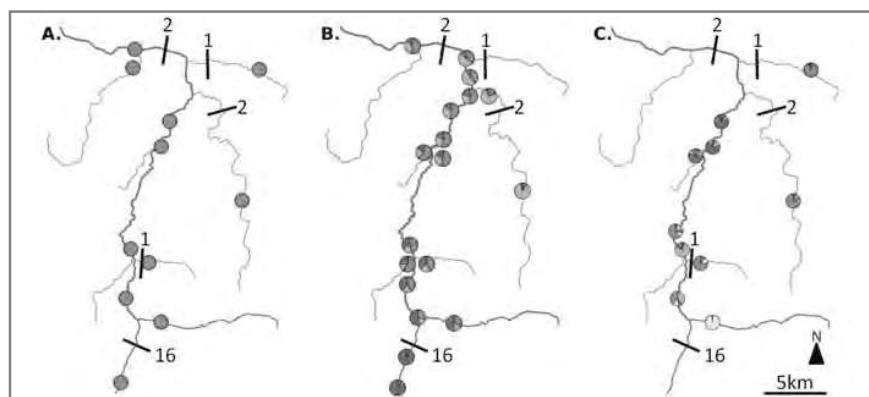


Bild 5. Populationsstruktur aquatischer Arten der Sense relativ zur Lage und Anzahl von Barrieren (schwarze Balken). Farben: die Zugehörigkeit von Individuen zu Populationen. **A.** Eintagsfliege. **B.** Groppe. **C.** Bachflohkrebs. Daten: A, C: Maria Alp; B: Julian Junker. Abbildung: Sonia Angelone.

Art	Fluss	Populationsstruktur	F_{ST}
Eintagsfliege	Sense	Kontinuierliche Population	-0.0006 ^{ns}
Bachflohkrebs	Sense	Räumlich strukturierte Population	0.2451 *
Groppe	Sense	Räumlich strukturierte Population	0.0614 *
Tamariske	Isar	Metapopulation	0.1226 *
Kiesbankgrashüpfer	Isar	Metapopulation	0.0309 *

Tabelle 3. Genetische Differenzierung (Box 1) zwischen Stichprobestellen an der Sense und an der Isar. Angegeben sind die Art, der untersuchte Fluss, die Populationsstruktur der Art, und der globale F_{ST} -Wert aus einer Analyse der Molekularen Varianz (F_{ST}); ns, statistisch nicht signifikant; *, statistisch signifikant.

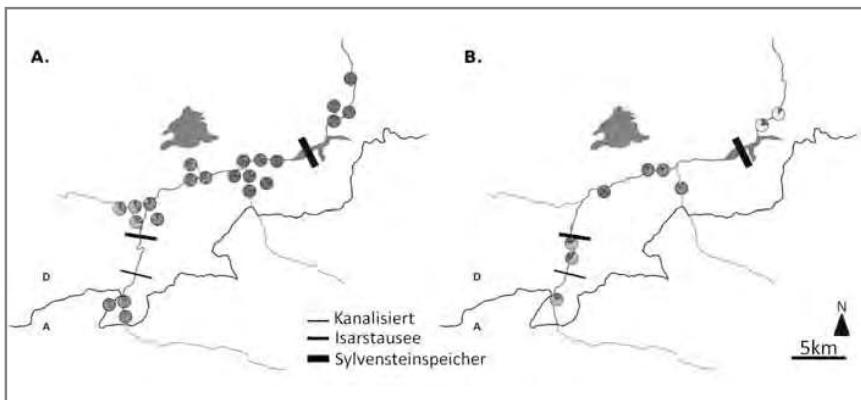


Bild 6. Populationsstruktur terrestrischer Arten der Isar im Grenzgebiet zwischen Deutschland (D) und Österreich (A), relativ zur Lage von Barrieren (schwarze Balken). Farben: Zugehörigkeit von Individuen zu Populationen. A. Kiesbankgrashüpfer. B. Tamariske. Daten: A: Theresa Karpati. B: Silke Werth. Abbildung: Sonia Angelone.

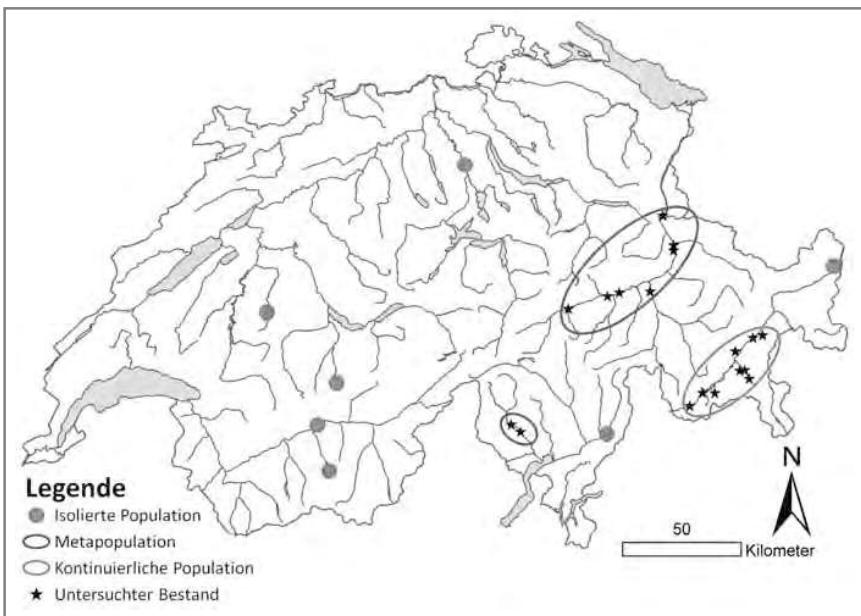


Bild 7. Populationsdynamik der Tamariske (*Myricaria germanica*) in der Schweiz, Quelle: Silke Werth.

untersucht (Junker et al., eingereicht). Weil die Art schwimmschwach ist, überraschte es nicht, dass zwischen den einzelnen Beprobungsstellen in der Sense eine deutliche genetische Differenzierung festgestellt wurde. Die genetischen Unterschiede zwischen Individuen von unterschiedlichen Standorten werden mit

zunehmender geographischer Distanz grösser. Allerdings fanden wir in einer weiteren Analyse, bei welcher wir den Einfluss der geographischen Distanz eliminiert hatten, ebenfalls eine positive Korrelation zwischen der Anzahl Barrieren und der genetischen Differenzierung zwischen den Standorten (Bild 5b). Die Populations-

struktur der Groppe in der Sense scheint insofern durch die Verbauungen beeinflusst zu werden (Junker, 2010; Junker et al., eingereicht). Die Groppe wies an der Sense eine relativ hohe genetische Differenzierung auf (Tabelle 3) und ebenfalls eine hohe genetische Diversität.

7.3 Populationsgenetische Struktur des Kiesbankgrashüpfers an der Isar

Der Kiesbankgrashüpfer (*Chorthippus parallelus*) ist eine in der Schweiz vom Aussterben bedrohte Heuschreckenart. Dieser Grashüpfer besiedelt Kiesbänke mit geringer Vegetationsdichte und hat als Kurzflügler nur ein geringes Ausbreitungspotenzial. Für diese Art stellten Staufen Barrieren für den Genfluss zwischen Populationen entlang der Isar dar (Bild 6a). Wir haben die populationsgenetische Struktur dieser Art mit fünf Mikrosatellitenmarkern an der Obern Isar in Deutschland untersucht (Karpati et al., in Vorbereitung). Der Flussabschnitt zwischen beiden Staufen fiel zwischen 1949 und 1990 jeden Sommer aufgrund von Ausleitungen trocken. Beim Kiesbankgrashüpfer wurde in diesem Flussabschnitt eine unerwartet grossräumige genetische Durchmischung nachgewiesen (Tabelle 3) und eine hohe genetische Diversität. Die geringen Abflussmengen förderten eine Vernetzung der Kiesbänke und somit auch die Durchmischung der Populationen dieser Art. Die seit 1990 vorgeschriebene Restwassermenge in der Isar führte hingegen zu einer zunehmenden Verbuschung der Kiesbänke, was für den Kiesbankgrashüpfer problematisch ist, da sein Lebensraum schrumpft.

7.4 Populationsgenetische Struktur der Tamariske

Die Tamariske (*Myricaria germanica*) ist ein den Vegetationstyp «Tamarisken-Weidengebüsche» (Moor, 1958) definierender Strauch, der in der Alluvialzone am Oberlauf von Fließgewässern vorkommt. Die Art ist heute aufgrund von Habitatverlust und mangelnder Dynamik im Zusammenhang mit der Begradigung und Verbauung von Flüssen in Mitteleuropa selten geworden. Die Tamariske pflanzt sich mit kleinen, flugfähigen Samen fort, die über Wind oder Wasser ausgetragen werden können; insofern hätten wir für diese Art hohen Genfluss erwartet und somit keine ausgeprägte Differenzierung zwischen Populationen innerhalb von Einzugsgebieten.

Wir haben diese Art mit 20 nukleären Mikrosatelliten untersucht (Werth,

Scheidegger, 2011). An der Oberen Isar in Süddeutschland fanden wir unterwartet eine deutliche genetische Differenzierung oberhalb und unterhalb von Stauseen, das heisst deutliche Unterschiede in der genetischen Zusammensetzung von Populationen (*Bild 6b*) (Werth et al., in Vorbereitung). Dies bedeutet, dass Stauseen für diese Pflanzenart schwer überwindbare Barrieren darstellen, obwohl die Tamariske dank ihrer durch Wind und Wasser verbreiteten Samen ein hohes Ausbreitungspotenzial hat. Die Art hatte eine relativ niedrige genetische Diversität, aber wies einen hohen Grad der genetischen Differenzierung auf, was typisch ist für Arten, die Metapopulationen bilden (*Tabelle 3*).

In der Schweiz zeigt die Tamariske am Oberlauf der Maggia und am Rhein Metapopulationen, während sie vor allem im Mittelland und im Wallis isolierte Populationen aufweist, und am Inn eine kontinuierliche Population bildet (*Bild 7*). Die Metapopulation an der Maggia haben einen Source-Sink-Charakter, wo die im obersten Bereich des Einzugsgebiets gelegenen Populationen die Quelle für Neubesiedlungen von Kiesbänken flussabwärts darstellen.

Am Schweizer Inn wiesen wir eine kontinuierliche Population für die Tamariske nach. Die genetische Diversität der Tamariskenbestände am Inn war sehr niedrig und liess darauf schliessen, dass die Art das Gebiet entweder durch einige wenige Individuen besiedelt haben muss, oder dass die Bestände durch einen so genannten «genetischen Flaschenhals» gegangen sein müssen bevor sie sich räumlich ausgedehnt haben (*Box 2*). In beiden Fällen gehen wir davon aus, dass die Tamarisken historisch vernetzt gewesen sein müssen, etwa dadurch, dass we-

Genetischer Flaschenhals und genetische Drift

Bei einem genetischen Flaschenhals sind Populationen über mehrere Generationen hinweg klein und verlieren viel ihrer ursprünglichen genetischen Vielfalt durch genetische Drift. Die genetische Drift ist eine durch Zufall bedingte Verschiebung der Allelfrequenz, bei der meist seltene Allele verschwinden, aber auch ursprünglich selten vorkommende Allele an Häufigkeit zunehmen können. Falls Populationen über viele Generationen hinweg klein sind, kann die genetische Drift zur Fixierung einzelner Allele in bestimmten Populationen führen.

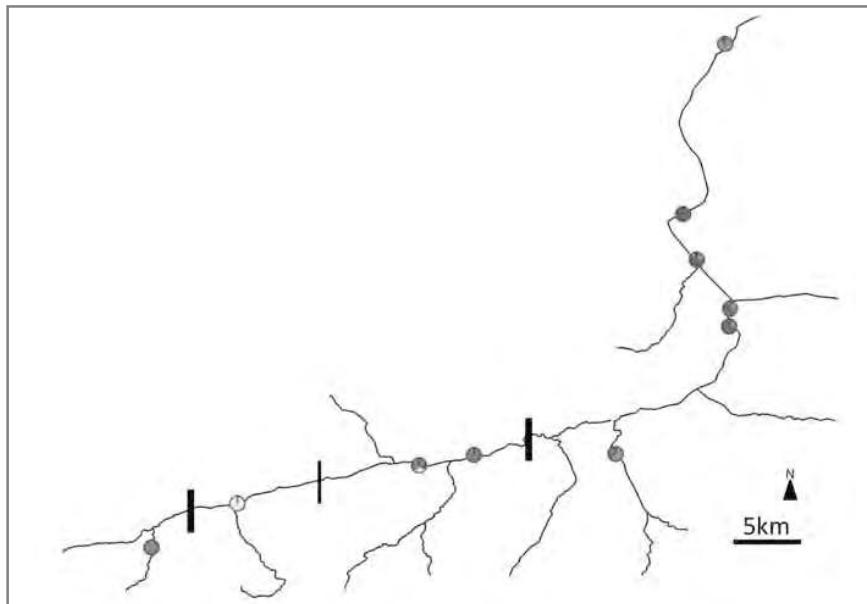


Bild 8. Populationsstruktur der Tamariske am Rhein in der Schweiz, relativ zur geografischen Lage natürlicher und anthropogener Barrieren (schwarze Balken, breit: Schluchten, schmal: kanalisierte Abschnitte mit wenigen Kiesinseln). Quelle: Silke Werth.

nige, eng verwandte Individuen das Gebiet besiedelten. Aufgrund dieser historischen Effekte ist die Diversität am Inn zu niedrig, um genetisch verschiedene Populationen nachzuweisen.

Unsere Ergebnisse für die Deutsche Tamariske vom Rhein in der Schweiz zeigen deutlich, dass auch natürliche Barrieren wie etwa Schluchten (dicke Balken, *Bild 8*) einen Effekt auf die genetische Struktur haben können – die lokalen Populationen der Tamariske wiesen deutliche genetische Unterschiede oberhalb und unterhalb dieser Barrieren auf, während der unterhalb gelegene Flussabschnitt, der keine Barrieren aufwies, die genetisch ähnlicheren Bestände hatte. Ein kanalisierte Flussabschnitt zeigte keine deutliche Barrierefunktion (schmaler Balken, *Bild 8*). Eine weitere Beobachtung war, dass die Tamariskenpopulationen im Unterlauf meist eine Mischung verschiedener genetischer Gruppen aufwiesen, während am Oberlauf häufig reine Vorkommen gefunden wurden. Dieses Ergebnis deutete an, dass eine Ausbreitung der Samen mit dem Wasser für diese Art eine wichtige Rolle spielen könnte.

8. Massnahmen zur Verbesserung der Vernetzung

8.1 Verbesserung der longitudinalen Vernetzung für die Fischfauna durch Blockrampen

Zur Wiederherstellung der Wanderkorridore für Fische bei Wehren und Dämmen

werden technische Fischtreppen oder naturnahe Umgehungsgerinne gebaut. Eine weitere Massnahme ist die Entfernung von Wanderhindernissen, zum Beispiel Wehre oder künstliche Abstürze. Im Kanton Aargau wurden die Kosten für die Beseitigung solcher Hindernisse je nach Gewässer auf 40 000 bis 100 000 Franken pro Meter Absturzhöhe geschätzt (Berner, 2006). Die Sanierung von Überfällen sollte nicht nach dem Zufallsprinzip erfolgen, sondern eine Priorisierungsanalyse über die zu entfernenden Hindernisse ist vorrangig durchzuführen (Zitek et al., 2007; Fahrni, 2011). Als Ersatz zur Sohlenstabilisierung werden bei der Entfernung von Überfällen Blockrampen gebaut. Eine Blockrampe ist eine mit Steinblöcken befestigte Fließgewässerstrecke mit erhöhtem Gefälle, welche die Fischgängigkeit ermöglichen soll. Verschiedene Faktoren sind entscheidend beim Bau von unterschiedlichen Blockrampentypen. Die Stabilität, insbesondere des Rampenfusses, muss bei einem Hochwasserereignis gewährleistet sein. Die Blockrampe, beziehungsweise ihr Gefälle, muss so dimensioniert sein, dass für Fische geeignete Fließgeschwindigkeiten und Wassertiefen entstehen. Als Richtwert wird in der Literatur eine maximale Fließgeschwindigkeit von 1.6 bis 2.0 m/s definiert (DVWK, 1996). Dabei muss allerdings beachtet werden, dass die Schwimm- und Springleistungen der einzelnen Fischarten voneinander verschieden sind. Es gilt, sowohl die im Gewässer vorkommende als auch die potentielle Fischfauna zu berück-

Blockkramptyp und Gefälle	Foto	Fischart	Aufstiegserfolg der markierten Fische	Bemerkungen
Dorfbach Oftringen • klassisch • 9.4 %		Bachforelle	▪ grosse Bachforellen: sehr gut ▪ kleine Bachforellen: eingeschränkt	Die Unterstände auf der Rampe werden von vielen Individuen als Habitat benutzt.
Wyna • klassisch-betoniert • 13.4 %		Bachforelle, Groppe	▪ grosse Bachforellen: sehr gut ▪ kleine Bachforellen: eingeschränkt ▪ Groppe: kein Aufstieg festgestellt	
Staffeleggbach • Becken- und Querriegelstruktur • 6.1 %		Groppe	▪ kein Aufstieg festgestellt	Geringe Fliessgeschwindigkeiten und Ruhebecken. Vertikale Abstürze von 15 cm werden von Groppen nicht überquert.
Sissle • strukturiert mit Querriegel • 3.6 %		Elritze	▪ kein Aufstieg festgestellt	Geringe Fliessgeschwindigkeiten. Weitere Experimente zum Verhalten der Elritzen nötig.
Glatt • klassisch • 8.9 %		Bachforelle; Cypriniden (Karpfenartige); Alet, Barbe, Gründling, Rotauge	▪ grosse Bachforelle: sehr gut ▪ kleine Bachforellen, grosse Alet, Barbe, Gründling: eingeschränkt ▪ kleine Alet, Rotauge: kein Aufstieg festgestellt	Sehr hohe Fliessgeschwindigkeiten.

Tabelle 4. Ausgewählte Resultate zur Erfolgskontrolle für den Fischaufstieg an Blockkrampen (kleine Individuen: <200 mm; grosse Individuen: ≥200 mm. Bewertung Aufstiegsrate: >75% sehr gut; 1-35% eingeschränkt).

sichtigen, welche sich nach Fischregion unterscheidet (Illies, 1961). An verschiedenen Blockkrampen wurden Erfolgskontrollen zum Fischaufstieg durchgeführt.

Fische wurden oberhalb der Rampe gefangen, markiert und unter die Rampe versetzt. Die Rückwanderung der markierten Fische über die Rampe bestimmte die Durchgängigkeit der Rampen für verschiedene Fischarten und deren Größenklassen (Weibel, Peter, eingereicht; Weibel et al., in Vorbereitung). Es zeigte sich, dass die Aufwärtswanderung je nach Fischart, Größenklasse der Individuen und Blockrampe unterschiedlich effizient ist (Tab. 4). Während die schwimmstarke Bachforelle auch über steile Rampen mit Gefälle >6% wanderte, hatten die Kleinfischart Groppe und die Cypriniden (Karpfenartige) Schwierigkeiten, solchen Rampen zu durchschwimmen. Auch für kleine Bachforellen war die Durchgängigkeit eingeschränkt. Gerade in der Aeschenregion, wo mehrere Fischarten vorkommen, soll das Gefälle der Rampen den leistungsschwächeren Cypriniden (z.B. Strömer, Nase, Gründling) angepasst werden. Es

zeigte sich, dass der Bau von Blockkrampen zur Wiederherstellung der Durchwanderbarkeit sinnvoll ist. Allerdings muss die Blockrampe an die jeweilige Fischzone angepasst sein. Unsere Ergebnisse zeigten, dass eine Blockrampe nur dann relativ steil gebaut sein darf, wenn die Bachforelle die einzige vorkommende Fischart ist. Um das ökologische Potential von Blockkrampen auszuschöpfen, sind Erfolgskontrollen über den Fischaufstieg empfehlenswert.

8.2 Vernetzung aquatischer und terrestrischer Ökosysteme bei Revitalisierungen

Bei Flussrevitalisierungen ist generell zu berücksichtigen, dass die revitalisierten Strecken mit möglichst naturnahen Flussabschnitten vernetzt werden. Besonders wichtig für die Vernetzung der Fliessgewässer ist eine Anbindung der Seitenzuflüsse (Ammann, 2006). Hier können oftmals mit geringem flussbaulichem Aufwand erstaunliche Ergebnisse erzielt werden, indem Einmündungen aufgeweitet werden, was die Durchgängigkeit für verschiedene Organismen verbessern

kann (Ribeiro et al., 2011). Eine Anbindung der Seitengewässer an artenreiche Hauptgewässer kann zu raschen Erfolgen führen, wie zu einer Erhöhung der Artenzahlen der aquatischen Fauna innerhalb kurzer Zeit. So wurde etwa die Anzahl der Fischarten des Liechtensteiner Binnenkanals durch die Vernetzung mit dem Hauptgewässer Alpenrhein im Zuge einer Revitalisierung von sechs Arten auf 16 erhöht (Bohl et al., 2004). Auch die Auenstandorte sollten durch Revitalisierungen miteinander vernetzt werden. Dabei ist auf den Raumbedarf vieler Auenarten zu achten.

Die Vernetzung von Fliessgewässern ist von massgeblicher Bedeutung, nicht nur für die Erhaltung und Wiederherstellung der typischen Artenvielfalt der Flusslandschaften, sondern auch für den Ablauf der natürlichen ökologischen Prozesse sowie für den Geschiebehaushalt. Die Wiederherstellung der Vernetzung der Fliessgewässer wird in den nächsten Jahren und Jahrzehnten im Fokus des Revitalisierungsgeschehens in der Schweiz stehen.

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- Schlüsselwörter**
Laterale Vernetzung, longitudinale Vernetzung,
- vertikale Vernetzung, Populationsgenetik, ge-netische Differenzierung, Bachflohkrebs (*Gam-marus fossarum*), Eintagsfliege (*Baetis rhodani*), Groppe (*Cottus gobio*), Kiesbankgrashüpfer (*Chorthippus pullus*), Tamariske (*Myricaria ger-manica*), Sense, Isar, Flussrevitalisierungen.
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Erklärung

gemäss Art. 28 Abs. 2 RSL 05

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Studiengang: Ecology and Evolution.....

Bachelor Master Dissertation

Titel der Arbeit: On the importance of longitudinal river connectivity for fishes

LeiterIn der Arbeit: Prof. Dr. Ole Seehausen

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetzes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

Luzern, 24. März 2014.....

Ort/Datum

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Unterschrift

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