universität wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Recruitment of 0+ fish in the main stem of the Danube River east of Vienna“

verfasst von / submitted by

Tobias Flor, BSc

angestrebter akademischer Grad / in partial fulfillment of the requirements for the degree of

Master of Science (MSc)

Wien, 2021 / Vienna, 2021

Studienkennzahl lt. Studienblatt / degree program code as it appears on the student record sheet:	UA 066 833
Studienrichtung lt. Studienblatt / degree program as it appears on the student record sheet:	Masterstudium Ecology and Ecosystems UG2002
Betreut von / Supervisor:	ao. Univ.-Prof. Dr. Hubert Keckeis

Table of Contents

Abstract

The world wide biodiversity crisis did not stop at the surface of the freshwater realm. Especially under threat are riverine fishes, as their natural habitats have been severely affected by anthropogenic degradation and exploitation. Riverine fish diversity and stocks are losing their most basic possibility to replenish by recruitment because spawning and nursery sites are getting scarce or are disconnected from regulation measures only improving navigation or flood control. As recruitment research was largely done in marine fisheries it is still necessary to fill in the white spots of drivers in large rivers, like the Danube. Here, in a free flowing section of the Danube River downstream of Vienna, Austria, this work surveyed recruitment as temporal and spatial variation of abundance and length of fish early stages. These were sampled before river engineering measures took place in 2007 and afterwards in both 2014 and 2017 in distinct mesohabitats located in an experimental section and two reference sections using a modified point-abundance-sampling (PAS) approach. A before-after-control-impact (BACI) design and linear mixed-effect modeling were applied for analysis. The results are discussed with regard to two important abiotic factors of discharge and water temperature. Temporal abundance variation was probably largely defined by the heavy impact of larger scale abiotic effects on the specific mesohabitat geomorphologies, whereas spatially low flow and depth bay mesohabitats were preferred by fish larvae. The enlargement of a gravel bar was revealed as the most valuable restoration measure for abundance, although longer term monitoring is needed to confirm a sustainable benefit for recruitment.

Zusammenfassung

Die weltweite Biodiversitätskrise hat nicht an der Oberfläche der Süßwasserwelt halt gemacht. Besonders bedroht sind Fluss-Fische, da ihre natürlichen Habitate schwer durch anthropogene Schädigung und Ausbeutung beeinträchtigt wurden. Die Diversität und die Bestände der Fluss-Fische sind durch die immer mehr eingeschränkten Möglichkeiten der Regeneration durch Rekrutierung bedroht, da Laichplätze und Jungfischhabitate durch Regulierungsmaßnahmen, welche nur Schifffahrt oder Hochwasserschutz verbessern, rar oder unzugänglich werden. Da die Rekrutierungsforschung größtenteils in der marinen Fischerei durchgeführt wurde, ist es noch notwendig, die weißen Flecken der Einflussfaktoren in großen Flüssen, wie in der Donau, zu füllen. Hier, in einem frei fließenden Abschnitt der Donau flussabwärts von Wien, Österreich, wurde in dieser Arbeit die Rekrutierung als zeitliche und räumliche Variation der Abundanz und Länge von frühen Entwicklungsstadien von Fischen untersucht. Diese wurden vor flussbaulichen Maßnahmen im Jahr 2007 und danach in den Jahren 2014 und 2017 in verschiedenen Mesohabitaten in einem Versuchs- und zwei Referenzabschnitten mit einem modifizierten Point-Abundance-Sampling-Ansatz (PAS) besammelt. Für die Beprobung wurde ein Before-After-Control-Impact-Design (BACI) und für die

Analyse eine lineare Mixed-Effect-Modellierung herangezogen. Die Ergebnisse werden im Hinblick auf die abiotischen Faktoren Durchfluss und Wassertemperatur diskutiert. Die zeitliche Variation der Abundanz wurde vermutlich weitgehend durch den starken Einfluss großräumiger abiotischer Effekte auf die spezifischen Mesohabitat-Geomorphologien bestimmt, während räumlich Bucht-Mesohabitate mit geringer Strömung und Tiefe von den Fischlarven bevorzugt wurden. Die Vergrößerung einer Schotterbank erwies sich als die wertvollste Restaurierungsmaßnahme für die Abundanz, obwohl ein längerfristiges Monitoring erforderlich wäre, um einen nachhaltigen Nutzen für die Rekrutierung zu bestätigen.

Introduction

The biodiversity in freshwater ecosystems is decreasing dramatically worldwide, with a speed highly elevated compared to the terrestrial realm (Albert et al., 2021; Collen et al., 2014; Dudgeon et al., 2006). Riverine fish species are most threatened and their rare and patchy distribution led to a higher extinction risk for small, more specialized and big anadromous species (Reynolds et al., 2005; Sheldon, 1988). The multitude of threats include loss and degradation of habitats, alien invaders, excess exploitation, pollution and climate change (Arthington et al., 2016; Dudgeon, 2019). In the temperate western hemisphere up to over a third of the freshwater fish species are imperiled, with increasing extinction rates which already have met species loss levels in tropical forest ecosystems (Freyhof & Brooks, 2011; Ricciardi & Rasmussen, 1999). The decline of riverine and especially rheophilic species was caused by the degradation and decoupling of shallow spawning and nursery sites, which are crucial for population success through reproduction and recruitment (Aarts et al., 2004; Keckeis et al., 1996; Pander et al., 2017; Schiemer et al., 2001).

In order to understand population dynamics, it is crucial to understand fish recruitment and its drivers, which still is not completely uncovered (Chambers & Trippel, 2012). Recruitment is defined as the amount of 0+ fish adding to a population each year after hatching, with the biggest hurdles being earlier stages than juveniles, which experience the highest mortalities (Cowan & Shaw, 2002; Humphries et al., 2019; King et al., 2013). Minor differences in the survival and growth can already result in fluctuations in the yearly recruitment over orders of magnitude (Cowan & Shaw, 2002). The abiotic and biotic factors influencing survival of fish larvae and recruitment are considered similar in marine and freshwater environments and include in streams spatial habitat heterogeneity, flow velocity and patterns, water temperature and depth, discharge, nutrient input, size and concentration of food and predators, fish species and traits, adult fish condition at spawning and abundance and behavior of adults and larvae (Cowan & Shaw, 2002; Humphries et al., 2019; Schiemer et al., 2001). High spatial heterogeneity or habitat structure is probably most important in shaping all other factors (Schiemer et al., 2001). The more heterogeneous a habitat is, the higher the probability is for an actual habitat being present where larvae and prey aggregate at the same time due to optimal conditions (Humphries et al., 2019). The dispersal to and the retention in such nursery sites makes connectivity of spawning and nursery sites a major issue (Schludermann et al., 2012). Only with increased swimming performance, spatial heterogeneity gets less important (Schiemer et al., 2001). Flow velocity and patterns are guiding dispersal and retention of not only fish larvae, but also food particles and prey. Water temperature is mainly shaped by geography and varies with specific water depth and throughout the season, hence fish larvae are found along a spatial and temporal gradient depending on developmental stage and species (Keckeis & Schiemer, 2002). Another important factor is nutrient input,

which, unlike in marine systems, is heavily influenced by terrestrial sources in running waters. Linked by primary production, nutrient input relates to reproduction of micro-zooplankton prey (Humphries et al., 2019). Abundance of appropriately sized food is especially important for the transition of feeding from endogenous yolk to exogenous food items. Enhanced food availability for larvae attracts predators which, together with density induced cannibalism, is the main reason for mortality in eggs and larvae (Cowan & Shaw, 2002). Predation pressure does not only decimate, but also can increase the ratio of food to larvae (Humphries et al., 2019).

The fish species as well as the structure and condition of the adult fish spawning population determines the hatch size and the yolk supply and therefore initial swimming performance for dispersal and time left after feeding transition to find appropriately sized food (Humphries et al., 2019; Keckeis & Schiemer, 2002). Adult fish compete over spawning grounds with suitable substrate and flow patterns, which makes space in streams a limiting factor (Cowan & Shaw, 2002). Hatched larvae are drifted downstream and disperse actively to inshore nursery grounds, where they encounter slow and stable flow and less turbulence (Schiemer et al., 2001; Schludermann et al., 2012). The larvae aggregate at shallow sites, such as sheltered bays, which act as flood refuges, preventing wash out and production sites of fine food particles and zooplankton (Schiemer et al., 2001; Winkler et al., 1997). During ontogenetic development, the requirements of larvae and juveniles change and so gradients in the nursery habitats and of the factors shaping recruitment are needed (Schiemer et al., 2001).

River regulation and engineering is forcing the exact opposite, creating homogenous river morphologies with less physical and structural gradients for optimal navigation, flood control and hydropower generation like in the Danube River (Weller, 2009). In the Danube and other European rivers the main and side channels are strongly regulated or degraded and a high number of threatened riverine species face a shortage of inaccessible spawning and nursery sites (Aarts et al., 2004). Such a lack of free flowing sections of sufficient length affect fish community structure (Braaten et al., 2008). Most vulnerable to such inadequate conditions is the rheophilic fish guild and migrating species which are hindered in completing their life cycles (Braaten et al., 2008; Kujawa & Glińska-Lewczuk, 2011). In the rivers Rhine, Meuse, Danube, Rhone and Larraun, regulation and channelization decreased, degraded and disconnected spawning sites. This had severe effects on riverine and rheophilic species in reducing their richness and the biomass and abundance of adult fish, restraining the recruitment base (Aarts et al., 2004; Oscoz et al., 2005). Regulation, damming and channelization reduces availability, number, size, types and quality of spawning and nursery sites, diminishing recruitment in riverine and rheophilic species like common nase (*Chondrostoma nasus* L., 1758) and changing larvae community structure in the remaining habitats (Jurajda, 1999;

Keckeis & Schiemer, 2002). By changing river flow dynamics when creating impoundments and cutting off floodplains, spawning and nursery sites become inundated or inaccessible by interrupting the dispersal of larvae, affecting the survival and recruitment negatively (Braaten et al., 2008; Jurajda et al., 2001). Longitudinal obstructions like dams were shown to decrease fish larvae abundance, to delay and shorten their temporal occurrence and reduce rare taxa (Song et al., 2019). River regulation measures can empower alien species like e.g. gobies which can decrease recruitment of native fish species by competition, predation and displacement (Qin et al., 2019; Ramler & Keckeis, 2019a). In the Danube River rheophilic specialists avoided sites occupied by invasive gobies (Ramler & Keckeis, 2019c). Riprap and other artificial, steep and linear shoreline types are avoided by fish larvae and at high flow and depth they would be washed out of such unsuitable habitats (Lechner et al., 2014; Schiemer et al., 2001). Through regulation, slow flow nursery sites are degraded to fast flow sites and larval densities drop dramatically when the flow velocity exceeds their swimming capabilities (Humphries et al., 2006; Keckeis & Schiemer, 2002). Low temperatures in temperate rivers decrease muscular performance while swimming, making altered flow conditions even more drastic for larvae (Hunt von Herbing, 2002). Gravel banks in regulated rivers with shore embankments are flooded under high water conditions resulting in high mortalities in larval communities (Humphries et al., 2006; Schiemer et al., 2001). Therefore recruitment of fish is highly influenced by river regulation and the patterns of low flow sites available which emphasizes the importance of heterogeneous river and shore morphologies (Humphries et al., 2006).

Most of the research in recruitment is done in marine systems and there is much less information on recruitment of fish in rivers (Cowan & Shaw, 2002) like the Danube. The free flowing stretch downstream of Vienna is inhabited by 80% of Austria's fish species (Tockner et al., 1998). Free flowing stretches play an important role in spawning and recruitment and should be prioritized for conservation and restoration (Wang et al., 2019). Important to consider when restoring spawning and nursery grounds are the course and the shores of the main channel and also tributaries and side arms (Kujawa & Glińska-Lewczuk, 2011). In contrast to channelized, fast flow sites, inshore low flow refuge areas enhance distribution and survival of e.g. larval rheophilic cyprinids (Keckeis & Schiemer, 2002). Especially rheophilic cyprinids are main target species for river restoration, because their eggs and larvae depend on near-natural interstitial and hydrological conditions to successfully develop and recruit (Duerregger et al., 2018). Such can involve sheltered bays and riparian vegetation, which when implemented in restoration measures, have a higher diversity and abundance of 0+ fish compared to still channelized sites (Langler & Smith, 2001). Eroded restored sites (Keckeis, 2014), steeply angled banks and rip-raps offer unfavorable flow conditions during most water

levels for fish larvae, but restored near-natural heterogeneous shores with shallow, flat angled bank sites and slow flow together with side arm reconnection where found to promote 0+ fish abundances (Pander et al., 2017; Ramler & Keckeis, 2019b; Villwock, 2016). Shoreline modifications back to a more natural state can also have negative impacts on invasive species, which makes it a powerful tool for restoration and supporting native populations (Ramler & Keckeis, 2019a). Lateral reconnection of gentle shorelines, secondary channels and other floodplain water bodies is generally agreed on to be the most powerful restoration measure with highly positive effects on 0+ and adult fish abundance and diversity mediated through connectivity and heterogeneity of depth and flow (Arthington et al., 2016; Grift et al., 2001; Grift et al., 2003; Sheldon, 1988; Tockner et al., 1998).

This study analyzed the abundance fluctuations of fish early stages within and among three non-consecutive years and different nurseries or mesohabitats in a still heavily regulated river section in a free flowing stretch of the Austrian Danube River. In such a large river 0+ fish abundance was shown to be an excellent indicator for surveying restoration projects, functional habitat quality and henceforth recruitment (Pander et al., 2017; Schiemer et al., 2001; Schiemer & Spindler, 1989). Restoration measures in this area aimed to recreate spawning and nursery sites or meso- and microhabitats suitable for spawning, successful growth and recruitment. The 0+ fish abundance in this study was compared before and after restoration measures were set and between sections and mesohabitats that were either restored or remained in their original state (BACI design; Smith, 2014). In order to better understand fluctuations in larval abundance, water temperature, discharge, larval length and developmental stage were included in the considerations. The actual measures surveyed in this study included modification of groynes and creation of a side channel for a more natural bank side flow, rip-rap removal, gravel bar extension and side arm reconnection at the upper confluent. It was expected that: [1] After restoration the improved suitability for 0+ fish of the mesohabitats within the experimental section should increase overall abundance in this section compared to previously similar reference sections. [2] The increased heterogeneity and connectivity in the modified mesohabitats should increase 0+ fish abundances therein. Opening the groyne roots will create a gentle sloping, shallow shore with a slow longitudinal flow. The new side channel shall provide protection from ship induced waves and offer low depth and flow microhabitats. The removal of rip-rap and the gravel bar extension will enlarge the near-natural shore area supporting more 0+ fish in future. Permanent reconnection of the side arm shall improve the connectivity and availability for rheophilic 0+ fish at every water level. [3] If the measures increased the habitat quality at nursery sites sufficiently, an increase in abundance should be sustainable and maintained over multiple years after restoration. These results will increase the knowledge about temporal and spatial variations in fish

recruitment between years and additionally reveal temporal dimensions within each sampling series in the main stem of a free-flowing section of this large River.

Material and Methods

Study site and river engineering measures

The Danube River is around 2850 km long, drains 805 000 km² and has a discharge of 6450 m^3s^{-1} at its delta. Originating in Germany it crosses 10 countries and three basins (Vienna, Pannonian and Dacian) until it reaches the Black Sea in Romania. This makes it the second largest river in Europe (Keckeis & Schiemer, 2002; Olariu et a., 2018). In the upper section of the Danube River (from the source at river kilometer 2850 to1750) 56 dams for hydropower generation significantly alter the formerly free-flowing river. Even the last three free-flowing stretches in this section are still heavily regulated, straightened and large parts of the shores are stabilized by rip-rap creating steep banks. One of them, downstream of Vienna to the Slovakian border, contains the largest floodplain and the biggest riparian forest of Central Europe and therefore was declared a National Park in 1996 (“Alluvial Zone National Park”) (Keckeis & Schiemer, 2002; Reckendorfer et al., 2005). At Hainburg the main stem of the river is roughly 300m wide and the 30-year mean (1981-2010) of the water level is about 278 cm with a mean discharge of 1930m^3s^{-1} (viadonau, 2012). The discharge regime in the upper section is pluvio-nival influenced (Stagl & Hattermann, 2015; Wimmer et al., 2012), and it reveals large, stochastically occurring variations within a year.

In 2005/2006 the pilot-project phase of the largest river restoration project of Central Europe, the Integrated River Engineering Project (IREP) started in this section in order to improve the situation for navigation and ecological conditions through a process oriented restoration program which included the evaluation of hydrological engineering and an interdisciplinary monitoring program (Klasz et al., 2009; Ramler & Keckeis, 2019; Reckendorfer et al., 2005). A before-after-control-impact design (BACI; Smith et al., 1993) with several sites (Conquest, 2000) was applied for the fish ecological program, where the pilot-project-stretch for the engineering measures at Bad Deutsch-Altenburg (BDA) was the experimental section (N, river km from 1884.5 to 1887.8) and two unchanged sections at Witzelsdorf (WITZ, river km 1892.6 to 1892.7) and Hainburg (HAIN, river km 1881.8 to 1882.9) served as simultaneously sampled reference sections (R and RN, respectively or R in general for reference) (Fig. 1). Because of an unforeseeable necessary river management intervention in November 2007, the section WITZ was replaced by HAIN. The section WITZ was thus only used in 2007, but was simultaneously sampled with HAIN in 2007 and then replaced by HAIN for 2014 and 2017. The mesohabitats (MH) in both sections were similar regarding the choriotopic structure, abiotic conditions and fish community characteristics (Loisl et al., 2014).

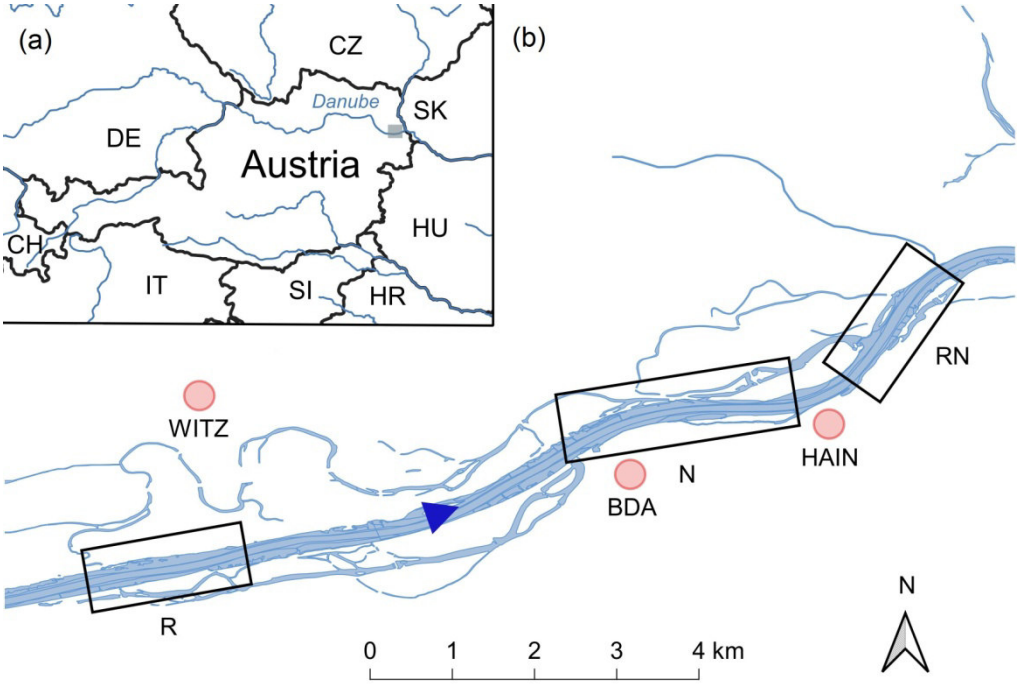


Fig. 1 (a) Map of Austria with the river Danube and the sampling area (gray square). (b) Map of the locations of the studied river sections (black rectangles) named after the villages closed by (red circles). R – reference, N – experimental, RN – reference new, WITZ – Witzelsdorf, BDA – Bad Deutsch-Altenburg, HAIN – Hainburg. Blue arrow indicates direction of flow.

Five different mesohabitat types were visually classified beforehand, mostly based on their structure and morphology, and examined: gravel bar (SB), groyne field (BU), side channel (BU_1), side arm (SA) and the upstream end of a newly constructed confluence of a side arm ("Johler Arm", SA_1) (Fig. 2). The mesohabitats represent natural river elements (except for the groyne field) and are highly dynamic areas which are strongly affected by erosion and deposition. Depending on the water level varying areas are emerged or they might be over-flown as a whole. Although groynes are mainly constructed to improve navigability, they have huge impacts in hydrological dynamics and on river biota. Depending on their angle to the shore and their height, they alter flow patterns, velocity, and contribute to sedimentation or erosion (Klasz et al., 2009). Therefore, they affect inshore fish habitats. The side channel of BU_1 was not present in either of the R sections because it was entirely constructed in N during the engineering measures. It is sheltered from waves by a gravel island in front, but still connected to the main channel. Flow and water depth are completely dependent on the water level of the River. This means that during low water large, dry areas and close to stagnant, shallow zones form, as well as during high water levels the complete flooding and over-flowing of mesohabitats. After the construction of the side channel, sampling was done within and not in the main channel. The SA at WITZ is built up by several islands and gravel bars, and can disappear under the water line during high water events. HAINs SA is the end of the cut off "Spittellauer Arm" and is just connected at its downstream end, therefore resembling a

bay character. The sampled SA behind a following island was included in this MH due to similar conditions. At BDA the SAs upstream confluence was not connected to the main channel any longer. It was almost dried up before the measures were set. After reconnection the new MH was called SA_1 (Tab. 1).

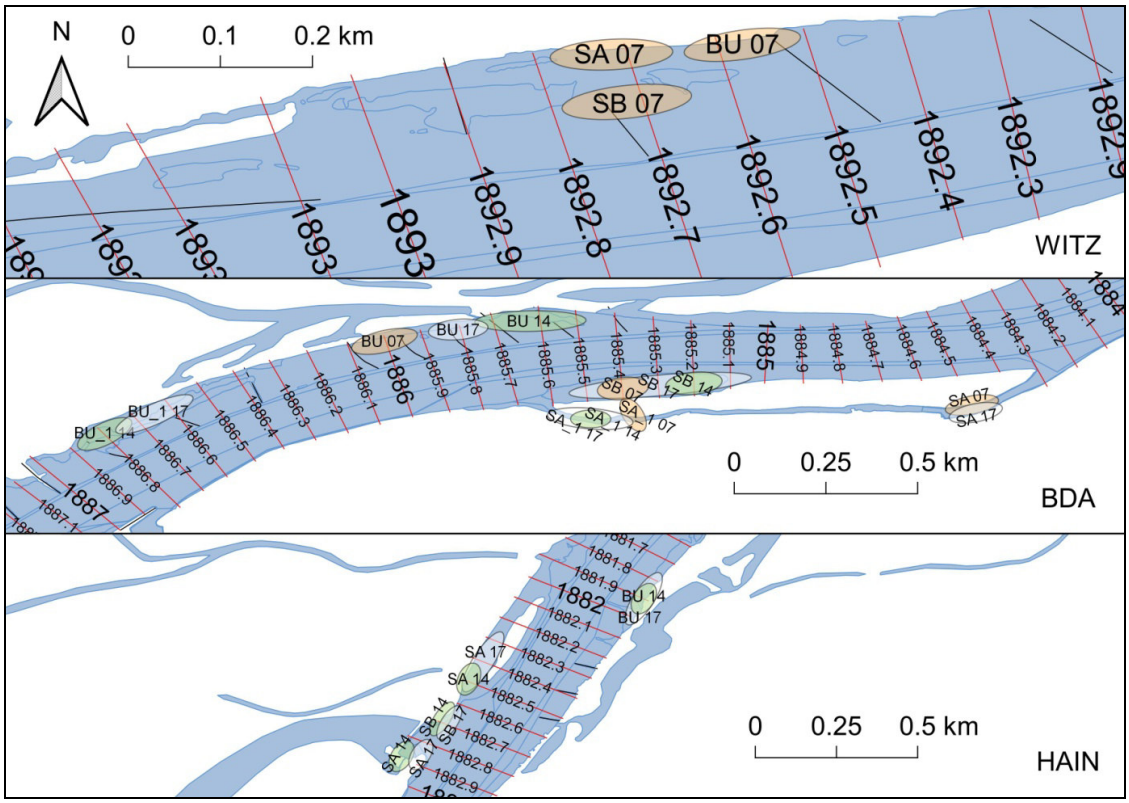


Fig. 2 Map of the mesohabitats (MH) in the three sections, in Witzelsdorf (WITZ, above), Bad Deutsch-Altenburg (BDA, middle) and in Hainburg (HAIN, below). Numbers on red lines represent river km. The number after each MH code points to the sampling year as well as the color (orange – 2007, green – 2014 and white – 2017). SB – gravel bar, BU – groine field, BU_1 – side channel, SA – side arm, SA_1 – side arm entry Johler Arm, WITZ – Witzelsdorf, BDA – Bad Deutsch-Altenburg, HAIN – Hainburg.

Tab. 1 Location (river kilometer) of the sampled mesohabitats within each section and year. SB – gravel bar, BU – groyne field, SA – side arm, N – experimental, R/RN – reference/reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures. SB, BU and BU_1 were located in the main channel.

Year	Section	SB	BU	BU_1	SA	SA_1
2007	R	1892.7	1892.6	-	1892.7	-
	N	1885.4	1886.0	-	1884.5	1885.4
2014	RN	1882.7	1881.9	-	1882.9 & 1882.5	-
	N	1885.2	1885.5-1885.7	1886.8	-	1885.5
2017	RN	1882.7	1881.8-1882.0	-	1882.3-1882.5 & 1882.8-1882.9	-
	N	1885.1-1885.5	1885.8	1886.6-1886.7	1884.5	1885.4-1885.6

The engineering measures were carried out between 2007 and 2012 (Ramler & Keckeis, 2018). The engineering measures set at BDA can be summarized in four packages (Fig. 3).

[1] Groyne modification I: All the stabilizing riprap as well as the inshore root parts of the groynes were removed. An approx. 500 m long gravel island was deposited which created a small side channel along the shore within the main stem. [2] Groyne modification II: Groynes were de-rooted from the shore to create a bank side flow and the rest was rebuilt in a declinant angle and lowered in height. At the bank itself the rip-rap was partly removed to create a berm. [3] Bank restoration: The rip-rap was completely removed and an already existing gravel bar in front of that was extended and enlarged. The affected area is basically a bigger island created by a former just periodically connected side arm. The shore further downstream of this area remained stabilized to prevent erosion. [4] Side arm reconnection: The above-mentioned side arm, called “Johler Arm”, was reconnected at its upstream end and is now permanently connected. These four measures were intended to initiate shore erosion and deposition dynamics with the natural substrate resulting in shallow and gradual rising shores, more natural flow patterns and better wave protection of especially 0+ fish habitats (Keckeis, 2014; Ramler & Keckeis, 2019a, 2019b).

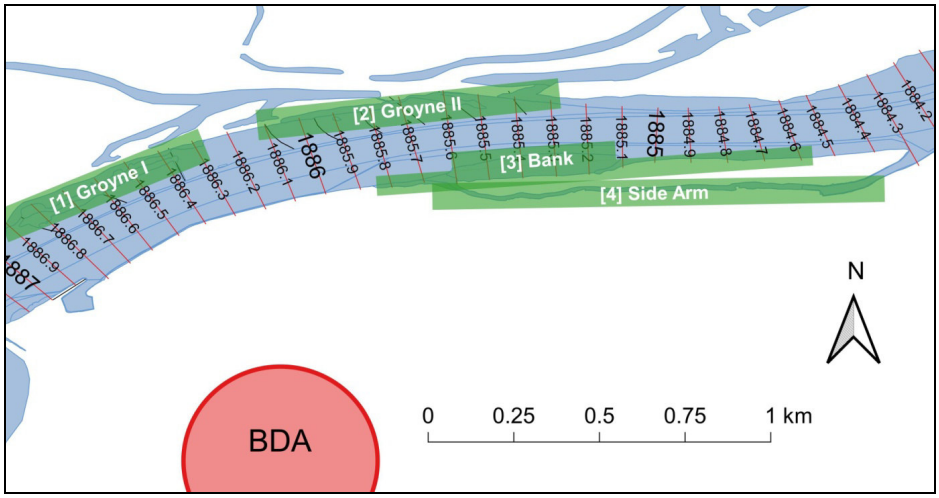


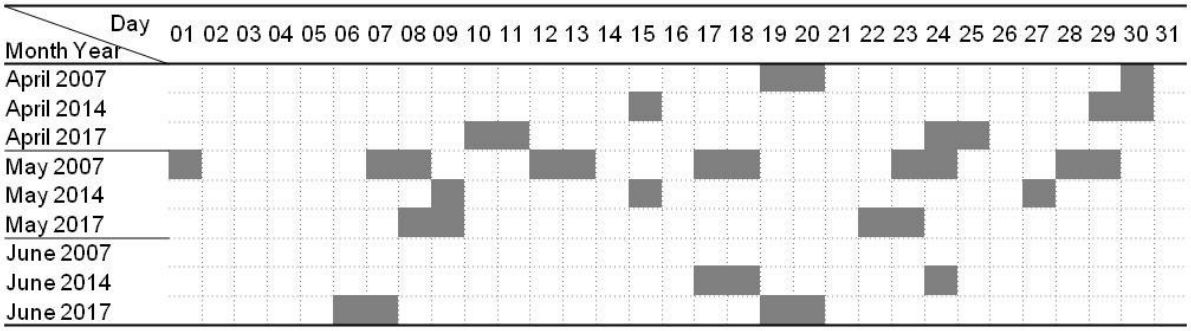
Fig. 3 Location of the four measures (green rectangles) taken in the experimental section Bad Deutsch-Altenburg (BDA). Numbers on the red lines in the river represent river km.

Sampling of early stages

Early stages of fish were sampled in 2007, 2014 and 2017 from April to June in infrequent intervals of two to 14 days (Tab. 2) during the period from the first occurrence to the end of June (April – June). A modified point-abundance-sampling (PAS) approach was used following Persat & Copp (1989). At every mesohabitat up to 30 samples (microhabitats, points) were taken with a dip net with a 2.5 m long wooden handle, the mesh size was 400 µm. The net opening was semicircular (width = 45 cm, height = 30 cm), the depth of the net was approx. 40 cm (Fig. 4). Moving the net in the water two to three times like an infinity sign filtered approximately a volume of 0.9 m^3. Additionally, at every sampling point water depth and flow velocity were measured with measuring stick and a flow meter (FLO-MATE 2000, Marsh-

McBirney Inc.®, Loveland, CO, USA). Water temperature was taken as well (WTW Cond 330i, Xylem Analytics GmbH & Co. KG, Weilheim, GER). Each sample was sieved with a 400 µm mesh, in order to collect and to transfer the fish larvae through a funnel into small glass tubes. The caught fish larvae were anesthetized with carbon dioxide from sparkling water and preserved in 95 % ethanol. In the lab, they were determined to the family level (Peňáz, 2001), and their total length was measured to the nearest mm using a Microscope (Nikon SMZ-U, Zoom 1:10, Nikon Corp., Tokyo, JP) with a camera (Nikon Digital Sight DS-Fi-1, Nikon Corp., Tokyo, JP) and an imaging software (NIS-Elements BR 3.00, SP6, Nikon Corp., Tokyo, JP).

Tab. 2 Overview of the sampling days in the different years. Gray denotes the sampled dates in the respective month and year.



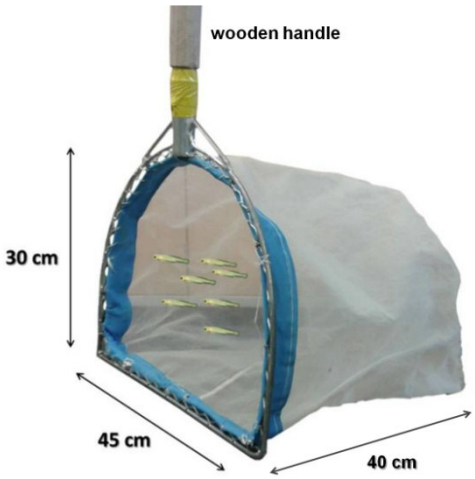


Fig. 4 Semi-circular shaped dip net used for point-abundance-sampling. Width is 45 cm, height 30 cm, depth of the net approx. 40 cm with a mesh size of 400 µm. The wooden handle is 2.5 m long. Changed after Villwock (2016).

Material and Methods

Statistical analysis

For statistical analysis, the abundance data were transformed using $\ln(x+1)$, in which x was the original value (McCune & Grace, 2002). Length data were transformed using $log10$. For tests on general influence of reference sections, R and RN (reference and reference new, respectively) were both coded as R only for the statistical analysis. To test whether there were differences in abiotic (temperature and discharge) or biotic variables (abundance and size) between the sampling years a Kruskal-Wallis test for global differences, and a post-hoc Dunn´s test (Dinno, 2017; Dunn, 1964) to assess the differences between single years was performed. The error rate of multiple pair wise comparisons was corrected using false-discovery-rate (FDR) (Benjamini & Hochberg, 1995). To distinguish the effects of river engineering measures and other factors on fish larvae abundances, a before-after-control-impact design was used. For this the river sections, as well as specific mesohabitats between sections were compared with each other. Linear mixed-effect models (Pinheiro et al., 2020; Zuur et al., 2009) were conducted to test for differences in sections and specific mesohabitats using abundance and total length as response variables, time (before – after) and section (control – impact) as predictors and year (2007 – 2014 – 2017) as random factor. Possible significant effects of the measures were revealed by the interaction term of time and section. For testing on differences in abundance within each sampling year, a generalized linear model with a following ANOVA was conducted. The model and family with the smallest deviance was chosen. Three factors were used: Section, mesohabitats and an interaction of both. Section and mesohabitats were both chosen to reveal within year differences. The interaction term was used to reveal a possible influence of the section itself on abundance by testing within section differences of mesohabitats. For every section within a year a post-hoc Dunn´s test was conducted to explore specific differences between the single mesohabitats. The level of significance, except for corrected values, was set to $p < 0.05$. For the statistical analysis, the program R version 3.6.1 (The R Foundation for Statistical Computing, Vienna, AT) was used. For graphs the programs IBM SPSS Statistics 26 (IBM Corp., Armonk, NY), SigmaPlot version 14.0 (Systat Software, Inc., San Jose, CA, USA) and Microsoft Excel version 1808 (Microsoft Corp., Redmont, WA, USA) were used.

Results

Abiotic parameters

The daily average water temperature during the investigation periods of the three years under study ranged from 8.4 to 22.1 °C, the overall average was 15.2 ± 3.5 °C. The maximum and minimum temperatures of 2007, 2014 and 2017, were 21.8 °C, 19.6°C and 22.1 °C and 8.4°C, 10.6°C and 9.6°C respectively, and the average temperatures within these yearly periods were 16.1 °C ± 3.5 °C, 14.6 °C ± 2.8 °C and 14.9 °C ± 4.0 °C (Fig. 5). The temperature in all three years increased gradually during the sampling period. The sampling series 2007 started as the coldest year in April, in the mid of April temperatures raised rapidly and then they were consistently higher compared to the other two years under study. Temperatures in 2014, at the beginning of April were comparatively high, but two pronounced drops occurred at the end of May and at the beginning of June. Comparable high temperatures were also observed at the beginning of April in 2017, but after the mid of April temperatures dropped down and until end of May, in which they were lower compared to the other two years under study. Temperatures rose again after this drop and gradually increased until the end of the sampling period.

The water temperatures of the years were significantly different (Kruskal-Wallis, $\chi^2 = 10.898$, df = 2, $p < 0.01$). A post-hoc Dunn´s test with FDR correction on water temperature revealed significant differences between 2007 and 2014 ($p < 0.01$) and between 2007 and 2017 ($p < 0.01$), but not between 2014 and 2017 ($p = 0.33$).

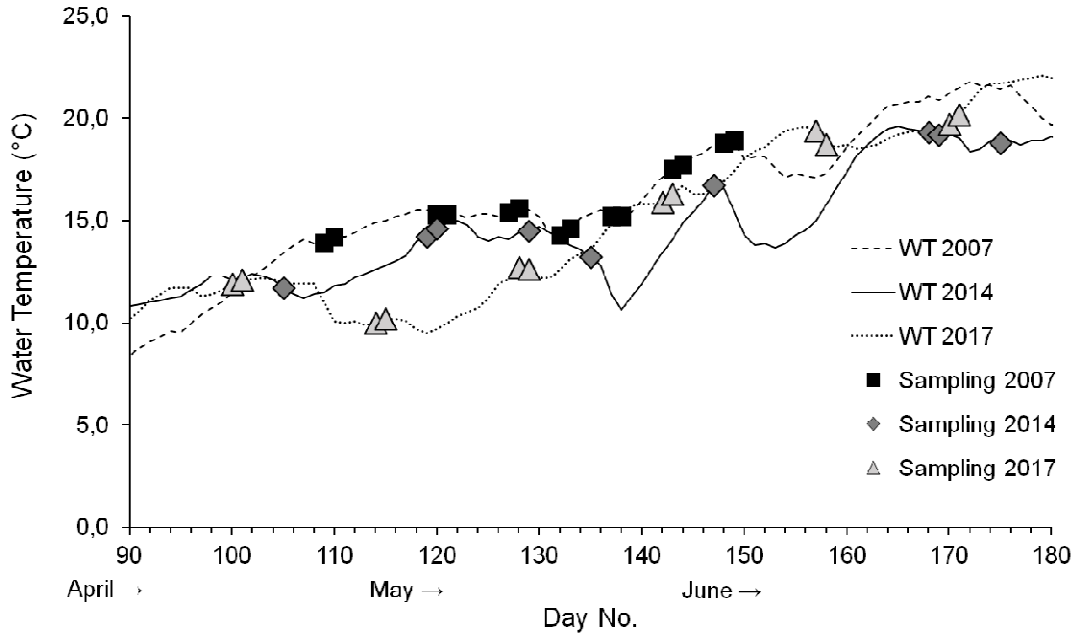


Fig. 5 Seasonal course of water temperature (daily means) at the water gauge in Hainburg from the different years under study. Days where samples were taken are marked with symbols. WT – water temperature. Data provided by viadonau (http://www.viadonau.org).

Results

The discharge in all sampling seasons ranged between 1090 m^3s^{-1} and 5246 m^3s^{-1} with an overall average of 1759.0 m^3s^{-1} ± 586 SD. The discharge in 2007 ranged from 1090 – 3801 m^3s^{-1} with a mean of 1579.6 m^3s^{-1} ± 387.28 SD. The discharge in 2014 ranged from 1143 - 5246 m^3s^{-1} (the maximum represents a yearly high-water event, HQ1) with a mean of 1836.9 m^3s^{-1} ± 772.70 SD. The discharge in 2017 ranged from 1240 - 3589 m^3s^{-1} with a mean of 1860.7 m^3s^{-1} ± 480.28 SD. Concerning discharge all three sampling periods started with comparatively low discharge, floods occurred during May until mid of June, and at the end of the sampling seasons the water level dropped down to a similar level between the three years under study. During the 2007 season, two moderate floods occurred in mid of May and at the beginning of June. The sampling period in 2014 also revealed two subsequent major high water events during the period of mid of May until beginning of June. The sampling period in 2017 had elevated discharge levels with two moderate floods at the beginning and mid of May. The majority of samples were taken during intermediate and low discharge levels (Fig. 6). In discharge there were significant differences between the sampled years (Kruskal-Wallis, $\chi^2 = 18.05$, df = 2, $p < 0.001$). A post-hoc Dunn´s test with FDR correction on discharge revealed significant differences between 2007 and 2017 ($p < 0.01$) and between 2014 and 2017 ($p < 0.05$), but not between 2007 and 2014 ($p = 0.034$).

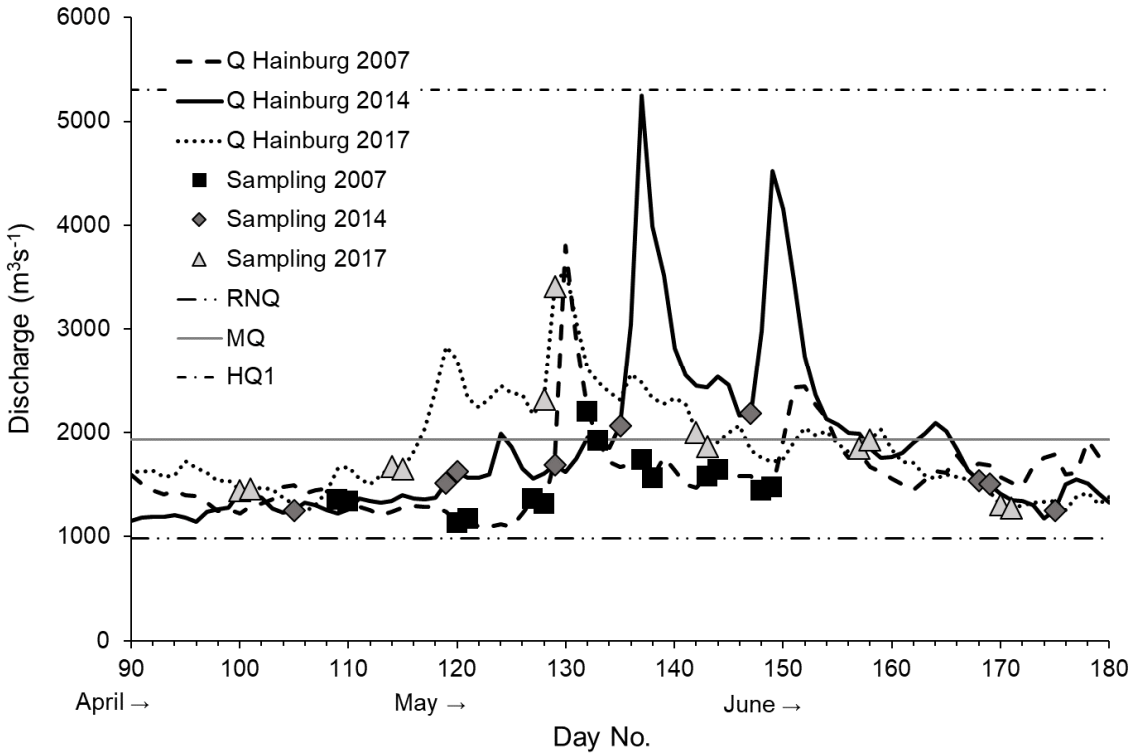


Fig. 6 Seasonal course of discharge (daily means) during the three years under study. Days where samples were taken are marked with symbols. Q Hainburg – discharge at water gauge Hainburg, The horizontal straight lines indicate navigationally important discharge levels of the Danube, where RNQ – lowest navigable discharge (980 m^3s^{-1}), MQ – mean discharge (1930 m^3s^{-1}), HQ1 – yearly Highwater event (5300 m^3s^{-1}). Discharge data made available by viadonau. Data provided by viadonau (http://www.viadonau.org).

Results

Individual number and catch composition

A total of 17977 individuals were caught, 4321 in 2007, 12892 in 2014, and 764 in 2017. In 2007 most individuals were caught in the groyne field mesohabitat with 2 times more in the reference section than in the experimental. The lowest individual number was caught at the gravel bars. Most individuals in 2014 were caught at the gravel bars in the experimental section, which was also the biggest catch of the survey, and with factor 3.7 less in the groyne fields and 3.5 times less in the side arm of the reference section. The numbers were very low for all other mesohabitats in this year. Most individuals in 2017 were caught in the side arm of the reference section and all other mesohabitats were low (Tab. 3). 5497 individuals from the total catch were identified composed of mainly Cyprinids (5460 individuals; 99.3 %) and then, in decreasing order, Gasterosteidae (18 individuals; 0.3 %), Percidae (9 individuals; 0.7 %), Gobiidae (6 individuals; 0.1 %), and Cottidae (2 individuals 0.03 %); 2 individuals were unidentifiable (0.03 %). The developmental stage by far most abundant in the catch was L2 (12701 individuals; 70.7 %), followed by, in decreasing order, L3 (2641 individuals; 14.7 %), L4 (1333 individuals; 7.4 %), L5 (715 individuals; 4.0 %), L1 (340 individuals; 2.0 %), L6 (125 individuals; 0.7 %), J1 (59 individuals; 0.3 %) and J2 (5 individuals; 0.03 %). In 55 individuals the stage was unknown (0.3 %).

Tab. 3 Sample size (n) and total number of individuals observed in each mesohabitat within the different sections. SB – gravel bar, BU – groyne field, SA – side arm. N – experimental, R/RN – reference/reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures. For N_BU_1 and N_SA_1 the data of N_BU and N_SA, respectively, act as base. SB, BU and BU_1 were located in the main channel.

Year	Section		SB	BU	BU_1	SA	SA_1
2007	N	Sample Size (n)	(190)	(190)	-	(95)	(95)
		No. of Ind.	77	1072	-	490	121
	R	Sample Size (n)	(190)	(190)	-	(189)	-
		No. of Ind.	30	2189	-	342	-
2014	N	Sample Size (n)	(276)	(90)	(90)	-	(79)
		No. of Ind.	8190	23	59	-	24
	RN	Sample Size (n)	(150)	(150)	-	(120)	-
		No. of Ind.	31	2202	-	2363	-
2017	N	Sample Size (n)	(180)	(180)	(180)	(75)	(105)
		No. of Ind.	42	4	99	17	13
	RN	Sample Size (n)	(176)	(178)	-	(330)	-
		No. of Ind.	13	46	-	530	-

0-catches were observed in an overwhelmingly large number (2909 catches; 83.7 %). The majority of catches revealed 1-10 individuals (445 catches; 12.7 %), and catches with higher number of fishes were less frequent. The absolute frequency of 0-catches in 2007 was 914

(80.3 %), in 2014 749 (78.4 %) and 2017 1246 (88.8 %). The absolute frequency of catches with 1-10 individuals in 2007 was 168 (14.8 %), in 2014 138 (14.5 %) and in 2017 139 (9.9 %). The absolute frequency of catch sizes between 11-100 individuals in 2007 was 45 (4.0 %), in 2014 45 (4.7 %) and 2017 19 (1.4 %). The absolute frequency of catch sizes between 101 and 1000 individuals in 2007 was 12 (1.1 %), in 2014 19 (2.0 %) and in 2017 there were no such big catches. Only in 2014 4 catches (0.4 %) containing 1001- 3000 individuals were observed (Fig. 7).

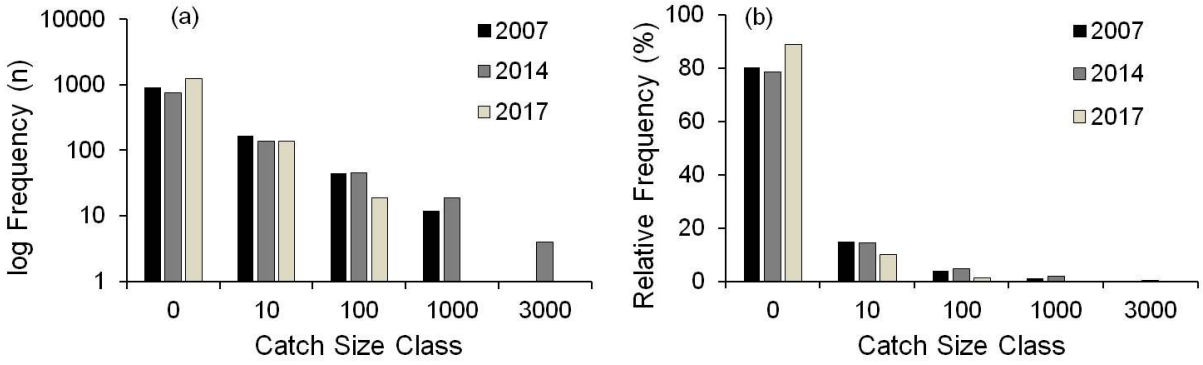


Fig. 7 Frequency distribution of catch sizes of the three surveys. (a) absolute frequency (note logarithmic scale of y –axis) and (b) a relative frequency. 0-catches by far dominate both distributions.

Spatio-temporal patterns of abundance

First larvae appeared in the middle to end of April. The temporal course of abundance revealed a bi-modal pattern. After a fast increase in abundance the values tended to decrease in May and a second increase in mid of June could be observed in 2014. The temporal distribution of fish larvae abundance showed a more similar pattern for 2007 and 2014, whereas it was different in 2017. In 2007 first larvae occurred end of April and abundance increased to mid of May followed by a decrease until the beginning of June. In 2014 first larvae occurred mid of April and abundance increased fast to mid of May followed by a slow decrease to mid of June. There was a second increase towards the end of June. In 2017 first larvae occurred mid of April, but earlier than the sampled years before. There was a low increase in abundance to the mid of May which then stayed constant until end of June (Fig. 8).

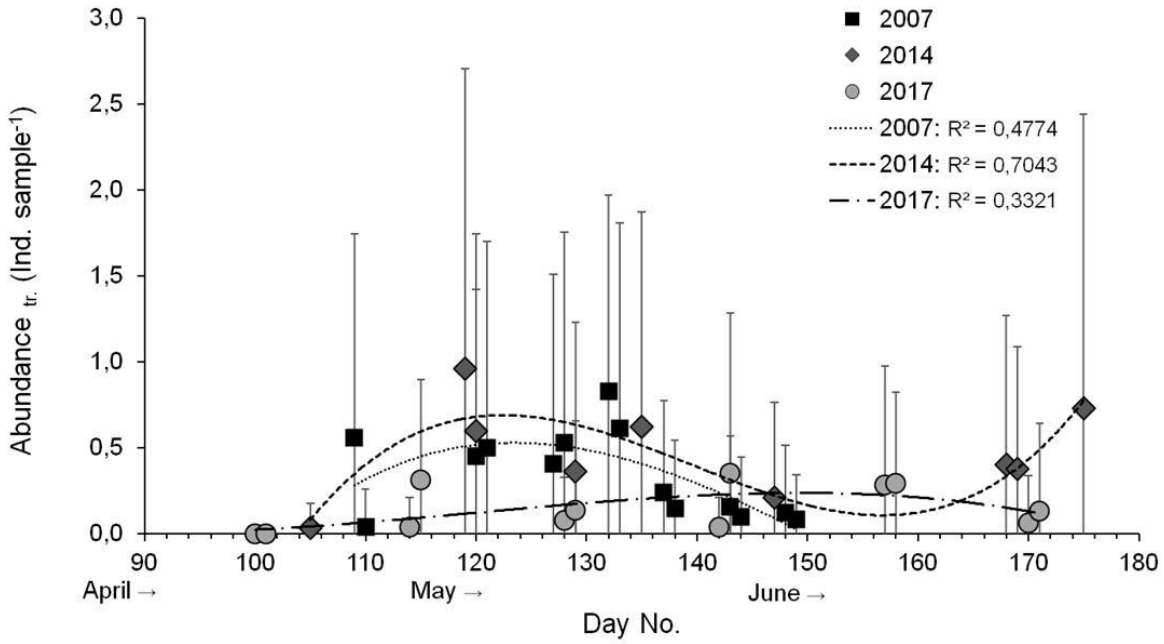


Fig. 8 Seasonal course of fish larvae abundance of three different survey years. The dotted lines indicate the temporal course for the single years (fitted third grade polynomial functions). Data shows means ± standard deviation of transformed values.

Between years the overall abundances of fish larvae were highest in 2014 and lowest in 2017 (Fig. 10a). In abundance there was a significant difference between all years (Kruskal-Wallis, $\chi^2 = 62.37$, df = 2, $p < 0.001$). A post-hoc Dunn´s test with FDR correction on abundance revealed no significant differences between 2007 and 2014 ($p = 0.10$), but between 2007 and 2017 ($p < 0.001$) and 2014 and 2017 ($p < 0.001$). Taking the sections into account, again 2014 showed the highest abundances and 2017 the lowest.

The abundance within each sampling year between the sections in 2007 was not significantly different (GLM, $p = 0.756$), whereas in 2014 it was almost significantly different (GLM. $p = 0.084$) and in 2017 it was significantly different (GLM, $p < 0.001$). The within-year abundance between the mesohabitats was significantly different for all years under investigation (GLM, all $p < 0.001$). The interaction term, indicating an influence of the section itself on the abundance in each mesohabitat was significant for 2007 (GLM, $p < 0.001$), 2014 (GLM, $p < 0.001$) and 2017 (GLM, $p < 0.01$) (Tab. 4). The abundance in 2007 in the experimental section was highest and similar in the groyne field and the side arm and lowest in the gravel bar (Fig. 9a). In abundance most of the mesohabitats were significantly different, except for side arm and groyne field and side arm and upper confluence of the side arm (Tab. 5a). The abundance in the control section of 2007 was highest in the groyne field, whereas gravel bar and side arm were low (Fig. 9b). The abundance in every mesohabitat pair except for side arm and gravel bar was significantly different (Tab. 5b). The abundance in the experimental section of 2014 was highest in the gravel bar, whereas groyne field, side channel and upper confluence of the side arm were low (Fig. 9c). The abundance in the mesohabitat pairs groyne field and gravel bar, side channel and gravel bar and upper confluence of the side arm and gravel bar

were significantly different to each other (Tab. 5c). The abundance in the control section of 2014 was highest in the side arm, intermediate in the groyne field and lowest in the gravel bar (Fig. 9d). Concerning abundance, all mesohabitats were significantly different to each other (Tab. 5d). The abundance in the experimental section of 2017 was low in all mesohabitats, with the groyne field being the highest (Fig. 9e). In terms of abundance, just the groyne field and the side channel were significantly different to each other (Tab. 5e). The abundance in the control section of 2017 was highest in the side arm and low in the groyne field and gravel bar (Fig. 9f). Regarding abundance, just the mesohabitats groyne field and gravel bar were not significantly different to each other (Tab. 5f).

Tab. 4 Results of the ANOVA on the GLM (generalized linear model) on transformed abundances of within section mesohabitat differences per year. Significant p-values are marked bold. Factors: sections, MH and Sec x MH – effect of sections on abundance in MH. Sec – section, MH - mesohabitats.

predictor	DF	Deviance	Resid. DF	Resid. Dev.	F-value	p-value
2007						
Section	1	0.081	1137	963.47	0.105	0.756
MH	3	70.546	1134	892.93	30.481	**<0.001**
Sec x MH	2	19.609	1132	873.32	12.709	**<0.001**
2014						
Section	1	3.794	953	1298.5	3.001	0.084
MH	4	50.638	949	1247.9	10.013	**<0.001**
Sec x MH	1	49.289	948	1198.6	38.985	**<0.001**
2017						
Section	1	5.216	1402	323.04	23.565	**<0.001**
MH	4	11.469	1398	311.57	12.953	**<0.001**
Sec x MH	2	2.567	1396	309.00	5.799	**<0.01**

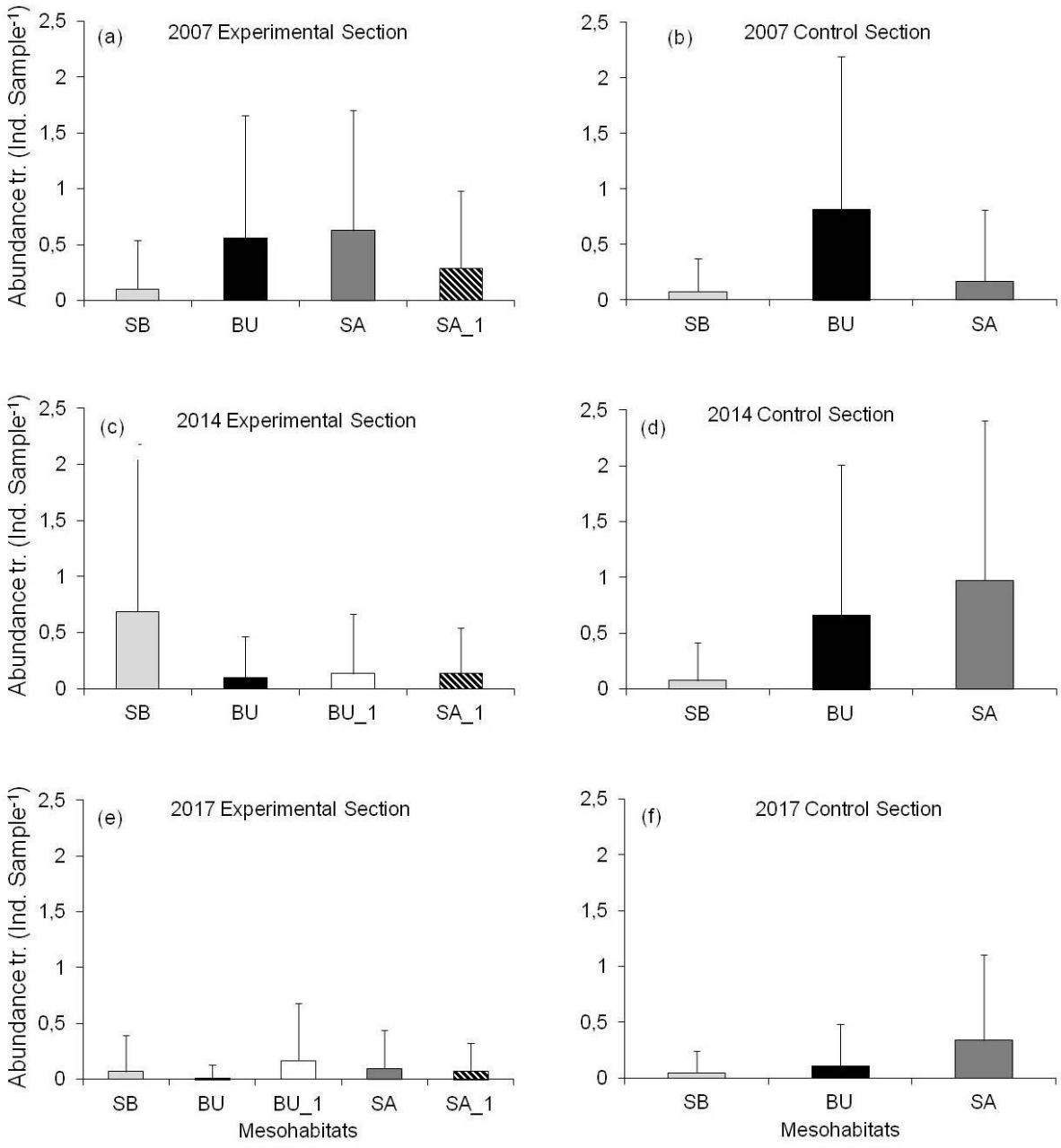


Fig. 9 Comparison of fish larvae abundance within year per section for mesohabitat types. SB, BU and BU_1 were located in the main channel. Mean transformed values are shown with + standard deviation. SB – gravel bar, BU – groyne field, SA – side arm, N – experimental, R/RN – reference/reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures.

Tab. 5 "Post hoc comparison": abundances within river sections between years. (a) 2007 experimental section (χ2 = 40.698, df = 3, p = < 0.001), (b) 2007 control section (χ2 = 73.330, df = 2, p = < 0.001) and (c) 2014 experimental section (χ2 = 23.491, df = 3, p = < 0.001), (d) 2014 control section (χ2 = 59.064, df = 2, p = < 0.001), (e) 2017 experimental section (χ2 = 18.304, df = 4, p = < 0.001), (e) 2017 control section (χ2 = 36.375, df = 2, p = < 0.001). Numbers shown are p-values with significant values marked bold. Exper. – experimental, SB – gravel bar, BU – groyne field, SA – side arm. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures.

(a)

Exper. 2007	BU	SA	SA_1
SA	0.141		
SA_1	0.032	**0.009**	
SB	**<0.001**	**<0.001**	**0.013**

(b)

Control 2007	BU	SA
SA	**<0.001**	
SB	**<0.001**	0.104

(c)

Exper. 2014	BU	BU_1	SA_1
BU_1	0.454		
SA_1	0.472	0.527	
SB	**<0.001**	**<0.001**	**0.002**

(d)

Control 2014	BU	SA
SA	**0.003**	
SB	**<0.001**	**<0.001**

(e)

Exper. 2017	BU	BU_1	SA	SA_1
BU_1	**<0.001**			
SA	0.027	0.238		
SA_1	0.051	0.182	0.419	
SB	0.068	0.035	0.264	0.251

(f)

Control 2017	BU	SA
SA	**<0.001**	
SB	0.077	**<0.001**

Comparing the abundance between years and sections, experimental and control in 2007 were similar. Abundance in 2014 and 2017 was higher in the control section (Fig. 10b). The abundance of all years between control and experimental section was significantly different (LMM, $p < 0.05$). Abundance was significantly different between sections before and after the measures where set (LMM, $p < 0.01$). The measures showed a significant effect on abundance (LMM, $p < 0.05$) between sections, which is due to the lower abundance in the experimental sections in 2014 and 2017 (Tab. 6). So, the measures affected the temporal abundance pattern and decreased overall abundance in the experimental section.

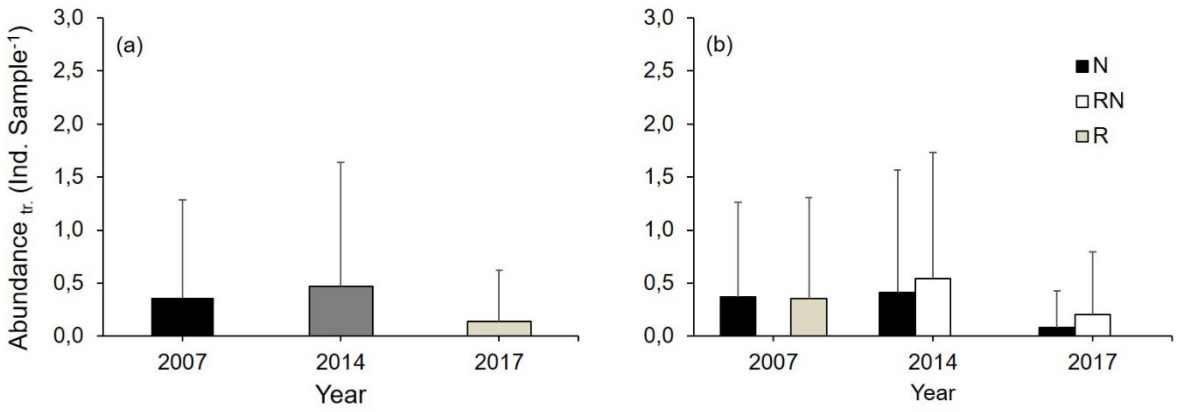


Fig. 10 Comparison of average yearly abundances of fish larvae. (a) Average ± standard deviation of total abundance for every sampling year. (b) Average abundances ± Standard Deviation at experimental and reference sections. Data show means of transformed values with + standard deviation. N – experimental, R/RN – reference/reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014.

Tab. 6 Results of the LMM (linear mixed effect model) on the abundance in the river sections and the single mesohabitats. Significant p-values are marked bold. Factors: CI – sections (control, impact), BA – year (before, after) and CI x BA – effect of measures. SB – gravel bar, BU – groyne field, SA – side arm. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures. SB, BU and BU_1 were located in the main channel.

Abundance									
predictor	numDF	denDF	F-value	p-value	predictor	numDF	denDF	F-value	p-value
Sections					**BU_1**				
CI	1	3493	7.126	**0.018**	CI	1	973	10.646	**0.001**
BA	1	1	0.036	**0.008**	BA	1	1	2.355	0.368
CI x BA	1	3493	5.122	**0.024**	CI x BA	1	973	0.447	0.504
SB					**SA**				
CI	1	1157	23.826	**<0.001**	CI	1	804	1.861	0.173
BA	1	1	0.249	0.705	BA	1	1	0.372	0.651
CI x BA	1	1157	9.260	**0.002**	CI x BA	1	804	19.224	**<0.001**
BU					**SA_1**				
CI	1	973	19.397	**<0.001**	CI	1	913	22.912	**<0.001**
BA	1	1	2.159	0.380	BA	1	1	0.404	0.639
CI x BA	1	973	0.018	0.893	CI x BA	1	913	23.058	**<0.001**

The overall abundances between the different mesohabitats revealed different spatio-temporal patterns. The abundance varied between mesohabitats in different years and no constant pattern could be observed. Very low abundance in 2017 in all mesohabitats could be observed, abundance was highest in the side arm, followed by the side channel. In abundance generally the mesohabitats were significantly different to each other (Kruskal-Wallis, $\chi^2 = 67.918$, df = 4, $p < 0.001$). A post-hoc Dunn´s test with FDR correction on general abundance over all years revealed significant differences between groyne field and side channel, side arm and side channel, groyne field and upper confluence of the side arm, side arm and it´s upper confluence, gravel bar and groyne field and side arm and gravel bar (Tab. 7). The highest mean abundance in decreasing order had the mesohabitat gravel bar (7.2 ± 99.3), followed by the groyne field (5.7 ± 40.0), the side arm (4.6 ± 47.9), the side channel (0.6 ± 3.8) and the upper confluence of the side arm (0.6 ± 3.8). The abundance in the gravel bar mesohabitat was low in 2007 and 2017 and highest in 2014 (Fig. 11a). The highest abundance in the groyne field could be observed in 2007, which gradually decreased to 2017. The abundance in the side channel, which was a modified version of the previous mesohabitat, decreased drastically from 2007 to 2014 and increased slightly to 2017 (Fig. 11b). By far the highest abundance in the side arm was observed in 2014, whereas 2017 was just slightly lower than 2007. The abundance in the upper confluence of the side arm, which was modified during the measures, was slightly lower than in the side arm itself in 2007 and decreased every year (Fig. 11c).

Tab. 7 Results of Dunn´s Multiple Comparison Test with FDR (false discovery rate) correction on overall between mesohabitat transformed abundances. Kruskal-Wallis H = 67.918, df = 4. Numbers shown are p-values with significant values marked bold. MH – mesohabitats, SB – gravel bar, BU – groyne field, SA – side arm. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures. SB, BU and BU_1 were located in the main channel.

MH	BU	BU_1	SA	SA_1
BU_1	**<0.001**			
SA	0.063	**<0.001**		
SA_1	**0.001**	0.298	**<0.001**	
SB	**<0.001**	0.485	**<0.001**	0.253

Two mesohabitats revealed a similar temporal abundance pattern. The highest abundance in 2014 had the gravel bar in the experimental section and the side arm in the control section. In perspective of abundance, all the other mesohabitats, including the section congeners of the aforementioned were either decreasing over the years or stayed similar.

The abundances between sections and years at the gravel bar of the experimental section were low in 2007, 6.7 times higher in 2014 and again very low in 2017. Low abundances at the gravel bar in the control sections were observed during all sampling series (Fig. 12a). In abundance a significant difference (LMM, $p < 0.001$) between the two sections could be observed. No significant differences of abundances between the years were found (LMM, $p = 0.71$). The restoration measures had a significant effect (LMM, $p < 0.01$) on abundance, so the increase in abundance at the gravel bar in 2014 was affected by the inshore modifications (Tab. 6).

The abundance between sections at the groyne field of the experimental section was highest in 2007, but decreased 5.46 times in 2014 and was even lower in 2017. The highest abundance in the control section was observed in 2007, which decreased in 2014 and even further in 2007 (Fig. 12b). Concerning abundance, a significant difference (LMM, $p < 0.001$) between the two sections could be observed. Regarding abundance, no significant differences between the years were found (LMM, $p = 0.38$) and also no significant effect of the measures (LMM, $p = 0.89$) on abundance could be found in this mesohabitat (Tab. 6).

The abundance between sections in the side channel, which is a modified groyne field in the experimental section, was highest in its original state in 2007, much lower in 2014 and stayed at a similar level in 2017 (Fig. 12b). The pendant in the control section was the aforementioned groyne field. Between the two sections a significant difference (LMM, $p < 0.001$) in abundance could be observed. In terms of abundance, no significant differences between the years were found (LMM, $p = 0.37$), as well as no significant effect of the measures (LMM, $p = 0.50$) on abundance could be observed in this mesohabitat (Tab. 6).

The abundance between sections in the side arm in the experimental section was highest in 2007 and was low in 2017. The lowest abundance in the control section was observed in

2007, which increased 5.73 times in 2014 to its highest value and decreased again 2.87 times in 2017 (Fig. 12c). In perspective of abundance, no significant difference (LMM, $p = 0.17$) between the two sections could be observed. In abundance, no significant differences between the years were found (LMM, $p = 0.65$). In this case, a significant effect (LMM, $p < 0.001$) of the measures on abundance could be found causing a decrease of the abundance after the restoration (Tab. 6).

The abundance between sections in the upper confluence of the side arm, which is also a modified mesohabitat in the experimental section, was highest in its original state in 2007, decreased slightly in 2014 and again in 2017 (Fig. 12c). The pendant in the control section was the aforementioned side arm. Concerning abundance, a significant difference (LMM, $p < 0.01$) between the two sections could be observed. Regarding abundance, no significant differences between the years were found (LMM, $p = 0.639$). A significant effect (LMM, $p < 0.001$) of the restoration measures on abundance could be found in this mesohabitat, causing a decrease of the abundance after the restoration (Tab. 6).

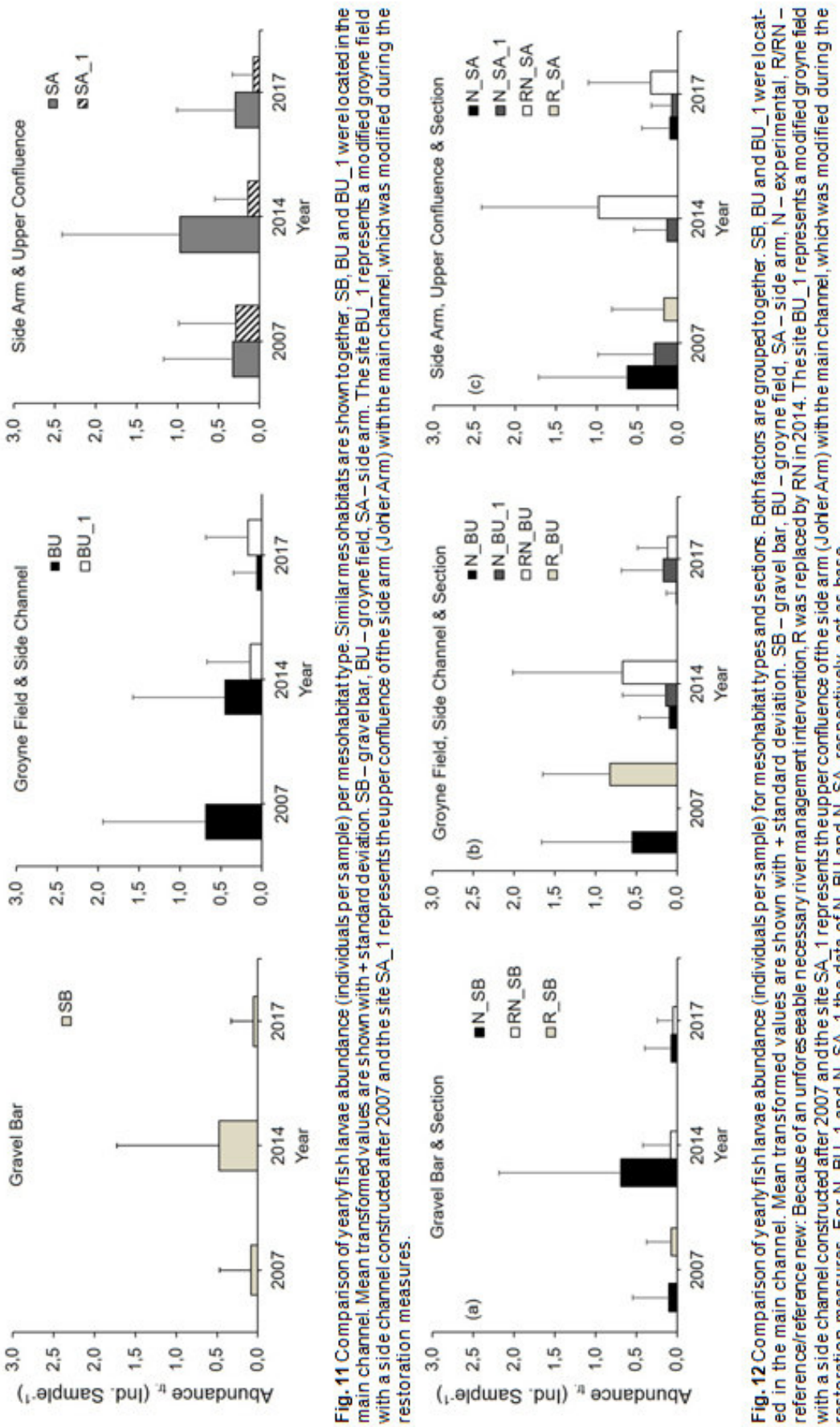


Fig. 11 Comparison of yearly fish larvae abundance (individuals per sample) per mesohabitat type. Similar mesohabitats are shown together, SB, BU and BU_1 were located in the main channel. Mean transformed values are shown with + standard deviation. SB – gravel bar, BU – groyne field, SA – side arm. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures.

Fig. 12 Comparison of yearly fish larvae abundance (individuals per sample) for mesohabitat types and sections. Both factors are grouped together. SB, BU and BU_1 were located in the main channel. Mean transformed values are shown with + standard deviation. SB – gravel bar, BU – groyne field, SA – side arm, N – experimental, R/RN – reference/reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures. For N_BU_1 and N_SA_1 the data of N_BU and N_SA, respectively, act as base.

Results

Spatio-temporal size distribution of early stages of fish

The overall size range of the caught larvae and juvenile fishes ranged from 6.2 to 34.5 mm total length. Total larval sizes slightly decreased from to 2007 to 2017. In 2007, the length ranged from 6.7 to 34.5 mm with a mean of 14.3 mm ± 3.3 SD and a median of 14.2 mm. The larval length in 2014 ranged from 6.3 to 34.3 mm with a mean of 10.8 mm ± 2.7 SD and a median of 10.14 mm. Larval length in 2017 ranged from 6.2 to 27.3 mm with a mean of 11.6 mm ± 4.1 SD and a median of 9.93 mm (Fig. 13). Larval length between the sampled years was significantly different (Kruskal-Wallis, $\chi^2 = 752.83$, df = 2, $p < 0.001$).

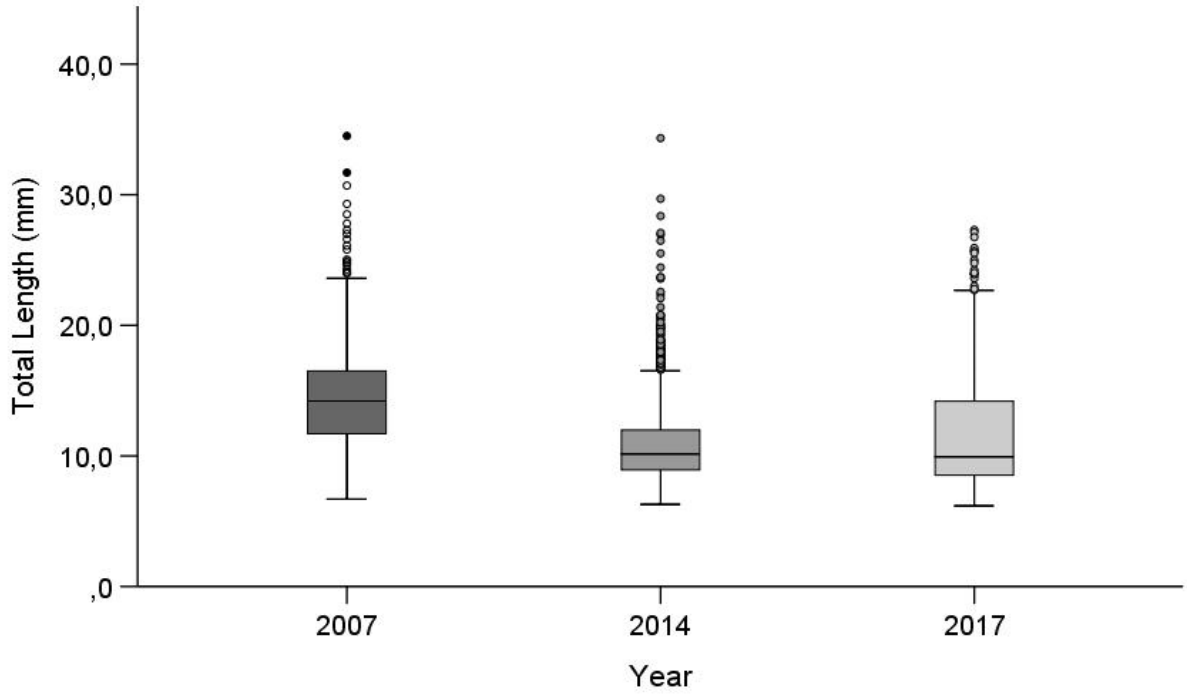


Fig. 13 Comparison of sizes of the early stages between the three sampling series. Boxes show inter quartile range (IQR, 25-75%) with the median indicated as line, whiskers are IQR*1.5, dots show outlier of the data.

Larval length increased linearly during the sampling season in all years under study. Additionally, multiple cohorts of larvae were observed within each sampling season. Larval length within years in 2007 gradually increased from mid of April until beginning of June. A pronounced decrease of average size of the larval assemblage was observed in early June. A similar pattern was found within year in 2014; however the average sizes were distinctly lower than in 2007. During the sampling dates at the end of June very small larvae could be observed again. Within year 2017 two growth cohorts could be observed, one comparable to the series in 2007 and 2014 for the period from end of April to mid of May and a second one from the end of May to the end of June. The second growth cohort appeared earlier in 2017 compared to the other two sampling series in 2007 and 2014 (Fig. 14).

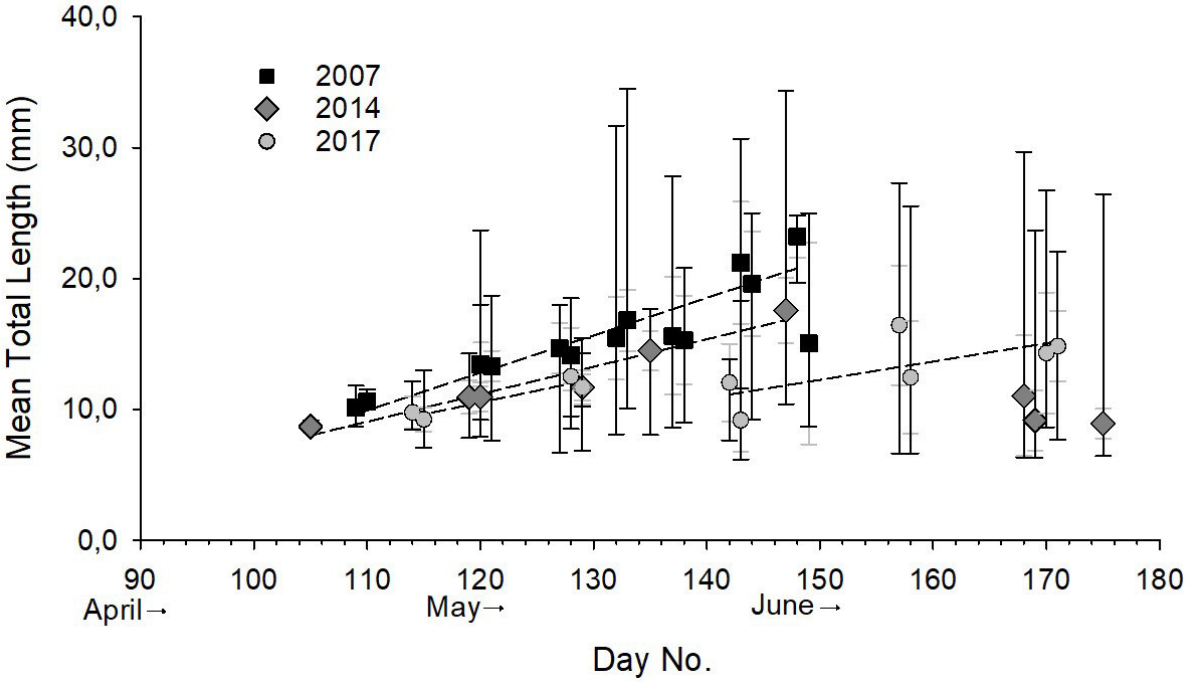


Fig. 14 Temporal course of the mean total length (mm) of fish larvae sampled in three years with ± standard deviation shown as grey error bar caps and ranges as black error bar caps. Temporal scale is shown on the x-axis as day numbers with beginning of months indicated below. Days where samples were taken are marked with symbols.

Larval length between sections was lower in the reference sections in the last two sampling series, whereas in the experimental section more fluctuations could be observed. Larval length between years and sections in 2014´s experimental section was lower than in 2007, but was higher again in 2017. In the size of early stages, the most pronounced differences between the two river sections were found during the last survey in 2017 (Fig. 15). Concerning larval length, a significant difference (LMM, $p < 0.001$) between experimental and reference sections could be observed. Regarding larval length, no significant difference was observed before and after restoration measures were set (LMM, $p = 0.12$), whereas a significant effect (LMM, $p < 0.01$) of the restoration measures on larval length could be found caused by the bigger larvae in the experimental section (Tab. 8). In terms of larval length, there was no significant difference between the sections in 2007 (Mann-Whitney, $U = 432500$, $p = 0.08$) and 2014 (Mann-Whitney, $U = 1080100$, $p = 0.26$). In perspective of larval length, there was a significant difference (Mann-Whitney, $U = 84198$, $p < 0.001$) between the sections in 2017, which was due to the bigger size of larvae in the experimental section.

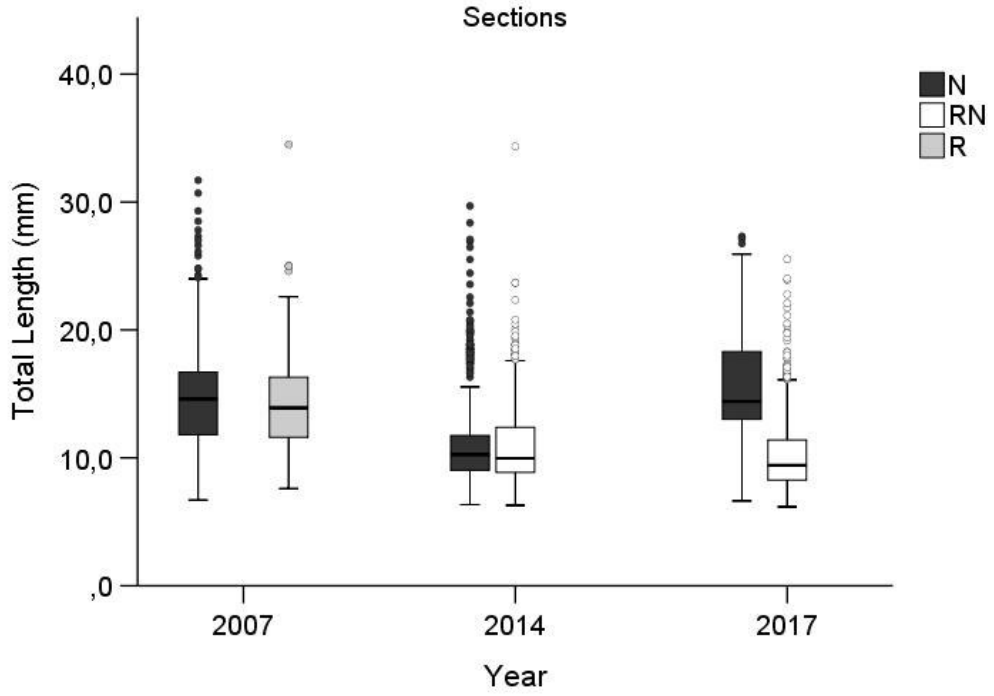


Fig. 15 Comparison of yearly fish larvae length in three sections. Graph shows total mean length in mm. Mean total length (mm) of fish larvae sampled in three years separated over three section types. Boxes show inter quartile range (25-75%) with median as line, whiskers are IQN*1.5, dots show outlier of the data. N – experimental, R – reference, RN –reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014.

Tab. 8 Results of the LMM (linear mixed effect modeling) on the fish larval length in the sections overall and the single mesohabitats. Significant p-values are marked bold. Factors: CI – sections, BA – year and CI x BA – effect of measures. SB – gravel bar, BU – groyne field. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures.

Length									
predictor	numDF	denDF	F-value	p-value	predictor	numDF	denDF	F-value	p-value
Sections					**BU_1**				
CI	1	5489	42.206	**<0.001**	CI	1	2139	128.130	**<0.001**
BA	1	1	27.203	0.121	BA	1	1	132.690	0.055
CI x BA	1	5489	7.143	**0.008**	CI x BA	1	2139	191.910	**<0.001**
SB					**SA**				
CI	1	1578	13.507	**<0.001**	CI	1	1610	0.032	0.857
BA	1	1	0.040	0.875	BA	1	1	165.763	**0.049**
CI x BA	1	1578	0.937	0.333	CI x BA	1	1610	13.029	**<0.001**
BU					**SA_1**				
CI	1	2010	0.044	0.834	CI	1	1487	99.045	**<0.001**
BA	1	1	0.942	0.510	BA	1	1	95.546	0.065
CI x BA	1	2010	4.667	**0.031**	CI x BA	1	1487	72.467	**<0.001**

In larval length between years, most of the mesohabitats showed a similar temporal size pattern of decreasing larval length in each sampling period, with exception of the gravel bars and the upper confluence of the side arm. Larval length was similar in all mesohabitats in 2007. Larval length at the gravel bar was lower in 2014 than in 2007, but was highest in 2017. Larval length in the groyne field was lower in 2014 than in 2007 and even lower in 2017. Larval length in the side channel, which is a modified groyne field, was slightly higher in its modified state in 2014 than in 2007 and was lower in 2017. Larval length in the side arm was lower in 2014 than 2007 and was similar in 2017. Larval length in the upper confluence of the side arm, which was modified in 2014, was higher in 2014 and much lower in 2017 (Fig. 16).

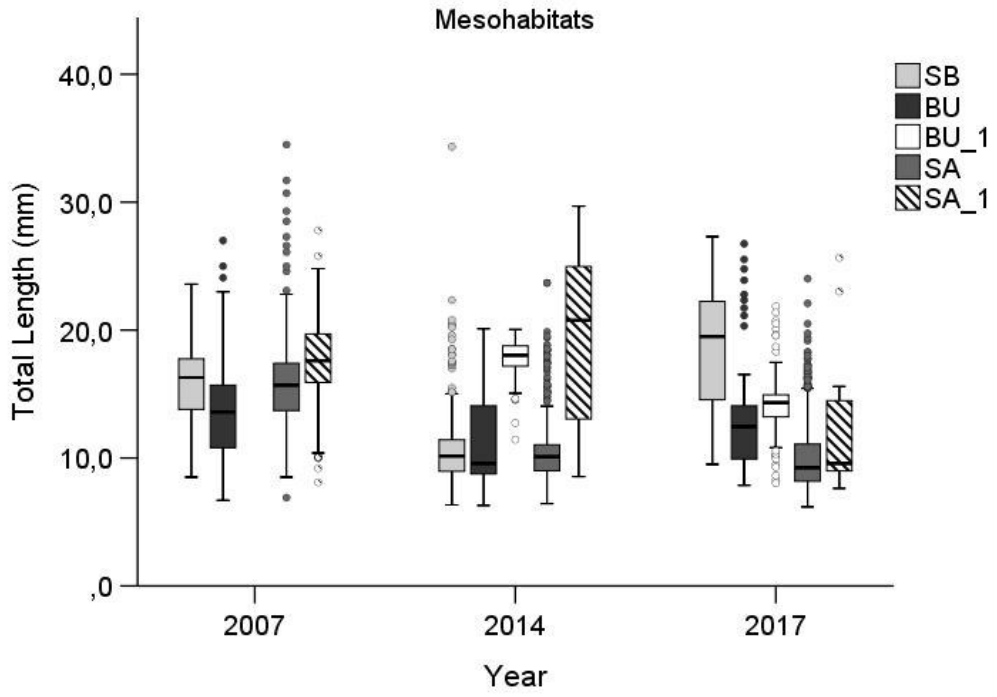


Fig. 16 Comparison of yearly fish larvae length in five mesohabitat types. Graph shows total mean length in mm. Boxes show inter quartile range (25-75%) with median as line, whiskers are IQN*1.5, dots show outlier of the data. SB – gravel bar, BU – groyne field, BU_1 – side channel, SA – side arm, SA_1 – side arm entry Johler Arm.

Concerning larval length between years and sections, some mesohabitats revealed similar temporal patterns. In the experimental section the gravel bar and the groyne field both had lowest lengths in 2014 and were highest in 2017. Regarding larval length, the side channel and the upper confluence of the side arm were highest in 2014 and lowest in 2017. In the control section larval length in the gravel bar and the groyne field was highest in 2007 and lowest in 2014, whereas in the side arm larval length was lower every sampled year. The larval length between years and sections at the gravel bar fluctuated in the last two sampling periods in opposite directions between the sections. Larval length at the gravel bar in the

experimental section in 2014 was lower than in 2007 and was high in 2017. Larval length at the gravel bar in the control section was higher in 2014 than in 2007 and lower in 2017 (Fig. 17). In terms of larval length, at the gravel bar a significant difference (LMM, $p < 0.001$) between experimental and reference section could be observed. In perspective of the larval length at the gravel bar no significant differences between the years (LMM, $p = 0.875$) and no significant effect (LMM, $p = 0.33$) of the measures could be found (Tab. 8).

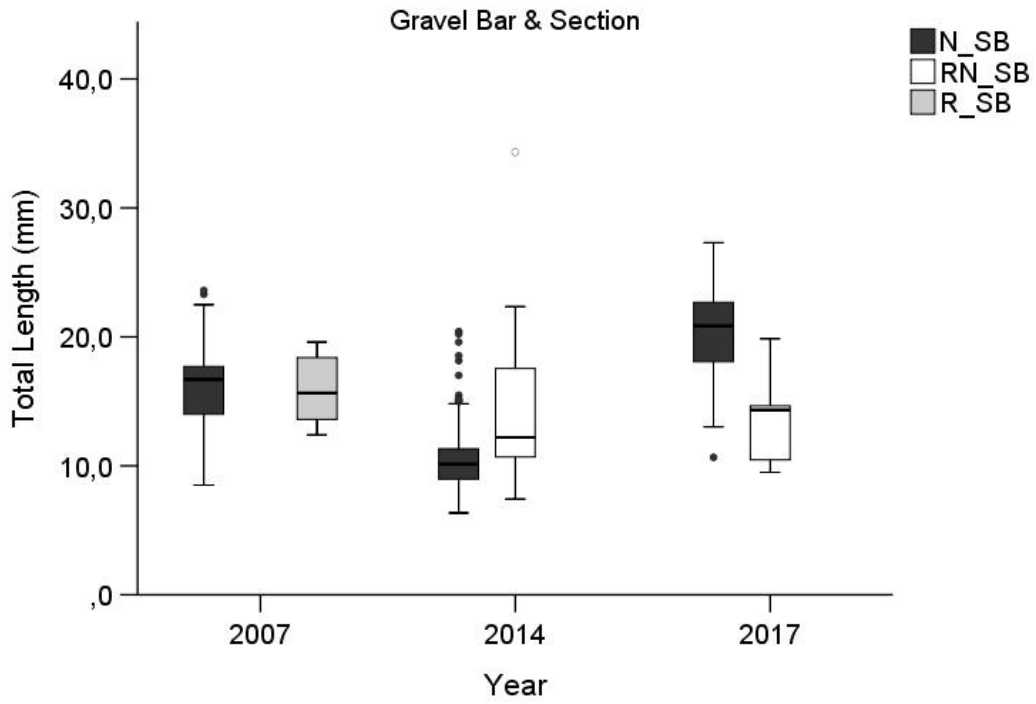


Fig. 17 Comparison of yearly fish larvae length in gravel bar type mesohabitats situated in an experimental and reference sections. Graph shows total mean length in mm. Boxes show inter quartile range (25-75%) with median as line, whiskers are IQN*1.5, dots show outlier of the data. SB – gravel bar, N – experimental, R – reference, RN –reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014.

The larval length between years and sections in the groyne field fluctuated within and between the two sections, no consistent pattern was visible. Larval length in the experimental section was higher in 2007 than in 2014 and highest in 2017. Larval length in the control section was highest in 2007, lower in 2014 and lowest in 2017. Larval length in the side channel, which is an after 2007 modified groyne field, was highest in 2014 and similar in 2007 and 2017 (Fig. 18). Larval length in the groyne field was not significantly different between the sections (LMM, $p = 0.83$) or the years (LMM, $p = 0.51$). A significant effect (LMM, $p < 0.05$) of the measures on larval length could be observed, which is expressed in larger sizes of early stages at the modified groyne field. Larval length in the side channel was significantly different (LMM, $p < 0.001$) between the sections. In larval length no significant difference (LMM, $p = 0.06$) between the years could be found. A significant effect of the measures (LMM, $p <$

0.001) on larval length could be found, caused by the bigger larval sizes in the side channel compared to the reference and the previous state of this mesohabitat (Tab. 7).

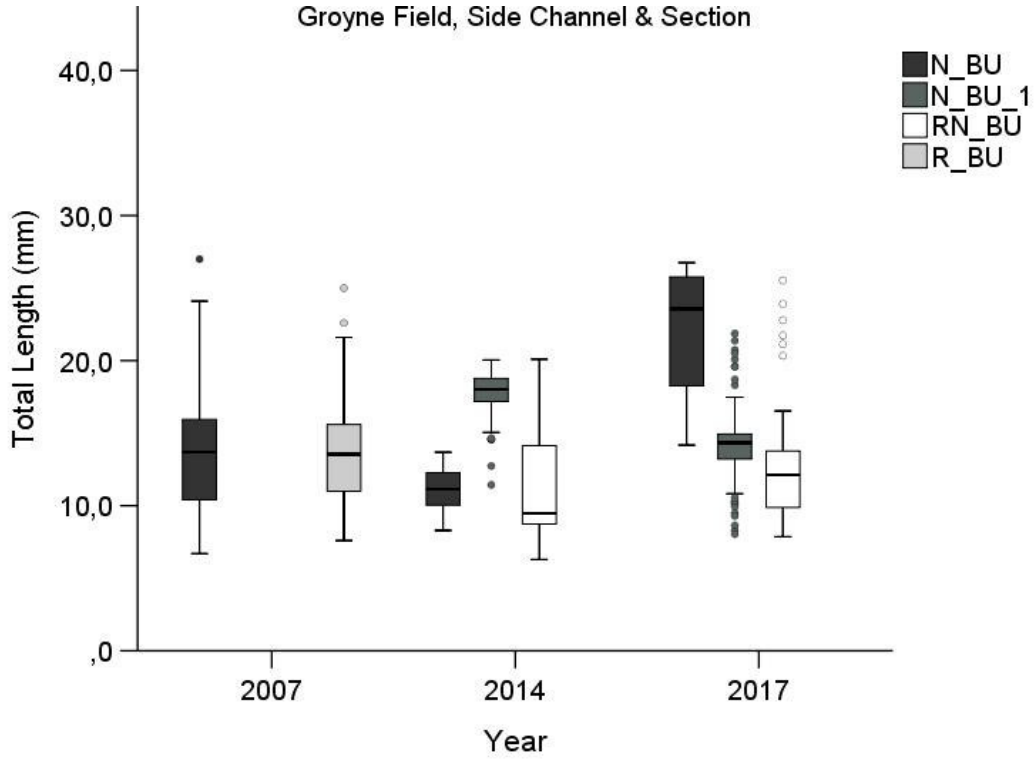


Fig. 18 Comparison of yearly fish larvae length in groyne type mesohabitats situated in an experimental and reference sections. Graph shows total mean length in mm. Boxes show inter quartile range (25-75%) with median as line, whiskers are IQN*1.5, dots show outlier of the data. BU – groyne field, BU_1 – side channel, N – experimental, R – reference, RN –reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 for which the data of N_BU acts as base.

Concerning larval length between year and section of the side arm mesohabitat no temporal pattern could be found. Larval length in the experimental section was higher in 2007 than in 2017. Larval length in the control section was highest in 2007 and similarly low in 2014 and 2017. Larval length in the upper confluence of the side arm was high in 2007, highest in 2014 and much lower in 2017 (Fig. 19). Regarding larval length of the side arm no significant differences between the sections (LMM, $p = 0.86$) could be found. In terms of larval length, there was a significant difference (LMM, $p < 0.05$) between the years and a significant effect (LMM, $p < 0.001$) of the measures caused by the low larval lengths in 2017 and influenced by the gap in 2014. In larval length of the upper confluence of the side arm a significant difference (LMM, $p < 0.001$) between the sections could be found. In perspective of larval length, no significant difference between the years (LMM, $p = 0.065$) could be found. Here, the measures had a significant effect (LMM, $p < 0.001$) on larval length, which led to higher lengths in 2014 (Tab. 7).

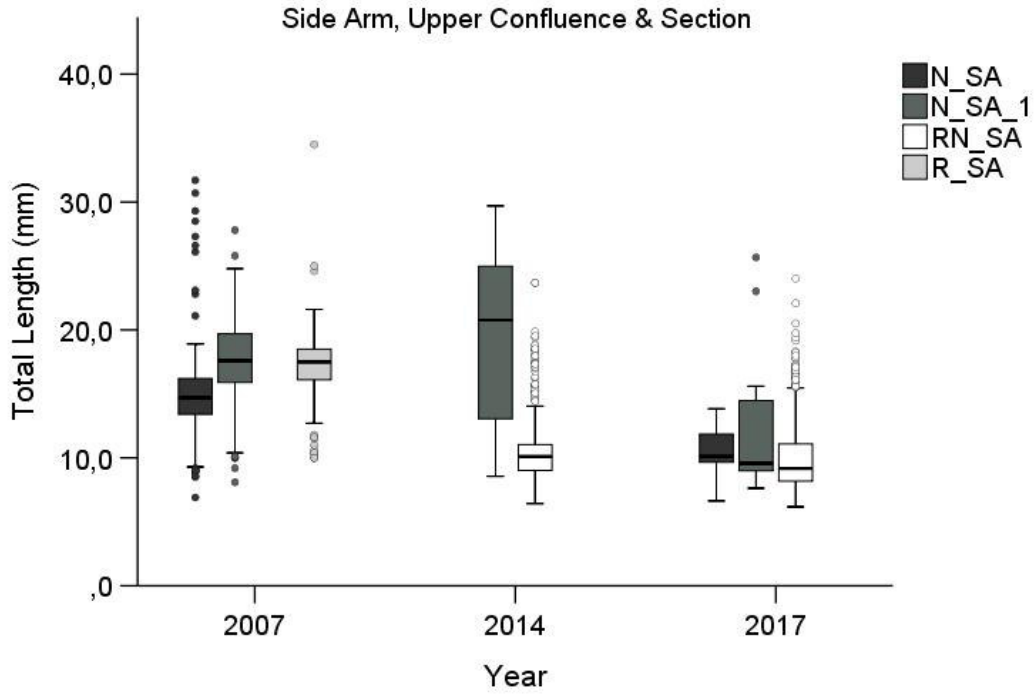


Fig. 19 Comparison of yearly fish larvae length in side arm type mesohabitats situated in an experimental and reference sections. Graph shows total mean length in mm. Boxes show inter quartile range (25-75%) with median as line, whiskers are IQN*1.5, dots show outlier of the data. SA – side arm, SA_1 – side arm entry Johler Arm, N – experimental, R – reference, RN –reference new: Because of an unforeseeable necessary river management intervention, R was replaced by RN in 2014. SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures. For N_SA_1 the data of N_SA acts as base.

To avoid fixation effects when testing larval lengths of different years against each other, a within year larval length comparison between single mesohabitats was performed. Larval length in 2007 between the single mesohabitats was significantly different (Kruskal-Wallis, χ^2 = 186.69, df = 3, $p < 0.001$). A post-hoc Dunn´s test with FDR correction on larval length between mesohabitats revealed which mesohabitats in 2007 were significantly different in larval size and which were more similar. Larval length was different between most of the mesohabitats in 2007. Larval length differed in the side arm mesohabitats in 2007 from its upper confluence with the main channel, the gravel bars and the groyne fields. Larval length also differed in the latter from the upper confluence of the side arm and the gravel bar, which in turn differed from the upper confluence of the side arm. Concerning larval length, the only mesohabitat-pair that was similar was the side arm and the gravel bar, where larvae of similar size were caught in this year (Tab. 9a).

Larval length in 2014 between the mesohabitats was significantly different (Kruskal-Wallis, χ^2 = 189.41, df = 4, $p < 0.001$). A post-hoc Dunn´s test with FDR correction on larval length revealed, that similarly to 2007, most of the mesohabitats were significantly different in larval length to each other. Regarding larval length, the groyne field differed significantly from the side channel, the side arm and the upper confluence of the side arm. In terms of larval

length, the side channel differed from the groyne field, the side arm and the gravel bar. In perspective of larval length, the side arm differed from the groyne fields, the side channel and its upper confluence with the main stem. Larval length differed in the latter from the groyne field, the side arm and the gravel bar, which in larval length differed from the side channel and the upper confluence of the side arm. Larval length did not differ in the pairs of the side channel and the upper confluence of the side arm, the gravel bar and the groyne field and the side arm and the gravel bar. In these mesohabitat pairs larvae must have had similar sizes in 2014 (Tab. 9b)

Larval length in 2017 between the mesohabitats was also significantly different (Kruskal-Wallis, $\chi^2 = 232.74$, df = 4, $p < 0.001$). A post-hoc Dunn´s test with FDR correction on larval length revealed, as already mentioned for 2007 and 2014, that almost all mesohabitats were significantly different in larval size in 2017. In larval length the side channel differed from the groyne fields, the side arm, the upper confluence of the side arm and the gravel bar. Concerning larval length, the groyne fields differed from the side channel, the side arm and the gravel bar. Regarding larval length, the side arm differed from the groyne fields, the side channel and the gravel bar. In terms of larval length, the upper confluence of the side arm differed from the gravel bar and the side channel. Larval length in the gravel bar differed from the groyne fields, the side channel, the side arm and its upper confluence. Larval length in 2017 was only similar in two pairs of mesohabitats, the groyne fields and the upper confluence and the side arm and its upper confluence (Tab. 9c). Larval length was only similar over more years in one pair, which was the side arm and the gravel bar in 2007 and 2014. This could indicate that there is no or just a weak effect directly after the measures on fish larval size in these two mesohabitats.

Tab. 9 Results of Dunn´s Multiple Comparison Test with FDR (false discovery rate) correction on within-year differences of transformed length between mesohabitats of (a) 2007 (H=186.689, df=3), (b) 2014 (H=189.413, df=4) and (c) 2017 (H=232.745, df=4). Numbers shown are p-values with significant values marked bold. MH – mesohabitats, SB – gravel bar, BU – groyne field, SA – side arm. The site BU_1 represents a modified groyne field with a side channel constructed after 2007 and the site SA_1 represents the upper confluence of the side arm (Johler Arm) with the main channel, which was modified during the restoration measures.

(a)

MH 2007	BU	SA	SA_1
SA	**<0.001**		
SA_1	**<0.001**	**<0.001**	
SB	**<0.001**	0.357	**<0.001**

(b)

MH 2014	BU	BU_1	SA	SA_1
BU_1	**<0.001**			
SA	**0.019**	**<0.001**		
SA_1	**<0.001**	0.034	**<0.001**	
SB	0.045	**<0.001**	0.211	**<0.001**

(c)

MH 2017	BU	BU_1	SA	SA_1
BU_1	**0.020**			
SA	**<0.001**	**<0.001**		
SA_1	0.165	**0.020**	0.057	
SB	**<0.001**	**0.011**	**<0.001**	**<0.001**

Discussion

A positive relationship between size and developmental stage could be observed, however the increase in size between the stages is not constant. Smaller differences in larval length were observed between developmental stages L1 to L2, as well as L3 to L6. Larger differences in larval length were observed between developmental stages L3 to L4, as well as L6 to J1 and J1 to J2. A larger difference in larval size in 2007 was also observed between developmental stages L5 to L6. Larval length was higher in 2007 than in 2014 in every developmental stage (Fig. 20).

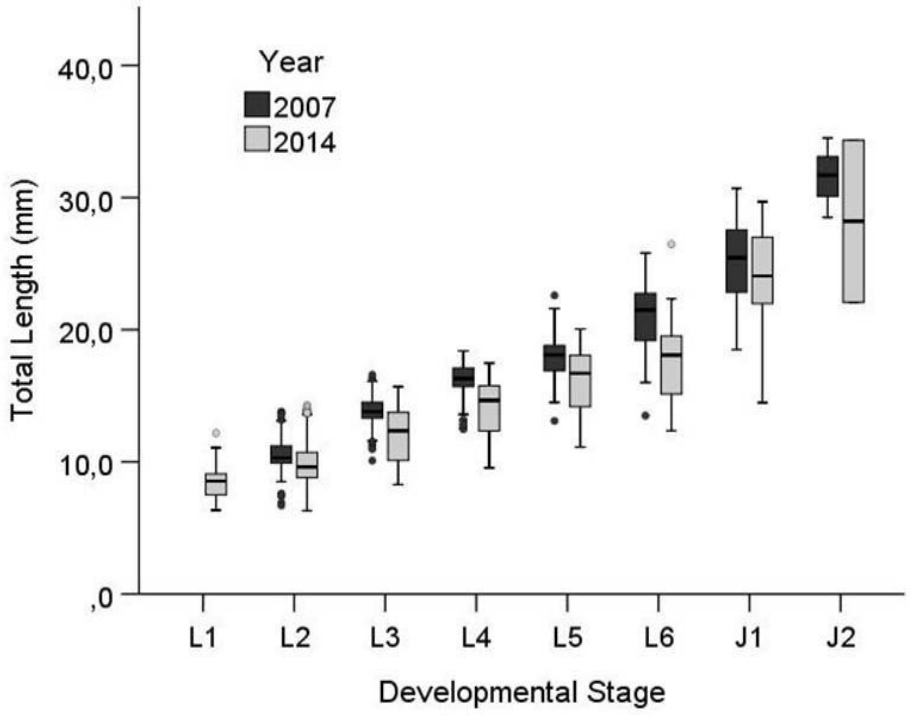


Fig. 20 Mean total length (mm) of fish larvae related to their developmental stage separated for two years. Boxes show inter quartile range (25-75%) with median as line, whiskers are IQN*1.5, dots show outlier of the data.

Discussion

Water temperature

Water temperature is probably the most important factor affecting development, survival and growth of fish in early stages (Pauly, 1980). Additionally, it is considered even more influential on growth than food abundance (Meekan et al., 2003), an increase in temperature and therefore in growth has to be compensated by a higher food intake (Houde, 1989). This relationship is not only valid for fish early stages, higher temperatures also boost primary (Hein et al., 1999) and prey production (Matzinger, 2009). In temperate rivers water temperature is mainly guided by the seasons and discharge. Rising temperatures in spring triggers spawning at certain thresholds, e.g. at 8 °C for many fish species in the Danube River (Keckeis, 1997). The course of the temperature thereafter is of vital importance for egg, larval and juvenile development and is often a deciding component for the recruitment success (Blaxter,

1991). For the three surveyed years the mean water temperature was significantly different between all years but 2014 and 2017. However, the individual temperature courses over the sampling seasons were very different even between the two last years. Even though 2007 had the highest average temperature, both 2007 and 2014 showed high temperatures at the beginning of the sampling season, especially in May. This should be advantageous for critical early stages, as in the Danube River downstream of Vienna, fish larvae were found to predominantly emerge during this month (Winkler et al., 1997). Higher water temperatures early in the reproductive season led to a higher abundance of several fish species larvae in the Paraná River Basin, Brazil (Hermes-Silva et al., 2009), enhanced fish larval growth and survival in seasonal tributaries of the Sacramento River, USA (Lorig et al., 2013) and in the lower Oder River, Germany (Wolter, 2007). 2017 displayed not only the lowest average water temperature of the three sampling seasons, but also a serious and long lasting temperature drop in April. Lower temperatures during the development of fish larvae, especially very early in the season, could be detrimental for the recruitment success, as it was shown in a three year ichthyoplankton survey in the upper Uruguay River, southern Brazil, where the year with the lowest water temperature showed a decreased abundance and a reduced richness in taxa and larval stages (Reynalte-Tataje et al., 2012).

Discharge

River discharge is shaping various other factors in connection with the specific geomorphology and thus strongly influencing the aquatic biota. In the Danube River discharge was found to affect flow velocity, water depth and water temperature in main channel habitats (Keckeis et al., 1997). Another study at the Danube River on fish larvae drift and dispersal highlighted the association of discharge and connectivity having major impact on the recruitment success (Schludermann et al., 2012). This relation was also discovered earlier to directly connect to fish richness in 15 river systems all over the US (Horwitz, 1978). Further discharge is crucial for the retentive capacity of a river habitat, which is the capability to retain and protect fish larvae from overcritical currents and potential wash-out at high-water events, therefore fostering recruitment (Schiemer et al., 2001). Retention was also found to be significant for the reproduction and abundance of fine zooplankton prey in 0+ fish habitats in the main stem of the River Danube (Reckendorfer et al., 1999). The discharge during this study was not different between 2007 and 2014, but in 2017 it was different from all other surveyed years. Accordingly, the individual yearly courses showed in majority the same patterns for 2007 and 2014, but not for 2017. Both first years showed a very low discharge in April and May, with the lowest average in 2007. This can be very beneficial for the abundance of early fish larvae stages, as low depths and currents were shown to decrease fish larvae drift densities in the same free flowing stretch of the Danube River (Lechner et al., 2014) and even increase ac-

tive dispersal to nursery sites, as a 20 year review on 0+ fishes in European streams showed (Copp, 2010). As larvae grow larger their muscular performance increases with the ability to withstand passively entering the drift and disperse at higher discharge conditions (Hunt von Herbing, 2002; Mann & Bass, 1997; Wolter & Sukhodolov, 2008). In 2017, the discharge not only had the highest average, but was elevated in April and with floods at the beginning of May during the critical time of the smallest larvae present. At this time of the reproductive season this could have detrimental effects on the abundance and survival of fish larvae through wash-out, as it was shown in a work over 4 breeding seasons at two regulated Australian lowland rivers, where timely critical increased discharge or high water events were assumed to be the causes of lower abundances of fish early stages (Humphries et al., 2002).

Temporal larvae distribution

In the first two sampling years high numbers of fish larvae could be caught using the PAS method, similarly to another Danube River study using PAS, which caught high larvae numbers in the first and low numbers in the second year, probably reasoning in increased flow velocities due to restoration measures (Keckeis, 2014). Another Danube River work on fish larvae abundance over one reproductive season also reported high numbers of fish larvae, which according to the author originated in small sampled microhabitat sizes and a high catch efficiency using the PAS method (Götsch, 2008). In a study on recruitment in the Great Ouse River, UK, just low numbers of juvenile fish could be sampled, although PAS electrofishing was used, which might be attributed to the late time of sampling in August and a very dry summer (Copp, 1990). Much higher numbers of fish early stages are regularly sampled in large rivers using drift nets, e.g. a two month Danube River drift study on early stages with slightly over 29000 caught larvae (Ramler et al., 2016). The comparably high numbers of 2007 and 2014 in this work were possibly due to low discharge conditions creating good retention at the studied nursery sites and higher temperatures early in the season fostering larval and zooplankton prey growth. These two series also revealed the steepest increases in caught larval sizes over the sampling seasons (Fig. 14). The exceptional high individual number of 2014 (Tab. 3) was due to a mass catch, which will be discussed below. The low individual number caught in 2017 was probably caused by directly opposing abiotic conditions, elevated discharge washing out larvae and lower temperatures reducing growth and survival of larvae and prey. The high number of 0-catches in all years showed the patchy distribution of fish and their larvae (Sheldon, 1988) and could also be explained in the stochasticity and small sampled areas of the point-abundance-sampling, and the omittance of an attractant like an electrical current when electro fishing.

In all years under study the first larvae were caught starting mid of April, whereas in 2007 and 2014 a peak in abundance in May and a second peak at the end of June in 2014 could

be observed. The same bimodal pattern, with an abundance peak in May and July, was also observed in the Tallahatchie River, USA, where temporal variation of fish early stages abundance was studied (Turner et al., 1994) and in the Meuse River, France, where early stages were sampled from April to September over two years and first larvae appeared in April with a maximum abundance in May (Latli et al., 2019). The second peak in June was also observed by Götsch (2008) in the Danube River, who inferred a second hatching event, which should also be the case in this work. The very low and almost even abundance over the whole season in 2017 might be attributed to wash-out and lower survival of larvae due to the elevated discharge and an early drop in temperature with flooding at the same time.

Abundance and length distributions

The gravel bar mesohabitats generally showed very low abundances in all years, except for the enormous number in 2014, which was already mentioned above. The reason for this peak in abundance was probably the formation of a shallow bay at the previously enlarged gravel bar in the experimental section caused by the interplay of water level and discharge. Fish larvae and juveniles were shown to actively disperse from gravel bars to bay structures for their shallow geomorphology and therefore warmer water temperatures and less predation risk, e.g. for 0+ Barbel in the River Sieg, Germany (Bischoff & Freyhof, 1999) or in the River Ourthe, Belgium (Baras & Nindaba, 1999). Furthermore, the larvae smallest in length of all seasons were found in this mesohabitat, pointing to a very well connected or nearby spawning site, as well as a successful spawning season. An explanation for the low abundances over all years in all the other gravel bars surveyed, could be the exposure of these habitat type to ship induced waves, wreaking havoc on early stages of fish, contrary to the protection and refuge bay structures offer (Jungwirth et al., 1993; Kucera-Hirzinger et al., 2009; Liedermann et al., 2014; Schludermann et al., 2014). The larger larvae found in all gravel bars with low abundance could be explained by inappropriate flow and water depth above or at the edges of the gravel bars, requiring the higher swimming capacity of larger larvae or juveniles (Mann & Bass, 1997). Nevertheless, gravel bars are important nursery sites, as it was shown for rheophilic fishes in a strongly regulated stretch of the Morava River, Czech Republic (Jurajda, 1999) or through the dominance of cyprinid larvae in the drift downstream of gravel bars in the Danube River at Vienna, Austria (Meulenbroek et al., 2018) or as spawning grounds for cyprinids and salmonids in a two-year study of six streams in Germany (Mueller, Pander, & Geist, 2014).

In the groyne field mesohabitats no general pattern in abundance could be observed, except that in 2007 and 2014 overall high abundances of fish larvae could be observed there. This is contrary to a three-year study on 0+ fish habitats in the lower Rhine River, Germany, which

attested groyne fields a generally lower value for riverine fish larvae than other mesohabitat types (Grift et al., 2003). Despite these findings, the corresponding mesohabitats of the present work were very eroded and sedimented, at least before the restoration and still after in the reference section, which was found to substantially increase morphological heterogeneity in a study at the Elbe River, Germany (Henning & Hentschel, 2013). Thus they probably acted more like gravel bars, offering suitable microhabitats and conditions for larvae, but at the same time offer protection from wash-out caused by ship-induced waves (Schludermann et al., 2014). The low abundances at the restored groyne field in 2014, despite improved connectivity through opened groyne roots, was also found at this mesohabitat by Ramler & Keckeis (2019b) with whom is agreed upon here that a lack of sedimentation at the newly built groynes and therefore less microhabitats, made it poorly suitable for fish larvae. Although abundances were low at the restored groynes, much smaller larvae could be found, suggesting that larger larvae benefitted from the enhanced connectivity to leave this mesohabitat. Even with substantial differences in suitability for fish larvae, all groyne fields showed low abundances in 2017. Concerning the elevated discharge early in this year´s season, the groyne fields might have been overflown and large numbers of smaller fish larvae in earlier developmental stages were washed out. The poor response in abundance to the creation of the side channel was not expected, as this measure effectively protected larvae from ship induced waves in the Austrian Danube River (Kucera-Hirzinger et al., 2009) and was shown to be an essential nursery site for rheophilic fish larvae in a five-year monitoring at the Waal River, NL (Simons et al., 2001). Although it is possible that the specific location of the side channel between an unmodified and a modified groyne field decreased the connectivity and availability for smaller sized larvae, which was also found by Ramler & Keckeis (2019b) for the same site. This could be underlined by the fact that just larger larvae and juveniles, with accordingly higher swimming performance, could be found there.

The side arm mesohabitats showed a very inconsistent abundance distribution over the sampled years, although high abundances were observed in 2007, particularly in 2014 and to some extent even in 2017. The common factor for the specific side arms, in which high abundances were collected, was their cut-off side arm character. So high abundances were detected in 2007 at the side arm in the experimental section, in 2014 at the new reference side arm with an especially high abundance and in 2017 again at the new reference side arm, which all resembled more low flow bay habitats with all the protective and advantageous conditions for fish larvae already stated further above. Besides the high abundances, these side arm mesohabitats accommodated the larvae smallest in length, suggesting a high retentive capacity of those specific side arms. The low abundances at the reference side arm in 2007 and both mesohabitats in the restored side arm in 2014 were probably caused by

their morphology, resembling fully connected, higher flow sites less suitable for smaller, earlier stage larvae. This was also observed in an experimental study at the Australian Broken River, where increasing the flow velocity through reconnection in former low flow sites decreased larval fish abundance (Humphries et al., 2006). In 2017, additional to the higher flow conditions in the experimental side arm, elevated discharge could have washed out even more larvae of the restored mesohabitat, probably accounting for this second year of low abundances therein. Nevertheless, after the restoration of the side arm fish larvae or juveniles caught were larger in length in the newly created upper confluence, where flow was high and the channel width narrower. At the same time smaller sized larvae were caught at the restored downstream end. This contrasting result originated probably in a larger channel width and a gravel shore/bay on the right side, where small larvae could be retained within. Although the measures seemed to have a negative effect on the general abundance on this reconnected side arm during the investigation, the two sampled mesohabitats within promoted different larval sizes through their specific habitat morphology. Side arm habitats as lateral extensions of the main channel were found to increases nutrient and particle input, boosting primary and secondary production as food source for fish larvae, generally being required by rheophilic fish and increase the abundance of their adults in the Austrian Danube River (Hein et al., 1999; Hirzinger et al., 2004; Schmutz et al., 2014) or serve as nursery and spawning sites as found in the lower Rhine River, Germany (Grift, 2001), thus being vital elements for the riverine fish fauna.

Overall low depth and slow flow bay habitats, like the restored gravel bar, the reference side arm and old, sedimented reference groyne fields harbored the most and the smallest larvae and seem therefore ideal to enhance early and plentiful recruitment. Higher flow velocity sites, like the fully connected reference side arm in 2007, the restored side arm in the experimental section and most of the surveyed gravel bars were found to have lower abundances, but more importantly, larvae and juveniles larger in size, indicating not only a habitat shift, but a supportive role for more developed stages. This means no single mesohabitat or measure surveyed in this work could provide suitable conditions for fish early stages of all sizes and at all water levels. Of all measures in the experimental section which should increase abundance through more heterogeneity and connectivity for 0+ fish, just the removal of riprap and the enlargement of the gravel bar increased the abundance of the fish larvae therein. All other measures (groyne root opening, side channel creation and side arm reconnection) had negative effects on the abundance of 0+ fish, although it seemed they still supported larger fish larvae and juveniles. On behalf of just one measure, enlargement of the gravel bar, which increased abundance just for one series, no sustainable or sufficient increase in habitat quality as nursery sites could be identified for the modifications overall during the survey.

Discussion

At the larger scale perspective of sections, the abundances of 2007 and 2014 revealed the highest values, with the latter even higher. On the contrary was 2017 with very low abundances for both sections. In 2007 the abundances revealed no significant differences between reference and experimental section, as the mesohabitats of one type were assumed to be similar in their geomorphology across sections and therefore should have been influenced to the same extent by the abiotic conditions. Small differences with higher abundances in the reference groyne field were balanced at the section scale by higher abundances at the unmodified experimental side arm. Not only were abundances similarly high for both sections in this series, but larval sizes of 2007 where the highest of all series and did not differ significantly either. Additionally, larvae in 2007 were bigger in every developmental stage than in 2014. In early 2007 discharge decreased to a very low level, probably enhancing retention and therefore abundance. The water temperatures of this series were among the highest of all sampling series, which might explain higher survival and faster development of larvae and food organisms in shallow microhabitats.

Although after the restoration in 2014 abundance in both sections was higher compared to the previous series, the experimental section revealed a lower abundance than the reference. A survey of all fish age classes using electro fishing of restored sections in the upper Main River (Germany) and a tributary contrastingly found an increase of fish reproduction and recruitment compared to unrestored sites (Lüderitz et al., 2011). The upper Main River at their study sites is not navigable and the restoration measures were far more extensive, transforming the reach into a near-natural meandering and highly dynamic network of multiple gravel channels interconnected in a mosaic like pattern to lakes and floodplains. Similarly, a review on 36 restoration projects on small to medium rivers in Germany concluded that a substantially modification of reach morphology yielded in significantly higher diversity and abundances of fish larvae and juveniles (Lorenz et al., 2013). In contrast, the Danube River sections assessed in the present work are important for navigation and modifications just were applied to selected mesohabitats, not transforming the cross- and longitudinal section as a whole. The modification of the experimental mesohabitats might have decreased their retentive capacity of all but the modified gravel bar, causing the overall lower abundance of the experimental section in this series. Another reason for the sectional abundance difference might as well be the change of the reference section in 2014. The new reference mesohabitats could have exhibited a much higher retentive capacity than in the previous series, thus fostering abundance even more. Although, as in the first series, no significant differences in larval sizes were found, the median sizes were much lower than in 2007. This could either be indicative for a very successful spawning season, a good connectivity from spawning to nursery sites or supporting the high retention and survival of smaller larvae with-

in both sections. Nevertheless, early rising and continuously high water temperatures together with low but slowly increasing discharge in 2014 provided suitable conditions for development and growth as well as larger areas of nursery habitats.

The comparably much lower abundances of both sections in 2017 could have been caused by the washout of smaller larvae by elevated discharge early in the season paired with dropping water temperatures lowering the larvae's swimming performance. The significant difference in abundance between both sections might be explained by a higher retentive capacity of the mesohabitats in the reference section even at higher water levels, buffering such unfavorable abiotic conditions. Higher retention and abiotic buffering at the bay structured reference side arm and sedimented, aged reference groyne fields might also explain the significant size difference between the sections of this series. The higher proportion of larger larvae in the experimental section might result from the washout of small larvae at elevated flow from less retentive or protective mesohabitats like the reconnected side arm, the enlarged gravel bar or an overflown groyne field with open roots. A Danube River study on adult fish at the same sections surveyed in this work found species assemblages differ at the scale of mesohabitats with the main driving force being the hydro-morphological conditions (Loisl et al., 2014). However, in the present work, both sections had generally similar minimum larval lengths, so both included suitable mesohabitats for small larval stages. Nonetheless in the experimental section larger larvae were caught, which together with a lower abundance would point to generally less retentive capacity or less mesohabitats with high retentive capacity. The restoration of the mesohabitats within the experimental section did not improved the suitability for 0+ fish in a way that would have increased overall abundance compared to the reference section.

Conclusion

The driving forces of fish early stages abundance variations between years uncovered in this survey were the abiotic factors discharge and water temperature interacting with the geomorphologies of the each specific mesohabitat. During the two years with low discharge and high water temperatures, generally higher abundances were found, whereas at elevated discharge and low temperatures lower abundances were discovered. Temporal courses within a series are dependent on discharge and water temperature as well. Early and generally higher temperatures as well as low discharge led to faster and higher rise in larval abundance. Elevated discharge and low temperatures led to slower rises and generally lower abundances. Water temperature was found to be directly proportional related to abundance, while discharge was inversely related to it.

Water temperature was likewise important for larval size, promoting growth, but discharge was observed to be even more influential in this survey. Larger larvae occurred in lower

abundances and mostly at higher flows, while smaller larvae were often observed in higher abundances and at low flow mesohabitats. If the high abundances of smaller sized larvae originated in more successful spawning or higher survival could not be completely resolved.

Spatially most valuable and seemingly preferred by fish early stages were mesohabitats resembling bays with shallow depths and low flow, which in all years under study displayed higher abundances. They might have offered more protection against ship-induced waves and to some extent flooding, like the bay structure of the enlarged gravel bar, the aged and sedimented reference groyne fields and the cut-off reference side arm.
The latter two mesohabitats and therefore the majority of the preferred sites were located in the unmodified reference sections. The increase of heterogeneity and connectivity to enhance abundance in the restored mesohabitats was only really achieved through the removal of riprap and enlargement of the gravel bar in the experimental section. As this was the only measure of all applied yielding positive results in terms of abundance, also no general abundance increase was observed in the experimental section compared to the reference. As this effect was only observed in one series, also no sufficient and sustainable increase over multiple years could be observed. The two post-restoration years were not sufficient to rule out the heavy impact of the larger scale abiotic factors assessed and fully explain abundance variations. For this, long term and regularly conducted yearly monitoring of the 0+ fish abundances would be necessary to evaluate if the restoration measures resulted in a sustainable advantage for fish recruitment.

Discussion

Acknowledgments

First and foremost, I would like to thank Hubert Keckeis for the opportunity and his thorough and patient supervision of my thesis. I would like to thank Randy Teal for all the great inspirations and for kindly improving the English. Then I am thankful to all my colleagues who were involved in the field sampling and lab processing: Dominik Altmann, Vinzenz Bammer, Bernhard Berger, Christian Fesl, Simon Götsch, Magdalena Hirtl, Hansjörg Hoyer, Philip Kerschbaumer, Reinhard Krusch, Georg Rakowitz, David Ramler, Stefan Rösler, Elisabeth Schludermann, Michael Schöfbenker, Maximilian Sehr, Astrid Toth, Holger Villwock, Sylvia Wanzenböck, Julia Weber and Bernhard Zens. This work was a §27 research project of the University of Vienna, embedded in the Integrated River Engineering Project (IREP), which was financed by the Austrian Ministry for Transport, Innovation and Technology, the European Commission´s Trans-European Transport Network and the Viadonau Österreichische Wasserstraßen-Gesellschaft mbH. The project was coordinated by the WasserCluster Lunz. I am very grateful for the overwhelming support of my family including Monika, Roman, Niklas, Katharina and Manfred, even during the difficult times of a pandemic. Finally, and above all, thank you Sophie for your patience and for going every path with me.

Danksagung

In erster Linie möchte ich mich bei Hubert Keckeis für die Möglichkeit und seine gründliche und geduldige Betreuung meiner Arbeit bedanken. Randy Teal möchte ich für all die großartigen Inspirationen und für die freundlicherweise übernommene sprachliche Korrektur danken. Dann bedanke ich mich bei all meinen Kollegen, die am Sammeln im Feld und der Bearbeitung der Proben im Labor beteiligt waren: Dominik Altmann, Vinzenz Bammer, Bernhard Berger, Christian Fesl, Simon Götsch, Magdalena Hirtl, Hansjörg Hoyer, Philip Kerschbaumer, Reinhard Krusch, Georg Rakowitz, David Ramler, Stefan Rösler, Elisabeth Schludermann, Michael Schöfbenker, Maximilian Sehr, Astrid Toth, Holger Villwock, Sylvia Wanzenböck, Julia Weber und Bernhard Zens. Diese Arbeit war ein §27-Forschungsprojekt der Universität Wien, eingebettet in das Integrated River Engineering Project (IREP), das vom österreichischen Bundesministerium für Verkehr, Innovation und Technologie, dem Trans-European Transport Network der Europäischen Kommission und der Viadonau Österreichische Wasserstraßen-Gesellschaft mbH finanziert wurde. Koordiniert wurde das Projekt durch den WasserCluster Lunz. Ich bin sehr dankbar für die überwältigende Unterstützung meiner Familie, einschließlich Monika, Roman, Niklas, Katharina und Manfred, auch in den schwierigen Zeiten einer Pandemie. Abschließend und vor allem danke ich dir, Sophie, für deine Geduld und dass du jeden Weg mit mir gehst.

Literature

Aarts, B. G. W., Van Den Brink, F. W. B., & Nienhuis, P. H. (2004). Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: The transversal floodplain gradient. *River Research and Applications*, *20*(1), 3–23.

Albert, J. S., Destouni, G., Duke-Sylvester, S. M., Magurran, A. E., Oberdorff, T., Reis, R. E., … Ripple, W. J. (2021). Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio*, *50*(1), 85–94.

Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J. (2016). Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), 838–857.

Baras, E., & Nindaba, J. (1999). Diel dynamics of habitat use by riverine young-of-the-year Barbus barbus and Chondrostoma nasus (Cyprinidae). *Archiv Fur Hydrobiologie*, *146*(4), 431–448.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Jounal of the Royal Statistical Society. Series B (Methodological)*, *57*(1), 289–300.

Bischoff, A., & Freyhof, J. (1999). Seasonal shifts in day-time resource use of 0+ barbel, Barbus barbus. *Environmental Biology of Fishes*, *56*, 199–212.

Blaxter, J. H. S. (1991). The effect of temperature on larval fishes. *Netherlands Journal of Zoology*, *42*(2–3), 336–357.

Braaten, P. J., Fuller, D. B., Holte, L. D., Lott, R. D., Holte, L. D., Viste, W., … Legare, R. G. (2008). Drift Dynamics of Larval Pallid Sturgeon and Shovelnose Sturgeon in a Natural Side Channel of the Upper Missouri River, Montana. *North American Journal of Fisheries Management*, *28*(3), 808–826.

Chambers, R. C., & Trippel, E. (2012). *Early life history and recruitment in fish populations*. Dordrecht, NL: Springer Science & Business Media.

Collen, B., Whitton, F., Dyer, E. E., Baillie, J. E. M., Cumberlidge, N., Darwall, W. R. T., … Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, *23*(1), 40–51.

Conquest, L. L. (2000). Analysis and Interpretation of Ecological Field Data Using BACI Designs : Discussion. *Journal of Agricultural, Biological, and Environmental Statistics*, *5*(3), 293–296.

Copp, G. H. (1990). Effect of regulation on 0+ fish recruitment in the great ouse, a lowland river. *Regulated Rivers: Research & Management*, *5*(3), 251–263.

Copp, G. H. (2010). Patterns of diel activity and species richness in young and small fishes of European streams: A review of 20 years of point abundance sampling by electrofishing. *Fish and Fisheries*, *11*(4), 439–460.

Literature

Cowan, J. H., & Shaw, R. F. (2002). Recruitment. In L. A. Fuiman & R. G. Werner (Eds.), *Fishery Science - The Unique Contributions of Early Life Stages*. Oxford, UK: Blackwell Science Ltd.

Dinno, A. (2017). dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. *R Package Version 1.3.5*.

Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology*, *29*(19), 960–967.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, *81*(2).

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., & Geist, J. (2018). The importance of stream interstitial conditions for the early-life-stage development of the European nase (Chondrostoma nasus L.). *Ecology of Freshwater Fish*, *27*(4), 920–932.

Dunn, O. J. (1964). Multiple Comparisons Using Rank Sums. *Technometrics*, *6*(3), 241–252.

Freyhof, J., & Brooks, E. (2011). *European Red List of Freshwater Fishes*. *Luxembourg: Publications Office of the European Union*.

Götsch, S. (2008). *Bestandsentwicklung von Fischlarven in verschiedenen Uferzonen der Donau bei Hainburg*. University of Vienna.

Grift, R., Buijse, A. D., Densen, W. L. T. van, & Klein Breteler, J. G. P. (2001). Restoration of the river-floodplain interaction: benefits for the fish community in the River Rhine. *River Systems*, *12*(2–4), 173–185.

Grift, R. E. (2001). *How fish benefit from floodplain restoration along the lower River Rhine*. Wageningen University.

Grift, R. E., Buijse, A. D., Van Densen, W. L. T., Machiels, M. A. M., Kranenbarg, J., Klein Breteler, J. G. P., & Backx, J. J. G. M. (2003). Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. *River Research and Applications*, *19*(4), 353–374.

Hein, T., Heiler, G., Pennetzdorfer, D., Riedler, P., Schagerl, M., & Schiemer, F. (1999). The Danube Restoration Project: Functional aspects and planktonic productivity in the floodplain system. *Regulated Rivers: Research and Management*, *15*(1–3), 259–270.

Henning, M., & Hentschel, B. (2013). Sedimentation and flow patterns induced by regular and modified groynes on the River Elbe, Germany. *Ecohydrology*, *6*(4), 598–610.

Hermes-Silva, S., Reynalte-Tataje, D., & Zaniboni-Filho, E. (2009). Spatial and temporal distribution of ichthyoplankton in the Upper Uruguay river, Brazil. *Brazilian Archives of Biology and Technology*, *52*(4), 933–944.

Literature

Hirzinger, V., Keckeis, H., Nemeschkal, H. L., & Schiemer, F. (2004). The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. *River Research and Applications*, *20*(2), 137–149.

Horwitz, R. J. (1978). Temporal Variability Patterns and the Distributional Patterns of Stream Fishes. *Ecological Monographs*, *48*(3), 307–321.

Houde, E. D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin*, *87*(3), 471–495.

Humphries, P., Cook, R. A., Richardson, A. J., & Serafini, L. G. (2006). Creating a disturbance: Manipulating slackwaters in a lowland river. *River Research and Applications*, *22*(5), 525–542.

Humphries, P., King, A., McCasker, N., Kopf, R., Stoffels, R., Zampatti, B. P., & Price, A. (2019). Riverscape recruitment: a conceptual synthesis of drivers of fish recruitment in rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(2), 213–225.

Humphries, P., Serafini, L. G., & King, A. J. (2002). River regulation and fish larvae: Variation through space and time. *Freshwater Biology*, *47*(7), 1307–1331.

Hunt von Herbing, I. (2002). Effects of temperature on larval fish swimming performance: The importance of physics to physiology. *Journal of Fish Biology*, *61*(4), 865–876.

Jungwirth, M., Moog, O., & Muhar, S. (1993). Effects of river bed restructuring on fish and benthos of a fifth order stream, melk, Austria. *Regulated Rivers: Research & Management*, *8*(1–2), 195–204.

Jurajda, P. (1999). Comparative nursery habitat use by 0+ fish in a modified lowland river. *River Research and Applications*, *15*(1–3), 113–124.

Jurajda, P., Reichard, M., Hohausova, E., & Cerny, J. (2001). Comparison of 0+ fish communities between regulated-channelized and floodplain stretches of the River Morava. *River Systems*, *12*(2–4), 187–202.

Keckeis, H. (2014). Short-term effects of inshore restoration measures on early stages, benthic species, and the sublittoral fish assemblage in a large river (Danube, Austria). *Hydrobiologia*, *729*(1), 61–76.

Keckeis, H., Frankiewicz, P., & Schiemer, F. (1996). The importance of inshore areas for spawning nase Chondrostoma nasus (Cyprinidae) in a free-flowing section of a large river (Danube, Austria). *River Systems*, *10*(1–4), 51–64.

Keckeis, H., Lechner, A., & Ramler, D. (2014). Bestimmung früher Entwicklungsstadien heimischer Fische 300148 PP Fischökologie - Drift und Habitatwahl von Donaufischen. University of Vienna.

Keckeis, H., & Schiemer, F. (2002). Understanding conservation issues of the Danube river. In L. A. Fuiman & R. G. Werner (Eds.), *Fishery Science. The unique contributions of early life stages* (pp. 272–288). Oxford, UK: Blackwell Science Ltd.

Literature

Keckeis, H., Winkler, G., Flore, L., Reckendorfer, W., & Schiemer, F. (1997). Spatial and seasonal characteristics of 0+ fish nursery habitats of Nase, Chondrostoma nasus in the river Danube, Austria. *Folia Zoologica*, *46*(Suppl. 1), 133–150.

King, A., Humphries, P., & McCasker, N. (2013). Reproduction and early life history. In P. Humphries & K. Walker (Eds.), *Ecology of Australian freshwater fishes* (pp. 159–192). Melbourne, AU: CSIRO Publishing.

Klasz, G., Krouzecky, N., Reckendorfer, W., Schmalfuß, R., & Schlögl, R. (2009). New hydro-engineering approaches : river bank renaturation and groyne redesign along the Danube east of Vienna. *Österreichische Ingenieur- Und Architekten-Zeitschrift*, *154*(1-6), 1–10.

Kucera-Hirzinger, V., Schludermann, E., Zornig, H., Weissenbacher, A., Schabuss, M., & Schiemer, F. (2009). Potential effects of navigation-induced wave wash on the early life history stages of riverine fish. *Aquatic Sciences*, *71*(1), 94–102.

Kujawa, R. & Glińska-Lewczuk, K. (2011). The Impact of Regulation and Hydrotechnical Works in River Channels on the Rheophilic Cyprinidae Fish. *Contem. Probl. Manag. Environ. Prot.*, 7. 233–248.

Langler, G. J. & Smith, C. (2001). Effects of habitat enhancement on 0-group fishes in a lowland river. *River Research and Applications*, *17*(6), 677–686.

Latli, A., Michel, L. N., Lepoint, G., & Kestemont, P. (2019). River habitat homogenisation enhances trophic competition and promotes individual specialisation among young of the year fish. *Freshwater Biology*, *64*(3).

Lechner, A., Keckeis, H., Schludermann, E., Humphries, P., McCasker, N., & Tritthart, M. (2014). Hydraulic forces impact larval fish drift in the free flowing section of a large European river. *Ecohydrology*, *7*(2), 648–658.

Liedermann, M., Tritthart, M., Gmeiner, P., Hinterleitner, M., Schludermann, E., Keckeis, H., & Habersack, H. (2014). Typification of vessel-induced waves and their interaction with different bank types, including management implications for river restoration projects. *Hydrobiologia*, *729*(1), 17–31.

Loisl, F., Singer, G., & Keckeis, H. (2014). Method-integrated fish assemblage structure at two spatial scales along a free-flowing stretch of the Austrian Danube. *Hydrobiologia*, *729*(1), 77–94.

Lorenz, A. W., Stoll, S., Sundermann, A., & Haase, P. (2013). Do adult and YOY fish benefit from river restoration measures? *Ecological Engineering*, *61*(PA), 174–181.

Lorig, R. C., Marchetti, M. P., & Kopp, G. (2013). Spatial and temporal distribution of native fish larvae in seasonal and perennial tributaries of the Sacramento River, CA, USA. *Journal of Freshwater Ecology*, *28*(2), 179–197.

Literature

Lüderitz, V., Speierl, T., Langheinrich, U., Völkl, W., & Gersberg, R. M. (2011). Restoration of the Upper Main and Rodach rivers - The success and its measurement. *Ecological Engineering*, *37*(12), 2044–2055.

Mann, R. H. K., & Bass, J. A. B. (1997). The critical water velocities of larval roach (Rutilus rutilus) and dace (Leuciscus leuciscus) and implications for river management. *Regulated Rivers: Research and Management*, *13*(3), 295–301.

Matzinger, M. (2009). *Nahrungszusammensetzung unterschiedlicher Entwicklungsstadien von Jungfischen der Donau*. University of Vienna.

McCune, B., & Grace, J. B. (2002). *Analysis of Ecological Communities*. *Analysis of Ecological Communities*. Gleneden Beach, OR, USA: MjM Software Design.

Meekan, M. G., Carleton, J. H., McKinnon, A. D., Flynn, K., & Furnas, M. (2003). What determines the growth of tropical reef fish larvae in the plankton: Food or temperature? *Marine Ecology Progress Series*, *256*(Houde 1989), 193–204.

Meulenbroek, P., Drexler, S., Huemer, D., Gruber, S., Krumböck, S., Rauch, P., … Waidbacher, H. (2018). Species-specific fish larvae drift in anthropogenically constructed riparian zones on the Vienna impoundment of the River Danube, Austria: Species occurrence, frequencies, and seasonal patterns based on DNA barcoding. *River Research and Applications*, *34*(7), 854–862.

Mueller, M., Pander, J., & Geist, J. (2014). The ecological value of stream restoration measures: An evaluation on ecosystem and target species scales. *Ecological Engineering*, *62*, 129–139.

Muhar, S., Schmutz, S., & Jungwirth, M. (1995). River restoration concepts - goals and perspectives. *Hydrobiologia*, *303*(1–3), 183–194.

Olariu, C., Krezsek, C., & Jipa, D. C. (2018). The Danube River inception: Evidence for a 4 Ma continental-scale river born from segmented ParaTethys basins. *Terra Nova*, *30*(1), 63–71.

Oscoz, J., Leunda, P. M., Miranda, R., García-Fresca, C., Campos, F., & Escala, M. C. (2005). River channelization effects on fish population structure in the Larraun river (Northern Spain). *Hydrobiologia*, *543*(1), 191–198.

Pander, J., Mueller, M., Knott, J., Egg, L., & Geist, J. (2017). Is it Worth the Money? The Functionality of Engineered Shallow Stream Banks as Habitat for Juvenile Fishes in Heavily Modified Water Bodies. *River Research and Applications*, *33*(1), 63–72.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, *39*(2), 175–192.

Persat, H., & Copp, G. H. (1989). Electrofishing and Point Abundance Sampling for the

Ichthyology of Large Rivers. In I. G. Cowx (Ed.), *Developments in Electrofishing* (pp. 203–215). Oxford, UK: Fishing News Books.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & R Core Team. (2020). nlme: Linear and Nonlinear Mixed Effects Models. *R Package Version 3.1-148*.

Qin, J., Cheng, F., Zhang, L., Schmidt, B. V., Liu, J., & Xie, S. (2019). Invasions of two estuarine gobiid species interactively induced from water diversion and saltwater intrusion. *Management of Biological Invasions*, *10*(1), 139–150.

Ramler, D., Ahnelt, H., Nemeschkal, H. L., & Keckeis, H. (2016). The drift of early life stages of Percidae and Gobiidae (Pisces: Teleostei) in a free-flowing section of the Austrian Danube. *Hydrobiologia*, *781*(1), 199–216.

Ramler, David, & Keckeis, H. (2018). Erste Ergebnisse des Fischmonitorings im Rahmen des Flussbaulichen Gesamtprojekts östlich von Wien: ein Überblick. *Österreichs Fischerei*, *71*(4).

Ramler, David, & Keckeis, H. (2019a). Effects of hydraulic engineering restoration measures on invasive gobies in a large river (Danube, Austria). *Biological Invasions*, *22*, 437–453.

Ramler, David, & Keckeis, H. (2019b). Effects of large-river restoration measures on ecological fish guilds and focal species of conservation in a large European river (Danube, Austria). *Science of the Total Environment*, *686*, 1076–1089.

Ramler, David, & Keckeis, H. (2019c). Occurrence of non-native fishes in the Danube east of Vienna (Austria) and potential interactions of invasive gobiids with native fishes. *Journal of Applied Ichthyology*, (April), 850–862.

Ramler, David, Keckeis, H., & Ahnelt, H. (2014). Gattungsbestimmung bei Embryonal-, Larval- und Juvenilstadien der Barsche (Percidae) und Meergrundeln (Gobiidae) Österreichs. *Österreichs Fischerei*, *67*, 299–307.

Reckendorfer, W., Keckeis, H., Winkler, G., & Schiemer, F. (1999). Zooplankton abundance in the River Danube, Austria: The significance of inshore retention. *Freshwater Biology*, *41*(3), 583–591.

Reckendorfer, Walter, Schmalfuss, R., Baumgartner, C., Habersack, H., Hohensinner, S., Jungwirth, M., & Schiemer, F. (2005). The Integrated River Engineering Project for the free-flowing Danube in the Austrian Alluvial Zone National Park : contradictory goals and mutual solutions. *Archiv für Hydrobiologie*, *15*(Suppl. 155/1-4), 613–630.

Reynalte-Tataje, D. A., Zaniboni-Filho, E., Bialetzki, A., & Agostinho, A. A. (2012). Temporal variability of fish larvae assemblages: Influence of natural and anthropogenic disturbances. *Neotropical Ichthyology*, *10*(4), 837–846.

Reynolds, J. D., Webb, T. J., & Hawkins, L. A. (2005). Life history and ecological correlates of extinction risk in European freshwater fishes. *Canadian Journal of Fisheries and*

Aquatic Sciences, *62*(4), 854–862.

Ricciardi, A., & Rasmussen, J. B. (1999). Extinction Rates of North American Freshwater Fauna Published by : Wiley for Society for Conservation Biology Linked references are available on JSTOR for this article : Extinction Rates of North American Freshwater Fauna. *Society for Conservation Biology*, *13*(5), 1220–1222.

Schiemer, F., Keckeis, H., Reckendorfer, W., & Winkler, G. (2001). The “inshore retention concept” and its significance for large rivers. *River Systems*, *12*(2–4), 509–516.

Schiemer, F., Keckeis, H., Winkler, G., & Flore, L. (2001). Large rivers: the relevance of ecotonal structure and hydrological properties for the fish fauna. *River Systems*, *12*(2–4), 487–508.

Schiemer, F., & Spindler, T. (1989). Endangered Fish Species of the Danube River in Austria. *Regulated Rivers: Research & Management*, *4*(June), 397-407.

Schludermann, E., Liedermann, M., Hoyer, H., Tritthart, M., Habersack, H., & Keckeis, H. (2014). Effects of vessel-induced waves on the YOY-fish assemblage at two different habitat types in the main stem of a large river (Danube, Austria). *Hydrobiologia*, *729*(1), 3–15.

Schludermann, Elisabeth, Tritthart, M., Humphries, P., & Keckeis, H. (2012). Dispersal and retention of larval fish in a potential nursery habitat of a large temperate river: an experimental study. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(8), 1302–1315.

Schmutz, S., Kremser, H., Melcher, A., Jungwirth, M., Muhar, S., Waidbacher, H., & Zauner, G. (2014). Ecological effects of rehabilitation measures at the Austrian Danube: a meta-analysis of fish assemblages. *Hydrobiologia*, *729*(1), 49–60.

Sheldon, A. L. (1988). Conservation of Stream Fishes: Patterns of Diversity, Rarity, and Risk. *Conservation Biology*, *2*(2), 149–156.

Simons, J. H. E. J., Barker, C., Schropp, M. H. I., Jans, L. H., Kok, F. R., & Grift, R. E. (2001). Man-made secondary channels along the river rhine (the Netherlands); results of post-project monitoring. *River Research and Applications*, *17*(4–5), 473–491.

Smith, E. P. (2014). BACI Design . *Wiley StatsRef: Statistics Reference Online*, 1–12.

Smith, E. P., Orvos, D. R., & Cairns Jr., J. (1993). Impact assessment using the before-after-control-impact (BACI) model: concerns and comments. *Canadian Journal of Fisheries and Aquatic Sciences 50: 627–637.*

Song, Y., Cheng, F., Ren, P., Wang, Z., & Xie, S. (2019). Longitudinal recovery gradients of drifting larval fish assemblages in the middle reach of the yangtze river: Impact of the three gorges dam and conservation implementation. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(12), 2256–2267.

Stagl, J. C., & Hattermann, F. F. (2015). Impacts of climate change on the hydrological

regime of the danube river and its tributaries using an ensemble of climate scenarios. *Water*, *7*(11), 6139–6172.

Tockner, K., Schiemer, F., & Ward, J. V. (1998). Conservation by restoration: The management concept for a river-floodplain system on the Danube river in Austria. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *8*(1), 71–86.

Turner, T. F., Trexler, J. C., Miller, G. L., & Toyer, K. E. (1994). Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. *Copeia*, *1994*(1), 174–183.

viadonau. (2012). *Die kennzeichnenden Wasserstände der österreichischen Donau*. Vienna, AT: via donau - Österreichische Wasserstraßen-Gesellschaft mbH.

Villwock, H. (2016). *Of Larvae and Men Anthropogenic impact on the abundance and distribution of 0+fish in a large river (Austrian Danube).* University of Vienna.

Wang, Z., Cheng, F., Hou, G., Song, Y., Thundiparambil Sathrajith, A., & Xie, S. (2019). Distribution of Botia superciliaris (Günther, 1892) ichthyoplankton in the upper mainstem of the Yangtze River preimpoundment and postimpoundment of the upstream dam cascade. *River Research and Applications*, *35*(7), 1053–1061.

Weller, P. (2009). The Danube River– The Most International River Basin. In *Handbook of Catchment Management* (pp. 287–302).

Wimmer, R., Wintersberger, H., & Parthl, G. (2012). *Hydromorphologische Leitbilder - Fließgewässertypisierung in Österreich*. Vienna, AT: Austrian Federal Ministry of Agriculture, Forestry, Environment and Water Management.

Winkler, G., Keckeis, H., Reckendorfer, W., & Schiemer, F. (1997). Temporal and spatial dynamics of 0+ Chondrostoma nasus, at the inshore zone of a large river. *Folia Zoologica*, *46*((Suppl. 1)), 151–168.

Wolter, C. (2007). Temperature influence on the fish assemblage structure in a large lowland river, the lower Oder River, Germany. *Ecology of Freshwater Fish*, *16*(4), 493–503.

Wolter, Christian, & Sukhodolov, A. (2008). Random Displacement Versus Habitat Choice of Fish Larvae in Rivers. *River Research and Applications*, *24*, 661–672.

Zuur, A., Leno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science & Business Media.