universität
wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Fish assemblages at different inshore mesohabitats in the main stem of the Danube east of Vienna"

verfasst von / submitted by

Dipl.-Ing. Astrid Toth, Bakk.techn.

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

Master of Science (MSc)

Wien, 2016 / Vienna 2016

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

1 Table of Contents

2 Abstract

Inshore zones in large rivers are essential as fish spawning grounds, as nursery habitats and are therefore important for recruitment. They provide shelter from predators as well as from harsh physical conditions (e.g. during flood events). This study was conducted in the Danube River (Alluvial Zone National Park) in Bad Deutsch-Altenburg and Hainburg from early March to late December 2014. Four different inshore mesohabitat types were sampled by means of wading electrofishing to compare the seasonal occurrence and distribution of fish assemblages: gravel bars, side arms (both considered natural), as well as artificially constructed rip raps and groyne fields.

A total of 37 species were found in these inshore habitats. The flow velocity, the water depth, and the discharge were used to analyze the relation between fish abundance and the hydraulic conditions. The environment-species relationship indicated that the changes in fish assemblages were mainly influenced by the discharge amount and by season. Fish abundance increased significantly with increasing discharge; it was highest in the summer (July and August).

Fish assemblages differed significantly between mesohabitat types. Although the species number was almost equally high at the gravel bars, in the side arms, and groyne fields, some species were most abundant in the side arms. The lowest species numbers were observed in the rip raps. Moreover, the assemblages also changed significantly during the sampling period. The four most abundant species (*Alburnus alburnus*, *Neogobius melanostomus*, *Chondostroma nasus*, *Barbus barbus*) showed a species- specific seasonal pattern.

The hydro-morphological characteristics of the shores and their capacity to buffer the effects of water level fluctuations, as well as the lateral connectivity, are significant for the occurrence and abundance of inshore fish assemblages.

3 Zusammenfassung

In großen Flüssen spielen Uferzonen eine bedeutende Rolle als Laich- und Aufwuchshabitate und spielen daher eine wichtige Rolle für den Fischbestand. Außerdem bieten sie Schutz vor Räubern, ebenso wie vor rauen Umweltbedingungen (z.B. während Hochwässern). Diese Studie wurde in der Donau (Nationalpark Donauauen) in Bad Deutsch-Altenburg und Hainburg von März bis Dezember 2014 durchgeführt. Um das saisonale Vorkommen und die saisonale Verteilung von Fischgemeinschaften zu vergleichen, wurden vier unterschiedliche Mesohabitate mittels Handanode beprobt: Schotterbänke und Seitenarme, beide können als naturnahe Habitate angesehen werden, sowie Blockwürfe und Buhnenfelder, welche als künstlich geschaffene Habitate gelten.

In Summe wurden 37 Arten in den Uferhabitaten bestimmt. Um den Zusammenhang zwischen der Abundanz von Fischen und den hydraulischen Bedingungen zu testen, wurden die Fließgeschwindigkeit, die Wassertiefe und der Abfluss herangezogen. Die Ergebnisse zeigten, dass die Wechselwirkung zwischen Umwelt und Arten am stärksten durch den Abfluss beeinflusst werden. Die Fischabundanz stieg signifikant mit ansteigendem Abfluss und war am höchsten in den Sommermonaten (Juli, August).

Fischgemeinschaften unterschieden sich signifikant zwischen den verschiedenen Habitaten. Obwohl die Anzahl der vorkommenden Arten auf den Schotterbänken, in den Seitenarmen und Buhnenfeldern in etwa gleich groß war, kamen einige Arten in größerer Anzahl in den Seitenarmen vor. Die wenigsten Fischarten wurden in den Blockwürfen verzeichnet. Außerdem konnten signifikante Unterschiede in den Fischgemeinschaften festgestellt werden. Die vier häufigsten Arten (*Alburnus alburnus*, *Neogobius melanostomus*, *Chondostroma nasus* und *Barbus barbus*) zeigten ein artenspezifisches, saisonales Muster der Abundanz.

Die hydro-morphologischen Eigenschaften der Ufer und die damit verbundene Pufferkapazität bei Hochwässern, als auch die laterale Konnektivität sind ausschlaggebend für das Auftreten und die Abundanz von Fischgemeinschaften und einzelner Arten.

4 Introduction

The Austrian part of the Danube has undergone immense environmental changes, because of flood protection, navigation, and the construction of hydroelectric power dams (Tockner et al., 2009; Schiemer and Spindler, 1989). These measures resulted in ecological degradation caused by the disconnection of the side arms, embankment construction that reduced shore heterogeneity, and the resulting habitat loss. For fishes, these changes led to a decrease and even loss of spawning and nursery habitats (Dolédec, 2015; Keckeis, 2013; Loisl et al., 2013; Strayer, 2010; King et al., 2009; Jungwirth et al., 2003).

Especially for early and juvenile stages of fish, the spatial heterogeneity of inshore habitats is important for survival (Humphries and Lake, 2000). Diverse inshore habitats, connected side arms, and floodplains offer refuges from harsh physical conditions (i.e. stochastic flood events; Schlosser, 1991). The characteristics of the shore influence its capacity to buffer water level fluctuations (Daufresne et al., 2015; Loisl et al., 2013; Strayer, 2010; Jackson, 2001; Oberdorff, 2001; Schiemer, 2000; Poff et al., 1997; Schiemer and Spindler, 1989). Accordingly, depending on the shore type, environmental or seasonal changes in discharge may affect the fish assemblages. This can lead to an emigration or an immigration of individuals. Assemblage variability increases with increasing flow or with discharge variability (Poff and Zimmermann, 2010; Strayer, 2010; Oberdorff, 2001).

Zones with a higher structural complexity support more biota than more uniform zones with a low structural complexity. An important factor for biodiversity is the connectivity within and between different shore zones. Especially for fishes that require different habitat types during their life cycle, this connectivity plays a crucial role for recruitment (Strayer, 2010; Zeug and Winemiller, 2008; Amoros, 2002; Jackson et al., 2001). High fish diversity is an important indicator of the ecological status of a river due to fish life cycles and the resulting habitat requirements (Loisl et al., 2013; Schiemer and Spindler, 1989).

Inshore zones of rivers generally consist of habitats with intensive nutrient cycling. Such zones have a high retention capacity that enhances nutrient cycling and therefore phyto- and zooplankton production (Jungwirth et al., 2003; Schiemer et al., 2001; Reckendorfer et al., 1999). Plankton as well as other invertebrates and algae are an important food source for young stages of fishes (Kottelat and Freyhof, 2007; Fuiman and Werner, 2002; Reckendorfer et al., 2001). In general, more individuals and more fish species occur in food rich habitats (Grenouillet, 2002).

An additional ecological function of inshore zones is protection from aquatic and terrestrial predators (Jungwirth et al., 2003; Grenouillet, 2002; Jackson et al., 2001; Schiemer, 2000; Mittelbach 1981). Juveniles or adults of small-sized fish species inhabit shallow waters to avoid predators in deeper areas of the stem. This can lead to more intense competitive interactions in such shore zones (Schlosser, 1991). Fish communities can change in response to the presence or absence of specific predators (Jackson et al., 2001).

A multitude of environmental factors also define fish assemblages. Some studies have analysed fish assemblages in terms of their habitat preferences as well as their relation to abiotic and biotic factors. The present study was conducted in the Alluvial Zone National Park, where natural and artificial inshore mesohabitats were investigated. In this context, Erős et al. (2008) specified that the species pool remains the same in natural and artificial shorelines in the Danube in Hungary. Nevertheless, native fish species prefer natural habitats. Watkins et al. (2015) showed that more species were found in side-channel habitats of the Lower Kootenai River in Idaho than in the main channel, and that non-native species prefer newly rehabilitated habitats. Gormann and Karr (1978) reported that fish communities are more stable in natural habitats than in modified streams (in Panama and Indiana). Nevertheless, according to Oberdorff et al. (2001) the variability and persistence of fish assemblages decreased with environmental variability (e.g. discharge variability) in streams of north-western France.

This study was designed to compare the temporal and spatial occurrence and distribution of fish assemblages at the inshore zones of two different river sections of the free-flowing stem of the Danube River between Bad Deutsch-Altenburg and Hainburg, Austria. To analyse the relation between fish abundance and the hydraulic conditions, different inshore zones were sampled. They vary in their morphology, substrate composition, and hydraulic conditions: gravel bars, side arms (both considered natural), and the artificially constructed rip raps and groyne fields. Based on the different shore morphology, a changing discharge can lead to a changing availability, connectivity, and quality of microhabitats and refugia (Schiemer, 2000). The following hypotheses were put forward: (1) The riparian zones in the main stem of the Danube are characterized by diverse fish assemblages. (2) The composition of these fish assemblages varies among the different mesohabitats. (3) Important factors are the hydro-morphological conditions, the flow conditions (water level and its change over time) as well as the seasonal development of individual species.

The study was conducted to gain more information about the occurrence and the distribution of fish assemblages in differently structured inshore habitats over a one-year period. This knowledge should highlight the importance of the inshore habitats of a main channel: Due to the loss of lateral connectivity, these inshore habitats become increasingly important as nursery habitats and as refugia (e.g. stochastic flood events, Jungwirth et al., 2003; Schiemer, 2000; Schlosser, 1991).

Hence, this study should provide essential information for further rehabilitation measures in large rivers: It offers detailed information about seasonal and temporal changes in abundance of numerous characteristic species and neobiota in different inshore habitats.

5 Material and Methods

5.1 River sections

Sampling was conducted along inshore zones located in the main channel of the Danube River east of Vienna, Austria. Within the area between Bad Deutsch-Altenburg and Hainburg, two river sections with a length of 2 and 3 km, respectively, were investigated. Sampling took place once a month in bi-weekly to monthly intervals from early March 2014 to late December 2014. In each sampling area, four different mesohabitats – groyne fields, side arms, rip raps, and gravel bars – were sampled.

The sampling area Bad Deutsch-Altenburg extended from river kilometre 1884.00 to river kilometre 1887.00. The side arm (1884.55), the rip rap (1884.80) and the gravel bar (1885.40) were on the right shore. The groyne field (1886.04) and the gravel bar (1886.85) were on the left shore of the Danube River. The river section Hainburg extended from river kilometre 1881.00 to river kilometre 1883.00. The side arm (1882.90), the rip rap (1881.25), and the gravel bar (1882.10) were on the right shore, the groyne fields (1882.00; 1882.15) on the left shore (Fig. 1).

Figure 1: Description and location of sampled mesohabitats in the river section Bad Deutsch Altenburg (N) and Hainburg (RN). ri = right shore, le = left shore. Symbols reflect the sampled transects.

5.1.1 Mesohabitats

Groyne field

A groyne is a transverse structure in a river – a small dam made of stones, gravel or rocks – which are built at a specific angle to the flow. The construction starts at the riverbank with the root and ends with a head at the regulation line. They are designed to control floods, to lead water in the navigation channel, and to protect the shore from erosion (Yossef, 2015). Depending on the water level, the sampling was conducted between these transverse structures along the shores, where the flow velocity was less than in the main channel. The substrate of the groyne fields was composed of natural gravel with small gravel-bars at low-flow-conditions. The groyne fields in the river sections were formed differently. In Bad Deutsch-Altenburg the cross-profile of the shore showed a stepped characteristic with a steep rip rap, a steep shore dominated by soil, and a flat gravel bar. In contrast, the longitudinal profile of the shore in Hainburg was formed as a flat gravel bar with a pool and a steep shore crisscrossed with roots at the end. Hence, depending on the structure of the shore and the water level, the vegetation was flooded. In Bad Deutsch-Altenburg, grass and small shrubs were flooded; in Hainburg, beside grass and shrubs, deadwood, wood debris and branches of trees were found in the water of both groyne fields sampled (Fig. 2).

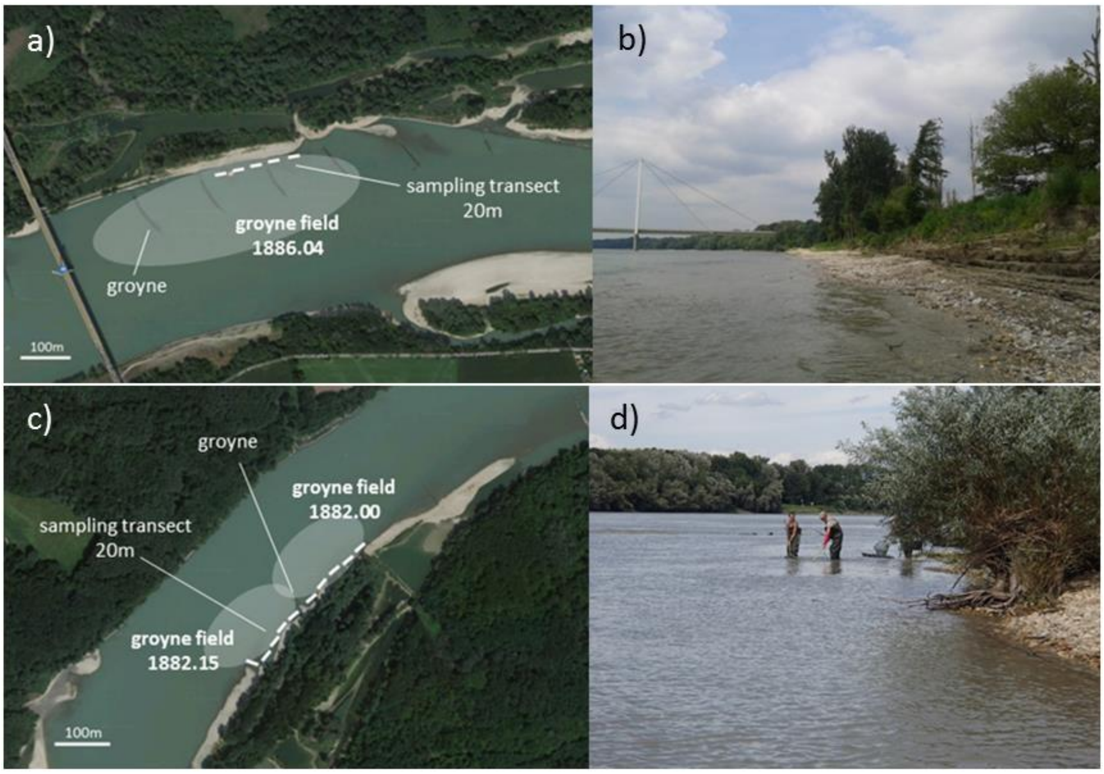

Figure 2: Description and location of the groyne fields (GR) in the river sections Bad Deutsch Altenburg (N; a, b) and Hainburg (RN; c, d). a) GR in N at low-water level; b) GR in N in June 2014, mean-flow conditions, left shore; c) GRs in RN at low-water level; d) GR in RN in August 2014, mean-flow conditions, right shore (Fig. 6). Further information about flow velocity and water depth, see Tab. 1 and Tab. 2; lines represent the sampled transects.

Rip rap

The rip rap is an artificial construction made of armour stones to protect the shores from water erosion. In Bad Deutsch-Altenburg, branches of trees hung in the water during high-water conditions. In Hainburg the stream "Russbach" entered into the Danube downstream of the rip rap. The shore in Bad Deutsch-Altenburg was steeper than the shore in Hainburg, where shallow and step areas alternated (Fig. 3).

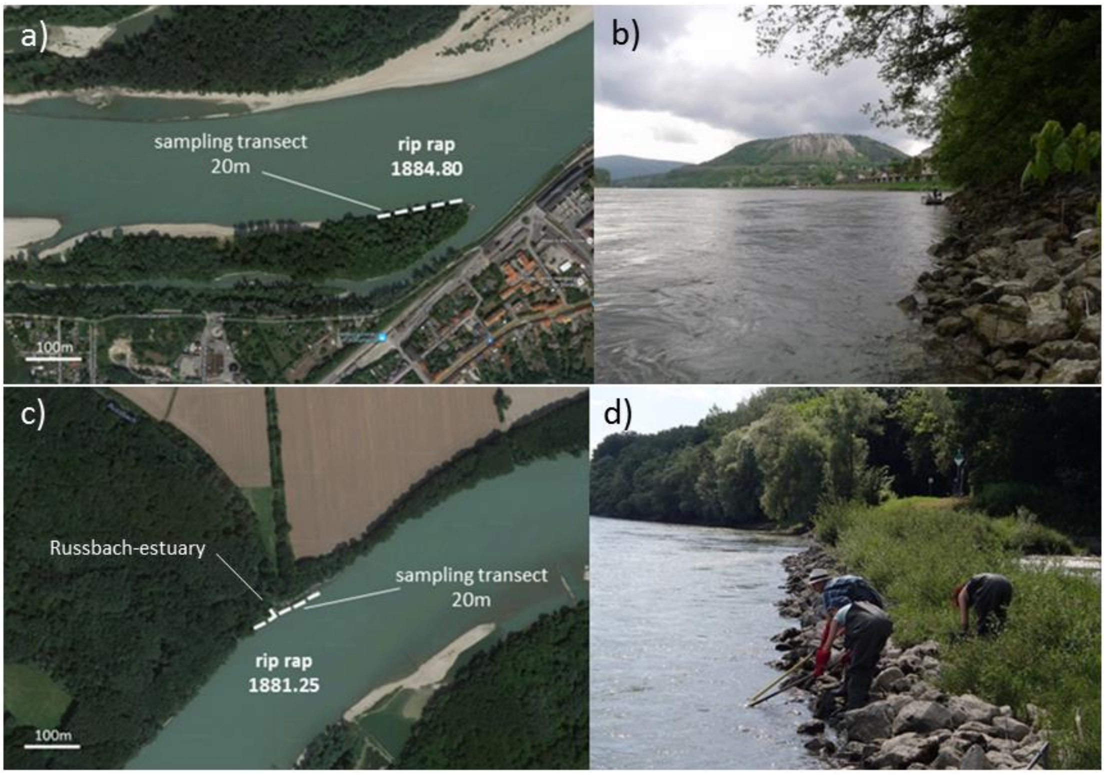

Figure 3: Description and location of the rip raps (RR) in the river sections Bad Deutsch Altenburg (N; a, b) and Hainburg (RN; c, d). a) RR in N at lower-water level; b) RR in N in May 2014 at mean-water level, right shore; c) RR in RN at low-water level; d) RR in RN in June 2014 at mean-water level; left shore (Fig. 6). Further information about flow velocity and water depth, see Tab. 1 and Tab. 2; lines represent the sampled transects.

Side arm

The side arm "Johlerarm" in Bad Deutsch-Altenburg was permanently connected to the main channel on both ends, whereas the side arm in Hainburg was temporary connected to the main channel on one end (Fig. 4). In Bad Deutsch-Altenburg the substrate of the side arms was composed of silt and gravel. The shores were overgrown by reeds and grass, which were flooded at the high water level. In Hainburg the substrate consisted mainly of mud along with large stones from the ripraps.

Figure 4: Description and location of the side arms (SA) in the river sections Bad Deutsch Altenburg (N; a, b) and Hainburg (RN; c, d). a) SA in N at low-water level; b) Sa in N in May 2014 at high-water level, right shore; c) SA in RN at low-water level; d) SA in RN in August 2014 at high-water level, left shore (Fig. 6). Further information about flow velocity and water depth, see Tab. 1 and Tab. 2; lines represent the sampled transects.

Gravel bar

A gravel bar is an elevated area at the shores of a river with a lower depth gradient towards the sublittoral compared to the other mesohabitat types. In Bad Deutsch-Altenburg, one gravel bar on the left shore (Fig. 5, a, b) and one on the right shore (Fig. 5, c, d) were sampled. The gravel bar (1886.85) on the left shore was located at a restored groyne field. The groynes were modified from river kilometre 1886.90 to 1885.80 from February 2012 to July 2014. In front of this mesohabitat, a gravel island was heaped during the restoration measures. Depending on the water level, this island was flooded and, along the shore, branches of trees and wood debris hung into the water. The sediment was dominated by gravel and fine sediment. The gravel bar (1885.40) on the right shore was characterised by a very shallow slope towards the navigation channel; it was very homogeneous regarding water depth. In Hainburg (Fig. 5) the gravel bar had a shallow, homogeneous slope. The sampling transects were located on both sides of the gravel bar, one side facing the main channel and the other side facing the shore. Depending on the water level, the side facing the shore provided habitats with low flow velocity. The substrate was composed of gravel and sand.

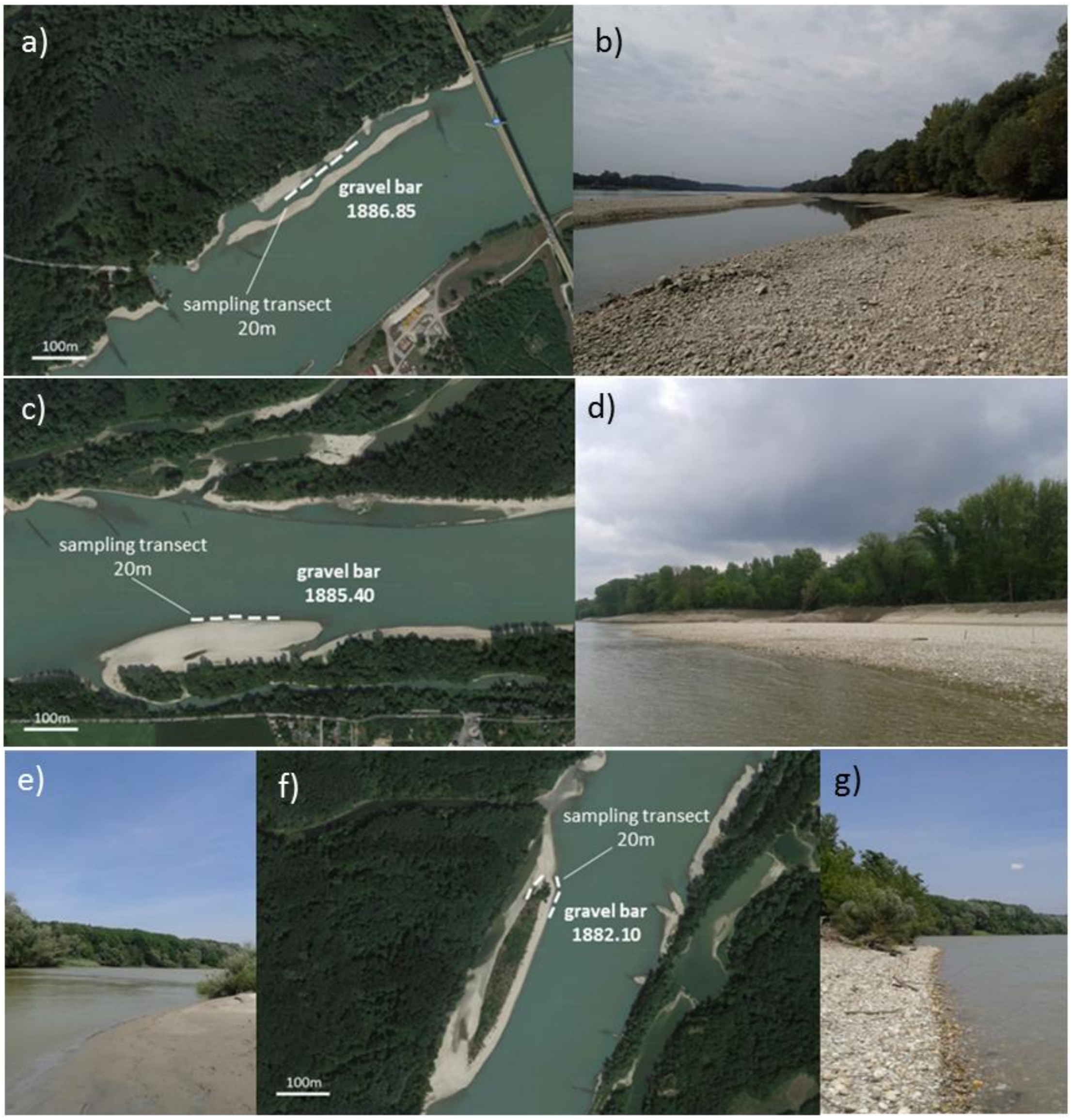

Figure 5: Description and location of the gravel bars (GB) in the river sections Bad Deutsch Altenburg (N; a-d) and Hainburg (RN; e-g). a) GB in N at low-water level; b) GB in N in September 2015 at low-water level, left shore; c) GB in N at low-water level; d) GB in N in May 2014 at mean-water level, right shore; e) GB (facing the shore) in RN in May 2014 at mean-water level, left shore; f) GB in RN at low-water level; g) GB (facing the stream) in RN in May 2014 at mean-water level, left shore (Fig. 6). Further information about flow velocity and water depth, see Tab. 1 and Tab. 2; lines represent the sampled transects.

5.2 Wading electrofishing

The littoral habitats of the Danube River were sampled by means of wading electrofishing, which provides valuable information about fish assemblages and their change over time as well as relative abundances (BONAR et al., 2009). A 300-500 Volt generator (EL 62 II) with continuous direct current (2-4 Ampere) was used. At each sampling site, 5 line transects with 20 m length each were sampled by wading upstream along the shore (Figs. 2-5). One person used the anode, two others collected the fishes with a dip net (mesh size: 4mm). The collected fishes were kept in a bucket filled with fresh river water. Individuals from each catch were determined to species level, counted, and total lengths (TL) measured. All fishes were released back into the river. When more than 30 individuals of one species were caught, the individual number was recorded and a subsample of 30 individuals was measured. Additionally, the flow velocity (m s^{-1}) and the water depth (m) were measured three times in each of the 5 transects per site. Conductivity (µS cm^{-1}) and the water temperature (°C) were recorded once per sampling date at every sampling site.

5.3 Statistical analyses

Data analyses

Catch data were standardized by the fishing time (catch per unit effort expressed as individuals per minute) as a measure of fish abundance (Guy and Brown, 2007).

For further analyses and comparisons, and because the data set consisted of a high number of "zeros", the abundance values (CPUE, Ind. min^{-1}) were transformed after McCune and Grace (2002).

Species number, the Shannon-Wiener Index, and Evenness (Magurran, 2004) were calculated in order to compare the spatial and temporal biodiversity of the different mesohabitats in each sampling area. The Kruskal-Wallis-Test was used for multiple comparisons of abundance and diversity indices (species number, Shannon-Wiener index, and Evenness) among the mesohabitats (combined data of both river sections), among the mesohabitats of each river section, and for temporal changes (seasonal patterns). The Mann-Whitney-U-Test was conducted to test the differences of the mesohabitats within a river section. Furthermore, the Kruskal-Wallis-Test was used to test the ecological guilds among the mesohabitats (combined data of the river sections) and among the mesohabitats of each river section. The Mann-Whitney-U-Test was conducted to test the differences of the guilds between the same habitat types of the river sections.

A generalized linear model was applied to conduct a multiple comparison of the environmental variables (water depth, flow velocity) between the river sections, among the mesohabitats (combined data of both river sections), as well as to test the variation among different mesohabitats of the river sections. Accordingly, these comparisons were made for the temporal change. For the variable water depth the “gaussian distribution”, and for the variable flow velocity the “quasipoisson distribution” were used, after testing for normal distribution (Shapiro-Wilk-Test).

Spearman-correlation-analysis was applied in order to relate the discharge with the environmental variables (water depth, flow velocity), and with the abundance (Ind. min^{-1}) per river section, per mesohabitat, and per mesohabitat of each river section.

Differences of fish assemblages among mesohabitats, as well as seasonal changes were analysed by non-metric Multidimensional Scaling (NMDS) and an analysis of similarity (ANOSIM). The graphs of the NMDS show centroids (mean values of each calculated point of NMDS 1 and NMDS 2) with the standard deviation. An R-value (ANOSIM) close to 1 indicates a complete separation of the fish communities, and an R-value close to 0 implies no segregation (Clarke and Warwick, 2001). With an R-value between 0.5 and 0.75 the fish communities differ clearly, but an overlap is indicated; with an R-value between 0.25 and 0.5 the fish communities indicate a clear overlap; at $R<0.25$ the fish communities are relatively similar and difficult to distinguish.

A redundancy analysis (RDA) was carried out to analyse the variability of the species composition in relation with environmental factors (discharge, water depth, flow velocity, water temperature; Lepš and Šmilauer, 2003). For this analysis, combined data (sum of the 5 single transects per site and date) were used.

MS Excel was used for data input, transformation of data, and formatting the matrices for further analyses. The statistical analyses were done in PRIMER 6 & PERMANOVA, IBM SPSS Statistics 20, Canoco 4.5, in R (3.2.5) using R-Studio, and the graphs were produced in SigmaPlot 12.5.

6 Results

6.1 River discharge and abiotic conditions

During the year of investigation (2014) the water level was characterised by relatively high fluctuations. Six flood events occurred, of which three events – one in May, one in August, and one in October – were higher than the highest navigable water level (HSW). During the sampling period the average discharge was 1795 ± 732 $m^3 s^{-1}$. Average-flow conditions occurred from March to May and from November to December, whereas high water levels occurred from June to September (Fig. 6). At the sampling dates, the lowest discharge was 1144 $m^3 s^{-1}$ on 21 March and the highest discharge was 2841 $m^3 s^{-1}$ on 14 August.

During this sampling period the mean water temperature was 13 ± 4 °C. The temperature curve showed a clear seasonal pattern and ranged from 7.0°C in March to 21.0°C in July and down to 4.0°C in December. The water temperature decreased temporarily during every flood event. At the sampling dates, the lowest temperature measured was 6.0°C on 11 December, the highest was 21.0°C on 25 July (Fig. 6).

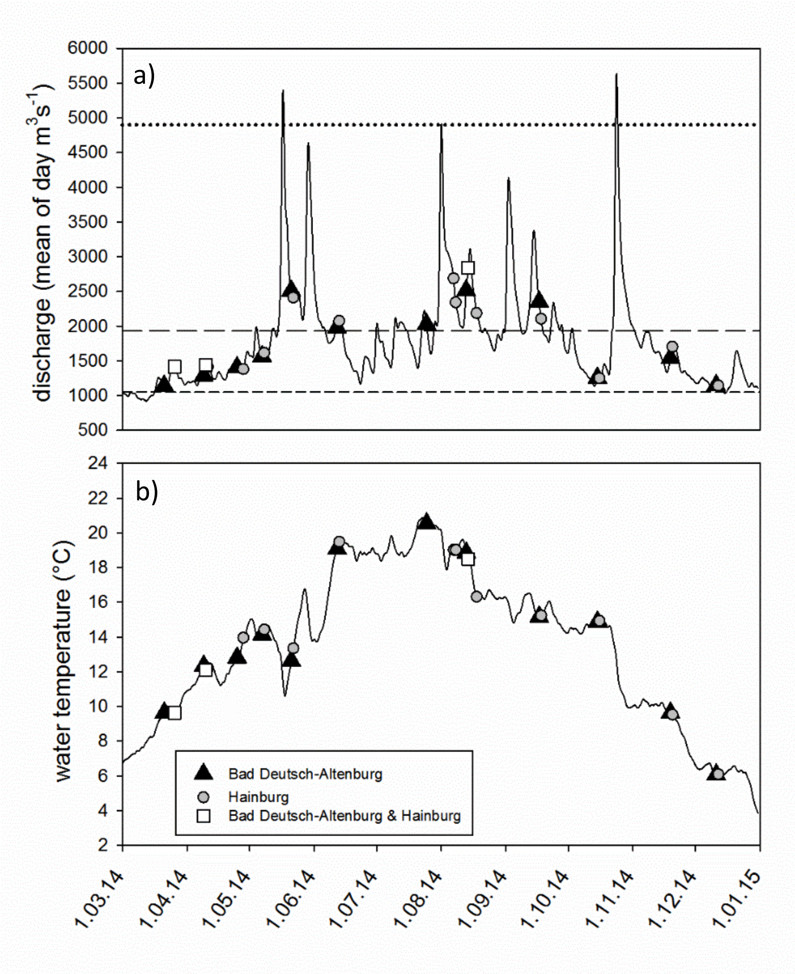

Figure 6: a) Average daily discharge at the water gauge Hainburg from March 2014 to January 2015. Dotted line highest navigable water level (HSW). Long-dashed line: long-term annual mean-flow (MW) conditions. Short-dashed line: low-water level (RNW). b) Average daily water temperature at the water gauge Hainburg from March 2014 to January 2015. Symbols show sampling dates at the different river sections. Data provided by viadonau.

6.1.1 Spatial pattern

The mean water depth at the sampling sites in Bad Deutsch-Altenburg was 0.43 ± 0.16 m and in Hainburg 0.45 ± 0.13 m. These values do not differ significantly. The water depth differed highly significant among the mesohabitats (combined data of both river sections, $p<0.001$, deviance=2.38), with a range from 0.36-0.53 m, and also among the mesohabitats within each river section ($p<0.001$, deviance=0.30), with a range from 0.36-0.54 m in Bad Deutsch-Altenburg and from 0.38-0.51 m in Hainburg.

The mean flow velocity in Bad Deutsch-Altenburg was 0.22 ± 0.17 m s^{-1} and in Hainburg 0.12 ± 0.16 m s^{-1}. In the mesohabitats it ranged from 0.11 m s^{-1} to 0.25 m s^{-1}. The flow velocities of the mesohabitats of each river section ranged from 0.16-0.26 m s^{-1} in Bad Deutsch-Altenburg and from 0.02-0.22 m s^{-1} in Hainburg. The flow velocity showed a highly significant difference between the sections (p<0.001, deviance=8.34), among the mesohabitats (combined data of both river sections, p<0.000, deviance=7.00), and among the mesohabitats within each section (p<0.001, deviance=11.10; Tab. 1, Fig. 7, Fig. 8).

Table 1: The median, the mean, the standard deviation (SD), the maximum (max), and the minimum (min) of the water depth, and the flow velocity in the river sections (N=Bad Deutsch-Altenburg, RN=Hainburg), the mesohabitats (GB=gravel bar, GR=groyne field, RR=rip rap, SA=side arm), and in the mesohabitats within each river sections (N_GB, N_GR, N_RR, N_SA, RN_GB, RN_GR, RN_RR, RN_SA).

	water depth (m)					flow velocity (m s^{-1})				
	median	**mean**	**SD**	**max**	**min**	**median**	**mean**	**SD**	**max**	**min**
N	0.43	0.43	0.16	1.00	0.11	0.20	0.22	0.17	0.80	<0.01
RN	0.44	0.45	0.13	0.91	0.08	0.06	0.12	0.16	1.74	<0.01
GB	0.35	0.36	0.13	0.90	0.11	0.21	0.25	0.21	1.74	<0.01
GR	0.42	0.42	0.13	0.91	0.18	0.08	0.13	0.12	0.47	<0.01
RR	0.50	0.51	0.11	0.90	0.26	0.16	0.19	0.13	0.62	0.017
SA	0.52	0.53	0.16	1.00	0.08	0.03	0.11	0.19	0.80	<0.01
N_GB	0.34	0.36	0.14	0.90	0.11	0.24	0.26	0.17	0.76	0.02
N_GR	0.37	0.38	0.12	0.64	0.18	0.23	0.22	0.13	0.47	<0.01
N_RR	0.54	0.54	0.12	0.90	0.30	0.14	0.16	0.12	0.48	0.017
N_SA	0.54	0.54	0.16	1.00	0.25	0.13	0.22	0.24	0.80	0.01
RN_GB	0.38	0.38	0.10	0.61	0.16	0.14	0.22	0.26	1.74	<0.01
RN_GR	0.42	0.44	0.13	0.91	0.19	0.05	0.07	0.07	0.36	<0.01
RN_RR	0.48	0.47	0.09	0.62	0.26	0.18	0.21	0.14	0.62	0.03
RN_SA	0.50	0.51	0.15	0.89	0.08	0.02	0.02	0.02	0.12	<0.01

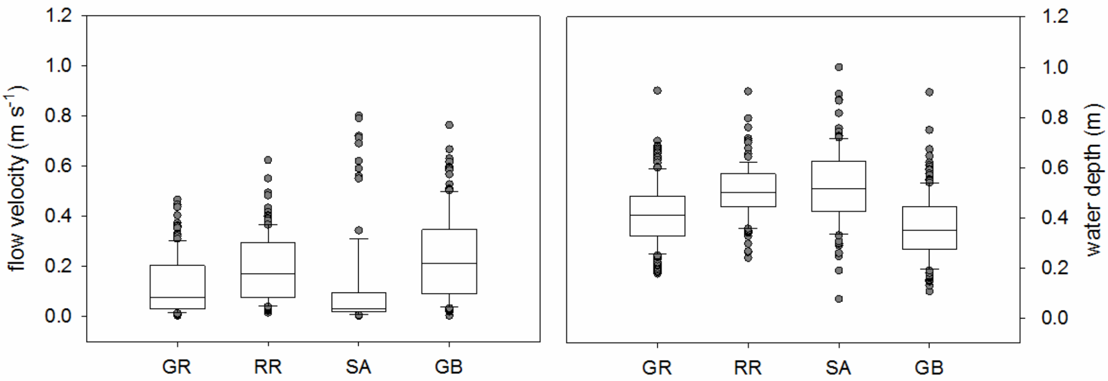

Figure 7: Box-Whisker-Plots of flow velocity and water depth in the investigated mesohabitats (combined data of both river sections; GR=groyne field; SA=side arm; RR=rip rap; GB=gravel bar).

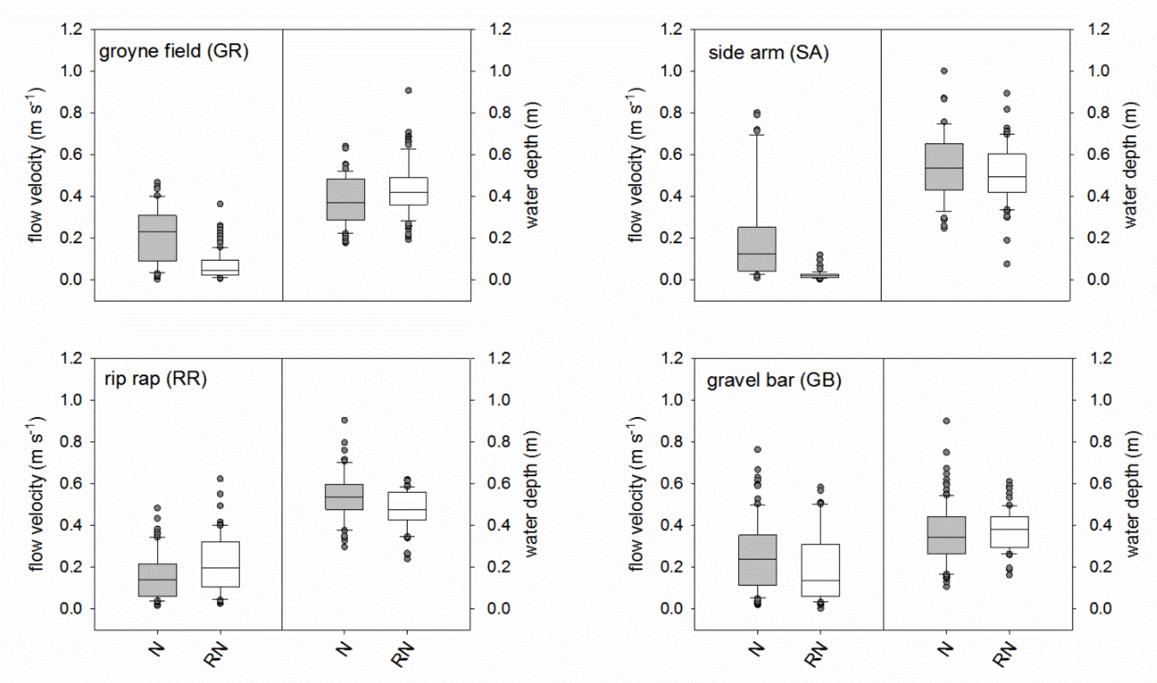

Figure 8: Box-Whisker-Plots of flow velocity and water depth from different mesohabitats (groyne field, side arm, rip rap, gravel bar) in two river sections (N=Bad Deutsch-Altenburg; RN=Hainburg).

6.1.2 Seasonal pattern

Fig. 9 and Fig. 10 show the seasonal changes of water depth and the flow velocity from March to December of the mesohabitats in each river section. In Bad Deutsch-Altenburg the mean water depth of all sampling sites ranged from 0.34 to 0.49 m, in Hainburg from 0.40 to 0.49 m. Despite these small differences, water depth differed significantly between the river sections ($p=0.03$, deviance=0.24). Water depth at the gravel bars ranged from 0.25 to 0.43 m, in the groyne fields from 0.22 to 0.47 m, along the rip raps from 0.41 to 0.63 m, and in the side arms from 0.41 to 0.58 m. Among the mesohabitats ($p<0.001$, deviance=1.05) the water depth differed highly significantly among the different months (combined data of both river sections). In Bad Deutsch-Altenburg the mean value at the gravel bars ranged from 0.23 to 0.44 m, in the groyne field from 0.22 to 0.49 m, along the rip rap from 0.41 to 0.76 m, and in the side arm from 0.31 to 0.78 m. In Hainburg the respective values were 0.28 to 0.46 m, 0.37 to 0.48 m, 0.39 to 0.53 m, and 0.48 to 0.56 m. Among the mesohabitats of each section the water depth varied highly significantly ($p=0.007$, deviance=0.62) over the sampling period.

In Bad Deutsch-Altenburg the flow velocity at all sampling sites ranged from 0.16 to 0.29 m s^{-1}, in Hainburg from 0.09 to 0.15 m s^{-1}. At the gravel bars the mean values ranged from 0.17 to 0.34 m s-

^{1}, in the groyne fields from 0.06 to 0.28 m s^{-1}, along the rip raps from 0.12 to 0.28 m s^{-1}, and in the side arms from 0.02 to 0.23 m s^{-1} (combined data of both river sections). In Bad Deutsch-Altenburg the respective values were 0.17-0.42 m s^{-1} (gravel bars), 0.12-0.32 m s^{-1} (groyne field), 0.12-0.28 m s^{-1} (rip rap), and 0.02-0.23 m s^{-1} (side arm), and in Hainburg 0.11-0.50 m s^{-1} (gravel bar), 0.03-0.15 m s^{-1} (groyne fields), 0.07-0.30 m s^{-1} (rip rap), and 0.01-0.05 m s^{-1} (side arm). The flow velocity between the sections showed no significant difference, whereas the flow velocity varied highly significantly among the mesohabitats ($p<0.001$, deviance=7.02) and among the mesohabitats of each section ($p=0.002$, deviance=4.58; Tab. 2, Fig. 9, and Fig. 10).

Table 2: Mean water depth and mean flow velocity per sampling transect of the sections (N=Bad Deutsch-Altenburg, RN=Hainburg), the mesohabitats (GB=gravel bar, GR=groyne field, RR=rip rap, SA=side arm), and the mesohabitats of each section (N_GB, N_GR, N_RR, N_SA, RN_GB, RN_GR, RN_RR, RN_SA) from March (Mar) to December (Dec) 2014.

	Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
					mean water depth (m)					
N	0.40	0.40	0.48	0.42	0.34	0.49	0.45	0.47	0.45	0.40
RN	0.40	0.45	0.45	0.45		0.43	0.49	0.43	0.46	0.46
GB	0.25	0.30	0.38	0.37	0.32	0.41	0.43	0.35	0.37	0.43
GR	0.40	0.41	0.47	0.34	0.22	0.41	0.41	0.47	0.44	0.38
RR	0.43	0.51	0.50	0.63	0.41	0.48	0.57	0.45	0.55	0.52
SA	0.50	0.54	0.55	0.43	0.56	0.58	0.53	0.58	0.52	0.41
N_GB	0.23	0.25	0.41	0.36	0.32	0.44	0.44	0.37	0.34	0.42
N_GR	0.44	0.39	0.46	0.24	0.22	0.41	0.30	0.49	0.47	0.32
N_RR	0.41	0.54	0.54	0.76	0.41	0.52	0.60	0.50	0.58	0.53
N_SA	0.51	0.57	0.61	0.31	0.56	0.78	0.48	0.61	0.53	0.34
RN_GB	0.28	0.41	0.34	0.38		0.38	0.41	0.30	0.43	0.46
RN_GR	0.37	0.43	0.48	0.43		0.41	0.47	0.46	0.43	0.41
RN_RR	0.44	0.48	0.46	0.49		0.45	0.53	0.39	0.52	0.50
RN_SA	0.49	0.51	0.50	0.48		0.52	0.56	0.55	0.52	0.49
	Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
					mean flow velocity (m s^{-1})					
N	0.16	0.23	0.23	0.26	0.25	0.22	0.29	0.22	0.21	0.16
RN	0.11	0.09	0.13	0.13		0.15	0.14	0.10	0.11	0.15
GB	0.17	0.17	0.23	0.25	0.34	0.30	0.34	0.21	0.22	0.30
GR	0.12	0.09	0.12	0.16	0.28	0.12	0.18	0.16	0.14	0.06
RR	0.15	0.17	0.21	0.28	0.12	0.21	0.20	0.14	0.16	0.18
SA	0.10	0.23	0.15	0.02	0.04	0.03	0.04	0.10	0.09	0.06
N_GB	0.20	0.17	0.24	0.29	0.34	0.31	0.42	0.25	0.25	0.20
N_GR	0.16	0.17	0.25	0.25	0.28	0.22	0.32	0.20	0.23	0.12
N_RR	0.13	0.19	0.12	0.28	0.12	0.14	0.15	0.22	0.15	0.17
N_SA	0.17	0.43	0.34	0.02	0.04	0.05	0.03	0.17	0.16	0.12
RN_GB	0.14	0.18	0.22	0.15		0.29	0.19	0.11	0.17	0.50
RN_GR	0.07	0.04	0.05	0.06		0.09	0.11	0.15	0.09	0.03
RN_RR	0.18	0.16	0.30	0.27		0.24	0.26	0.07	0.17	0.18
RN_SA	0.03	0.02	0.02	0.02		0.03	0.05	0.02	0.03	0.01

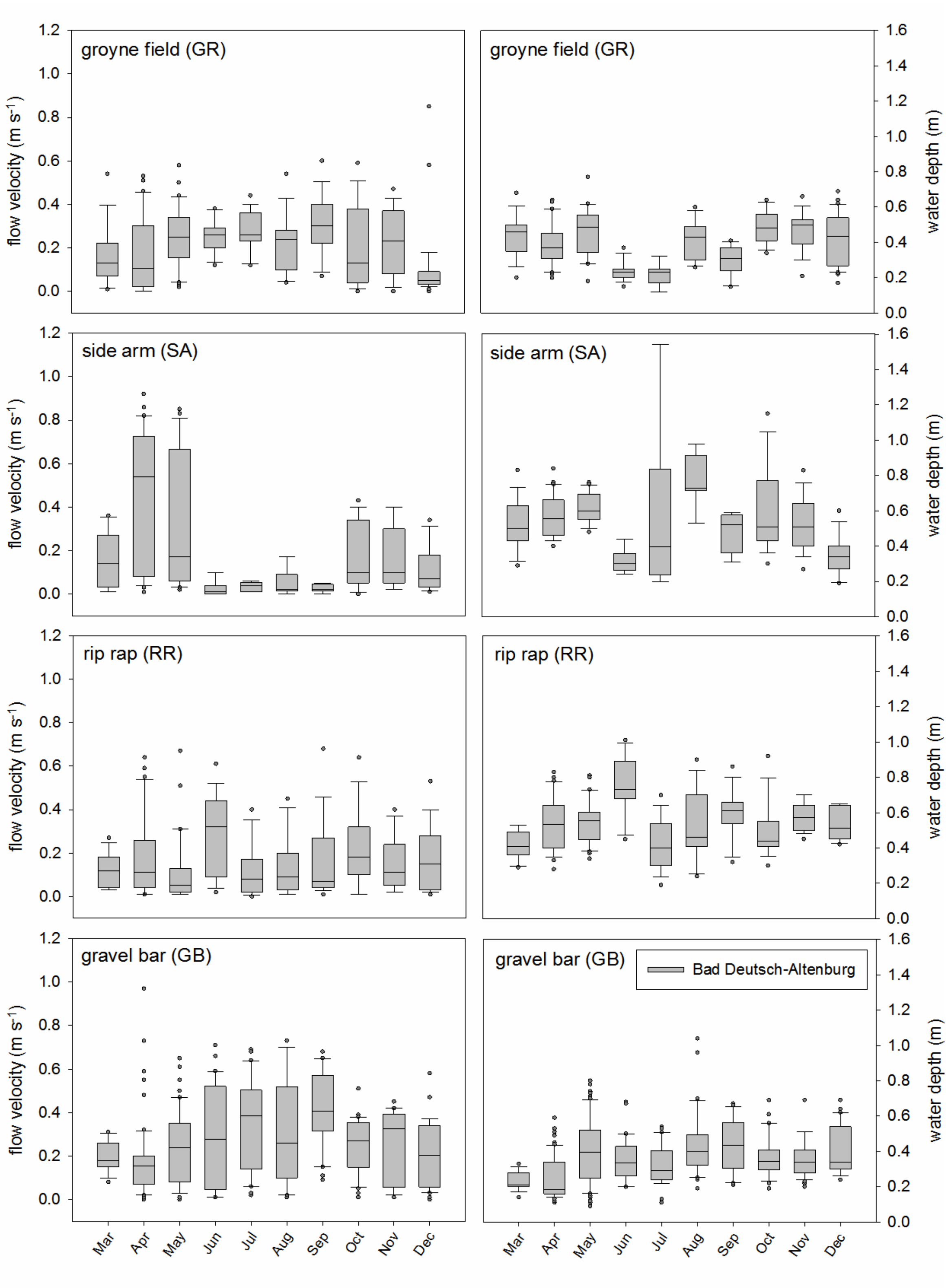

Figure 9: Box-Whisker-Plots of the seasonal pattern) of flow velocity and water depth in different mesohabitats (groyne field, side arm, rip rap, gravel bar) at the river section Bad Deutsch Altenburg (N).

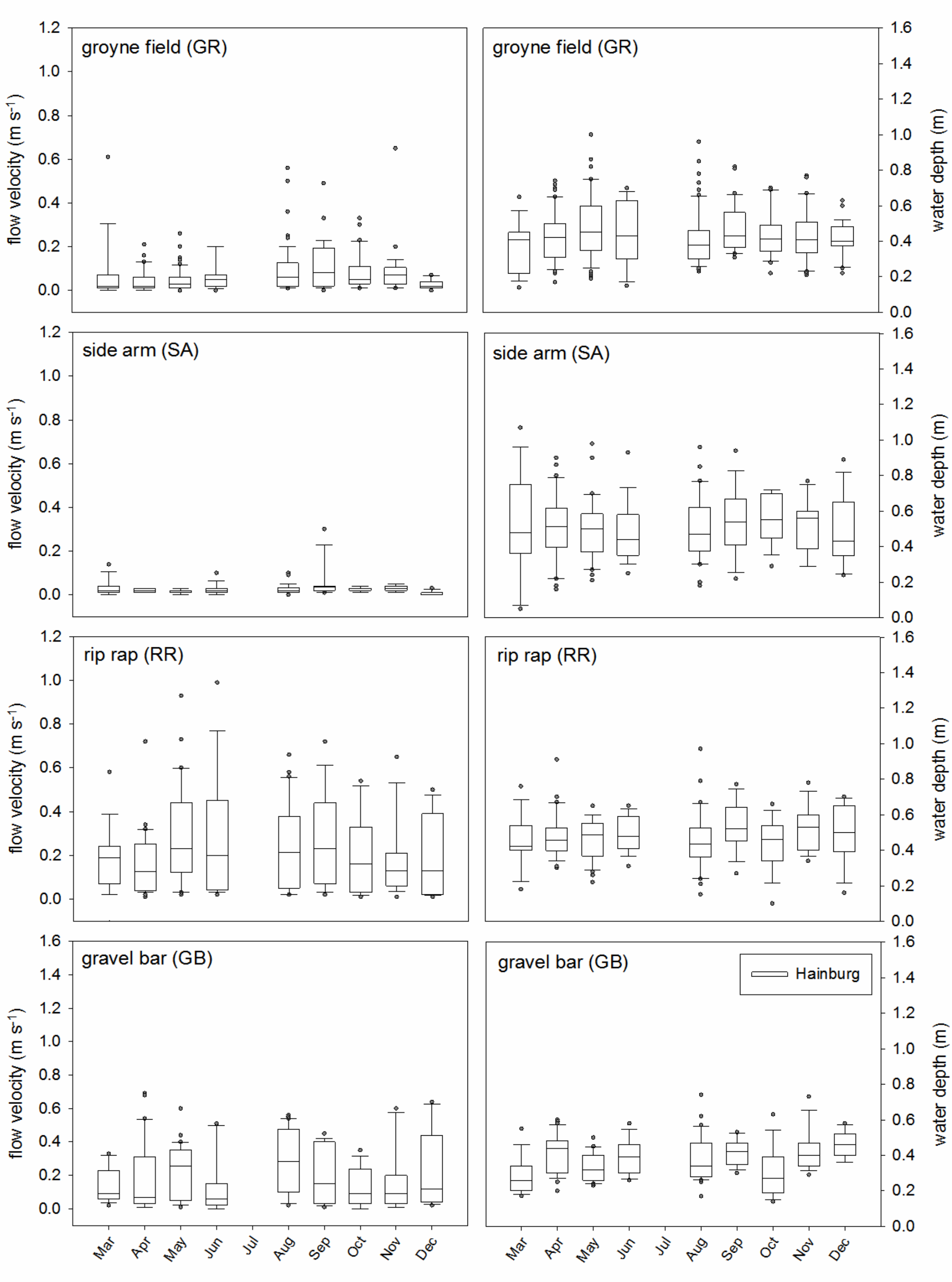

Figure 10: Box-Whisker-Plots of the seasonal pattern (March to December 2014) of flow velocity and water depth in different mesohabitats (groyne field, side arm, rip rap, gravel bar) at the river section Hainburg (RN).

6.1.3 Relationship among hydrological parameters

The discharge influenced the flow velocity and the water depth in the main stem of the Danube, in the river sections, and in the mesohabitats. This is reflected in the relationships between discharge and water depth, and discharge and flow velocity, as well as between water depth and flow velocity (Fig. 11-14).

Generally, higher discharges led to higher flow velocities (n=569, p=0.004, Spearman=0.121). Both river sections showed a positive trend, with a small increase of 0.03 m s^{-1} per 1000 m^3 s^{-1} in Bad Deutsch-Altenburg and 0.04 m s^{-1} per 1000 m^3 s^{-1} in Hainburg, but at different levels (Fig. 11a, Tab. 2). In the river sections the correlations between discharge and flow velocities were significantly positive in Bad Deutsch-Altenburg (n=282, p=0.045, Spearman=0.120) and in Hainburg (n=287, p=0.01, Spearman=0.200).

The correlation between the discharge and the water depth in the Danube (0.03 m per 1000 m^3 s^{-1}, combined data of both river sections) and in the river section Bad Deutsch-Altenburg, respectively, was slightly positive, but not significant; this relationship at Hainburg was slightly negative, but significant (n=287, p=0.016, Spearman=-0.143, Fig. 11c).

The correlation between water depth and flow velocity was slightly negative in the Danube (0.05 m s^{-1} per 1m, combined data of both river sections), at Bad Deutsch-Altenburg (0.035 m s^{-1} per 1m) and Hainburg (0.036 m s^{-1} per 1m). The flow velocity in the inshore habitats of the whole sampling reach (combined data of both river sections, n=569, p=0.002, Spearman=-0.128) and at Hainburg (n=287, p=0.016, Spearman=-0.143) showed a slight but significant decrease with increasing water depth (Fig. 11b).

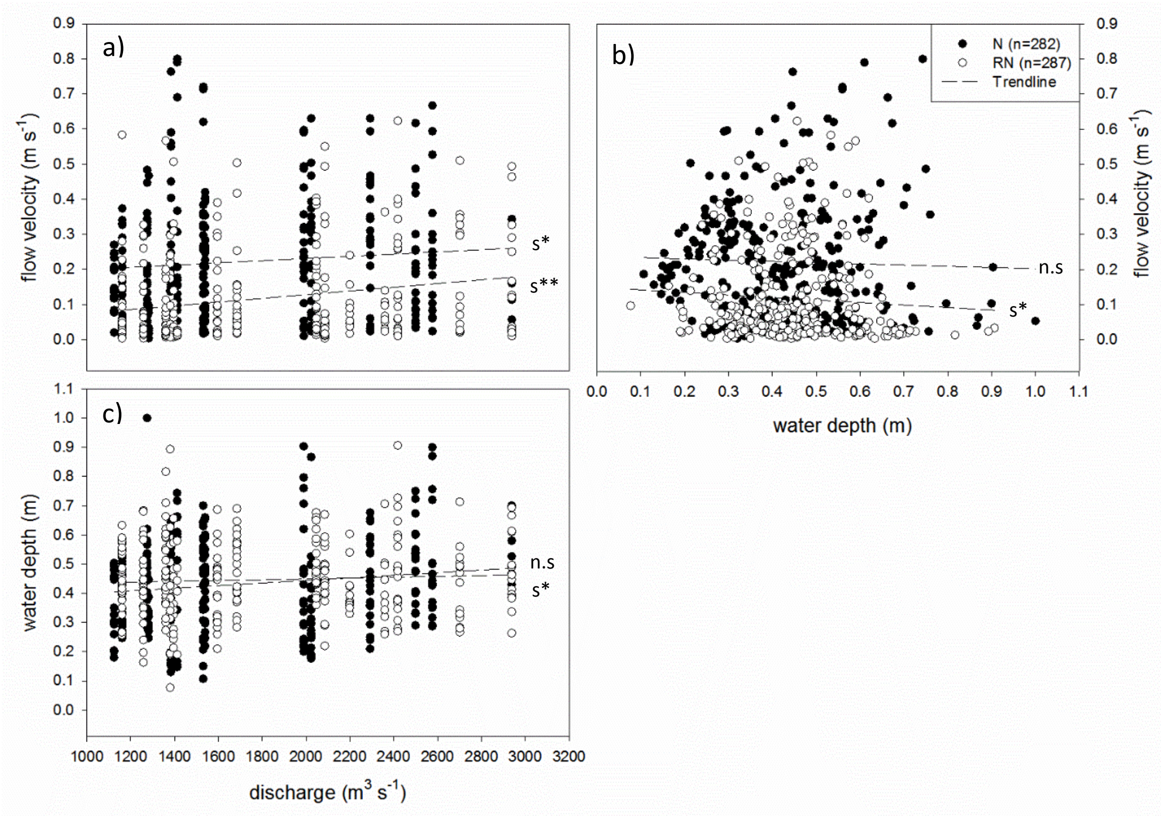

Figure 11: Correlation between a) the discharge and flow velocity b) water depth and flow velocity, and c) discharge and water depth in the river sections (Bad Deutsch-Altenburg=N, Hainburg=RN). Regression line indicates the trend of the data. n=number of samples. Significant (s *** if p<0.001; s ** if p<0.01; s* if p<0.05); not significant (n.s.).

In general the relationship (positive or negative) between discharge and flow velocity depended on the characteristics of the shores, hence on the mesohabitat. Six out of the eight sites revealed a significant relationship (Fig. 12).

In the groyne fields the correlation between discharge and flow velocity was slightly positive (0.04 m s^{-1} per 1000 m^3 s^{-1}). In all groyne field measurements (combined data of both river sections; n=167, p=0.002, Spearman=0.233) and at Hainburg (n=107, p=0.004, Spearman=0.280) the relationship was highly significant. At Bad Deutsch-Altenburg (n=60, p=0.012, Spearman=0.323) the correlation was significantly positive.

In all rip rap measurements (combined data of both river sections) the correlation between discharge and flow velocity was slightly positive (0.03 m s^{-1} per 1000 m^3 s^{-1}), although not significant, and highly significant positive at Hainburg (n=60, p=0.01, Spearman=0.330), whereas at Bad Deutsch-Altenburg it was negative and not significant.

In all side arm measurements (combined data of both river sections) the correlation between discharge and flow velocity was slightly negative (0.08 m s^{-1} per 1000 m^3 s^{-1}), although not significant, and highly significant negative at Bad Deutsch-Altenburg (n=47, p=0.009, Spearman=-0.377). The relation at Hainburg was positive and not significant.

In the gravel bars, the correlation between flow velocity and discharge was slightly positive (0.075 m s^{-1} per 1000 m^3 s^{-1}). In all gravel bar measurements (combined data of both river sections; n=175, p=0.000, Spearman=0.267) and at Bad Deutsch-Altenburg (n=115, p=0.001, Spearman=0.300) it was highly significantly positive, at Hainburg (n=60, p=0.036, Spearman=0.272) significantly positive.

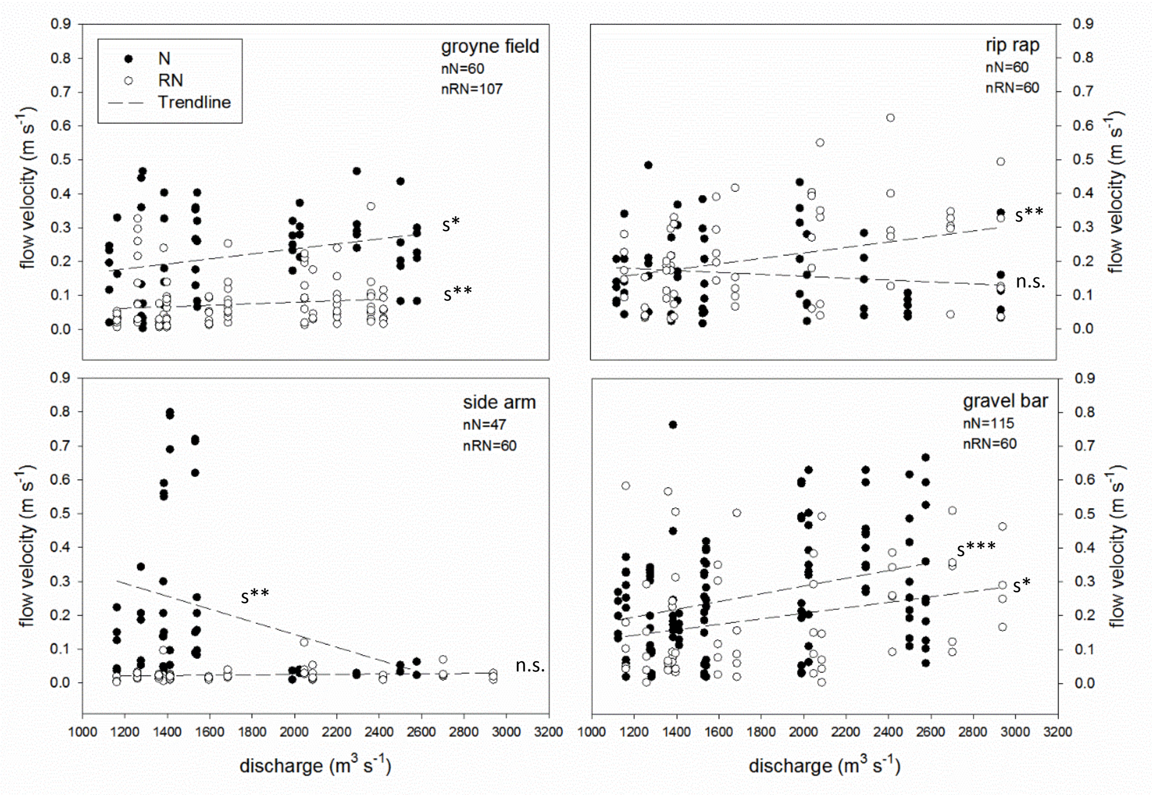

Figure 12: Correlation between discharge and flow velocity of the different river sections (Bad Deutsch-Altenburg=N and Hainburg=RN). Regression line indicates the trend of the data. n=number of samples. Significant (s *** if p<0.001; s ** if p<0.01; s* if p<0.05); not significant (n.s.).

The water depth was influenced to a lesser extent by increasing discharge than the flow velocity. Three out of the eight sites revealed a significant relationship between discharge and water depth (Fig. 13). The groyne field in Bad Deutsch-Altenburg showed a significant but slightly negative relation (n=60, p=0.041, Spearman=-0.265), whereas the water depth in the Bad Deutsch-Altenburg side arm (n=47, p=0.015, Spearman=0.351) increased little, but significantly. At the gravel bar in Bad Deutsch-Altenburg (n=115, p<0.001, Spearman=0.343) water depth increased highly significantly but minimally.

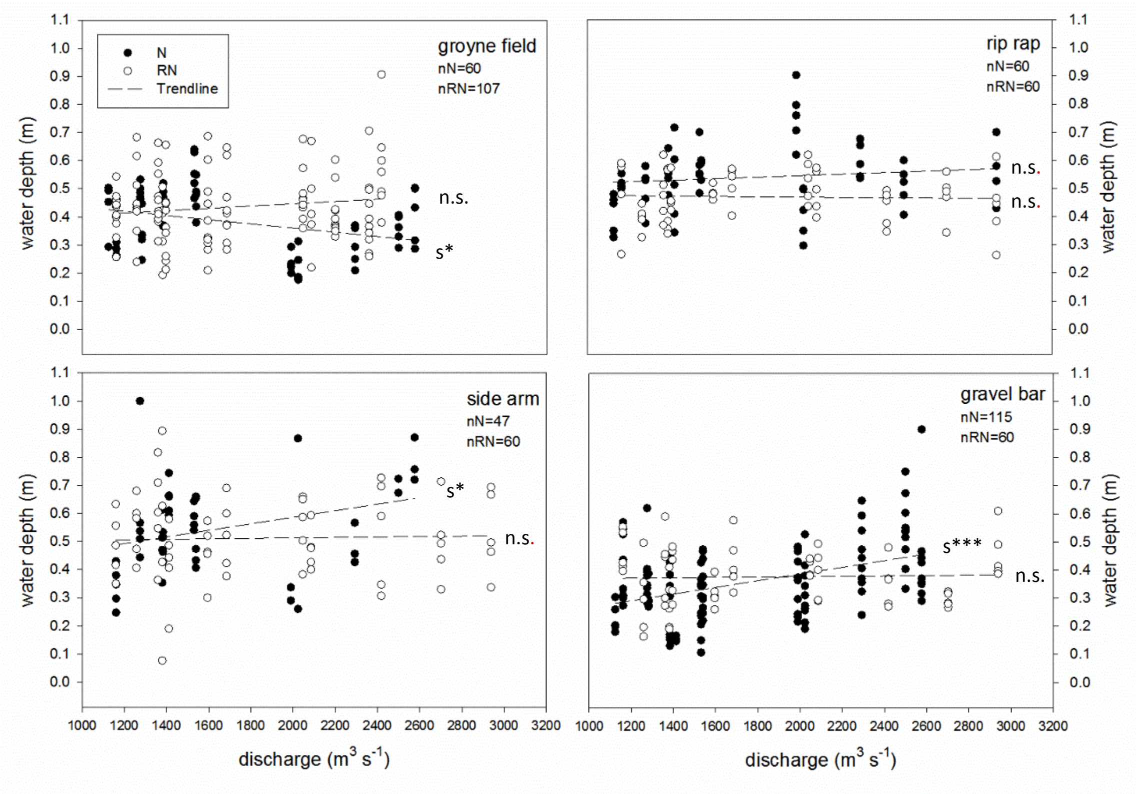

Figure 13: Correlation between discharge and water depth of the different river sections (Bad Deutsch-Altenburg=N and Hainburg=RN. Regression line indicates the trend of the data. n=number of samples. Significant (s *** if p<0.001; s ** if p<0.01; s* if p<0.05); not significant (n.s.).

Fig.14 shows the correlation between water depth and flow velocity of the mesohabitats at both river sections. At the groyne field in Hainburg (n=107, p=0.018, Spearman=-0.229), flow velocity significantly decreased with water depth. Based on the combined data of both river sections, the flow velocity clearly decreased (0.228 m s^{-1} per 1m). The rip rap, the gravel bar, and the side arm showed no significant trend, although the flow velocity clearly increased (0.34 m s^{-1} per 1m) at the gravel bars (combined data).

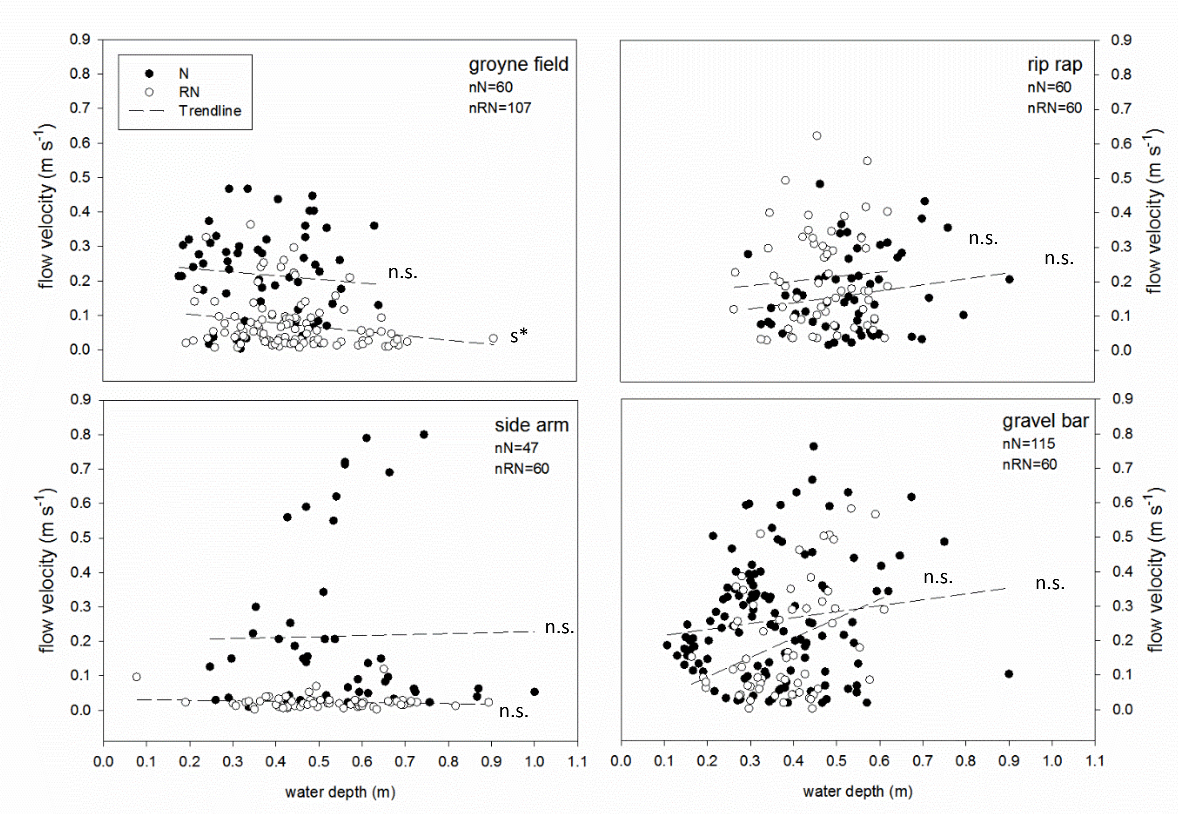

Figure 14: Correlation between water depth and flow velocity of the different mesohabitats at Bad Deutsch Altenburg=N and Hainburg=RN. Regression line indicates the trend of the data. n=number of samples. Significant (s *** if p<0.001; s ** if p<0.01; s* if p<0.05); not significant (n.s.).

6.2 Abundance, diversity indices and assemblage structure

6.2.1 Spatial pattern

6.2.1.1 Species assemblages in the river sections Bad Deutsch Altenburg and Hainburg

The overall species number was 37 (combined data of both river sections), 29 in Bad Deutsch-Altenburg, and 32 in Hainburg (Tab. 3; Tab. 5). Of these, 2 species belong to the rhithralic guild, 10 to the rheophilic A, 6 to the rheophilic B, 12 species to the eurytopic, 2 to the stagnophilic guild, and 5 species are neobiota. The species schneider (*Alburnoides bipunctatus*), common carp (*Cyprinus carpio*), stone moroko (*Pseudoraspora parva*), trout (*Salmo trutta*) and the Danube streber (*Zingel streber*) were caught only at Bad Deutsch-Altenburg. Bream (*Abramis brama*), blue bream (*Ballerus ballerus*), Danube bream (*Ballerus sapa*), stone loach (*Barbatula barbatula*), spined loach (*Cobitis elongatoides*), pike (*Esox lucius*), pumpkinseed (*Lepomis gibbosus*) and bitterling (*Rhodeus amarus*) were caught only at Hainburg.

Table 3: Fish species list from the Danube River in Bad Deutsch-Altenburg (N) and Hainburg (RN) during the sampling period from March to December 2014. Listed are species names, common names (in English and German), the ecological guild after Schiemer & Waidbacher (1992) and the classification after FFH (Flora-Fauna-Habitat-Richtlinie). RT=rhithral, RA=rheophil A, RB=rheophil B, EU=euryotope, ST=stagnophil; NB=neobiota;

species	common name (engl.)	common name (germ.)	abbreviation	FFH	ecol. guild	river section	
Abramis brama	bream	Brachse	Abr_bra		EU		RN
Alburnoides bipunctatus	schneider	Schneider	Alb_bip		RA	N	
Alburnus alburnus	Danube bleak	Laube	Alb_alb		EU	N	RN
Aspius aspius	asp	Schied	Asp_asp	II	RB	N	RN
Babka gymnotrachelus	racer goby	Nackthalsgrundel	Neo_gym		NB	N	RN
Ballerus ballerus	blue bream	Zope	Bal_bal		RB		RN
Ballerus sapa	Danube bream	Zobel	Bal_sap		RB		RN
Barbatula barbatula	stone loach	Bachschmerle	Barb_barb		RA		RN
Barbus barbus	barbel	Barbe	Bar_bar	V	RA	N	RN
Blicca bjoerkna	white bream	Güster	Bli_bjo		RB	N	RN
Carassius gibelio	prussian carp	Giebel	Car_gib		EU	N	RN
Carassius sp.			Car_sp				RN
Chondrostoma nasus	nase	Nase	Cho_nas		RA	N	RN
Cobitis elongatoides	spined loach	Steinbeißer	Cob_elo	II	RB		RN
Cottus gobio	bullhead	Koppe	Cot_gob	II	RA	N	RN
Cyprinidae sp.			Cyp_sp			N	RN
Cyprinus carpio	common carp	Karpfen	Cyp_car		EU	N	
Esox lucius	pike	Hecht	Eso_luc		EU		RN
Gasterosteus aculeatus	three-spined stickleback	Stichling	Gas_acu		ST	N	RN
Gymnocephalus cernua	ruffe	Kaulbarsch	Gym_cer		EU	N	RN
Gymnocephalus schraetser	schraetzer	Schrätzer	Gym_sch	II, V	RA	N	RN
Lepomis gibbosus	pumpkinseed	Sonnenbarsch	Lep_gib		NB		RN
Leuciscus idus	ide	Nerfling	Leu_idu		RB	N	RN
Leuciscus leuciscus	common dace	Hasel	Leu_leu		RA	N	RN
Lota lota	burbot	Quappe	Lot_lot		RT	N	RN
Neogobius melanostomus	round goby	Schwarzmundgrundel	Neo_mel		NB	N	RN
Neogobius sp.			Neo_sp				RN
Perca fluviatilis	european perch	Flußbarsch	Per_flu		EU	N	RN
Percidae sp.			Per_sp				RN
Ponticola kessleri	bighead goby	Kesslergrundel	Neo_kes		NB	N	RN
Proterorhinus semilunaris	western tubenose goby	Halbmondgrundel	Pro_sem		EU	N	RN
Pseudorasbora parva	stone moroko	Blaubandbärbling	Pse_par		NB	N	
Rhodeus amarus	bitterling	Bitterling	Rho_ama	II	ST		RN
Romanogobio vladykovi	white-finned gudgeon	Weißflossengründling	Rom_vla	II	RA	N	RN
Rutilus rutilus	roach	Rotauge	Rut_rut		EU	N	RN
Salmo trutta	trout	Bachforelle	Sal_tru		RT	N	
Sander lucioperca	pike-perch	Zander	San_luc		EU	N	RN
Silurus glanis	wels catfish	Wels	Sil_gla		EU	N	RN
Squalius cephalus	chub	Aitel	Squ_cep		EU	N	RN
Vimba vimba	vimba bream	Rußnase	Vim_vim		RA	N	RN
Zingel streber	danube streber	Streber	Zin_str	II	RA	N	
Total species number		**37**				**29**	**32**

The most abundant species of the total catch was the eurytope bleak (*Alburnus alburnus*, 0.32 ± 0.96 Ind. min^{-1}), followed by the invasive species round goby (*Neogobius melanostomus*, 0.19 ± 0.38 Ind. min^{-1}), nase (*Chondostroma nasus*, RA, 0.11 ± 0.48 Ind. min^{-1}) and barbel (*Barbus barbus*, RA, 0.08 ± 0.22 Ind. min^{-1}, Fig. 15).

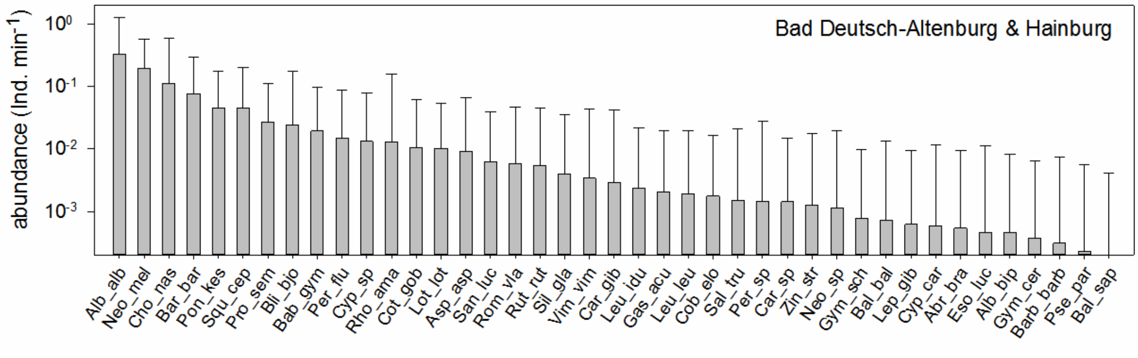

Figure 15: Mean abundance (+standard deviation SD) of all species caught in Bad Deutsch Altenburg (N) and Hainburg (RN) over a sampling period from March to December 2014 by wading electrofishing. Species abbreviations from Tab. 3. Note logarithmic scale on y-axis.

In Bad Deutsch-Altenburg and Hainburg, 2 and 1 species of the rheophilic guild were captured, respectively, of which burbot (*Lota lota*, RT) was the most abundant species, followed by trout (*Salmo trutta*, RT). In the rheophilic A guild, we found 9 species in Bad Deutsch-Altenburg and 8 species in Hainburg, of which nase (*Chondostroma nasus*, RA) and barbel (*Barbus barbus*; RA) were the most abundant. In the rheophilic B guild, 3 species were recorded in Bad Deutsch-Altenburg, 6 species in Hainburg: white bream (*Blicca bjoerkna*, RB) and asp (*Aspius aspius*, RB) were the most abundant. The euryotopic guild contained 10 species in Bad Deutsch-Altenburg and 11 species in Hainburg, of which bleak (*Alburnus alburnus*, EU) and chub (*Squalius cephalus*, EU) were the most abundant. In Bad Deutsch-Altenburg and in Hainburg we caught 1 and 2 species of the stagnophilic guild, respectively. The most abundant species in this guild was bitterling (*Rhodeus amarus*, ST). Overall, 5 neobiota were identified, namely pumpkinseed (*Lepomis gibbosus*), stone moroko (*Pseudoraspora parva*), racer goby (*Babka gymnotrachelus*), round goby (*Neogobius melanostomus*), and bighead goby (*Ponticola kessleri*). Round goby (*Neogobius melanostomus*, NB), followed by bighead goby (*Ponticola kessleri*, NB), were the most abundant invasive species (Fig. 16).

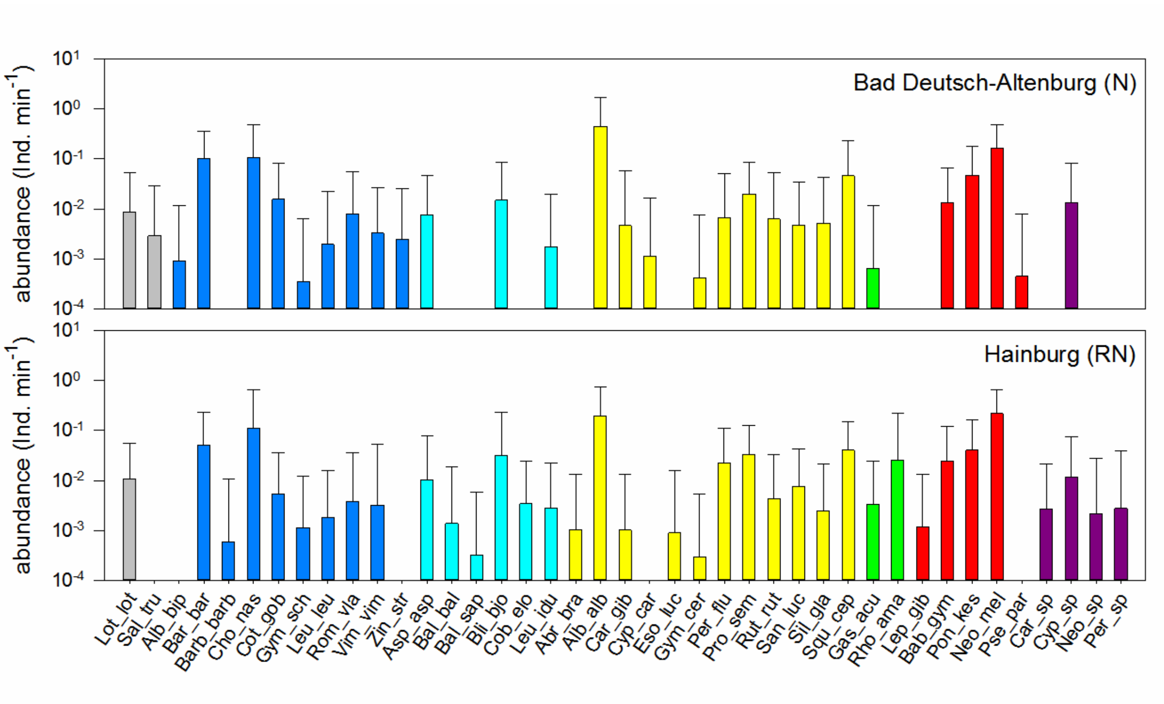

Figure 16: Mean abundance (+ standard deviation SD) of all fish species caught in two river sections of the River Danube, at Bad Deutsch-Altenburg (N) and Hainburg (RN). Colours indicate ecological guilds after Schiemer & Waidbacher, (1992). Grey: rhithral (RT); dark blue: rheophilic A (RA); light blue: rheophilic B (RB); yellow: eurytopic (EU); green: stagnophilic (ST); red: neobiota (NB); violet: unidentified species; Method – wading electrofishing (sampling period: March to December 2014). Species abbreviations from Tab. 3. Note logarithmic scale on y-axis.

Table 4: Median, mean, standard deviation (SD), maximum (max), and minimum (min) of the abundance (CPUE), and the diversity indices (species number, Evenness, and Shannon) of two river sections (N=Bad Deutsch-Altenburg, RN=Hainburg) and four different mesohabitats (GB=gravel bar, GR=gravel bar, RR=rip rap, SA=side arm), and the mesohabitats of each river section (N_GB, N_GR, N_RR, N_SA, RN_GB, RN_GR, RN_RR, RN_SA).

	abundance (CPUE, Ind. min^{-1})					species number (S)				
	median	mean	SD	max	min	median	mean	SD	max	min
N	0.58	1.06	1.48	12.67	0.00	2	2	2	10	0
RN	0.50	0.88	1.18	7.20	0.00	2	2	2	15	0
GB	0.33	0.89	1.60	12.67	0.00	1	2	2	8	0
GR	0.71	1.05	1.16	7.00	0.00	2	2	2	10	0
RR	0.50	0.93	1.03	5.89	0.00	2	2	2	11	0
SA	0.43	1.02	1.46	8.47	0.00	2	3	3	15	0
N_GB	0.40	0.88	1.61	12.67	0.00	1	2	2	8	0
N_GR	1.00	1.40	1.30	7.00	0.00	3	3	2	10	0
N_RR	0.74	1.12	1.18	5.89	0.00	2	2	1	5	0
N_SA	0.20	0.99	1.69	8.47	0.00	1	2	3	8	0
RN_GB	0.25	0.91	1.60	7.20	0.00	1	2	2	8	0
RN_GR	0.60	0.85	1.02	4.47	0.00	2	2	2	9	0
RN_RR	0.47	0.74	0.81	3.43	0.00	2	2	2	11	0
RN_SA	0.61	1.05	1.27	5.96	0.00	2	3	3	15	0

	Evenness (E)					Shannon (H')				
	median	mean	SD	max	min	median	mean	SD	max	min
N	0.91	0.82	0.20	1.00	0.14	0.50	0.52	0.53	1.84	0.00
RN	0.92	0.84	0.17	1.00	0.30	0.50	0.54	0.60	2.22	0.00
GB	0.92	0.84	0.20	1.00	0.19	0.00	0.35	0.50	1.72	0.00
GR	0.92	0.85	0.15	1.00	0.30	0.64	0.63	0.56	1.87	0.00
RR	0.91	0.81	0.21	1.00	0.14	0.64	0.60	0.51	2.22	0.00
SA	0.88	0.82	0.17	1.00	0.33	0.37	0.59	0.68	2.14	0.00
N_GB	0.92	0.86	0.19	1.00	0.19	0.00	0.36	0.50	1.71	0.00
N_GR	0.87	0.84	0.15	1.00	0.50	0.89	0.82	0.50	1.75	0.00
N_RR	0.87	0.78	0.24	1.00	0.14	0.64	0.62	0.41	1.61	0.00
N_SA	0.89	0.82	0.20	1.00	0.41	0.00	0.40	0.61	1.84	0.00
RN_GB	0.90	0.79	0.21	1.00	0.37	0.00	0.33	0.50	1.72	0.00
RN_GR	0.92	0.86	0.15	1.00	0.30	0.49	0.52	0.57	1.87	0.00
RN_RR	0.95	0.87	0.17	1.00	0.40	0.62	0.58	0.60	2.22	0.00
RN_SA	0.88	0.83	0.16	1.00	0.33	0.69	0.74	0.70	2.14	0.00

At the scale of the river sections, the abundance and the biodiversity indices (species number, Shannon-Wiener Index, and Evenness) are not significantly different. The Evenness is relatively high in both river sections, indicating that the abundances of the species are equally distributed (Fig. 17).

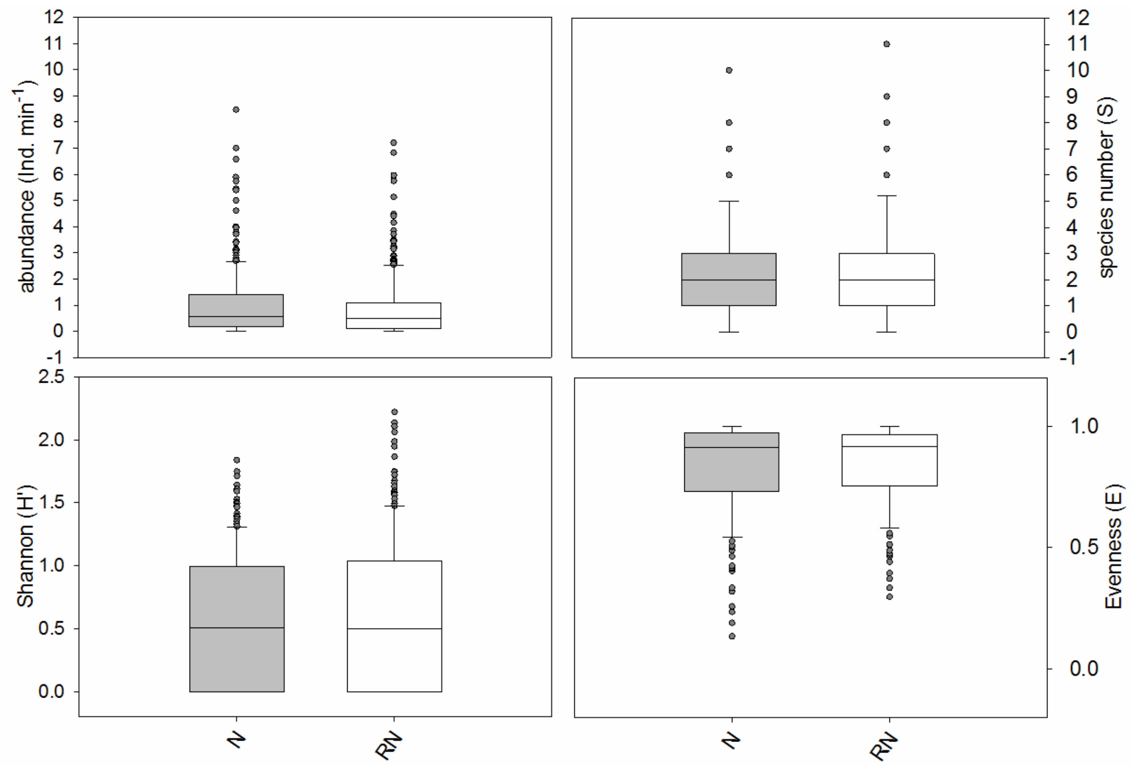

Figure 17: Box-Whisker-Plots of abundance (Ind. min^{-1}) and biodiversity indices (species number, Shannon, Evenness) of each river section (Bad Deutsch-Altenburg N & Hainburg RN).

Analysis of similarity (ANOSIM) revealed a significant but small difference between the two assemblages of the two river sections. The Global R and the distance of the centroids are small (ANOSIM; R = 0.009, p = 0.016, nN=221, nRN=216) and the variability of the values are high, pointing to a high similarity of the species assemblages and their abundances (Fig. 18).

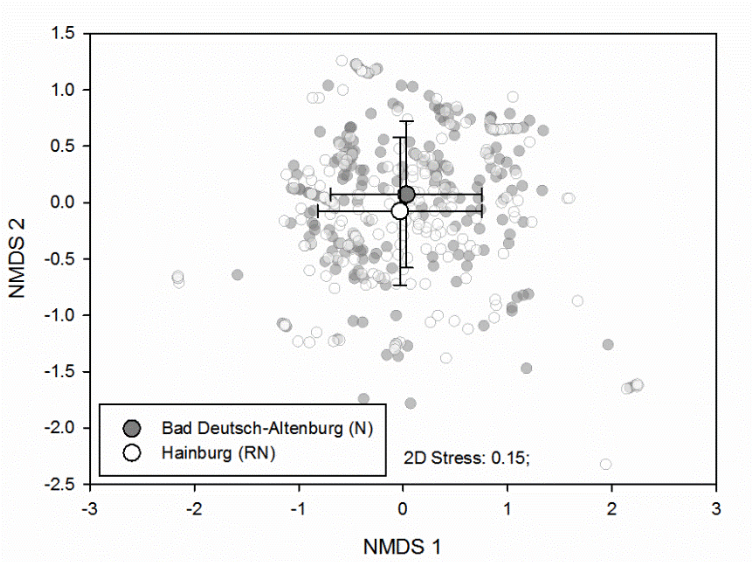

Figure 18: NMDS-analysis of the catch data (abundance of each species, Ind. min^{-1}) of each sampling event (n=569), separated in Bad Deutsch-Altenburg (N) and Hainburg (RN). Resemblance matrix based on Bray-Curtis-dissimilarities between samples.

6.2.1.2 Comparison of species assemblages of different mesohabitats

groyne field

The groyne fields at the two river sections yielded 21 species. The most abundant in Bad Deutsch-Altenburg was the round goby (*Neogobius melanostomus*), followed by bleak (*Alburnus alburnus*), barbel (*Barbus barbus*), nase (*Chondostroma nasus*) and bighead goby (*Ponticola kessleri*). In Hainburg the most abundant fish was round goby (*Neogobius melanostomus*), followed by bleak (*Alburnus alburnus*), nase (*Chondostroma nasus*), bighead goby (*Ponticola kessleri*) and chub (*Squalius cephalus*).

side arm

In the side arms at Bad Deutsch-Altenburg and Hainburg yielded 20 and 24 species, respectively. The most abundant in Bad Deutsch-Altenburg was bleak (*Alburnus alburnus*), followed by chub (*Squalius cephalus*), nase (*Chondostroma nasus*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*). In Hainburg the most abundant fish was round goby (*Neogobius melanostomus*), followed by bleak (*Alburnus alburnus*), bitterling (*Rhodeus amarus*), European perch (*Perca fluviatilis*), and racer goby (*Babka gymnotrachelus*).

rip rap

The rip rap at Bad Deutsch-Altenburg and Hainburg yielded 16 and 23 species, respectively. In the former, the most abundant fish was bleak (*Alburnus alburnus*), followed by round goby (*Neogobius melanostomus*), barbel (*Barbus barbus*), bighead goby (*Ponticola kessleri*) and burbot (*Lota lota*). In the latter site, the most abundant species was round goby (*Neogobius melanostomus*), followed by bleak (*Alburnus alburnus*), barbel (*Barbus barbus*), burbot (*Lota lota*) and chub (*Squalius cephalus*).

gravel bar

The gravel bars yielded 22 species in Bad Deutsch-Altenburg, 14 in Hainburg. The four most abundant species were the same in both river sections. Abundance differed: the most abundant species in Bad Deutsch-Altenburg was bleak (*Alburnus alburnus*), followed by nase (*Chondostroma nasus*), barbel (*Barbus barbus*), the round goby (*Neogobius melanostomus*) and bighead goby (*Ponticola kessleri*). In contrast, the most abundant fish in Hainburg was nase (*Chondostroma *nasus*), followed by bleak (*Alburnus alburnus*), the round goby (*Neogobius melanostomus*), barbel (*Barbus barbus*) and western tubenose goby (*Proterorhinus semilunaris*).

Burbot (*Lota lota*) was the most abundant along the rip raps. The groyne fields at both river sections yielded three individuals. In contrast, this species was absent in the side arms and at the gravel bars. Roach (*Rutilus rutilus*) was abundant only in the side arms. One individual was recorded in the groyne field and at the gravel bar in Bad Deutsch-Altenburg, respectively, and one individual along the rip rap and in the groyne field in Hainburg, respectively (Tab. 3).

Table 5: List of fish species caught in the Danube River in each mesohabitat in Bad Deutsch-Altenburg (N) and Hainburg (RN) from March to December 2014. Listed are species names, common names, abbreviations, mean CPUE (Ind. min^{-1}) of each river section, number of individuals per mesohabitat and river section, and total number of individuals of each species.

			Bad Deutsch Altenburg (N)				mean CPUE (N)	Hainburg (RN)				mean CPUE (RN)	number of
species	**common name**	**abbreviation**	**GR**	**SA**	**RR**	**GB**	**(Ind min^{-1})**	**GR**	**SA**	**RR**	**GB**	**(Ind min^{-1})**	**individuals**
Abramis brama	bream	Abr_bra								2		0.001	2
Alburnoides bipunctatus	schneider	Alb_bip			2		0.001						2
Alburnus alburnus	danube bleak	Alb_alb	147	195	251	247	0.446	168	76	83	69	0.192	1236
Aspius aspius	asp	Asp_asp	9	2	2	2	0.007	3	22	1	5	0.010	46
Babka gymnotrachelus	racer goby	Bab_gym	12	6		4	0.013	2	43	2	13	0.024	82
Ballerus ballerus	blue bream	Bal_bal							7			0.001	7
Ballerus sapa	Danube bream	Bal_sap								1			1
Barbatula barbatula	stone loach	Barb_barb						1				0.001	1
Barbus barbus	barbel	Bar_bar	110	1	32	51	0.102	18	22	36	22	0.052	292
Blicca bjoerkna	white bream	Bli_bjo	13	19	3	3	0.015	24	31	11		0.031	104
Carassius gibelio	prussian carp	Car_gib	7			1	0.005		1	1		0.001	10
Carassius sp.		Car_sp							3	4		0.003	7
Chondrostoma nasus	nase	Cho_nas	87	30	13	94	0.106	72	10	12	151	0.110	469
Cobitis elongatoides	spined loach	Cob_elo							9			0.004	9
Cottus gobio	bullhead	Cot_gob	16	1	5	9	0.016	6		3	1	0.005	41
Cyprinidae sp.		Cyp_sp	2	12	3	8	0.014	3	31	1	2	0.014	62
Cyprinus carpio	common carp	Cyp_car	1			1	0.001						2
Esox lucius	pike	Eso_luc							2			0.001	2
Gasterosteus aculeatus	three-spined stickleback	Gas_acu				1	0.001		3	4	1	0.004	9
Gymnocephalus cernua	ruffe	Gym_cer		1					1				2
Gymnocephalus schraetser	schraetzer	Gym_sch				1		1		1	1	0.001	4
Lepomis gibbosus	pumpkinseed	Lep_gib							3			0.001	3
Leuciscus idus	ide	Leu_idu		4			0.002	3	6	1		0.003	14
Leuciscus leuciscus	common dace	Leu_leu	3	3			0.002		5	1	2	0.002	14
Lota lota	burbot	Lot_lot	2		16		0.009	1		19		0.011	38
Neogobius melanostomus	round goby	Neo_mel	150	7	129	48	0.165	177	95	120	62	0.215	788
Neogobius sp.		Neo_sp							6			0.002	6
Perca fluviatilis	european perch	Per_flu	1	7	1	3	0.007	12	64	2	2	0.024	92
Percidae sp.		Per_sp						3				0.003	3
Ponticola kessleri	bighead goby	Pon_kes	49	2	22	19	0.047	43	20	10	10	0.040	175
Proterorhinus semilunaris	western tubenose goby	Pro_sem	19	6	4	8	0.020	15	33	7	14	0.032	106
Pseudoraspora parva	stone moroko	Pse_par		1									1
Rhodeus amarus	bitterling	Rho_ama						5	117			0.027	122
Romanogobio vladykovi	white-finned gudgeon	Rom_vla	9			5	0.008	4				0.004	18
Rutilus rutilus	roach	Rut_rut	1	13		1	0.006	1	17	1		0.005	34
Salmo trutta	trout	Sal_tru	1		1	2	0.003						4
Sander lucioperca	pike-perch	San_luc	1	5		3	0.005	4	19	1		0.007	33
Silurus glanis	wels catfish	Sil_gla		1	10		0.005			5		0.002	16
Squalius cephalus	chub	Squ_cep	11	47	10	17	0.046	43	31	11	7	0.042	177
Vimba vimba	vimba bream	Vim_vim	1	3		4	0.003	5	2			0.003	15
Zingel streber	Danube streber	Zin_str			3	1	0.002						4
sum of individuals			652	366	507	533		614	679	340	362		4053
total species number []	**[37]**		**[21]**	**[20]**	**[16]**	**[22]**	**[29]**	**[21]**	**[24]**	**[23]**	**[14]**	**[32]**	

Fig. 19 compares the abundance and the biodiversity indices (species number, Shannon-Wiener Index, Evenness) of the mesohabitats of the two river sections. Abundance, species number, and the Shannon-Wiener Index differed highly significantly among all samples of the mesohabitats (combined data of the river sections). Evenness was not significantly different. The abundance varied highly significantly in Bad Deutsch-Altenburg but not in Hainburg. In both river sections the species number and the Shannon-Wiener Index differed highly significantly among the mesohabitats, whereas Evenness did not differ significantly (see Tab. S1).

The mean abundance at the groyne field (1.40 Ind. min^{-1}) and the rip rap (1.12 Ind. min^{-1}) in Bad Deutsch-Altenburg was higher than in the corresponding habitats (0.85 Ind. min^{-1}; 0.74 Ind. min^{-1}) in Hainburg. The abundance at the gravel bar and side arm were similar. The mean of Shannon-Wiener Index of the side arms differed between the river sections (0.40, and 0.74, respectively). It also varied among the groyne fields (0.82 in Bad Deutsch-Altenburg, 0.52 Ind. min^{-1} in Hainburg). The mean of the Evenness was very similar in every habitat of the river sections, ranging from 0.79-0.87 (Tab. 4).

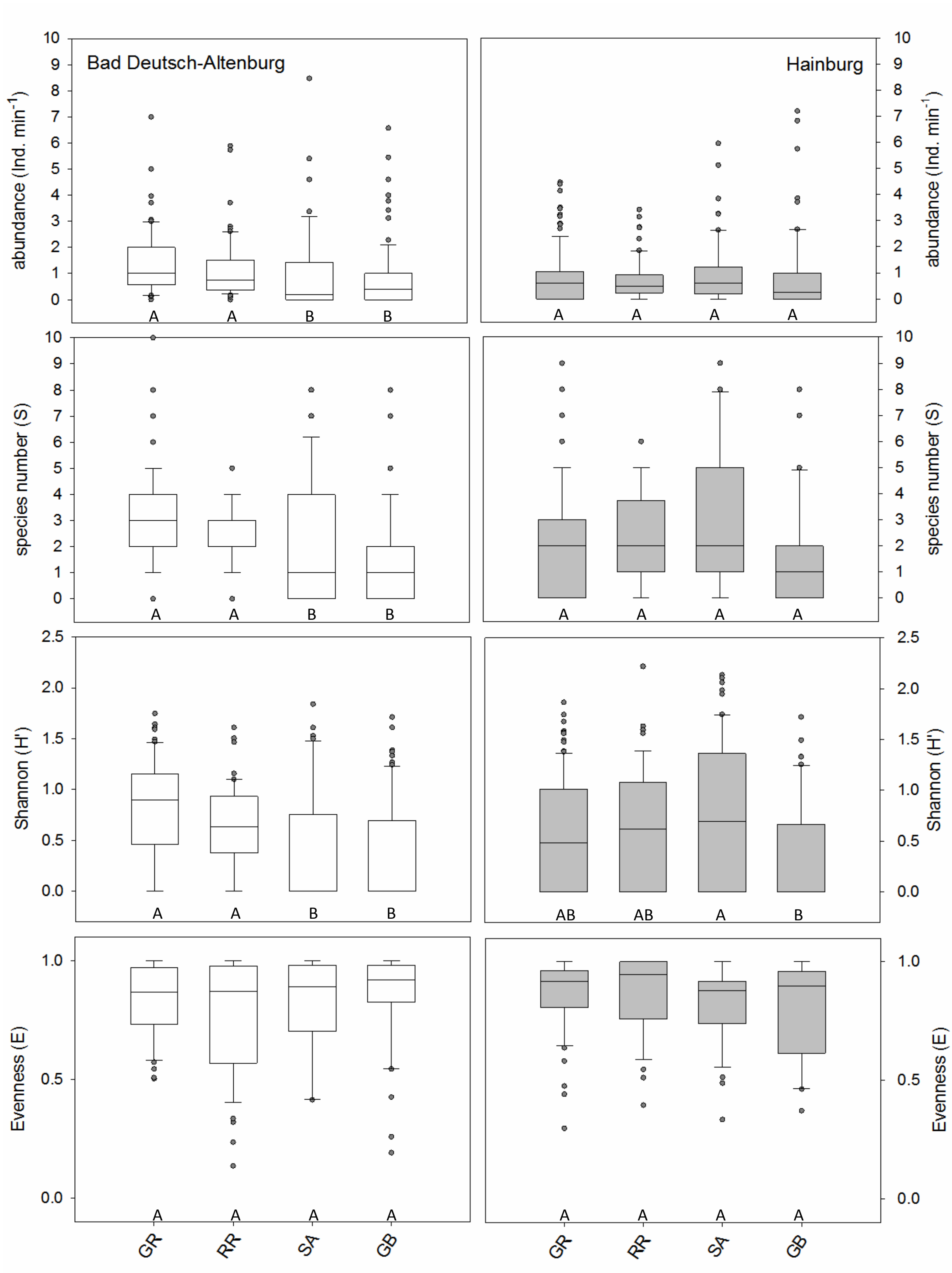

Figure 19: Box-Whisker-Plots of abundance (Ind. min^{-1}) and biodiversity indices (species number, Shannon-Wiener Index, Evenness) of different mesohabitats (GR=groyne field, RR=rip rap, SA=side arm, GB=gravel bar) in two river sections (Bad Deutsch-Altenburg N and Hainburg RN). Letters (A, AB, B) symbolize the statistical differences among the mesohabitats within a river section.

A comparison of fish assemblages of the mesohabitats of the two sections by non-metric Multidimensional scaling (NMDS) is shown in Fig. 20. No significant differences between the fish assemblages of the groyne fields, the side arms, the rip raps, and the gravel bars between Bad Deutsch-Altenburg and Hainburg were found. The fish assemblages of different mesohabitats did differ significantly: Both side arms differed significantly from almost every other habitat, whereas only a few significant differences were evident among these other habitats (Tab. S2).

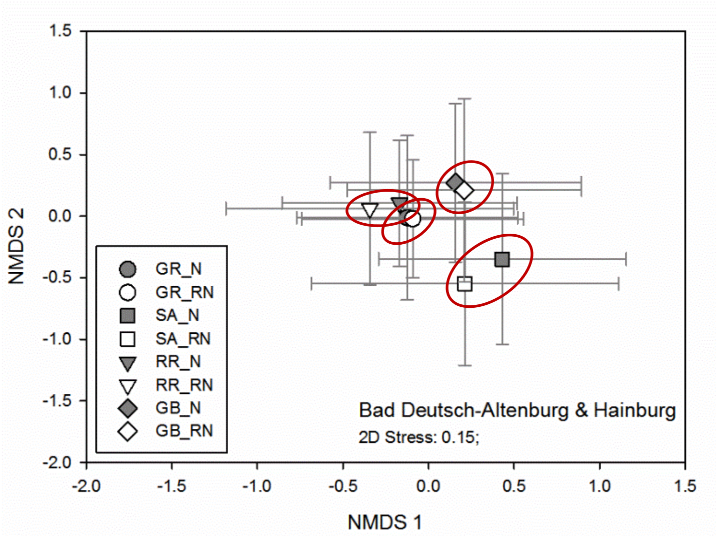

Figure 20: NMDS-analysis of the catch data (abundance of each species, Ind. min^{-1}), separated by mesohabitats: groyne fields (GR), side arms (SA), rip raps (RR), gravel bars (GB) of the two river sections (Bad Deutsch-Altenburg N, and Hainburg RN). Red circles indicate similar mesohabitat types in the two river sections. Resemblance matrix based on Bray-Curtis-dissimilarities between samples.

6.2.2 Seasonal pattern

6.2.2.1 Species assemblages over the sampling period

The seasonal abundance of species differed between the river sections. In Bad Deutsch-Altenburg, the abundance of bleak (*Alburnus alburnus*), nase (*Chondostroma nasus*) and chub (*Squalius cephalus*) peaked in summer. Barbel (*Barbus barbus*) was most abundant in April and May, and bighead goby (*Ponticola kessleri*) in autumn and winter. Round goby showed two peaks in May and October. In Hainburg the abundance of several species, i.e. bleak (*Alburnus alburnus*), nase (*Chondostroma nasus*), bighead goby (*Ponticola kessleri*), the round goby (*Neogobius melanostomus*), European perch (*Perca fluviatilis*), bitterling (*Rhodeus amarus*), roach (*Rutilus rutilus*), pike (*Sander lucioperca*), and chub (*Squalius cephalus*) showed a peak after the flood event in August. Additionally, bleak (*Alburnus alburnus*) showed a peak after the flood event in May, and round goby (*Neogobius melanostomus*) in April, May and October (Tab. 6).

Table 6: List of fish species caught in the Danube River in Bad Deutsch-Altenburg (N) and Hainburg (RN) from March to December 2014. Listed are species names, common names, abbreviations, number of individuals of every sampling area and of each month per sampling area (N,RN), the total number of individuals of each species, and the mean CPUE (Ind. min-1) of each species.

species	common name	abbreviation	Bad Deutsch Altenburg (N)										number of individuals	Hainburg (RN)									number of individuals	total number of individuals	mean CPUE (Ind. min^{-1})
			Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		Mar	Apr	May	Jun	Aug	Sep	Oct	Nov	Dec			
Abramis brama	bream	Abr_bra											0								2		2	2	0.001
Alburnoides bipunctatus	schneider	Alb_bip							1		1		2										0	2	0.000
Alburnus alburnus	danube bleak	Alb_alb	36	9	121	108	208	243	111	3		1	840	2	42	109	7	163	45	6		22	396	1236	0.318
Aspius aspius	asp	Asp_asp					2	6	7				15				12	16	3				31	46	0.009
Babka ymnotrachelus	racer goby	Bab_gym					4	2	4	5	3	4	22		2			12	12	17	11	6	60	82	0.019
Ballerus ballerus	blue bream	Bal_bal											0					7					7	7	0.001
Ballerus sapa	Danube bream	Bal_sap											0					1					1	1	0.000
Barbatula barbatula	stone loach	Barb_barb											0	1									1	1	0.000
Barbus barbus	barbel	Bar_bar	10	51	78	5	14	22	10	4			194	4	32	28	3	25	2	4			98	292	0.077
Blicca bjoerkna	white bream	Bli_bjo			10	2		23		3			38		6	3	3	24	3	26		1	66	104	0.023
Carassius gibelio	prussian carp	Car_gib								8			8						1	1			2	10	0.003
Carassius sp.		Car_sp											0					4	3				7	7	0.001
Chondrostoma nasus	nase	Cho_nas			31	1	23	145	24				224		1	24		215	5				245	469	0.108
Cobitis elongatoides	spined loach	Cob_elo											0	1		2	1	1	2	2			9	9	0.002
Cottus gobio	bullhead	Cot_gob	2	1	1	2			1	15	3	6	31		1	1	1	3		3		1	10	41	0.010
Cyprinidae sp.		Cyp_sp			4	10		2	7	2			23		1	11	1	24					37	60	0.014
Cyprinus carpio	common carp	Cyp_car					1	1					2										0	2	0.001
Esox lucius	pike	Eso_luc											0			2							2	2	0.000
Gasterosteus aculeatus	three-spined stickleback	Gas_acu				1							1	1	1	1		1			2	2	8	9	0.002
Gymnocephalus cernua	ruffe	Gym_cer			1								1							1			1	2	0.000
Gymnocephalus schraetser	schraetzer	Gym_sch						1					1					3					3	4	0.001
Lepomis gibbosus	pumpkinseed	Lep_gib											0	1	1					1			3	3	0.001
Leuciscus idus	ide	Leu_idu					1	2	1				4		1			9					10	14	0.002
Leuciscus leuciscus	common dace	Leu_leu					2	4					6	1				7					8	14	0.002
Lota lota	burbot	Lot_lot		1	3					6	2	6	18	1	3	1	4	1		5	5		20	38	0.010
Neogobius melanostomus	round goby	Neo_mel	22	46	66	35	23	19	9	82	14	18	334	4	62	61	11	114	31	129	23	19	454	788	0.190
Neogobius sp.		Neo_sp											0		6								6	6	0.001
Perca fluviatilis	european perch	Per_flu			2	2	2	2	2		2		12	1		5	1	60	6	1	4	2	80	92	0.016
Percidae sp.		Per_sp											0				3						3	3	0.001
Ponticola kessleri	bighead goby	Pon_kes	2	2	5	2	2	12	17	14	21	15	92		2		2	37	7	16	10	9	83	175	0.044
Proterorhinus semilunaris	western tubenose goby	Pro_sem	1	6	8	3	2	2	1	8	3	3	37	6	4	11	2	18	5	5	8	10	69	106	0.026
Pseudoraspora parva	stone moroko	Pse_par							1				1										0	1	0.000
Rhodeus amarus	bitterling	Rho_ama											0					101	12	1	4	4	122	122	0.014
Romanogobio vladykovi	white-finned gudgeon	Rom_vla	2					2			7	3	14							1		3	4	18	0.006
Rutilus rutilus	roach	Rut_rut			9	1		3	1	1			15	1				16			2		19	34	0.005
Salmo trutta	trout	Sal_tru			2	1	1						4										0	4	0.001
Sander lucioperca	pike-perch	San_luc			1	1	1	5	1				9		1	3		18		1		1	24	33	0.006
Silurus glanis	wels catfish	Sil_gla			5				2	3	1		11			1	1	2	1				5	16	0.004
Squalius cephalus	chub	Squ_cep		2	2	2	4	14	26	12	8	15	85	3	7	6		42	18	3	6	7	92	177	0.044
Vimba vimba	vimba bream	Vim_vim			1		1	5		1			8				1	6					7	15	0.003
Zingel streber	Danube streber	Zin_str					1				3		4										0	4	0.001
number of individuals month^{-1}			75	118	350	176	292	515	226	167	68	71	**2058**	27	173	269	53	930	156	223	77	87	**1995**	**4053**	
species number month^{-1}			7	8	17	14	17	19	17	14	12	9	**29**	13	15	15	13	25	15	18	11	13	**32**		

Fig.21 shows monthly values of the abundance and the diversity indices (species number, Evenness, and Shannon-Wiener Index) during the sampling period. All these parameters differed highly significantly over the sampling period (combined data of both river sections) and for the data of each river section (see Tab. S1, Fig. 22, and Fig. 23). In Bad Deutsch-Altenburg the abundance and the species number were relatively high in May, June, September, and October in contrast to March, April, November and December. The abundance and species numbers were highest in July and August. Hainburg shows a similar pattern: species number and abundance were highest in August but were lower in March, April, November, and December. In summary, abundance, species number, and the Shannon-Wiener Index clearly increased in summer (June to October) in both river sections, while Evenness decreased in these months, which indicated an increasing abundance of a few species (e.g. *Alburnus alburnus*, *Chondostroma nasus*, *Neogobius melanostomus*; see Fig. 21, Fig. 24, Tab. 6).

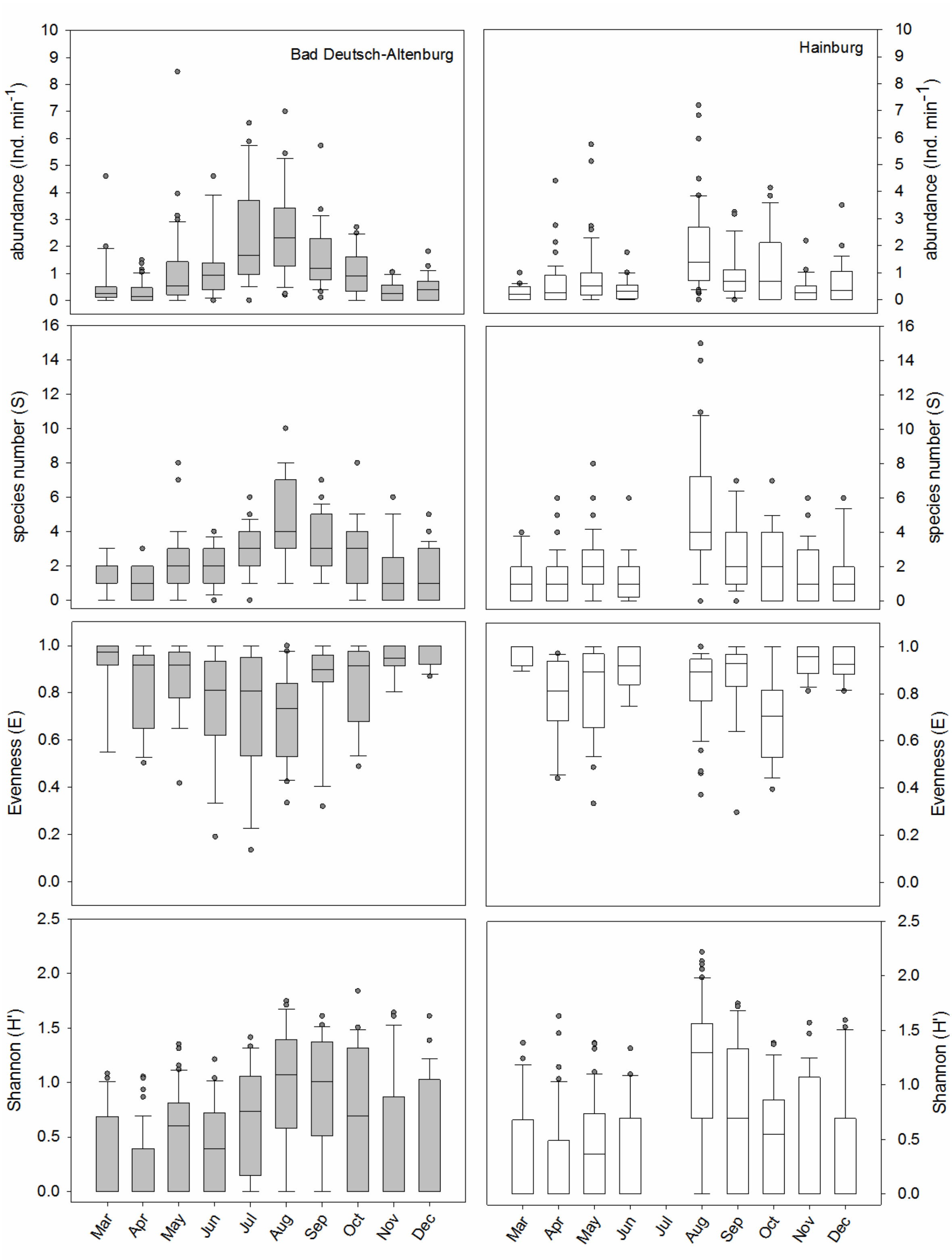

Figure 21: Box-Whisker-Plots of abundance (Ind. min^{-1}) and biodiversity indices (species number, Shannon-Wiener Index, Evenness) at Bad Deutsch-Altenburg (N) and Hainburg (RN) from March to December 2014. In July, no data available for Hainburg.

6.2.2.2 Comparison of species assemblages over the sampling period

Fig. 22 compares the assemblages between different months (combined data of both sections). The centroids of March and April, May to September, and October to December represented three groups, which differed highly significantly from each other (Tab. S2, Tab. S3).

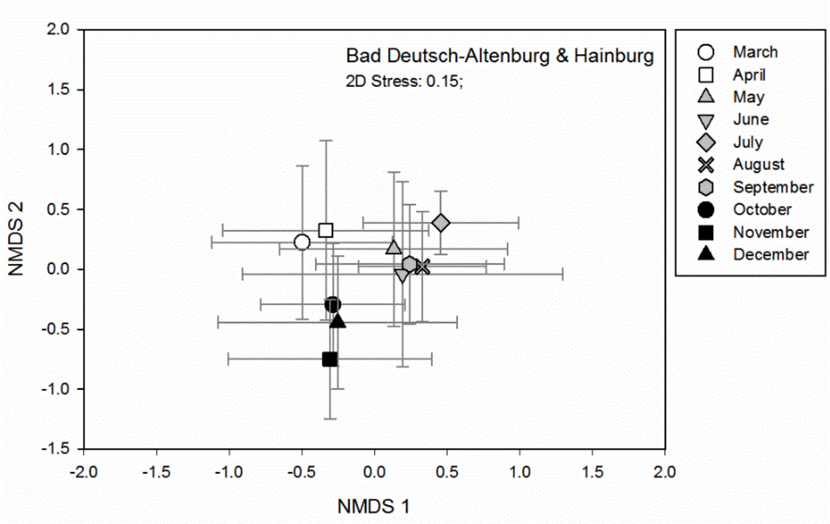

Figure 22: NMDS-analysis of the catch data (abundance of each species, Ind. min^{-1}) by month (March to December 2014). Resemblance matrix based on Bray-Curtis-dissimilarities between samples.

Fig. 23 shows the analyses of the species assemblages for each river section with regard to monthly changes. In Bad Deutsch-Altenburg the centroids of March and April, May to September, and October to December formed groups which differed highly significantly from each other. In Hainburg the distances of the centroids were significant, but smaller (Tab. S2, Tab. S3).

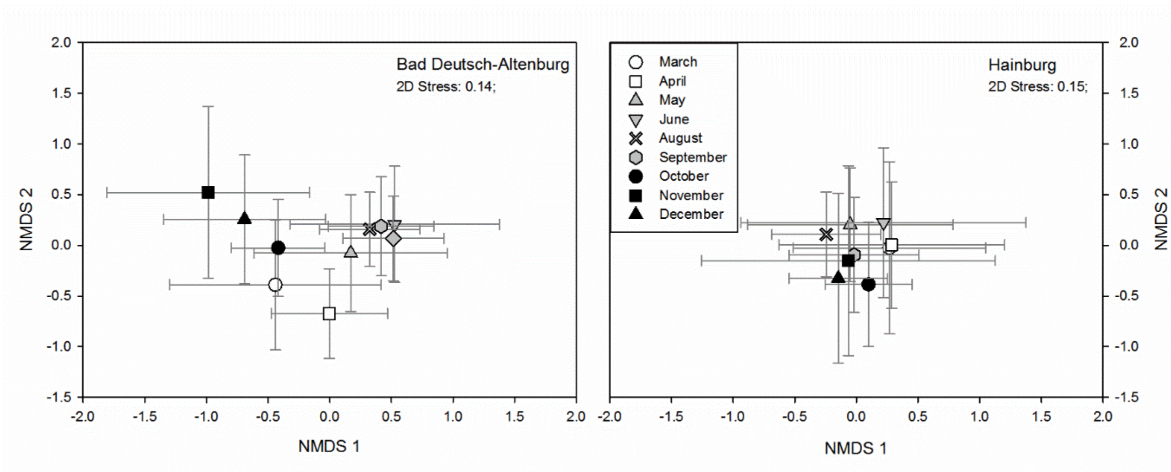

Figure 23: NMDS-analysis of the catch data (abundance of each species, Ind. min^{-1}) of Bad Deutsch-Altenburg (N) and Hainburg (RN) by month (March to December 2014). Resemblance matrix based on Bray-Curtis-dissimilarities between samples.

Fig. 24 shows the seasonal changes in abundance of the four most abundant species in both river sections. The abundance of bleak (*Alburnus alburnus*), nase (*Chondostroma nasus*), and round goby (*Neogobius melanostomus*) fluctuated over the year, whereas barbel (*Barbus barbus*) showed a more consistent pattern. In Bad Deutsch-Altenburg, bleak was most abundant in July. Nase showed a relatively small peak in August, and the round goby (*Neogobius melanostomus*) in October. Barbel increased slightly in abundance in April and May. In Hainburg the seasonal pattern was similar. Bleak was most abundant in May and August. Nase peaked in August, the round goby (*Neogobius melanostomus*) in October. Barbel abundance increased slightly in April and May.

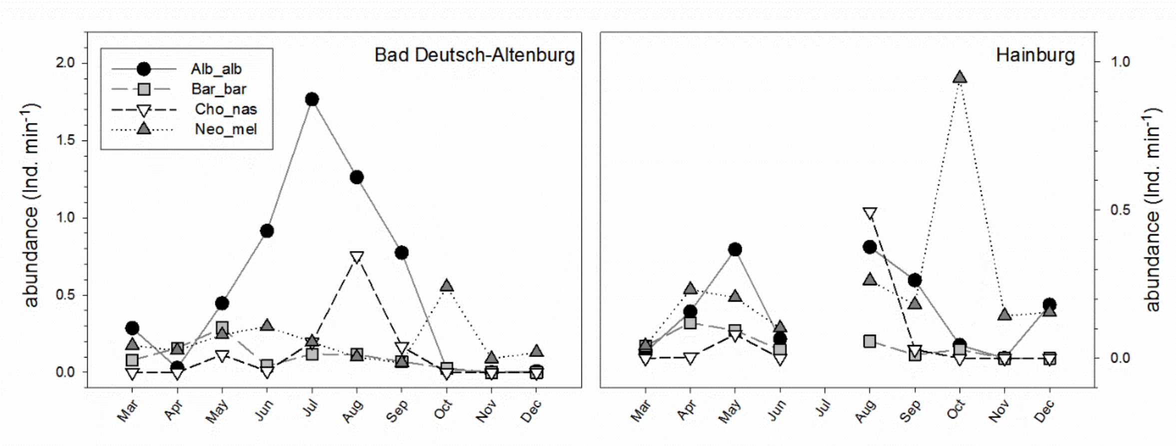

Figure 24: Monthly changes of abundance (Ind. min^{-1}) of bleak (*Alburnus alburnus*=Alb_alb), barbel (*Barbus barbus*=Bar_bar), nase (*Chondostroma nasus*=Cho_nas) and round goby (*Neogobius melanostomus*=Neo_mel) in Bad Deutsch-Altenburg and Hainburg. Note different scales of y-axes. In July, no data available for Hainburg.

6.2.3 Species accumulation curves

Species accumulation curves were calculated for both river sections, for each river section (Bad Deutsch-Altenburg, Hainburg), and for the mesohabitats of the river sections (Fig. 25). The total species number (29) was higher in Hainburg than in Bad Deutsch-Altenburg (32). Regarding mesohabitats, in Bad Deutsch-Altenburg, more species were found in the groyne field and at the gravel bars than in the corresponding habitats in Hainburg. This situation was reversed at the rip raps and in the side arms.

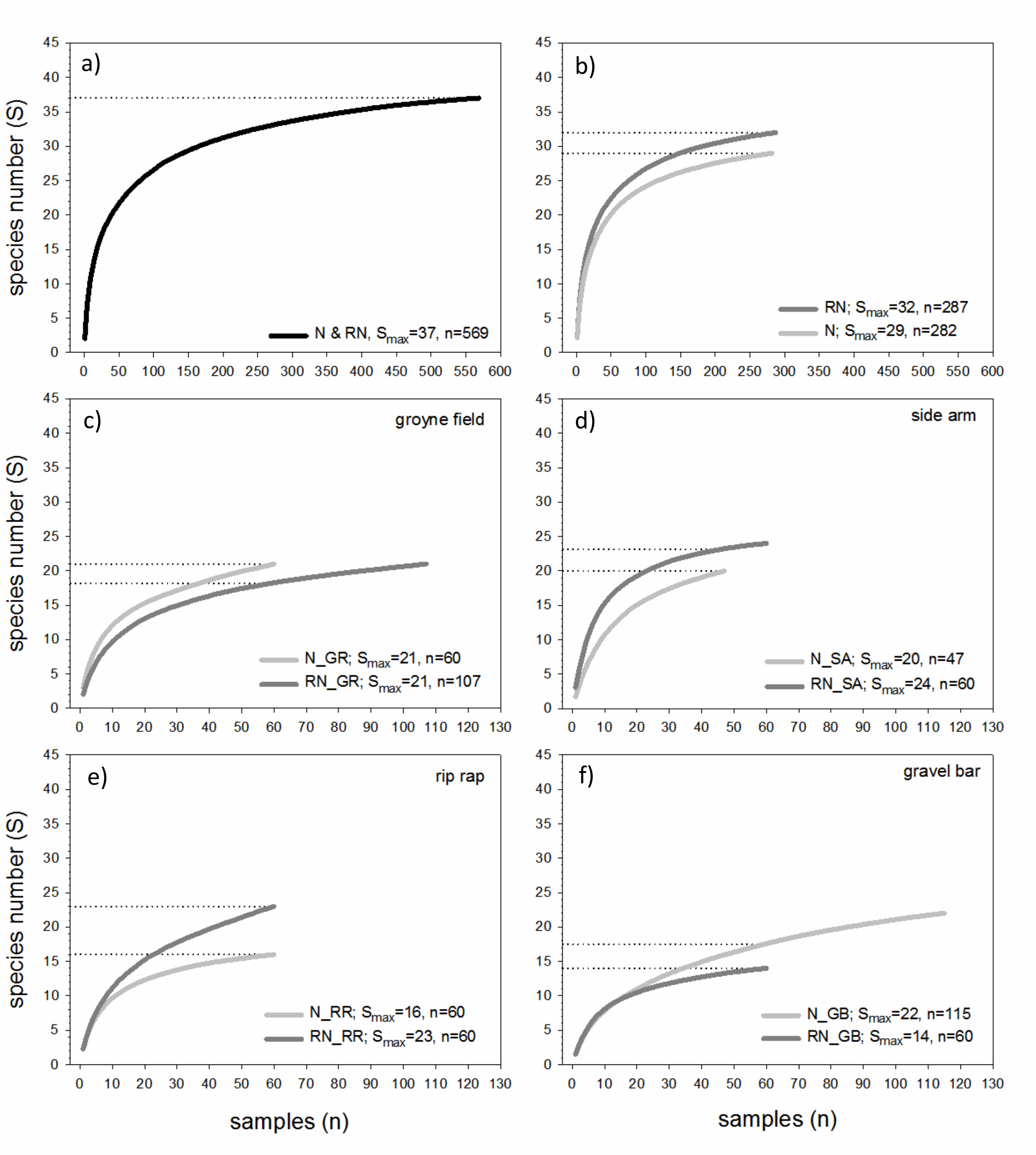

Figure 25: Species accumulation curves for a) the total catch, b) for Bad Deutsch-Altenburg (N), and Hainburg (RN), c) for the groyne field in N and RN and d) for the side arm in N and RN, e) for the rip rap in N and RN, f) for the gravel bar in N and RN. X-axis: number of samples.

6.2.4 Relationship between fish abundance and discharge, as well as other hydraulic parameters

We conducted an RDA to explain the variability of the species data based on the measured environmental variables (flow velocity, water depth, and water temperature) and discharge. The results showed that 23.5% of the total variability in the species data is explained by all four canonical axes (Tab. 7). The first axis (RD-a1) explains 18.5% and the second axis (RD-a2) 3.0%. The variables water temperature and discharge are associated with RD-a1, and the variables water depth and flow velocity are linked with RD-a2. Hence, the variability of the species data is mainly influenced by the discharge, followed by water temperature. Bleak (*Alburnus alburnus*), nase (*Chondostroma nasus*), and barbel (*Barbus barbus*) are connected with the RD-a1, while the round goby (*Neogobius melanostomus*) and white bream (*Blicca bjoerkna*) are associated with RD-a2 (Tab. 7, Tab. 8). Nase and bleak had higher abundances at high discharge. Round goby (*Neogobius melanostomus*) was more abundant at lower water level. Finally, the species number increased with higher discharge (Fig. 26).

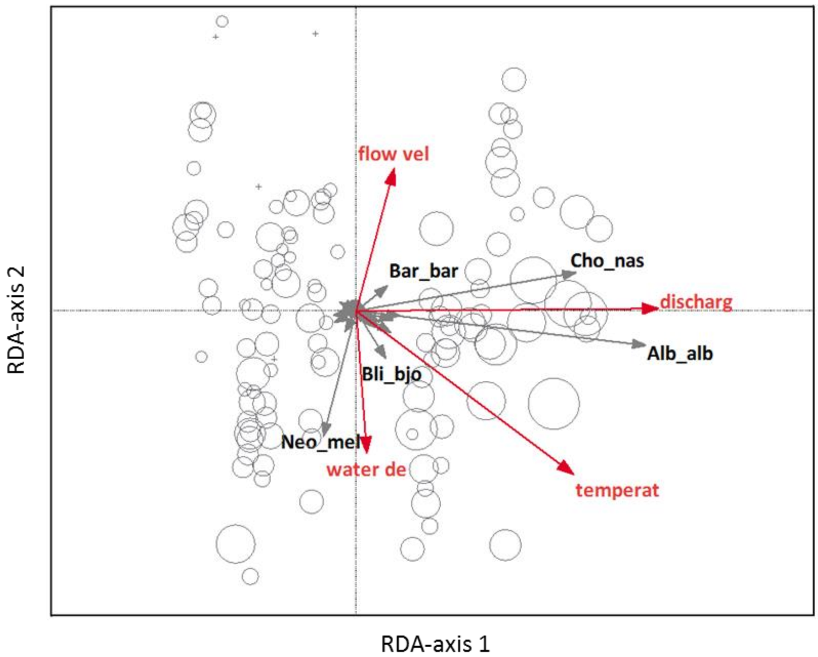

Figure 26: RDA of the species data (Ind. min^{-1}) and the environmental data (n=117, flow velocity, discharge, water depth, water temperature). The species belonging to the arrows in the center are: Alb_bip, Asp_asp, Car_gib, Cob_elo, Cot_gob, Cyp_car, Gas_acu, Gym_cer, Gym_sch, Lep_gib, Leu_idu, Leu_leu, Lot_lot, Bab_gym, Pon_kes, Per_flu, Pro_sem, Rho_ama, Rom_vla, Rut_rut, Sal_tru, San_luc, Sil_gla, Squ_cep, Vim_vim, Zin_str (Tab. S4); Grey circles represent the species number of each sampling event. Species abbreviations from Tab. 3.

Table 7: Eigenvalues of the canonical axes, the cumulative variance of the species data, the sum of all canonical eigenvalues, test of significance of the canonical axes of the RDA (Fig. 26).

	RD-a1	**RD-a2**	**RD-a3**	**RD-a4**
Eigenvalues	0.185	0.030	0.016	0.004
Cumulative percentage variance of species data	18.5	21.5	23.1	23.5
Sum of all canonical eigenvalues		Total variance		0.235
Test of significance (Monte Carlo) of the canonical axes				
First canonical axis:	F-ratio: 25.376			
	P-value: 0.0020			
of all canonical axis:	F-ratio: 8.601			
	P-value: 0.0020			

Table 8: Relation of the environmental variables to the RDA-axes and the relation of the species to the RDA-axes. Alb_alb= bleak, Cho_nas= nase, Bar_bar= barbel, Neo_mel= round goby, Bli_bjo= white bream.

Inter set correlations of environmental variables with axes				
NAME	AX1	AX2	AX3	AX4
	0.1949	0.0451	0.041	0.0085
water depth	0.0254	-0.2328	-0.1346	0.1655
flow velocity	0.09	0.2335	0.3411	0.0663
water temperature	0.5125	-0.2675	0.1644	-0.046
discharge	0.7129	0.0041	-0.052	0.0074

Cumulative fit per species as fraction of variance of species						
NAME	AX1	AX2	AX3	AX4	VAR(y)	% EXPL
	0.1847	0.0302	0.0162	0.0038		
Alb_ alb	0.3748	0.3801	0.3813	0.3836	9.26	38.36
Cho_ nas	0.4227	0.4356	0.4356	0.4422	4.72	44.22
Bar_ bar	0.016	0.0262	0.0879	0.0892	2.55	8.92
Neo_ mel	0.0088	0.1378	0.1478	0.1503	5.02	15.03
Bli_ bjo	0.0322	0.114	0.1341	0.1387	1.13	13.87

The abundance increased highly significantly with increasing discharge in the main stem of the Danube (combined data of both river sections, n=569, p<0.001, Spearman=0.320), and in each river section, Bad Deutsch-Altenburg (n=282, p<0.001, Spearman=0.387) and Hainburg (n=287, p<0.001, Spearman=0.273; Fig. 27). Our results indicated that the abundance increased especially in summer. In August and September the discharge was above mean water level. Additionally, abundance increased slightly with the high water level in May (Fig. 6, Fig. 21).

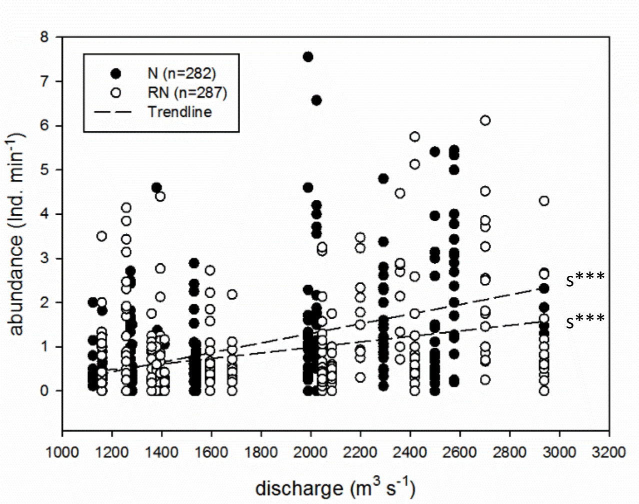

Figure 27: Correlation between discharge ($m^3\ s^{-1}$) and fish abundance (Ind. min^{-1}) in Bad Deutsch-Altenburg (N) and Hainburg (RN). Regression line indicates the trend of the data. n=number of samples. Significant (s *** if p<0.001; s ** if p<0.01; s* if p<0.05); not significant (n.s.).

In all mesohabitat types of both river sections, the correlation between fish abundance and discharge was positive. The gravel bars (n=175, p=0.000, Spearman=0.291), groyne fields (n=167, p= 0.000, Spearman=0.489) and rip raps (n=120, p=0.008, Spearman=0.240) of both river sections (combined data) showed a highly significant increase in abundance with discharge, while the correlation was significantly positive in the side arms (n=107, p=0.031, Spearman=0.208). Nevertheless, at the river section level, the significance of the correlation between and within habitat types varied: The groyne fields showed a highly significant increase in the abundance with increasing discharge in Bad Deutsch-Altenburg (n=60, p=0.000, Spearman=0.615) and in Hainburg (n=107, p=0.000, Spearman=0.371), and the same was true for the gravel bars in Bad Deutsch-Altenburg (n=115, p=0.000, Spearman=0.337). The correlations of the rip rap in Bad Deutsch-Altenburg (n=60, p=0.012, Spearman= 0.322) and in Hainburg (n=60, p=0.036, Spearman=0.271) were significantly positive (Fig. 28).

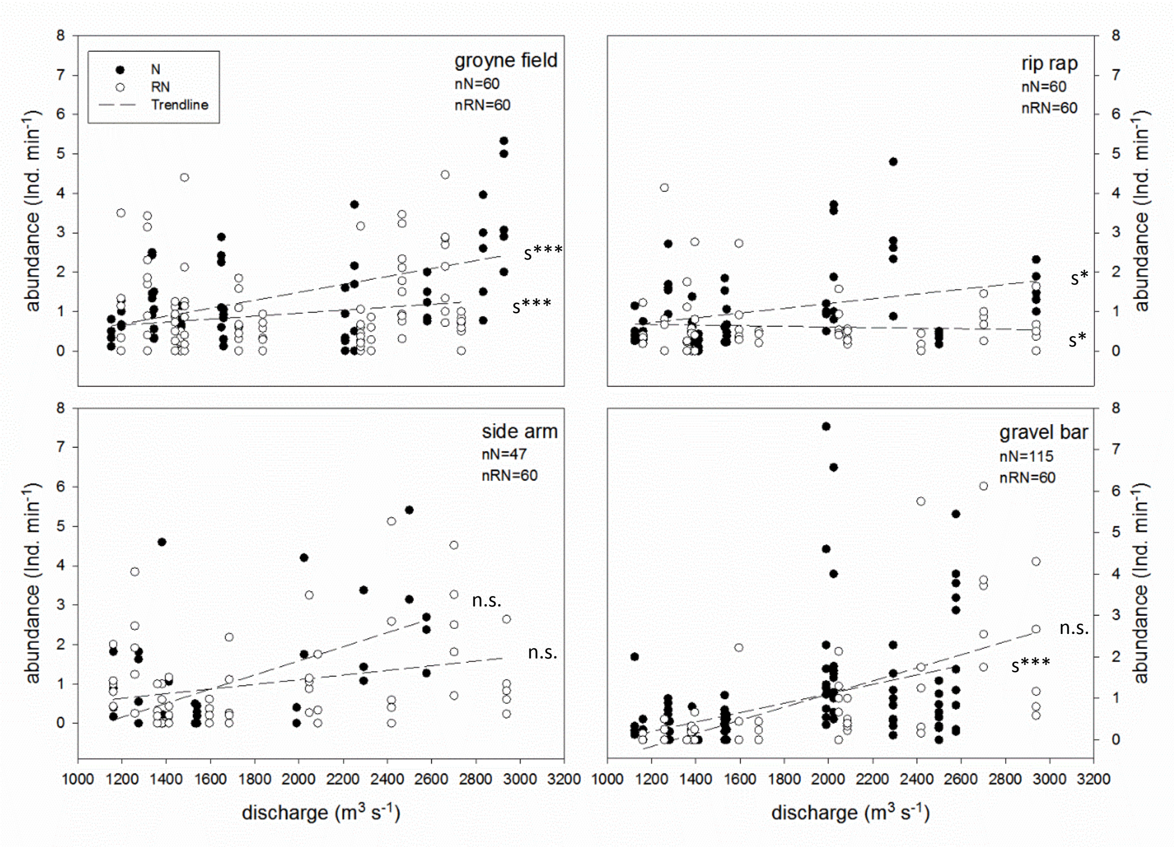

Figure 28: Correlation between discharge (m^3 s^{-1}) and fish abundance in different mesohabitats (gravel bar, groyne field, rip rap, side arm), and the mesohabitats of each river section (Bad Deutsch-Altenburg N and Hainburg RN). Regression line indicates the trend of the data. n=number of samples. Significant (s *** if p<0.001; s ** if p<0.01; s* if p<0.05); not significant (n.s.).

6.2.5 Spatial distribution of ecological guilds

Fish assemblages of the same mesohabitat types (gravel bar, groyne field, rip rap) were characterised by a similar structure and were composed of similar ecological guilds irrespective of river section. Despite this similar pattern the percentage of the guilds varied in these three mesohabitats. The groyne fields and gravel bars contained a higher proportion of the rheophilic A guild compared to the side arms and rip raps. Fishes of the rhithralic guild were found only along the rip raps. The side arms showed a higher variability in their composition of ecological guilds (see also Fig. 20). In contrast to the side arm in Bad Deutsch-Altenburg, representatives of the stagnophilic guild were found in the Hainburg side arm.

The mesohabitats differed significantly from each other (combined data of both river sections, Kruskal-Wallis-Test: Chi-Square= 15.326, p= 0.002, d.f.= 3, n= 569). The mesohabitats differed highly significantly from each other at Bad Deutsch-Altenburg (Kruskal-Wallis-Test: Chi-Square= 29.047, p= 0.000, d.f.= 3, n= 282), but not at Hainburg. In the groyne fields the neobiota (U-test, p=0.004, nN=60, nRN=107) and the guild rheophilic A (U-test, p=0.000, nN=60, nRN=107) differed highly significantly between Bad Deutsch-Altenburg and Hainburg. In the side arms the neobiota (U-test, p=0.001, nN=47, nRN=60) and the stagnophilic guild (U-test, p=0.006, nN=47, nRN=60) differed highly significantly between the two river sections. Along the rip raps and at the gravel bars there was no significant difference of the guilds between the two river sections (Fig.29, Tab.9).

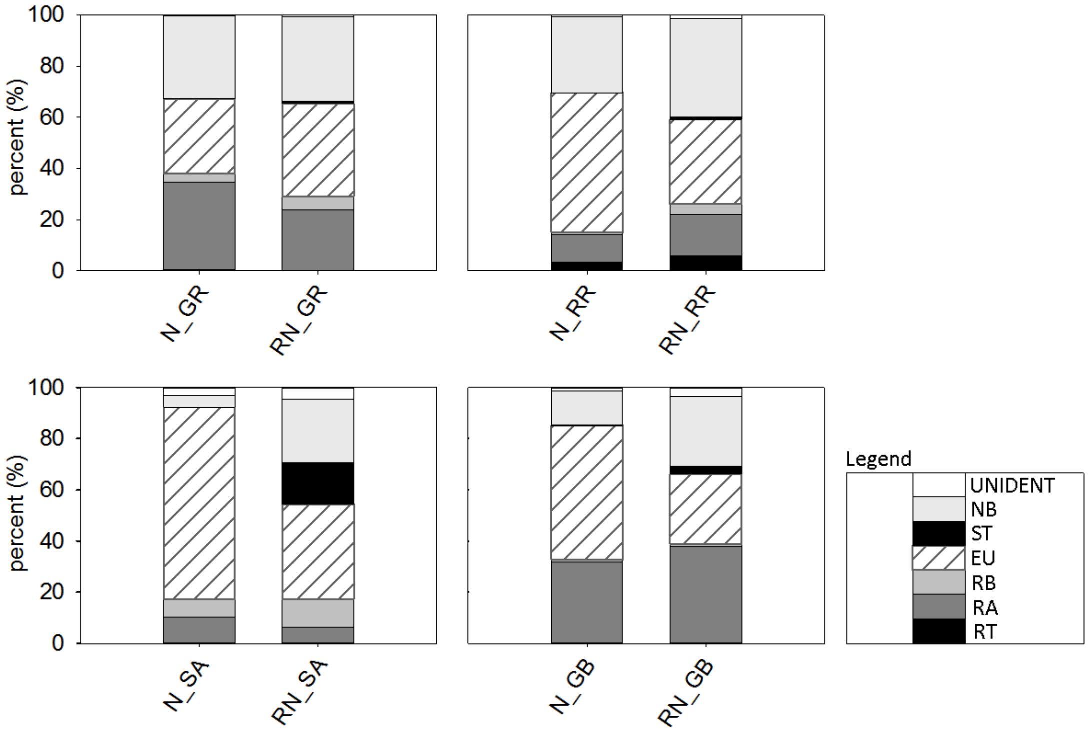

Figure 29: Ecological guilds (Schiemer & Waidbacher, 1992) in percent % of the mesohabitats (groyne field GR, rip rap RR, side arm SA, gravel bar GB) at Bad Deutsch-Altenburg (N) and Hainburg (RN). RT (rhithralic), RA (rheophilic A), RB (rheophilic B), EU (eurytopic), ST (stagnophilic), NB (Neobiota, exotic fishes), UNIDENT (fishes could not be identified at species level in the field).

Table 9: Mean abundance (Ind. min^{-1} ± standard deviation SD) and number of individuals [Ind.] of each guild in different mesohabitats (groyne field GR, side arm SA, rip rap RR, gravel bar GB) at Bad Deutsch-Altenburg (N) and Hainburg (RN) from March to December 2014; bold = significant differences.

	RT		**RA**		**RB**		**EU**		**ST**		**NB**		**UNIDENT**		**total abundance**	
	mean	± SD	mean	± SD	mean	± SD	mean	± SD	mean	± SD	mean	± SD	mean	± SD	mean	± SD
N	0.051		0.924		0.118		2.246		0.002		0.977		0.089	0.450	1.057	1.485
[Ind.]	[22]		[484]		[57]		[1020]		[1]		[449]		[25]		[2058]	
RN	0.050		0.710		0.202		1.230		0.141		1.102		0.185	0.859	0.880	1.180
[Ind.]	[20]		[367]		[124]		[692]		[130]		[600]		[53]		[1986]	
GR																
N	0.008	0.039	**0.470**	**0.611**	0.040	0.110	0.401	0.859	0.000	0.000	**0.470**	**0.458**	0.033	0.181	1.399	1.298
[Ind.]	[3]		**[221]**		[22]		[187]		[0]		**[210]**		[2]		[645]	
RN	0.001	0.012	**0.182**	**0.655**	0.045	0.134	0.314	0.615	0.008	0.053	**0.305**	**0.472**	0.056	0.269	0.868	1.139
[Ind.]	[1]		**[158]**		[34]		[242]		[6]		**[218]**		[6]		[665]	
SA																
N	0.000	0.000	0.090	0.201	0.059	0.149	0.754	1.463	**0.000**	**0.000**	**0.053**	**0.106**	0.255	0.765	0.989	1.685
[Ind.]	[0]		[38]		[25]		[275]		**[0]**		**[16]**		[12]		[366]	
RN	0.000	0.000	0.069	0.217	0.127	0.434	0.437	0.782	**0.111**	**0.421**	**0.304**	**0.486**	0.517	1.359	1.101	1.298
[Ind.]	[0]		[44]		[74]		[254]		**[111]**		**[170]**		[31]		684	
RR																
N	0.039	0.087	0.118	0.190	0.010	0.048	0.593	1.201	0.000	0.000	0.349	0.462	0.050	0.287	1.116	1.182
[Ind.]	[17]		[55]		[5]		[276]		[0]		[151]		[3]		[507]	
RN	0.049	0.084	0.117	0.264	0.023	0.071	0.215	0.363	0.006	0.028	0.279	0.580	0.083	0.279	0.700	0.823
[Ind.]	[19]		[52]		[13]		[107]		[3]		[124]		[5]		[323]	
GB																
N	0.004	0.033	0.247	0.587	0.008	0.047	0.498	1.426	0.002	0.017	0.106	0.221	0.070	0.434	0.876	1.611
[Ind.]	[2]		[170]		[5]		[282]		[1]		[72]		[8]		[540]	
RN	0.000	0.000	0.342	0.917	0.006	0.027	0.264	0.524	0.015	0.076	0.214	0.538	0.183	1.172	0.861	1.405
[Ind.]	[0]		[122]		[3]		[89]		[10]		[88]		[11]		[323]	
N & RN	0.011	0.047	0.209	0.556	0.037	0.169	0.423	1.003	0.016	0.144	0.253	0.448	0.137	0.689	0.968	1.341
[Ind.]	[42]		[860]		[181]		[1712]		[131]		[1049]		[78]		[4053]	

6.2.6 Size structure

The mean size (total length) of fishes at the inshore habitats in the main stem of the Danube was 7.20 ± 4.17 cm. In Bad Deutsch-Altenburg, size ranged from 1.50 to 43.00 cm. The size class with the highest number of individuals was 6.00 to 6.99 cm. In Hainburg, size ranged from 2.00 to 58.00 cm. Fishes with a size between 2.00 and 15.00 cm were most abundant. In contrast to Bad Deutsch-Altenburg, the 4.00 to 4.99 cm size class had the most fish (Fig. 30). Although the difference was rather small, the total length (cm) differed highly significantly (Kruskal-Wallis-Test: Chi-square= 38.695, $p<0.001$, d.f.=1, nN=2058, nRN=1995) between the two river sections (mean total length ± standard deviation SD cm = 7.30 ± 4.00 cm in Bad Deutsch-Altenburg, 6.90 ± 4.30 cm in Hainburg, Fig. 31, Tab. 10). In the gravel bars and groyne fields, fish size ranged from 2.00 to 20.00 cm and from 1.50 to 30.00 cm, respectively. In contrast, the range in the rip raps and side arms ranged from 2.00 to 43.00 cm and from 1.50 to 58.00 cm, respectively.

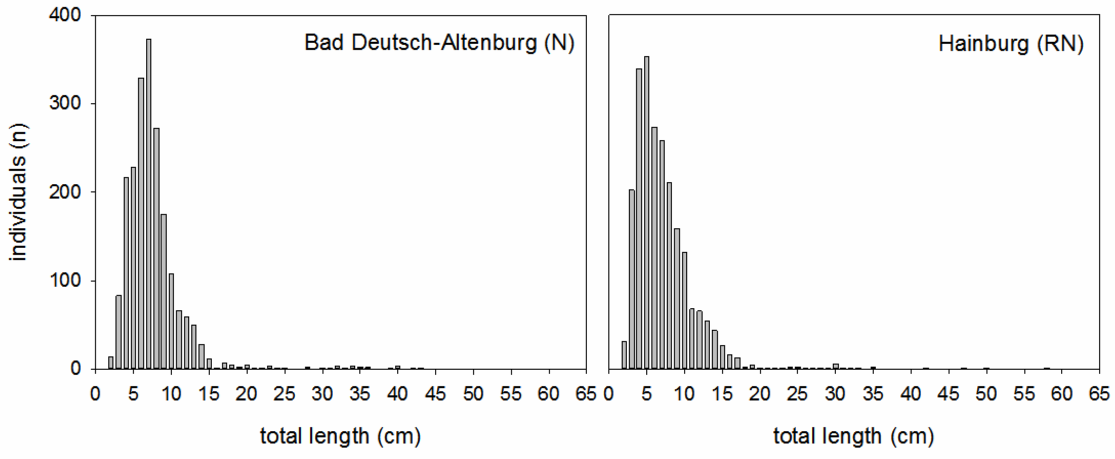

Figure 30: Frequency distribution of the total length (cm) of fishes caught in the inshore habitats at Bad Deutsch-Altenburg and Hainburg.

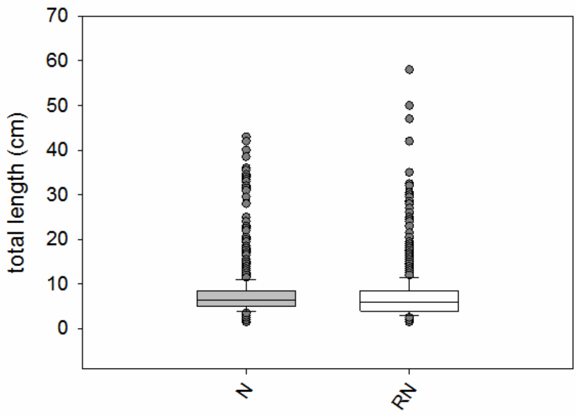

Figure 31: Box-Whisker-Plots of fish size (total length, cm) at Bad Deutsch-Altenburg and Hainburg.

Table 10: Mean size (total length, cm) of fishes in different mesohabitats (gravel bar GB, groyne field GR, rip rap RR, side arm SA) at Bad Deutsch-Altenburg (N) and Hainburg (RN) from March to December 2014. SD=standard deviation, min=minimum, max=maximum.

	total length (cm)				
	median	**mean**	**SD**	**max**	**min**
N	6.83	7.36	4.03	43.00	1.50
RN	6.00	6.96	4.31	58.00	2.00
GB	6.50	6.67	2.85	20.00	2.00
GR	6.50	7.16	3.18	30.00	1.50
RR	7.00	8.76	6.24	47.00	2.00
SA	5.50	6.28	3.70	58.00	1.50
N_GB	6.50	6.79	2.75	20.00	2.00
N_GR	7.00	7.58	2.92	29.50	1.50
N_RR	7.00	8.24	6.09	43.00	2.00
N_SA	6.50	6.59	3.40	42.00	1.50
RN_GB	6.00	6.50	2.99	17.50	2.00
RN_GR	6.00	6.72	3.38	30.00	2.00
RN_RR	7.75	9.53	6.39	47.00	2.00
RN_SA	5.00	6.12	3.85	58.00	2.00

Fig. 32 compares species-specific sizes (total length in cm) in the inshore areas of the main stem of the Danube River. The assemblage consisted of juveniles of characteristic species, as well as of adults of small-sized species (e.g. *Rhodeus amarus*, *Gasterosteus aculeatus*, Gymnocephalus schraetser, *Alburnoides bipunctatus*, *Romanogobio vladykovi*, *Cobitis elongatoides*, *Cottus gobio*, *Proterorhinus semilunaris*, *Neogobius melanostomus*, *Babka gymnotrachelus*, *Ponticola kessleri*). The above species have a total length (TL) of approx. 5-10 cm, and Neogobius sp. attained up to 20 cm.

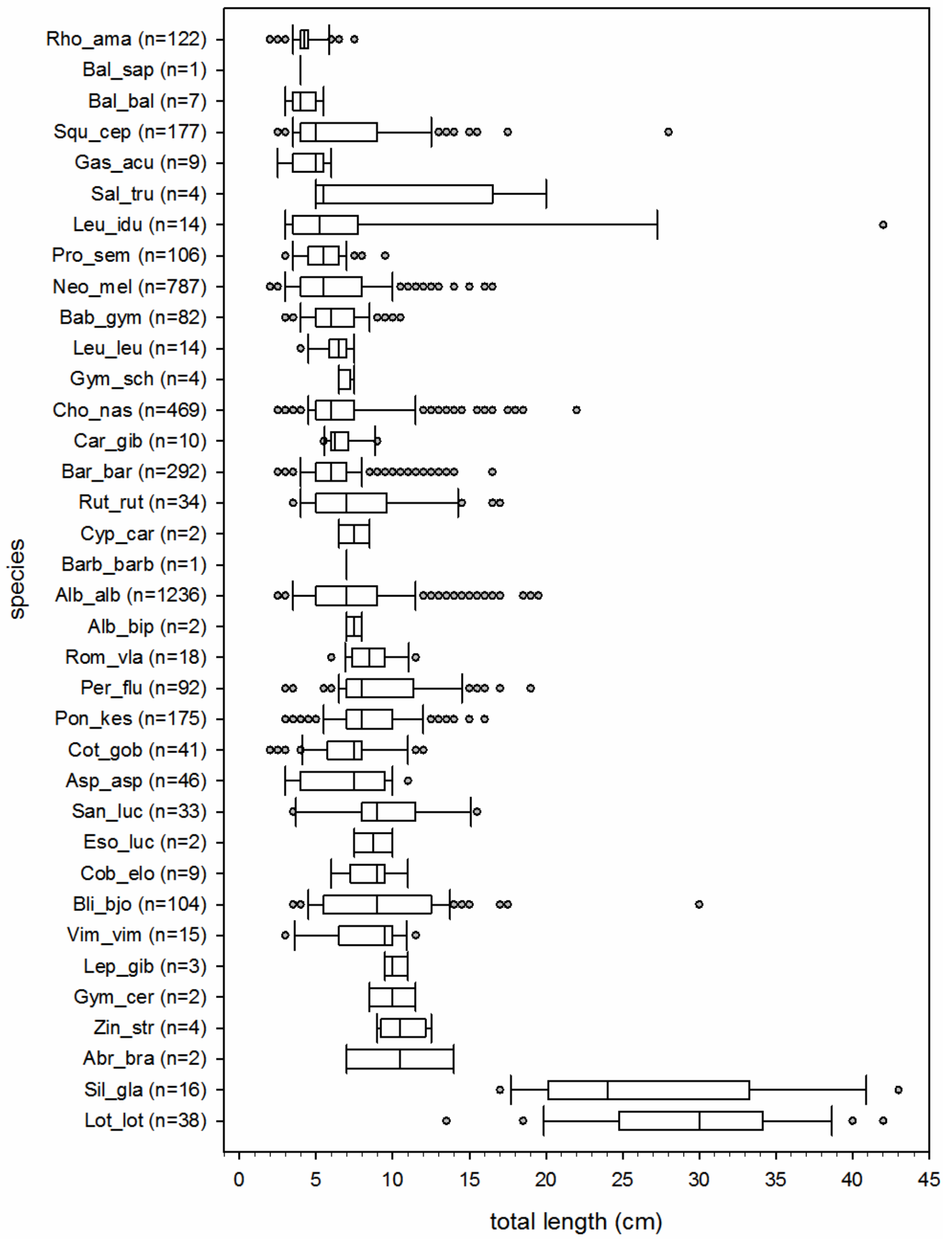

Figure 32: Box-Whisker-Plots of total length (cm) of the fish species caught in inshore mesohabitats from March to December 2014 at Bad Deutsch-Altenburg and Hainburg. Species abbreviations from Tab. 3; n=numbers of samples.

7 Discussion

7.1 Spatial pattern

River sections Bad Deutsch Altenburg and Hainburg

A high number of fish species (37) from five guilds were caught in the inshore zones of the main stem of the Danube in Bad Deutsch-Altenburg and Hainburg (Tab. 3). Schiemer and Waidbacher (1992), Jungwirth et al. (2003) list 57 native fish species in the Danube River. Schiemer et al. (1991) recorded 50 species in the free-flowing stretch downstream of Vienna. The present study reports approx. 75% of these species in the 8 sampled inshore mesohabitats. In this context, Loisl et al. (2014), Schiemer and Waidbacher (1992) stated that usually more diverse fish assemblages are present in the inshore areas than in the sublittoral and benthic habitats of the main channel in the free-flowing sections of the Danube River. In this study, fish assemblages showed a significant but very small difference between the river sections (NMDS with conducted ANOSIM, Fig.18). Additionally, the abundances of these numerous species were relative equally distributed (Evenness approx. 0.8) within the river sections. The conclusion is that both investigated river sections provide a relatively high and similar diversity of habitats.

The main channel is important for the riverine fishes in terms of recruitment. The numerous juvenile fishes, e.g. nase (*Chondostroma nasus*), barbel (*Barbus barbus*), and chub (*Squalius cephalus*), that occurred regularly in different sections and mesohabitats (Fig. 32) demonstrate successful reproduction in the vicinity of different inshore habitats. Habitats (main channel, laterally connected habitats, e.g. side arm) must provide conditions for the larvae to hatch and to survive until they are juveniles (for example suitable oxygen content and flow velocity; Humphries and Lake, 2000). Strayer (2010) underlined that suitable habitats for spawning and for recruitment, as well as their connectivity are important. The numerous species caught show that differently structured habitats are essential in the Danube to ensure sustainable populations.

Mesohabitats

The fish assemblages in the different mesohabitats are, with the exception of the side arms, relative similar to each other Fig. 20). This result supports the findings of Erős et al. (2008), who showed that the fish assemblages do not differ significantly in artificial and natural shorelines of the Danube in Hungary. Nevertheless, different numbers of species were found among the mesohabitats of both river sections investigated here, as well as within the same type of mesohabitats (Fig. 25, Tab.

5). Jackson (2001), Gorman and Karr (1978) emphasized the importance of structural diversity to enhance species number because inter- and intraspecific competition is reduced. The present study supports this hypothesis: The gravel bars in Bad Deutsch-Altenburg harboured more species than the same habitat type in Hainburg. One potential explanation is the recent reconstruction in Bad Deutsch-Altenburg (heaped island, see chapter 5.1.1). Furthermore, clearly more species were caught along the rip rap in Hainburg than in the correlating habitat in Bad Deutsch-Altenburg. This specific rip rap showed a high diversity of microhabitats because a small stream (Russbach) separates this mesohabitat. Moreover, this small stream forms a confluence with the Danube. Also, more species were present in the side arm at Hainburg than in the side channel at Bad Deutsch-Altenburg. The side arm of Hainburg is characterized by a high inshore heterogeneity; it is not permanently connected on both ends and has no permanent through-flow. While the Bad Deutsch-Altenburg side channel shows a lower inshore heterogeneity, it is permanently connected upstream and downstream to the main stem and exhibited a permanent through-flow. These results indicate that mesohabitats with a higher structural diversity, as well as mesohabitats that are connected to other water bodies (e.g. side arm and rip rap in Hainburg), support more species. In this context, Stoffels et al. (2015) showed that the duration and heterogeneity of the lateral hydrological connectivity among water bodies are important for spatial differences in fish assemblages.

Wintersberger (1996b, 1996d) showed that bleak (*Alburnus alburnus*) has adapted to a broad range of environmental conditions and that it was most abundant in lentic habitats. Schiemer and Spindler (1989) proved that eurytopic species (e.g. bleak) were found in all habitats. Bleak was also the most abundant species in this study supporting Tarkus (2010) and Zauner et al. 2007), followed by nase (*Chondostroma nasus*), barbel (*Barbus barbus*), and the neobiota round goby (*Neogobius melanostomus*). These four species were the four most abundant ones in the gravel bars, whereas in the rip raps and the groyne fields at least three of them were among the first five most abundant species. The side arms in both river sections differed significantly from the groyne fields, rip raps and gravel bars concerning the most abundant species. In the side arms, two of these species were among the most abundant. Moreover, numerous species occur only or in higher numbers in the side arms (Tab.5).

Rheophilic species (e.g. *Chondostroma nasus, Barbus barbus*) spawn in the inshore zones of the river itself (Keckeis et al. 1996; Schiemer and Spindler, 1989). Thus, Schiemer et al. (1991) found abundant freshly-hatched larvae in the Danube. Keckeis et al. (1996) concluded that the spawning areas and the nursery habitats must be close to each other, based on the high mortality rate of eggs and larvae under high mechanical stress. Additionally, nase prefer moderate to fast-flowing current in rivers with rock or gravel bottom. Early juveniles are benthic and prefer shallow shoreline habitats (Kottelat and Freyhof, 2007). In this study they were therefore found in greater abundances at the gravel bars and groyne fields of both river sections in the Danube River. Additionally, the mean flow velocity was higher at the gravel bars than in the other habitat types. Barbel, which prefer gravel bottoms and fast currents in rivers (Kottelat and Freyhof, 2007), were most abundant in the reconstructed groyne field (enhanced flow velocity along the shoreline) in Bad Deutsch-Altenburg. This groyne field is located downstream of numerous gravel bars, which might, along with the groyne field itself, have served as spawning grounds. Barbel spawn at shallow riffles, and feeding larvae drift to nearby shallow inshore habitats, where they stay until they are juveniles. Neogobius sp. is abundant at riverbeds and in shallow littoral inshore zones (Bammer, 2010; Zauner et al., 2007).

Watkins et al. (2015) showed for the Lower Kootenai River in Idaho that non-native species also apparently exhibited higher relative abundances in newly rehabilitated areas than native species. The neobiota round goby (*Neogobius melanostomus*) favours rocky inshore habitats (Kottelat and Freyhof, 2007). According to Loisl (2012) and Zauner et al. (2007), Neogobius sp. is most abundant in anthropogenically constructed rip raps and groyne fields. Accordingly, in the present study they were most abundant in these artificial habitats, with an exception of the Bad Deutsch-Altenburg side arm.

The distribution and proportion of the guilds reflect the results on the occurrence and abundance of species in distinct mesohabitats: due to the abundant nase (*Chondostroma nasus*) and barbel (*Barbus barbus*), the percentage of the rheophilic guild is higher in the gravel bars and groyne fields than in the side arms and rip raps. In every sampled habitat (except the side arm in Bad Deutsch-Altenburg) the proportion of the neobiota (e.g. *Neogobius melanostomus*) is relatively high, as is the percentage of the euryotopic species (e.g. *Alburnus alburnus*). Burbot (*Lota lota*) was more abundant along the rip raps, which mirrors the percentage of the rhithralic guild in this habitat type. Furthermore, the high species number in the side arm and the rip rap in Hainburg means that more guilds are represented in these habitats (Tab. 5, Fig. 29).

7.2 Seasonal pattern

Poff and Zimmermann, 2010 observed a clear seasonal pattern: as flow increased, the number of species and therefore habitat biodiversity increased. As the factor "discharge" interacts with the parameter season (Fladung et al., 2003), the same pattern was evident in the present samples. Discharge and abundance were positively correlated in the groyne fields as well as along the rip raps in both river sections, and at the gravel bars in Bad Deutsch-Altenburg. Additionally, abundance increased in summer (July, August, September), as did species number and the Shannon-Wiener Index in these months; Evenness, however, decreased (Fig. 21). As represented in the present samples, this leads to the assumption, that, despite a higher number of species, only a few species showed a strong increase in abundance (e.g. *Alburnus alburnus, Chondostroma nasus*, Tab. 6, Fig. 24). The RDA analysis supports this interpretation: a clear association of these two species with discharge and water temperature was shown (increasing abundance with increasing discharge and increasing water temperature; Fig. 26, Tab. 7, and Tab. 8; see also Fig. 27).

The four most abundant species showed a seasonal pattern (Fig. 24). The abundance of bleak (*Alburnus alburnus*) in Hainburg showed two peaks, one in May and one in August. This could reflect flood events and the resulting high water level in May and August (Fig. 6). The highest abundance however, occurred in July in Bad Deutsch-Altenburg during mean-flow conditions (constantly increasing from April to July, and constantly decreasing from July to October, Fig. 24). This could point to spawning activities of the bleak, which spawn between May and August at a temperature above 12°C (Kottelat and Freyhof, 2007). An additional reason could be enhanced predator pressure (e.g. by *Aspius aspius*). Furthermore, the round goby (*Neogobius melanostomus*) showed a peak in October during low-water level in both river sections, while the other species declined. In this context, Watkins et al. (2015) showed a great predation and competition effect from non-native fish species on native species. Thus, the decreased abundance in October of bleak, nase (*Chondostroma nasus*), and barbel (*Barbus barbus*) could lead to this sudden increase of the round goby (Fig. 24).

The variability of the species (abundance, occurrence) was mainly affected by discharge and water temperature, but also by flow velocity and water depth (Fig. 26, Tab. 7, and Tab. 8). Shore structure and slope are decisive for the hydraulic conditions (water level, flow velocity, water depth) in inshore habitat and thus for the habitat availability for juveniles: Fladung et al. (2003) reported that the most important factors for fish assemblages in the Elbe River were slope, flow velocity, predominant substrate, water depth, and water level. The present findings showed that the flow velocity increased significantly, but slightly, with increasing discharge in the groyne fields and gravel bars of both river sections, and in the rip rap of Hainburg. Brunke et al. (2001) concluded that the relationship between discharge and flow velocity differed with the gradient of the slope and the structure of the distinct mesohabitats. Fladung et al. (2003) further showed that the factors “slope of a shore” and “water depth” were the key factors for adult and juvenile fishes for their habitat choice in the Elbe River. The present results indicate that the correlation of discharge and water depth depended on the slope and structure of the inshore habitats. Steep shorelines, e.g. the side channel in Bad Deutsch Altenburg, showed a significant positive correlation. Overall, the water depth in the inshore habitats increased only slightly with discharge. Both factors, flow velocity and water depth, were minimally influenced by increasing discharge in the inshore mesohabitats. This leads to the conclusion that these habitats show stable abiotic conditions, even at flow conditions above mean-water level. Moreover, the flow velocity was little influenced by increasing water depth in the various mesohabitats (Fig. 6, Fig. 9, and Fig. 13). Finally, fish abundance in the inshore areas in both river sections investigated here increased significantly with increasing discharge. This correlation varied among the different habitats (between and within sections; Fig. 27, Fig. 28). Based on the fact that flow velocity and water depth of the inshore habitats were little influenced by stronger discharge, the investigated inshore mesohabitats show a refugial-capacity: After an August flood event in Hainburg, the individual numbers of some species (*Alburnus alburnus*, *Chondostroma nasus*, *Neogobius melanostomus*, *Perca fluviatilis*, *Squalius cephalus*, *Sander lucioperca*, *Rhodeus amarus*) clearly increased along the shoreline (Fig. 6, Tab. 6). Bitterling (*Rhodeus amarus*) was very abundant only in the Hainburg side arm, which was flowed through. Numerous juvenile nase (*Chondostroma nasus*) were found after this flood event at a slow-flowing, shallow, vegetated area behind the island (gravel bar) in Hainburg (Tab. 5, Tab. 6). These results emphasize the importance of diverse inshore habitats in a mainstream (Jungwirth et al., 2003; Schiemer, 2000; Schlosser, 1991; Mittelbach, 1980), especially of side arms and bays, which provide a greater shore heterogeneity and potential as refugia during flood events (Schiemer et al., 2001).

Daufresne et al. (2015) concluded that long-term and time-lagged environmental effects, which may alter the stability of fish dynamics, complicate specifying the annual variability of fish assemblages. Fishes do not react immediately to environmental changes. Moreover, the difficulty to sample in large stems could blur the effects of such annual variability. Lamouroux and Olivier (2015) stated that biotic interactions, interactive effects of river-floodplain restoration, long-term effects of dam constructions, and climate change are among the factors which make it difficult to predict annual fish variability. Accordingly, the present study proves that specific inshore habitats were used in higher abundance at high-water level. Additionally, the results showed a positive relationship between discharge and abundance, as well as a seasonal pattern of both discharge and abundance (see above, Fig. 6, Fig. 21). The RDA however, shows that discharge explains only 18.5% of the variability of the fish assemblages (Fig. 26, Tab. 7, and Tab. 8). Additionally, bleak (*Alburnus alburnus*) showed a different seasonal pattern between the two river sections (see chapter 7.2, Fig. 24). In interpreting these results (supporting Schiemer et al., 1991; Schlosser, 1991), other factors no doubt also influence the annual variability in fish assemblages, e.g. ontogenetic habitat shifts, spawning events, and predator pressure.

7.3 Conclusion

This study underlined the complexity of the interaction between fish assemblages and a changing environment (discharge, flow velocity, water depth). Multiple factors influenced the inshore fish assemblages of the Danube River in Bad Deutsch-Altenburg and Hainburg: The data indicated a change in fish assemblages and fish abundance due to changes in discharge. The rising water level changed - depending on the shore characteristics (slope, structural diversity) - the hydro-morphological conditions (e.g. flow velocity, water depth) minimally. Thus, the abiotic conditions of the inshore habitats were stable, even with flood events above mean-water level. As discharge and fish abundance showed a seasonal pattern, also other factors (ontogenetic habitat shifts, spawning events, predator pressure) influenced the annual variability of fish assemblages. Further, in interpreting the results, the annual variability of fish assemblages is mainly influenced by the abundance of certain fish (e.g. *Alburnus alburnus, Chondostroma nasus, Neogobius melanostomus*). The present results emphasize the importance of instream inshore habitats and their lateral and longitudinal connectivity. They act as refugia and as potential spawning- and nursery grounds for larvae and juveniles, making them essential for reproduction and recruitment. Hence, improving the inshore habitats of the main channel and their connectivity is crucial for sustainable fish populations. Accordingly, further renaturation efforts require additional long-term surveys of fish species and fish assemblages and their reaction to altered environmental conditions in order to provide physical habitats that meet the habitat requirements and characteristics of native fish species and fish assemblages.

8 Danksagung

An dieser Stelle möchte ich mich ganz herzlich bei meinem Betreuer Prof. Dr. Hubert Keckeis für seine Unterstützung, und dass ich Teil dieses interessanten Projektes sein durfte, bedanken.

Außerdem gilt mein besonderer Dank der Fischtruppe (Reinhard Krusch, David Ramler, Maximilian Sehr, Holger Villwock und Bernhard Zens) für ihre tatkräftige Unterstützung - sei es beim Fischen auf der wundervollen Donau, oder durch ihren Humor und ihr Verständnis im Alltag.

Meinen warmherzigen Dank möchte ich auch gegenüber meiner Familie und meinen Freunden ausdrücken. DANKE, dass ihr mein Leben schöner und reicher macht.

9 Acknowledgement

I wish to express my warm thanks to my supervisor Prof. Dr. Hubert Keckeis for his support and for enabling my participation in this interesting project.

Furthermore, my special thanks go to the fishing team (Reinhard Krusch, David Ramler, Maximilian Sehr, Holger Villwock, Bernhard Zens) for their active support while fishing on the wonderful Danube and for their humor and understanding.

My warm-hearted thanks to my family and my friends. THANK YOU for enriching my life and making it more beautiful.

10 References

Amoros, C., Bornette, G., 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology, 47(4), pp.761-776.

Bammer, V. E. (2010). Benthische Fischartenassoziationen in unterschiedlichen Mesohabitaten der Donau bei Hainburg unter Berücksichtigung eingewanderter Meeresgrundeln. Diplomarbeit. Wien.

Bonar, S.A., Hubert, W.A., Willis, D.W., 2009. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society.

Brunke, M., Hoffmann, A., Pusch, M., 2001. Use of mesohabitat-specific relationships between flow velocity and river discharge to assess invertebrate minimum flow requirements. Regulated Rivers: Research & Management Rivers, 17(September 2000), pp.667-676.

Clarke, K. R., Warwick, R.M., 2001. Change In marine communities. An approach to statistical analysis and interpretation. 2nd Edition. PRIMER-E Ltd. UK: Plymouth Marine Laboratary.

Daufresne, M., Veslot, J., Capra, H., Carrel, G., Poirel, A., Olivier, J.-M., Lamouroux, N., 2015. Fish community dynamics (1985-2010) in multiple reaches of a large river subjected to flow restoration and other environmental changes. Freshwater Biology, 60, pp.1176-1191.

Dolédec, S., Castella, E., Forcellini, M., Olivier, J.-M., Paillex, A., Sagnes, P., 2015. The generality of changes in trait compositions of fish and invertebrate communities after flow restoration in a large river (French Rhône). Freshwater Biology, 60, pp.1147-1161.

Erős, T., Tóth, B., Sevcsik, A., Schmera, D., 2008. Comparison of Fish Assemblage Diversity in Natural and Artificial Rip-Rap Habitats in the Littoral Zone of a Large River (River Danube, Hungary). International Review of Hydrobiology, 93(1), pp.88-105.

Fladung, E., Scholten, M., Thiel, R., 2003. Modelling the habitat preferences of preadult and adult fishes on the shoreline of the large, lowland Elbe River. Journal of Applied Ichthyology, 19(5), pp.303-314.

Fuiman, L. A., Werner, R. G., 2002. Fishery Science. The unique contributions of early life stages. Blackwell Science Ltd, Oxford.

Gormann, O.T., Karr, J.R., 1978. Habitat Structure and Stream Fish Communities. Ecology, 59(3), pp.507-515.

Guy, C. S., Brown, M. L. (Eds), 2007. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Grenouillet, G., Pont, D., Seip, K., 2002. Abundance and species richness as a function of food resources and vegetation structure: juvenile fish assemblages in rivers. Ecography, 6(March), pp.641-650.

Humphries, P., Lake, P.S., 2000. Fish larvae and the management of regulated rivers. Regulated Rivers Research & Management, 432(May 1999), pp.421-432.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D., 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences, 58(1), pp.157-170.

Jungwirth, M., Haidvogel, G., Moog, O., Muhar, S., Schmutz, S., 2003. Angewandte Fischökologie an Fließgewässern. Wien. Facultas. 547 pp.

Keckeis, H., 2013. 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), pp.1-16.

Keckeis, H., Frankiewicz, P., Schiemer, F., 1996. The importance of inshore areas for spawning nase *Chondostroma nasus* (Cyprinidae) in a free-flowing section of a large river (Danube, Austria). Archiv für Hydrobiologie. Official journal of the International Association of Theoretical and Applied Limnology. 113(1-4), pp.51-64.

King, A.J., Tonkin, Z., Mahoney, J., 2009. Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. River Research Applications, 25, pp.1205-1218.

Kottelat, M., Freyhof, J., 2007. Handbook of European freshwater fishes. Kottelat, Cornol, Switzerland and Freyhof, Berlin, Germany.

Lamouroux, N., Olivier, J.-M., 2015. Testing predictions of changes in fish abundance and community structure after flow restoration in four reaches of a large river (French Rhône). Freshwater Biology, 60, pp.1118-1130.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data using CANOCO. Cambridge University Press, Cambridge, UK.

Loisl, F. 2012. Comparison of the fish assemblage of three Danube segments on the basis of different sampling methods. Diplomarbeit. Wien.

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, pp.77-94.

Magurran, Anne E., 2004. Measuring biological diversity: Blackwell Publishing.

McCune, B., Grace, J.B. (2002). Analysis of ecological communities. Gleneden Beach, Oregon: MjM Software Design.

Mittelbach, G.G., 1981. Foraging Efficiency and Body Size: A Study of optimal diet and Habitat Use by Bluegills. Ecology, 62(5), pp.1370-1386.

Oberdorff, T., Hugueny, B., Vigneron, T., 2001. Is assemblage variability related to environmental variability? An answer for riverine fish. Oikos, 93(3), pp.419-428.

Poff, N.L., Zimmerman, J.K.H., 2010. Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. Freshwater Biology, 55(1), pp.194-205.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.S., 1997. The Natural Flow Regime: A paradigm for river conservation and restoration N. BioScience, 47(11), pp.769-784.

Reckendorfer, W., Keckeis, H., Tiitu, V., Winkler, G., Zornig, H., Schiemer, F., 2001. Diet shifts in 0+ nase, *Chondostroma nasus*. Size-specific differences and the effect of food availability. Archiv für Hydrobiologie (Suppl.) (Large Rivers), 135(2-4), pp.425-440.

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), pp.583-591.

Schiemer, F., Keckeis, H., Reckendorfer, W., Winkler, G., 2001. The “inshore retention concept” and its significance for large rivers. Archiv für Hydrobiologie (Suppl.) (Large Rivers), 135(2), pp.509-516.

Schiemer, F., 2000. Fish as indicators for the assessment of the ecological integrity of large rivers. Hydrobiologia, 422, pp.271–278.

Schiemer F., Waidbacher H. 1992. Strategies for Conservation of a Danubian Fish Fauna. In Boon, P. J., P. Calow & G. E. Petts (eds), River Conservation and Management, pp.364-382.

Schiemer, F., Spindler, T., Wintersberger, H., Schneider, A., & Chovanec, A., 1991. Fish fry associations: important indicators for the ecological status of large rivers. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie. Verhandlungen IVTLAP, 24(4), pp.2497-2500.

Schiemer F., Spindler T. 1989. Endangered fish species of the Danube River in Austria. Regulated Rivers: Research & Management, 4, pp.397-407.

Schlosser, J., 1991. Fish Ecology : A Perspective Landscape affect fish populations and their community dynamics. BioScience, 41(10), pp.704–712.

Stoffels, R.J., Rehwinkel, R.A., Price, A.E., Fagan, W.F., 2015. Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly. Aquatic Sciences.

Strayer, D.L., Findlay, S.E.G., 2010. Ecology of freshwater shore zones. Aquatic Sciences, 72(2), pp.127-163.

Tarkus, M., Volkmann, C., Drexler, S.-S., Waidbacher, H., Straif, M., 2010. Assessment of the ecological functionality of anthropogenically created habitats in the impoundment of the hydropower plant Freudenau (Vienna, Austria) with bi- and multivariate statistical analyses. Zoologia, 27(1), pp.92-98.

Tockner, K., Robinson, C.T., Uehlinger, U., 2009. Rivers of Europe. London. Academic Press.

Watkins, C.J., Stevens, B.S., Quist, M.C., Shepard, B.B., Ireland, S.C., 2015. Patterns of Fish Assemblage Structure and Habitat Use among Main- and Side-Channel Environments in the Lower Kootenai River, Idaho. Transactions of the American Fisheries Society.

Wintersberger, H., 1996b. Species assemblages and habitat selection of larval and juvenile fishes in the River Danube. pp.14-23. Dissertation. Wien.

Wintersberger, H., 1996d. Size-dependent use of fish larvae and 0+ juveniles in the River Danube. pp.48-65. Dissertation. Wien.

Yossef, M.F.M., 2005. Morphodynamics of rivers with groynes. Delft. Delft University of Technology.

Zauner, G.; Ratschan, C.; Mühlbaumer, M., 2007. Fischfauna der Donau im östlichen Machland unter besonderer Berücksichtigung der FFH-Schutzgüter und ihres Erhaltungszustands; Maßnahmen und Potenzial für Revitalisierung. In: Österreichs Fischerei, 60, pp.194-206.

11 Supplement

Table S1: Results of the Kruskal-Wallis-Test

Mesohabitats	Chi-Square	p	d.f.	n
Bad Deutsch-Altenburg (N) & Hainburg (RN)				
abundance	17.337	0.001	3	569
species number (S)	30.393	0.000	3	569
Shannon-Wiener Index (H')	27.570	0.000	3	569
Evenness (E)	2.023	0.568	3	309
Bad Deutsch-Altenburg (N)				
abundance	29.047	0.000	3	282
species number (S)	44.591	0.000	3	282
Shannon-Wiener Index (H')	38.108	0.000	3	282
Evenness (E)	3.683	0.298	3	160
Hainburg (RN)				
abundance	5.004	0.172	3	287
species number (S)	12.036	0.007	3	287
Shannon-Wiener Index (H')	13.159	0.128	3	287
Evenness (E)	5.685	0.004	3	149

Sampling Period (Mar-Dec)	Chi-Square	p	d.f.	n
Bad Deutsch-Altenburg (N) & Hainburg (RN)				
abundance	149.033	0.000	9	569
species number (S)	140.682	0.000	9	569
Shannon-Wiener Index (H')	117.796	0.000	9	569
Evenness (E)	42.867	0.000	9	309
Bad Deutsch-Altenburg (N)				
abundance	100.049	0.000	9	282
species number (S)	77.244	0.000	9	282
Shannon-Wiener Index (H')	55.358	0.000	9	282
Evenness (E)	29.785	0.000	9	160
Hainburg (RN)				
abundance	63.299	0.000	8	287
species number (S)	69.133	0.000	8	287
Shannon-Wiener Index (H')	66.816	0.000	8	287
Evenness (E)	26.499	0.001	8	149

Table S2: Results of the Anosim I

Bad Deutsch Altenburg (N) & Hainburg (RN)

n		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
nN=16, nRN=12	**Mar**					p=0.001, R=0.36	p=0.001, R=0.424	p=0.001, R=0.195	p=0.001, R=0.215	p=0.001, R=0.192	
nN=26, nRN=32	**Apr**				p=0.001, R=0.187	p=0.001, R=0.299	p=0.001, R=0.374	p=0.001, R=0.241		p=0.001, R=0.282	p=0.001, R=0.258
nN=37, nRN=36	**May**									p=0.001, R=0.283	p=0.001, R=0.191
nN=20, nRN=15	**Jun**						p=0.001, R=0.278				
nN=21, nRN=0	**Jul**								p=0.001, R=0.43	p=0.001, R=0.456	p=0.001, R=0.283
nN=32,nRN=49	**Aug**								p=0.001,R=0.367	p=0.001,R=0.482	p=0.001,R=0.379
nN=23, nRN=23	**Sep**								p=0.001, R=0.209	p=0.001,R=0.227	
nN=20, nRN=17	**Oct**										
nN=17, nRN=16	**Nov**										
nN=18, nRN=16	**Dec**										

Bad Deutsch Altenburg (N)

n		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
nN=16	**Mar**					p=0.001,R=0.484	p=0.001,R=0.529	p=0.001,R=0.424		p=0.001,R=0.286	
nN=26	**Apr**				p=0.001,R=0.349	p=0.001,R=0.532	p=0.001,R=0.566	p=0.001,R=0.463	p=0.001,R=0.309	p=0.001,R0.463	p=0.001,R=0.392
nN=37	**May**									p=0.001,R=0.316	
nN=20	**Jun**									p=0.001,R=0.25	
nN=21	**Jul**								p=0.001,R=0.521	p=0.001,R=0.561	p=0.001,R=0.488
nN=32	**Aug**								p=0.001,R=0.57	p=0.001,R=0.55	p=0.001,R=0.507
nN=23	**Sep**								p=0.001,R=0.446	p=0.001,R=0.41	p=0.001, R=0.381
nN=20	**Oct**										
nN=17	**Nov**										
nN=18	**Dec**										

Hainburg (RN)

n		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
nRN=12	**Mar**						p=0.001,R=0.479	p=0.003,R=0.219	p=0.001,R=0.285		
nRN=32	**Apr**						p=0.001,R=0.277				
nRN=36	**May**									p=0.001,R=0.254	
nRN=15	**Jun**						p=0.001,R=0.372				
nRN=0	**Jul**										
nRN=49	**Aug**								p=0.001,R=0.254	p=0.001,R=0.416	p=0.002,R=0.262
nRN=23	**Sep**										
nRN=17	**Oct**										
nRN=16	**Nov**										
nRN=16	**Dec**										

n		N_GB	N_GR	N_RR	N_SA	RN_GB	RN_GR	RN_RR	RN_SA
n=77	**N_GB**				p=0.003,R=0.122		p=0.001,R=0.116		p=0.001,R=0.172
n=58	**N_GR**				p=0.001,R=0.306				p=0.001,R=0.177
n=58	**N_RR**				p=0.001,R=0.247	p=0.001,R=0.124			p=0.001,R=0.188
n=28	**N_SA**						p=0.001,R=0.278	p=0.001,R=0.129	
n=38	**RN_GB**						p=0.001,R=0.197		p=0.001,R=0.131
n=80	**RN_GR**								p=0.001,R=0.199
n=51	**RN_RR**								p=0.001,R=0.154
n=47	**RN_SA**								

Table S3: Results of the Anosim II

Group 1: March, April				
Group 2: May, June, July, August, September				
Group 3: October, November, December				
Bad Deutsch-Altenburg (N) & Hainburg (RN)				
n		1	2	3
nN=42, nRN=44	1		p=0.001, R=0.184	p=0.001, R=0.185
nN=133, nRN=123	2			p=0.001, R=0.220
nN=55, nRN=49	3			
Bad Deutsch-Altenburg (N)				
n		1	2	3
nN=42	1		p=0.001, R=0.249	p=0.001, R=0.212
nN=133	2			p=0.001, R=0.339
nN=55	3			
Hainburg (RN)				
n		1	2	3
nRN=44	1		p=0.001, R=0.109	p=0.001, R=0.185
nRN=123	2			p=0.018, R=0.033
nRN=49	3			

Table S4: Relation of the species to the RDA-axes

		Cumulative fit per species as fraction of variance of species					
N	NAME	AX1	AX2	AX3	AX4	VAR(y)	% EXPL
		0.1847	0.0302	0.0162	0.0038		
1	Alb_alb	0.3748	0.3801	0.3813	0.3836	9.26	38.36
2	Alb_bip	0.0016	0.0016	0.011	0.0357	0.01	3.57
3	Asp_asp	0.1285	0.1361	0.1362	0.1431	0.43	14.31
4	Bar_bar	0.016	0.0262	0.0879	0.0892	2.55	8.92
5	Bli_bjo	0.0322	0.114	0.1341	0.1387	1.13	13.87
6	Car_gib	0.0114	0.0316	0.043	0.0435	0.1	4.35
7	Car_sp	0.0297	0.0304	0.0322	0.0405	0.05	4.05
8	Cho_nas	0.4227	0.4356	0.4356	0.4422	4.72	44.22
9	Cob_elo	0.0004	0.0624	0.1124	0.1127	0.05	11.27
10	Cot_gob	0.0501	0.064	0.0733	0.0743	0.39	7.43
11	Cyp_car	0.0166	0.0166	0.0648	0.0648	0.01	6.48
12	Gas_acu	0.0036	0.0076	0.0218	0.0222	0.04	2.22
13	Gym_cer	0.0026	0.0142	0.0426	0.0624	0.02	6.24
14	Gym_sch	0.0865	0.0865	0.0867	0.0953	0.02	9.53
15	Lep_gib	0.0196	0.048	0.0683	0.0717	0.02	7.17
16	Leu_idu	0.0629	0.1146	0.1397	0.1449	0.09	14.49
17	Leu_leu	0.085	0.0929	0.0951	0.0952	0.1	9.52
18	Lot_lot	0.0482	0.05	0.05	0.0739	0.44	7.39
19	Bab_gym	0.0006	0.0016	0.0059	0.0075	0.84	0.75
20	Pon_kes	0.0006	0.002	0.0059	0.0078	1.54	0.78
21	Neo_mel	0.0088	0.1378	0.1478	0.1503	5.02	15.03
22	Per_flu	0.0672	0.093	0.2117	0.2217	0.74	22.17
23	Pro_sem	0.0065	0.0287	0.0301	0.0307	0.8	3.07
24	Rho_ama	0.0203	0.0306	0.0935	0.0966	0.71	9.66
25	Rom_vla	0.04	0.052	0.0786	0.0786	0.26	7.86
26	Rut_rut	0.0528	0.0644	0.103	0.1304	0.4	13.04
27	Sal_tru	0.0289	0.0317	0.0353	0.0456	0.04	4.56
28	San_luc	0.0737	0.1248	0.2002	0.2024	0.22	20.24
29	Sil_gla	0	0.0012	0.0057	0.0231	0.19	2.31
30	Squ_cep	0.0496	0.0502	0.1005	0.102	1.61	10.2
31	Vim_vim	0.0434	0.0578	0.0649	0.0733	0.15	7.33
32	Zin_str	0.0001	0.0001	0.0054	0.0071	0.04	0.71