Original Articles

Ecological indicators for restoration success: Development of fish diversity in a large restored floodplain over twelve years

Joachim Pander, Elisabeth Winter, Juergen Geist[*]

Aquatic Systems Biology Unit, TUM School of Life Sciences, Technical University of Munich, Mühlenweg 22, Freising D-85350, Germany

ABSTRACT

The restoration of rivers and their floodplains is complex, requires substantial financial efforts, intensive stakeholder involvement and long recovery times, making the identification of appropriate ecological indicators for restoration success a key challenge. Herein, one of the largest floodplain restorations along the European Danube was repeatedly assessed over a 12-year period. Changes in the fish community composition in relation to chemical and morphological habitat variables were assessed in all three restored habitat types free-flowing rivers (RS), reconnected oxbows (OS), and small floodplain ponds (FP) which are only temporarily connected to the main stem Danube. Fish species composition of RS, OS, FP and the Danube differed significantly. Species numbers (34 detected in 2022) remained largely constant since the last monitoring in 2013, whereas abundance increased by 15%. Small-bodied target species with short generation times were able to establish populations comprising all size classes shortly after restoration, whilst large-bodied species needed a decade after the restoration for full demographic representation. Highly specialised species such as the rheophilic *Chondrostoma nasus* used restored RS only during the life stages spawning and juvenile growth. Restoration increased habitat heterogeneity and the initialized hydromorphological processes are still ongoing, supporting the high species diversity. The observed differences in colonization patterns can be explained by species-specific life histories, resulting in diverse short and long-term responses of different fish species and life stages following restoration. Consequently, a comprehensive assessment of restoration success only becomes possible if multiple fish species as ecological indicators are combined in a long-term monitoring.

1. Introduction

Freshwater biodiversity is critically threatened, with stream ecosystems being the most heavily affected (Reid et al., 2019; Tickner et al., 2020). Large river ecosystems have been strongly altered by anthropogenic activities such as river straightening, bank stabilization, impoundments, hydropower use and the disconnection from their former floodplain (Dynesius and Nilsson, 1994; Ward et al., 1999; Dudgeon et al., 2006; Best, 2019). Due to the irreversibility of some of these changes (Auerswald et al., 2019), restoration of large river systems is most complex, requires substantial financial efforts and intensive stakeholder involvement (Geist & Hawkins, 2016). Depending on species and system properties, biological responses on the population level, i.e. recovery times, can vary but are considered long in large river systems compared to life-stage- or species-specific habitat restoration measures (Pander & Geist, 2013). To understand the processes driving successful restoration in complex systems such as floodplains and for an

evidence-based information of river restoration, long-term monitoring using appropriate ecological indicators is needed (Frissell et al., 1986), yet often lacking (Pander & Geist, 2013). Documented monitoring efforts exceeding three to five years are hardly found in the scientific literature (but see Wyżga et al., 2021; Louhi et al., 2016). This not only results in challenges related to monitoring and assessing restoration success, but also in determining appropriate ecological indicators which are needed to monitor success against pre-defined restoration goals (Geist, 2015; Pander & Geist, 2013). Understanding which life stages and species are most suitable as indicators typically depends on spatio-temporally resolved long-term data from taxonomic groups with specific habitat requirements, long generation times and lag phases between action and response such as fishes.

Renewed funding from the German Federal Agency for Nature Conservation (BfN) provided the opportunity to investigate one of the largest floodplain restorations along the Danube over a total of 12 years (Pander et al., 2015a). The first monitoring before restoration was

---

carried out in 2010, the early post restoration monitoring in 2011 and it was repeated in 2013. The follow-up project started nine years later and included a complete monitoring of all sites again in 2022. It comprised the same field surveys as in the first monitoring round to assess the long-term development of the fish community. The first monitoring had investigated the initial colonization of aquatic habitats, the colonization rate, species diversity, the presence of neozoa (Pander et al., 2015a; Pander et al., 2018) and effects of ecological floodings on aquatic biodiversity (Pander et al., 2019). Other scientific questions included the functionality and availability of key habitats for the reproduction of rheophilic fish species (Pander et al., 2017) and the colonization dynamics of macroinvertebrates with a particular focus on invasive gammarids (Pander et al., 2016). During the initial study, it was a key finding that the various aquatic habitats across the floodplain were colonized very differently and strongly seasonally dependent by fish from the Danube, the pre-existing Danube oxbow lakes and floodplain ponds. Three months after restoration work was completed, over 90 % of the species from the adjacent Danube were already present in the project area (Pander et al., 2015a; Pander et al., 2018). It was also shown that the distance and connectivity to the Danube had a strong effect on colonization and that habitats close to the Danube generally held the highest diversity of fish species (Pander et al., 2018). As hardly any new species could be detected after the 2011 surveys, it was assumed that supply biotopes at a greater distance would have to be better connected for further development in the project area and that the colonisation of rare species, such as Danube percids, could only be expected in the longer term. Danube percids generally include various perch species that are often restricted to the Danube and Dniester catchment (Fricke et al., 2024) and are highly threatened in their populations today. Prominent representatives of this group are *Zingel streber* Siebold 1863, *Zingel zingel* L. 1766, *Gymnocephalus schraetser* L. 1766 and *Gymnocephalus baloni* Holčík & Hensel 1974. Another important question in the first monitoring round was whether the ecological floodings carried out to increase groundwater level diversity in the riparian forest could also have an effect on the fish species composition in the aquatic habitats. It turned out that naturally occurring floods had a greater impact on the fish species community due to the significantly higher volumes of water flowing into the project area (Pander et al., 2019). As the Danube is one of the most important distribution corridors for aquatic neobiota in Bavaria (Brandner et al., 2013), it was of particular interest to what extent the project area was colonized by neozoa and whether restoration measures can increase the resilience of aquatic habitats against colonization by invasive species. In the case of fish, the focus was primarily on the various goby species from the Black Sea region, which were present in the Danube at the time of commissioning of the restoration project. Whilst gobies of Ponto-Caspian origin such as the round goby (*Neogobius melanostomus* Pallas 1814) used to be quite abundant in the main stem Danube for more than a decade (Cerwenka et al., 2023), they could not be detected in the restored floodplain during the first study period until 2013. Other neozoa such as the *Pseudorasbora parva* Temminck & Schlegel 1846 or *Carassius gibelio* Bloch 1782 were present, but only in low numbers, questioning their long-term performance in the restored floodplain system.

In this study, the specific questions 12 years after implementation of this large-scale restoration were:

(i) has the fish community in the project area reached a climax stage comprising the same community composition and individual numbers or has it further changed since the last survey nine years ago?

(ii) have rare Danube species or species with complex life cycles and habitat requirements, which were already detected in the first survey period, now been able to increase their population covering all size classes?

(iii) have other species of the Danube catchment area, such as the relatively rare Danube percids, been able to colonize the project area?

(iv) how has the situation of neozoa developed in the project area? Have non-native gobies, been able to colonize the project area in the

meantime?

2. Material and methods

2.1. Study area

The study was carried out at the Danube River between the cities Neuburg an der Donau and Ingolstadt (Fig. 1), 68 km north of Munich (Stammel et al., 2012, Pander et al., 2015a). The study site is located at the right bank of the Danube within the largest remaining contiguous alluvial forest, in direct proximity to the power plant Bergheim (km 2,470; 48°45′00.74″N, 11°15′57.79″E to km 2,459; 48° 44′13.58″N, 11°19′54.07″E). The discharge at this upper Danube stretch (mean annual discharge = 313 m³ s⁻¹) is highly influenced by two major alpine rivers, the Iller and the Lech which both are characterised by snowmelt-induced summer peak flows. Like many major European rivers, the Danube was subject to substantial changes of its river hydraulics and sediment regime over the centuries. Main drivers of degradation were flood protection, hydropower use and reclamation of land resulting in channel straightening, embankment, reduced sediment transport, interruption of the river continuum, and disconnection from the floodplain. Nowadays 58 hydropower plants within its first 1000 km flow course interrupt the Danube's longitudinal and lateral connectivity (Habersack et al., 2016).

2.2. Floodplain restoration

To antagonise the negative effects on the floodplain caused by intensive damming and hydropower use of the power plants Bergheim and Ingolstadt, a secondary floodplain channel, the Ottheinrichbach (OHB) was constructed and opened in June 2010. The new OHB was intended to laterally reconnect the Danube with its former floodplain, increase groundwater levels, provide additional freshwater habitat and restore fish migration by bypassing the hydropower plant Bergheim. The discharge of the new floodplain river is permanent, ranges between 1.5
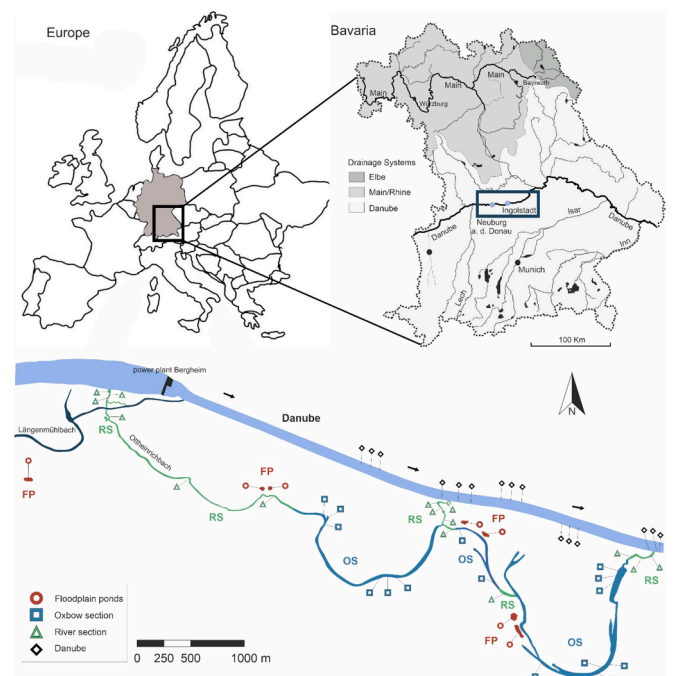
Fig. 1. Map of the study site with the location of the three different assessed habitats river sections (RS), oxbow sections (OS), floodplain ponds (FP) and study sections of the Danube. RS, OS and FP were sampled in 2010, 2011, 2013 and 2022. Please note that the study sections of the Danube were only sampled in 2022.

$m^3 s^{-1}$ and 5 $m^3 s^{-1}$, and is dynamically regulated according to the discharge of the Danube. In addition, the OHB and its floodplain can be flooded artificially (ecological flooding) with a maximum of 30 $m^3 s^{-1}$ during high flow conditions of the Danube (Discharge Danube > 600 m^3 s^{-1}, Stammel et al., 2012; Pander et al., 2019). The flow course of the OHB has a total length of 9 km and was built according to a nature-oriented construction scheme with additional structural improvements like boulders and dead wood accumulations. In some sections, gravel, which became available from the dredging of the new river course, was also introduced. Besides the newly built sections, the river consists of temporary Danube tributaries (Zeller Kanal) and former disconnected oxbows of different successional stages as described in Stammel et al. (2012). In spatial proximity and along the whole flow course of the OHB, several permanent small floodplain ponds exist (Fig. 1). These small ponds may also contribute to fish diversity since they are connected to the OHB and to the Danube during high flow conditions (e.g. ecological flooding, Pander et al., 2019).

2.3. Study design

To allow comparisons between the initial monitoring carried out between the years 2010 and 2013 and the recent development, the same study design was applied across years to assess the changes in fish community patterns in relation to habitat restoration 12 years after its implementation. The pre-restoration monitoring was carried out in 2010, the early post-restoration monitoring started in 2011 and was repeated in 2013. The follow-up project started nine years later in 2022. The three main habitat types (Fig. 2) as identified and defined in the year 2010 were re-assessed, comprising river sections (RS, in 2010 new built and existing river sections), oxbow sections (OS, comprising shallow, deep, narrow and wide habitats) and floodplain ponds (FP, small aquatic ponds only connected to the systems during ecological flooding). The sampling sections in the Danube were only assessed during the monitoring in 2022. The assessment of the fish community was carried out seasonally in all habitats in spring (April 2022) and summer (August 2022). In RS and OS respectively 15 study sections, 30 m each, were evenly distributed throughout the study area. These were set up in the first monitoring and now assessed again. As in the first monitoring, the same 7 FP habitats were sampled.

2.4. Fish community assessment

The fish community was assessed in all 30 m study sections of all habitats (15 RS, 15 OS and 7 FP) using an electrofishing generator (EFKO FEG 11000, EFKO Elektrofischfanggeräte GmbH, Leutkirch, Germany). The study sections were consecutively sampled with the same electrofishing crew at all sampling dates working from downstream to upstream direction according to Pander et al. (2015a). The deeper oxbow sections were sampled from a boat during all sampling events whilst all RS and FP were fished wading. A single anode was used and stunned fish were collected with a dipnet. Fish from each study segment were kept in plastic tanks with oxygen supply until identification and measurement. Fish and lampreys were identified to species level and their total length (TL) was measured to the closest cm. All fish were then immediately released into the same study sections from which they were collected and no mortality was detected during the electrofishing.

2.5. Abiotic habitat variables including macrophytes and dead wood

Like in the previous sampling years between 2010 and 2013, important abiotic habitat variables were recorded in 2022 immediately after the electrofishing at the same day and with the previously applied measurement design in all study sections as described in Pander et al. (2015). Substrate samples were taken using a substratum box sampler, producing samples ranging from 7 kg to 10 kg (Pander et al., 2015b).
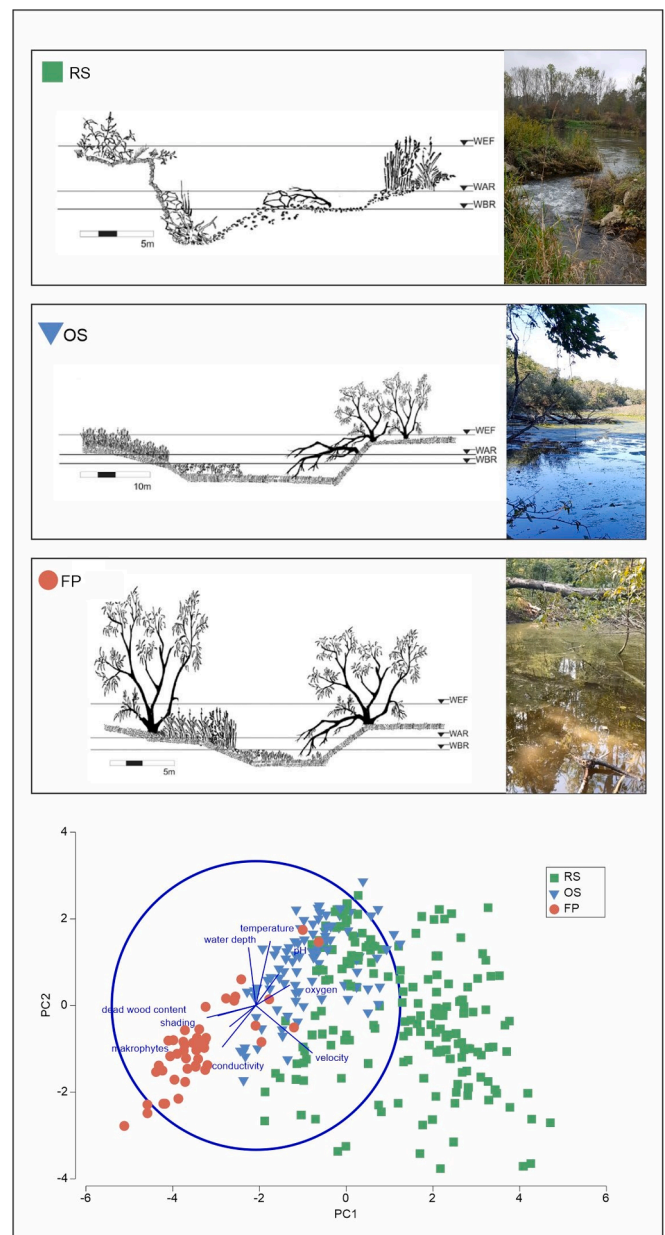
Fig. 2. Illustration of the assessed three different habitat types river sections (RS), oxbow sections (OS), floodplain ponds (FP) and PCA of the measured abiotic habitat variables indicating structural and chemical differences of habitat conditions; these variables were also integrated in the BEST analysis. WEF = water level major ecological flooding, WAR = mean water level, WBR = low water level. Explained variability of PC1 = 34.4 % and PC2 = 16.0 %. Blue circle indicates 100 % correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Grain sizes were fractioned with a wet-sieving tower (Fritsch, Idar-Oberstein, Germany) of decreasing mesh sizes (63, 20, 6.3, 2.0 and 0.85 mm) in the lab. Water depth (Wd, cm) and current speed 5 cm above substrate (vg, $m s^{-1}$,) as well as 5 cm below surface (vs) were measured with 9 replicates in each study section according to Pander et al. (2015a) using an electromagnetic flowmeter Ott MF pro (Ott, Kempten, Deutschland). Readings of electric conductance (EC, μS cm^{-1}, corrected to 20 °C), dissolved oxygen concentration (O_2, mg L^{-1}), pH value (pH), and temperature (T, °C) were taken in open water using a handheld Multi 3430 (WTW, Weilheim, Germany).

2.6. Data analysis

Numbers of individuals, species richness, Shannon diversity (Shannon & Weaver, 1949) and Evenness (Pielou, 1966) were calculated as measures of alpha-diversity from the overall species abundance matrix using the DIVERSE procedure in PRIMERv7 (Plymouth Marine Laboratory, Plymouth, United Kingdom). Diversity measures and abiotic data were analysed for their temporal trends in the different habitat types using univariate statistics. All data were tested for normality using the Shapiro-Wilk-test. Since data were not normally distributed, Kruskal-Wallis-tests and Bonferroni-corrected post-Hoc pairwise Mann-Whitney-U tests were used. From the sieved substratum samples, the percentage of each grain fraction as described above was determined, and the geometric mean particle diameter (dg, mm) was calculated according to Sinowski & Auerswald (1999). To illustrate the changes of substratum composition in narrow OS over time, a timeline of cumulative sieving lines from the partitioned grain sizes of a selected narrow OS were plotted. Individual species-specific traits that potentially determine colonisation success such as current preference, spawning behaviour, size and generation time were derived from Jungwirth et al. (2003) and Zauner & Eberstaller (1999). Conservation status of freshwater fish was derived from the Red Lists of Bavaria (Effenberger et al., 2021) and Germany (Freyhof et al., 2023).

Principal component analyses (PCA) based on Euclidean distance were used to assess differences of habitat conditions using the measured abiotic habitat variables. The PCA allowed an overlay with the measured variables indicating the strength of correlation to the arrangement of habitat types in the ordination plot. Environmental variables were standardized using the "normalize function" in Primer v7 for environmental variables.

To analyse differences in aquatic community composition between sampling years and the assessed habitat types RS, OS and FP, Bray-Curtis Similarities (Bray & Curtis, 1957; Clarke et al., 2014) were calculated from the overall fish abundance matrix in PRIMERv7. Using the Bray-Curtis resemblance matrices, analysis of variance (ANOVA, Anderson et al., 2008) was carried out to test for significant differences in the overall aquatic community between sampling years and habitat types. Based on the overall Bray-Curtis resemblance matrix, non-metric multidimensional scaling (NMDS) applying the bootstrap function in PRIMERv7 was performed to visualize changes of the aquatic community between habitats RS OS, FP and the Danube in the sampling years 2010, 2011, 2013 and 2022. A similarity percentage analysis (SIMPER) as previously applied in Pander et al. (2015b; 2018) was carried out to determine the relative contribution of individual fish species to the in-group similarity and between-group dissimilarity of habitat types. To identify relations between fish community data and environmental data, biota-environmental stepwise matching (BEST) analyses was conducted, using the biota-environmental matching (Bio-Env) method to identify the significant relationships between fish community composition and the assessed physicochemical habitat variables within fluvial habitats and ponds (Bio-Env; Clarke et al., 2014).

3. Results

3.1. Abiotic habitat development

The PCA indicated structural and chemical differences between the three habitat types RS, OS and FP (Fig. 2) with an explained variability of PC1 = 34.4 % and PC2 = 16.0 %. The main difference between habitats was a higher content of deadwood and macrophyte coverage as well as a higher percentage of shading in FP in contrast to OS and RS (Table 1). In addition, RS habitats are characterised by higher flow-velocity, coarse gravel substrate (Table 1) and a large variability in water depth. This is also supported by BEST-analysis which identified current speed, water depth, pH and the coverage of macrophytes and deadwood as well as EC and O₂ as explaining variables for habitat differences (BEST, R = 0.68). As evident from the PCA visualization, some RS and OS habitats overlap in their spatial arrangement. This overlap is largely attributed to the variable current speed in narrow OS. Here, deadwood accumulations successively narrowed the profile of the flow course, increased water depth and current speed, resulting in a succession towards flowing habitats 12 years after restoration. This also led to a change in substratum composition from formerly fine sediment dominated stagnant aquatic habitats in the year 2010 before restoration (almost 80 % fines < 0.85 mm) to gravel dominated habitats with less than 35 % fines in 2022 (Fig. 3).
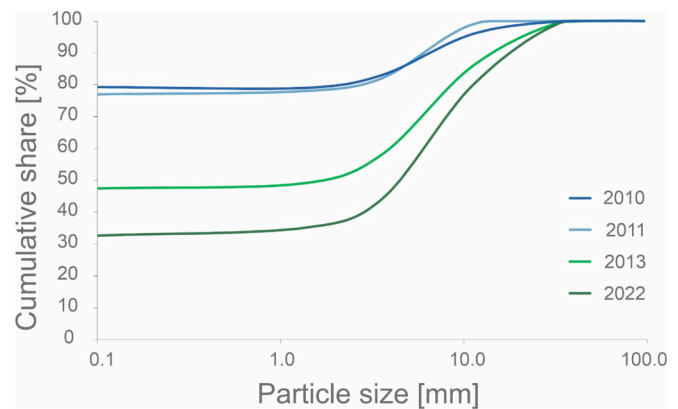

Fig. 3. Change in sediment composition in one of the reconnected narrow oxbow habitats between 2010 (before restoration), 2011 (shortly after restoration), 2013 (three years after restoration) and 2022 (12 years after restoration). Cumulative share of grain sizes according to Sinowski & Auerswald (1999).

Table 1
Abiotic habitat variables given as means, pooled from the study sections of the respective habitat types, river sections (RS), reconnected oxbows (OS) and floodplain ponds (FP). WD = water depth, v = current velocity (pooled from both readings, above substrate as well as below surface), EC = electric conductance, O₂ = dissolved oxygen T = water temperature, pH = pH value, dg = mean particle diameter (Sinowski & Auerswald 1999), M = macrophytes coverage, DW = dead wood.

	Year	WD [cm]	v [ms⁻¹]	EC [µScm⁻¹]	O₂ [mgL⁻¹]	T [°C]	pH	dg [mm]	M [%]	DW [%]
RS	2010	41	0.11	682	10.9	15.0	8.1	2.6	6	3
	2011	66	0.38	541	10.7	15.9	8.1	6.9	5	5
	2013	62	0.41	542	10.2	14.5	8.5	6.9	10	5
	2022	54	0.30	480	9.9	19.3	8.1	6.9	7	18
OS	2010	57	0.00	885	11.5	15.9	8.0	0.2	17	12
	2011	92	0.05	556	10.7	17.0	8.2	0.3	10	14
	2013	74	0.07	563	11.4	14.9	8.4	0.4	20	16
	2022	67	0.09	492	8.2	18.6	8.0	0.9	36	19
FP	2010	43	0.00	758	5.3	14.0	7.6	0.1	70	32
	2011	64	0.00	704	6.2	16.0	7.7	0.2	70	32
	2013	62	0.00	676	5.3	13.5	7.7	0.2	72	30
	2022	32	0.00	537	3.8	18.1	7.5	0.2	68	38

3.2. Fish catches in 2022

In total, 17,574 fish were caught in the sampling year 2022. Catch numbers ranged from 8,921 individuals in river sections (RS), to 5,539 individuals in reconnected oxbow sections (OS), 613 individuals in floodplain ponds (FP) and 2,501 individuals in the Danube (Table 2).

In 2022, 34 species were detected out of 16 different fish families that were highly dominated by cyprinids (50 %). Compared to 2010, before the Ottheinrichbach was put into operation, this was a significant increase in the number of species (1.3 fold) and individuals (10 fold, Table 2). Since 2010 there was a constantly increasing number of species (26–34), with only one new species detected in 2022, the non-native round goby (*N. melanostomus*). Bitterling (*Rhodeus amarus* Bloch 1782) was the most common fish with 4,548 individuals (Table 3). Other abundant species were the chub (*Squalius cephalus* Linnaeus 1758) with 2,429 individuals and the round goby (*N. melanostomus*) with 2,169 individuals, predominantly found in the Danube (1,348) and river sections (693). The lowest numbers of individuals were found in burbot (*Lota lota* Linnaeus 1758), European bullhead (*Cottus gobio* Linnaeus 1758), brown trout (*Salmo trutta* Linnaeus 1758), Eurasian pike-perch (*Sander lucioperca* Linnaeus 1758), Eurasian ruffe (*Gymnocephalus cernua* Linnaeus 1758) und European brook lamprey (*Lampetra planeri* Bloch 1784). Former species records of minnow (*Phoxinus phoxinus* Linnaeus 1758, one specimen) and European grayling (*Thymallus thymallus* Linnaeus 1758, 17 specimens) could not be confirmed in 2022 (Table 3). The Danube percid Baloń's ruffe (*G. baloni*) was also not detected in 2022. However, it was also only found in very small numbers (two individuals) in the former samplings in 2011 and 2013. Another Danube percid, the streber (*Z. streber*) slightly increased its density on low level from 3 individuals in 2013 to 12 individuals over all size classes in 2022. Zingel (*Z. zingel*) and schraetser (*G. schraetser*) that potentially occur in the Danube upstream of the study area (not frequently and in very low numbers) could still not be detected in the restored floodplain.

3.3. Fish community composition

Multivariate community analyses between the assessed habitat types revealed significant differences between all habitat types RS, OS, FP and the Danube (ANOSIM, global test R = 0.507, p < 0.001). The development of the fish community over time in RS, OS and FP comprised habitat-specific patterns with a significant initial change of the fish community between pre- and post-restoration in the habitats RS, OS and FP (Figs. 4, 5). The initial change was strongest in FP (ANOSIM, R = 0.271, p < 0.001) compared to OS (ANOSIM, R = 0.088, p < 0.01) and RS (ANOSIM, R = 0.038, p < 0.05) habitats (Fig. 5). Subsequently, community composition in OS and FP comprised only marginal changes in the following years. In RS, fish community pattern over time revealed a strong change. Although there was already an observed initial significant change in fish community composition after the restoration in 2010 in these habitats, the change was subsequently ongoing over the years and seemed to become successively stronger until 2022 as evident from increasing R-values (ANOSIM, global test R = 0.51, p < 0.001, Fig. 5). Variability of community composition within sampling years

was largest in FP habitats in 2013 and smallest in RS and the Danube in 2022. Compared to the variability of the fish community in the main stem Danube, the restoration of the aquatic habitats added a large diversity of different habitat specific fish communities to the riverscape (Fig. 4).

RS, OS, FP and Danube were characterized by different species that occurred steadily in the respective replicates of the habitat type according to SIMPER. RS was characterized by high abundances of *S. cephalus*, *Alburnus alburnus* Linnaeus 1758, *Gobio gobio* Linnaeus 1758, *Rutilus rutilus* Linnaeus 1758 and *Gasterosteus aculeatus* Linnaeus 1758, OS instead was characterized by *R. rutilus, A. alburnus* and additionally by *R. amarus* and *Perca fluviatilis* Linnaeus 1758. In OS and the Danube, only one species was steadily present per habitat according to SIMPER. In OS, this was the stagnophilic *Carassius carassius* Linnaeus 1758, and in the Danube the invasive species *N. melanostomus*. Species that explained the dissimilarity between RS, OS and FP according to SIMPER were for example the rheophilic *Barbus barbus* Linnaeus 1758 with much higher abundances in RS, the stagnophilic *R. amarus* with higher abundances in OS and the stagnophilic *C. carassius* with higher abundances in FP. The dissimilarity between the Danube and the floodplain habitats RS OS and FP was largely attributed to very high abundances of the invasive *N. melanostomus* in the main stem of the Danube, comprising a strong population with all size classes (Fig. 6).

3.4. Population development of selected species

Of the 34 fish species detected in 2022, 20 species revealed a full population demographic structure comprising all size classes. This was four species more compared to the sampling in 2013. In general, four different population trends were identified in the restored habitats: Firstly, there were fish species that already had a complete population structure before the restoration in 2010, such as *S. cephalus*, *R. rutilus* or *Esox lucius* Linnaeus 1758 (Fig. 7, Fig. 8). Secondly, for some species, a pronounced increase in the number of individuals and a closing of gaps in the population structure (size classes) was found, shortly after the opening of the Ottheinrichbach. Thirdly, some species were only able to build up a full population structure (e.g. *B. barbus* and *Barbatula barbatula* Linnaeus 1758) in the second monitoring run (12 years after restoration). Fourthly, there were species which, despite high numbers of individuals in individual size classes, did not build up a complete population structure (comprising all size classes) in 2022 (e.g. *Chondrostoma nasus* Linnaeus 1758, Fig. 8), indicating a lack of habitat suitability for specific life stages. For instance, in the case of *C. nasus*, it is remarkable that across years, only large (> 40 cm TL) individuals could be caught in spring and predominantly only small (up to 20 cm long) individuals in summer (Fig. 8), suggesting that only specific size/age-classes of this species use the restored habitats. In addition to the completion of size classes, higher abundances of some species were found compared to previous years. This increase in the number of individuals was particularly true for the generalist *G. gobio*, a species where all size classes successively increased. *Leuciscus leuciscus* Linnaeus 1758 had an initial rapid increase in the number of individuals (until 2011) and then a stagnation in the development with a subsequent decline in larger specimens. In 2022, however, more individuals with ≤ 5 cm and ≤ 10 cm were detected again. Fish, such as the rheophilic *B. barbatula*, also showed a positive population trend, with significantly higher numbers of individuals in 2022 (Fig. 8).

4. Discussion

Nine years after the last assessment of the Danube floodplain restoration in Bavaria (MONDAU I, Pander et al., 2015a, Pander et al., 2018), the monitoring was repeated in order to investigate the long-term effects of the restoration on the fish population development, with a strong focus on species with long generation times. The monitoring in 2022, 12 years after the restoration, revealed that only one fish species was able to

Table 2
Individuals (N), species numbers (S) per sampling year and accumulated species numbers (Overall S) across different sampling years, before restoration, three month after restoration, one year after restoration and three years as well as 12 years after restoration. H = Shannon diversity, J = Evenness.

	N	S	Overall S	H	J
Before restoration	1,740	26	26	2.26	0.74
Three month after restoration	5,253	30	32	2.32	0.70
One year after restoration	8,829	31	34	2.37	0.69
Three years after restoration	15,288	34	36	2.18	0.62
Twelve years after restoration	17,574	34	37	2.54	0.72

Table 3

Individual numbers of total fish catch in the habitats river sections (RS), reconnected oxbows (OS), flood plain ponds (FP) and the Danube in the year 2022. Total = Total catch of species across habitats, Reproduction (RP): PL = phyto-lithophil, L = lithophil, M = marin, PS = psammophil, P = phytophil, SP = speleophil, LP = litho-pelagophil, O = ostracophil, current preference (CP): ind = indifferent, rheo = rheophil, limn = limnophil and conservation status Red List Bavaria = RL B (Effenberger et al. 2021) and Red List Germany = RL G (Freyhof et al. 2023): * = not threatened, V = early warning list, 1 = threatened with extinction, 2 = highly endangered, 3 = endangered,! = Bavarian responsibility, ◆ = not evaluated, Flora-Fauna- Habitat-Directive (FFH, https://www.ffh-gebiete.de/natura2000/ffh-anhang-ii/, last accessed 25 June 2024): Appendix II, IV, V; NL = not listed.

Species	FP	OS	RS	Danube	Total	RP	CP	RL B	RL G	FFH
Abramis brama	0	113	9	6	128	PL	ind	*	*	NL
Alburnoides bipunctatus	0	60	496	540	1,109	L	rheo	*	V	NL
Alburnus alburnus	0	466	874	50	2,434	PL	ind	*	*	NL
Anguilla anguilla	0	4	49	46	124	M	ind	3	2	NL
Barbatula barbatula	0	11	300	0	351	PS	rheo	*	*	NL
Barbus barbus	0	20	525	12	620	L	rheo	*!	V	V
Blicca bjoerkna	0	16	113	7	139	P	ind	V	*	NL
Carassius carassius	322	0	0	0	322	P	limn	1	2	NL
Carassius gibelio	0	0	15	1	16	P	ind	*	◆	NL
Chondrostoma nasus	0	7	68	0	75	L	rheo	3!	V	NL
Cottus gobio	1	0	0	0	1	SP	rheo	*	*	II
Cyprinus carpio	0	94	490	20	683	P	ind	V	*	NL
Esox lucius	0	130	43	11	187	P	ind	*	*	NL
Gasterosteus aculeatus	80	238	379	4	718	P	ind	*	*	NL
Gobio gobio	0	262	1,082	16	1,431	PS	rheo	*!	*	NL
Gymnocephalus cernua	0	2	0	3	5	PL	rheo	*	V	NL
Lampetra planeri	0	2	1	2	6	L	rheo	V	*	II
Leuciscus aspius	0	6	21	11	38	L	ind	*	*	II,V
Leuciscus idus	5	114	58	4	196	L	ind	*	*	NL
Leuciscus leuciscus	0	53	343	2	419	L	rheo	*	*	NL
Lota lota	0	0	0	3	3	LP	rheo	*	2	NL
Neogobius melanostomus	0	64	693	1,348	2,169	SP	ind	◆	◆	NL
Perca fluviatilis	0	100	25	43	178	PL	ind	*	*	NL
Pseudoraspora parva	0	10	7	0	22	PL	ind	◆	◆	NL
Rhodeus amarus	116	2,650	1,703	67	4,548	O	limn	*	*	II
Rutilus rutilus	0	270	166	10	457	PL	ind	*	*	NL
Salmo trutta fario	0	0	1	1	2	L	rheo	V	3	NL
Sander lucioperca	0	0	2	0	2	P	ind	*	*	NL
Scardinius erythrophthalmus	0	38	0	0	38	P	limn	*	*	NL
Silurus glanis	0	16	14	34	65	P	ind	*	*	NL
Squalius cephalus	6	651	1,388	259	2,429	L	ind	*	*	NL
Tinca tinca	84	134	38	1	257	P	limn	*	*	NL
Vimba vimba	0	8	6	0	14	L	rheo	V	2	NL
Zingel streber	0	0	12	0	12	L	rheo	2	2	II
Total 2022	613	5,539	8,921	2,501	**17,574**					
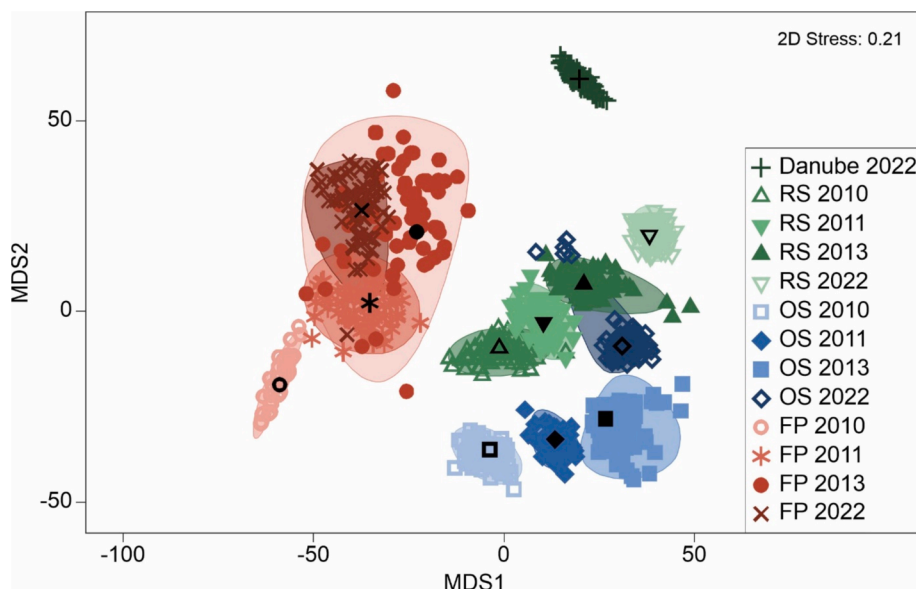
Fig. 4. Non-metric-multidimensional-scaling (NMDS) of the fish community composition from the data sets for the years 2010, 2011, 2013 and 2022. RS = river sections displayed in green colours, OS = oxbow sections displayed in blue colours and FP = floodplain ponds displayed in red colours. Black symbols indicate the average abundance of study sections across the respective habitat type RS, OS, FP and Danube and the respective sampling years 2010, 2011, 2013 and 2022. Please note that for the Danube only data from 2022 is available. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
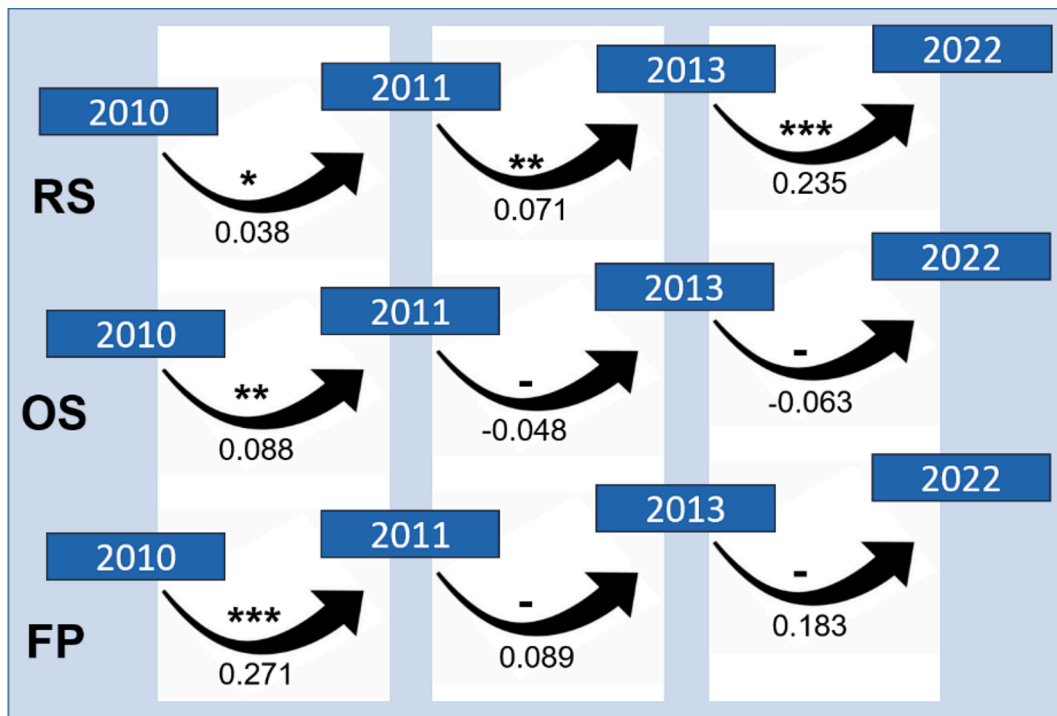
Fig. 5. Results of ANOSIM for the comparison between sampling years for each of the habitat type rivers (RS), reconnected oxbows (OS) and floodplain ponds (FP). ANOSIM, global test R = 0.453, $p < 0.001$. Asterisks above black arrows indicate level of significance. Values below black arrows indicate the R-values as derived from ANOSIM pairwise comparisons.
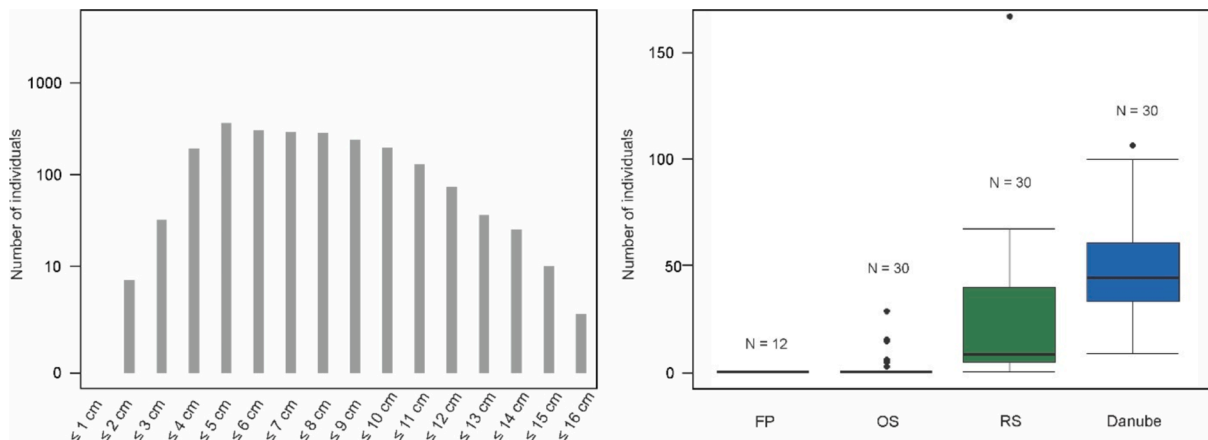

Fig. 6. Size classes of *Neogobius melanostomus* (left panel) and occurrence in floodplain ponds (FP), reconnected oxbows (OS), rivers (RS) and the main stem Danube in the year 2022 (right panel). N = number of sampled study sections. Please note that small fish (sizes ≤ 2 cm) may be underrepresented due to sampling limitations.

newly colonise the project area (the invasive *N. melanostomus*). At the same time, three other formerly detected species were not caught during the investigation in 2022. In the case of Baloń's ruffe (*G. baloni*), this is may be attributed due to changes in habitat connectivity and flow-velocity. In the case of minnow (*P. phoxinus*) and European grayling (*T. thymallus*), the rising water temperatures of the Danube can likely explain the observed declines in their abundance. However, these three species were already only detected in very low individual numbers in the system beforehand and may either have already been at the thresholds of their ecological tolerances at that time, or could simply have been missed in the sampling in the year 2022. On first glance, this change in number of species seems to indicate only marginal effects. However, shifts in community composition that were based on changes in number of specimens and the pronounced changes in demography gave important information on the functionality of the restoration measures and the

species-specific population development in the medium- and long-run. Remarkably, each of the three distinct habitat types revealed very different succession patterns: A continuous development of the fish species community (largely attributed to size class specific individual numbers) was observed in rivers, compared to generally rather stable populations over time in oxbows, and strongly fluctuating fish communities in floodplain ponds (driven by ecological flooding).

The phased long-term monitoring as applied herein, with an intensive yearly seasonal sampling in the beginning and subsequently longer periods between sampling events, indicated that the colonization and the subsequently ongoing population development is a temporally and spatially dynamic process. This development turned out to be highly dependent on habitat type with successively ongoing morphological changes as described herein. It also depended on species-specific life history traits and the complex interactions between species, supporting

Fig. 7. Length-frequency-distribution of selected small-bodied fish species in the restored aquatic habitats. Bars represent the sum of caught individuals from spring and summer samplings per year. Different colors indicate different size classes. Please note that the shaded area in bars for *Rhodeus amarus* in 2022 represents the results from the floodplain ponds with the most restricted connectivity to the Danube.

that fishes are ideal indicators of restoration success on all spatial and temporal levels (Weber & Peter, 2011). The advantage of a staggered monitoring as applied herein is that sudden improvements immediately after restoration can be detected (e.g. the fast colonization of some small-bodied fishes) as well as improvements towards long-term restoration targets (e.g. sustainable populations of long-lived specialist species such as *B. barbus*) that require more time to develop. As derived from this study, simple ecological indicators such as species counts and the presence of desired species can be used to evaluate early restoration effects. In contrast, complex developments integrating the presence of early life stages such as spawning and juvenile growth can only be detected in following monitoring phases, except for life-stage specific assessments using e.g. active bioindication with fish eggs to assess spawning ground quality (Pander & Geist 2013). Particularly the status of these early life stages of fish (target species) is informative for evaluating sustainable population development and allow a more differentiated and comprehensive assessment of restoration success (Pander & Geist, 2013). For large-growing and long-lived (often up to 15 years, Kottelat & Freyhof, 2007; Froese & Pauly, 2023) species like *B. barbus* and *C. nasus* present in the restored floodplain, restoration success could

only be fully evaluated after 12 years, with markedly different success (full population demography in *B. barbus*, only life-stage specific restoration success and no full population demography in *C. nasus*). These examples illustrate that projects without a long-term monitoring would not be able to comprehensively assess restoration success.

A widely yet often neglected factor in restoration monitoring is the consideration of species interactions potentially affecting the evaluation of success, particularly when restored habitats are colonised by non-indigenous or invasive species as detected in this study. The fact that *N. melanostomus* is a steadily occurring species in the largely degraded Danube as detected herein by SIMPER, but not in the restored habitats, points to a higher resilience of those against invasion which in turn can also be considered as an indication of restoration success.

When comparing fish communities of the restored habitats in the floodplain to the one in the Danube, it comes obvious that the diversity of community compositions in the restored floodplain is by far greater than in the Danube main stem. This can likely be explained by the degraded (straightened and dammed) river course of the Danube where hydropower plants interrupt the longitudinal and lateral connectivity which has led to a deterioration of habitat diversity over the last decades
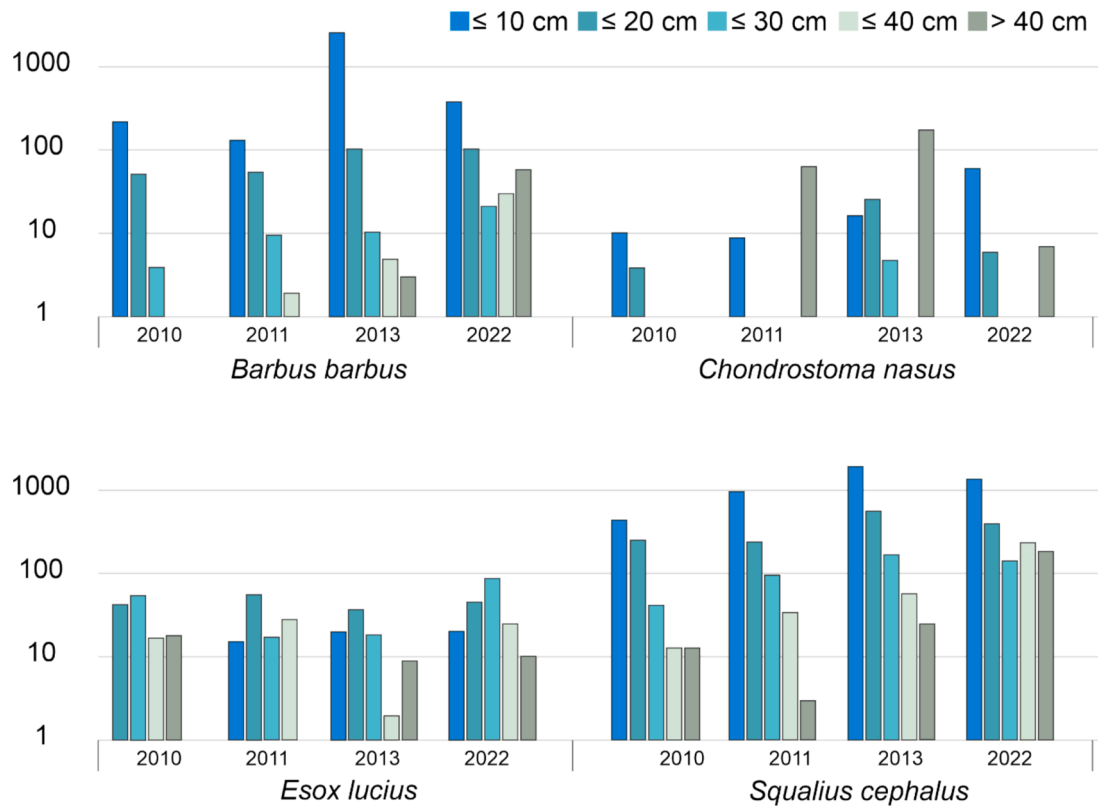
Fig. 8. Length-frequency-distribution of selected large-bodied fish species in the restored aquatic habitats. Bars represent the sum of caught individuals from spring and summer samplings per year. Different colors indicate different size classes.

(Schiemer et al., 1999; Habersack et al., 2016), facilitating the establishment of generalist non-native species (Brandner et al., 2018). The restoration-induced and increased habitat diversity and heterogeneity (Pander et al., 2018) provides an explanation for the resulting in high species diversity in the floodplain. In addition, the floodplain restoration reconnected important floodplain habitats, increased the amount of fast flowing RS sections in the OHB and improved the transport of dead wood as well as the relocation of gravel. These processes are an important prerequisite for the completion of life-cycles dependent on specific riverine habitats such as spawning grounds (Pander et al., 2023a; Pander et al., 2023b) and juvenile habitats (Pander et al., 2017) for rheophilic specialists. This was the basis for a significant development towards a rheophilic-dominated community with *B. barbus*, *G. gobio* and *B. barbatula* becoming steadily occurring species as detected by SIMPER in the riverine habitats of the OHB.

With the exception of the very narrow sections of OS that developed into riverine habitats, medium wide and wide OS revealed no significant changes in their fish community composition compared to the first monitoring, and the overall community in OS was still dominated by *R rutilus*, *P. fluviatilis* and *E. lucius*. The stability of the species composition (only an increase in individual numbers was detectable) in medium-wide and wide oxbows is likely attributed to the only marginal morphological changes in these habitats such as macrophyte growth as well as only marginal changes in water depth and current speed. In addition, the community in oxbows was highly dominated by generalist species with relatively short generation times that were already present before the restoration and had completed population demography development already in the first monitoring round two years after restoration. In the narrower sections of oxbow lakes, there is a tendency towards more current-adapted cyprinids such as *G. gobio*, which can be explained by an increase in current speed, a change in substratum composition from fine sediment-dominated habitats before restoration to gravel-dominated habitats in the subsequent years. This process was

largely driven by the connection of narrow OS to the OHB that caused deposition of dead wood which in turn narrowed cross profiles and increased current speed that forced the sedimentation of coarse grain sizes in the gravel fraction and transport of fines out of these habitats.

Due to the dry summer of 2022, no ecological flooding took place in the restored floodplain. The fish species composition of FP in particular is dependent on these regular floods since these are the only phases of connectivity to the other aquatic floodplain habitats. Accordingly, only rudimentary remnants of the fish species community from previous ecological floods were found in 2022, with relatively few individuals, often reaching their size and age limits. This is particularly evident in the case of some small-bodied species, such as *R. amarus* that included specimens with total lengths of up to 10 cm, which is the known maximum size for this species. A reproduction of *R. amarus* in FP is to date not possible due to a lack of large freshwater mussels which are a prerequisite for the reproduction of this species (Konečná et al., 2010). The only species in these mostly shallow habitats, which has been reproducing over the years regardless of ecological flooding, was *C. carassius*. This species is a limnophilic specialist that is adapted to macrophyte-rich small bodies of water, as they can tolerate temporary oxygen deficits (Vornanen et al., 2009) that were also detected in this study (on average 3.8 mg/L in the floodplain ponds).

The four different types of population developments (i, ii, iii, iv) can be explained by the different life history strategies, generation times, and species-specific sizes. Fish species that had a full population structure comprising high numbers of all size and age classes already before the restoration (i), mainly comprised generalist small- to medium-bodied species with known short generation time such as *R. rutilus*, *A. alburnus*, *S. cephalus* and *G. aculeatus* (Kottelat & Freyhof, 2007; Froese & Pauly, 2023). For those species, habitat quality before restoration was already sufficient. For species of type (ii), comprising a full population shortly after the restoration (two to three years), the short-term increase of the availability of riverine habitats and the increased

connectivity to the Danube and the oxbows improved their living conditions, matching the goals of the restoration effort. In combination with their short generation time, they were able to build up a full population structure shortly after the implementation of the restoration measures. Typical representatives for type (ii) in our study are small-bodied rheophilic species such as *B. barbatula* and *L. leuciscus*. Species of type (iii) that completed the population development after 12 years are medium to large-bodied rheophilic fishes that were dependent on clean gravel for spawning. These species were present in small numbers shortly after the restoration; however, the river dynamic processes that relocate gravel within the OHB and create spawning and juvenile habitats took some time to fully establish in terms of quality and connectivity. In addition, these species are more specialised than species of type (i and ii) when it comes to the quality of spawning grounds or juvenile habitats. A typical species for this colonisation type is *B. barbus*. This species is known to gather in small schools of three to five fish for spawning and it has a generation time of up to 15 years (Kottelat & Freyhof, 2007; Britton & Pegg, 2011; Froese & Pauly, 2023), making this species an ideal indicator for long-term functionality of restoration measures, in line with findings in Ramler & Keckeis (2019). Besides these successful colonisers, some species did not build up a full population structure comprising all size classes (iv). These are generally highly specialised species such as *C. nasus* or species that are generally very rare in the Danube itself like the Danube-percid *Z. streber* (Pander et al., 2015a; Leuner et al., 2013). In principle, *C. nasus* is − like *B. barbus* − a rheophilic cyprinid sharing the same fish ecological region (Leuner et al., 2013; Mueller et al., 2018). However, *C. nasus* has more specific habitat requirements when it comes to larval and juvenile development (Duerregger et al., 2018). During their early life stages, they change diet two times from the yolk sack to rotifers and later to algae which requires a precise match in timing of spawning, emergence, and juvenile growth with food availability (Reckendorfer et al., 2001; Pander et al., 2017). In addition, they have poor swimming abilities compared to juvenile *B. barbus* (Flore & Keckeis, 1998; Lechner et al., 2018), making them prone to be washed out of the study area during floods, with poor return rates. In this context, it is likely that adult *C. nasus* rely on larger and deeper riverine habitats than those available in the OHB which they only temporarily use during early life stages (spawning and juvenile phases). Consequently, this species benefits from the connectivity between OHB and the Danube so that the diverse habitat requirements of this species in the life cycle are met (Fig. 9). Other species of that colonisation type such as *S. trutta* or *T. thymallus* have meanwhile almost disappeared from the study site since warmer water temperatures in light of global change already exceed the optimum for those cold-stenothermic species (Kuhn et al., 2021; Pander et al., 2024).

The only newly detected species in the most recent monitoring was the invasive *N. melanostomus*. This species was first recorded in the Danube in 2004, 230 km downstream of the study site (Paintner & Seifert, 2006). From then on, this species successively spread along the Danube upstream, reaching the City of Kelheim in 2014 (Brandner et al., 2013) and the city of Vohburg in 2018 (Brandner et al., 2018). At the study site, the species is so far present in the OHB and to a lesser extend in narrow oxbows. In line with its speleophilic spawning strategy (Roche et al., 2021), it favors stony substrates (Sindilariu et al., 2006), which is particularly the case in the Danube due to intense bank rip-rap structures, and to a smaller extend in the OHB. As *N. melanostomus* is considered an invasive species and it is able to colonize new aquatic habitats very quickly, it also poses a threat to native species. Negative effects on the fish community in the study site have not yet been demonstrated, but cannot be ruled out in the long-run.

5. Conclusions

Restoration and the subsequently initialized succession processes in aquatic floodplain habitats are still developing and they continue improving functionality of the restoration over the 12-year time span,
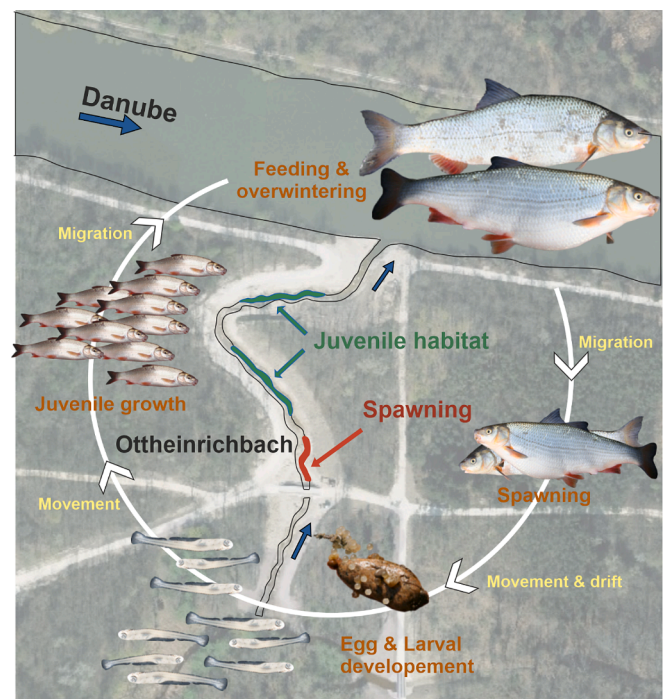
Fig. 9. Life cycle-specific habitat distribution in the heavily modified water body of the Danube and the restored floodplain. Life cycle fulfillment for highly sensitive riverine fish gets only possible with restoration measures beyond the main channel by restoring and reconnecting tributaries, oxbows and other aquatic floodplain habitats.

revealing that full indication of restoration effects of rivers and their floodplain systems may take decades. Since in practice there is a need to inform restoration management shortly after restoration as well as in the long-run, indicators are needed that allow the evaluation on different temporal and spatial scales. Since some fish species or their life stages immediately responding to environmental changes can ideally be used to indicate restoration-induced short-term changes of habitat quality as shown in the first three years of the study. In addition, fishes with complex life cycles and long generation times can indicate long-term functionality and sustainability of restoration measures.

As evident from this study, a staggered monitoring is ideal to cover short-term as well as mid- and long-term effects. A long-term monitoring is particularly helpful to detect species-specific responses of highly specialized, large-bodied and current-adapted species such as *C. nasus* comprising the longest generation time and therefore requiring the longest monitoring time span to detect success or failure. In addition, relationships between native fish communities and their invaders, in this case *N. melanostomus,* may need time to establish. However, in the long-run the integrity of the fish community can also be used as an indication tool (as proxy for restoration success) to evaluate the resilience of restored habitats against the invasion with non-desired species, particularly since *N. melanostomus* is known to favor anthropogenic rip rap in the Danube instead of restored natural river habitat.

The results herein indicate that large-scale floodplain restoration of aquatic habitats can at least partly compensate for habitat loss in degraded main stems of large rivers, However, some highly specialized species depend on full connectivity to the main river for optimal life-stage specific habitat match and population development.

CRediT authorship contribution statement

Joachim Pander: Funding acquisition, Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Writing – original draft, Visualization, Project administration. **Elisabeth Winter:** Data

curation, Investigation, Formal analysis, Writing – review & editing, Visualization. **Juergen Geist:** Conceptualization, Funding acquisition, Methodology, Validation, Resources, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Data availability

Data will be made available on request.

References

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. UK, PRIMER-E Ltd, Plymouth, p. 345.

Auerswald, K., Moyle, P., Seibert, S.P., Geist, J., 2019. HESS Opinions: Socio-economic and ecological trade-offs of flood management - benefits of a transdisciplinary approach. Hydrol. Earth Syst. Sci. 23, 1035–1044. https://doi.org/10.5194/hess-23-1035-2019.

Best, J., 2019. Anthropogenic stresses on the world's big rivers. Nat. Geosci. 12 (1), 7–21. https://doi.org/10.1038/s41561-018-0262-x.

Brandner, J., Cerwenka, A.F., Schliewen, U.K., Geist, J., 2013. Bigger is better: Characteristics of round gobies forming an invasion front in the Danube River. PLoS One 8 (9). https://doi.org/10.1371/journal.pone.0073036.

Brandner, J., Cerwenka, A.F., Schliewen, U.K., Geist, J., 2018. Invasion strategies in round goby (*Neogobius melanostomus*): Is bigger really better? PLoS One 13 (1). https://doi.org/10.1371/journal.pone.0190777.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland Forest communities of Southern Wisconsin. Ecol. Monogr. 27, 325–349. https://doi.org/10.2307/1942268.

Britton, J.R., Pegg, J., 2011. Ecology of European barbel *Barbus barbus*: implications for river, fishery, and conservation management. Rev. Fish. Sci. 19 (4), 321–330. https://doi.org/10.1080/10641262.2011.599886.

Cerwenka, A.F., Brandner, J., Dashinov, D., Geist, J., 2023. Small but Mighty: The Round Goby (*Neogobius melanostomus*) as a Model Species of Biological Invasions. Diversity 15 (4), 528. https://doi.org/10.3390/d15040528.

Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014. Change in marine communities: An approach to statistical analysis and interpretation, third ed. Plymouth, UK, PRIMER-E, p. 144.

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., Geist, J., 2018. The importance of stream interstitial conditions for the early-life-stage development of the European nase (*Chondrostoma nasus* L.). Ecol. Freshw. Fish 27, 920–932. https://doi.org/10.1111/eff.12403.

Dynesius, M., Nilsson, C., 1994. Fragmentation and flow regulation of river systems in the Northern third of the world. Science 266, 753–762.

Effenberger, M., Oehm, J., Schubert, M., Schliewen, U., Mayr, C. 2021. Rote Liste und Gesamtartenliste Bayern – Fische und Rundmäuler. Bayerisches Landesamt für Umwelt (ed). Germany, Augsburg, 50 p.

Flore, L., Keckeis, H. 1998. The effect of water current on foraging behaviour of the rheophilic cyprinid *Chondrostoma nasus* (L.) during ontogeny: evidence of a trade-off between energetic gain and swimming costs. Regulated Rivers: Research & Management. An International Journal Devoted to River Research and Management. 14(1), 141–154. 10.1002/(SICI)1099-1646(199801/02)14:1<141::AID-RRR492>3.0.CO;2-4.

Freyhof, J., Bowler, D., Broghammer, T., Friedrichs-Manthey, M., Heinze, S., Wolter, C., 2023. Rote Liste und Gesamtartenliste der sich im Süßwasser reproduzierenden Fische und Neunaugen (Pisces et Cyclostomata). Deutschlands – Naturschutz Und Biologische Vielfalt 170 (6), 63 S.

Fricke, R., Eschmeyer, W.N., Van der Laan, R. (eds) 2024. Eschmeyer's Catalog of Fishes: Genera, Species, References. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 12.11.2024.

Frissell, C.A., Liss, W.J., Warren, C.E., Hurley, M.D., 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manag. 10, 199–214. https://doi.org/10.1007/BF01867358.

Froese, R. and D. Pauly. Editors. 2023. FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2023).

Geist, J., 2015. Seven steps towards improving freshwater conservation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 25, 447–453. https://doi.org/10.1002/aqc.2576.

Geist, J., Hawkins, S.J., 2016. Habitat recovery and restoration in aquatic ecosystems: Current progress and future challenges. Aquat. Conserv. Mar. Freshwat. Ecosyst. 26, 942–962. https://doi.org/10.1002/aqc.2702.

Habersack, H., Hein, T., Stanica, A., Liska, I., Mair, R., Jäger, E., Hauer, C., Bradley, C., 2016. Challenges of river basin management: current status of, and prospects for, the River Danube from a river engineering perspective. Sci. Total Environ. 543, 828–845. https://doi.org/10.1016/j.scitotenv.2015.10.123.

Jungwirth, M., Haidvogl, G., Moog, O., Muhar, S., Schmutz, S., 2003. Angewandte Fischökologie an Fließgewässern. Facultas Verlags- und Buchhandels AG, Vienna.

Konečná, M., Smith, C., Reichard, M., 2010. Population and individual consequences of breeding resource availability in the European bitterling (*Rhodeus amarus*). Behav. Ecol. Sociobiol. 64, 1069–1079. https://doi.org/10.1007/s00265-010-0921-4.

Kottelat, M., Freyhof, J., 2007. Handbook of European freshwater fishes. Publications Kottelat, Cornol, Switzerland.

Kuhn, J., Casas-Mulet, R., Pander, J., Geist, J., 2021. Assessing stream thermal heterogeneity and cold-water patches from UAV-based imagery: a matter of classification methods and metrics. Remote Sens. (Basel) 13, 1379. https://doi.org/10.3390/rs13071379.

Lechner, A., Keckeis, H., Glas, M., Tritthart, M., Habersack, H., Andorfer, L., Humphries, P., 2018. The influence of discharge, current speed, and development on the downstream dispersal of larval nase (*Chondrostoma nasus*) in the River Danube. Can. J. Fish. Aquat. Sci. 75 (2), 247–259. https://doi.org/10.1139/cjfas-2016-0340.

Leuner, E., Schubert, M., Klein, M., 2013. Die Situation des Europäischen Aals (*Anguilla anguilla*) in Bayern. Bayerische Landesanstalt für Landwirtschaft, Freising.

Louhi, P., Vehanen, T., Huusko, A., Mäki-Petäys, A., Muotka, T., 2016. Long-term monitoring reveals the success of salmonid habitat restoration. Can. J. Fish. Aquat. Sci. 73 (12), 1733–1741. https://doi.org/10.1139/cjfas-2015-0546.

Mueller, M., Pander, J., Geist, J., 2018. Comprehensive analysis of > 30 years of data on stream fish population trends and conservation status in Bavaria. Germany. Biological Conservation. 226, 311–320. https://doi.org/10.1016/j.biocon.2018.08.006.

Paintner, S., Seifert, K., 2006. First record of the round goby, *Neogobius melanostomus* (Gobiidae), in the German Danube. Lauterbornia. 58, 101–107.

Pander, J., Geist, J., 2013. Ecological indicators for measuring stream restoration success. Ecol. Ind. 30, 106–118. https://doi.org/10.1016/j.ecolind.2013.01.039.

Pander, J., Mueller, M., Geist, J., 2015a. Succession of fish diversity after reconnecting a large floodplain to the upper Danube River. Ecol. Eng. 75, 41–50. https://doi.org/10.1016/j.ecoleng.2014.11.011.

Pander, J., Mueller, M., Geist, J., 2015b. A comparison of four stream substratum restoration techniques concerning interstitial conditions and downstream effects. River Res. Appl. 31 (2), 239–255. https://doi.org/10.1002/rra.2732.

Pander, J., Mueller, M., Sacher, M., Geist, J., 2016. The role of life history traits and habitat characteristics in the colonisation of a secondary floodplain by neobiota and indigenous macroinvertebrate species. Hydrobiologia 772, 229–245. https://doi.org/10.1007/s10750-016-2667-0.

Pander, J., Mueller, M., Knott, J., Egg, L., Geist, J., 2017. Is it worth the money? The functionality of engineered shallow stream banks as habitat for juvenile fishes in heavily modified water bodies. River Res. Appl. 33, 63–72. https://doi.org/10.1002/rra.3065.

Pander, J., Mueller, M., Geist, J., 2018. Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. Biol. Conserv. 217, 1–10. https://doi.org/10.1016/j.biocon.2017.10.024.

Pander, J., Knott, J., Mueller, M., Geist, J., 2019. Effects of environmental flows in a restored floodplain system on the community composition of fish, macroinvertebrates and macrophytes. Ecol. Eng. 132, 75–86. https://doi.org/10.1016/j.ecoleng.2019.04.003.

Pander, J., Casas-Mulet, R., Geist, J., 2023a. Hydropeaking impairs upstream salmonid spawning habitats in a restored Danube tributary. River Res. Appl. 39 (3), 389–400. https://doi.org/10.1002/rra.3953.

Pander, J., Casas-Mulet, R., Geist, J., 2023b. Contribution of a groundwater-influenced hinterland drainage system to the restoration of salmonid spawning grounds at the upper river Danube. Front. Environ. Sci. 11, 1124797. https://doi.org/10.3389/fenvs.2023.1124797.

Pander, J., Kuhn, J., Casas-Mulet, R., Habersetzer, L., Geist, J., 2024. Diurnal patterns of spatial stream temperature variations reveal the need for integrating thermal heterogeneity in riverscape habitat restoration. Sci. Total Environ. 918, 170786. https://doi.org/10.1016/j.scitotenv.2024.170786.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144. https://doi.org/10.1016/0022-5193(66)90013-0.

Ramler, D., Keckeis, H., 2019. Effects of large-river restoration measures on ecological fish guilds and focal species of conservation in a large European river (Danube, Austria). Sci. Total Environ. 686, 1076–1089. https://doi.org/10.1016/j.scitotenv.2019.05.373.

Reckendorfer, W., Keckeis, H., Tiitu, V., Winkler, G., Zornig, H., Schiemer, F., 2001. Diet shifts in 0+ nase, *Chondrostoma nasus*: size-specific differences and the effect of food. Archiv Fuer Hydrobiologie Supplement. 13512, 425–440. https://doi.org/10.1127/lr/12/2001/425.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Tayler, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94 (3), 849–873. https://doi.org/10.1111/brv.12480.

Roche, K.L., Šlapanský, M., Travnik, M., Janáč, M., Jurajda, P., 2021. The importance of rip-rap for round goby invasion success–a field habitat manipulation experiment. Journal of Vertebrate Biology. 70 (4), 1–11. https://doi.org/10.25225/jvb.21052.

Schiemer, F., Baumgartner, C., Tockner, K., 1999. Restoration of floodplain rivers: The 'Danube restoration project'. River Res. Appl. 15 (1–3), 231–244. https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<231::AID-RRR548>3.0.CO;2-5.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication, 1. University of Illinois Press, Urbana.

Sindilariu, P.-D., Freyhof, J., Wolter, C., 2006. Habitat use of juvenile fish in the lower Danube and the Danube delta: implications for ecotone connectivity. Hydrobiologia 571 (1), 51–61. https://doi.org/10.1007/s10750-006-0216-y.

Sinowski, W., Auerswald, K., 1999. Using relief parameters in a discriminant analysis to stratify geological areas with different spatial variability of soil properties. Geoderma 89, 113–128. https://doi.org/10.1016/S0016-7061(98)00127-X.

Stammel, B., Cyffka, B., Geist, J., Müller, M., Pander, J., Blasch, G., Fischer, P., Gruppe, A., Haas, F., Kilg, M., Lang, P., Schopf, R., Schwab, A., Utschik, H., Weißbrod, M., 2012. Floodplain restoration on the Upper Danube (Germany) by re-establishing water and sediment dynamics: a scientific monitoring as part of the implementation. River Syst. 20, 55–70. https://doi.org/10.1127/1868-5749/2011/020-0033.

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclère, D., Lynch, A.J., Leonard, P., McClain, M.E., Muruven, D., Olden, J.D., Ormerod, S.J., Robinson, J., Tharme, R.E., Thieme, M., Tockner, K., Wright, M., Young, L., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. Bioscience 70 (4), 330–342. https://doi.org/10.1093/biosci/biaa002.

Vornanen, M., Stecyk, J.A., Nilsson, G.E. 2009. The anoxia-tolerant crucian carp (*Carassius carassius* L.). In Fish physiology. 27, 397–441. Academic Press. 10.1016/S1546-5098(08)00009-5.

Ward, J.V., Tockner, K., Schiemer, F., 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regul. Rivers Res. Manag. 15, 125–139. https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E.

Weber, C., Peter, A., 2011. Success or failure? Do indicator selection and reference setting influence river rehabilitation outcome? N. Am. J. Fish Manag. 31 (3), 535–547. https://doi.org/10.1080/02755947.2011.595277.

Wyżga, B., Amirowicz, A., Bednarska, A., Bylak, A., Hajdukiewicz, H., Kędzior, R., Kukula, K., Liro, M., Mikus, P., Oglecki, P., Radecki-Pawlik, A., Zawiejska, J., 2021. Scientific monitoring of immediate and long-term effects of river restoration projects in the Polish Carpathians. Ecohydrol. Hydrobiol. 21 (2), 244–255. https://doi.org/10.1016/j.ecohyd.2020.11.005.

Zauner, G., Eberstaller, J., 1999. Klassifizierungsschema der österreichischen Flußfischfauna in Bezug auf deren Lebensraumansprüche. Österreichs Fischerei. 52, 198–205.