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Integration of Constructed Floodplain Ponds into Nature-Like Fish Passes Supports Fish Diversity in a Heavily Modified Water Body

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Abstract: Fish passes facilitate fish movement in fragmented river systems, yet they can also provide important habitat functions. This study investigated the fish community composition of different constructed habitat types (fluvial habitats, floodplain ponds) within fish passes in relation to habitat characteristics in order to deduce recommendations for fish-friendly designs of such structures. Fish community structures within passes differed significantly from those in the main river, comprising a high number of rheophilic species in fluvial habitats (*Thymallus thymallus*, *Hucho hucho*, *Salmo trutta*, *Cottus gobio*, *Chondrostoma nasus*, and *Barbus barbus*), and of stagnophilic species in floodplain ponds (*Rhodeus amarus*, *Scardinius erythrophthalmus*, *Misgurnus bipartitus*, and *Tinca tinca*). During summer, floodplain ponds also provided important juvenile habitats for the target species *C. nasus* and *B. barbus*. Differences between the two habitat types in fish abundance were mostly explained by differences in macrophyte coverage, gravel, boulders, temperature, and current speed. The findings of this study stress the important habitat functions of fish passes. They also suggest that integration of diverse habitat structures, especially of currently hardly considered constructed floodplain ponds into fish passes, can greatly enhance their fish communities and contribute to the restoration of several declining target species of conservation.

Keywords: river restoration; bypass channel; fish conservation; aquatic habitat; floodplain ponds; hydropower; fish stock management; fish migration

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1. Introduction

Habitat degradation and fragmentation of river systems caused by dams, weirs, and other barriers is considered a major challenge in restoring European fish populations [1]. For instance, impoundments that restrict river dynamic processes, such as sediment transport or other matter fluxes, have been identified as one of the major factors related to the decline of riverine fish species in the headwater areas of Elbe, Main, and Danube rivers [2,3]. Besides restoring habitat quality of rivers by improving structural richness, sediment transport and deadwood dynamics, the restoration of fish passage in fragmented rivers is high on the agenda [4–6]. Different techniques to restore fish migration, such as technical fish passes (e.g., vertical slot-pass; [7,8]) or solutions with nature-like construction schemes [9–11], have been applied in practice. These artificial structures have widely proven their valuable contributions to restore fish migration [12,13]. However, the restoration of fish communities in degraded rivers seems to be highly challenging and not only dependent on restoring connectivity, due to the manifold other restrictions in heavily modified water bodies (HMWB; [14]). In these waters, the natural river dynamic processes are strongly impaired [15–17], limiting the chances of restoring complete life cycles of specialized riverine fish species, such as *Thymallus thymallus* L., *Hucho hucho* L., *Salmo trutta* L., *Chondrostoma nasus* L., and *Barbus barbus* L. [18,19]. It has been proposed to restore fish habitats in highly degraded rivers by designing separate, parallel flowing river courses or channels outside the degraded systems using a portion of their natural discharge [19,20] as it is required for nature-like fish passes that initially were built to restore fish migration (reviewed in [21]). This initiated a discussion between ecologists, river managers and users, to which extend fish passes can provide important fish habitats potentially compensating the existing habitat loss in the main river. First studies on the contribution of nature-like fish passes to overall biodiversity of fishes indicated that these structures can be highly valuable refuges for rheophilic fishes [13,19,22], e.g., providing key habitats for reproduction [11,12].

Many countries developed extensive guidelines how fish passes have to be built (e.g., Germany; [23]), often primarily focussing on their role for fish passage. Nature-like solutions are generally built to mimic small streams with discharges between 0.3 m^3/s and 30 m^3/s comprising runs, riffles and pools [23,24], with a special focus on providing a widely functional migration corridor for the target species of conservation throughout the year [23]. Besides the fluvial habitats, nature-like solutions increasingly consider the lateral connectivity to stagnant waters in the floodplain. These additional aquatic habitats can comprise large structures, such as backwaters that evolved from ancient cut-off meanders or small floodplain ponds [25–28]. If such structures are absent, they can also be newly constructed.

In this study, we investigated the value of fluvial habitats and newly created and connected small floodplain ponds (further referred to as ponds) as habitat for the fish community in two nature-like fish passes in relation to their characteristics. In particular, we hypothesized that (i) fish community composition in the nature-like fish passes reflects the fish community composition of the main stem, and (ii) nature-like fish passes integrating stagnant waters provide habitat for both rheophilic and stagnophilic fish species, thus contributing to greater fish diversity. Furthermore, we hypothesized that (iii) fish pass systems can provide important juvenile habitats for rheophilic and stagnophilic species, as well.

2. Materials and Methods

2.1. Study Area

The study was carried out at two nature-like fish passes at the hydropower plant Gars (48°09′13.92″ N, 12°18′40.80″ E) and Stammham (48°14′50.67″ N, 12°51′57.03″ E), which are located at the heavily modified middle reach of the Bavarian Inn in Germany (Figure 1). The River Inn is a snow-melt dependent alpine river with relatively cold water temperatures (2.0–17 °C) and peak discharge in summer (mean annual discharge (MQ) in Summer 490 m^3/s) with turbid water (up to 200 nephelometric turbidity units (NTU)), and a clear water phase (often below 25 NTU) at low discharge (MQ 222 m^3/s) in winter. The River Inn is a highly altered alpine river due to flood protection and hydropower generation with many dams and 20 power plants. The loss of the former rich habitat mosaic comprising lentic floodplain habitats, as well as several river courses (Figure 2), impaired the recruitment of riverine fish species and severely reduced the amount of aquatic habitats of a water depth less than 1 m. The interruption of the river continuum due to the implemented power plants additionally impaired the connectivity of life stage specific habitats, with strong effects on migratory fish populations, particularly the target species considered in this study. The degradation of the River Inn created a strong need to restore fish migration and aquatic habitats, as well, which was partly realized by implementing nature-like fish passes.

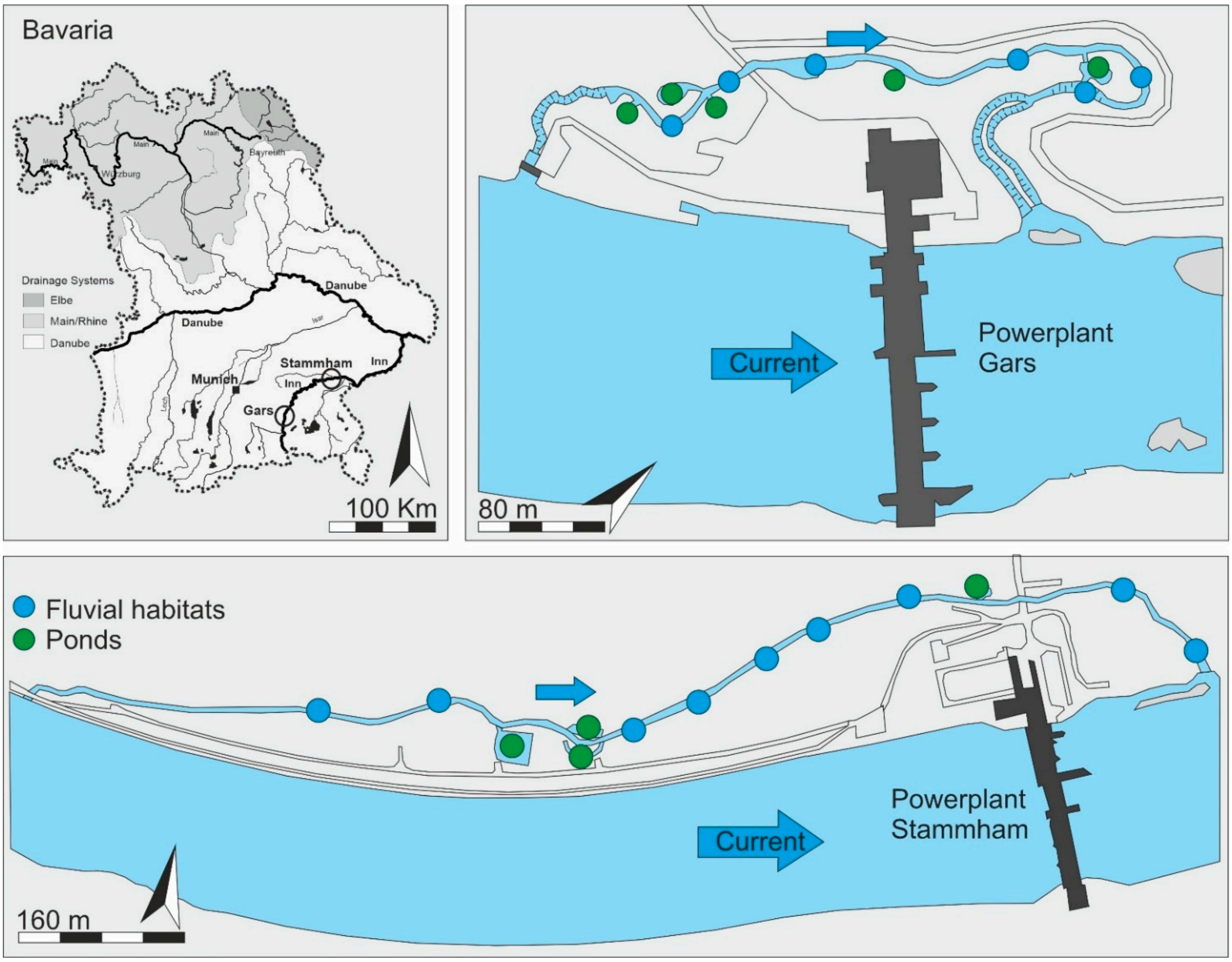

Figure 1. Map of Bavaria with the major rivers and drainage areas. Drainage system of the River Danube into which the River Inn drains is highlighted in light grey, with the location of the two fish passes Gars and Stammham, as well as the sampled fluvial habitats (blue) and ponds (green).

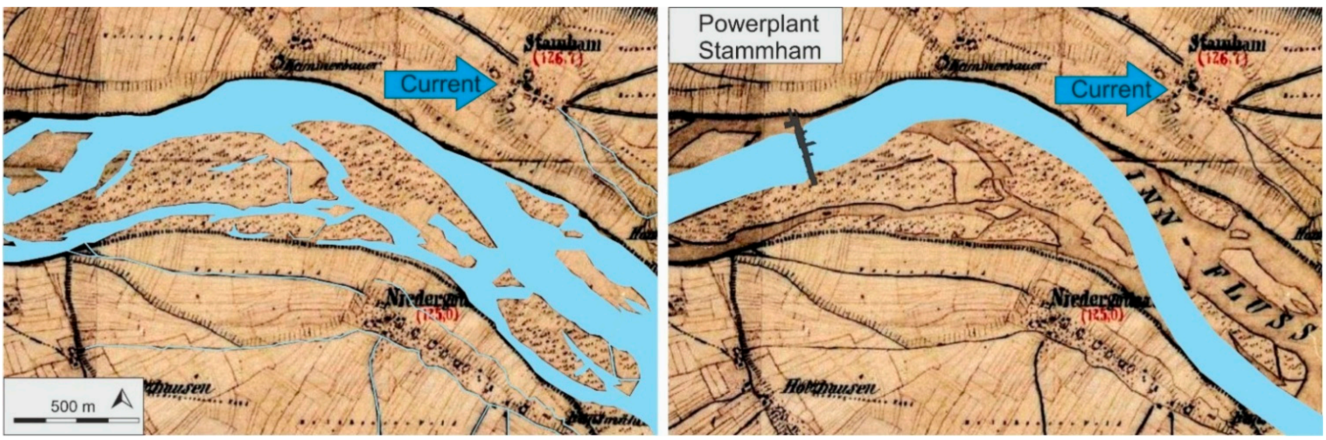

Figure 2. Illustration of the historic habitat mosaic of the River Inn comprising lentic as well as lotic habitats (**left panel**) compared the pre-restoration conditions after the implementation of the power plant Stammham in 1955 (**right panel**). The map was created based on the Bavarian "Positionsblätter", which dates back to the 1860s (https://geoportal.bayern.de/bayernatlas/?lang=de&topic=ba&bgLayer=historisch&catlogNodes=11,122&E=786779.49&N=5350979.79&zoom=11; last accessed on 24 March 2021). For post-restoration conditions, please see Figure 1.

The potential fish ecological region of the River Inn is the hyporhithral with historically widespread rheophilic specialists, such as *T. thymallus*, *H. hucho*, *S. trutta*, *Cottus gobio* L., *C. nasus*, and *B. barbus* [29], representing the largest part of the former natural fish community. Today, the rheophilic specialists are still present; however, their population density is rather low, and some of the more prominent species, such as *T. thymallus* and *H. hucho*, continue declining, although they are protected and stocked [30]. The fish community in the River Inn is now dominated by ubiquitous species, such as *Alburnus alburnus* L., *Rutilus rutilus* L., and *Squalius cephalus* L., as well as the stocked non-native *Oncorhynchus mykiss* Walbaum [30].

2.2. Characterization of the Fish Passes

Both fish passes (FP) were constructed with a nature-like construction scheme and finalized in 2015 (Gars) and 2016 (Stammham). With a length of 1500 m, the FP Stammham is more than double the length of Gars (670 m); however, its discharge and width are much smaller (Tables 1 and 2).

Table 1. Construction details of the two assessed fish passes Gars and Stammham.

Fish Pass	Year Built	Gradient [‰]	Length [m]	Height Difference [m]	Discharge [L s^{-1}]	Flow-Course [m]
Gars	2015	10	670	7.5	900	670
Stammham	2016	5.5	1500	8.5	350	1500

Table 2. Construction details of the fluvial habitats in Gars and Stammham. Values represent the mean and the range. CSB = current speed above bottom, CSS = current speed below surface, MA = submerged macrophytes in % coverage, DW = deadwood in % coverage, Veg = bank vegetation in % coverage. B = boulder in % coverage, G = gravel in % coverage, S = sand in % coverage, F = fines smaller 1 mm % coverage.

Fluvial habitats	Width [m]	Depth [m]	CSB [ms^{-1}]	CSS [ms^{-1}]	Area [m^2]	MA [%]	DW [%]	Veg [%]	B [%]	G [%]	S [%]	F [%]
Gars	4.83 3.10–7.00	0.43 0.10–1.12	0.43 0.00–1.44	0.61 0.00–2.07	146 120–177	2 0–5	5 0–10	7 0–25	34 25–50	67 50–70	23 15–35	11 5–15
Stammham	2.89 1.83–4.32	0.34 0.08–0.75	0.36 0.00–1.09	0.41 0.01–1.10	89 75–107	3 0–10	5 0–10	46 0–90	4 0–25	60 45–70	26 20–35	14 10–20

To create a high variability in aquatic habitats and to improve the fish diversity in the two fish passes, nine artificial ponds with different sizes and depth were built adjacent but connected to the flow course (Figures 1 and 3). In both FP, large stones and deadwood in form of dead rootstocks from forest clearance were placed for structural enrichment into the fluvial habitats, as well as into the small constructed ponds (Figure 3). The upstream connection of the FP was realized using an undershot sluice gate. At the upstream entrance of the FP Gars, a concrete structure (8 m × 4 m) was built to remove frequently occurring high loads of silt and sand. In contrast to Stammham, where the discharge was fixed to 350 L/s (comprising only water-level fluctuations in the cm range), the discharge in Gars (base flow of 900 L/s) can additionally be enhanced by applying environmental flows (e-flows; Reference [31]) of additional 900 L/s. This e-flow is mainly applied during the peak discharge phase of the River Inn in summer. Due to strongly fluctuating water levels in the tailwater of the power plant Gars, this FP was constructed with a second, parallel running fish passage structure of different height at the confluence to the River Inn. In Stammham, the downstream connection of the FP to the Inn was built like a natural tributary confluence (Table 1). The substrate introduced into the FP was gravel dominated with low percentage of sand and silt. In the ponds, accumulations of fine material built up to a thin layer of several cm (20–100 mm) over the originally introduced gravel comprising a grain size range of 0–65 mm. Depending on their depths, pond macrophyte coverage varied between 0–95%. In fluvial habitats, macrophytes were widely absent.

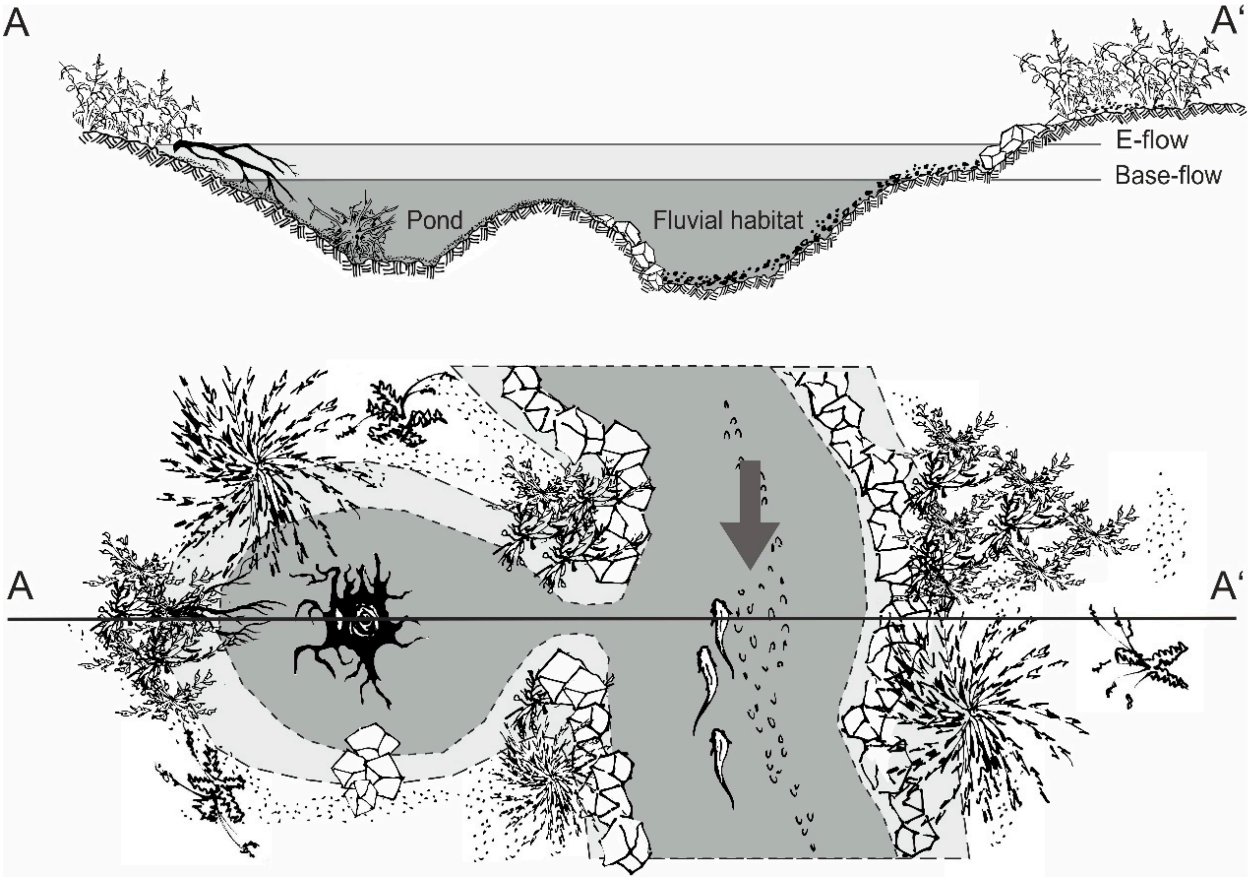

Figure 3. Schematic drawing (cross section and top-view) of the principle habitat types fluvial habitats and ponds, which were assessed in this study. Base-flow line indicates the water level at base-flow conditions (900 L s^{-1}). E-flow line indicates water level during the application of environmental flows (additionally to the base-flow another 900 L s^{-1} discharge can be provided in the fish pass). Note that e-flow conditions can only be applied in the fish pass Gars.

2.3. Fish Sampling

Fish community composition in both FP and their adjacent ponds was assessed in spring (March, May), summer (June, August), and late fall (October, December) 2019. To assess a representative length of more than 20% of the FP (suggested in [32]), 6 fluvial habitats (FS) were sampled in Gars and 9 in Stammham. In both fish passes, all available floodplain ponds were fully sampled, altogether comprising 9 ponds of different size and depth (Table 3). Each of the 15 fluvial habitats comprised 30 m in length [32] and differed slightly in the sampled area according to the respective river width (Table 2). All fluvial habitats and ponds were sampled with a land-based electrofishing generator of 8 kW (EFKO FEG 8000, EFKO-Elektrofischfanggeräte GmbH, Leutkirch, Germany) during stable weather and discharge conditions. All fluvial habitats and ponds were consecutively sampled within a 6-h period (9 a.m.–3 p.m.), working from downstream to upstream direction. A single anode was used and stunned fish were collected with a dipnet and transferred to a plastic tank. During all sampling events, the same persons handled the anode and the dipnet. The total length of all specimens was measured to the nearest cm. All individuals of lampreys, adults, as well as larvae, were determined to the family level Petromyzontidae. Fish and lampreys were immediately released after the length measurement at the location from which they had been collected. The same methodological approach was used across all sampling dates.

Table 3. Construction details of the constructed floodplain ponds in Gars and Stammham. Values represent the mean and the range. N = number of ponds, MA = submerged macrophytes in % coverage, DW = deadwood in % coverage, Veg = bank vegetation in % coverage. B = boulder in % coverage, G = gravel in % coverage, S = sand in % coverage, F = fines smaller 1 mm % coverage. NA = not available.

Floodplain Ponds	N	Length [m]	Width [m]	Depth Base-Flow [m]	Depth E-Flow [m]	Area Base-Flow [m^2]	Area E-Flow [m^2]	MA [%]	DW [%]	Veg [%]	B [%]	G [%]	S [%]	F [%]
Gars	5	15.52	8.10	0.32	0.50	66	115	38	10	4	2	7	28	65
		9.55–25.89	6.60–9.52	0.06–0.93	0.25–1.08	44–130	66–181	0–90	5–20	0–20	0–10	0–15	0–40	50–90
Stammham	4	26.00	11.70	0.51	NA	377	NA	58	8	4	3	13	26	61
		11.47–39.00	2.89–30.00	0.17–1.65	NA	67–1127	NA	10–95	5–15	0–10	0–10	0–40	20–30	30–75

For the fish community analyses of the River Inn, data from the governmental fish monitoring in context of the European Water Framework Directive was used. This data set includes 6 sampling locations at the Bavarian River Inn that were sampled in different seasons. Fish were caught according to a standardized national sampling protocol [33,34]. This standard included electrofishing from the boat or wading using an electrofishing generator with continuous voltage and a single anode by specifically trained personnel with in-depth training on correct species identification. All fish caught were assigned to species-specific size classes, and numbers were recorded, distinguishing juveniles, subadults, and adults [35].

2.4. Physicochemical Habitat Characteristics and Vegetation

To characterize structural and chemical habitat properties of the FPs, physicochemical habitat variables were recorded at the same time as the fish sampling was carried out (Tables 2–4). Habitat surface area (wetted area of ponds and fluvial habitats given in m^2), water depth (m), length of fluvial habitats (m), width of fluvial habitats (m), and current speed (Ott MF pro, Ott, Kempten, Germany) 5 cm above ground (m/s), as well as 5 cm below surface (m/s). The measurements were recorded at 9 measurement points distributed along three cross sections in each fluvial habitat and pond, respectively (Tables 2 and 3). Readings of electric conductance (EC, µS/cm, corrected to 20 °C), dissolved oxygen concentration (O_2, mg/L), pH value (pH), temperature (T, °C), and turbidity (Turb, NTU) were taken using the handheld devices Multi 3430, pH 3110, and pHotoFlex Turb (WTW, Weilheim, Germany), with three measurements per fluvial habitat or pond (Table 4). The relative composition of bed material was visually estimated in 10% steps according to the classification boulders (B), gravel (G), sand (S), and fines (F). The presence of bank vegetation (VEG), macrophytes (MA), and dead wood (DW) was documented in 5% steps (Tables 2 and 3, following Reference [19]).

2.5. Data Analysis

All multivariate analyses were computed using PRIMER v7 (Plymouth Marine Laboratory, Plymouth, UK). For all statistical analyses, significance was accepted at $p \leq 0.05$. To analyze differences in fish community composition, a catch per unit effort (CPUE) standardized to 10 m fished river length for the comparison of the Inn with FPs, and 10 m^2 for multivariate comparisons between FPs, seasons, and FP habitats was calculated. Due to the different data structure of the water framework sampling conducted in the main stem of the River Inn and the FP (sampling of 30 m fluvial habitats and ponds), the resemblance matrix for the non-metric multidimensional scaling (nMDS) for the comparison River Inn versus FP was calculated based on pooled seasonal data, which is displayed in Figure 4A. For the comparisons of fish community composition within the FPs, a second resemblance matrix was created using the full data resolution of all fluvial habitats and ponds during different seasons (spring, summer, and late fall; Figure 4B). Additionally, the bubble-function in PRIMERv7 was used to display the contribution of important target species for restoration, such as *B. barbus*, *C. nasus*, *H. hucho*, and *T. thymallus* (N = number of individuals), to the fish community composition (Figure 4C). 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 physico-chemical habitat variables within fluvial habitats and ponds (Bio-Env; Reference [36]). Abiotic habitat variables were plotted in the nMDS using the overlay function in PRIMER (Figure 4B). To test for significant differences between fish community composition of the River Inn and FPs, between FP Gars and FP Stammham, and between fluvial habitats and ponds in different seasons, one-way analysis of similarities (ANOSIM) based on Bray–Curtis similarities [37] calculated from species abundance and species length-frequency data [38] were computed. If variables amongst samples happened to be entirely zero, a zero-adjusted Bray–Curtis coefficient, including a virtual dummy variable being one for all objects, was used as suggested by Clarke et al. [39]. To identify the most common and steadily occurring species in the River Inn, among the FPs, FS, and ponds and at different seasons, a one-way Similarity Percentage Analysis (SIMPER; Reference [36]) was computed. Average dissimilarity values for the abundance of species for the respective comparisons Inn versus FPs, FP Gars versus FP Stammham, FS versus ponds, and the comparisons among different seasons were calculated (Table 5).

Table 4. Abiotic habitat variables measured in the two fish passes Gars and Stammham throughout the study period. Values represent Scheme 2. O_2 = dissolved oxygen, EC = electric conductance, pH, and turbidity. NA = not available.

	Gars Fluvial Habitats					**Gars Ponds**				
	T [°C]	**O_2 [mgl^{-1}]**	**EC [µscm^{-1}]**	**pH**	**Turbidity [NTU]**	**T [°C]**	**O_2 [mgl^{-1}]**	**EC [µscm^{-1}]**	**pH**	**Turbidity [NTU]**
March	6.4	12.1	385	8.2	16.3	7.6	14.2	358	8.5	12.3
	6.4–6.5	11.8–12.8	380–388	8.2–8.3	12.1–24.8	6.6–8.4	11.0–16.6	352–416	8.0–8.9	2.6–19.6
May	9.1	11.1	276	8.3	36.0	10.7	12.3	272	8.5	19.1
	8.6–9.4	11.0–11.1	273–279	8.2–8.5	28.5–45.1	8.8–12.5	11.0–15.3	263–280	8.3–8.9	6.9–35.3
June	13.8	10.2	194	NA	117.0	16.1	10.4	191	NA	60.5
	13.6–14.1	10.1–10.4	195–199	NA	101.6–134.9	14.3–20.5	9.3–11.2	169–197	NA	12.5–113.0
August	18.6	9.1	224	8.0	167.7	22.0	10.0	208	8.5	78
	18.2–19.1	7.8–9.7	218–231	7.9–8.1	139.0–215.2	18.9–27.2	7.2–13.3	150–225	7.6–9.7	5.5–141.8
October	11.8	10.9	330	8.1	16.4	13.3	11.6	303	8.4	7.3
	11.5–12.1	10.3–11.1	327–333	7.9–8.2	11.1–23.2	12.7–14.8	4.0–18.3	241–386	7.8–8.9	2.7–17.3
December	4.8	11.7	388	8.1	15.7	3.0	13.4	336	8.6	10.1
	4.7–4.9	11.1–11.9	359–393	7.9–8.2	10.1–25.6	2.4–3.4	10.3–16.2	275–362	8.1–8.8	0.5–22.9

	Stammham Fluvial Habitats					**Stammham Ponds**				
	T [°C]	**O_2 [mgl^{-1}]**	**EC [µscm^{-1}]**	**pH**	**Turbidity [NTU]**	**T [°C]**	**O_2 [mg^{-1}]**	**EC [µscm^{-1}]**	**pH**	**Turbidity [NTU]**
March	7.0	11.2	425	8.0	16.0	7.4	7.7	425	7.8	3.5
	6.6–7.1	11.0–11.7	379–441	7.9–8.1	10.6–26.3	6.7–9.1	1.2–13.0	405–442	6.7–8.5	0.2–8.7
May	9.0	11.0	327	8.2	20.3	13.3	10.7	369	8.2	4.4
	8.7–9.3	10.0–11.3	304–365	8.1–8.3	12.5–27.7	9.3–19.6	3.8–16.9	319–418	7.8–8.6	1.8–11.4
June	14.6	9.9	253	NA	72.2	17.9	9.3	295	NA	25.8
	14.0–14.8	9.7–10.1	234–288	NA	52.0–90.3	12.5–24.5	4.4–13.1	207–354	NA	2.2–74.6
August	19.1	8.8	264	8.0	79.9	23.3	12.7	269	8.6	27.9
	18.3–19.7	7.7–9.0	245–295	7.9–8.9	59.4–107.0	15.1–30.0	4.5–18.4	203–328	8.0–9.5	1.9–128.7
October	12.8	10.3	355	8.1	9.9	13.9	8.1	335	8.0	3.2
	12.3–13.2	9.5–11.0	342–379	7.9–8.2	5.8–17.1	11.6–15.8	1.8–10.9	297–376	7.5–8.5	1.1–5.6
December	5.1	11.2	407	8.1	17.1	5.6	8.0	388	7.9	7.4
	4.7–6.1	10.5–11.8	400–423	8.0–8.1	7.9–29.2	4.4–9.8	2.6–11.0	373–421	7.6–8.2	0.3–20.9

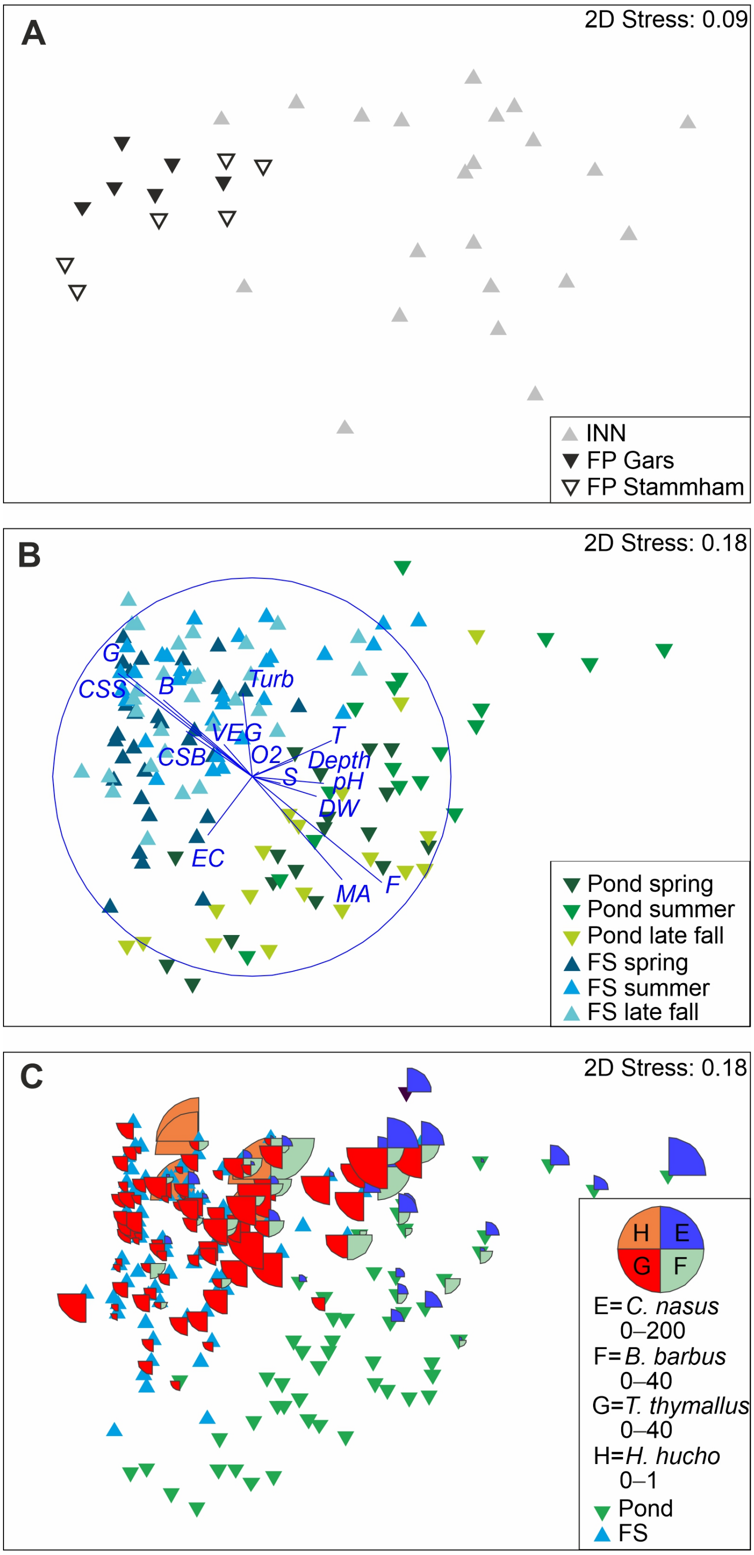

Figure 4. Non-metric multidimensional scaling (nMDS) comprising comparisons of fish community composition based on catch per unit effort (CPUE) abundance data. (**A**) The River Inn and the fish passes (Inn = grey triangles, black triangles, = fish pass Gars, open black triangles = fish pass Stammham), (**B**) comparison of the fish community composition in ponds (green triangles) versus fluvial habitats (blue triangles), and (**C**) proportion of target species in ponds or fluvial habitats displayed as pie size. Green triangles (ponds) and blue triangles (fluvial habitats). *C. nasus* = *Chondrostoma nasus*, *B. barbus* = *Barbus barbus*, *T. thymallus* = *Thymallus thymallus*, and *H. hucho* = *Hucho hucho*. Abbreviation of habitat variables refer to Tables 2–4. Turb = turbidity in NTU. 2D-Stress = stress value after Kruskal.

Table 5. Results of one-way analysis of similarities (ANOSIM) and Similarity Percentage Analysis (SIMPER) concerning pairwise comparisons of the two fish passes, different seasons, and between fluvial habitats and ponds. AVDIS = average dissimilarity, NA = not detected by SIMPER. FP = fish pass, FS = fluvial habitats, PO = floodplain ponds. For abbreviations of species, refer to Table 6.

	ANOSIM		**SIMPER**													
Comparisons	**R-Value**	***p*-Value**	**df**	**AVDIS**	**Bleak**	**Stonel**	**Barbel**	**Bullh**	**Nase**	**Stickle**	**Dace**	**Lamprey Larvae**	**Stomo**	**Bitter**	**Chub**	**Grayl**
FP–River Inn	0.482	**<0.001**	1	88.42	9.44–17.89	NA	NA	47.46–3.02	NA	52.95–0.30	NA	NA	NA	NA	76.57–7.13	12.96–0.71
FP Gars–FP Stammham	0.07	**<0.001**	1	83.28	NA	NA	NA	20.15–6.31	3.36–7.46	5.71–25.49	NA	0.00–6.04	NA	NA	18.71–25.36	2.26–5.29
FP spring–FP summer	0.134	**<0.001**	2	82.97	7.85–13.92	NA	NA	NA	1.17 –14.38	3.17–40.40	NA	2.46–5.44	NA	NA	2.73–58.19	1.69–5.15
FP summer–FP late fall	0.051	**<0.01**	2	81.22	NA	NA	NA	13.92–16.19	14.38–1.21	40.40–5.71	6.83–3.54	NA	NA	NA	58.19–6.02	5.15–4.88
FP spring– FP late fall	0.023	>0.05	2	82.31	NA	NA	NA	7.85–16.19	NA	3.17–5.71	NA	2.46–1.92	NA	NA	2.73–6.02	1.69–4.88
FS–PO	0.631	**<0.001**	1	92.62	NA	NA	NA	19.97–0.46	4.19–7.91	1.81–40.78	NA	NA	NA	NA	4.42–52.13	6.18–0.11
PO Gars–PO Stammham	0.122	**<0.01**	3	84.05	NA	3.70–0.58	NA	NA	6.23–10.00	12.53–76.08	7.63–5.46	NA	NA	NA	39.40–68.04	NA
FS Gars–FS Stammham	0.208	**<0.001**	3	72.10	NA	NA	NA	36.25–9.11	NA	NA	NA	0.00–8.50	NA	NA	1.47–6.39	3.97–7.65
PO Gars–FS Gars	0.795	**<0.001**	3	93.64	NA	NA	NA	0.83–36.25	NA	12.53–0.03	NA	NA	NA	NA	39.40–1.47	NA
PO Stammham–FS Stammham	0.635	**<0.001**	3	93.34	NA	NA	NA	0.00–9.11	10.00–6.33	76.08–3.00	NA	0.50–8.50	NA	9.42–0.13	68.04–6.39	0.00–7.65
FS spring–FS summer	0.181	**<0.001**	5	71.43	NA	NA	0.03–4.30	12.40–21.77	0.83–9.83	NA	NA	3.83–8.60	NA	NA	0.97–7.13	2.50–8.23
FS summer–FS late fall	0.009	>0.05	5	65.93	3.30–4.67	NA	NA	21.77–25.73	9.83–1.90	NA	NA	8.60–2.87	NA	NA	7.13–5.17	8.23 –7.80
FS spring–FS late fall	0.119	**<0.001**	5	70.00	NA	NA	NA	12.40–25.73	NA	NA	NA	3.83–2.87	NA	NA	0.97–5.17	2.50–7.80
PO spring–PO summer	0.201	**<0.001**	5	82.62	NA	NA	NA	NA	1.72–21.94	8.06–105.22	NA	NA	NA	NA	5.67 143.28	NA
PO summer–PO late fall	0.207	**<0.01**	5	85.21	NA	NA	NA	NA	21.94–0.06	105.22–9.06	NA	NA	NA	NA	143.28–7.44	NA
PO spring–PO late fall	0.017	>0.05	5	81.34	NA	2.56–1.72	NA	NA	NA	8.06–9.06	NA	NA	1.00–1.33	1.11–2.50	5.67–7.44	NA
PO spring–FS spring	0.699	**<0.001**	5	92.69	NA	2.56–0.70	NA	0.28–12.40	NA	8.06–0.23	NA	0.17–3.83	NA	NA	5.67–0.97	NA
PO summer–FS summer	0.644	**<0.001**	5	90.50	NA	NA	NA	0.83–21.77	21.94–9.83	105.22–1.50	NA	NA	NA	NA	143.28–7.13	0.00–8.23
PO late fall–FS late fall	0.723	**<0.001**	5	93.79	NA	NA	NA	0.28–25.73	NA	9.06–3.70	5.83–2.17	NA	NA	NA	7.44–5.17	0.00–7.80

Numbers in bold indicate significant differences for pairwise comparisons.

To display species preferential use of FS or ponds, a scatter plot based on pooled species abundance data from FPs (data was Log(X+1) transformed due to the highly unbalanced occurrence of species) was computed using the scatter plot function in PRIMERv7. To illustrate fish density of important or target species, cumulative bar plots for each month were displayed for FS and ponds, respectively. Additionally, length-frequency plots were computed for the most abundant species *S. cephalus* and the two target species of conservation *C. nasus* and *T. thymallus*.

Significant influences of abiotic parameters on fish species diversity in the ponds were assessed by computing a linear model (LM) as model assumptions regarding normal distribution of model residuals were met. Assumptions and model fit were assessed using the package "DHARMa" in R [40]. Species richness (numbers of species detected) as the response variable was linked to habitat variables described in Tables 2–4 as predictor variables. Data were visually checked for autocorrelation using autocorrelation (ACF) and partial autocorrelation (PACF) plots. To test whether possible temporal correlation of repeated sampling in the same habitat explained additional variability in the models, a linear mixed model (LMM) with the function "lmer" in the package "lme4" in R [41] was computed, including the sampling date (1–6) and site as random effects. Comparing models via akaike information criterion (AIC) values indicated no additional explanatory value to the model outcome when the random effects date and site were included. Hence, significances of main effects were tested in the initial model, excluding random effects, using an F test in the R "car" package [42].

3. Results

In the two fish passes 11,893 individuals of fish and lampreys were caught during the sampling survey. The 33 fish species detected belonged to nine families with Cyprinidae (55% of all species) dominating, followed by Salmonidae (15%) and Percidae (9%). The

Families Esocidae, Nemacheilidae, Cottidae, Cobitidae, and Gasterosteidae comprised only one species each (Table 6). Most abundant species were *S. cephalus* (27% of all individuals), followed by *Gasterosteus aculeatus* L. (20%), *C. gobio* (15%), *C. nasus* (7%), *T. thymallus* (5%), *A. alburnus* (4%), *Leuciscus leuciscus* L. (4%), *R. rutilus* (4%), *Barbatula barbatula* L. (3%), and *Rhodeus amarus* Bloch (2%). All other species only contributed less than 1% to the individuals (Table 6).

Table 6. List of detected species and their abbreviations used. INN = River Inn, FP = fish pass, CP = current preference, RL = Red List Germany, RLB = Red List Bavaria [43], FFH = protected species according to Flora Fauna Habitat Direction AnnexII and AnnexV [44]. Please note that the number of individuals are given as total catch numbers, which were not standardized to the length of sampled area here.

Species	Common Names	Abbreviation	INN	FP	Gars	Stammham	Family	CP	RL	RLB	FFH
Anguilla anguilla	European eel	Eel	225	0	0	0	Anguillidae	indifferent	3	F	NL
Abramis brama	Freshwater bream	Bream	162	5	4	1	Cyprinidae	indifferent	*	NL	NL
Alburnoides bipunctatus	Spirlin	Spirlin	85	19	7	12	Cyprinidae	rheophil	V	2	NL
Alburnus alburnus	Bleak	Bleak	1830	434	26	408	Cyprinidae	indifferent	*	V	NL
Aspius aspius	Asp	Asp	10	0	0	0	Cyprinidae	indifferent	3	3	Annex II
Barbatula barbatula	Stone loach	Stonel	70	305	191	114	Nemacheilidae	rheophil	*	V	NL
Barbus barbus	Barbel	Barbel	112	152	28	124	Cyprinidae	rheophil	*	3	Annex V
Blicca bjoerkna	White bream	Whitebr	1	1	0	1	Cyprinidae	indifferent	*	NL	NL
Carassius gibelio	Prussian carp	Cruci	1	2	0	2	Cyprinidae	indifferent	*	NL	NL
Chondrostoma nasus	Common nase	Nase	211	786	222	564	Cyprinidae	rheophil	V	2	NL
Cottus gobio	Bullhead	Bullh	507	1822	1330	492	Cottidae	rheophil	*	V	Annex II
Cyprinus carpio	Common carp	Carp	7	5	5	0	Cyprinidae	indifferent	*	NL	NL
Esox lucius	Northern pike	Pike	110	32	4	28	Esocidae	indifferent	*	NL	NL
Gasterosteus aculeatus	Three-spined stickleback	Stickle	15	2365	377	1988	Gasterosteidae	limnophil	*	V	NL
Gobio gobio	Gudgeon	Gudge	23	125	0	125	Cyprinidae	rheophil	*	V	NL
Gymnocephalus cernua	Ruffe	Ruffe	19	0	0	0	Percidae	indifferent	*	V	NL
Hucho hucho	Huchen	Huchen	22	6	3	3	Salmonidae	rheophil	2	3	Annex II
NA	Brook lamprey	Blamp	20	532	15	517	Petromyzontidae	rheophil	*	1	Annex II
Lepomis gibbosus	Pumpkinseed	Pumpk	0	9	2	7	Percidae	indifferent	*	NL	NL
Leucaspius delineatus	Belica	Belica	0	1	0	1	Cyprinidae	limnophil	*	3	NL
Leuciscus idus	Ide	Ide	26	0	0	0	Cyprinidae	indifferent	3	V	NL
Leuciscus leuciscus	Common dace	Dace	230	506	246	260	Cyprinidae	indifferent	*	V	NL
Lota lota	Burbot	Burb	235	2	2	0	Lotidae	indifferent	V	2	NL
Misgurnus anguillicaudatus	Pond loach	Pondl	0	2	2	0	Cobitidae	limnophil	◊	NL	NL
Oncorhynchus mykiss	Rainbow trout	Raintr	110	23	14	9	Salmonidae	rheophil	◊	NL	NL
Perca fluviatilis	European perch	Perch	89	76	29	47	Percidae	indifferent	*	NL	NL
Phoxinus phoxinus	Eurasian minnow	Minnow	28	6	0	6	Cyprinidae	indifferent	*	3	NL
Pseudorasbora parva	Stone moroko	Stomo	4	44	43	1	Cyprinidae	indifferent	◊	NL	NL
Rhodeus amarus	European bitterling	Bitter	5	233	0	233	Cyprinidae	limnophil	*	2	Annex II
Romanogobio vladykovi	Gudgeon	Wgudge	15	0	0	0	Cyprinidae	rheophil	2	2	Annex II
Rutilus rutilus	Roach	Roach	267	526	44	482	Cyprinidae	indifferent	*	NL	NL
Salmo trutta fario	Brown trout	Browntr	331	77	16	61	Salmonidae	rheophil	*	V	NL
Salvelinus fontinalis	Brook trout	Brooktr	4	1	1	0	Salmonidae	rheophil	◊	NL	NL
Sander lucioperca	Pike-pearch	Pikepe	12	1	0	1	Percidae	indifferent	*	NL	NL
Scardinius erythrophthalmus	Rudd	Rudd	4	2	1	1	Cyprinidae	limnophil	*	NL	NL
Silurus glanis	Wels catfish	Wels	3	0	0	0	Siluridae	indifferent	2	V	NL
Squalius cephalus	Chub	Chub	837	3213	1235	1978	Cyprinidae	indifferent	*	NL	NL
Thymallus thymallus	Grayling	Grayl	238	562	149	413	Salmonidae	rheophil	2	2	Annex V
Tinca tinca	Tench	Tench	1	29	6	23	Cyprinidae	limnophil	*	NL	NL

* = currently not threatened, ◊ = classification not possible.

Fish community composition in the fish passes based on pooled data over all sampling time points differed significantly from the River Inn (Figure 4, ANOSIM, R = 0.48, $p < 0.001$). According to SIMPER analysis, these differences were mainly attributed to the higher abundance of *C. gobio*, *S. cephalus*, *G. aculeatus*, *T. thymallus*, and Petromyzontidae in the fish passes and higher abundance of *A. alburnus* in the main river (Table 5). Species richness in the River Inn was higher (40 species) than in the fish passes with six more species being caught. These were mainly ubiquitous species except for the Danube-endemic rheophilic specialist *Romanogobio vladykovi* Fang. Three additional species (*Lepomis gibbosus* L., *Misgurnus bipartitus* Dybowski, and *Leucaspius delineates* Heckel) were exclusively caught in the fish passes (Table 6).

The community composition of the FP Gars differed significantly from the FP Stammham; however, the R-value was very low for this comparison (ANOSIM, R = 0.07, $p < 0.001$). According to SIMPER, the same set of species was identified as for the comparison Inn and FP (Table 5), with *C. gobio* being 3-fold more abundant in Gars and *S. cephalus*, *G. aculeatus*, *T. thymallus*, and Petromyzontidae being more abundant in Stammham. Throughout the year, fish community composition in FP changed significantly (ANOSIM, R = 0.058, $p < 0.001$) between spring (March and May), summer (June and August), and late fall (October and December) (Figure 4, Table 5). For example, SIMPER detected that species, such as *C. gobio*, increased in abundance from spring to late fall, whilst *S. cephalus*, *G. aculeatus*, and *C. nasus* reached their abundance peak in summer. *T. thymallus* was also detected with highest densities in summer, but, in contrast to the other species, it was still present in high abundances in the FP during late fall.

Fluvial habitats of the fish passes differed significantly from ponds in community composition (Figure 4, ANOSIM, R = 0.631, $p < 0.001$). BEST analysis detected macrophyte coverage, gravel, boulders, temperature and current speed at the surface as variables best fitting the ordination of abundance data in the nMDS ($R^2 = 0.74$, Figure 4). There was a higher proportion of macrophytes and a higher water temperature in ponds, and more gravel, boulders and higher current speed in fluvial habitats. According to SIMPER, differences in fish community structure among habitat types were mainly attributed to higher abundances of *T. thymallus* (56-fold), *C. gobio* (40-fold), *C. nasus* (1.9-fold) in fluvial habitats, and *G. aculeatus* (22-fold) and *S. cephalus* (12-fold) in ponds (Table 5). Five stagnophilic or indifferent species, such as *L. gibbosus*, *Scardinius erythrophthalmus* L., *M. bipartitus*, *Cyprinus carpio* L., and *Blicca bjoerkna* L., were exclusively detected in ponds (overall number of species here 26), whilst 6 mostly rheophilic species (e.g., *Salvelinus fontinalis* Mitchill, *Gobio gobio* L., *O. mykiss*, *H. Hucho*) were exclusively detected in fluvial habitats (28 species) of the FP (Figure 7, Table 6). *C. gobio* (99% individuals), *S. trutta* (99%), *T. thymallus* (99%), *B. barbus* (95%), and Petromyzontidae (97%) were almost exclusively detected in the fluvial habitats, and *R. amarus*, as well as *Pseudorasbora parva* Temmink & Schlegel, almost exclusively in ponds (Figure 7, Table 6).

However, it has to be noted that the abundance of species in fluvial habitats or ponds was strongly governed by seasonal effects (Figure 5). This was particularly true for species that are known to switch habitats during different stages of their life cycle, such as *C. nasus*. This species was very abundant in ponds during summer and disappeared almost entirely from this habitat in late fall (Figures 5 and 6). In contrast, other species, like *S. cephalus*, used ponds and fluvial habitats equally throughout the year in almost all size classes (Figure 6), whilst *R. amarus* and *P. parva* only used ponds comprising a population structure, including all size classes. In contrast, all size classes of the reophilic species *T. thymallus* were exclusively found in fluvial habitats. LM detected that species richness in the ponds was significantly influenced by the factors macrophyte coverage ($p < 0.05$), deadwood coverage ($p < 0.01$) and water depth ($p < 0.05$). For all detections of significances, the relationship between the variable and the response species richness was not linear with highest species diversity for macrophyte coverage at 75%, deadwood coverage between 5% and 10%, and water depth about 0.5 m to 1.0 m.

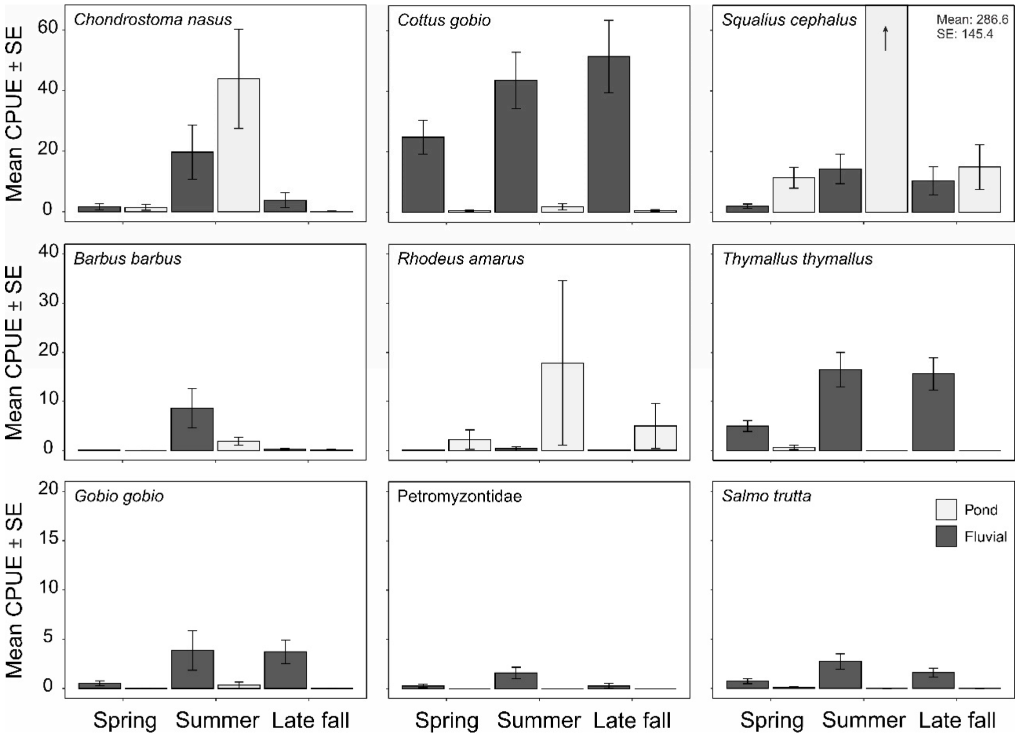

Figure 5. Seasonal distribution of the mean catch per unit effort ± standard error (CPUE ± SE) for selected target species of conservation. Different shades of grey indicate the habitat types ´pond´ (light grey) and ´fluvial habitat´ (dark grey). Outlier is marked with an arrow. Note the different scaling of the y-axis.

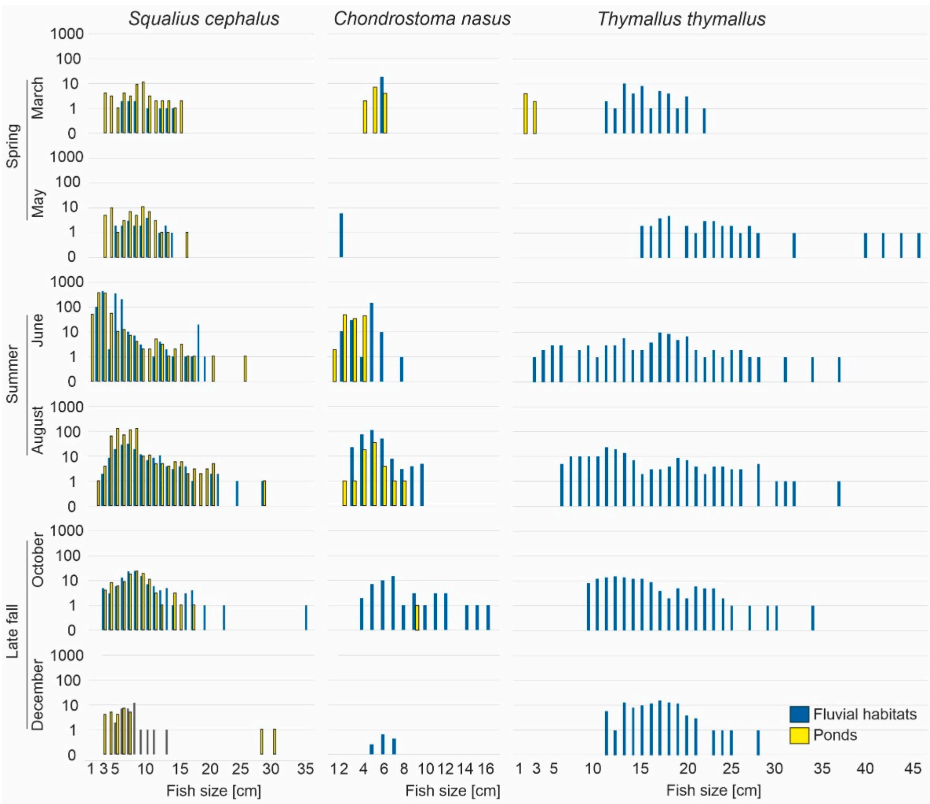

Figure 6. Length-frequency-distribution of *Squalius cephalus*, the most persistent fish species, as well as two other species with high conservation and indicator value, *Thymallus thymallus* and *Chondrostoma nasus*, in fluvial habitats (blue bars) and ponds (yellow bars), for the different sampling months between March and December and the seasons spring, summer, and late fall. Bars represent the sum of caught individuals.

4. Discussion

The findings of this study confirm the positive contribution of diverse habitats within constructed fish passes to the fish diversity of the River Inn. Fish diversity within the fish passes (33 species) largely resembled the species inventory of the River Inn (36 species), except for some rare species, such as *R. vladykovi*, that also occur at low densities in the main river [30]. Still, there were major differences in abundances of species between the fish passes and the main river.

As demonstrated herein, nature- like fish passes of high habitat diversity, comprising both fluvial habitats and stagnant waters, can at least partially contribute to the restoration of the formerly present habitat mosaic in this alpine river. In such large degraded alpine systems as the River Inn, the restoration of river dynamic processes, which govern high habitat and species diversity, is almost impossible due to the many restrictions in densely populated areas. From a fish conservation point of view, this makes near-natural watercourses that can at least partially fulfil these functions most valuable.

As expected, fluvial habitats within the fish passes comprised a rheophilic-dominated fish community, whilst ponds were largely dominated by stagnophilic fish species, or by species with indifferent current preferences. Consequently, both habitats contributed to a high species diversity in that system. However, it has to be considered that the fish community sampling in these small structures within a fish pass is likely more effective than in the larger main stem [46], potentially resulting in a bias towards an underestimation of species richness in the River Inn. This is also in compliance with the findings from Mollenhauer et al. [47], who demonstrated that fish detection probability can be affected by water depth and turbidity.

The populations of species, such as *T. thymallus*, *B. barbus*, and *C. nasus*, are under pressure in almost all rivers across their distribution range, particularly in the densest populated areas of central Europe, with their names on national and international red lists alike [43]. This makes them prominent target species for conservation. The fact that *T. thymallus* was detected in all size classes and that *C. nasus* and *B. barbus* were present in their most sensitive small size classes indicate that fluvial habitats and ponds in nature-like fish passes can provide important juvenile habitats, which are scarce in the main river. This should encourage river managers to follow the pathway of creating additional fluvial habitats and small ponds adjacent to the heavily modified and exploited main channel of rivers such as the Inn. The presence of early life stages of those target species and their seasonal habitat use, as detected herein for *C. nasus*, indicates that, besides habitat quality, connectivity between the source and all other habitats relevant for subsequent life stages is mandatory. A high degree of connectivity is particularly crucial when species have to change habitats for spawning or during larval drift. Thereby, it is crucial to match the timing of, e.g., spawning season [48,49] or emergence, with the accessibility of those life stage specific habitats. This is particularly important if species during their ontogeny change food sources, which happens usually simultaneously with a shift in habitat requirements. Such a situation is typical for *C. nasus* [50,51], which obviously moved seasonally between Inn, fluvial habitats in the fish passes and the ponds in our study. Other species may follow their food sources into the habitats, such as the apex predator *H. hucho* [52], or use the fish pass for spawning (*T. thymallus*), as previously proposed by Nagel et al. [53].

Ponds contributed to fish diversity by providing habitat for additional species, which prefer stagnant water conditions, such as *Tinca tinca* L., *S. erythrophthalmus*, the strictly protected *R. amarus* [43,44], or the invasive *P. parva* [54], and *M. bipartitus* [55]. Whilst the presence of additional species, such as *R. amarus*, can be accomplishable, the occurrence of *M. bipartitus* is not always desired since it is known to be an invasive species potentially replacing the indigenous *Misgurnus fossilis* L. [55,56]. In addition to the contribution to the overall diversity of the FP that was highest during the summer months, ponds provided habitat for species of high conservation value which has previously received little attention. This peak in diversity during summer can likely be attributed to higher structural density caused by macrophytes and bank vegetation, as well as more available habitat area, due to higher water levels, particularly in the ponds of fish pass Gars, where, during summer, the e-flow regime is applied. Besides the small life stages of the rheophilic *C. nasus*, the stagnophilic *R. amarus* [45] had peak densities in these ponds during summer. Usually, in braided high-energy rivers, like the River Inn, its distribution range is restricted to backwaters and small floodplain ponds [57], which all underlie strong river dynamic processes of habitat change [58–60]. In the historically (early 1960s) highly altered River Inn, the remaining backwaters have meanwhile undergone a successional development peaking often in a terminal phase. Some of those backwaters shifted towards terrestrial habitats, and others are being used for recreational purposes, such as angling or bathing lakes. Due to the restricted river dynamic processes, which consistently would have created new backwaters and floodplain ponds, such habitats are today widely lacking. Therefore, the construction of such structures can be important. However, it has to be noted that also artificially created floodplain ponds undergo rapid successional changes, which need to be mitigated in order to preserve high species richness. Particularly macrophyte coverage increased rapidly in the rather shallow ponds since their construction, restricting habitat area for at least some species. This creates the need for a partial maintenance by clear-cutting when macrophyte coverage exceeds 75% of pond area on a regular basis.

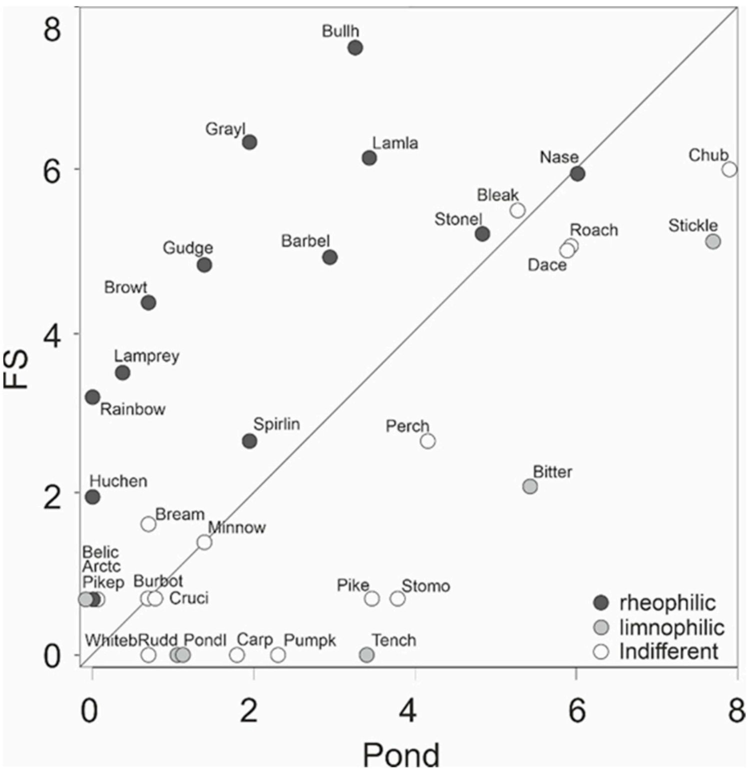

Figure 7. Scatterplot of pooled fish abundance data (based on Log(X + 1) transformed abundance data), distinguishing their primary occurrence in floodplain ponds and fluvial habitats (FS) of the fish passes Gars and Stammham. Shaded symbols indicate the different current preferences of species according to Reference [45]. For abbreviations of species, refer to Table 6.

The rich species inventory in the system must not obscure the fact that fish community composition in the highly degraded River Inn of today comprises a reduced set of riverine specialists that typically dominated the fish community in the past, originally comprising historically widespread and now undetected species, such as *Zingel streber* Siebold and *Zingel zingel* L. [30]. This underscores the finding that as good as the habitat quality of a fish pass might be, the species inventory largely depends on the source and if the source habitat is severely altered, an ecological integer fish community composition in restored areas or fish passes might be limited [27]. To date, it is not fully clear if the smaller size and discharge of a fish pass compared to the main river can still provide a suitable compensatory habitat, since it has not yet been proven if all riverine species can benefit from fish passes as permanent habitat or at least habitat for certain life stages. For example, *B. barbus*, *Z. zingel*, and *Z. streber* are known to prefer the strong flowing main current of rivers in their adult stages and only use riverbanks during early ontogeny [61,62]. In our study, *B. barbus* was present in the fish passes but only in small size-classes. *Z. zingel* and *Z. streber* could not be detected at all due to the earlier mentioned reasons for habitat degradation in the main river. If these rare species will respond positively to the installation of nature-like fish passes, they can only be determined on a long-term basis because it needs some time for them to reach a critical population size that can be detected reliably by fish population assessments (e.g., [18,63]).

5. Conclusions

This study underlines the important habitat role of fish passes, which can largely contribute to overall fish diversity in rivers, comprising typically rheophilic species in fluvial habitats and stagnophilic species in stagnant waters, such as the created floodplain ponds. Both, rheophilc and stagnophilic, species of high conservation value, such as, e.g., *T. thymallus*, *C. nasus*, *B. barbus*, *H. hucho*, and *R. amarus*, are rare in the main river. Some of those species, e.g., *T. thymallus*, even occurred in large numbers across all size classes in the fish passes, suggesting that fish passes can host a complete population of this species. Other species, which continue declining in the main river, were present in high numbers of small life stages in fluvial habitats, as well as ponds, indicating potential functionality of both habitat types as juvenile habitats. Provided regular maintenance to keep the small floodplain ponds open, high species diversity can be achieved in combination with fish passes.

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Informed Consent Statement: Not applicable.

Data Availability Statement: Data are available from the corresponding author upon reasonable request.

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Conflicts of Interest: The authors declare no conflict of interest.

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