



Seasonal and spatial variability of abiotic habitat conditions and fish community composition at tributary confluences in an alpine river network

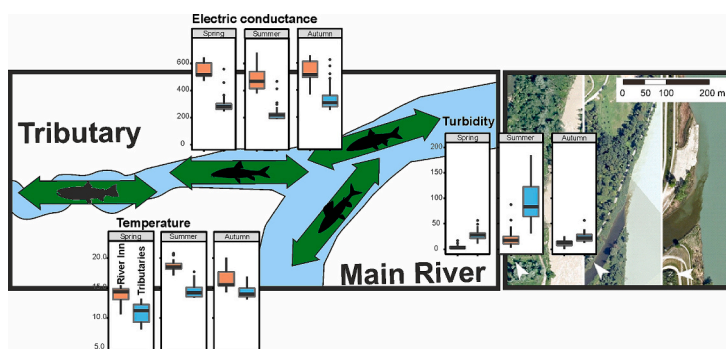
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HIGHLIGHTS

- Connectivity and habitat diversity are key drivers of alpine river fish diversity
- Strong abiotic differences between tributaries and main stem were detected
- Fish community distribution reflected differences in habitat conditions
- Completion of life cycles of target species depend on river network connectivity
- Conservation needs to focus on both connectivity and habitat integrity

GRAPHICAL ABSTRACT



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ABSTRACT

Habitat quality, diversity and connectivity are key variables governing biodiversity patterns, but existing conservation and restoration strategies hardly consider their important interlinkages in river networks. In order to develop best practice river network restoration strategies, fish diversity and the spatio-temporal occurrence of target species of conservation in relation to abiotic habitat conditions were assessed in the alpine River Inn network comprising main stem, tributaries and confluences. Fish sampling was carried out by standardized electrofishing during spring, summer and autumn. In addition, important physicochemical variables were collected to interlink abiotic habitat characteristics with the fish community patterns. Differences in the physicochemical habitat conditions between the main stem and the tributaries were particularly evident in turbidity, electrical conductivity and temperature. This was also reflected in seasonal distribution patterns of fishes which differed between tributaries and main stem, even at small spatial scales. Cyprinids such as common nase and barbel were generally found more frequently in the tributaries where they successfully reproduced. In contrast, cold-water adapted species such as grayling, brown trout and European bullhead were detected much more frequently in the River Inn main stem, mostly as juveniles. Across species, distribution patterns were strongly driven by spawning migration into tributaries in spring and back-drift of larvae and juveniles to the main stem between summer and autumn. Consequently, the diverse habitats of interconnected river networks are key in sustaining the life cycles of diverse and healthy fish populations, and they can provide refuge areas increasing the resilience of such systems. The findings are directly relevant for restoration projects in large alpine rivers to

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address two primary aspects: Firstly, to create heterogeneous habitat structures that reflect the diverse life cycle requirements of target species, and secondly, to improve multidimensional river network connectivity.

1. Introduction

Rivers are among the most threatened ecosystems on earth (Gleick, 2003; Pimm et al., 2001), which is reflected in the high degree of endangerment of many flow-dependent freshwater organisms (Jenkins, 2003; Ricciardi and Rasmussen, 1999). The threats are diverse and range from hydromorphological changes to river courses, the introduction of toxic substances and invasive species, overexploitation of freshwater resources, to climate change-related effects (Gorenz et al., 2025; Reid et al., 2019).

In particular, the hydromorphological alteration of river systems and the resulting disconnection of the main stems from their tributaries often impair the longitudinal and lateral connectivity of aquatic habitats, which is a key driver for biodiversity (Aarts et al., 2004; Pander and Geist, 2018; Ramler and Keckeis, 2019) and is often irreversible (Auerswald et al., 2019). This is particularly true for alpine rivers, as in their natural states, they typically have an extensive, widely branched riverbed and interconnected river network with its tributaries (Pander et al., 2021; Schiemer et al., 2020; Tockner et al., 2003). Other characteristics of alpine rivers include strong fluctuation in discharge, periods of high suspended sediment loads and comparatively cool temperatures during summer as a result of snow- and glacier-melt (Pander et al., 2022).

In Central Europe, alpine rivers are home to a number of specialized cold-water adapted fish species of high conservation priority such as the European bullhead (*Cottus gobio* L. 1758), brown trout (*Salmo trutta* L. 1758), huchen (*Hucho hucho* L. 1758) and grayling (*Thymallus thymallus* L. 1758). All of these are nowadays moderately to severely threatened in their populations (Mueller et al., 2018). In addition to the threat posed by morphological and structural habitat loss, these species are also increasingly threatened by climate change and the related estimated increase in water temperatures (Hari et al., 2006; Wild et al., 2024), which according to many forecasts will pose the greatest threat to native freshwater biodiversity in the coming decades (Markovic et al., 2014; Reid et al., 2019). Climate change does not solely affect rivers through rising water temperatures, which can reach a lethal threshold for sensitive species (summarised for salmonids in Smialek et al., 2021), but also through massive disruption of functional processes (Palmer and Ruhí, 2019) particularly in alpine regions. These include the shifting of discharge hydrographs of meltwater and glacier runoff dominated systems (Bard et al., 2015; Braun et al., 2017), the disruption of inter- and intraspecific synchronized migrations and spawning processes (Sternecker et al., 2014), the influence on food webs (Augustyniak et al., 2025) and severe restrictions in the temporal and spatial availability of fish habitats (Reid et al., 2019).

To mitigate such effects through conservation and restoration strategies, a comprehensive knowledge of the functional principles of alpine river networks and their biota is essential (Smialek et al., 2019), making integrative strategies of freshwater conservation and restoration and thus the consideration of entire river network structures a necessity (Geist, 2011). This especially applies to interactions of large rivers with their tributaries, and especially to alpine river systems where pronounced differences in habitat conditions can occur between smaller tributaries and main stem. For example, the River Inn represents an alpine river which is characterized by low discharges and a clear water phase in winter and, due to its glacier/ice melt runoff, high discharges of turbid and cold water during the summer. In contrast, most of its tributaries in the German section originate in the alpine foothills comprising clear and warmer water throughout the year. The interrelationship between habitat availability and aquatic diversity of large rivers and their tributaries is subject of many studies for lowland rivers (summarised in

Rice et al., 2008; Czeplédi et al., 2016), however, investigations that highlight the contribution of tributaries and their confluences to fish diversity in alpine rivers are scarce (but see Ward, 1994 for general ecology in high energy rivers, Nunn et al., 2010 for one tributary in a lowland river, and Clay et al., 2015 for macroinvertebrates in alpine rivers). The existence of (spawning) migrations of fishes from larger systems into tributaries is a general knowledge, available since centuries for natural or near natural rivers. However, little is known about these processes in highly modified rivers, particularly alpine streams where abiotic conditions may differ strongly in spatial proximity between summer-cold glacier-fed main stems and warmer tributaries.

The aim of the present study was to comprehensively investigate importance of the biotic and abiotic interaction of a glacier-induced, summer-cold alpine river system with its warmer tributaries using the Bavarian River Inn network as an example. For this purpose, fish community composition in relation to abiotic habitat conditions were studied across five important tributaries and the adjacent areas in the main stem River Inn in spring, summer and autumn.

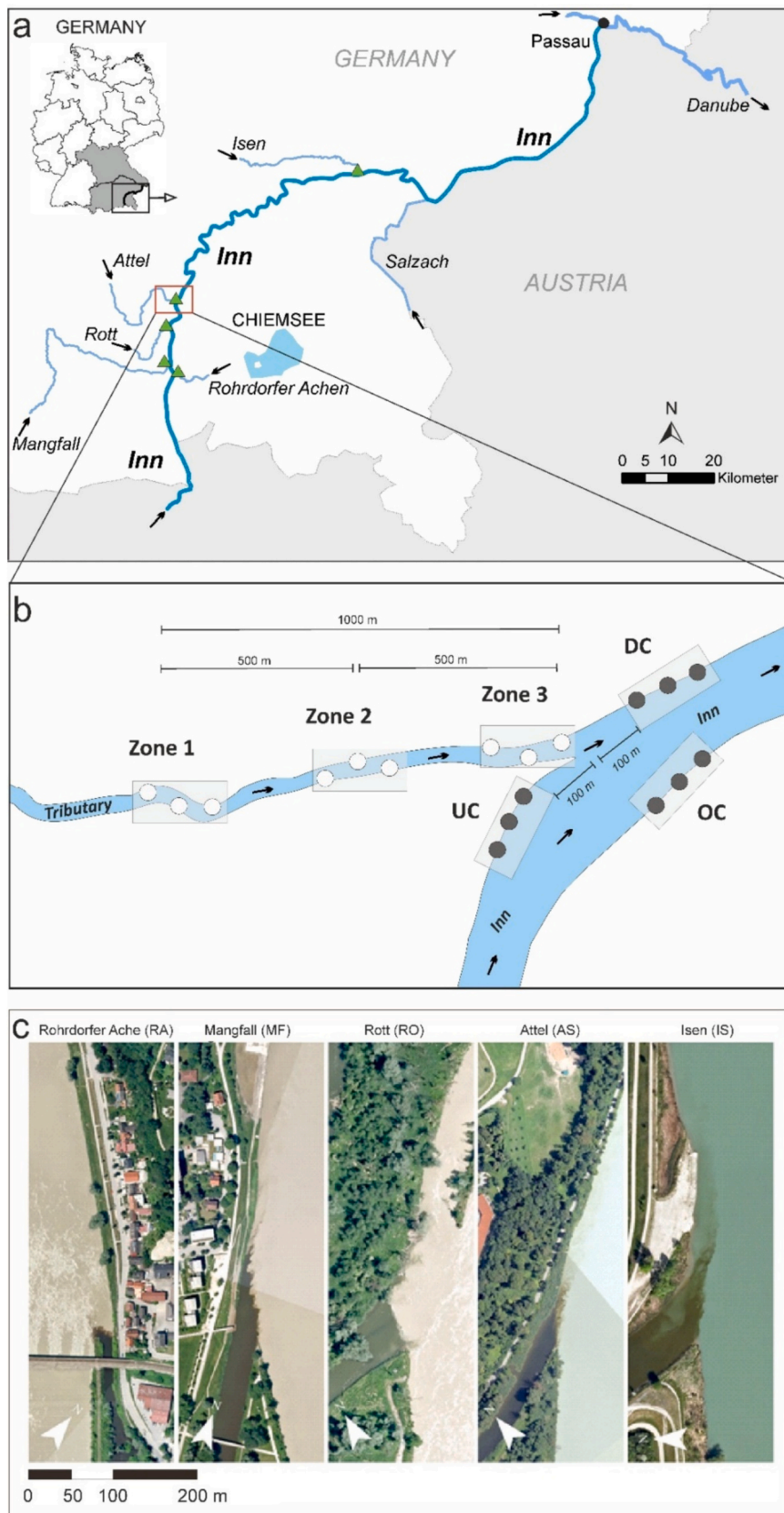
Specifically, the following two hypotheses were tested:

- I. The abiotic habitat characteristics, such as water temperature, turbidity or conductivity, differ significantly between tributaries and the main stem.
- II. These differences in abiotic habitat characteristics are reflected in the spatio-temporal composition of the fish species communities and fish sizes, with the rheophilic cyprinids barbel and common nase occurring more frequently in the comparably warm tributaries, while the cold water adapted salmonids grayling and brown trout increasingly use the colder River Inn as habitat.

2. Material and methods

2.1. Study design

Five important tributaries of the River Inn, the Mangfall (MF), Rohrdorfer Achen (RA), Rott (RO), Attel (AT), and Isen (IS) were selected for a representative characterization of the interaction with the main stem River Inn (Fig. 1a). To achieve a representative characterization of the confluences of our study rivers and the adjacent sites at the main stem River Inn, three zones were defined in each tributary as well as in the areas in spatial proximity to the mouth of the tributary in the Inn itself. The selected zones in the tributaries were the areas directly upstream of the mouth (zone 3) and further upstream ~500 m (zone 2) and ~1000 m (zone 1; Fig. 1b) and do not represent the full river network. This is mainly attributed to the many barriers in the tributaries that still hinder free fish movement and migration further upstream, but will likely be removed in the future according to the Bavarian river network restoration plan. In the main stem of the River Inn, the area downstream (DC) and upstream (UC) of the confluence of the tributary was investigated, as well as the bank opposite the confluence (OC) (Fig. 1b). The zones UC and OC served as a reference for areas not or less affected by the tributaries. To achieve a statistically robust design, each zone was sampled with three replicates of 30 m long sampling stretches at each season (Pander and Geist, 2010). 18 Sampling stretches were assessed for each tributary and season (spring, summer and autumn 2021), nine of them in the tributary and nine in the main stem of the River Inn, resulting in 270 sampled 30 m stretches in total (total fished river length 8.1 km).



(caption on next page)

Fig. 1. Map and magnification of the study area with the River Inn and the major tributaries (a), the zonation at the confluence with location of sampling stretches (b) and aerial photographs of each confluence (c). Please note the clear visual differences in turbidity between the main stem River Inn and tributaries resulting from the suspended load the River Inn carries due to its glacier-induced discharge during the summer. Green triangles indicate the assessed tributaries (a), Zone 3 = in close proximity upstream of the confluence in the tributary, Zone 2 = 500 m upstream of the confluence in the tributary, Zone 1 = 1000 m upstream of the confluence in the tributary (b). White dots indicate the sampling scheme within tributaries and grey dots indicate the principle of sampling stretch location in the main stem River Inn (b). DC = sampling stretches in the River Inn directly downstream of the confluence of the tributary, UC = sampling stretches in the River Inn directly upstream of the confluence of the tributary, OC = sampling stretches in the River Inn on the opposite riverbank of the confluence of the tributary (b). Black arrows indicate flow direction (a, b).

2.2. Study area

This study was conducted at the River Inn, a formerly braided river (www.geoportal.bayern.de/bayernatlas, last accessed 26 June 2025). Nowadays, this river is a structurally modified and straightened single channel with embankments for flood protection (Pander et al., 2021) that is intensively used for hydropower generation (21 run-of-river power plants on 200 km river, <https://www.innkraft-bayern.de/wasserkraftwerke-am-inn>, last accessed 18 June 2025). Despite its intense morphological alterations, the River Inn comprises a hydrograph characterized by low discharges and a clear water phase in winter and, due to its glacier/ice melt runoff, high discharges of turbid and cold water during summer. The five tributaries AT, IS, MF, RA, and RO (Fig. 1c, Table 1) are distributed along a 94 km stretch in the German section of the Inn. All tributaries are subject of river straightening with many transverse structures, often only a few kilometres upstream of the mouth. These structures which are classified as not passable for fish according to the water structure mapping of Bavaria's watercourses are being removed or modified within the next years. However, all sampling stretches of the respective tributaries and the Inn are freely passable and there are no weirs or sills between our sampling stretches and the main river that hinder free fish movement. The morphological status of all watercourses is predominantly classified as “heavily modified” (class 5) or “significantly modified” (class 4). Only four study stretches in the RA are categorized as “moderately modified” (class 3). Details of each of the study stretches are presented in Table 1.

2.3. Abiotic habitat characteristics

A series of physicochemical habitat variables of the open water crucial for fish habitat quality were measured according to Pander and Geist (2010), with measurements taken in the middle and at the upper and lower end of each 30 m sampling stretch.

The measurements to characterize physicochemistry,

Table 1

Characterization of the main stem Inn and the assessed tributaries. Rosenheim = location of water gauge in the River Inn upstream of the study area. Eschelbach = location of water gauge in the River Inn downstream of the study area. Fish passability = measured distance between confluence and the first not free fish passable obstacle in the tributary. Please note that fish passability in the River Inn is currently restricted in the study area at the hydropower plant Rosenheim. Distances given for fish passability in the River Inn are distances to the next hydropower plants located downstream (Feldkirchen = 14.4 km) and upstream (Nussdorf = 11.2 km).

Inn and tributaries	Length [km]	Mean discharge MQ [m ³ s ⁻¹]	Catchment [km ²]	Fish passability [km]
River Inn	518	316 (Rosenheim) 366 (Eschelbach)	26,072	14.4/11.2
Attel (AT)	40.3	3.9	331	1.9
Isen (IS)	81.0	5.6	586	3.7
Mangfall (MF)	58.0	17.6	1099	4.3
Rohrdorfer Achen (RA)	18.6	k. A.	171	9.2
Rott (RO)	25.7	k. A.	109	6.6

hydromorphology and structural habitat properties took place immediately after the fish sampling and were carried out between 14:00 and 16:00 on each sampling day.

Water temperature (T) [°C], oxygen concentration (O₂) [mg/L], electrical conductivity (EC) [µS/cm], pH value (pH) and turbidity (Turb) [NTU] were measured, using a WTW® Multimeter 340i and a WTW® Turb 355 IR (WTW GmbH, Weilheim, Germany). For hydromorphological characterization, the depth (D) [m] and current (CS) [m/s] were recorded using an Ott MFpro (Ott Hydromet GmbH, Kempten, Germany). For D, three values were recorded analogous to the physicochemical measurements, and the current was measured at the same three measuring points ten centimeters below the surface (CSS) and ten centimeters above the river bed (CSB). The structural habitat parameters investigated included the degree of shading (CC, expressed in canopy cover of the bank habitats) [%], the proportion of dead wood (DW) [%], and the macrophyte cover (M) [%] in the sampling stretches (Pander et al., 2024a).

Since spot measurements of T with handheld devices may not give an accurate picture over time, T as an important driver of fish community composition (Pander et al., 2024b) was recorded using data loggers (EL-USB-1, Lascar electronics, Wiltshire, UK) that were exposed in the sampling stretches. Three loggers were deployed in the River Inn main stem and two in each tributary in the section 1000 m upstream of the confluence (zone 1). The recordings were made at hourly intervals from 22 April 2021 to 22 September 2021, i.e. during the entire study period. Due to several flood events and the resulting relocation of substrate and deadwood in the RA, the data loggers in this tributary could not be recovered.

2.4. Fish sampling

Fish sampling was carried out by standardized electrofishing during the day between 10:00 and 15:00 along the river banks using a power unit with 8 kW output (EFKO FEG 8000) and one hand anode (Pander and Geist, 2010). Fishing was carried out in voltage level II with an electrical current of 10 to 17 A and approx. 400 V. Fish were sampled by boat, with wading being used only in very shallow sections of the tributaries. In addition to the boat and anode guide, the team consisted of another person to net the fish. Sampling was carried out at a slow and steady speed against the direction of flow and at a distance of approx. 2 m from the shoreline. Catch efficiency of electrofishing in deep sections (greater than 1.5 m water depth) of large open waters is generally limited and potentially creates a bias towards the catch of smaller specimens. We thus fished the River Inn towards the shoreline, applying the most representative sampling approach identified in a previous method comparison of different fish sampling approaches in the same river (Mueller et al., 2017). Consequently, data on the fish community composition may rather represent fish communities along the shorelines of this large river than the overall fish community composition. Fish were identified to species level and their individual total lengths were measured to the nearest cm. All individuals were carefully released immediately after measurement with the exception of a few juvenile fish and fish larvae that could not be exactly determined to species level in the field. These individuals were preserved in EtOH solution (96%) and identified in the laboratory with the aid of a binocular using the identification keys listed in Pander et al. (2017).

2.5. Statistical analysis

To assess hypothesis I, Principal Components Analysis (PCA) based on the Euclidean distance measure were used to investigate the differences between the main stem of the Inn and its tributaries on the basis of abiotic habitat variables. PCA enables the spatial representation of the individual study stretches and an overlay of the measured variables, represented as vector arrows, which illustrates the strength of the correlation with the arrangement of the studied water bodies in the ordination diagram. The environmental variables were standardized using the normalization function in PRIMER for Environmental Variables and visually checked for co-linearity. The variability of the abiotic variables depending on the habitat type (Inn main stem or tributary) and seasonal differences were visualized using boxplots created with the ‘ggplot2’ package in R (<https://www.R-project.org/>). (last accessed 28 November 2025).

To assess the composition of the fish community in the respective study stretches (hypothesis II), a Bray-Curtis Similarity Resemblance Matrix was created based on the differences in fish abundance data (standardized as catch per unit effort CPUE) between survey dates and studied stretches and visualized using non-metric multidimensional scaling (nMDS Clarke et al., 2014). To account for zero values if no fish were caught in individual stretches, the program can calculate dummy variables, as recommended by Clarke et al. (2014) as a standard procedure in PRIMER. A bootstrap nMDS was calculated based on the same Bray-Curtis similarity-resemblance matrix to visualize the differences in the fish species community between the studied zones. The ANOSIM (Analysis of Similarities) statistics was calculated to test for significant differences in fish species community composition and abiotic habitat conditions between habitat types, survey time points and surveyed zones. SIMPER (Similarity Percentages Analysis) analysis was used to identify abiotic variables and fish species that contribute most to the similarity between sampling dates and habitats (Pander et al., 2022). The “shade plot” function in PRIMER was used to display the spatio-

temporal occurrence of the individual fish species in a heatmap. All multivariate analyses were computed with PRIMER (Plymouth Routines in Multivariate Ecological Research, version idR v7, Auckland, New Zealand).

The univariate distribution of fish density (CPUE) and fish species, as well as the distribution of fish lengths of selected target species were visualized using raincloud plots and the package “ggplot2” in R (version 4.3.1; R Core Team, 2023). Significant differences at $p \leq 0.05$ were accepted for all statistical analyses.

3. Results

3.1. Habitat characteristics of main stem Inn and tributaries

The PCA analysis of the abiotic habitat parameters (explained variability PC1 = 18.8% and PC2 = 16.1%) revealed a clear difference in the abiotic habitat features between the main stem of the Inn and the tributaries (Fig. 2, ANOSIM: Global $R = 0.51$; $p < 0.001$). However, it must be noted that a large portion of the variance remains unexplained, likely due to other unmeasured variables or complex interactions.

As indicated by the arrangement of the sampling points along the PC1 axis in Fig. 2, differences in the physicochemical habitat conditions between the River Inn and the tributaries were particularly evident in turbidity, electrical conductivity and temperature. Mean Turb values of 49.8 NTU were measured in the River Inn, while only 12.0 NTU were documented in the tributaries. The mean EC in the River Inn was only about half as high (288 $\mu\text{S}/\text{cm}$) as in the tributaries (528 $\mu\text{S}/\text{cm}$). In the River Inn, the average T (individual measurements on the days of sampling) during the study period was 13.2 $^{\circ}\text{C}$, whereas it was 3 $^{\circ}\text{C}$ higher in the tributaries, at 16.2 $^{\circ}\text{C}$ (Fig. 3). The means of structural habitat features were highly similar between the River Inn and its tributaries in terms of the CC (Inn: 9%; tributaries 12%), and the proportion of DW (Inn: 6%; tributaries 8%). However, differences in the presence of M between the River Inn and its tributaries were recorded, as these were

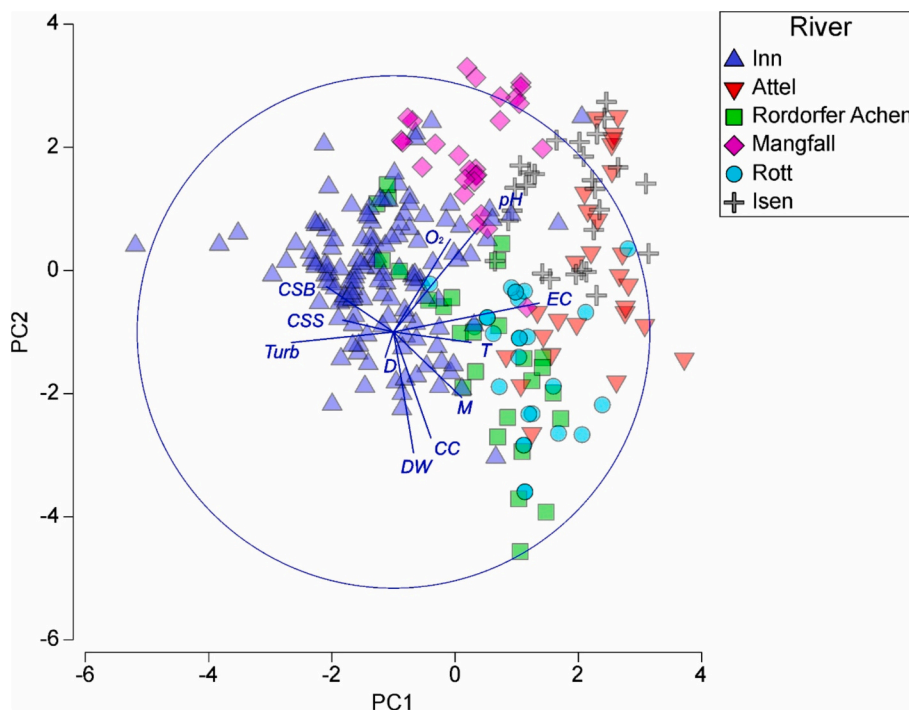


Fig. 2. PCA - Principal Component Analysis (PCA) of abiotic habitat variables of the River Inn and all assessed tributaries (explained variability PC1 = 18.8% and PC2 = 16.1%). The length of the vectors corresponds to the strength of the correlation (blue circle = 100%). EC = electric conductance standardized to 20 $^{\circ}\text{C}$ [$\mu\text{S cm}^{-1}$], pH = pH value, O₂ = oxygen concentration in milligrams per litre [mg L^{-1}], CSS = current speed 10 cm below surface in meters per second [m s^{-1}], CSB = current speed 10 cm above substratum in meters per second [m s^{-1}], T = temperature in degrees Celsius [$^{\circ}\text{C}$], Turb = turbidity as nephelometric turbidity unit [NTU], D = water depth [m]. CC = canopy cover in % coverage, DW = deadwood in % coverage, M = macrophytes in % coverage.

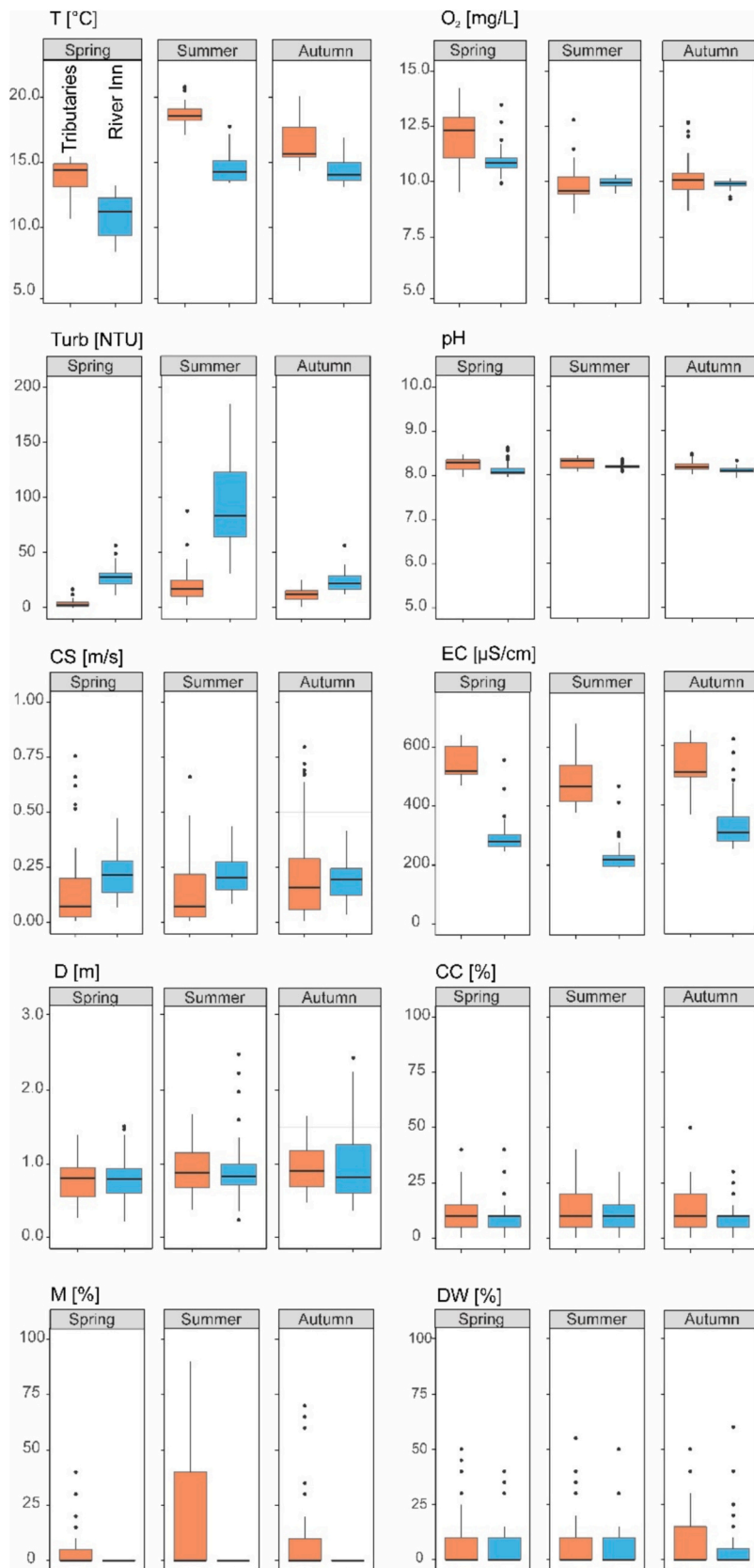


Fig. 3. Box-whisker-plot (25% quantile, median, 75% quantile, whisker: minimum and maximum values, circles represent outliers) of abiotic habitat variables of the main stem River Inn and the tributaries (results pooled for tributaries). Data points (n) per box = 135 (Current speed n = 270). EC = electric conductance standardized to 20 °C, pH = pH value, O₂ = dissolved oxygen, CS = current speed, T = temperature (point measurements during the electrofishing), Turb = turbidity, D = water depth. CC = canopy cover, DW = deadwood coverage, M = macrophytes coverage.

not documented at all in the River Inn, while in the tributaries they accounted for a mean of 11% habitat coverage (Fig. 3). However, there were also strong differences between the individual tributaries, as the occurrence of M was highest in the RA 31%, followed by the RO 15% and the AT 11%. No M were documented in the investigated sections of the MF and IS. The hydromorphological characteristics of mean D in the sampling stretches (River Inn: 0.9 m; tributaries: 0.9 m) and CS (v up = Inn: 0.0–1.3 m/s, tributaries: 0.0–1.5 m/s; v down = River Inn: 0.0–0.9 m/s, tributaries: 0.0–0.9 m/s) were very similar (Table 2). The evaluation of the permanent logger data shows that both the measured daily T maxima and the daily minima in the River Inn were distinctly lower than in the tributaries (Fig. Si1), which is particular evident for the IS that had highest T over the whole sampling period. The logger data revealed that the T profiles of the MF, RO and AT are very similar to each other.

A more detailed analysis according to the defined sampling stretches (zone 1 – zone 3 in the tributaries and DC, UC and OC in the River Inn) indicated that the water chemistry in the River Inn, below the confluence (zone DC), clearly differs from the reference sections above the confluence (UC) and on the opposite bank (OC) in terms of both higher mean T of about 1.1 °C and 37% higher mean EC values in DC. Comparing means of the section DC in the River Inn downstream of the confluence to the sampling stretches in the tributaries (Zones 1, 2 and 3), a by 2.3 °C higher mean temperature and 50% higher EC values in the zones of the tributaries were recorded (Table 2). This effect was attributable to the mixed water conditions and was also detectable up to 200 m downstream of the confluences. Mean values of Turb were 25% lower downstream of the confluences in DC than in the reference stretches in zones UC and OC, and no clear zonation could be determined for any variable between the study sections in the tributaries (zone 1 - zone 3).

3.2. General community composition - fish catches in the Inn and tributaries

A total of 23,352 individuals from 35 different fish species and one lamprey species were detected across all sampling stretches (Table Si2). This corresponds to a mean catch per unit effort (CPUE) of 86 fish per 30 m sampling stretch. The maximum number of individuals detected per sampling stretch was noticeably 1.6-fold higher in the tributaries (1221 individuals, mean CPUE = 123 fish per 30 m sampling stretch) than in the main stem Inn (755 individuals, mean CPUE = 50 fish). In the tributaries (Fig. 4), a five-fold higher individual density was evident between spring sampling (mean: 46, total: 389) and summer sampling (mean: 197, total: 1221). In comparison to the sampled shoreline habitats of the River Inn main stem, where an enormous increase in individual density can be seen between summer and fall (3.6-fold increase in individuals), the density in the tributaries dropped significantly from summer to fall (1.5-fold decrease of individuals) (Fig. 4).

Out of the 35 fish species, 11 belong to Leuciscidae (80% of all fish recorded), four to Salmonidae (including one species from the subfamily Thymallinae), four to Cyprinidae and three to the Percidae family. All other documented families (Acheilognathidae, Anguillidae, Centrarchidae, Cobitidae, Cottidae, Esocidae, Gasterosteidae, Lotidae, Nemacheilidae, Siluridae and Tincidae) were each represented by only one species. In addition, one species of the lamprey family Petromyzontidae was caught (Table Si2). According to Zauner and Eberstaller (1999), 18 of the caught fish species are classified according to their current preference as indifferent, eleven as rheophilic, six as limnophilic and one species can be classified as oligorheophilic. In general, the most frequently caught species were bleak (41%), common nase (18%), chub (8%), roach (5%) and European perch (4%), whilst only a few individuals of white bream, European catfish, asp, huchen, vimba bream, European eel and Prussian carp were caught (Table Si2).

Table 2
Abiotic characteristics of study rivers. EC = electric conductance standardized to 20 °C in microsiemens per centimetre [$\mu\text{S cm}^{-1}$], O₂ = oxygen concentration in milligrams per litre [mg L^{-1}], CSS = current speed 10 cm below surface in meters per second [m s^{-1}], CSB = current speed 10 cm above substratum in meters per second [m s^{-1}], T = temperature in degrees Celsius [°C], Turb = turbidity as nephelometric turbidity unit [NTU], D = water depth in centimeters [cm]. CC = canopy cover in % coverage, DW = deadwood in % coverage, M = macrophytes in % coverage.

		T	O ₂	EC	pH	Turb	D	CSS	CSB	CC	DW	M
Main Stem River Inn	Mean	13.9	10.3	352	8.2	41.3	0.82	0.28	0.15	7	8	0
	Min - Max	8.2–17.7	9.3–13.5	200–623	8.0–8.6	11.3–151.3	0.23–1.49	0.06–0.61	0.01–0.33	0–30	0–60	0–0
	Mean	12.8	10.2	257	8.1	55.6	0.66	0.26	0.17	9	5	0
	Min - Max	8.1–15.6	9.5–11.2	192–316	7.9–8.4	12.2–238.3	0.22–1.05	0.07–0.41	0.03–0.61	0–30	0–25	0–0
Tributaries	Mean	12.8	10.2	257	8.1	52.4	1.14	0.26	0.12	12	5	0
	Min - Max	8.1–15.1	9.2–11.7	190–320	8.0–8.4	13.0–156.7	0.30–2.49	0.08–0.46	0.01–0.31	5–40	0–30	0–0
	Mean	13.1	10.2	289	8.1	49.8	0.87	0.27	0.15	9	6	0
	Min - Max	8.1–17.7	9.2–13.5	190–623	7.9–8.6	11.3–238.3	0.22–2.49	0.06–0.61	0.01–0.61	0–40	0–60	0–0
Overall	Mean	16.0	10.7	534	8.3	9.4	0.86	0.29	0.19	15	12	11
	MIN - MAX	10.9–20.8	9.1–13.6	382–668	8.0–8.5	0.3–26.6	0.27–1.68	0.01–0.95	0.01–0.65	0–50	0–55	0–70
	Mean	16.0	10.6	532	8.2	11.8	0.90	0.28	0.10	10	6	19
Zone 2	MIN - MAX	10.9–20.8	8.6–13.8	382–669	8.0–8.5	0.4–87.6	0.46–1.60	0.01–0.76	0.00–0.62	0–30	0–50	0–90
	Mean	16.5	10.7	518	8.2	14.7	0.88	0.20	0.00	12	6	5
	MIN - MAX	10.6–20.1	8.7–14.2	368–679	8.1–8.4	0.1–57.0	0.42–1.42	0.01–1.03	0.01–0.57	0–50	0–40	0–80
Overall	Mean	16.2	10.7	528	8.2	12.0	0.88	0.22	0.14	12	8	12
	MIN - MAX	10.6–20.8	8.6–14.2	386–679	8.0–8.5	0.1–87.5	0.27–1.68	0.01–1.03	0.00–0.65	0–50	0–55	0–90

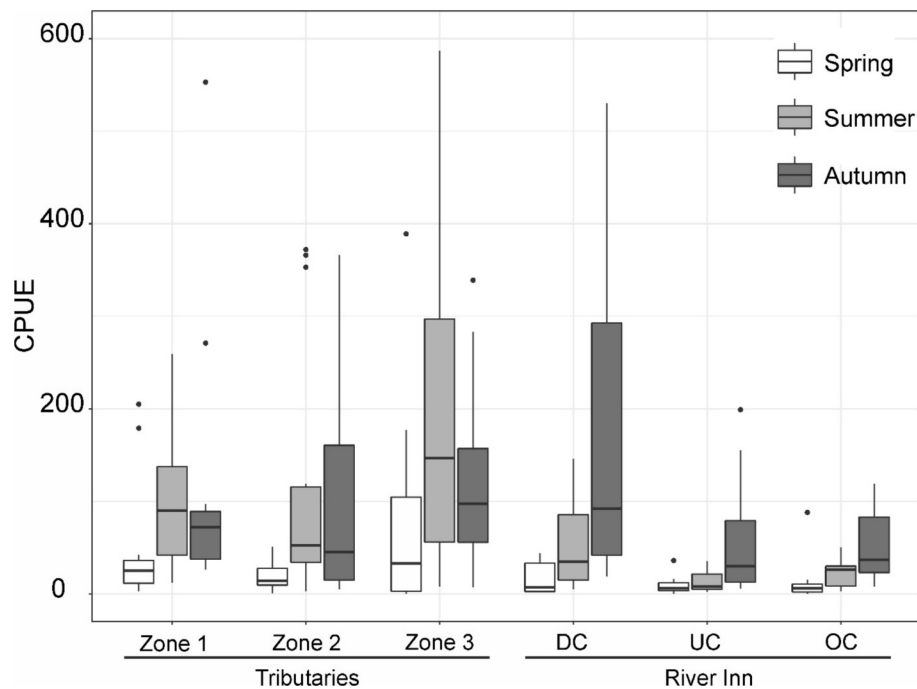


Fig. 4. Box-whisker-plot (25% quantile, median, 75% quantile, whisker: minimum and maximum values, outliers are indicated as black dots) of the seasonal fish density expressed as CPUE = catch per unit effort per 30 m sampling stretch, of the main stream of the River Inn and the tributaries (pooled data for all tributaries). Data points (N) per box = 45. OC = location at the opposite bank of the confluence of tributary and River Inn, UC = upstream of the confluence in the River Inn, DC = downstream of the confluence in the River Inn. Zone 3 = in close proximity upstream of the confluence in the tributary, Zone 2 = 500 m upstream of the confluence in the tributary, Zone 1 = 1000 m upstream of the confluence in the tributary.

3.3. Differences in species occurrence and taxonomic community composition between Inn and tributaries

3.3.1. General community composition

In general, the multivariate analysis revealed a great level of variability in the fish community compositions among the tributaries and the River Inn main stem (Fig. 5), with strong seasonal differences. They were strongest in the summer season as indicated by the pairwise comparisons of Inn and tributaries by ANOSIM (summer $R = 0.478$, spring $R = 0.127$ and fall $R = 0.128$, all $p < 0.001$, for detailed comparisons within rivers please see Table 3).

The family Leuciscidae was the most commonly detected both in the Inn (78%) and in the tributaries (81%). A comparison of the relative proportion of all Leuciscidae detected between the main stem Inn and the tributaries indicates that the majority of Leuciscidae (72%) were caught in the tributaries versus 28% in the River Inn, which is also reflected by the rheophilic target species common nase and barbel that were mainly recorded in tributaries (barbel = 76%, common nase = 85%). Fish species from the Salmonidae family (grayling, brown trout, rainbow trout, huchen) were caught to a share of 77% in the main stem of the River Inn and only to 23% in the tributaries. Regarding salmonids, it is noticeable that one tributary (15% of the total catch in MF) accounts for a large proportion of this family detected in these habitats. Representatives of the Percidae family (European perch, ruffe, pike-perch) were recorded in the tributaries to a share of 95%, whereas only 5% of all percids were documented in the Inn. A different picture emerges for the family Cottidae (only European bullhead) where 72% of the total records were in the Inn and only 28% in the tributaries. This is also true for representatives of Petromyzontidae where 86% were recorded in the Inn.

Across all survey dates and survey stretches, the total number of species recorded in the Inn and its tributaries was similar, with 32 and 33 species, respectively (Table Si2). During the assessed three seasons, most species in the River Inn were caught in summer (27 species) and fall (26 species) compared to spring when only 19 species were detected.

In the tributaries, this picture was different with more species caught in spring (30), 32 species caught in summer and 30 species caught in fall. The heatmap presenting the distribution patterns of species between the Inn and the tributaries indicates a high heterogeneity throughout the seasons with a river-specific strong concentration of individual species in summer and fall (Fig. 6). According to SIMPER analyses, the average dissimilarity between sampling stretches of the Inn and the tributaries was 85.9%. The bleak was very common in sampling stretches of the Inn and tributaries. However, it was two-fold more abundant in tributaries. This was also true for the chub. The European bullhead was 2.5-fold more abundant in the Inn whilst European perch (20.8-fold), roach (16.9-fold) and common nase (5.8-fold) were more abundant in tributaries.

3.3.2. Target species for conservation

Considering the distribution of the target species grayling, brown trout, huchen, common nase and barbel, a distinctive pattern of occurrence between the main stem of the River Inn and tributaries as well as within the tributaries was obvious. On the overarching data analysis over all tributaries and sampling stretches of the main stem Inn with the focus on the target species, only the European nase was detected by SIMPER to be common across sampling stretches in the Inn (617 individuals) or the tributaries (3551 overall and 2300 exclusively in MF). The other target species were rather sporadically detected, revealing a spotty distribution pattern over the study rivers. The huchen was only detected in low numbers in the Inn (3 individuals), whilst the brown trout was also detected in low numbers in the tributaries (9 individuals, Inn: 75 individuals). The grayling was only detected in two tributaries (20 and 9 individuals respectively) and the River Inn (64 individuals). The barbel was present in high numbers in one of the tributaries (overall 533 individuals, 462 solely in MF), and the Inn (168). In addition, European eel, and Prussian carp were caught exclusively in the Inn, whilst white bream, rudd, vimba bream and tench were only found in the tributaries.

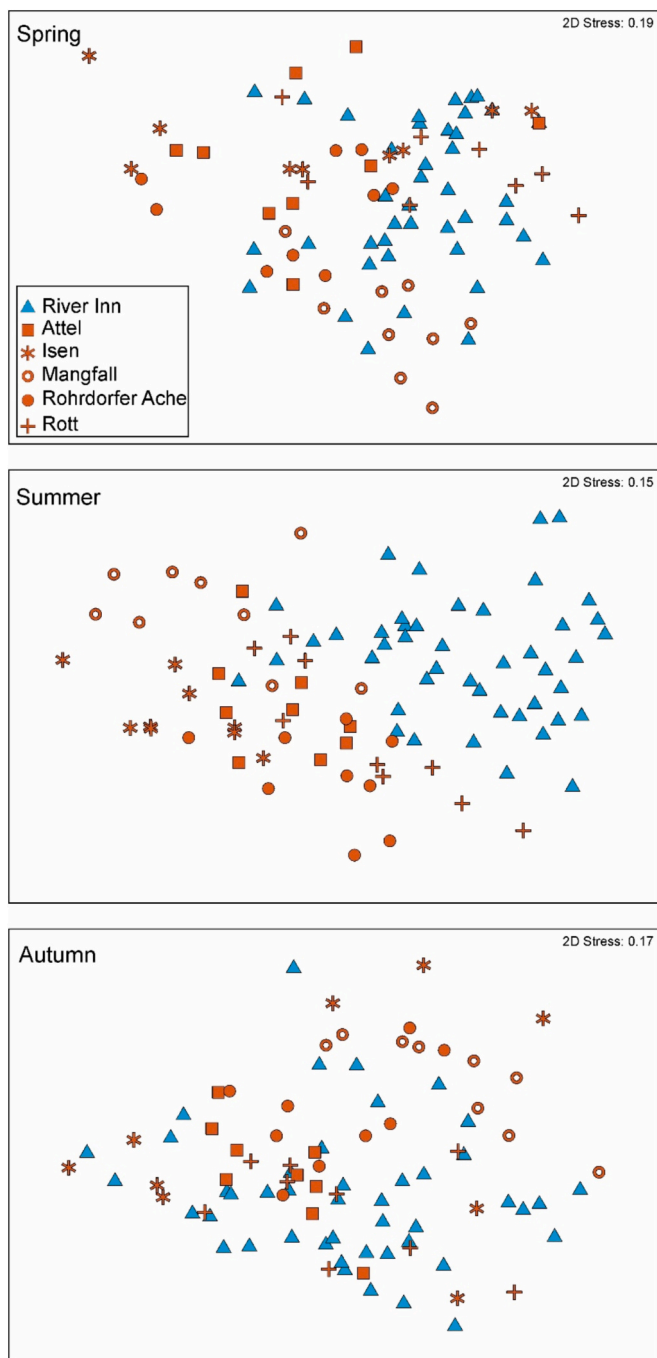


Fig. 5. Nonmetric multidimensional scaling (nMDS) of fish community composition based on fish-abundance data in the River Inn and the five assessed tributaries Attel, Isen, Mangfall, Rott, and Rohrdorfer Ache based on Bray-Curtis-Similarity, with each pictogram representing a distinctive sampling stretch. The distance between the circles (sampling stretch) corresponds to the similarity in fish community composition (small distance = large similarity). The three parts of the figure represent the sampling time points in spring, summer and autumn.

3.4. Fish community composition between the different zones sampled within the Inn and within the tributaries

Differences in fish community composition between the different zones and sampling stretches in the Inn and the tributaries were most pronounced during summer (Fig. 7, Global ANOSIM between zones in the River Inn and tributaries $R = 0.358, p < 0.001$, Table 4).

Despite their close proximity, the sampled stretches zone 3

Table 3

Seasonal comparison of the fish community composition by one-way analysis of similarities (ANOSIM) between the River Inn (Inn) and the tributaries AT = Attel, IS = Isen, MF = Mangfall, RA = Rohrdorfer Ache, RO = Rott.

Comparisons	Spring		Summer		Autumn	
	R	p-value	R	p-value	R	p-value
Global	0.322	<0.001	0.464	<0.001	0.201	<0.001
Inn - AT	0.404	<0.001	0.443	<0.001	-0.024	>0.05
Inn - IS	0.273	<0.05	0.743	<0.001	0.436	<0.001
Inn - MF	0.315	<0.001	0.658	<0.001	0.357	<0.001
Inn - RA	0.350	<0.001	0.474	<0.001	0.107	>0.05
Inn - RO	0.166	<0.05	0.365	<0.001	0.067	>0.05
AT - IS	-0.010	>0.05	0.336	<0.01	0.312	<0.001
AT - MF	0.501	<0.001	0.345	<0.01	0.686	<0.001
AT - RA	0.017	>0.05	0.184	<0.05	0.145	<0.05
AT - RO	0.311	<0.01	0.214	<0.05	0.125	<0.05
IS - MF	0.585	<0.001	0.386	<0.001	0.389	<0.001
IS - RA	0.139	>0.05	0.659	<0.001	0.271	<0.05
IS - RO	0.211	<0.05	0.698	<0.001	0.130	>0.05
MF - RA	0.504	<0.001	0.574	<0.001	0.391	<0.01
MF - RO	0.674	<0.001	0.556	<0.01	0.555	<0.01
RA - RO	0.350	<0.01	0.294	<0.01	0.123	>0.05

(confluence of tributaries) and UC (directly upstream site in the main stem River Inn) differed significantly from each other in fish community composition, particularly in summer (ANOSIM $R = 0.777, p < 0.001$). Within the sampled zones in the tributaries, significant differences could only be detected between zone 1 and zone 3 (as evident for all three seasons, Table 4). Within the River Inn, DC downstream of the confluence between tributary and main stem only differed significantly in summer and fall from OC and UC (most pronounced in summer, Table 4). The sampling stretch at the opposite bank of the confluence OC did not differ in fish community composition from the site UC located in the river Inn directly upstream of the confluence (Fig. 7, Table 4). These findings are in line with the results of the CPUE in the sampling stretches. Whilst CPUE increased in the three zones of tributaries throughout seasons from spring to fall (most pronounced in zone 3), in the River Inn main stem, only in DC an increase in CPUE throughout the seasons could be detected. Comparing zone 3, located directly upstream of the confluence, and DC, located directly downstream of the confluence, the high CPUE detected in summer in zone 3 (decreased in fall here) was detected further downstream in the main stem in DC in fall (Fig. 4). Fish size of target species such as grayling (maximum size 47 cm) and brown trout (maximum size 48 cm) was larger in spring in the tributaries compared to the main stem where mostly smaller individuals <12 cm were detected in most dense populations during summer (Fig. 8). No adult or juvenile brown trout could be detected in fall in the tributaries. For the rheophilic Cypriniformes nase and barbel, a similar trend was detected with many adult nase and barbel concentrating in the tributaries in spring. Later in the year in summer and fall, a concentration of juveniles in the Inn and the tributaries could be detected, indicating successful reproduction (Fig. 8). In contrast to the salmonids, a large proportion of adult specimens of barbel (maximum size of 74 cm) and nase (maximum size of 56 cm) also used the tributaries during summer and fall (Fig. 8).

4. Discussion

Using the example of an alpine river system, this study highlights the importance of interconnected river networks between main stem and tributaries contributing to habitat heterogeneity and resulting diverse fish community structures. Riverine fish developed complex life cycles during their evolution, requiring specific heterogenous habitats in the sequence of certain stages of life from egg to spawner. Consequently, there are many factors determining healthy populations with connectivity and habitat integrity being the most important ones. As evident from the results of our study, connectivity between tributaries and the

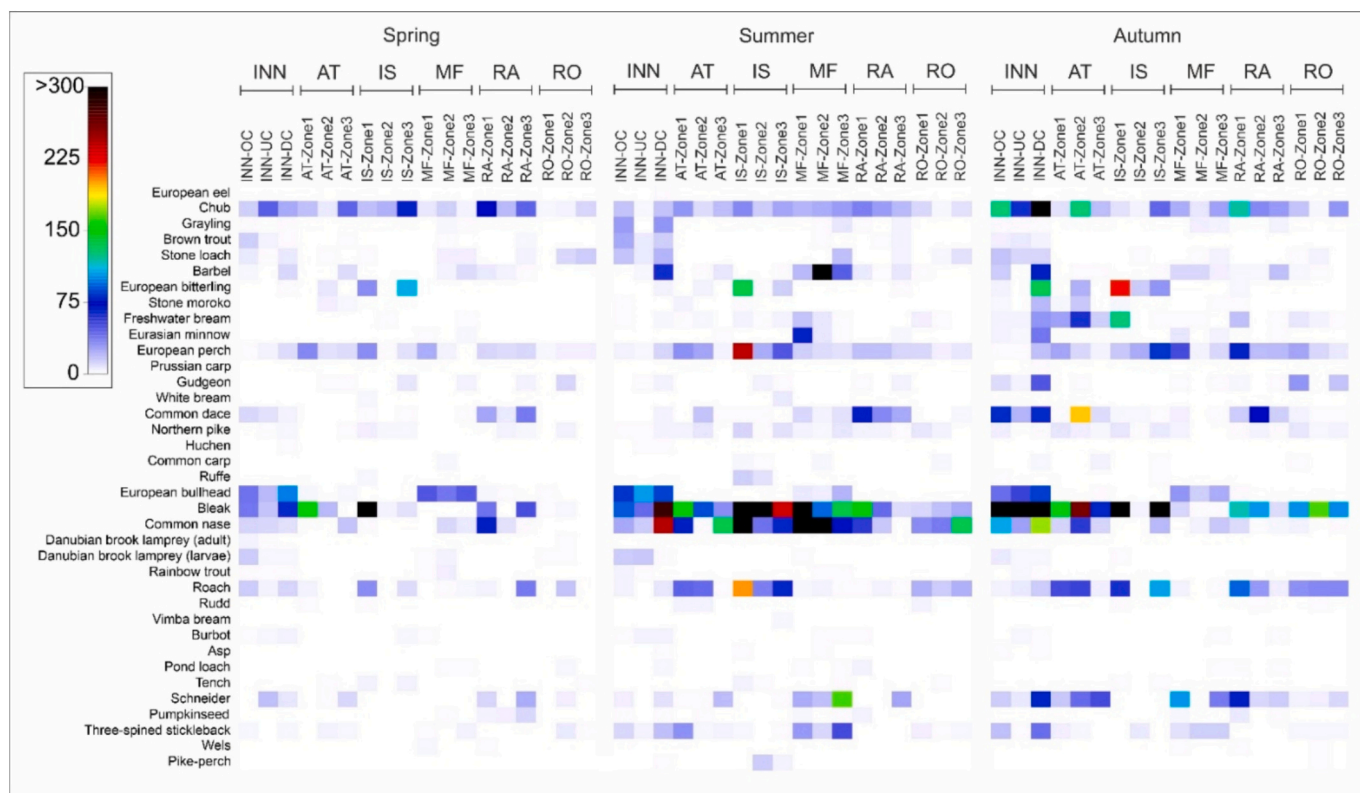


Fig. 6. Shade plot of the spatial-seasonal distribution of all fish species between the tributaries (AT = Attel, IS = Isen, MF = Mangfall, RA = Rohrdorfer Achen, RO = Rott) and the INN = River Inn main stem. The code of sampling stretches corresponds to the schematic description given in Fig. 1. OC = location at the opposite bank of the confluence of tributary and River Inn, UC = upstream of the confluence in the River Inn, DC = downstream of the confluence in the River Inn. Zone 3 = in close proximity upstream of the confluence in the tributary, Zone 2 = 500 m upstream of the confluence in the tributary, Zone 1 = 1000 m upstream of the confluence in the tributary.

main stem are crucial for providing access to the diverse physical habitats such as spawning grounds, juvenile habitats, feeding habitats or habitats for shelter in winter that cannot be solely found in the main stem of the River Inn. This matches previous findings (e.g. Rice et al., 2008; Czeglédi et al., 2016) specifying the diverse needs of different fish species during different life stages and at different seasons. Besides the important contribution of tributaries in alpine systems to overall fish species diversity as well as for reproduction and juvenile growth, fish communities turned out to be highly variable across seasons and were very different between tributaries and main stem. These community shifts can mostly be explained by spawning runs of adult fish in spring into the tributaries (Nagel et al., 2020) and their back migration to the main stem as well as juvenile movements in summer between spawning sites in the tributaries and juvenile habitats of low current and higher temperatures at the confluences with the River Inn main stem. Later in the year in fall, when these fish had completed their development from larvae to young of the year juveniles, they were detected further downstream of the confluences in the main stem. These fish community shifts are highly driven by temperature distribution patterns in the river network and the availability of structural suitable habitats such as shallow water zones (Pander et al., 2017), and they depend on full connectivity throughout the year between the main stem River Inn and its tributaries.

In principle, this alpine river network must be seen as an overarching habitat system, in which several species fulfill their complex life cycles that they evolutionary developed. The harsh environmental conditions in terms of extremely fast fluctuating discharges and low temperatures in this glacier melt-induced system forces fish to search for conditions suitable for reproduction. For doing so, species such as common nase, barbel, grayling and brown trout developed two principal strategies.

Firstly, they can either start early to spawn in the main stem River Inn before the glacier runoff with high loads of fines start impairing the interstitial zones and egg-development (Soulsby et al., 2001). This is usually evident at the River Inn in the beginning of May. Secondly, they can carry out spawning migrations into the tributaries where these high loads of fines do not occur and where they find spawning grounds and habitats for early life stages. Some fish species may use both options. The utilization of different strategies of individuals of the same species may increase the reproduction success in these highly dynamic environments. The loss of one spawning possibility (i.e. limited access to tributaries and unsuitable environmental conditions therein) may therefore reduce the survival probability for the species in a longer-term perspective.

It is likely that the presence of brown trout in the River Inn indicates either successful reproduction of the wild strains in the River Inn itself or the success of the various stocking projects with brown trout eggs in the tributaries. In this context, genetic analysis could be used to clarify the contribution of stocking programs to the overall population. With regard to grayling, based on the significant number of juvenile fish, successful reproduction in the River Inn itself still seems possible and probable. Whether this is limited to the diversion section and the near-natural bypass waters (Nagel et al., 2021) or also takes place in the main river itself should be clarified by further investigations. In summary, it can be stated that the River Inn appears to be significantly more important as a habitat for the cold water adapted species grayling and brown trout compared to the tributaries investigated.

Spawning is highly driven by water temperature and cyprinids such as common nase and barbel are triggered by higher water temperatures (Rakowitz et al., 2008) than salmonids. Cyprinids evolutionary adapted in a sense that they carry out spawning migrations into the tributaries (e.

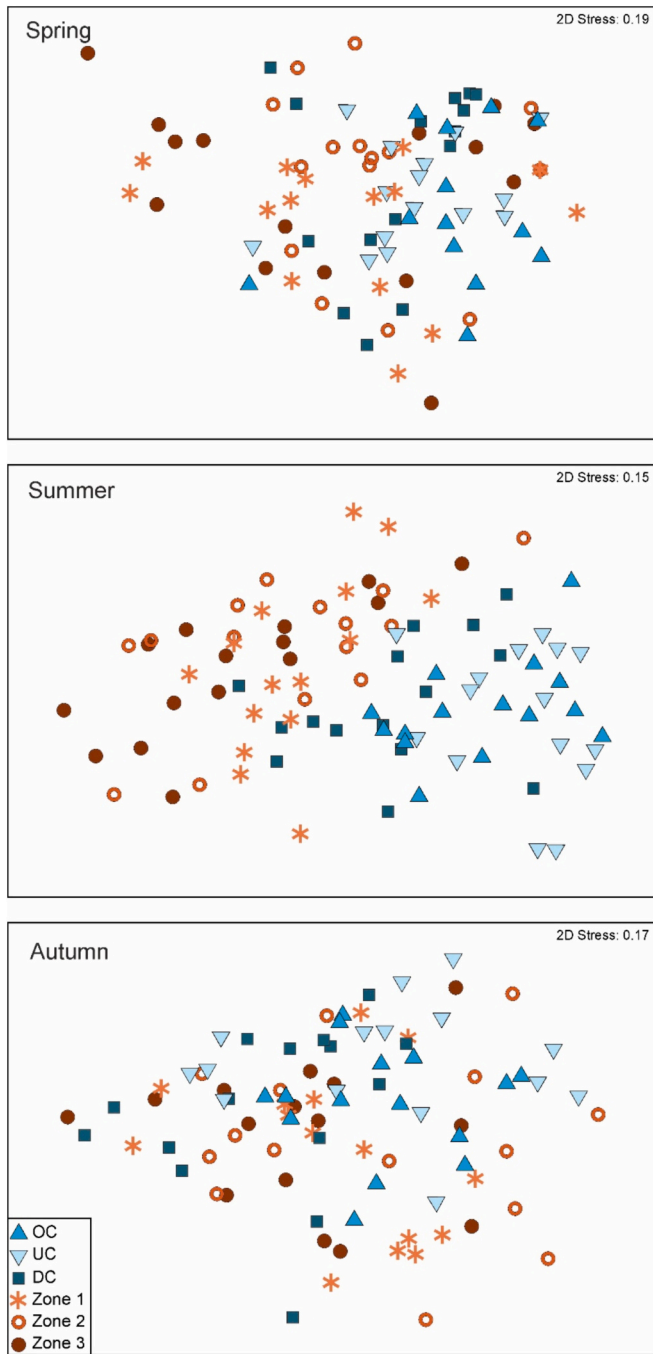


Fig. 7. Nonmetric multidimensional scaling (nMDS) of fish community composition based on fish-abundance data in the different sampled zones in the River Inn and the tributaries based on Bray-Curtis-Similarity, with each pictogram representing a distinctive sampling stretch. OC = location at the opposite bank of the confluence of tributary and River Inn, UC = upstream of the confluence in the River Inn, DC = downstream of the confluence in the River Inn. Zone 3 = in close proximity upstream of the confluence in the tributary, Zone 2 = 500 m upstream of the confluence in the tributary, Zone 1 = 1000 m upstream of the confluence in the tributary. The distance between the circles (sampling stretch) corresponds to the similarity in fish community composition (small distance = large similarity). The three parts of the figure represent the sampling time points in spring, summer and autumn.

g. Keckeis, 2001; Pander et al., 2024b), most likely to avoid the low temperatures in the glacier induced discharge of the River Inn and the high loads of fines typically originating from the glacier runoff (Arora et al., 2014). These high loads of fines are reflected in high turbidity

Table 4

Seasonal comparison of the fish community composition by one-way analysis of similarities (ANOSIM) between the different sampled zones in the River Inn and the tributaries. UC = upstream of the confluence in the River Inn, DC = downstream of the confluence in the River Inn and OC = location at the opposite bank of the confluence of tributary and River Inn. Zone 1 = 1000 m upstream of the confluence located in the tributary, Zone 2 = 500 m upstream of the confluence in the tributary and Zone 3 = in close proximity upstream of the confluence in the tributary.

Comparisons	Spring		Summer		Autumn	
	R	p-value	R	p-value	R	p-value
Global	0.110	<0.001	0.358	<0.001	0.127	<0.001
OC - UC	0.065	>0.05	0.063	>0.05	0.033	>0.05
OC - DC	0.013	>0.05	0.120	<0.05	0.153	<0.01
UC - DC	0.065	>0.05	0.277	<0.01	0.110	<0.05
OC - Zone 1	0.296	<0.001	0.629	<0.001	0.147	<0.001
OC - Zone 2	0.187	<0.01	0.498	<0.001	0.156	<0.05
OC - Zone 3	0.153	<0.05	0.700	<0.001	0.272	<0.01
UC - Zone 1	0.219	<0.001	0.783	<0.001	0.220	<0.01
UC - Zone 2	0.119	<0.05	0.640	<0.001	0.141	<0.05
UC - Zone 3	0.152	<0.05	0.777	<0.001	0.240	<0.01
DC - Zone 1	0.163	<0.01	0.212	<0.01	0.137	<0.05
DC - Zone 2	0.046	>0.05	0.180	<0.01	0.139	<0.05
DC - Zone 3	0.070	>0.05	0.342	<0.001	0.089	<0.05
Zone 1 - Zone 2	-0.021	>0.05	0.033	>0.05	0.049	>0.05
Zone 1 - Zone 3	0.081	<0.05	0.089	<0.05	0.011	>0.05
Zone 2 - Zone 3	0.033	>0.05	0.016	>0.05	0.010	>0.05

values measured herein in the main stem River Inn (increasing from spring to fall), potentially infiltrating and clogging any available gravel in the riverbed of the main stem (Sear, 1993; Pander et al., 2022). This can exert negative effects on hatching and emergence success in salmonids and cyprinids likewise (Nagel et al., 2020; Wild et al., 2024). The tributaries assessed are not glacier fed and originate in a subalpine terrain, mostly within scree fields of glacier remaining of the ice age. These tributaries are substituted with a wide range of grain sizes from those scree fields and were formed by the hydraulic forces of the rivers resulting in habitats for critical life stages such as fast overflow gravelly spawning grounds and shallow sand dominated juvenile habitats comprising less current, however, their river morphology is highly degraded. In addition, these tributaries are warmer than the River Inn main stem that originates from much higher altitudes. Their slightly higher temperatures - particularly early in the year - are preferred conditions by rheophilic cyprinids as also evident from the large catch numbers of common nase that were documented in tributaries between spring and summer. The size-specific analysis indicates that almost exclusively adult common nase were caught in spring, using the tributaries to spawn at this time of year (Nagel et al., 2020; Nagel et al., 2021). In summer and fall, on the other hand, mostly juvenile common nase were detected, which indicates successful reproduction by the adult fish. Similar patterns also occurred for barbel, where mostly adults over 50 cm length were recorded in the tributaries in spring and fourteen times the number of barbels were detected in the tributaries in summer, with the majority being juveniles <5 cm. Later in the year, when temperatures get too warm in the tributaries, cold-water adapted species migrate back to the colder main stem and are then widely absent in tributaries as evident for brown trout (no more detections in fall in tributaries). This species regularly carries out spawning migrations into tributaries as also described for other systems (Gosset et al., 2006; Slavík et al., 2012). However, we cannot rule out that homogenous degraded habitat structures, fisheries or other factors may also explain the absence of brown trout in tributaries later in the year.

This interlinkage of tributaries and River Inn is also reflected in the different zones that were sampled in the tributaries and downstream of the confluences. In these zones, CPUE subsequently increases during the seasons and peaks in high numbers downstream of the confluence in the River Inn main stem. Considering the enormous volume of water, the high turbidity loads and the resulting severely limited effectiveness of

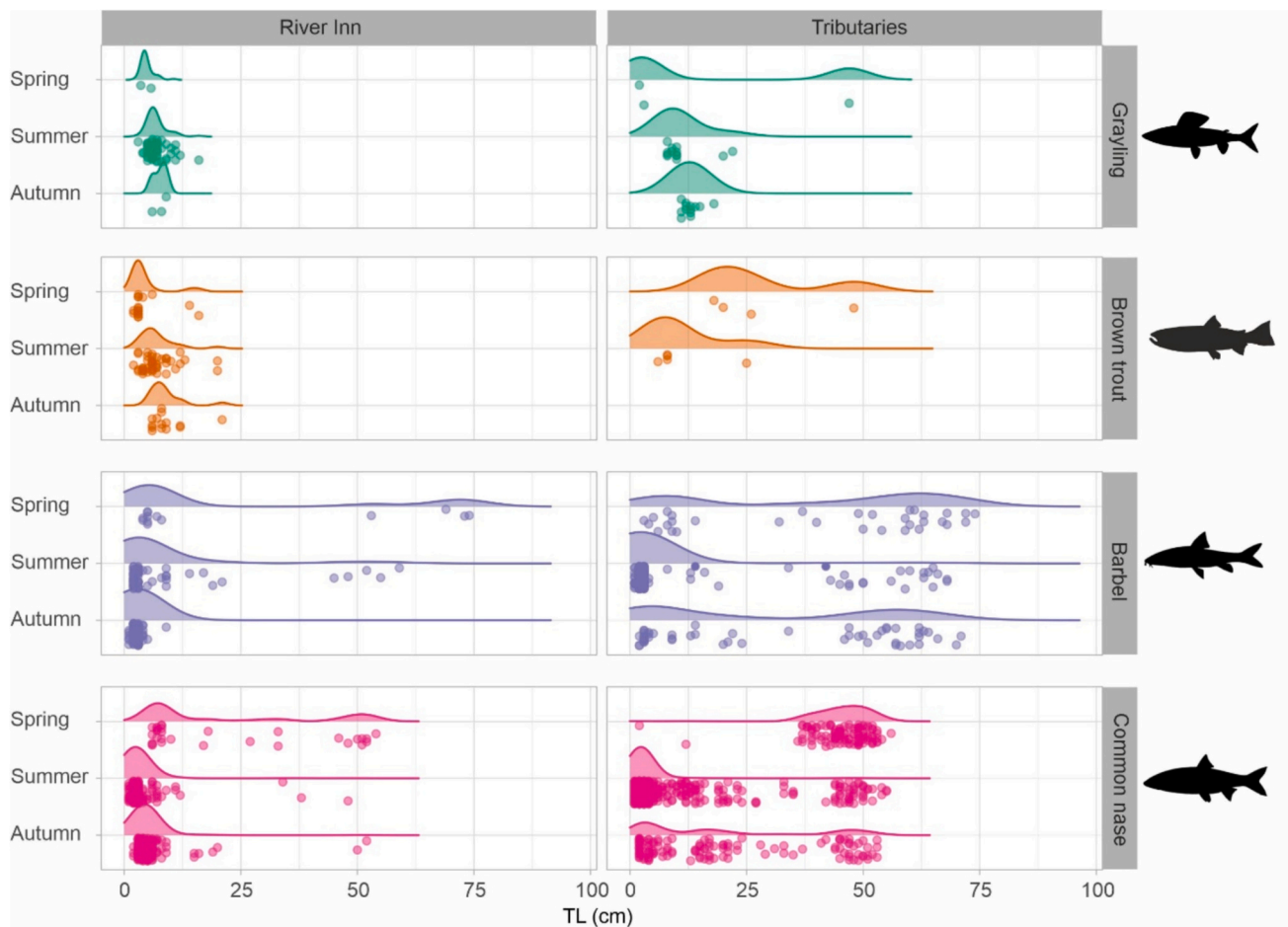


Fig. 8. Seasonal and spatial length distributions (total length = TL) of the selected target species grayling (*Thymallus thymallus*), brown trout (*Salmo trutta*), barbel (*Barbus barbus*), and common nase (*Chondrostoma nasus*) in the River Inn and the tributaries (pooled data). Each dot represents a caught fish in the respective habitat. Shaded curves indicate the modelled length distribution for the River Inn and the tributaries at the time of recording.

electrofishing (Lyon et al., 2014) in the River Inn, the evidence of juvenile brown trout and grayling in the samples is certainly remarkable. The fish ecological importance of the confluence (zone 3) and the areas further downstream in the main stem River Inn (DC) also becomes clear when CPUE is analyzed on a seasonal basis. At each survey time, the density of individuals was higher in the confluence areas than in the upper sections 500 m (zone 2) and 1000 m (zone 1) upstream in the tributaries. This pattern is particularly evident in summer and is largely due to an enormous increase in juvenile fish, which have obviously found suitable, flow-calmed conditions in the confluence. In the examined sections of the River Inn main stem, a significantly higher fish density was documented from summer on in the area below the confluence in DC compared to sections that were considered as reference upstream the confluence UC or on the opposite bank in OC. This underpins the importance of confluences and their downstream areas for fish diversity in alpine systems. This is in line with the findings of Rice et al. (2008, and references therein) who summarised several positive effects of tributaries and their confluences on structuring riverine habitat, increasing productivity, providing local refugia and enhancing network heterogeneity, all contributing to high diversity of aquatic life, particular the diversity of fishes (Pracheil et al., 2013).

The findings of our study can be used for upcoming restoration projects in large alpine rivers to address two primary aspects: Firstly, to create heterogeneous habitat structures that reflect the life cycle requirements of the target species to support diverse fish communities, and secondly, to improve multidimensional connectivity as is currently being intensively investigated in this system by using a large telemetry

infrastructure (Nagel et al., 2025).

5. Conclusions

As river networks with a largely alpine catchment area, such as the River Inn, are at the same time among the most heavily modified watercourses, but are also home to a number of specialized and highly endangered fish species, effective protection strategies for these ecosystems are of great importance. To implement targeted conservation measures, such as habitat improvements and improvements of connectivity, a systemic understanding of these systems is essential. This includes differences in habitat quality throughout seasons such as water temperature, conductivity and turbidity and subsequently following differences in fish community composition throughout the year.

The different habitat conditions described above lead to pronounced differences in the composition of fish communities within small spatial scales: rheophilic cyprinids such as common nase and barbel were found much more frequently in the tributaries and, as the spatio-temporal composition of the size classes indicated, successfully reproduced there. In contrast, cold-water adapted species such as grayling, brown trout and European bullhead were detected much more frequently in the bank habitats of the River Inn, mostly as juveniles, which indicates natural reproduction there. This underpins the particular value of the summer-cold main stem River Inn as a refuge for these species, especially in the expected further increase in water temperatures over the coming decades.

The more detailed spatial analysis according to the various zones

investigated revealed that the confluences as well as the areas downstream in the main stem are of very high fish ecological importance, informing restoration management of their high value for the restoration of connectivity and of juvenile habitats in otherwise often highly modified systems.

CRedit authorship contribution statement

Joachim Pander: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christoffer Nagel:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Juergen Geist:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2026.181401>.

Data availability

Data will be made available on request.

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