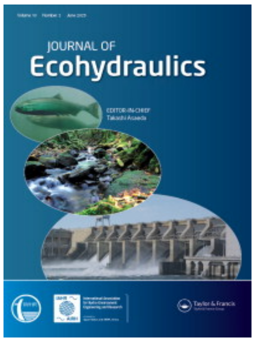

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A check-up of the opening of a fish migratory axis on multi-dimensional and multi-annual scales

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ABSTRACT

River fragmentation disrupts essential fish migrations, threatening aquatic ecosystems. In 2021, a fishway was installed at the Coo waterfall on the Amblève River to restore ecological continuity. This study combined a multi-annual and multi-dimensional approach with electrofishing and fishway monitoring over three years to assess fish populations before and after the fishway's opening. Before installation, upstream populations were less diverse, with 13 species compared to 20 species downstream (diversity indices: H′ = 1.21 vs. 2.93). After the fishway's opening, a diverse and equitably distributed community used it (H′ = 2.02 and $J = 0.71$). The fishway facilitated migrations throughout the year, with an opening effect observed for barbel and pike (50% captured during the first year). Seasonal patterns revealed adult migrations during spawning (April to July) and juvenile movements in autumn. Results highlighted that spirlin, absent upstream before the fishway, were captured in large numbers in the fishway, demonstrating their role in facilitating recolonisation. Recapture data confirmed that some individuals moved freely between upstream and downstream habitats by re-using the fishway. This study underscores the value of multi-method, multi-year monitoring to understand fish population responses to river defragmentation and highlights the importance of fishways in restoring connectivity and enabling ecological recovery.

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1. Introduction

Rivers are fragmented by more than 1.2 million obstacles in Europe (Belletti et al. 2020). The fragmentation of riverine habitats is a major environmental issue and has far-reaching consequences for aquatic ecosystems. These barriers interrupt the connectivity between habitats essential for many fish species that rely on access to different functional habitats to complete their life cycle, including spawning, feeding and growth (Haworth and Bestgen 2024; Kowal et al. 2024). Physical barriers can hinder these migrations, creating genetic isolates, reducing genetic diversity, and making populations more vulnerable to environmental stressors (Yamamoto et al. 2004; Falke and Gido 2006; Moccetti et al. 2024). Moreover, barriers disrupt hydrological and sedimentary regimes, affecting the quality of habitats and modifying biotic communities (Poff and Hart 2002; Baldan et al. 2023; Haworth and Bestgen 2024).

The adoption of the European Union Water Framework Directive (2000/60/EC) has played a crucial role in highlighting the damaging impacts of river fragmentation and has catalysed substantial river restoration efforts across Europe. The demolition of dams and the installation of crossing devices have been used as solutions to restore connectivity (Benitez et al. 2018; Silva et al. 2018; Ovidio et al. 2020). Although dam removal is the best solution, this alternative is relatively costly and not always feasible, depending on the site's topography (Dodd et al. 2017; Barbarossa and Schmitt 2024). Building a fishway is an alternative that facilitates fish movements, enabling them to explore and use habitats both upstream and downstream of the obstacle (Roscoe & Hinch 2010; Benitez et al. 2015; Gelder et al. 2023). In recent years, fishways have evolved to become suitable for multiple species with less restrictive characteristics in terms of swimming capacity (Benitez et al. 2015; Grimardias et al. 2022). Numerous studies on potamodromous species have highlighted their ability to travel tens or even hundreds of kilometres (García-Vega et al. 2018; Ovidio et al. 2023; Gelder et al. 2024b). Consequently, these species, like diadromous species, are also severely affected by anthropogenic barriers and the consequential loss of longitudinal connectivity.

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Although many watercourses have been defragmented, relatively few studies have been conducted following this defragmentation (Poff and Hart 2002; Jones et al. 2023; Gelder et al. 2024b). Most studies have focused on the physical aspects (e.g. flow, temperature, sediment) or on the effectiveness of the fishway, with few studies concentrating on the ecological aspect, taking into account changes in fish communities (Ryan Bellmore et al. 2017; Cook and Sullivan 2018; Romão et al. 2018; Dębowski et al. 2022; Gelder et al. 2024a). In addition, few studies include data on the initial state of fish populations prior to site defragmentation, which would enable a complete before and after analysis of habitat defragmentation (Tummers et al. 2016; Jones et al. 2023; Bower et al. 2024). When installing a fishway, it is interesting to include monitoring of individuals using a telemetry device (Panagiotopoulos et al. 2024). Several studies have highlighted the use of the fishway and the dynamics of individual colonisation towards newly available habitats (Legrand et al. 2020; Benitez et al. 2022; Gelder et al. 2023). However, the performance of these facilities requires rigorous evaluation. With the increasing number of crossing devices being installed, it seems important to have an overall view of fish population evolution compared to the initial state in order to determine the impact of defragmentation on fish populations.

The Amblève River has several dams that impede the free movement of fish, the most important of which is the Coo waterfall, which is 11.8 m high. In 2021, a fishway was installed at the foot of the Coo waterfall to restore upstream movement and fully restore ecological continuity. This study aims to determine the utilisation of the fishway from the opening during a three consecutive years period and to study the impact of habitat defragmentation on fish populations by observing the state of these populations downstream and upstream of the obstacle before and after the opening of the migratory axis. To do this, we conducted electrofishing before and after the opening of the migratory axis and monitored the individuals using the fishway since its opening. The combination of these methods allows us to determine the number, biomass and size of individuals per species captured in the fishway, which can then be related to individuals present downstream and upstream of the waterfall. This makes it possible to determine the use of the fishway on a seasonal and multi-annual scale and whether the abundance, biomass and size of individuals captured by species are representative of the fish populations present downstream and upstream before the opening of the migratory axis. The result of this study contributes to the management and restoration of fragmented river ecosystems.

2. Materials and methods

2.1. Study area and monitoring

The Coo waterfall is located in the Amblève River, in the Meuse basin. The Amblève River is the Ourthe's largest tributary, with a catchment area of 1,076.79 km^2, a length of 88.4 km and an average annual discharge of 19.3 m^3/s (Figure 1A). The downstream section of the river is qualified as a grayling/barbel fish zone (Huet 1949), with 23 different species recorded (Gelder et al. 2024a). The Coo waterfall is one of the major obstacles in the Amblève River. This semi-artificial barrier, 11.8 m high, was created during the Middle Ages through the artificial cutoff of a meander. Until 1970, a natural meander on the left bank of the Amblève River allowed fish to bypass the Coo waterfall. However, in 1970, the construction of the Coo pumped-storage hydropower plant transformed this meander into a water storage reservoir, cutting it off from the main flow and making the waterfall completely impassable for upstream migration, although downstream passage remains possible *via* the waterfall. In addition, a small hydroelectric facility, the Coo Dérivation Plant, diverts part of the river's flow upstream of the waterfall into a inlet channel to power a turbine, and discharges it downstream *via* a restitution channel on the left bank of the waterfall (Figure 1B). To restore the connectivity, a capture–transport fishway equipped with a 2.8 × 1.9 × 1.8 m capture cage was built in 2021 in the restitution channel of the Coo derivation hydroelectric power station, 100 m from the foot of the waterfall, on the left bank. The cage includes a cone entrance that prevents most fish from exiting once inside. This fishway is unique in Belgium, as it requires manual transport of fish upstream due to the lack of any hydraulic connection between downstream and upstream sections.

Monitoring of the capture cage started on 15 March 2021 and continued at intervals of one to four times per week. The monitoring frequency increased during periods of intense migration and decreased during periods of low captures. Fish captured in the cage were identified at the species level, weighed (± 1 g) and measured (± 1 mm, fork length) after anaesthesia (Eugenol, 0.1 mL L^{-1}). Non-chipped individuals over 200 mm in length were marked with a radio frequency identification (RFID) tag in the intraperitoneal cavity in order to identify them for potential recaptures. The individuals were then placed in a tank of water with oxygen to recover (+/− 20 min). After recovery, the fish were manually transported in oxygenated tanks using a vehicle and released into the main river channel with a tank, 500 m upstream of the waterfall, at a

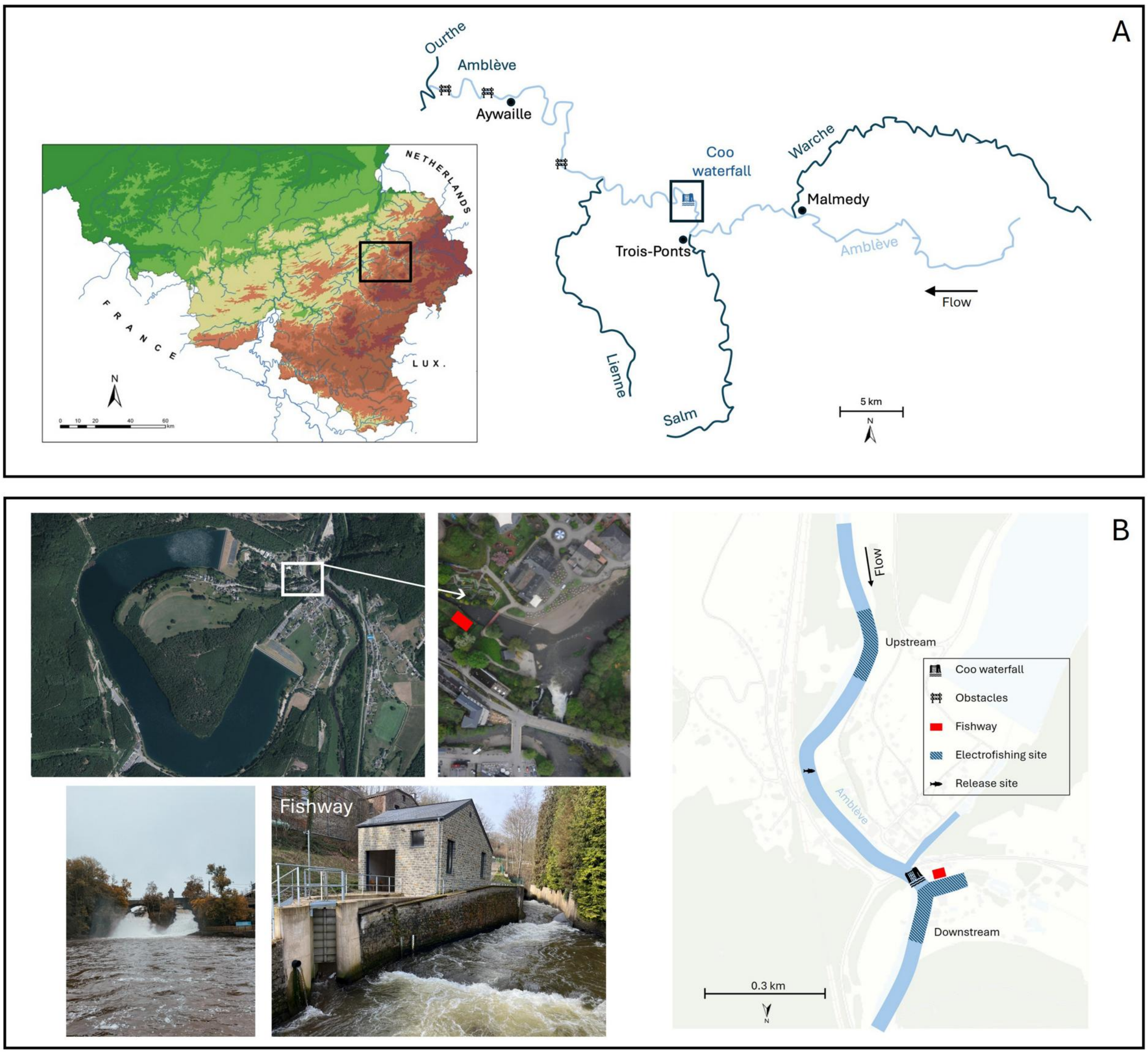

Figure 1. Maps of the Amblève river with the coo waterfall (A). Pictures showing aerial views of the coo site, the waterfall, the fishway, and schematic representation of the electrofishing sites and the fish release point upstream (B).

sufficient distance from the inlet channel to ensure they remained in the natural river flow. The release site provides sufficient depth, moderate current, and the presence of rocks offering shelter. All fish were released the day of capture, with no holding period beyond recovery. This protocol ensured a rapid release to minimise stress.

2.2. Electrofishing and fish inventories

Fish inventories were carried out using a two-pass electrofishing (EFKO 7000) technique with a hand net (diameter 40 × 40 cm, mesh 2 × 2 mm) along a 150 m stretch of the river at two different sites (Figure 1B): one upstream and one downstream of the waterfall. A total of 10 electrofishing were carried out from 2005 to 2023: six 150 m downstream (August 2005, October 2010, March 2011, May 2011, November 2011 and April 2014) and four 700 m upstream of the waterfall (August 2005, April 2021, March 2022 and June 2023). All sampled sites are located within the barbel/grayling fish zonation, characterised by moderate current, well-oxygenated water and coarse substrates, providing comparable habitat conditions. At each electrofishing session, all individuals of all species were captured in order to obtain a complete inventory of the site. The fish were then anaesthetised with 0.1 mL/L of a solution of Eugenol, counted, measured (±1 mm, fork length) and weighed (±1 g). Individuals longer than 200 mm were scanned to check whether they had been chipped. Individuals captured during the first passage were kept in tanks in the river with oxygen during the second passage. At the end of the session, all the individuals were released on the site.

2.3. Data analysis

In order to determine the state of the populations upstream and downstream before the opening of the migratory axis, we combined the data from six electrofishing samples downstream (August 2005, October 2010, March 2011, May 2011, November 2011 and April 2014) and two upstream (August 2005 and April 2021). Although the fishway was installed on 15 March 2021, we assumed that the electrofishing carried out on 1 April 2021 still reflected the initial state in view of the short lead time. Abundance and biomass data for each species, obtained during electrofishing, were combined and expressed in terms of proportions to smooth out the potential recaptures of the same individual during different electrofishing sessions, and these were represented by a histogram. We chose to use data from several electrofishing samples to minimise seasonal biases and provide a more accurate representation of the population dynamics. The abundance and biomass of the upstream and downstream populations were compared using the Mann–Whitney test for all species present in the Amblève River. To assess the biodiversity of the fish community, the following biodiversity indexes were applied to characterise the alpha and beta diversity of the fish communities:

- **Species richness (*S*)**: the number of species present on a site
- **Shannon–Wiener diversity index (*H'*)**: measures the species diversity by considering both the number of species (richness) and the relative abundance of each species (evenness)
  $H' = -\sum p_i \ \ln \ p_i$ (Shannon and Weiner 1963)
- **Simpson's diversity index (D_s)**: measures species diversity by assessing the probability that two randomly selected individuals from a community belong to different species, emphasising dominance.
  $D_s = 1 - \sum n_i(n_i - 1)/N(N - 1)$ (Simpson 1949)
- **Pielou's index (*J*):** measures the species evenness, calculated as the ratio of the Shannon–Wiener diversity index (*H'*) to the logarithm of species richness (*S*)
  $J = H'/\ln S$ (Pielou 1966)
- **Bray–Curtis dissimilarity index (D_{BC}):** measures the dissimilarity between two samples based on species abundance.

$$D_{BC} = \sum (xi + yi)/\sum |xi - yi|$$

where *S* represents the number of species on a site, n_i is the total number of individuals occurring for each species *i*, *N* is the total number of individuals, p_i is the relative abundance of each species, x_i is the abundance of species *i* in the sample x, and y_i is the abundance of species *i* in the sample y. The alpha diversity index was calculated for the upstream part of the waterfall (before and after the opening), the downstream part of the waterfall (before the opening) and the fishway. Beta diversity was calculated between upstream and downstream sites before the opening of the migratory axis, downstream of the fishway (before opening), and upstream of the fishway (after opening). For upstream populations after opening, abundances are based on two electrofishing surveys (March 2023 and June 2023). Beta diversity was not calculated between the fishway and upstream of the waterfall before it was opened because individuals could not move from downstream to upstream at that time.

The use of the fishway was studied for three years, from 15 March 2021 to 15 March 2024. Abundance, biomass and size data were grouped by species and by monitoring year in terms of total abundance, total biomass and minimum, maximum and mean size. The abundance and biomass data were then transformed into proportions covering the three years of monitoring for comparison with downstream data. Spearman's rank correlation test was used to assess the relationships between the abundance and biomass found in the fishway and those downstream. The Mann–Whitney test was also used to compare the abundance and biomass between downstream and upstream of the fishway. To analyse the dynamic of capture in the fishway, we used cumulative curves for native species with a minimum of 10 individuals captured. The number of captures was expressed as a proportion, where 100% represented the total number of individuals captured throughout the three consecutive years of monitoring. A chi-square test was used to determine whether the captures were homogeneous or heterogeneously distributed over the three years compared to a theoretical number of captures (corresponding to the total capture divided by the number of years of monitoring). To analyse the use of the fishway throughout the year, we added up the monthly capture data over three years for species with a minimum of ten individuals captured during that period. A distinction was made between adults and juveniles by size of individual (Philippart and Vranken 1983): adult trout (*Salmo trutta*) $\geq$ 250 mm, barbel (*Barbus barbus*) $\geq$ 250 mm, chub (*Squalius cephalus*) $\geq$ 160 mm, spirlin (*Alburnoides bipunctatus*) $\geq$50 mm, grayling (*Thymallus thymallus*) $\geq$ 240 mm, loach (*Barbatula barbatula*) $\geq$ 50 mm, bullhead (*Cottus rhenanus*) $\geq$ 50 mm, roach (*Rutilus rutilus*) $\geq$ 150 mm, gudgeon (*Gobio gobio*) $\geq$ 70 mm, minnow (*Phoxinus phoxinus*) $\geq$ 45 mm, pike (*Esox lucius*) $\geq$ 35 mm and perch (*Perca fluviatilis*) $\geq$ 100 mm. We compared whether juveniles and adults were captured at the same time of the year by performing a Mann–Whitney test according to the months of capture.

We studied the size ranges of individuals belonging to three species with a minimum of 20 individuals captured per year of monitoring: barbel, chub and trout. We combined, in boxplot form, the size data from individuals captured during electrofishing downstream before the opening of the axis and the size data from individuals captured in the fishway capture trap for each year of monitoring. The size ranges were then compared between the different periods using a Kruskal–Wallis (KW) test, and a post hoc Dunn test was conducted to identify which periods differed.

Statistical tests were performed using the R Studio statistical programme version 3.6.1 packages vegan, car, FSA, ggplot2, tidyr and dplyr, and the significant threshold was set at 5%.

3. Results

3.1. Initial status of populations upstream/downstream

The most abundant species in terms of the number of individuals was the minnow both upstream and downstream, with 76.7% and 40% of capture, respectively. In terms of biomass, barbel was the most important species upstream and downstream, with 59% and 51.4%, respectively. A significant difference was identified between the proportions of the abundance of species present upstream and those present downstream (KW test, $p < .05$), but no significant difference was observed between the proportion of biomass downstream and upstream (KW test, $p > .05$; Figure 2).

The species richness (S) showed a greater number of species present downstream of the waterfall, with 20 species downstream and 13 species upstream. Shannon–Wiener, Simpson's, and Pielou's diversity indexes showed a diverse and equitably distributed fish community downstream ($H' = 2.93$, $D_s = 0.79$ and $J = 0.98$), and a community composed of dominant species upstream ($H' = 1.21$, $D_s = 0.39$ and $J = 0.47$), with abundance distributed unevenly between species. The beta diversity indicated a dissimilarity between upstream and downstream fish populations ($D_{BC} = 0.44$), indicating a difference in the composition of the two communities (Table 1).

3.2. Use of the fishway and comparison with downstream populations

Since the opening of the fishway on 15 March 2021, 17 species and 2,328 individuals have been captured in the capture cage for a total biomass of 333.7 kg. The fishway was used by a diverse and equitably distributed community ($H' = 2.02$, $D_s = 0.81$ and $J = 0.71$; Table 1). Over the three years, the community was consistently dominated by rheophilic species, which represented more than 70% of the total

Table 1. Alpha diversity index with species richness (S), Shannon–wiener diversity index (H'), Simpson's diversity index (D_s), Pielou's index (J) and beta diversity with Bray–Curtis dissimilarity index (D_{BC}) for upstream, downstream and fishway populations.

	Alpha diversity					Beta diversity
	S	*H'*	*Ds*	*J*		D_{BC}
Upstream	13	1.21	0.39	0.47	Upstream–downstream	0.44
Downstream	20	2.93	0.79	0.98	Downstream–fishway	0.60
Fishway	17	2.02	0.81	0.71	Upstream^a–fishway	0.70
Upstream^a	11	1.71	0.76	0.71		

D_s, J and D_{BC} ranged from 0 to 1.

[a] After the opening of the migratory axis.

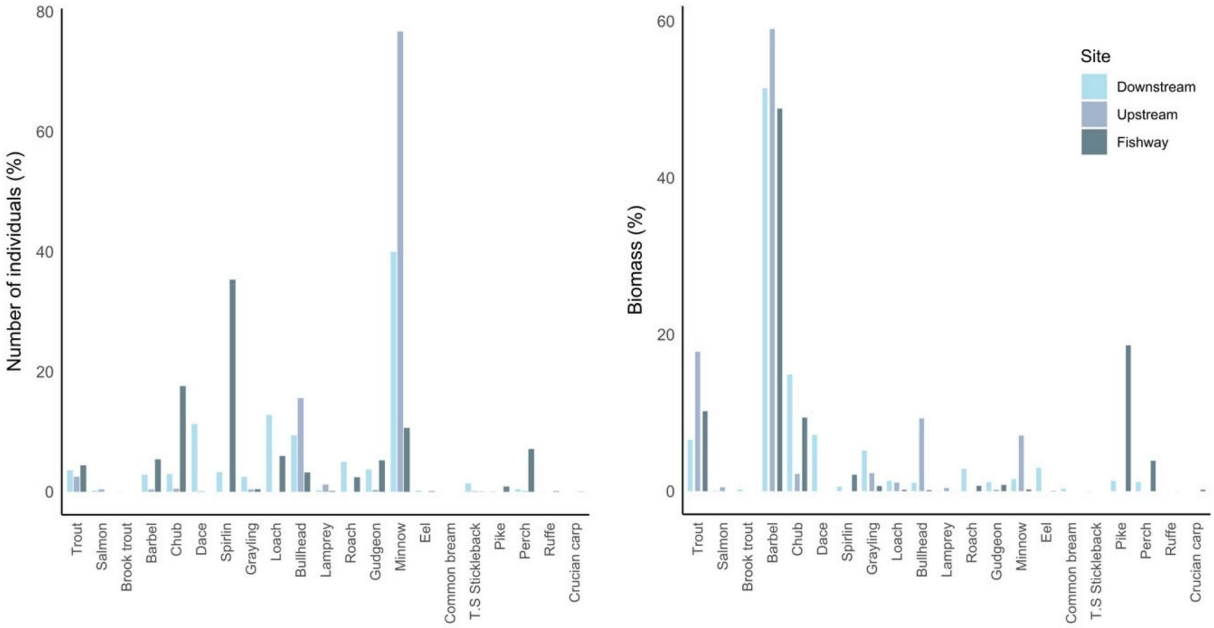

Figure 2. Proportion of the number of individuals captured and the biomass by species (%) upstream and downstream of the waterfall before the opening of the migratory axis and in the fishway.

Table 2. Percentage of individuals captured per flow guild, number of individuals captured in the fishway (n), number of individuals marked (n_{tag}) with the number of recaptures in brackets, biomass (g), range size (mm): min, max and mean per species by years of monitoring.

		2021–2022						2022–2023						2023-2024					
Species					Size (mm)						Size (mm)						Size (mm)		
Common name	Latin name	*n*	*ntag*	g	min	max	mean	*n*	*ntag*	g	min	max	mean	*n*	*ntag*	g	min	max	mean
Rheophilic species (%)		**80.2**%						**72.4**%						**72.7**%					
Trout	*Salmo trutta*	37	34 (2)	18276	125	608	334	43	36 (6)	11194	82	505	282	23	8 (2)	4590	105	600	247
Rainbow trout[a]	*Oncorhynchus mykiss*	13	–	9144	211	510	379	7	–	3404	184	473	347	1	–	628	376	376	376
Barbel	*Barbus barbus*	69	68 (8)	111267	171	648	455	34	18 (6)	36145	50	655	331	23	9 (1)	15581	93	640	246
Chub	*Squalius cephalus*	30	20	6424	97	372	235	302	51 (1)	18781	45	345	145	78	18 (2)	6174	64	310	156
Spirlin	*Alburnoides bipunctatus*	42	–	295	58	109	81	766	–	6598	44	119	86	15	–	126	72	105	84
Grayling	*Thymallus thymallus*	2	2	526	266	293	280	8	8	1692	210	318	264	–	–	–	–	–	–
Loach	*Barbatula barbatula*	2	–	13,9	85	97	91	48	–	228	54	105	85	89	–	370	55	105	74
Bullhead	*Cottus rhenanus*	3	–	16	67	85	74	61	–	360	30	114	72	11	–	68	50	105	72
Lamprey	*Lampetra planeri*	–	–	–	–	–	–	1	–	14	151	151	151	2	–	8	92	167	130
Eurytopic species (%)		**9.7**%						**19.9**%						**17.9**%					
Roach	*Rutilus rutilus*	3	3	594	195	266	221	27	2	1346	56	203	132	26	–	376	63	153	93
Gudgeon	*Gobio gobio*	2	–	26	101	102	102	117	–	2620	50	146	118	3	–	44	97	113	103
Minnow	*Phoxinus phoxinus*	18	–	37	45	65	57	204	–	705	34	98	59	26	–	33	32	65	43
Eel	*Anguilla anguilla*	1	1	82	398	398	398	–	–	–	–	–	–	1	1	90	384	384	384
T.S stickleback	*Gasterosteus aculeatus*	–	–	–	–	–	–	1	–	2	55	55	55	–	–	–	–	–	–
Limnophilic species (%)		**10.1**%						**7.7**%						**9.3**%					
Pike	*Esox lucius*	16	8	47967	418	850	661	3	2	9050	578	793	669	1	1	5150	840	840	840
Perch	*Perca fluviatilis*	6	–	1536	221	285	245	132	11	9238	65	289	154	28	1	2198	80	236	160
Crucian carp	*Carassius carassius*	1	–	670	312	312	312	–	–	–	–	–	–	–	2	–	–	–	–
Ruffe	*Gymnocephalus cernua*	2	–	33	103	105	104	–	–	–	–	–	–	–	–	–	–	–	–
Total		247	136 (10)	196907	–	–	–	1754	128 (13)	101377	–	–	–	327	40 (5)	35436	–	–	–

[a]: non-native species.

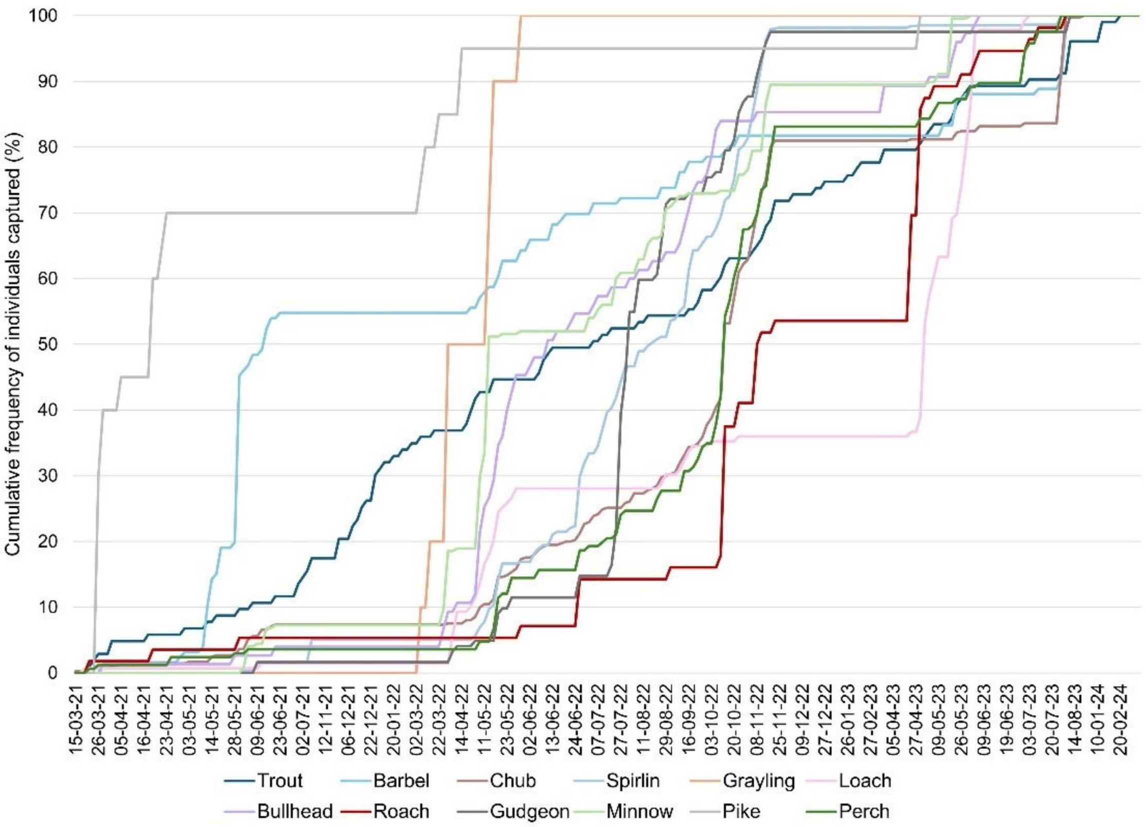

Figure 3. Cumulative frequency of individuals captured (%) per species according to the monitoring days during three consecutive years.

individuals captured each year (82.7% between 2021 and 2022, 72.4% between 2022 and 2023 and 72.7% between 2023 and 2024). The most abundant species was the barbel between 2021 and 2022 ($n = 69$), the spirlin between 2022 and 2023 ($n = 766$), and the loach between 2023 and 2024 ($n = 89$).

In terms of biomass, the highest total biomass was in the first year of monitoring, with 196,907 g, after which the biomass decreased from year to year. The barbel was the dominant species during the three years of monitoring (11.3, 36.1 and 15.6 kg, respectively), representing 48.8% of the biomass. The largest species captured in each year was pike (850, 793 and 840 mm, respectively). The smallest species captured was the minnow between 2021 and 2022 and 2023 and 2024 (size = 45 mm and 32 mm, respectively) and the gudgeon between 2022 and 2023 (size = 30 mm). During the three years of monitoring, 304 individuals were tagged with RFID tags, including 136 between 2021 and 2022, 128 between 2022 and 2023 and 40 between 2023 and 2024. Of the 306 individuals marked, 28 were recaptured in the fishway, and four were recaptured upstream during electrofishing (Table 2).

[a]Non-native species.

The most abundant species captured in the fishway after three years of monitoring was the spirlin (35.3%). No dace was captured in the fishway, and 11.3% were counted downstream. The Spearman's rank correlation test showed a significant correlation between the fish populations present downstream of the waterfall and those captured in the fishway during the three years of monitoring ($\rho = 0.58$, $p < .01$; Figure 2). The Bray–Curtis dissimilarity index showed greater similarity with downstream populations ($D_{BC} = 0.60$) than upstream ($D_{BC} = 0.70$; Table 1). No significant differences were observed between the biomass and abundance of species present downstream and those captured in the fishway and between species present upstream and those captured in the fishway (Mann–Whitney test, $p > .05$).

The cumulative frequency of fish captured during the three consecutive years of monitoring showed that trout was homogeneously captured over the monitoring period (Chi^2 test, $p > .05$). The other species had a heterogeneous capture distribution: barbel, chub, spirlin, grayling, loach, bullhead, roach, gudgeon, minnow, pike and perch (Chi^2 test, $p < .05$). Pike and barbel reached 50% of their capture in the first year of monitoring, after 17 and 42 days of monitoring, respectively. Several species reached 50% of their capture during the second year of monitoring: the grayling (after 83 days), the trout (after 115 days of monitoring), the chub (after 144 days), the spirlin (after 128 days), the bullhead (after 105 days), the roach (after 151 days), the gudgeon (after 123 days), the minnow (after 92 days) and

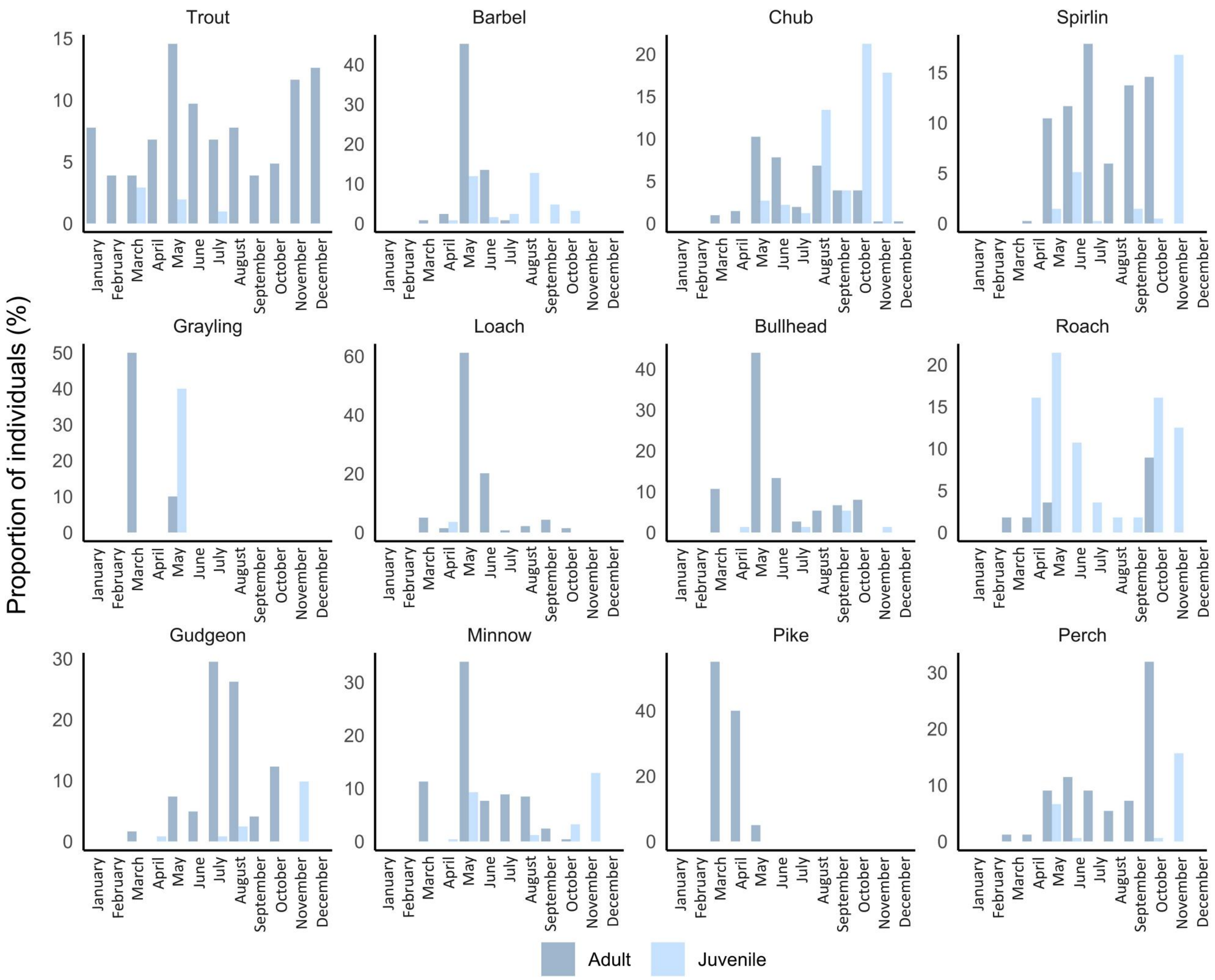

Figure 4. Histograms of the periodicity of captures throughout the year (by months) expressed as a percentage of individuals captured for each species (trout, barbel, chub, spirlin, grayling, loach, bullhead, roach, gudgeon, minnow, pike and perch) with a distinction between adults and juveniles.

the perch (after 144 days). The loach had 50% of their capture in the last year of monitoring, after 188 days of monitoring (Figure 3).

The periodicity of fish captured showed that some species were captured evenly throughout the year, while other species had peaks at specific times. Trout were captured throughout the year, with the highest capture rate in May ($n = 16.5\%$). Some species (chub, spirlin, perch, roach and gudgeon) were not or poorly captured during the winter (December, January and February) but were captured during the rest of the year with the highest capture rates in July (spirlin = 18.1% and gudgeon = 30.3%) and October (chub = 25.1%, roach = 25% and perch = 32.5%). We observed that other species had capture peaks at specific times of the year, like the barbel, the loach, the bullhead and the minnow, with 57.1%, 61.1%, 44% and 43.1%, respectively, of the capture rate in May. The pike was mainly captured in March and April, with 55% and 40%, respectively, of captures, and only adults were captured. The periodicity with which juveniles were captured was significantly different from that of adults for the barbel, the chub, the grayling, the bullhead, the minnow and the perch (Mann–Whitney test, $p < .05$). The highest captured rate of juveniles occurred during the autumn for chub ($n = 21.2\%$ in October), spirlin ($n = 16.8\%$ in November), gudgeon ($n = 9.8\%$ in November) and minnow ($n = 12.9\%$ in November). The barbel and the grayling had their highest number of juvenile captures in summer, with 12.7% in August and 40.0% in May, respectively. Most of the roach captured were juveniles, with the highest captured rate in May ($n = 21.4\%$; Figure 4).

Analysis of the sizes of the individuals captured showed that the median size of the individuals captured during the first year of monitoring (2021–2022) after the opening of the migratory axis was very significantly greater than the median size of the individuals present downstream for all species (Dunn test, $p < .001$): the barbel, 494 mm and 372 mm; the chub, 222 mm and 115 mm; and the trou,t 324 mm and 197 mm, respectively. The median size of individuals for barbel and chub was also significantly greater in 2021–2022 than in the

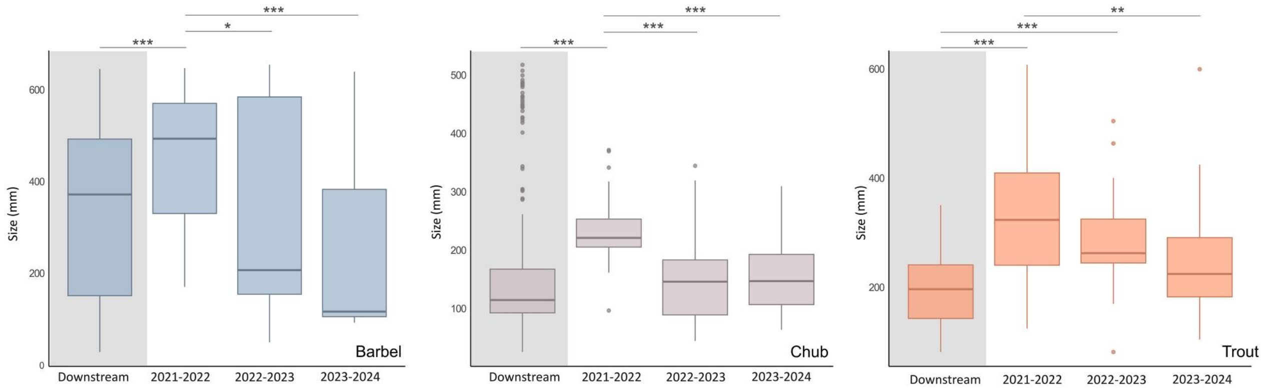

Figure 5. Size distribution of individuals captured downstream of the waterfall before the opening of the migratory axis (grey background) and individuals captured within the fishway during the three years following the opening of the migratory axis. The horizontal line inside the triangle is the median, rectangle extremities are first and third quartiles, the end of the whiskers are 5 and 95 quantiles, and round dots are outliers. Level of significance: * $p < .05$; ** $p < .01$; *** $p < .001$.

following two years (2022–2023 and 2023–2024), with 208 mm for barbel and 146 mm for chub in 2022–2023 and 117 mm for babel and 148 mm for chub in 2023–2024. Although the median sizes of the trout were smaller in 2022–2023 (263 mm) and 2023–2024 (225 mm) compared to the first year, a significant difference was only observed between 2021–2022 and 2023–2024 (Dunn test, $p < .01$; Figure 5).

4. Discussion

Multi-dimensional and multi-annual analysis is a good strategy for determining the effect of defragmentation on a river section. The use of fishways through seasons has mainly been studied using automatic video recordings (Hatry et al. 2016; Grimardias et al. 2022), although some studies have used hand-held monitoring of individuals captured in cages to obtain the identification of each species as well as biometric data (Benitez et al. 2022; Tan et al. 2024). Some studies have also examined the impact of opening up the migratory axis on the fish populations present upstream and downstream of the obstacle using electrofishing (Tummers et al. 2016; Birnie-Gauvin et al. 2020). In our study, we examined the fishway use and the state of fish populations upstream and downstream to obtain an overall view of the impact of defragmentation by combining several complementary methods and analysis over several years to analyse what happens before, during and after the opening of a migratory axis.

Our results revealed differences between the fish populations upstream and downstream of the waterfall before the opening of the migratory axis, with a more diverse and equitably distributed community downstream. We can hypothesise the historical impact of the waterfall, which represented an obstacle to upstream migration for more than 50 years, limiting the specific diversity upstream (Junker et al. 2012; Coleman et al. 2018; Vega-Retter et al. 2020). The difference in species richness between upstream and downstream could also be explained by hydromorphological conditions upstream that would be less favourable to some species (e.g. ubiquitous or limnophilic species) present downstream of the waterfall. Although the entire site is located in a grayling/barbel zone, it is likely that hydromorphological conditions differ locally between the upstream and downstream sectors of the waterfall. These potential differences could influence habitat suitability for certain species. In addition, as downstream migration was possible, the populations present upstream could feed the populations present downstream and thus contribute to equitability. Valenzuela-Aguayo et al. (2019) showed that natural or anthropogenic barriers annihilated upstream gene flow but that downstream movements remained possible despite major falls, enabling downstream populations to be fed. Tan et al. (2024) also showed that alpha diversity indices were higher downstream of a 7.8 m high obstacle before the opening of the migratory axis, with greater species richness and greater equitability between species.

As upstream migration was previously impossible, the recolonisation of species absent upstream and present downstream could not occur. Given that the removal of the Coo waterfall is not an option, recolonisation was only achievable through the installation of a crossing device. The installation of the fishway has enabled upstream movements to be re-established. Ideally, the entrance to the fishway would be located directly adjacent to the obstacle. However, due to topographic and landscape constraints, it was positioned 100 m away on the left bank of the waterfall. Despite this suboptimal placement, results demonstrated that more than 2,000 individuals from 17 of the 20 downstream species used the fishway and used new habitats available upstream, as shown by the four individuals recaptured upstream during electrofishing. However, a complementary study by Gelder et al. (2024) estimated the efficiency of the fishway at 7.9%, suggesting that the quantity of fish using the fishway underrepresents the real number of fish attempting to migrate upstream. Nevertheless, the structure is used by a wide range of species, confirming its multi-species functionality, and discussions are ongoing to improve its overall efficiency. In addition, the populations using the fishway were significantly correlated with those downstream, confirming that the fishway effectively facilitates upstream migration of the established population (Tan et al. 2024). The fishway was mainly used by rheophilic species, which is consistent with the habitat characteristics of this sector of the Amblève River. The results also showed that the spirlin was the most abundant species captured during the second year of monitoring, with 766 individuals. This capture peak could potentially reflect the capture of a migrating school of this gregarious species, which may contribute to interannual variation in fishway use (Prchalová et al. 2011; Benitez et al. 2015). No spirlin were captured during electrofishing upstream of the waterfall prior to the opening of the migratory axis, underscoring the fishway's role in enabling the recolonisation of species previously absent upstream (Tummers et al. 2016; Kiffney et al. 2018). In terms of biomass, total biomass decreased from year to year, with the highest total biomass during the year following the opening of the migratory axis, which suggests an opening effect (Benitez et al. 2015). Although spirlin and loach were captured in much higher numbers over the last two years of monitoring compared to barbel (766 spirlin vs. 34 barbel between 2022 and 2023 and 89 loach vs. 23 barbel between 2023 and 2024), underlining the importance of the multi-species nature of the fishway, barbel accounted for the highest biomass each year due to their larger size. Chub were also captured in large numbers, but the average size of these individuals indicated that they were mostly juveniles (mean size $\leq$ 160 mm), while the barbel were, on average, adults (mean size $\geq$ 250 mm). The abundance and biomass of some species decreased over the monitoring period, while for others, the biomass and abundance fluctuated from year to year. This trend was also shown by the cumulative frequency of individuals captured which showed that for some species an opening effect has been visible, such as for barbel and pike, which reached 50% of their captures in the first year. The barbel is a species known in the literature to move regularly and over great distances (Ovidio et al. 2007; Le Pichon et al. 2016). What we observed for pike can be associated with quick colonisation, with 17 individuals captured in the first year of monitoring, followed by a large decrease in the number of individuals captured in the next two years (Gelder et al. 2023). The majority of species (grayling, trout, chub, spirlin, bullhead, roach, gudgeon and minnow) reached 50% of their captures during the second year, and the loach reached this during the last year of monitoring. Except for trout, which were homogeneously captured throughout the year, the other species showed notable variations in their captures from one year to the next. Captures can fluctuate based on environmental conditions. Although we did not analyse the temperature and flow data as part of this study, it is likely that environmental conditions during 2022–2023 and 2023–2024 were favourable for stimulating the migration of these species and consequently increased the number of fish captured. Fishway monitoring over several consecutive years has enabled us to analyse in greater detail the colonisation dynamics of fish populations on a multi-annual scale, as well as on a seasonal scale.

The periodicity of captures showed that adult individuals were mainly captured during the months corresponding to the species spawning period, between April and July and between March and April for the pike (Prchalová et al. 2011). These potamodromous species are known in the literature to migrate upstream during the spawning period to find suitable habitats (Ovidio et al. 2007; Benitez et al. 2015; Romão et al. 2019; Gelder et al. 2023). Significant differences between captures of adults and juveniles were observed, with a higher capture rate in summer and autumn. To meet their ontogenic needs and allow them to grow, juveniles take advantage of optimal environmental conditions to move around in search of suitable habitats. Benitez et al. (2022) showed that juveniles moved mainly during the summer when temperatures were higher and flow lower. The movements of juveniles may be explained in the following ways: (i) after spawning in spring/early summer, the individuals have reached a sufficient size in autumn to swim against the current and migrate upstream, and (ii) individuals migrate to find suitable habitats to overwinter (Prchalová et al. 2011). These results show that juveniles are also able to use the fishway, enabling ecological recovery for the entire life cycle of the fish. Analysis of the size of the individuals showed that significantly larger individuals first colonised the fishway compared with the individuals present downstream and the individuals that used the fishway during the second and third year of monitoring. Larger individuals are known to have better swimming capacity and are, therefore, better able to cross larger currents (Baudoin et al. 2015; Grimardias et al. 2022; Eggers et al. 2024). They are also more likely to cover greater distances in response to the need of migratory individuals to explore and have larger home ranges, likely resulting in extended movements over longer distances (Minns 1995; Woolnough et al. 2009; Burbank et al. 2023;). Griffiths (2006) showed that resident individuals were smaller in size than migratory potamodromous fish. It is likely that, depending on environmental conditions, if food resources become scarce and available habitats less suitable, some individuals will adopt migratory behaviour. The opening up of the migratory axis has enabled individuals to gain access to new habitats and to balance the use of different habitats. Moreover, the marking individuals revealed that some fish moved downstream, crossed the waterfall and re-used the fishway. Consequently, these results proved that the individuals could cross the waterfall and decide to move back downstream, probably to return to known habitats. Although the number of recaptures upstream is low compared with the number of individuals marked, it is very likely that the individuals moved and dispersed upstream, as demonstrated by Gelder et al. (2023) in the same study site.

5. Conclusion

This study contributes to the growing body of knowledge on river defragmentation and the response of fish populations to the opening of a migratory axis. It highlights the importance of understanding the states of fish populations downstream of an obstacle before the installation of a fishway. This knowledge is crucial for selecting the right type of device and placing it in the optimal location (Jones et al. 2023; Bower et al. 2024). Very few studies have analysed the effect over several years of restoring connectivity on fish populations. Our study emphasises the need for continuous monitoring over several years to fully understand the dynamics involved, taking into account the initial state of the populations before the opening of the migratory axis as well as what happens within the fishway as soon as it is opened. The results showed the importance of opening up the migratory axis upstream for spawning and accessing other functional habitats or completing their life cycle not only for diadromous species but also for potamodromous species (Romão et al. 2018; Bao et al. 2019). We demonstrated the usefulness of the multi-species nature of the fishway, which has enabled many species, including those considered less migratory and juveniles with varying swimming capacities, to benefit from this opening. Indeed, potamodromous species also migrate within rivers, and studying their movements can offer important insights for future management strategies. In addition, our capture periodicity results showed that the fishway is used throughout the year and not only during the spawning period, showing the importance of keeping this type of device open continuously (Benitez et al. 2022; Gelder et al. 2023). In order to obtain a complete overview and refine our understanding of habitat connectivity, it would be interesting to continue the monitoring and to carry out new electrofishing upstream of the site after several decades of opening in order to study any changes in the populations upstream of the waterfall.

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Disclosure statement

The authors report there are no competing interests to declare.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Baldan D, Cunillera-Montcusí D, Funk A, Piniewski M, Cañedo-Argüelles M, Hein T. 2023. The effects of longitudinal fragmentation on riverine beta diversity are modulated by fragmentation intensity. Sci Total Environ. 903:166703. doi: 10.1016/j.scitotenv.2023.166703.

Bao J, Li W, Zhang C, Mi X, Li H, Zhao X, Cao N, Twardek WM, Cooke SJ, Duan M. 2019. Quantitative assessment of fish passage efficiency at a vertical-slot fishway on the Daduhe River in Southwest China. Ecol Eng. 141:105597. doi: 10.1016/j.ecoleng.2019.105597.

Barbarossa V, Schmitt RJP. 2024. Strategic restoration-development mitigates tradeoffs between hydropower and fish habitat fragmentation in the Mekong. One Earth. 7(6):1096–1107. doi: 10.1016/j.oneear.2024.05.009.

Baudoin J-M, Burgun V, Chanseau M, Larinier M, Ovidio M, Sremski W, Steinbach P, Voegtle B. 2015. Assessing the passage of obstacles by fish. Concepts, Design and Application. Onema: paris, France.

Belletti B, Garcia De Leaniz C, Jones J, Bizzi S, Börger L, Segura G, Castelletti A, Van De Bund W, Aarestrup K, Barry J, et al. 2020. More than one million barriers fragment Europe's rivers. Nature. 588(7838):436–441. doi: 10.1038/s41586-020-3005-2.

Benitez J-P, Dierckx A, Nzau Matondo B, Rollin X, Ovidio M. 2018. Movement behaviours of potamodromous fish within a large anthropised river after the reestablishment of the longitudinal connectivity. Fish Res. 207:140–149. doi: 10.1016/j.fishres.2018.06.008.

Benitez J-P, Dierckx A, Rimbaud G, Nzau Matondo B, Renardy S, Rollin X, Gillet A, Dumonceau F, Poncin P, Philippart J-C, et al. 2022. Assessment of fish abundance, biodiversity and movement periodicity changes in a large river over a 20-year period. Environments. 9(2):22. doi: 10.3390/environments9020022.

Benitez J-P, Nzau Matondo B, Dierckx A, Ovidio M. 2015. An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. Aquat Ecol. 49(4):481–497. doi: 10.1007/s10452-015-9541-4.

Birnie-Gauvin K, Nielsen J, Frandsen SB, Olsen H-M, Aarestrup K. 2020. Catchment-scale effects of river fragmentation: a case study on restoring connectivity. J Environ Manage. 264:110408. doi: 10.1016/j.jenvman.2020.110408.

Bower LM, Marion CA, Scott M, Kubach K, Gelder A. 2024. Fish assemblage and functional trait responses to small-dam removal. Freshwater Biology. 69(8):1043–1056. doi: 10.1111/fwb.14288.

Burbank J, Gao K, Power M. 2023. Factors influencing the home range of freshwater fishes. Ecol Freshwater Fish. 32(4):916–925. doi: 10.1111/eff.12732.

Coleman RA, Gauffre B, Pavlova A, Beheregaray LB, Kearns J, Lyon J, Sasaki M, Leblois R, Sgro C, Sunnucks P. 2018. Artificial barriers prevent genetic recovery of small isolated populations of a low-mobility freshwater fish. Heredity (Edinb). 120(6):515–532. doi: 10.1038/s41437-017-0008-3.

Cook DR, Sullivan SMP. 2018. Associations between riffle development and aquatic biota following lowhead dam removal. Environ Monit Assess. 190(6):339. doi: 10.1007/s10661-018-6716-1.

Dębowski P, Bernaś R, Radtke G, Święcki W. 2022. Assessment of the effectiveness of fish passage through the vertical-slot fishway at the main dam on the longest Baltic River. Fisheries & Aquatic Life. 30(4):175–183. doi: 10.2478/aopf-2022-0016.

Dodd JR, Cowx IG, Bolland JD. 2017. Efficiency of a nature-like bypass channel for restoring longitudinal connectivity for a river-resident population of brown trout. J Environ Manage. 204(Pt 1):318–326. doi: 10.1016/j.jenvman.2017.09.004.

Eggers F, Schiavon A, Calles O, Watz J, Comoglio C, Candiotto A, Nyqvist D. 2024. Fish behaviour in a vertical slot fishway: multi-species upstream passage success, size selectivity and diel passage patterns in a large Italian river. River Research & Apps. 41(4):849–863. doi: 10.1002/rra.4409.

Falke JA, Gido KB. 2006. Effects of reservoir connectivity on stream fish assemblages in the Great Plains. Can J Fish Aquat Sci. 63(3):480–493. doi: 10.1139/f05-233.

García-Vega A, Sanz-Ronda FJ, Fernandes Celestino L, Makrakis S, Leunda PM. 2018. Potamodromous brown trout movements in the North of the Iberian Peninsula: modelling past, present and future based on continuous fishway monitoring. Sci Total Environ. 640–641:1521–1536. doi: 10.1016/j.scitotenv.2018.05.339.

Gelder J, Benitez J-P, Colson D, Sonny D, Ovidio M. 2024a. Evaluating the efficiency of a fishway installed near a high, artificially created waterfall. River Research & Apps. 41(3):624–637. doi: 10.1002/rra.4398.

Gelder J, Benitez J-P, Ovidio M. 2023. Multi-year analysis of the fish colonisation dynamic in three newly installed fishways in medium sized Belgian rivers. Knowl Manag Aquat Ecosyst. 424:12. doi: 10.1051/kmae/2023009.

Gelder J, Benitez J-P, Ovidio M. 2024b. What do fish do after passing through a fishway? A radio-telemetry study on patrimonial holobiotic species. Ecol Freshwater Fish. 33(3):16. doi: 10.1111/eff.12782.

Griffiths D. 2006. Pattern and process in the ecological biogeography of European freshwater fish. J Anim Ecol. 75(3):734–751. 10.1111/j.1365-2656.2006.01094.x. 16689956

Grimardias D, Chasserieau C, Beaufils M, Cattanéo F. 2022. Ecological connectivity of the upper Rhône River: upstream fish passage at two successive large hydroelectric dams for partially migratory species. Ecol Eng. 178:106545. doi: 10.1016/j.ecoleng.2022.106545.

Hatry C, Thiem JD, Hatin D, Dumont P, Smokorowski KE, Cooke SJ. 2016. Fishway approach behaviour and passage of three redhorse species (Moxostoma anisurum, M. carinatum, and M. macrolepidotum) in the Richelieu River, Quebec. Environ Biol Fish. 99(2-3):249–263. doi: 10.1007/s10641-016-0471-3.

Haworth MR, Bestgen KR. 2024. Low-head dam fragmentation, habitat alteration, and invasive predators degrade a Western United States stream fish assemblage. Ecol Freshwater Fish. 33(3):e12773. doi: 10.1111/eff.12773.

Huet M. 1949. Aperçu des relations entre la pente et les populations piscicoles des eaux courantes. Schweiz Z Hydrologie. 11(3-4):332–351. doi: 10.1007/BF02503356.

Jones AC, Meiners SJ, Effert-Fanta E, Thomas T, Smith SCF, Colombo RE. 2023. Low-head dam removal increases functional diversity of stream fish assemblages. River Research & Apps. 39(1):3–20. doi: 10.1002/rra.4063.

Junker J, Peter A, Wagner CE, Mwaiko S, Germann B, Seehausen O, Keller I. 2012. River fragmentation increases localized population genetic structure and enhances asymmetry of dispersal in bullhead (*Cottus gobio*). Conserv Genet. 13(2):545–556. doi: 10.1007/s10592-011-0306-x.

Kiffney PM, Cram B, Faulds PL, Burton K, Koehler M, Quinn TP. 2018. Spatiotemporal patterns of mountain whitefish (*Prosopium williamsoni*) in response to a restoration of longitudinal connectivity. Ecol Freshwater Fish. 27(4):1037–1053. doi: 10.1111/eff.12413.

Kowal JL, Funk A, Unfer G, Baldan D, Haidvogl G, Hauer C, Ferreira MT, Branco P, Schinegger R, Hein T. 2024. River continuum disruptions in a highly altered system: the perspective of potamodromous fish. Ecol Indic. 164:112130. doi: 10.1016/j.ecolind.2024.112130.

Legrand M, Briand C, Buisson L, Artur G, Azam D, Baisez A, Barracou D, Bourré N, Carry L, Caudal A-L, et al. 2020. Contrasting trends between species and catchments in diadromous fish counts over the last 30 years in France. Knowl Manag Aquat Ecosyst. 421(421):7. doi: 10.1051/kmae/2019046.

Le Pichon C, Tales É, Gorges G, Baudry J, Boët P. 2016. Using a continuous riverscape survey to examine the effects of the spatial structure of functional habitats on fish distribution. J Freshwater Ecol. 31(1):1–19. doi: 10.1080/02705060.2015.1035345.

Minns CK. 1995. Allometry of home range size in lake and river fishes. Can J Fish Aquat Sci. 52(7):1499–1508. doi: 10.1139/f95-144.

Moccetti P, Dodd JR, Joyce DA, Nunn AD, Gillespie B, Bolland JD. 2024. Genetic consequences of improved river connectivity in brown trout (*Salmo trutta* L.). Evol Appl. 17(4):e13660. doi: 10.1111/eva.13660.

Ovidio M, Dierckx A, Benitez J-P. 2023. Movement behaviour and fishway performance for endemic and exotic species in a large anthropized river. Limnologica. 99:126061. doi: 10.1016/j.limno.2023.126061.

Ovidio M, Parkinson D, Philippart J-C, Baras E. 2007. Multiyear homing and fidelity to residence areas by individual barbel (*Barbus barbus*). Belg J Zool. 137: 183–190. doi: 137.: 183–190

Ovidio M, Sonny D, Watthez Q, Goffaux D, Detrait O, Orban P, Nzau Matondo B, Renardy S, Dierckx A, Benitez J-P. 2020. Evaluation of the performance of successive multispecies improved fishways to reconnect a rehabilitated river. Wetlands Ecol Manage. 28(4):641–654. doi: 10.1007/s11273-020-09737-w.

Panagiotopoulos P, Buijse AD, Winter HV, Nagelkerke LAJ. 2024. A large-scale passage evaluation for multiple fish species: lessons from 82 fishways in lowland rivers and brooks. Ecol Eng. 199:107158. doi: 10.1016/j.ecoleng.2023.107158.

Philippart J-C, Vranken M. 1983. Atlas des poissons de Wallonie: distribution, écologie, éthologie, pêche, conservation, *Cahiers d'éthologie*, 3 (supplément 1-2) | 1983, 1–395

Pielou EC. 1966. Species-diversity and pattern-diversity in the study of ecological succession. J Theor Biol. 10(2): 370–383. doi: 10.1016/0022-5193(66)90133-0.

Poff NL, Hart DD. 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience. 52(8):659. doi: 10.1641/0006-3568(2002)052[0659:HDVAWI]2.0.CO;2.

Prchalová M, Horký P, SlavíK O, VetešNíK L, Halačka K. 2011. Fish occurrence in the fishpass on the lowland section of the River Elbe, Czech Republic, with respect to water temperature, water flow and fish size. Folia Zoologica. 60(2):104–114. doi: 10.25225/fozo.v60.i2.a4.2011.

Romão F, Branco P, Quaresma AL, Amaral SD, Pinheiro AN. 2018. Effectiveness of a multi-slot vertical slot fishway versus a standard vertical slot fishway for potamodromous cyprinids. Hydrobiologia. 816(1):153–163. doi: 10.1007/s10750-018-3580-5.

Romão F, Quaresma AL, Santos JM, Branco P, Pinheiro AN. 2019. Cyprinid passage performance in an experimental multislot fishway across distinct seasons. Mar Freshwater Res. 70(6):881. doi: 10.1071/MF18232.

Roscoe DW, Hinch SG. 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. Fish and Fisheries. 11(1): 12–33. doi: 10.1111/j.1467-2979.2009.00333.x.

Ryan Bellmore J, Duda JJ, Craig LS, Greene SL, Torgersen CE, Collins MJ, Vittum K. 2017. Status and trends of dam removal research in the United States. WIREs Water. 4(2):e1164. doi: 10.1002/wat2.1164.

Shannon CE, Weiner W. 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana, 127 p.

Silva AT, Lucas MC, Castro-Santos T, Katopodis C, Baumgartner LJ, Thiem JD, Aarestrup K, Pompeu PS, O'Brien GC, Braun DC, et al. 2018. The future of fish passage science, engineering, and practice. Fish Fish. 19(2):340–362. doi: 10.1111/faf.12258.

Simpson EH. 1949. Measurement of diversity. Nature. 163(4148):688–688. doi: 10.1038/163688a0.

Tan J, Sun J, Wang Y, Tian H, Cheng B, Qing J, Yan X, Sun G, Ke S, Kattel GR, et al. 2024. Fish community dynamics following the low-head dam removal and newly installed fish passage in a headstream tributary of Jinsha River, Southwest China. Sci Total Environ. 954:176774. doi: 10.1016/j.scitotenv.2024.176774.

Tummers JS, Hudson S, Lucas MC. 2016. Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach. Sci Total Environ. 569–570:850–860. doi: 10.1016/j.scitotenv.2016.06.207.

Valenzuela-Aguayo F, McCracken GR, Manosalva A, Habit E, Ruzzante DE. 2019. Human-induced habitat fragmentation effects on connectivity, diversity, and population persistence of an endemic fish, Percilia irwini, in the Biobío River basin (Chile). Evol Appl. 13(4):794–807. 10.1111/eva.12901. 32211068

Vega-Retter C, Muñoz-Rojas P, Rojas-Hernández N, Copaja S, Flores-Prado L, Véliz D. 2020. Dammed river: short- and long-term consequences for fish species inhabiting a river in a Mediterranean climate in central Chile. Aquatic Conservation. 30(12):2254–2268. doi: 10.1002/aqc.3425.

Woolnough DA, Downing JA, Newton TJ. 2009. Fish movement and habitat use depends on water body size and shape. Ecol Freshwater Fish. 18(1):83–91. doi: 10.1111/j.1600-0633.2008.00326.x.

Yamamoto S, Morita K, Koizumi I, Maekawa K. 2004. Genetic differentiation of white-spotted charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial–temporal changes in gene frequencies. Conservation Genetics. 5(4):529–538. doi: 10.1023/B:COGE.0000041029.38961.a0.