RESEARCH ARTICLE

Evaluating the Efficiency of a Fishway Installed Near a High, Artificially Created Waterfall

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ABSTRACT

The installation of fishways is the most common method to restore connectivity and allow fish to carry out their life cycle. However, the performance and efficiency of fishways are still highly variable, particularly for freshwater potamodromous species. We aimed to determine the passage efficiency of a fishway installed in 2021 downstream of the Coo waterfall in Belgium to allow upstream migration and crossing of the 11.8 m height. We double-marked 38 individuals (RFID tag and radio transmitter) belonging to three species (*Barbus barbus*, *Salmo trutta* and *Thymallus thymallus*) from upstream and then released them 1.2 km downstream of the waterfall. A total of five automatic detection antennas were installed downstream of the waterfall and within the fishway, and the individuals were tracked with manual radio telemetry. We used several behavioural metrics to assess efficiency and attractiveness. The results indicate a lack of attractiveness of the fishway (overall rate of attraction < 25%). There was a higher detections at the waterfall (26 detections) than at the restitution channel (12 detections), where the entrance of the fishway was located. For individuals that reached the fishway entrance, the fishway efficiency was 12.5% for barbel and 6.3% for trout, with an average fishway entrance searching delay of 25 days for barbel. The lack of attractiveness led to numerous back-and-forth movements by individuals to find the entrance and the search for a substitute spawning habitat downstream. Our results indicate the need to improve the attractiveness of the fishway, in particular by improving the attraction flow.

1 | Introduction

Freshwater potamodromous fish are known to move regularly from one habitat to another to meet their ecological needs. They can travel great distances, particularly during their migration periods (Benitez et al. 2015; Benitez and Ovidio 2018; García-Vega, Sanz-Ronda, and Fuentes-Pérez 2017). The ecological continuity of the river is essential for these movements and underscores the necessity of having diverse, accessible and interconnected functional habitats to support robust population dynamics (Consuegra et al. 2021; Romão et al. 2018). However, many anthropogenic fishways have been installed on rivers in recent decades to meet human needs, with the consequence of fragmenting rivers, restricting access to different habitats and isolating populations (Birnie-Gauvin et al. 2020; Cooke and Hinch 2013). Today, more than 1.2 million obstacles are present on European rivers (Belletti et al. 2020). These structures modify the hydromorphology of the river and the substrate movement dynamics, thereby impacting the quality of habitats (Baudoin et al. 2015; Carpenter, Stanley, and Vander Zanden 2011), as well as altering the migratory movements of fish (De Leeuw and Winter 2008; Ovidio et al. 2021).

In order to restore connectivity and access to functional habitats and to allow genetic mixing, different models of fishways have been installed worldwide (Gelder, Benitez, and Ovidio 2023; Mameri et al. 2019; Silva et al. 2018). The type of fishway installed will depend on the infrastructure, the target species, the size of the individuals and the hydraulic conditions of the segment (Lothian et al. 2019; Ovidio et al. 2017; Romão et al. 2019). Initially designed for diadromous species such as salmonids, fishways have evolved to encompass a wider range of species (Alvarez-Vázquez et al. 2008; Grimardias et al. 2022; Nunn and Cowx 2012). Several factors need to be considered when designing a fishway. An essential point is that fish must find the entrance and be attracted to enter the fishway. For this reason, studies can be carried out before the installation to determine the ideal location for the entrance to the fishway, where a stronger current is often created to attract individuals (Bunt 2001; Noonan, Grant, and Jackson 2012; Romão et al. 2017). However, it is essential to carry out post-installation studies to determine the fishway's effectiveness (Roscoe and Hinch 2010; Woolsey et al. 2007). Although many studies have been carried out on this subject in recent years, they have generally only used automatic individual detection systems placed on the infrastructure (Forty, Spees, and Lucas 2016; Grimardias et al. 2022; Hatry et al. 2016). It is essential to study the effectiveness of fishways at a multi-species scale using different methods to gain an overall view of the efficiency of the fishway (Bao et al. 2019; Ovidio et al. 2020). It is also very relevant to analyse the behaviour of the fish when they approach the fishway (Silva et al. 2011).

Today, there are over 4800 obstacles on Belgian rivers, of which approximately 2700 are potentially impassable (unpublished data from SPW's Walloon region). The Amblève River has seven main obstacles to fish mobility, including the Coo waterfall, an 11.8 m high obstacle, which has been an impassable barrier for 50 years (Gelder, Benitez, and Ovidio 2024; Ovidio and Philippart 2008). In 2021, a fishway was installed on this particular site to restore connectivity, and 21 fish species have been captured, but quantitatively, some species are poorly represented (Gelder et al. 2023). We hypothesised that the presence of the waterfall may attract fish in the wrong direction and prevent them from heading towards the fishway. The objective of this study was to evaluate the fishway performance using the following combination of telemetry: (i) automatic telemetry via integrated transponder tag Radio Frequency IDentification (RFID) and (ii) manual radiotelemetry using a radio transmitter in order to determine the pre-crossing behaviour of individuals through the fishway. To meet this objective, individuals belonging to three fish species were tagged: the barbel (*Barbus barbus*), the trout (*Salmo trutta*) and the grayling (*Thymallus thymallus*).

2 | Material and Method

2.1 | Study Area and Fishway Monitoring

The Coo waterfall is located in the Amblève River in the Meuse Basin in southeast Belgium, 39.7 km from the confluence with the Ourthe River. The average annual discharge of the Amblève River is 19.3 m^3/s with good ecological and physicochemical water quality (Public Service of Wallonia—DEE). Downstream of the Coo waterfall is qualified as a grayling/barbel fish zone (Huet 1949). The Coo waterfall is an artificial obstacle that is 11.8 m high and was created during the Middle Ages to cut a meander. The installation of a pumped storage plant in 1970 made the obstacle impassable for fish during upstream migration by diverting the natural arm of the river to power the turbine and release water downstream into a restitution channel (Gelder, Benitez, and Ovidio 2024). A capture–transport fishway was installed in 2021 on the left bank of the waterfall, within the restitution canal of the Coo derivation hydroelectric power station. The fishway is equipped with a 2.8 × 1.9 × 1.8 m capture cage monitored one to three times per week (Figure 1). After their capture in the fishway, fish are transported by car upstream of the obstacle. This is the unique capture–transport fishway in Belgium because the 11.8 m height difference makes it very complicated and expensive to install a classical fishway.

The fishway has been monitored since 15 March 2021. Fish captured in the cage were anaesthetised in a solution of 2-phenoxy-ethanol (0.2 mL/L), sexed, identified, weighed (±1 g) and measured (±1 mm, fork length). The individuals were then transported to a release point 30 m upstream of the waterfall (Gelder et al. 2023). To date, 21 different fish species have been captured, and the three more abundant species are spirlin (*Alburnoides bipunctatus*), chub (*Squalius cephalus*) and minnow (*Phoxinus phoxinus*).

2.2 | Electrofishing and Fish Tagging

The study was carried out from 23 March 2022 to 10 January 2023. Electrofishing (Elektrofischfanggeräte EFKO 7000) was used at four different sites (S) upstream of the waterfall. S1 (23 March 2022), S2 (23 March 2022), S3 (14 April 2022) and S4 (11 October 2022) are 10.3, 4, 0.47 and 4.7 km upstream, respectively. Electrofishing captured 38 individuals belonging to three different rheophilic species (grayling, $n = 6$; barbel, $n = 16$; trout, $n = 16$). We chose species known in the literature for their mobility and/or their upstream migration during the spawning period and their homing behaviour so that they would want to return to their capture site (García-Vega et al. 2022; Ovidio et al. 2004, 2007). The date of the electrofishing was chosen to precede the spawning period of the species. However, no grayling of sufficient size was caught in the pre-spawning period (early March). Consequently, a second sample was obtained at the end of March (Table 1; Figure 2A). The grayling is a species known to reproduce from March to May when the temperature rises to 7°C–11°C (Ovidio et al. 2004; Parkinson, Philippart, and Baras 1999). These conditions had not yet been reached before the start of the study, so we assumed that the individuals had not yet reproduced. Captured individuals were anaesthetised (2 mL/L of 2-phenoxy-ethanol), weighed, measured and sexed. Only individuals whose weight/transmitter index did not exceed 2.5% were tagged (Ovidio et al. 2020). Two types of tags were implanted in all individuals in their intraperitoneal cavity according to the method used by Gelder, Benitez, and Ovidio (2024): a RFID tag (134.2 kHz, 23 × 3 mm, 0.7 g) and a radio transmitter (Sigma Eight MST-930, 30 × 8 mm, 3.7 g, 235 mm antenna, 150.34 MHz, pulse rate 1.5 s). In order to match the weight/transmitter index ≤ 2.5%, individuals had to

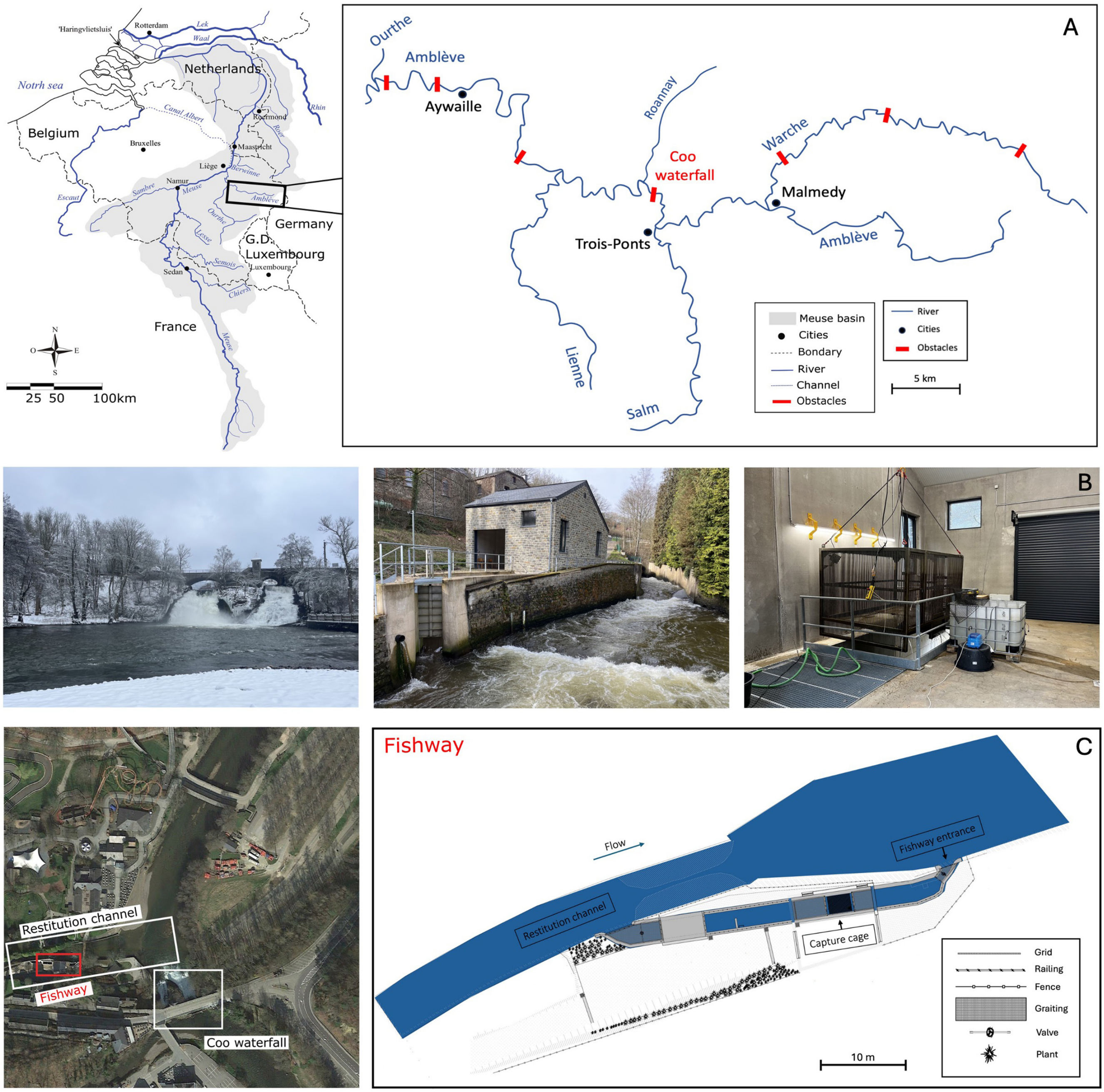

FIGURE 1 | Map of the Amblève River with its seven dams (A) with pictures showing the waterfall, the fishway and the capture cage (B) and an aerial view of the site with the schematic plan of the fishway (C). [Color figure can be viewed at wileyonlinelibrary.com]

weigh at least ≤150 g. The fish were then transported, on the same day as the electrofishing, in a 600 L tank with a bubbler system in a vehicle for 1.2 km downstream of the waterfall, where they were released.

2.3 | System for Fish Detection and Environmental Variables

A total of three radio antennas and two RFID antennas were installed on the Coo waterfall site to analyse the movements of individuals as they approached the waterfall and fishway. Around the waterfall, two aerial radio antennas and one underwater antenna were installed. One of these aerial antennas was installed at the entrance of the site 160 m downstream of the waterfall (A0). The second antenna was located 10 m downstream of the waterfall (A1) to detect fish approaching the waterfall. The underwater antenna was located at the entrance to the hydroelectric power station's restitution canal (A2) throughout the width of the canal 36 m downstream of the fishway. Around the fishway, two RFID antennas were placed: one at the entrance of the fishway (A3) and a second antenna at the entrance of the capture cage 10 m upstream of the entrance (A4) to confirm the passage of individuals in the fishway (Figure 2B). The RFID and radio antenna stations were operational from the start of the study (March 2022).

TABLE 1 | Biometric characteristics of individuals tagged: Number of individuals marked (*N*), mean size ± SD (fork length, mm), mean weight ± SD (g), sex (M = male, F = female, + = mature, I = indeterminate) and date and sites of capture.

Species	*N*	Mean size ± SD (mm)	Mean weight ± SD (g)	Sex	Capture site	Date of capture
Grayling	6	302.7 ± 17.7	323.7 ± 51.7	4 M/2 F$^+$	S1, S2, S3	23/03/2022 and 14/04/2022
Barbel	16	561.6 ± 74.0	2810.6 ± 1130.5	5 M/9 F/2 I	S2, S3	23/03/2022 and 14/04/2022
Trout	16	275.1 ± 40.2	240.9 ± 105.2	7 M$^+$/5 F/4 I	S4	11/10/2022

Radio antennas were used to analyse the approaching behaviour of individuals within the site. RFID antennas were used to analyse the movements of individuals in a narrower zone, the fishway and determine the performance of the crossing device. The selected orientation and spacing of these antennas were specifically configured to prevent any overlapping in their respective detection ranges.

The data obtained by the antennas enabled us to study several behavioural metrics (Ovidio et al. 2017):

- *Approach rate*—the percentage of individuals detected by radio and RFID antennas (A0, A1, A2, A3 and A4) compared to the total number of individuals detected at the previous antenna, except the approach rate for A0 representing the number of individuals detected in A0 relative to the total number of individuals released.
- *Arrival delay*—time elapsed (h) between the discharge of the individual and its first detection by antenna (A0, A1 and A2 are radio antennas, and A3 and A4 are RFID antennas).
- *Cumulative time spent at antenna*—time (in hours) spent by each individual at antennas A0, A1 and A2.
- *Rate of attraction*—the percentage of individuals detected by A3 (RFID antenna) compared to the number of individuals detected at A0 (radio antenna).
- *Fishway entrance searching delay*—the time interval between the first detection at A0 (radio antenna) and the first detection at A3 (RFID antenna).
- *Fishway transit time*—the time interval between the first detection by A3 (RFID antenna) and the first detection by A4 (RFID antenna).
- *Fishway efficiency*—the ratio between the total number of individuals released and the number of individuals transported upstream the waterfall after passing through the fishway.
- *Adjusted efficiency*—the ratio between the number of individuals detected by A4 (RFID antenna) and the number of individuals transported upstream of the waterfall after passing through the fishway.

Active manual radiotracking was also used to locate individuals one to three times per week on foot using a directional three-element-folding Yagi antenna connected to a receiver (Lotek SRX1200-M2). An audible beep was emitted when an individual was detected, and the receiver displayed the identifier of the fish detected. The detection range was about 300 m but varied according to the topography and environmental conditions. Tracking was used to obtain the precise position of the individuals, which cannot be obtained with fixed antennas, in order to analyse their pre-crossing behaviour. The water flow and temperature were recorded hourly and obtained by the Hydrometry-Wallonia Public Service and temperature data loggers (Tidbit Onset), respectively.

2.4 | Statistical Analyses

Detection data from the antennas were first processed globally, indicating the number and proportion of individuals detected per species, as well as the number of individuals per species captured. These data enabled us to determine the approach rate metrics as well as the efficiency and adjusted efficiency of the fishway. We used the Chi-square test to compare the number of detections between A1 (waterfall) and A2 (restitution channel). The arrival delay for individuals to reach each antenna was analysed for each species by calculating the median, first and third quartile (Q1 and Q3). We compared the arrival delay between each antenna for each species using non-parametric Kruskal–Wallis tests. Dunn's post hoc multiple comparison test was used when the Kruskal–Wallis test result was significant to determine which antennas are different from each other in terms of arrival delay. A violin plot was used to represent the arrival delay at the antennas for each species as well as statistical differences. Data relating to RFID antennas for grayling were not considered due to the limited availability of only one data point. The time taken to find the fishway entrance and the time taken to pass through the fishway were expressed in days, hours and seconds.

The time spent by each individual at each antenna was illustrated by cumulative histograms representing the cumulative time for each fish. These graphs were produced individually for each species. A Kruskal–Wallis test was performed to determine significant differences in median cumulative time spent at three antennas (A0, A1, and A2) for all species, and a post hoc Dunn test was conducted to identify which antennas differed when the results were significant.

The movements made by each individual were represented for each species using a movement curve graph with a distinction made between individuals that passed through the fishway and were released upstream and those that remained downstream.

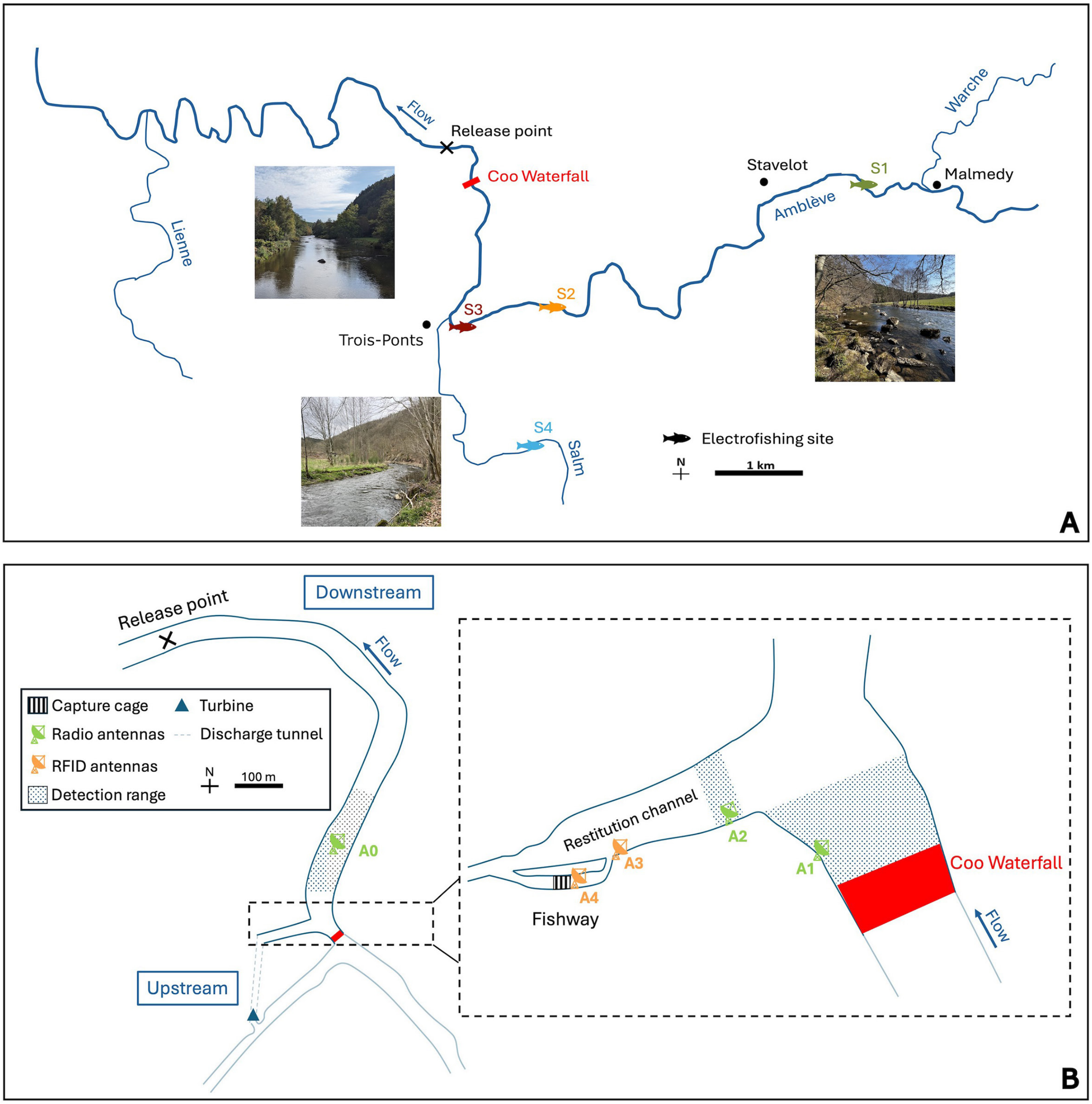

FIGURE 2 | (A) Map showing the electrofishing sites (S1, S2, S3 and S4) upstream of the Coo waterfall, the release point downstream and images illustrating the different environments along the river, and (B) diagram showing the layout of radio (A0, A1 and A2) and RFID (A3 and A4) antennas and their range of detection within the study site (waterfall and fishway). [Color figure can be viewed at wileyonlinelibrary.com]

Water temperature, flow rate and waterfall position were integrated. The flow and temperature values correspond to the average temperature and flow values of the day before tracking. The graphs represent the distances travelled by each individual from their release point (represented by a fish) between two manual radiotracking.

The flow and temperature values correspond to the average temperature and flow values of the day before tracking. Statistical tests were performed using the R statistical programme (the R Foundation for Statistical Computing, Vienna, Austria, version 3.6.1.), and the significant threshold was set at 5%.

3 | Results

3.1 | Study Site Approach Rate: Attraction and Efficiency of Fishway

The results showed that 89.5% of tagged individuals ($n = 34$ individuals) reached A0, representing the entrance to the study site. Barbel showed an approach rate of 100% with all individuals detected at A0. The approach rate was 87.5% for trout ($n = 14$ individuals) and 66.7% for grayling ($n = 4$ individuals). Of the individuals detected at A0, 26 (76.5% of detection at A0) were detected at the foot of the waterfall in A1: four grayling (approach rate 100% of individuals detected in A0), 15 barbel (approach rate 93.8%) and seven trout (approach rate 50%). Within the restitution channel, two grayling (approach rate = 50% of individuals detected in A2), eight barbel (approach rate = 53.3%) and two trout (approach rate = 28.6%) were detected at A2. The number of individuals detected at A1 (waterfall) was significantly greater than the number detected at A2 (restitution channel; Chi^2 test, $p < 0.001$). It should be noted that two grayling (O1 and O5) and one trout (T9) were considered lost from the start of the study, as they were never located after being released, either by mobile tracking or by fixed antennas.

Detection data from RFID antennas (A3 and A4) could not be collected for trout due to a technical failure of the RFID station. However, individuals must pass through the restitution channel and be detected by A2 before arriving at the fishway (A3). Knowing that 1 individual was captured and released upstream of the waterfall, we can deduce that at least 1 trout was detected in A3 and A4 and a maximum of 2 trout, bearing in mind that individuals can turn around once they arrive at the entrance to the fishway (as was the case for 2 barbel detected in A4 but not captured in the cage).

A total of four barbel (50% of individuals detected in A2), one grayling (50% of individuals detected in A2) and from one to two trout (50%–100% of individuals detected in A2) were detected at A3 (fishway entrance). At A0, 16 barbel, 14 trout and four grayling were detected. As a result, the fishway had an attraction rate of 25% for barbel and grayling, and an attraction rate of 7.2%–14.3% for trout. At the entrance to the capture trap, A4 detected a total of four barbel (100% of the barbel detected in A3), one to two trout (50%–100% of the trout detected in A3) while no grayling were detected. Within the capture trap, two barbel (of the four individuals detected in A4) and one trout (of the one to two individuals detected in A4) were captured and released upstream of the waterfall. This corresponds to a total fishway efficiency rate of 7.9% ($n = 3$ of the 38 individuals marked), with 12.5% for barbel and 6.3% for trout. The adjusted efficiency was 50% for barbel, with four individuals detected in A4 and two individuals released upstream and 50%–100% for the trout with one to two individuals detected in A4 and one individual released upstream (Table 2).

3.2 | Arrival Delay at the Antennas and Fishway Entrance Search/Transit Time

The grayling had a median arrival delay at A0 of 56 h and 11 min (Q1 = 46 h and 28 min; Q3 = 73 h and 38 min) after being released at the release point. At A1, grayling had a median arrival delay of 109 h and 51 min (Q1 = 57 h and 30 min; Q3 = 481 h and 15 min). For A2, the grayling median arrival delay was 259 h and 24 min post-release (Q1 = 180 h and 4 min; Q3 = 856 h and 39 min). At A3, one grayling (O6) was detected after 111 h and 37 min. For barbel, the median arrival delay at A0 was of 112 h and 53 min (Q1 = 12 h and 25 min; Q3 = 235 h and 54 min). At A1, barbel had a median arrival delay of 219 h and 41 min (Q1 = 90 h and 4 min; Q3 = 457 h and 34 min). At A2, the barbel median arrival delay was 726 h and 42 min (Q1 = 581 h and 12 min; Q3 = 981 h and 2 min). Four barbel (B3, B5, B6 and B15) were detected in A3 with a median arrival delay of 449 h and 19 min (Q1 = 293 h and 18 min; Q3 = 839 h and 36 min). The median arrival delay to A4 for the four barbel detected at A3 was 546 h (Q1 = 462 h and 13 min; Q3 = 839 h and 39 min). The trout had a median arrival delay at A0 of 12 h (Q1 = 10 h and 26 min; Q3 = 14 h and 20 min). At A1, the median arrival delay was 21 h and 37 min (Q1 = 16 h and 23 min; Q3 = 23 h and 17 min). The two trout detected in A2 (T6 and T10) had arrival delays of 18 h and 15 min and 13 h and 32 min, respectively. The data for antennas A3 and A4 could not be analysed.

Significant differences in arrival delay were observed in barbel (Kruskal–Wallis, $p = 0.002$) and trout (Kruskal–Wallis, $p < 0.001$) between antennas A1 and A2 (Dunn's test, $p = 0.02$) and between A0 and A2 (Dunn's test, $p < 0.001$) for barbel and between antennas A0 and A1 (Dunn's test, $p = 0.001$) and between A0 and A2 for trout (Dunn's test, $p = 0.007$; Figure 3).

TABLE 2 | Number and proportion of fish detected by fixed antennas at the system entrance (A0), at the foot of the waterfall (A1), at the restitution channel (A2), at the fishway entrance (A3), at the fishway capture cage entrance (A4), with approach rate and attraction rate and number and proportion of fish discharged upstream of the waterfall with fishway efficiency and adjusted efficiency.

Antenna	*N* grayling = 6	*N* barbel = 16	*N* trout = 16	*N* total = 38
A0 (radio antenna) (approach rate)	4 (66.7%)	16 (100%)	14 (87.5%)	34 (89.5%)
A1 (radio antenna)	4 (100%)	15 (93.8%)	7 (50%)	26 (76.5%)
A2 (radio antenna)	2 (50%)	8 (53.3%)	2 (28.6%)	12 (46.2%)
A3 (RFID antenna)	1 (50%)	4 (50%)	1–2[a] (50%–100%)	6–7[a] (50%–58.3%)
Attraction rate	25%	25%	7.2%–14.3%[a]	17.6%–20.6%[a]
A4 (RFID antenna)	0	4 (100%)	1–2[a] (50%–100%)	5–6[a] (from 71.4% to 100%)
Individuals captured in the cage (fishway efficiency)	0	2 (12.5%)	1 (6.3%)	3 (7.9%)
Adjusted fishway efficiency	0	50%	50%–100%[a]	50%–60%[a]

[a]Total taking into account the detection of minimum 1 to maximum 2 trout in A3 and A4.

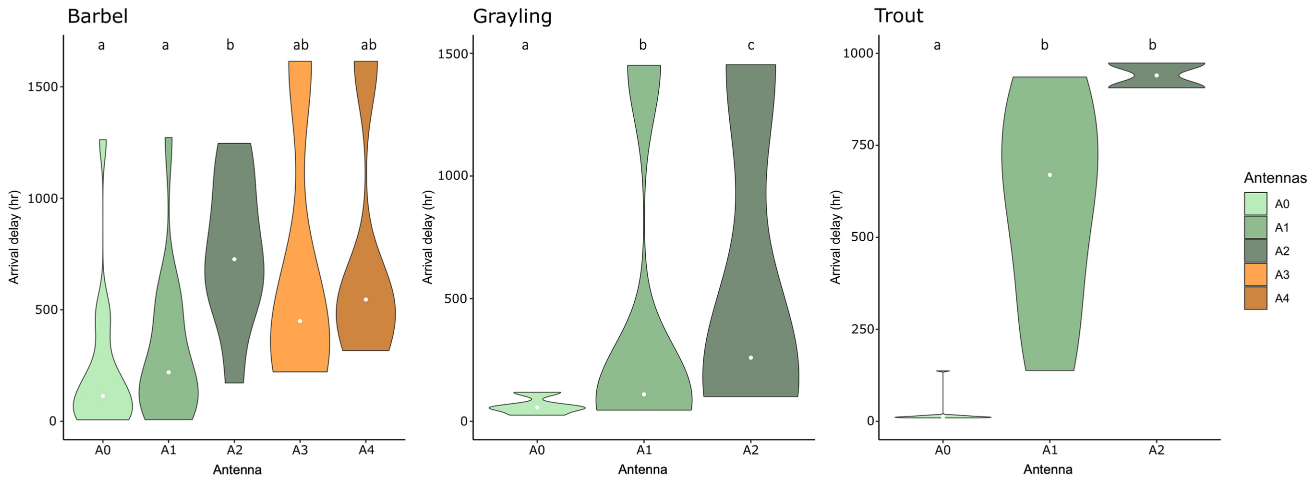

FIGURE 3 | Arrival delay (h) of individuals grouped by species at each antenna. The white point represents the median arrival delay per antenna. Species sharing at least one common letter (above each violin plot) did not differ at the 0.05 level of significance. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 | Fishway entrance searching delay and fishway transit time by individuals having reached RFID antennas (A3 and/or A4) and their averages for barbel.

Species	ID	Fishway entrance searching delay	Average searching delay for barbel	Fishway transit time	Average fishway transit time of barbel
Barbel	B3	4 days 20:15:04	25 days 03:30:05 ± 20 days 21:51:22	00:02:31	3 days 05:52:26 ± 4 days 20:44:50
	B5	66 days 23:12:49		00:00:28	
	B6	8 days 17:42:58		12 days 23:22:07	
	B15	20 days 00:49:29		00:04:39	
Grayling	O6	2 days 10:01:43	—	—	—

Note: Delays are expressed in days (hours:minutes:seconds).

Of the five individuals that reached the fishway (detected in A3), grayling (O6) had the shortest searching delay of around 2 days and 10 h (Table 3). Searching delay for the four barbel ranged from 4 days and 20 h to 66 days and 23 h, with an overall average of 25 days (±20 days and 22 h). Only barbel showed a fishway transit time, with an average of 3 days (±4 days and 21 h) and times ranging from 28 s to 12 days and 23 h (Table 3).

3.3 | Cumulative Time Spent at the Antennas

The results of cumulative time spent near the antennas showed that four individuals spent more than 250 h near the detection antennas (all antennas combined): one grayling (O4: 528 h 30 min), two barbel (B5: 256 h 15 min and B16: 528 h 30 min) and one trout (T13: 252 h). T11 spent 237 h 30 min and trout T6 spent 155 h in total near the detection antennas. The results showed two trends for the remaining individuals: (i) individuals who spent between 50 and 150 h near the antennas with five barbel (B1, B3, B4, B8 and B10), one grayling (O2) and two trout (T4 and T10) and (ii) individuals who spent less than 50 h near antennas, with nine barbel, (B2, B6, B7, B9, B11, B12, B13, B14 and B15), two grayling (O3 and O6) and nine trout (T1, T3, T5, T7, T8, T12, T14, T15 and T16). The antenna most visited varied from one individual to another. For individuals who spent less than 150 h at antennas, A0 was the most frequently visited. Individuals B6 and B15, who had a low cumulative detection time (less than 40 h cumulative), spent more time at A3 and A4 than the others (1 h 15 min and 1 h 45 min, respectively). These are the individuals that were captured in the capture cage (Figure 4A).

The median time spent with radio antennas for barbel was 15 h 30 min in A0, 7 h in A1 and 15 min in A2. For grayling, 24 h in A0, 21 h 30 min in A1 and 1 h 30 min in A2. The median time spent for trout was 23 h 30 min in A0, 11 h 30 min in A1 and < 15 min in A2. Therefore, the waterfall seemed more attractive than the restitution channel but no significant differences were observed in terms of median time spent for the three species between A1 and A2 (Dunn test, $p = 0.21$). Significant differences were observed between A0 and A2 (Kruskal-Wallis, $p = 0.03$—Dunn test, $p = 0.02$).

3.4 | Movements of Individuals via Manual Radiotelemetry

Manual radiotelemetry showed that individuals O2, O3 and O4, released on 23 March 2022, remained at the entrance of the study site until early April. O2 and O4 then moved 4 and 1.2 km downstream, respectively, from the fishway. Individual

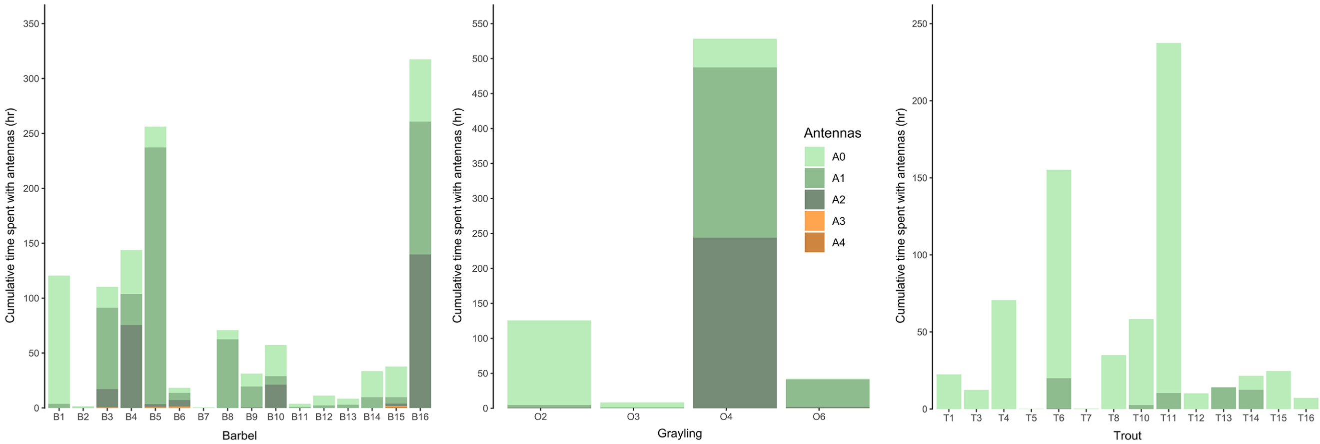

FIGURE 4 | Cumulative time (h) spent at each antenna (A0, A1, A2, A3 and A4) per individual/species. [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 | Locations of grayling (A), trout (B) and barbel (C), which stayed downstream of the waterfall, in relation to the Coo fishway capture cage, as a function of time and associated mean temperature (°C) and flow rate (m^3/s). [Color figure can be viewed at wileyonlinelibrary.com]

O6 was released on 14 April 2022 and was detected at the system entrance 2 days later and moved downstream 3 days later up to 5.1 km downstream of the fishway. Grayling O2, O4 and O6 then remained stable in their movements, with the exception of individual O4, which made exploratory movements with an amplitude of around 1 km around the released point. Individual O3 was last located 322 m downstream of the fishway approximately 1 month after its release (Figure 5A).

T12 and T15 were never detected by mobile tracking since their release on 11 October. On 17 October, T14 was located 100 m downstream of the fishway. T11 was located 500 m downstream of the fishway in the last week of October. T2, T3, T4, T5, T7 and T14 were lost between 17 October and 24 October and were localised between one and four times during manual tracking. T2 was located 1.9 km downstream of the fishway on 24 October, and T3, T4, T5 and T7 were last located between 1.2 and 1.1 km downstream of the fishway. T13 travelled the furthest downstream, with its last detection on 6 December, 6.5 km downstream of the fishway. T10 moved upstream and downstream between 1.1 and 3 km downstream of the fishway. T1 and T16 remained relatively close to the release point, and T8 rapidly moved downstream and stabilised 2.1 km downstream of the fishway (Figure 5B).

B14 made a major downstream migration of around 6.7 km downstream of the waterfall during the first fortnight of May before returning to the study site. A few days later, it made a second downstream movement of 2.3 km before returning to the study site, where it remained. Individual B16, initially stationary, moved 4.2 km downstream of the fishway on 30 May and remained stationary thereafter. B11 made numerous round trips 2 days after reaching the waterfall, finally descending 4.2 km. B1, B2, B7 and B12 moved downstream from 19 April to end up around 2.3 km downstream of the fishway. On 11 May, B2, B7 and B12 were found together, and B2 was found dead on 18 May. The other three individuals moved back and forth over an amplitude of around 500 m. Individuals B3, B5, B9, B10, B14 and B13 moved upstream and downstream for 2 weeks (from 20 April to 4 May). On 9 May, B5, B10, B14 and B3 stabilised at the released point with B8 (1.2 km downstream of the fishway) and B13 moved downstream up to 2.4 km. On 23 May, all the individuals (except B13) were located 1.3 km downstream of the fishway. B9 and B10 remained static for 1 month. From 31 May onwards, the other individuals made numerous movements between the fishway and 1.2 km downstream (Figure 5C).

Of all the individuals tracked, three individuals (B6, B15 and T6) reached the capture cage and were discharged upstream of the waterfall. After reaching the study site, B6 and B15 moved back and forth for around 20 days before being detected at the entrance to the capture cage. The two individuals were released upstream of the cascade on 9 May. Individual B15 was lost following its release and was not detected by the fixed antennas, suggesting that the individual had remained upstream. Individual B6 was found on 11 May, 2.5 km upstream of the waterfall, in a confluence of the Amblève (Salm River) and spawned with other barbel. B6 was located for the last time on 24 June, which was the last location before the end of the transmitter's life, 1 km upstream of the waterfall. T6 moved between A0, A1 and A2 for 4 days before being captured and released upstream of the waterfall on 22 November. On 23 November, it was located at A0, but it was not detected at A2; it appears that it tumbled down the discharge tunnel. It was last located on 22 December downstream of the confluence with the Roannay River (approximatively 2.5 km downstream of the waterfall; Figure 6).

4 | Discussion

The number of studies on fishway performance is increasing in the literature but remains limited relative to the high diversity of typology in thousands of fishways in the world (Bunt, Castro-Santos, and Haro 2012; Dębowski et al. 2022; Nestler and Gosselin 2023; Panagiotopoulos et al. 2024; Roscoe and Hinch 2010; Sun et al. 2023). The fishway studied in this paper presents an original configuration that had not previously been investigated. As highlighted by Castro-Santos, Cotel, and Webb (2009) and Silva et al. (2018), the effectiveness of a crossing device can be finely assessed in three main phases: (i) fish approach, (ii) fish entry and (iii) fish passage. By studying these different phases, it is possible to highlight a more holistic evaluation of the performance of the fishways. The fish approach phase near the fishway is a crucial point, but it has been poorly studied in the literature compared to the other phases (Bunt, Castro-Santos, and Haro 2012; Ovidio et al. 2017). The use of a combination of RFID and automatic and mobile radio telemetry enabled us to study these three phases with the use of standardised behavioural metrics. The study was performed on freshwater fish species, which have been studied less frequently than migratory fish species (Ovidio et al. 2020). These species will benefit from the reopening of the migratory route because they are the most representative of the study area. However, diadromous species are also concerned to a lesser extent.

In our study, the individuals were captured upstream of the waterfall. Apart from those considered lost at the start of the study, most of the fish moved upstream and were detected at the system entrance (89.5% of individuals) after being released downstream. These results demonstrate the value of using individuals who come from upstream to stimulate homing behaviour to find their original habitat when assessing the efficiency of a fishway (Armstrong and Herbert 1997; Dodd et al. 2023; Ovidio et al. 2017). In addition, we chose to capture individuals before the spawning period in order to maximise the chances of upstream migration at the time of reproduction (Ovidio et al. 2017). These choices enabled us to use fish with an important motivation to move upstream.

Our results showed that the median arrival delay in the system for the three species was similar to data obtained in previous studies involving barbel, trout and grayling, ranging from 1 to 4 days (Dębowski et al. 2022; Ovidio et al. 2017). The numerous back-and-forth movements made by individuals suggests intensive habitat search behaviour to find spawning habitats (Gelder, Benitez, and Ovidio 2024; Panchan et al. 2022). The cumulative time spent at the antennas showed that the restitution channel (A2) was less attractive than the waterfall (A1) for the three species. In addition, all individuals detected in the restitution channel (A2) were first detected at the waterfall, demonstrating its greatest attractiveness. In their

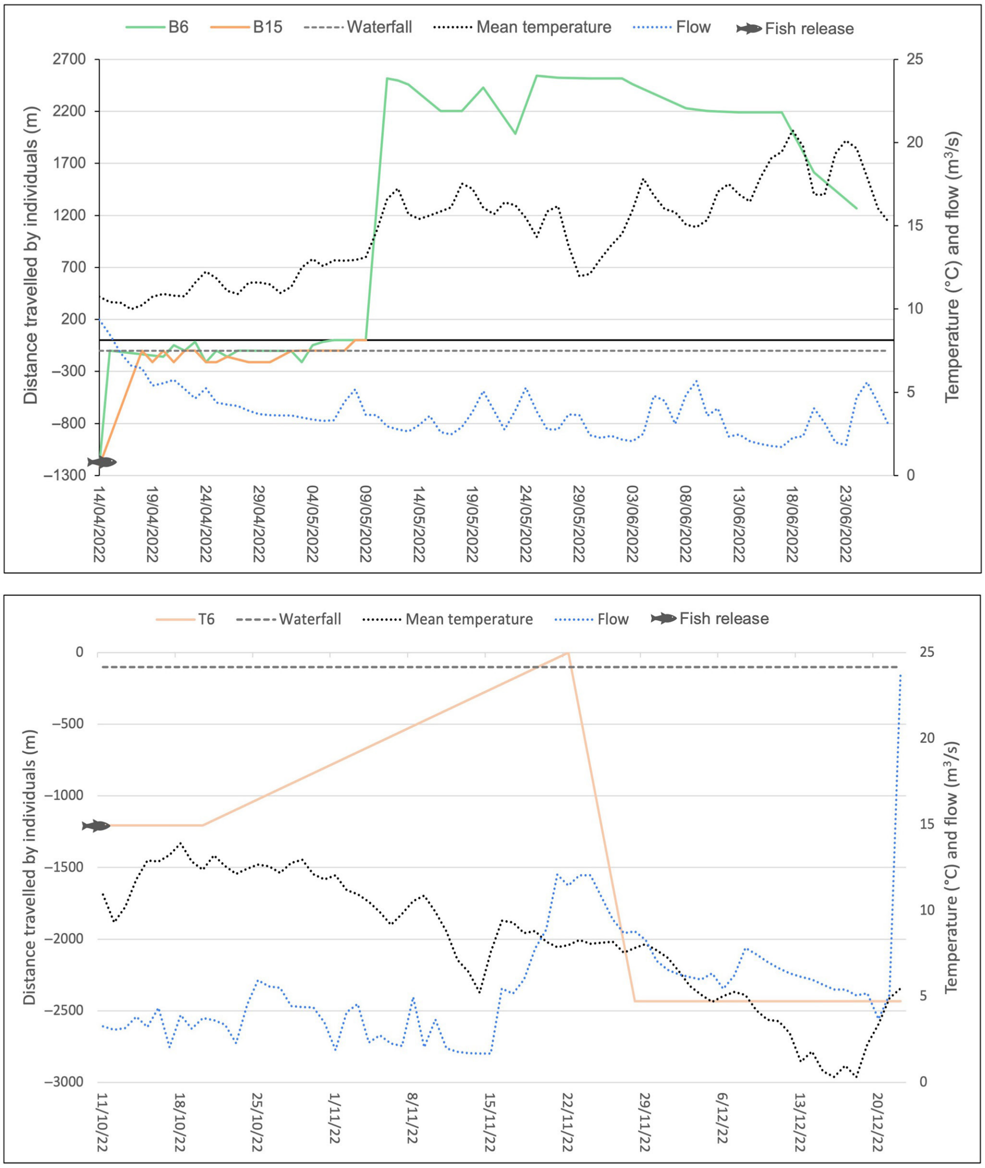

FIGURE 6 | Location of barbel B6 and B15 released on 14 April 2022 and trout T6 released on 11 October 2022 that had passed through the fishway, in relation to the Coo fishway capture cage, as a function of time and associated mean temperature (°C) and flow rate (m³/s). [Color figure can be viewed at wileyonlinelibrary.com]

meta-analysis, Sun et al. (2023) obtained a fishway attraction rate of 49% for non-salmonids and 63% for salmonids. Ovidio et al. (2017) showed an attraction rate of 20.5% for grayling, 48.9% for trout and 41% for barbel on the Bocq River (Belgium). Grimardias et al. (2022) obtained the same rates as Ovidio et al. (2017) for barbel on the Rhône River (France). Our results indicate an overall attraction rate of 25% for barbel (non-salmonids) and grayling (salmonids) and an attraction rate of 7.2%–14.3% for the trout (salmonids), corresponding to a total attraction rate of 17.6%–20.6%. By compiling data from 29 vertical slot fishways, Bunt, Castro-Santos, and Haro (2012) deduced that the average attraction rate for a vertical slot type fishway was 63% by combining salmonids and non-salmonids. We can reasonably think that low or medium passage performances constitute an improvement (i.e., for gene flow effects and metapopulation reconnection) compared to the absence of connections. However, it is still complicated to assess the demographic gain for a population from fishway improvement or restoration (Ovidio et al. 2020). Some studies have shown that the factor limiting the effectiveness of fishways is their attractiveness (Grimardias et al. 2022; Ovidio et al. 2017; Roscoe and Hinch 2010). Therefore, the location of the fishway entrance is crucial to its success (Bunt 2001; Katopodis and Williams 2012). An attraction flow is necessary to increase the water current at the entrance of the fishway (Cooke and Hinch 2013; Noonan, Grant, and Jackson 2012; Romão et al. 2018). The lack of attractiveness of the restitution channel, where the entrance of the fishway is located, can be explained by the flow at the time of the study, which was particularly low. Moreover, the turbine was not operating, which may have had an impact on the motivation of individuals to use this way (Bao et al. 2019). During the spawning period, fish are stimulated to migrate against the current (Bunt 2001; Prchalová et al. 2011). However, a flow that is too low can slow down this stimulation and stop individuals from migrating to spawn (Bunt, Castro-Santos, and Haro 2012; Maynard, Kinnison, and Zydlewski 2017; Sprankle 2005). In addition, prior to the study, a current flow was present on the right bank of the restitution channel, which attracted fish to the entrance of the fishway (Benitez et al. 2015; Gelder et al. 2023). However, the floods in July 2021 (the year before this study) resulted in the clogging of the right bank, consequently eliminating the current flow that was present prior to this study. This lack of flow may have affected the attractiveness (Laine, Jokivirta, and Katopodis 2002), as observed by Calles and Greenberg (2005) in Sweden where a low flow at the entrance to the fishway compared with other years resulted in a lower number of individuals reaching the fishway. This lack of attractiveness is linked to the movements detected during manual telemetry. The numerous movements of the individuals, particularly the back-and-forth movements made by the barbel between the fishway site and downstream, suggest that the individuals were unable to quickly find the entrance to the fishway despite the motivation to migrate upstream and therefore reflect the search for a potential new spawning area. In their study in the United Kingdom, Gutmann Roberts, Hindes, and Britton (2019) showed that dams had an impacted on the upstream migration of barbels, which alternately found spawning habitats within 1 km downstream of the dam. Although other individuals were detected at the entrance to the site (A0), they were only found to be located downstream of the site with telemetry. For these individuals, it is possible that they found alternative suitable spawning habitats because there are many habitats available spawning site downstream of the obstacle. It is likely that these individuals discovered new habitats to which they did not previously have access and settled there, because they not found the entrance to the fishway and had to remain downstream (Calles and Greenberg 2005, 2007; De Leeuw and Winter 2008). The fact that there were detections at the antennas (A0 and A1) would suggest this hypothesis.

The total fishway efficiency obtained was 7.9%, which was 50%–60% once adjusted. Of the six to seven individuals detected at the entrance of the fishway (A3), five to six were detected at the entrance to the capture cage (A4), and three were captured and released upstream. These results indicate that even if individuals enter the fishway, they do not necessarily complete their passage through (Dębowski et al. 2022; Grimardias et al. 2022) even if the distance between the entrance to the fishway and the capture cage is small, which it was in the context of our study. The probability of crossing a fishway varies greatly depending on the species and the type of crossing device considered (Calles and Greenberg 2005; Grimardias et al. 2022; Forty, Spees, and Lucas 2016; Noonan, Grant, and Jackson 2012; Ovidio et al. 2020; Silva et al. 2012; Tummers, Hudson, and Lucas 2016; Weibel and Peter 2013). As a result, the rate at which a fishway is used is rarely predictable. However, Noonan, Grant, and Jackson (2012) determined via a meta-analysis that the average passage efficiency of salmonids is 62%, and that of non-salmonids is on average 21%. Sun et al. (2023) showed a mean passage efficiency of 70% for salmonids and 42% for Cypriniformes (including Cyprinidae). In our study, the fishway efficiency was lower (6.3% for salmonids and 12.5% for non-salmonids), suggesting that the lack of attractiveness of the fishway is the limiting factor.

The barbel that used the fishway had an average searching delay of 25 days and an average of 3 days to pass through the fishway and be captured in the cage, which represents a significant delay, particularly during the spawning period (Schilt 2007). Although one individual in our study was observed reproducing, long search and passage times can make it impossible for individuals to reach their spawning site (Thiem et al. 2013). Although some individuals manage to find new spawning habitats downstream of an obstacle, Lucas and Baras (2001) and Roscoe et al. (2011) showed that these delays can reduce spawning success by missing their spawning window or reducing the time spent on the spawning site, thereby minimising the chances of successful spawning. Interesting behaviours were observed in individuals captured and released upstream. Barbel B6 quickly moved upstream and was visually observed spawning with other barbel in a tributary of the Amblève before returning to its original capture site. These results suggest that the individual had returned to a spawning site that it had probably frequented in previous years. Many fish species, including barbel, are known to have an important fidelity to their spawning site (Baras 1995; Gelder, Benitez, and Ovidio 2024; Ovidio et al. 2007; Panchan et al. 2022). Trout T16 moved downstream of the waterfall within 24 h of being released upstream. Trout T16 descended the cascade within 24 h of being released upstream and was then located near a tributary of the Amblève. Trout are known to migrate to tributaries during their spawning period in order to find a suitable spawning site (García-Vega et al. 2018; Ovidio et al. 1998; Piecuch et al. 2007). Therefore, it is possible that this individual spawned in this tributary.

Our study highlighted a lack of attractiveness at the Coo fishway, which consequently affects its performance. In addition, the time taken to find the entrance to the fishway was relatively long. Although achieving 100% efficiency is extremely rare (Noonan, Grant, and Jackson 2012), the ideal situation is for individuals to find the entrance to the fishway and pass through as quickly as possible so as not to disrupt their migration times, particularly during the spawning period (Ovidio et al. 2017; Roscoe et al. 2011; Thiem et al. 2013). However, each site has its own characteristics and must be studied as a unique case, taking into account the ichthyofauna present (Dębowski et al. 2022; Noonan, Grant, and Jackson 2012). In our case, the configuration of the Coo waterfall restricted the choice of the type of fishway by requiring a low-cost device that can overcome such a high fall. In addition, landscape and touristic constraints, as well as the space available, led to the choice of a capture-transport type fishway located in the restitution channel. As a fish elevator was not possible because it would disfigure the waterfall site, this solution was the best alternative to the constraints imposed by the site, although, ideally, the crossing device should be closer to the waterfall. In this context, increasing the attraction flow at the entrance to the fishway would increase its attractiveness and allow individuals wishing to migrate upstream to find the entrance and complete their life cycle (Bao et al. 2019; Cooke and Hinch 2013; Romão et al. 2018). The aim of this paper is to identify the performance of the devices and to highlight any weaknesses with a view to improving future designs.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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