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What do fish do after passing through a fishway? A radio-telemetry study on patrimonial holobiotic species

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Abstract

The restoration of longitudinal connectivity in rivers allows fish to colonise new habitats. However, there is a lack of information regarding the behaviour of fish when they colonise the newly opened river stretch. We used manual radiotelemetry to tracked individuals belonging to four species (trout, nase, grayling and barbel) after their release upstream of two obstacles in the Amblève River. We observed a diversity of movement behaviours and habitats used among the studied species. All the species used potential spawning habitats with distances travelled upstream reaching 2.4 km for the grayling, 7.0 km for the barbel, 16.9 km for the nase and 18.0 km for the trout, which also use tributaries and sub-tributaries of the Amblève River. Post-reproduction downstream behaviours were observed in all species, but this was made difficult by the absence of downstream migration devices at dams that forced fish to seek alternative habitats. Our study suggested that allowing fish to move upstream with fishways is beneficial as the species succeeded in reaching spawning grounds, but a holistic approach combined with the installations of devices or an opening of gates to allow post-reproduction downstream migrations would allow them to completely accomplish their biological cycle.

KEYWORDS
defragmentation, ecological benefit, migratory axis, potamodromous species, radiotelemetry

1 | INTRODUCTION

Rivers are characterised by a great diversity and heterogeneity of habitats, which can be extremely variable over time and offer a great diversity of ecological niches for many fish species (Townsend, 1989). They are considered to be the epitome of connectivity (Wiens, 2002) through a mosaic of functional habitats between which aquatic organisms move (Hilty et al., 2012; Ovidio et al., 2020). However, most rivers are fragmented by various physical barriers that affect connectivity and limit access to functional habitats (Birnie-Gauvin et al., 2020; Consuegra et al., 2021; Sheer & Steel, 2006). The reconnection of longitudinal connectivity to make functional habitats accessible is one of the most

important measures in river restoration projects and management plans (Gelder, Benitez, & Ovidio, 2023; Roni et al., 2002). The installation of barrier-circumvention devices, such as fishways, allows the re-establishment of upstream migration routes and allows individuals to continue their movements to different habitats to feed, rest or reproduce (Mameri et al., 2019; Ovidio et al., 2023; Weibel & Peter, 2013). Fishways have evolved to become holistic, to allow a wide variety of fish species of different swimming capacity and size to use them (Alvarez-Vázquez et al., 2008; Benitez et al., 2015; Grimardias et al., 2022). Indeed, over the past few years, a substantial effort has been made in most European countries to consider patrimonial holobiotic fish as priority species for restoration of ecological continuity additionally to diadromous

species (e.g. salmon or eel; Foulds & Lucas, 2013; Laine et al., 2002; Nunn & Cowx, 2012). Some species are very exigent in terms of their spawning habitats (lithophilic, phytophilic) and must migrate several dozen kilometres to complete their biological cycle (Baras et al., 1994; De Leeuw & Winter, 2008; García-Vega et al., 2018; Ovidio et al., 2023; Ovidio & Philippart, 2002).

Fishway monitoring (manual monitoring, automatic counters) has been used to analyse species diversity as well as biometric characteristics of fish and their timing of migration (Benitez et al., 2015, 2022; De Leeuw & Winter, 2008; Gelder, Benitez, & Ovidio, 2023; Gelder, Benitez, Ovidio, Dierckx, & Sonny, 2023; Knaepkens et al., 2006; Prchalová et al., 2011; Stuart & Berghuis, 2002). It has shown that a wide diversity of species in various life stages and sizes develop behaviours with frequent movements throughout the year. Some studies have rather focused on the performance of fishways, either using tagging and installation of Radio Frequency Identification (RFID) or Radio-antennas (Bao et al., 2019; Davies et al., 2007; Lucas et al., 1999; Ovidio et al., 2017, 2020, 2023). Results are quite variable in terms of passage performance, with many studies having quite encouraging results and others having worse (Birnie-Gauvin et al., 2018; Foulds & Lucas, 2013; Grimardias et al., 2022; Ovidio et al., 2020, 2023).

Despite the increasingly frequent installation of fishways, very few studies have focused on the ecological benefit and gain of opening a migratory axis for different species (Tummers et al., 2016). This type of study can be realised on a short or long-timescale at the level of the individual and/or the populations to highlight an adaptation sequence (behaviour reproduction physiology genetic) in the newly opened river section. On a short time scale, such studies require intensive and regular monitoring of individual behaviour after the passage of the fishways to obtain qualitative data on the habitats exploited or their ability to reproduce in the newly opened river stretch. Manual radiotelemetry is human costly but makes it possible to follow individuals everywhere at any time and to determine the occupied habitats and the movements carried out as well as to observe potential reproductive events after the passage of a fishway (Ovidio, 1999).

Many fishways have been installed in Belgium in the last 20 years to restore connectivity, and a large part of them have been evaluated in terms of passage intensity and/or performance (Benitez et al., 2015, 2018, 2022; Ovidio et al., 2017, 2020, 2023). However, there have been no studies performed yet to follow the detailed behaviour of fish once they have been released upstream of these fishways. The objective of this study is to determine the ecological benefit of the exploration of new habitats of a selection of fish species, once released after their passage through two different fishways of the Amblève River, using manual radio-telemetry techniques. To determine the ecological benefit of habitat restoration on the Amblève River, four species of holobiotic fish were tagged and radio-tracked after their capture in two fishways. From the results of the radio-tracking, our study aimed to analyse: (1) fish behaviours upstream of the two fishways based on their movements and habitats occupation, (2) the mobility indicators of each individual based on the distance travelled between two locations, (3) the exploration behaviours of individuals (permanent or punctual occupation) after reopening the migratory axis and (4) determine whether temperature and flow are environmental factors influencing the movement of individuals.

2 | MATERIALS AND METHODS

2.1 | Study area

The Amblève River (up-land river, Southern Belgium) is a tributary of the Ourthe River located in the Belgian Meuse River basin with an average annual discharge of $19.3 \, m^3/s$. Its ecological status is good (i.e. Public Service of Wallonia – DEE) with a total of 23 species potentially present in the river, and its downstream part is situated in a grayling/barbel fish zone (Huet, 1949). Many physical obstacles are present on the Amblève River, including the hydroelectric dam of Lorcé and the Coo waterfall (Figure 1). Two fishways were installed in 2007 and 2021 and allow access to high-quality functional habitats for exigent fish species. These devices are equipped with a monitoring capture cage (Benitez et al., 2015; Gelder, Benitez, & Ovidio, 2023; Gelder, Benitez, Ovidio, Dierckx, & Sonny, 2023), and the fish are manually released upstream after biometric analyses.

The first study site was the hydroelectric dam of Lorcé, located 22.9 km upstream of the confluence with the Ourthe River. Since its construction in 1932, the hydroelectric dam has been impassable outside of rare periods, when the turbines were not in operation (repair work, opening of spillways, high floods). Lorcé dam creates a small $50,000 \, m^3/s$ reservoir, with no accumulation capacity, which feeds a pressure pipeline to the Heid de Goreux hydroelectric power station. The dam has two mobile gates 24 m wide, creating a drop of delta height of 3.3 m. Next to the two regulator gates is an emptying gate, whose purpose is to completely empty the reservoir, increase the flood discharge flow and until 1993, allow $3 \, m^3/s$ of compensation discharge to pass as overflow. However, this compensation discharge also turns a micro-turbine (3.5 m drop, $3 \, m^3/s$ water flow, 85 kW maximum power; mean annual production 450,000 kWh). This small turbine is fed through a large trash rack made of vertical bars spaced 4 cm apart. The Amblève River has a minimum flow of $3 \, m^3/s$ upstream of the hydroelectric power station of Heid de Goreux, located 8 km downstream from the dam. At the end of 2007, the dam of Lorcé was equipped with a 67 m long vertical-slot pool (15 pools) and multi-specific types of fishway. A capture cage with dimensions of $1.7 \times 1.1 \times 1.5 \, m$ and a grid of $1 \times 1 \, cm$ was installed at the end of the pools.

The Coo waterfall, located 39.7 km upstream with the confluence of the Ourthe River, is an artificial obstacle 11.8 m high, created during the Middle Ages, following a meander overlap, but a natural river arm located on the left bank still allowed the circumvention of the waterfall. In 1970, the waterfall became an impassable obstacle for upstream migration, following the construction of a pumped
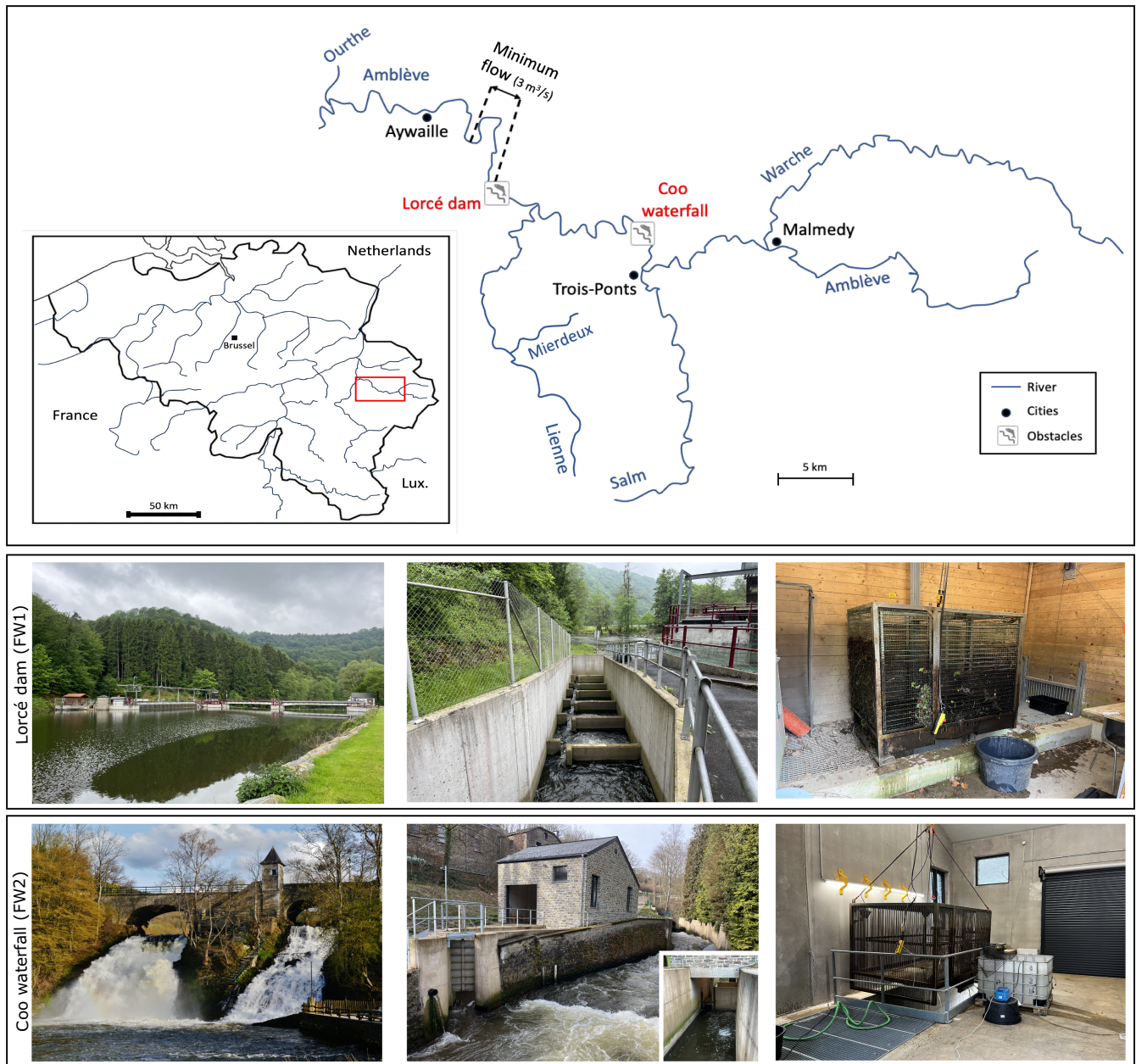
FIGURE 1 Location of study sites: the Lorcé dam (FW1) with a minimum flow of 3 m³/s over 8 km downstream of the dam and the Coo waterfall (FW2) in the Amblève River in the south of Belgium, and pictures showing obstacles, fishway configurations and capture cages of each site.

storage plant, which deflected the natural arm to power the turbine and discharge water downstream of the waterfall into a restitution channel. A transport-capture device was installed in 2021. The entrance to the crossing is 45 m before the end of the restitution channel, on the right bank. The device has a capture cage measuring $2.8 \times 1.9 \times 1.8$ m.

Both capture cages were monitored on average 1–3 times per week (Figure 1). Between 2007 and 2016, 23 different species used the Lorcé fishway (FW1) (Gelder, Benitez, & Ovidio, 2023; Gelder, Benitez, Ovidio, Dierckx, & Sonny, 2023) and 21 species between 2021 and 2022 used the Coo fishway (FW2) (Gelder, Benitez, Ovidio, Dierckx, & Sonny, 2023). In terms of biomass, the dominant species

were barbel (42%), brown trout (29%), chub (5%) and grayling (4%) at FW1, and barbel (49%) and pike (19%) at FW2.

2.2 | Fish capture and tagging

Individuals of four fish species were radio-tracked after their passage through the FW1 ($n = 10$) and FW2 ($n = 11$): 2 brown trout (*Salmo trutta* L.), 3 grayling (*Thymallus thymallus* L.), 4 barbel (*Barbus barbus* L.) and 1 nase (*Chondrostoma nasus* L.) at FW1 and 11 barbel at FW2 (Table 1). These patrimonial species are representative of this sector of the Amblève River, and the restoration

TABLE 1 Characteristics of radio-tracked individuals (size, weight, weight of transmitter and sex with F=female, M=male and +=mature), their date and location of capture and start/end date of tracking.

No fish	Size (mm)	Weight (g)	Weight of transmitter (g)	Weight/transmitter index (%)	Sex	Capture location	Date of capture	Tracking start date	Tracking end date
T1	341	372	3.8	1.0	F	FW1	26/11/07	28/11/07	18/12/07
T2	326	310	3.8	1.2	M	FW1	26/11/07	28/11/07	25/02/08
G1	425	781	3.8	0.5	M	FW1	30/11/07	4/12/07	20/08/08
G2	306	328	3.8	1.2	F	FW1	5/03/08	7/03/08	16/07/08
G3	308	262	3.8	1.5	M	FW1	5/03/08	7/03/08	11/07/08
B1	488	1423	13.3	0.9	M	FW1	4/04/08	4/04/08	6/07/09
B2	525	1806	13.3	0.7	F	FW1	21/04/08	23/04/08	6/07/09
B3	480	1436	13.3	0.9	F	FW1	21/04/08	23/04/08	2/01/09
B4	589	2223	13.3	0.6	F	FW1	21/04/08	23/04/08	23/03/09
N1	500	1797	13.3	0.7	F	FW1	4/04/08	4/04/08	8/04/09
B5	620	3160	20.0	0.6	F	FW2	11/05/22	11/05/22	29/09/22
B6	655	3340	20.0	0.6	F	FW2	13/05/22	13/05/22	29/09/22
B7	397	832	20.0	2.4	F+	FW2	20/05/22	20/05/22	29/09/22
B8	620	3670	20.0	0.5	F	FW2	20/05/22	20/05/22	29/09/22
B9	527	2004	20.0	1.0	M+	FW2	30/05/22	30/05/22	29/09/22
B10	615	2674	20.0	0.7	F+	FW2	30/05/22	30/05/22	29/09/22
B11	568	2478	20.0	0.8	M+	FW2	2/06/22	2/06/22	29/09/22
B12	635	2622	20.0	0.8	M	FW2	13/06/22	13/06/22	29/09/22
B13	644	3662	20.0	0.5	F+	FW2	13/06/22	13/06/22	29/09/22
B14	586	2542	20.0	0.8	F+	FW2	17/06/22	17/06/22	29/09/22
B15	582	2260	20.0	0.9	M	FW2	4/07/22	4/07/22	29/09/22

of the hydromorphological quality of their habitats is considered to be a high priority in the Wallonia region of Belgium (Philippart & Ovidio, 2007). They are demanding species in terms of water quality and substrate for their reproduction (Britton & Pegg, 2011; Hayes et al., 2021; Ovidio et al., 1998, 2004, 2017; Ovidio & Philippart, 2008).

Fish were captured in the cage capture of FW1 and FW2 and were anaesthetised with 0.2 mL/L of a solution of 2-phenoxy-ethanol, measured (±1 mm, fork length), weighed (±1 g) and sexed. Fish were surgically equipped with a radio transmitter (ATS Inc. 40 MHz trailing whip antenna), whose weight/transmitter index did not exceed 2.5% (Ovidio et al., 2020; Renardy et al., 2022), in their intraperitoneal cavity through a 0.8–2 cm midventral incision, depending on the size of the transmitter, behind their pelvic fin (Ovidio & Philippart, 2002). The incision was closed with two or three independent stitches, using resorbable Vicryl sutures, and disinfected with eosin. The transmitters had a weight of 3.8 g with a life of 140 days (F1580 ATS Inc.) for the grayling and the trout, a weight of 13.3 g with a life of 242 days (F1835 ATS Inc.) for the barbel and nase at FW1, and a weight of 20 g with a life of 3 years (F1840 ATS Inc.) for the barbel at FW2. Fish were then transferred to a water basin for recovery and released after they recuperated their swimming capacities (approximately 20–30 min), directly upstream of the fishway at FW1 and 500 m upstream of the waterfall by the ease of access at FW2.

2.3 | Telemetry system and environmental variables

Active manual radio-tracking began the same day or the day after the individual was released. Fish from FW1 were tracked during the daytime for 3–7 days a week, and those from FW2 were tracked for 2–4 days a week, depending on the season and the amplitude of movements (breeding period, migration period or winter period). Individuals were tracked for a period between 1 and 15 months, depending on the life of the transmitters and losses (Table 1). We searched manually for the fish by car and on foot and located each one through triangulation from the banks of the river, using a diamond directional antenna (low-frequency loop) and a Fieldmaster radio receiver (ATS Inc.; Ovidio et al., 2007; Renardy et al., 2020). The location accuracy varies with river width and the distance between the fish and observer; in the Amblève River, the accuracy is estimated to be 1–4 m^2. Water temperature was recorded hourly by data loggers (Tidbit Onset), and water flow was continually monitored (data from the Hydrometry-Wallonia Public Service).

2.4 | Data analysis

Movements made by individuals were represented by species by site using displacement curves, where temperature and water flow were integrated. This graph represents the distance travelled by individuals during each tracking, from the point of discharge upstream (positive value) to downstream (negative value) of that point.

Fish mobility has been studied according to several spatial indicators (Table 2; Capra et al., 2018; Ovidio et al., 2007). Home range was calculated for each individual with maximum and minimum corresponding to the most upstream and downstream location, respectively. The most upstream location was compared for each individual and between sites; all species were combined using the Kruskal-Wallis test. The spatial indicators (HR, TND, MND and TRD) were represented as boxplots per site. Since one species was studied at FW2, only barbel data were used to compare the two sites. Barbel are known in the literature to travel centres of metres up to dozen of kilometres (Benitez et al., 2018; Britton & Pegg, 2011; Capra et al., 2018; De Leeuw & Winter, 2008; Ovidio et al., 2007). Each spatial indicator was compared between sites with the Mann–Whitney test (U test).

The influence of environmental factors (flow and temperature) on the net distance travelled between two subsequent locations and for each individual was represented by a bubble chart for each site. The net distance (Dn) travelled was illustrated by the size of the circle and the individuals by the colours of the circles with the x-axis representing temperature values and the y-axis flow values.

TABLE 2 Spatial indicators of fish mobility and their definitions.

Spatial indicators	Definitions
Longitudinal home range (HR)	Corresponding to the distance between the most upstream location and the most downstream location within a period.
Total net longitudinal distance travelled (TND)	Corresponding to the sum of the net distance separating two subsequent locations. Expressed in the absolute value of the raw travelled distance.
Mean net longitudinal distance travelled (MND)	Corresponding to the mean of the net distance travelled separating two subsequent locations. Expressed in the absolute value of the travelled distance.
Total real distance travelled (TRD)	corresponding to the sum of the real distance travelled separating two subsequent locations, positive in the upstream direction and negative in the downstream direction.

To understand how mean daily temperature and flow values (fixed effects) affect dn (response variable), we used linear mixed models (LMM). Dn has been log-transformed to obtain normal distributions. Individuals were nested within species as random effect at FW1 and only individuals were used as random effect at FW2 since only one species was studied. The most parsimonious model was selected after calculating Akaike information criteria (AIC) and AIC weights to determine the rank of each model tested. The best model was the model with the lowest AIC and the distance in AIC score (ΔAIC) from the best model was performed. Models with a distance score < 2 were considered equal (Zuur, 2009). We have calculated the conditional and marginal R^2 values to evaluate the performance of the model in explaining the proportion of variance. We used the 95% confident interval (CI) to determine if the variables have an effect on the net distance travelled of individuals. An effect was deemed important when the 95% CI did not include zero.

The flow and temperature values correspond to the average temperature and flow values of the day before tracking. We calculated the 25 and 75 percentile of flow values for each species to determine the TND for each individual according to flow percentile. Statistical tests were performed using the R Studio statistical programme version 3.6.1 packages MuMIn, lme4, sjPlot and ggplot2 and the significant threshold was set at 5%.

3 | RESULTS

3.1 | Behaviours upstream of the FW1

Trout 1 (T1) and T2 swiftly ascended the Amblève River after being released on 28 November 2007. They were found in the Lienne River a tributary, 11.8 and 8.1 km away, respectively, 6 and 2 days post-release from Lorcé dam upstream. T1 stayed near a suitable reproduction area for 3 days, then moved downstream and was found 0.1 km upstream of the dam on 15 December (5.2°C, 50.7 m³/s), before later being found deceased in the fishway. T2 moved further covering 5 km to reach the Mierdeux River, a Lienne tributary 17 km and then 18 km upstream of Lorcé dam on 4 December (7°C, 81.1 m³/s) and 23 January (5.8°C, 47.6 m³/s) and then probably died (transmitter found on the bank on 21 February; Figure 2a).

Grayling 1 (G1) was tagged on 4 December 2007 and until 17 March 2008, travelled between 0 and 0.8 km upstream of Lorcé dam. On 19 March (6°C, 53.9 m³/s) it migrated towards a potential spawning site, between 1.5 and 2.2 km upstream. G2 and G3, tagged on 7 March joined G1 on 31 March (8.2°C, 71 m³/s) and 4 April (8.2°C, 39.2 m³/s) likely for spawning. Graylings (G1, G2, G3) left the spawning area from 11 to 16 April. G1 and G2 returned 2 and 5 days after, respectively, G2 stayed 3 months between 2 and 2.4 km upstream and then moved downstream on 2 July (20°C, 5.7 m³/s) remaining 0.8 km upstream from the Lorce dam. G1 began post-spawning downstream migration in late April (13.1°C, 17.8 m³/s) and stabilised near the dam, crossing it on 20 August 2008 (16.6°C, 6.6 m³/s; Figure 2b).

Five days after tagging, Nase 1 (N1) rapidly migrated upstream on 21 April 2008 (11.0°C, 26.7 m³/s) reaching the base of the impassable 11.8 m Coo waterfall (Figure 1), 16.9 km from the Lorcé dam. It stayed there until 25 April and then returned upstream, where it was located 2.6 km from the dam on 28 April (13.1°C, 17.8 m³/s). It moved upstream, reaching 13.6 km from the dam on 5 May (14.4°C, 11.1 m³/s) and stayed until 11 May. After spawning, it migrated downstream (16.3°C, 7 m³/s), encountering the impassable downstream Lorcé dam. It stabilised upstream, 1.23 km from the dam until early October. N1 moved upstream from 19 January to 13 February 2009 and then downstream between 2.8 and 3 km upstream of the Lorcé dam where tracking ended (Figure 2c).

Barbel 1 (B1) and B2, B3 and B4 undertook rapid spawning migrations upstream, occupying sites between 2.1 and 7 km from the dam. B1 covered between 0.05 and 7 km upstream until 30 May. After spawning B1, B2 and B4 moved downstream on 2 June (18.3°C, 9 m³/s) and 4 June (17.6°C, 7.4 m³/s) 13 June (12.8°C, 18 m³/s), respectively, until encountering the impassable downstream dam. During summer, all fish stayed upstream (between 0 and 2 km). B4 remained near the dam until a signal loss in March 2009. B1 and B3 were located downstream on 15 and 24 September 2008. B1 returned to the dam in May 2009. B3 moved downstream, staying until tracking ended. In April 2009, B2 undertook a reproductive migration upstream (between 3.79 and 5.47 km from the dam) and then settled 0.02 km upstream, where tracking ended (Figure 2d).

3.2 | Behaviours upstream of the FW2

The 11 barbels were captured and tagged in FW2 between 11 May and 1 July 2022. B5 was located the day after its release 1.5 km upstream (17.2°C and 3.1 m³/s) from 20 May to 23 May. It then moved downstream on 25 May (14.3°C and 4 m³/s) and made short movements until the end of tracking. B6 remained 0.2 km from the release point before crossing-down the waterfall and being located downstream on 23 May (16.2°C and 4.3 m³/s) with B7 and B8 who were released on 20 May. They then stayed at the foot of the waterfall. On 6 October, B9 was located 2.1 km upstream (12.9°C and 4.7 m³/s) before moving downstream on 17 October (13.2°C and 2 m³/s), 0.3 km upstream from the release point. B10 was situated downstream of the waterfall on 6 June (16°C and 4.5 m³/s), where it stayed until 14 June (16.5°C and 2.3 m³/s), before continuing its downstream movement until 2.7 km downstream from the release point, where it stayed until the end. B11 moved upstream until 1.3 km before going down the waterfall on 14 June, where he stayed until 6 September before moving 2 km downstream (18.5°C and 1.5 m³/s). B12 maintained its position until the end near the release point. B13 and B15 were located in the same area during the entire tracking near the release point. B14 was located 2.1 km upstream on 24 June (19.6°C and 2.2 m³/s) before moving downstream on 29 June and remained 0.3 km upstream until the beginning of October when it was located 1.9 km upstream. B14 then made movements between 1.9 and 0.3 km upstream of the release point (Figure 3).

FIGURE 2 Variations of mean water flow (m³/s) and mean water temperature (°C) in the Amblève River and the position (km) of the radio-tagged trout T1 and T2 (a), grayling G1, G2 and G3 (b), nase N1 (c) and barbel B1, B2, B3 and B4 (d) relative to the discharge point: FW1 during the 2007–2009 study with X-axes that differ depending on the time and date of tracking.
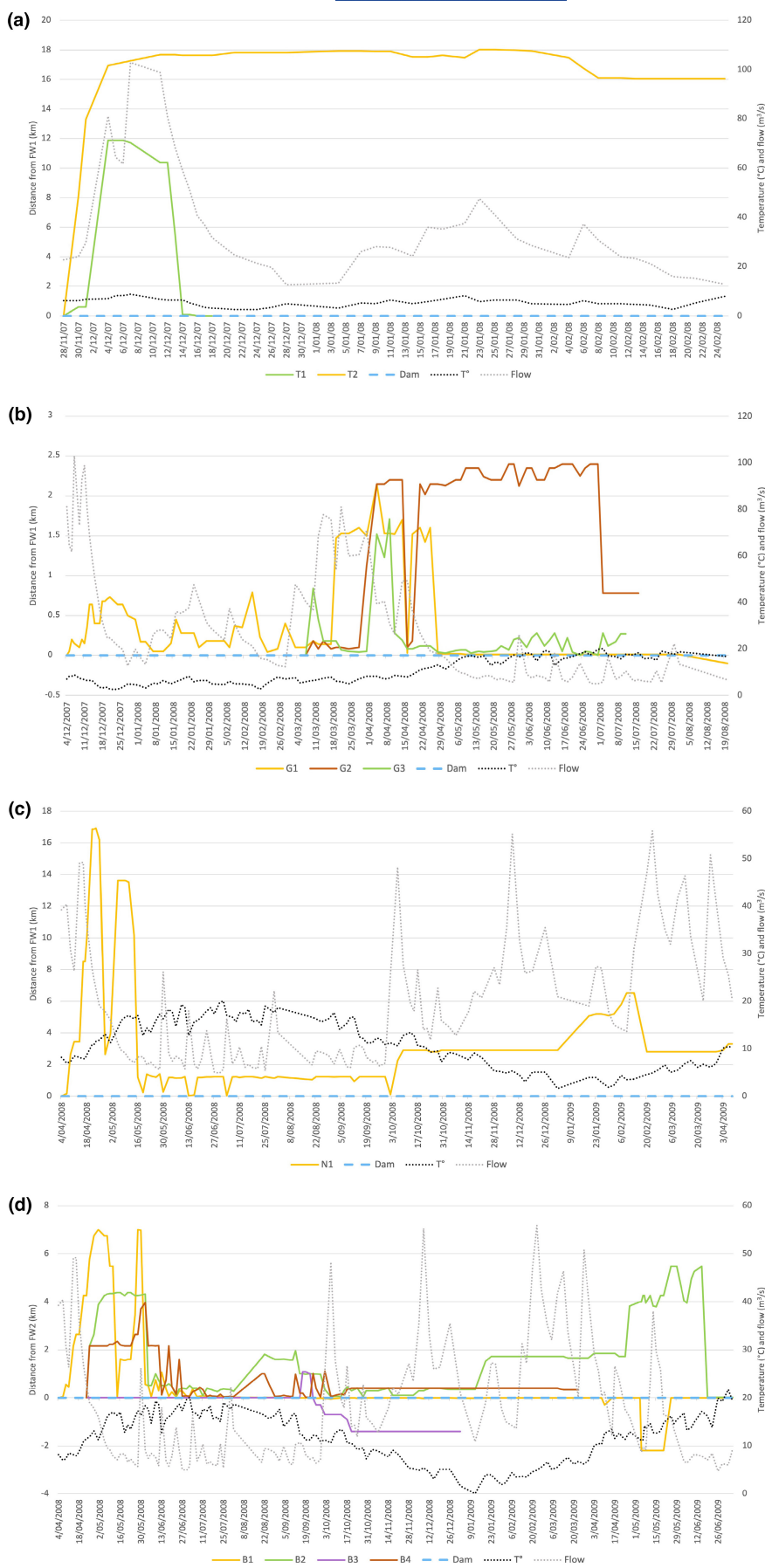
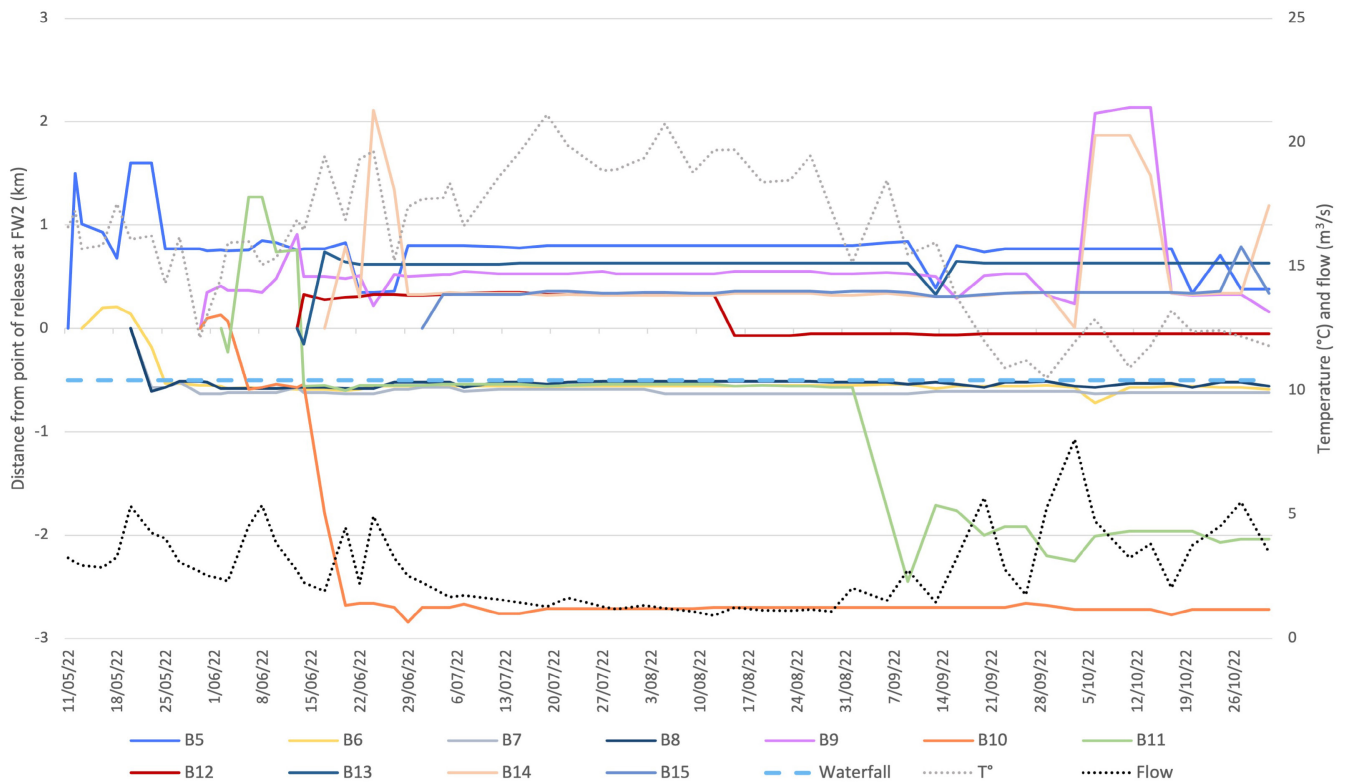**FIGURE 3** Variations of mean water flow (m³/s) and mean water temperature (°C) in the Amblève River and the position (km) of the radio-tagged barbels B5–B15 relative to the discharge point: 500 m upstream of FW2 during the 2022 study.

3.3 | Home range and stay in the new river stretch

Some individuals were located in the tributary and sub-tributary of the main stream (Amblève River); T1 and T2 at FW1 in the Lienne River and the Mierdeux River, respectively. Nase and trout are the species with the largest home range with 16.9 km (N1), 11.9 km (T1) and 18 km (T2) from FW1. Barbel and grayling exploited smaller home ranges ranging from 1.7 km (G3) to 2.4 km (G2) for the grayling, 2.5 km (B3) to 9.2 km (B1) for the barbel from FW1 and 0.4 km (B12) to 3.7 km (B11) for the barbel from FW2 (Table 3). Barbels tracked from FW1 had a wider home range than those tracked from FW2 (*U* test, $p < .05$; Figure 4). The greatest distance travelled upstream of a newly opened area was 7 km (B1) from FW1 and 2.1 km from FW2 (B9 and B14); significant differences were identified between individuals belonging to FW2 and between sites (KW test, $p < .05$). In total, 3 (G1, B1 and B3) of the 10 individuals tracked from FW1 moved downstream of the dam and 7 (B6, B7, B8, B10, B11, B12 and B13) of the 11 barbels from FW2 moved downstream of the release point; however, only five barbels moved down the waterfall (B6, B7, B8, B10 and B12; Table 3).

The TND was significantly greater for individuals tracked from FW1 (*U* test, $p < .05$) with, on average 24.9 km travelled from FW1 and 4.0 km from FW2. The greatest net total distance travelled was 37.8 km from FW1 (B1) and 9.7 km from FW2 (B14). For TRD, no significant difference was observed between the two sites (U test, $p > .05$) with, on average −0.3 km from FW1 and −0.4 from FW2. The greatest total real distance travelled was 0.3 km from FW1 (B4) and

1.2 km from FW2 (B14). No significant difference was observed for MND, with average net displacements ranging from 0 (B3) to 0.3 km (B1) and ranging from 0 (B6, B7, B8, B12, B13 and B15) to 0.2 km (B11 and B14) from FW2 (Table 3, Figure 4).

3.4 | Effects of environmental factors on the mobility of individuals

The model selection showed that temperature and flow have an effect on Dn, with lower AIC values and greater weight at FW1 (AIC = 2330.405, weight = 0.508) and FW2 (AIC = 940.216, weight = 0.778) and explained 2.2% at FW1 (marginal $R^2 = .022$) and 7.7% at FW2 (marginal $R^2 = .077$) of the model's total variance. Allowing for random effects, the model explained 8.4% (conditional $R^2 = .084$) of the variance at FW1 and 14.4% at FW2 (conditional $R^2 = .144$). However, at FW1 the flow did not seem to have a strong effect according to the distance in AIC score between the model selected and the model with only the temperature (Δ AIC < 2). The results of the LMM analyses showed that temperature and flow have a positive effect on the net distance travelled by individuals at FW1 (95% CI: 0.017–0.048 and 0.004–0.013, respectively) and FW2 (95% CI: 0.007–0.049 and 0.106–0.200; Table 4).

Model results suggest that increased flow and temperature had a positive influence on trout movements (estimate = 0.049 and 0.012, respectively). However, this effect was not confirmed by the statistical results (95% CI: −0.021 to 0.003 and −0.002 to 0.003)

TABLE 3 Spatial indicators of marked individuals (HR, TND, TRD and MND), minimum and maximum distance travelled (km) from point 0 corresponding to the place of discharge of individuals with negative values corresponding to the downstream of point 0.

No fish	HR (km)	Min (km)	Max (km)	TND (km)	TRD (km)	MND (km)
T1	11.9	0.0	11.9	23.8	0.0	1.7
T2	18.0	0.0	18.0	21.2	16.1	0.5
G1[a]	2.3	−0.1	2.2	13.7	−0.1	0.1
G2	2.4	0.0	2.4	10.4	0.8	0.2
G3	1.7	0.0	1.7	8.0	0.3	0.2
B1[a]	9.2	−2.2	7.0	37.8	0.0	0.3
B2	5.5	0.0	5.5	33.4	0.0	0.2
B3[a]	2.5	−1.4	1.1	3.6	−1.4	0.0
B4	4.0	0.0	4.0	24.8	0.3	0.2
N1	16.9	0.0	16.9	77.8	3.3	0.7
B5	1.6	0.0	1.6	7.5	0.4	0.1
B6[a]	0.9	−0.7	0.2	1.6	−0.6	0.0
B7[a]	0.6	−0.6	0.0	1.1	−0.6	0.0
B8[a]	0.6	−0.6	0.0	1.4	−0.6	0.0
B9	2.1	0.0	2.1	6.9	0.2	0.1
B10[a]	3.0	−2.8	0.1	3.8	−2.7	0.1
B11	3.7	−2.5	1.3	7.6	−2.0	0.2
B12[a]	0.4	−0.1	0.4	0.9	−0.1	0.0
B13	0.9	−0.2	0.7	1.8	0.6	0.0
B14	2.1	0.0	2.1	9.7	1.2	0.2
B15	0.8	0.0	0.8	1.4	0.3	0.0

[a]Corresponds to individuals found downstream of a physical barrier.

and depending on the individual, the greatest distance was travelled at low (12.8 km above 74.5 m³/s) or high flow rates (15.3 km under 34.3 m³/s). Graylings exhibited a slight tendency to cover shorter distances as temperature increased (estimate = −0.034) and conversely, when the flow rate increased (estimate = 0.001). The three graylings moved more at average flow rates (7.8 km (G1), 4.3 km (G2) and 4.8 km (G3) between 9.1 and 40.4 m³/s). The model confirmed the effect of temperature (95% CI: 0.027–0.067) on displacement but not flow (95% CI: −0.006 to 0.011). Nase covered greater distances at average flow rates (47.1 km between 8 and 26.7 m³/s), as well as when temperatures were between 10 and 17°C. However, no effect was observed (estimate = 0.046, 95% CI: −0.017 to 0.109 for the temperature and estimate = 0.014, 95% CI: −0.009 to 0.038 for the flow). Barbels at FW1 showed considerable variability in their movement patterns. Movements exceeding 2 km occurred when the temperature was above 10°C. Some individuals (B1, B2 and B4) covered greater distances at average flow rates (between 7.6 and 23.3 m³/s) and other (B3) covered a greater distance at low-flow rates (under 7.6 m³/s). The LMM showed that temperature has a positive effect on the displacement of barbels (estimate = 0.047, 95% CI: 0.027 to 0.067) but not the flow (estimate = 0.002, 95% CI: −0.006 to 0.010). At FW2, results showed that barbels tended to cover a larger distance (>0.5 km) as the flow rate increased beyond 2 m³/s, and temperatures ranged between 12.5 and 17.5°C. The model indicated a positive effect of both

environmental variables. However, greater total displacement was observed within each flow category (Tables 4 and 5, Figure 5).

4 | DISCUSSION

Individual tracking is a good strategy to determine the ecological added value following the defragmentation of a river section. Other studies that have used radiotelemetry focused on determining the efficiency of fishways (Grimardias et al., 2022; Ovidio et al., 2017) or the different habitats used and movement characteristics in rivers in the regular home range of the fish (Capra et al., 2017; De Leeuw & Winter, 2008; Gardner et al., 2013). However, few studies have studied the behaviour of individuals outside their established home range and continuously. Some authors have already tested the success of the translocation of individual fish (Ovidio et al., 2016, with nase) in different sections of the same river. Benitez et al. (2018) studied, on an *ad hoc* basis the movements of individuals after having been released upstream of a fishway, using RFID tags and fixed stations. Tummers et al. (2016) succeeded in demonstrating the importance of using different methods to assess the impact of habitat restoration on fish populations. Manual radio-telemetry enabled the authors to point out migration bottlenecks at some crossing lanes, allowing subsequent improvements to crossing devices. This study is unique in that it allowed for the collection of data on the detailed behaviour of individual fish
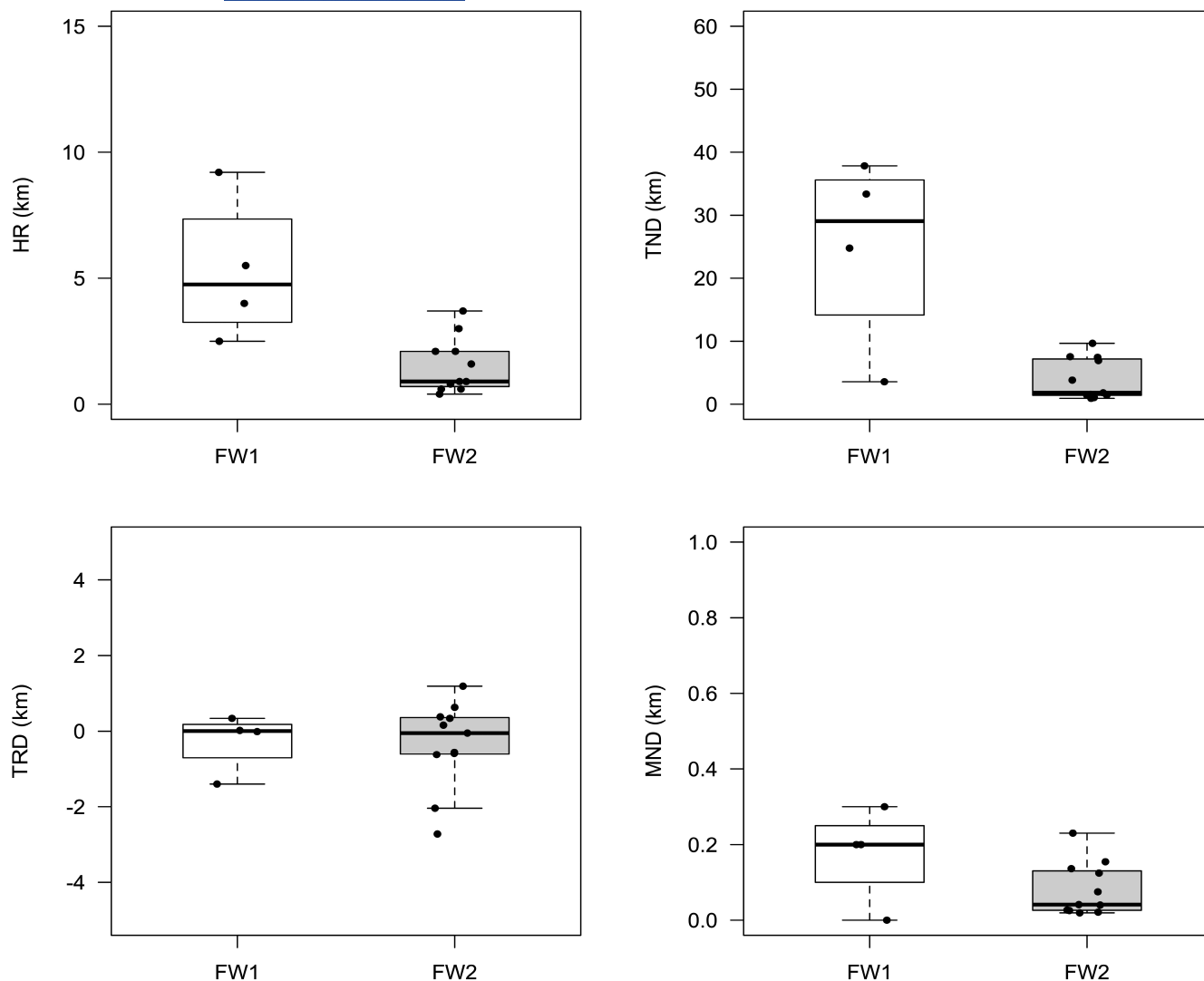
FIGURE 4 Boxplots of the four spatial indicators (HR, TND, TRD and MND) with barbels combined per site (FW1 and FW2). The end of the whiskers corresponds to the extreme values, and individuals are represented by a dot.

of different species after their passage in a fishway, during medium and long time periods and directly after the reopening of a migratory axis. Our results showed that most individuals succeeded in establishing themselves, definitively or temporarily, in the new open river stretch, and most species performed movement behaviours that are most probably associated with reproduction. This reinforces the validity of constructing fishways with associated positive responses from fish. Indeed, the results indicate that the reopening of the migratory axis is beneficial for fish since they have dispersed and made migration movements, despite a break in connectivity for several years (Benitez et al., 2018; García-Vega et al., 2022; Gelder, Benitez, & Ovidio, 2023; Gelder, Benitez, Ovidio, Dierckx, & Sonny, 2023).

Our results are restricted in terms of representativity and statistical output due to the low number of individuals tracked and the heterogeneous number of individuals per species. A more representative sample with the same number of individuals per species would have been better but was not possible with the captures in the fishway. However, this problem is compensated by the innovative and

qualitative approach with long-term tracking, accurate locations and the possibility to track the fish everywhere they moved, even after long distances travelled and entry into tributaries. The four radio-tracking species showed a diversity of movements after being released upstream of FW1 and FW2. The longest displacements took place during the migration period of the four species reported in the literature, certainly to search for spawning areas. At the FW1 site, the trout exploited a tributary of the Amblève River and even a sub-tributary, which are suitable reproductive habitats covering up to 18 km before moving downstream during autumn, which is a common behaviour for trout (Epple et al., 2022; García-Vega et al., 2022; Ovidio et al., 2004; Piecuch et al., 2007) and shows the importance of having a connection between mainstream and its tributaries during a reopening event. Trout began their migration at low temperatures (7°C) and during peak flow (81 m^3/s), which are known to act as stimuli for spawning migration (García-Vega et al., 2022; Ovidio et al., 1998; Piecuch et al., 2007). The nase covered a 17 km stretch upstream of FW1 during April, when the water temperature

TABLE 4 Linear mixed model (LMM) selection with factors affecting the net distance travelled at FW1 and FW2, with individuals nested within species at FW1 and individuals at FW2 as a random effect.

Response variable	Site	Model structure	AIC	Δ AIC	Weight
Net distance travelled (Dn)	FW1	Temp+Flow+(1|sp/ind)	2330.405	0.00	0.508
		Temp+(1|sp/ind)	2330.514	0.11	0.481
		Fow+(1|sp/ind)	2338.012	7.61	0.011
Net distance travelled (Dn)	FW2	Temp+Flow+(1|ind)	940.216	0.00	0.778
		Temp+(1|ind)	974.633	31.90	0.000
		Flow+(1|ind)	942.729	2.51	0.221

FW1

Random effects

Groups	Name	Variance	SD
Ind: sp	(Intercept)	0.0272	0.1650
sp	(Intercept)	0.0303	0.1741
Residual		0.8492	0.9215

Number of obs: 854, groups: ind: sp, 10; sp, 4

Fixed effects: all species	Estimate	SE	t value	95% CI
(Intercept)	−2.2062	0.1699	−12.978	[−2.538 to −1.868]
Temperature	0.0332	0.0079	4.201	[0.017–0.048]
Flow	0.0081	0.0023	3.516	[0.004–0.013]
Fixed effects: trout				
(Intercept)	−2.2358	0.6530	−3.424	[−2.413 to 1.714]
Temperature	0.0499	0.1370	0.364	[−0.310 to 0.549]
Flow	0.0119	0.0090	1.326	[−0.014 to 0.042]
Fixed effects: grayling				
(Intercept)	−1.3778	0.2287	−6.023	[0.127–0.540]
Temperature	−0.0341	0.0120	−2.623	[−0.021 to 0.004]
Flow	0.0012	0.0028	0.428	[−0.002 to 0.003]
Fixed effects: barbel				
(Intercept)	−2.4412	0.2229	−10.951	[−2.870 to −2.013]
Temperature	0.0473	0.0102	4.635	[0.027–0.067]
Flow	0.0022	0.0043	0.508	[−0.006 to 0.107]
Fixed effects: nase				
(Intercept)	−2.2667	0.5642	−4.017	[−3.385 to −1.149]
Temperature	0.0463	0.0319	1.452	[−0.017 to 0.109]
Flow	0.0145	0.0121	1.200	[−0.009 to 0.038]

FW2

Random effects

Groups	Name	Variance	SD
Ind	(Intercept)	0.0238	0.1543
Residual		0.3057	0.5529

Number of obs: 545, groups: ind, 11

Fixed effects: barbel	Estimate	SE	t value	95% CI
(Intercept)	−2.8922	0.2336	−12.380	[−3.349 to −2.435]
Temperature	0.0283	0.0109	2.591	[0.007–0.049]
Flow	0.1535	0.0239	6.400	[0.106–0.200]

Note: The table includes the AIC score, distance score from the model with the lowest AIC (Δ AIC) weight of each model and the summary of the model selected by site (FW1 and FW2) with a 95% confident interval (CI).

reached 10°C (Ovidio et al., 2016; Ovidio & Philippart, 2008) and was blocked at the foot of the Coo waterfall, which was an impassable obstacle at that time. This result shows the importance of re-establishing connectivity along the entire length of the river to enable individuals to take advantage of the maximum number of available habitats (Panchan et al., 2022). The graylings migrated over shorter distances and most particularly exploited an area of the Amblève situated between 1.5 and 2.5km upstream of FW1 near potential spawning areas. A barbel female, which was tracked for two reproduction seasons, expressed an interannual fidelity to the spawning site in the newly exploited reach as already observed by Ovidio et al. (2007) in the Ourthe river in the Belgian Ardennes. As observed for three barbels upstream of FW1, the same trend was observed at the FW2 site with upstream movements observed for five barbels, between May and late June, known to be the reproduction period (Britton & Pegg, 2011; Gutmann Roberts et al., 2019; Lucas & Batley, 1996; Ovidio et al., 2007). Moreover, spawning temperature conditions were reached as the water temperature was >13.5°C (observed by Benitez & Ovidio, 2018; Ovidio et al., 2007).

TABLE 5 Total net distance travelled (TND) per individual per site by category of flow percentile (m³/s; trout: P25 = 34.3 and P75 = 74.6; grayling P25 = 9.1 and P75 = 40.4; barbel at FW1: P25 = 7.6 and P75 = 23.3; nase: P25 = 8.0 and P75 = 26.7; barbel at FW2: P25 = 1.8 and P75 = 3.7).

	<P25	P25–P75	>P75
FW1			
T1	0.6	10.4	12.8
T2	15.3	1.6	4.4
G1	0.1	7.8	5.7
G2	2.6	4.3	3.5
G3	1.9	4.8	1.3
B1	13.0	20.3	4.6
B2	14.5	15.6	3.3
B3	1.7	1.4	0.5
B4	9.6	11.7	3.5
N1	7.8	47.1	22.8
Total	67.1	124.9	62.3
FW2			
B5	12.8	23.9	10.1
B6	0.0	0.6	0.9
B7	0.1	0.4	0.6
B8	0.1	0.4	0.9
B9	0.1	2.0	3.0
B10	0.1	3.5	0.2
B11	1.3	5.0	1.3
B12	0.5	0.5	0.0
B13	0.0	1.4	0.4
B14	0.1	4.1	4.3
B15	0.1	0.4	0.9
Total	15.2	42.2	22.7

The majority of these movements occurred during an increase in flow (Britton & Pegg, 2011; Lucas, 2000). The barbel is known in the literature to migrate over long distance during pre-spawning and the spawning period (Baras et al., 1994; Britton & Pegg, 2011; De Leeuw & Winter, 2008), sometimes covering up to 20km (Ovidio et al., 2007), but the distance covered by our barbel upstream of FW1 and FW2 reached up to 6 and 2km, respectively. This probably means that they used one of the first spawning sites that they discovered upstream of the obstacles with no need to look any further. Other upstream movements were also observed during autumn by three barbels, as observed by Benitez and Ovidio (2018); these movements can be associated with finding suitable habitats to overwinter. The behaviour observed confirms that all the species probably succeeded in reaching spawning areas after their release upstream of the fishway, which confirm the merits of their installations and the importance of their multispecies characteristics (Gelder, Benitez, & Ovidio, 2023; Gelder, Benitez, Ovidio, Dierckx, & Sonny, 2023; Ovidio et al., 2020). Results of the LMM are quite in accordance with the literature in terms of flow and temperature factors stimulating movements. Although they were already in the process of migrating when they were marked, environmental variables temperature and flow, showed an influence on the movements of individuals with a greater influence of temperature at FW1 although differences in the influence of variables were observed at the species level. These differences of importance may be associated with different monitoring periods depending on the site, but may also be linked to the preferences of species that may have different behaviours responses in the same river basin (Benitez & Ovidio, 2018; Lucas, 2000). After the spawning period during summer, the majority of individuals stabilised in specific habitats, where little movements were observed (Lucas & Batley, 1996; Ovidio et al., 2007). The Amblève River is located in a barbel zone (Huet, 1949) from Lorcé to the confluence with the Salm River; therefore, the Amblève River is full of suitable habitat for this species that could potentially limit search movements to achieve their biological functions.

Radio-tracking upstream from FW1 has shown that all the species tracked undertook post-spawning downstream migration, called post-reproduction homing behaviour (Ovidio, 1999; Ovidio & Philippart, 2002). But, they were interrupted by the dam associated with FW1 which, when the spillways are closed and all the water is turbined, makes this movement impossible: a trout rapidly moved downstream (before being found dead at FW1 probably of exhaustion after spawning), just as one grayling (Ovidio et al., 2004; Parkinson et al., 1999) and two of the four barbels, which finally managed to move downstream of FW1 dam by taking advantage of a low flow and the opening of the gates. The nase also shown this behaviour (Huber & Kirchhofer, 1998; Panchan et al., 2022) as the two other barbels were blocked several times at FW1, since the dam was impassable when the gates were not opened. In this case, for fish in the post-spawning phase, the only alternative to a forced and lethal passage through the turbines is an interruption of migration and the use of substitution habitats (Gutmann Roberts et al., 2019). This behaviour was observed by the nase and two of the barbel; our results
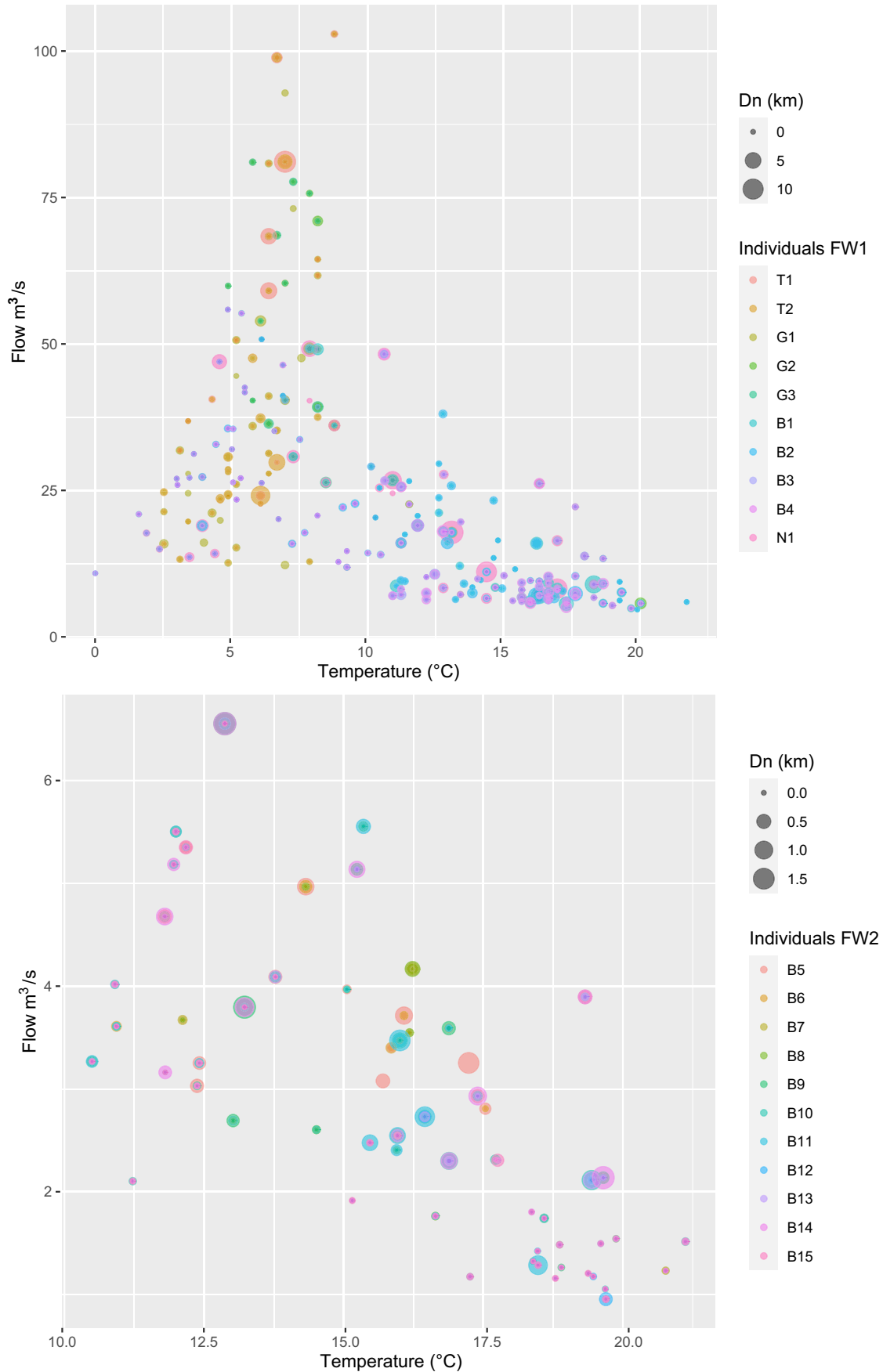
FIGURE 5 Bubble charts of the net distance travelled (Dn) by individuals between two subsequent locations depending on temperature (°C) and flow (m³/s) at FW1 and FW2 (x = temperature (°C), y = flow (m³/s), z = Dn (size of the circle) and colours = individuals).

showed that they established themselves in a new sector, where they were totally absent before the fishway was constructed. At FW2, five individuals rapidly moved down the waterfall after being released upstream. Except for one, these movements occurred during the migration period. It's however, difficult to know if they succeeded in spawning up the waterfall before their homing downstream. Indeed, the barbel is known in the literature for its fidelity to functional habitats (Baras, 1997; Ovidio et al., 2007; Panchan et al., 2022) and for its homing post-reproductive behaviour. Other individuals made downstream movements without crossing back over the waterfall after upstream displacement peaks, which may be tentatively associated with homing behaviour due to a fear of passing the waterfall. Our results showed that restoration of connectivity has enabled individuals to exploit punctually or permanently many different habitats. Access to new habitats therefore allows fish to have a greater diversity of available habitats, increasing the chances of matching their habitat preferences to reproduce, feed or rest, which leads to a boost in their fitness (Brönmark et al., 2014; Mawer et al., 2023). Moreover, this allows fish to increase genetic mixing with other populations and, therefore, increase genetic diversity to be able to combat climate change (Baldan et al., 2023; Lange et al., 2018).

This suggested that allowing the fish to move upstream with fishways is a first step for the ecological gain of rivers, but a holistic approach combined with the installation of devices to allow downstream migrations or an opening of gates for mobile devices would allow fish to perform all the natural movements. To prevent a holobiotic potamodromous species from accomplishing their post-reproductive homing behaviour is probably less imperative and constraining than for diadromous species as they succeed in finding alternative habitats. However, these results suggest that downstream movement has to be considered for a large part of these fish species in rivers.

Despite a small number of individuals studied, with precision in terms of tracking, our results encourage the importance of restoring free circulation both upstream and downstream to allow fish to achieve their complete biological cycle. These results can support the hypothesis that the parts of the river made accessible by the construction of a fishway can indeed be exploited by fish originating from the downstream part of FW1 and FW2 and that the ascending behaviours observed are not atypical compared to behaviours of the same species observed in their usual environments (Baras & Cherry, 1990; Britton & Pegg, 2011; Ovidio, 1999; Ovidio et al., 2004, 2016; Parkinson et al., 1999). It remains to be clarified whether the migrations towards spawning grounds materialise into successful reproduction and good survival levels of the earlier stages in the new habitat by undertaking complementary studies including a larger number of individuals tracked.

AUTHOR CONTRIBUTIONS

Writing of the article: J. Gelder, M. Ovidio and J.P. Benitez. Conceived and designed the investigation: J. Gelder, M. Ovidio and J.P. Benitez. Performed field and/or laboratory work: J. Gelder, M. Ovidio, J.P. Benitez. Analysed the data: J. Gelder and J.P. Benitez. Contributed materials, reagents and/or analysis tools: M. Ovidio. Paper proof-reading: J. Gelder, M. Ovidio and J.P. Benitez. Research project funding: M. Ovidio.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict 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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