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PRIMARY RESEARCH PAPER

What happens beyond the obstacle? Long-term fishway post-passage behaviour of potamodromous fish

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Abstract River defragmentation is essential to restore longitudinal connectivity and allow fish populations to access the full range of functional habitats they require. Yet, little is known about how individuals move and use habitats after a passage in a fishway. Over three consecutive years, we used manual radiotelemetry to track 31 individuals (21 barbel *Barbus barbus*, 10 chub *Squalius cephalus*) released upstream of two major barriers on the Amblève River (Belgium). Post-passage behaviour showed marked inter-individual variability, falling into three main profiles: long-term upstream residency, rapid downstream return, and upstream exploration before moving downstream an obstacle. Barbel exhibited larger home ranges (min = 0.5, max = 25.8, mean = 6.0 km) than chub (min = 0.5, max = 4.3, mean = 1.7 km), and were more likely to move downstream an obstacle (67% vs. 20%). Moving downstream of an obstacle increased significatively during the spawning period (estimate = 4.13, 95% CI 1.99–6.87) and with higher factor condition (estimate = 1.25, 95% CI 0.21–2.35), but significatively decreased with higher flow. High inter-individual variability suggests that movements are partly driven by intrinsic behavioural traits. These findings help understand river defragmentation advantages as a whole, by revealing what fish do once they have passed an obstacle.

Keywords Defragmentation · Potamodromous species · Radiotelemetry · Fishway · Migratory axis

Introduction

Freshwater ecosystems are among the most threatened habitats on Earth, facing severe pressure from a variety of human-induced alterations. One of the most negative and long-standing of these pressures is the fragmentation of river networks by physical barriers such as dams, weirs, and hydropower installations (Belletti et al., 2020; Felin et al., 2025). These structures break the natural continuity of river systems, preventing or limiting the movement of aquatic organisms, altering sediment transport, and modifying flow regimes (Nilsson et al., 2005; Dudgeon et al., 2006; Duarte et al., 2021; Baird et al., 2024). For migratory fish species, in particular, such disruptions can have profound consequences on population dynamics, reproductive success, and genetic connectivity (Scruton et al., 2008; Lange et al., 2018; Baldan et al., 2023; Dean et al., 2023).

In response to these challenges, river restoration initiatives have increasingly focused on improving

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longitudinal connectivity. The complete removal of a dam remains the most effective way to restore longitudinal connectivity, but it is not always a realistic option (Tummers et al., 2016; Dodd et al., 2017; Bellmore et al., 2019; Bower et al., 2024). The costs associated with deconstruction, along with the essential services provided by the structure, such as hydropower generation, water supply, or flood regulation, can present significant constraints (Bellmore et al., 2019; Barbarossa & Schmitt, 2024). As a result, many dams are conserved. In such cases, a key measure has been the installation of fishways. These structures re-establish connectivity to functional habitats, including feeding, refuge, and spawning areas, while preserving the human uses of the barrier (Roscoe & Hinch, 2010; Marques et al., 2018; Mameri et al., 2019; Lothian et al., 2020; Ovidio et al., 2023). Numerous studies have focused on evaluating the effectiveness of fishways, the way they are used by fish populations, and their impacts at the scale of fish communities. These studies typically assess whether individuals are able to locate and enter the fishway, how long they take to pass through it, and whether they successfully emerge upstream/downstream, all key indicators for measuring passage performance (Stuart & Mallen-Cooper, 1999; Noonan et al., 2012; Silva et al., 2012; Cooke & Hinch, 2013; Weibel & Peter, 2013; Tummers et al., 2016; Romão et al., 2018; Bao et al., 2019; Dębowski et al., 2022; Gelder et al., 2024a; Iaia et al., 2025). In parallel, other research has examined the effects of fishways on the composition, diversity, or structure of fish communities in upstream and/or downstream sections of the river (Benitez et al., 2015, 2018; Sun et al., 2022; Gelder et al., 2023; Tan et al., 2024). Such studies are essential for understanding how fish species respond to river defragmentation efforts. They also help to identify limitations in the design or functioning of fishways that may reduce their effectiveness. As such, they provide valuable guidance for managers in optimising restoration strategies.

Despite the extensive research dedicated to the efficiency and design of fishways, a key component of the river defragmentation process remains largely overlooked: the post-passage behaviours of individuals after they have passed an obstacle. Do they continue their migration? Do they remain nearby? Do they actually make use of the newly accessible habitats? These aspects are still rarely explored in the scientific literature, and when they are, studies are often restricted to specific points such as fishways (Benitez et al., 2018; Tétard et al., 2025), which limits our ability to fully evaluate the ecological outcomes of connectivity restoration measures. Studying this post-passage phase is therefore essential to evaluate the long-term success of such interventions and to ensure they result in genuine ecological gain. To better understand fish behaviour after crossing an obstacle in the context of habitat defragmentation, it is essential to obtain precise data on their movements. Manual radiotelemetry is particularly well suited to this objective, as it allows for the accurate localisation of tracked individuals at any time and wherever they may be along the monitored river section (Huber & Kirchhofer, 1998; Ovidio, 1999; Ovidio et al., 2020; Calles et al., 2021; Bravo-Córdoba et al., 2023; Renardy et al., 2023; Gelder et al., 2024b; Popp et al., 2024; Kucukali et al., 2025). Although this method does not allow for the simultaneous tracking of large numbers of individuals, it provides highly detailed and reliable information which are crucial for studying individual behavioural responses.

The Amblève River, located in the Belgian Ardennes, is fragmented by nine barriers, among these two are significant: the Coo waterfall and the Lorcé hydroelectric dam. Both of these major obstacles have been equipped with fishways, effectively reconnecting upstream habitats and restoring longitudinal connectivity. This study aims to investigate the behaviour of fish after successfully passing these structures, specifically, what do individuals do once they are upstream? To address this question, we carried out a continuous, three-year monitoring using manual radiotelemetry on the Ambleve River, on two cyprinid species: chub [*Squalius cephalus* (Linnaeus, 1758)] and barbel [*Barbus barbus* (Linnaeus, 1758)]. Individuals were tracked manually, without seasonal interruption, making this, to our knowledge, the first study of its kind to combine location accuracy and temporal continuity. It is precisely this original approach that gives this study its innovative character. We focused our analysis on several complementary aspects: (i) the spatial behaviour of individuals based on their movements and their occupation of the river stretch; (ii) mobility indicators derived from displacement metrics between successive tracking sessions; (iii) a comparison of exploratory behaviour between individuals in upstream, newly accessible habitats versus downstream sectors; (iv) and finally, an examination of the factors potentially influencing post-passage outcomes, specifically, why some individuals remain upstream while others move back downstream. This work is fully aligned with current efforts to restore ecological continuity in river systems, by providing new insights into the post-passage phase, a component still largely overlooked, yet crucial for assessing the real outcomes of river defragmentation.

Materials and methods

Study site

The Amblève river, the main tributary of the Ourthe River in the Belgian Meuse basin, drains a catchment area of around 1077 km^2, flows for 88.4 km and has an average annual flow of 19.3 m^3/s. From its confluence with the Warche River to its confluence with the Ourthe River, the Amblève River belongs to the 'grayling/barbel' zone (Huet, 1949), characterised by cool, well-oxygenated waters with a steady current, perfectly suited to rheophilous species. Along this river, nine weirs and dams interrupt longitudinal connectivity, including two major ones: the hydroelectric dam at Lorcé and the semi-artificial waterfall at Coo (Fig. 1).

The Lorcé dam, built in the 1930s, 22.9 km upstream of its confluence with the Ourthe River, creates an approximately 3.3 m head and supplies the Heid-de-Goreux power station, 8 km downstream. To restore upstream migration, a 67-m-long, 15-pool vertical-slot fishway installed in 2007, that incorporates a 1.7 × 1.1 × 1.5 m capture cage that enables scientific monitoring of fish use. The fishway was non-functional from 2016 to 2022. It was reopened in November 2022 (Fig. 1).

The Coo waterfall, located 17 km upstream of Lorcé dam, has a drop of 11.8 m. The waterfall was formed in the Middle Ages following a meander overlap. In 1970, the meander was used to create a reservoir feeding a pumped-storage hydroelectric power station. The water from the turbine is returned to the river via a restitution channel located on the left bank downstream of the waterfall. From that point onwards, the waterfall became totally impassable for fish moving upstream. To restore connectivity, a capture-transport fishway was installed in the restitution channel in 2021. The device has two basins leading to a 2.8 × 1.9 × 1.8 m capture cage.

Both capture cages were monitored one to three times per week, and the individuals captured were released upstream of the obstacle.

Fish capture and tagging

A total of 31 individuals were captured and tagged during the study period, comprising 21 barbels (*Barbus barbus*) and 10 chubs (*Squalius cephalus*) (Table 1). Most of the fish ($n = 28$) were captured at the Coo fishway, while three individuals were capture at Lorcé fishway. Both species are rheophilic and representative of the local fish community, as the Amblève River is located in a grayling/barbel zone, characterised by well-oxygenated, fast-flowing habitats particularly favourable to rheophilic species. Following capture, fish were anaesthetised using a solution of Eugenol at a concentration of 0.1 mL/L. The fish was considered anaesthetised when it was losing equilibrium and can no longer maintain a ventral position, typically after approximately five minutes of anaesthetic exposure. Each individual was then weighed (± 1 g), measured (total length, ± 1 mm) and sexed when possible. A surgical procedure was carried out to implant the radio transmitter (ATS Inc., 40 or 48 MHz with trailing whip antenna) into the intraperitoneal cavity. The weight/transmitter index was kept at or below 2.5% to minimise the physiological impact of tagging (Ovidio et al., 2020; Gelder et al., 2024a, b). A small incision of approximately 1 to 2 cm was made posterior to the pelvic fins, and the transmitter was inserted carefully into the body cavity. The incision was then closed using three absorbable sutures (Vicryl), disinfected with eosin solution. The fish was placed in an aerated recovery tank until full recovery from anaesthesia and restoration of swimming ability (± 20 to 30 min). Once recovered, individuals were transported in oxygenated tanks and released approximately 500 m upstream of the obstacle from which they were originally captured.

Three different types of radio transmitters (ATS Inc.) were used during the study: the F1840 model (20 g) with an estimated battery life of three years, the F1835 model (14 g) with a battery life of 629 days, and the F1580 model (3.6 g) with a

Fig. 1 Map of the Amblève River and its nine barriers to longitudinal connectivity. The two study sites, Lorcé dam and Coo waterfall, are indicated and illustrated on the map

battery life of 441 days. Tagging was carried out continuously over a period of three years, with the first individual tagged on 11 May 2022 and the last on 17 July 2024 (Table 1).

Radiotelemetry tracking

Tracking began on 11 May 2022 and ended on 26 June 2025. Individuals were tracked continuously throughout the year, with a frequency ranging from

Table 1 Individual characteristics of fish monitored by radio telemetry: species, individual ID, date of capture and first location, capture site, transmitter weight (g), body weight (g), transmitter-to-body weight ratio (%), total length (mm), sex (F: female, M: male, I: indeterminate, +: sexually mature) and date of the end of the tracking

Species	ID	Date of capture and first location	Site	Transmitter weight	Weight (g)	Weight/transmitter index (%)	Size (mm)	Sex	End of the tracking
Barbel	B1	2022-05-11	Coo	20	3160	0.6	620	F	26-06-25
Barbel	B2	2022-05-13	Coo	20	3340	0.6	655	F	26-06-25
Barbel	B3	2022-05-20	Coo	20	832	2.4	397	F+	26-06-25
Barbel	B4	2022-05-20	Coo	20	3670	0.5	620	F	26-06-25
Barbel	B5	2022-05-30	Coo	20	2004	1.0	527	M+	26-06-25
Barbel	B6	2022-05-30	Coo	20	2674	0.7	615	F+	26-06-25
Barbel	B7	2022-06-02	Coo	20	2478	0.8	568	M+	21-08-23
Barbel	B8	2022-06-13	Coo	20	2622	0.8	635	M?	26-06-25
Barbel	B9	2022-06-13	Coo	20	3662	0.5	644	F+	26-06-25
Barbel	B10	2022-06-17	Coo	20	2542	0.8	586	F+	26-06-25
Barbel	B11	2022-07-04	Coo	20	2260	0.9	582	M?	24-01-24
Barbel	B12	2024-05-16	Coo	14	1664	0.8	501	I	26-06-25
Barbel	B13	2024-05-16	Coo	14	1468	1.0	536	F+	26-06-25
Barbel	B14	2024-05-16	Coo	14	3780	0.4	632	I	26-06-25
Barbel	B15	2024-05-29	Lorcé	14	1056	1.3	440	F+	26-06-25
Barbel	B16	2024-06-06	Coo	14	2668	0.5	575	F	26-06-25
Barbel	B17	2024-06-19	Coo	14	3550	0.4	668	F	26-06-25
Barbel	B18	2024-06-28	Coo	14	2350	0.6	582	F+	26-06-25
Barbel	B19	2024-07-23	Coo	14	1940	0.7	550	F	26-06-25
Barbel	B20	2024-08-01	Lorcé	14	2246	0.6	570	F	26-06-25
Barbel	B21	2024-08-01	Lorcé	14	2420	0.6	590	I	26-06-25
Chub	C1	2023-05-23	Coo	3.6	150	2.4	220	M+	30-05-23
Chub	C2	2023-06-12	Coo	3.6	2040	0.2	531	F?	26-06-25
Chub	C3	2023-08-09	Coo	3.6	278	1.3	269	I	26-06-25
Chub	C4	2023-08-09	Coo	3.6	302	1.2	271	I	26-06-25
Chub	C5	2024-05-16	Coo	3.6	258	1.4	269	M+	21-06-24
Chub	C6	2024-05-16	Coo	3.6	236	1.5	259	M+	26-06-25
Chub	C7	2024-05-16	Coo	3.6	236	1.5	260	I	26-06-25
Chub	C8	2024-05-17	Coo	3.6	232	1.6	288	I	26-06-25
Chub	C9	2024-06-24	Coo	3.6	332	1.1	287	I	26-06-25
Chub	C10	2024-07-17	Coo	3.6	300	1.2	270	I	26-06-25

two to four times per week depending on the season and the intensity of fish movements. During the spawning period, tracking frequency was increased to better capture short-term behavioural changes. The period of individual tracking ranged from 445 days (approximately one year and two months) to 1142 days (around three years and one month), depending on transmitter lifespan and potential loss of tagged individuals.

Tracking was conducted using a two-step protocol. Initial detection was performed using an omnidirectional antenna installed on a car. Once a signal was detected, the observer proceeded on foot with a diamond directional antenna and a Fieldmaster radio receiver (ATS inc.) to determine the fish's precise location. The position of the fish was estimated by triangulation from the riverbank, which involves taking signal from at least three different angles and intersecting the lines to infer the point of emission. Depending on river depth and the observer's distance from the river, spatial accuracy varied between approximately 1 and 4 m^2. For each detection, the individual's position was recorded by marking the corresponding location point on Google Maps, which provided the geographical coordinates. During each tracking session, the activity of tagged individuals was systematically checked. Once a signal was detected, the directional antenna was kept pointed at the fish for two minutes, while listening to variations in the signal intensity emitted by the transmitter. Characteristic fluctuations in the signal indicated that the individual was alive, even when relatively stationary, due to body movements required to maintain position. This procedure ensured that all individuals were indeed alive. There were no spatial limits imposed on the tracking area: individuals were monitored regardless of how far upstream or downstream they moved within the river. When a fish signal could not be detected during a tracking session, an extended search was conducted using the antenna on the car, covering up to 15 km upstream (as far as the confluence with the Warche River) and up to 40 km downstream of the Coo waterfall, including a 10 km section within the Ourthe River. This search effort was repeated over a two-week period during each tracking to relocate missing individuals.

Water temperature was measured hourly using data loggers (Tidbit Onset), while water flow was continuously monitored using data provided by the Hydrometry-Wallonia Public Service.

Data processing

Based on the GPS coordinates recorded in Google Maps for each detection, the locations were subsequently imported into Google Earth, which allowed the calculation of the linear distance travelled between two consecutive tracking sessions. Movements were represented as longitudinal curves, with flow and temperature data displayed on a secondary axis. The graphs show the distance travelled by each individual between consecutive tracking sessions throughout the monitoring period, with upstream movements relative to the obstacle represented as positive values, and downstream movements as negative. In order to maintain acceptable legibility despite the large number of individuals, the individuals were grouped by species and by site, then subdivided. In the case of the chub, two sub-groups were distinguished: (i) individuals that remained upstream and (ii) individuals that moved downstream of the obstacle. For barbel tagged at Coo, four categories were retained: (i) individuals that explored the upstream section before moving downstream of the obstacle; (ii) individuals that rapidly moved downstream of the obstacle (within three weeks after release), (iii) individuals that remained upstream, (iv) individuals with a home range > 10 km.Individuals tagged at Lorcé were considered separately.

In addition to the visualisation of individual displacements, several spatial indicators were calculated to quantify fish mobility throughout the monitoring period (Ovidio et al., 2007; Capra et al., 2018; Gelder et al., 2024b):

- **HR (Home Range)** the linear distance between the most upstream and the most downstream recorded positions for each individual.
- **TU (Time Upstream)** the percentage of days an individual was located upstream of the obstacle from which it originated, relative to the total number of days it was tracked over the entire monitoring period.
- **TND (Total Net Distance)** the sum of the net (absolute) distances travelled between two successive locations.
- **MND (Mean Net Distance)** the average of the net (absolute) distances travelled between two successive locations.
- **MedND (Median Net Distance)**: the median of the net (absolute) distances travelled between two successive locations, excluding cases with no movement (i.e. zero values). This indicator reflects the median distance travelled in instances where displacement occurred.

To better understand the influence of position relative to the obstacle on individual mobility, the total net distance (TND) was calculated separately for movements that occurred upstream and, when applicable, downstream of the obstacle. Thus, for each fish, an upstream TND and a downstream TND were distinguished, depending on the sectors in which movements took place. These data were visually represented using boxplots, separately for barbel and chub. However, for chub, the downstream group included only two individuals, which was insufficient to generate a meaningful boxplot or perform a statistical comparison. Therefore, a Mann–Whitney (U test) was performed only for barbel to statistically assess whether significant differences existed between the total net distances travelled upstream and downstream.

To model the probability that an individual moves downstream of an obstacle after passage (binary outcome: 1 = descended, 0 = not descended), we used a Bayesian mixed-effects logistic regression. We considered eight candidate fixed effects as explanatory variables: daily discharge, daily temperature, degree days, condition factor (K) an index of fish well-being defined as the relationship between body mass and length, body size, species and a binary indicator of whether the date falls within the species' reproductive period. Sex was not included as a covariate in the model due to an unbalanced number of males compared to females, both across species and within individual species. Two random intercepts were specified to account for repeated measures: one for individual fish (1|id) and one for sampling date (1|date). Given the rarity of passage events, weakly informative priors (Normal(0, 2.5)) were used to stabilise estimates. We then performed an exhaustive model search over all 256 possible combinations of the eight predictors. Model comparison was based on PSIS-LOO, which provides measure of model fit with an estimate of expected log predictive density (elpd). Higher elpd values indicate better model fit, and models were ranked accordingly. Differences in elpd (Δ elpd) were calculated relative to the top model, and models with Δ elpd < 2 were considered to have equivalent predictive performance (Vehtari et al., 2017). The final model was re-estimated using Markov chain Monte Carlo (MCMC) with four chains, each running 4000 iterations (1000 warm-up). Convergence was confirmed by inspecting the potential scale reduction factor ($\hat{R} \approx 1$). Model parameters were summarised using posterior means (estimate) and 95% credible intervals. An effect was considered meaningful when the 95% credible interval did not include zero, indicating a robust association with the response variable. We calculated both the conditional and marginal Bayesian R^2 values to assess model performance in explaining variance in the response. The marginal R^2 reflects the variance explained by the fixed effects alone, while the conditional R^2 accounts for both fixed and random effects. Additionally, we conducted posterior predictive checks (PPCs) to evaluate the model's ability to reproduce the distributional structure of the observed data.

Statistical analyses were performed using R version 4.4.2 and RStudio version 2024.09.1, with the packages dplyr 1.1.4, lubridate 1.9.4, brms 2.22.0, loo 2.8.0, performance 0.15.0, caret 7.0–1, tidyr 1.3.1, and ggplot2 4.0.0. The significant threshold was set at 5%.

Results

Movement behaviour of individuals

Movement data revealed distinct individual patterns. Several barbel (B2, B3, B4, B6, B7, B14, B16) moved downstream of the Coo waterfall within 3 (B3, B4)–18 days (B16) post-release (Fig. 2A–B). After descent, some (B2, B3, B4, B7) adopted sedentary behaviour near the waterfall (0.5 to 1 km from the release site), while others (B6, B14, B16) established downstream positions at 2.7 km, 4.3 km, and 8.7 km, respectively from the release site. Occasional exploratory movements were observed, notably by B3, B4 and B14. For example, B3 exhibited two downstream displacements (1.4 km) in November 2023 and March 2025 (48.5 and 7.7 m^3/s; 6.1 and 6.5 °C), followed by an upstream movement in May 2025 (2.2 m^3/s, 13.2 °C) and a return to its previous position eight days later (3.9 m^3/s, 14.2 °C). Similar patterns were observed for B7 and B14. B4 also displayed greater mobility, with two round trips downstream between May and June 2023. Notably, it re-used the Coo fishway on 28 October 2024 (15.6 m^3/s, 12.2 °C) and undertook a 2 km round trip in May 2025 (2.1 m^3/s, 14.4 °C) before returning to its previous location.

Four individuals (B9, B11, B12, B19) initially explored upstream (0.5–1 km) from three months to 1.5 years before moving downstream of the waterfall (Fig. 2C). Notably, B11 moved 1.2 km upstream in November 2023 (3.7 m^3/s, 9.9 °C), then moved downstream of the waterfall in December (20.6 m^3/s, 6.3 °C). After descent, B9, B11, and B12 first settled just below the waterfall before progressively moving downstream, reaching maximum distances of 1.7 km (B9), 2.8 km (B11), and 1.7 km (B12). They each briefly returned to the waterfall between

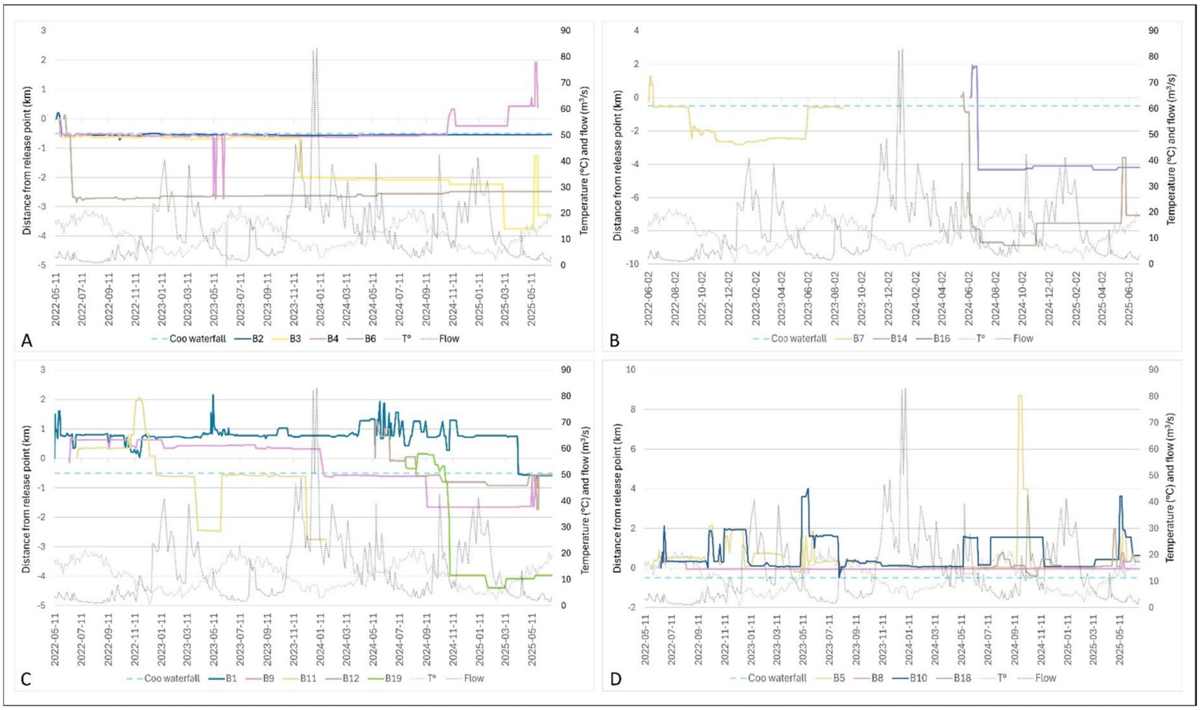

Fig. 2 Positions of tagged barbel at the Coo waterfall recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the waterfall), along with water temperature (°C) and flow (m^3/s) variations over the study period

early May and early June (<3.7 m^3/s; >13.5 °C). In contrast, B19 stabilised at 4.0–4.4 km downstream with no upstream return. B1, also performed multiple upstream movements before finally moving downstream of the waterfall on 10 April 2025 (2.94 m^3/s; 9.4 °C). In addition, B1 explored twice a tributary of the Amblève—the Salm—covering ≈ 2 km upstream and remaining there for two days in May 2023 (6.5–14.1 °C) and four days in April 2024 (17.6–13.2 °C) before re-entering the mainstem.

Among individuals that remained upstream of the Coo waterfall (B5, B8, B10, B18; Fig. 2D), B8 was sedentary near the release point, while B5 and B10 made regular upstream movements during the spawning period (between April and June). B5 made several back-and-forth movements between the release point and an area located 1.7 to 2 km upstream, and reached 8.7 km upstream in September 2024 (4.6 m^3/s, 14.6 °C). B10 made similar repeated trips to areas located 1.5 to 2 km upstream and reached 4 km in May 2023 and 3.6 km in May 2025 (<6 m^3/s; >14 °C). Two barbel (B13, B17) showed wide-ranging movements (Fig. 3A). B13 moved downstream of the Coo waterfall (23.8 m^3/s; 13.1 °C) and Lorcé dam (27.8 m^3/s, 12.9 °C) within 5 and 15 days respectively, reaching 24.7 km downstream. B17 remained 3–4 km upstream for over three months before movind downstream of the waterfall in October 2024 (12.0 m^3/s; 12.3 °C), and settling 16.7 km downstream. Three fish tagged at Lorcé (B15, B20, B21) remained within 2 km upstream of release (Fig. 3B), except B15, which made a brief 10.3 km upstream excursion in May 2025 (2.1 m^3/s, 14.4 °C) before returning.

Most chub (C2, C3, C4, C6, C7, C8, C9, C10) remained upstream of the Coo waterfall with activity within a range of 0 to 2.5 km from the release site (Fig. 4A). C2 and C3 made repeated upstream movements during 2023 (up to 1.7 and 2.5 km) under varying flow and temperature conditions. C6 reached 1.2 km during June 2024 (8.4 m^3/s; 14.2 °C) and 2.5 km during June 2025 (3.1 m^3/s; 13.4 °C), corresponding to the spawning period (between April and June). C4 stayed just above the waterfall without moving downstream. Others (C6,

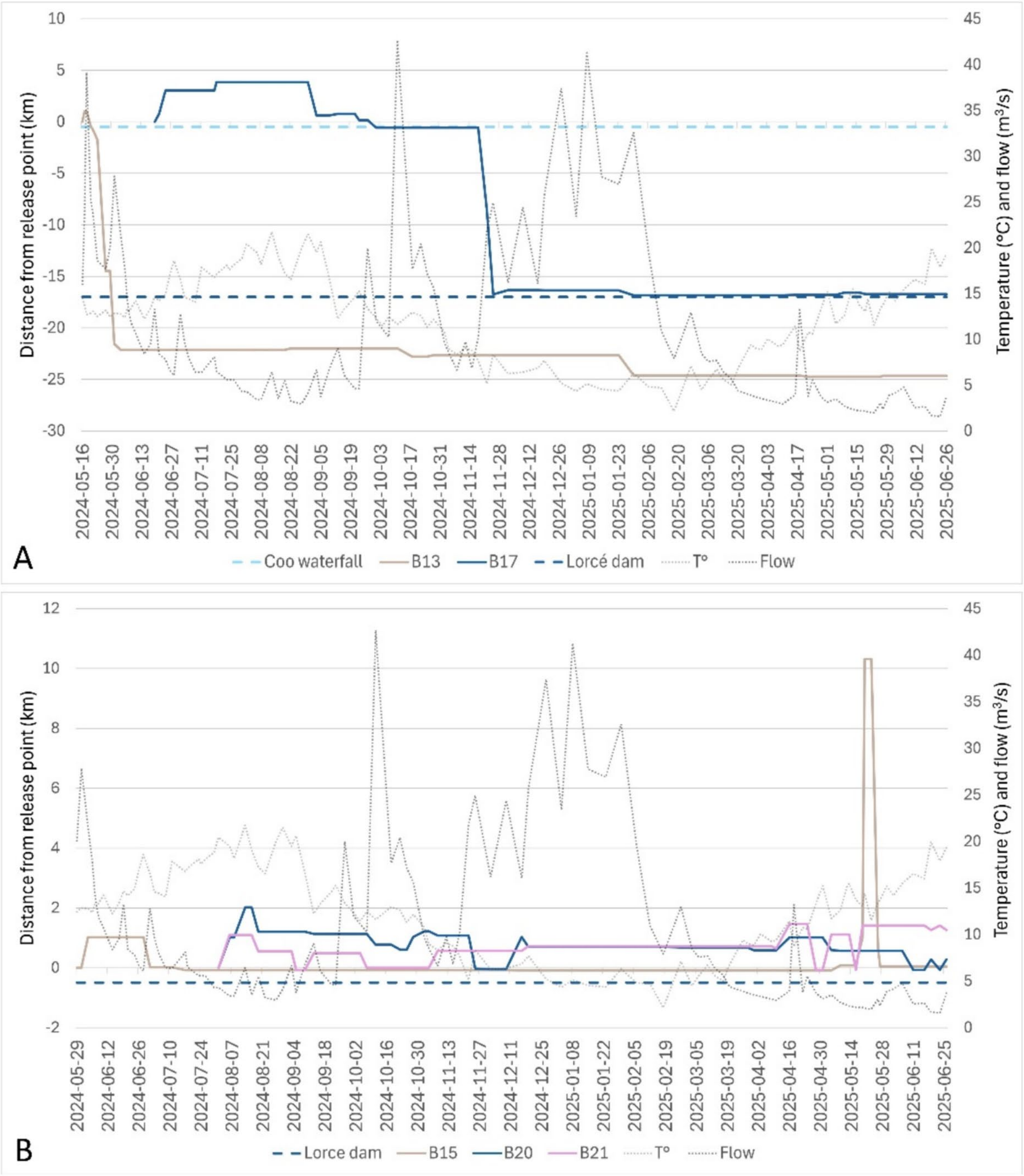

Fig. 3 Positions of tagged barbel at the Coo waterfall (**A**) and the Lorcé dam (**B**) recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the obstacle), along with water temperature (°C) and flow (m^3/s) variations over the study period

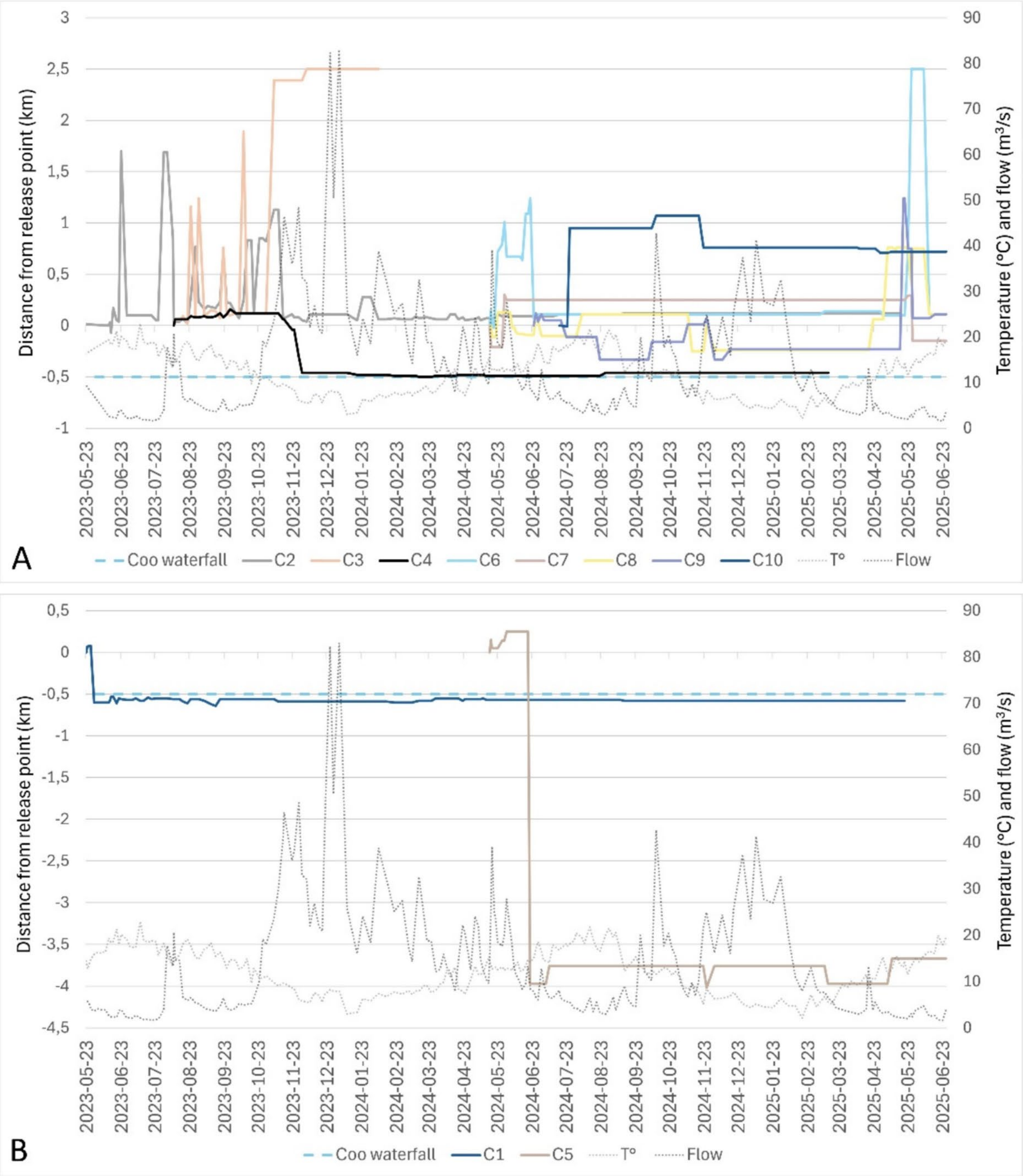

Fig. 4 Positions of tagged chub at the Coo waterfall recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the waterfall), along with water temperature (°C) and flow (m^3/s) variations over the study period

C7, C8, C9) showed less frequent or smaller movements, such as C9 which reached 1.2 km upstream in late May 2025 (2.2 m^3/s; 13 °C). Two chub (C1, C5) moved downstream of the waterfall (Fig. 4B). C1 moved downstream of the waterfall shortly after being released (3.6 m^3/s, 15.8 °C) and remained close downstream (0.6 km from the release site), while C5 first explored upstream (up to 0.4 km) before moving downstream in early June 2024 (8.4 m^3/s, 114.2 °C) and stabilising 4 km downstream.

Home range and displacement metrics

After having crossed the obstacles, the trajectories of the fish showed great heterogeneity. For barbel, TU indicated contrasting residency behaviours, with individuals spending anywhere from 0.3% (B3) to the entirety, 100% (B5, B8, B10, B15, B18, B20 and B21), of their monitored time upstream. Their home range extended from 0.46 km (B8) to 25.76 km (B13) with a mean of 6.02 km. Two other individuals stood out: B17, with 20.70 km, and B15, with 10.40 km. The analysis of minimum and maximum values revealed that B13 (min = − 24.74 km; max = 1.02 km) and B17 (min = − 16.82 km; max = 3.85 km) mainly exploited areas located downstream of the obstacle, whereas B15 (min = − 0.09 km; max = 10.31 km) developed most of its home range upstream. The daily movements of barbel oscillated on average between 0.01 and 0.32 km, but the median of daily movements, during movement phases, could reach 0.80 km. In terms of net total distance travelled, B5 and B10 showed the greatest distances with 50.18 km and 40.45 km respectively. Moving downstream of the obstacle was frequent with 66.7% of individuals: 14 barbel out of 21 moved downstream of the Coo waterfall, and B13 also moved downstream of the Lorcé dam. The results also showed an event of fishway reuse by B4, which moved downstream of the waterfall and then reused the Coo fishway. For chub, home ranges were more restricted, from 0.51 km (C7) to 4.27 km (C5) with a mean of 1.66 km. This latter individual mainly occupied the downstream section (min = − 4.02 km; max = 0.25 km). Average daily movements ranged between 0.02 km and 0.08 km, with median values stretching from 0.03 km to 0.23 km. The greatest net distances recorded in chub were 14.86 km for C2 and 14.62 km for C3, that is approximately 2.8 to 3.5 times lower than those observed in barbel. Finally, moving downstream of the obstacle remained marginal with 20% of individuals: two chub (C1 and C5) out of 10 tagged moved downstream of the Coo waterfall (Table 2).

The total net distances (TND) calculated from individual movement data revealed differences between species and depending on their location relative to the obstacles. Barbel travelled a greater median distance of 5.8 km upstream, with values ranging from 0.67 km to 50 km, compared to the downstream movements, where the median distance was 3.95 km, ranging from 0.59 km to 23.64 km. However, no significant difference was observed between upstream and downstream movements (p value = 0.43). For chub, movements were more restricted, with upstream TND ranging from 1.33 km to 14.86 km (median = 4.67 km). However, no significant difference was found between the upstream distances travelled by chub and barbel (p value = 0.47). The two individuals that moved downstream of the Coo waterfall travelled 0.73 km and 4.95 km, respectively (Fig. 5).

What drives fish to move downstream of obstacles?

Model selection revealed that the best predictive model included the variables daily discharge (flow), daily temperature (temp), condition factor (K), species, and repro, along with random intercepts for individuals (id) and sampling dates (date). This model had the highest ELPD (–61.85) and a stacking weight of 0.37, indicating a 37% probability of being the best model among the 256 combinations tested. Competing models showed slightly lower predictive performance (Δ ELPD < 2), suggesting similar support from the data (Table 3).

Posterior summaries of the final model showed that daily discharge (flow), daily temperature (temp), condition factor (K), the period of reproduction (repro) and species (sp) had 95% credible intervals that did not include zero, indicating robust associations with the probability of moving downstream of an obstacle. Daily discharge (flow) had significant negative effect and daily temperature (temp) had significant positive effect on the probability of moving downstream of an obstacle (flow: estimate = − 3.99, 95% CI − 6.59 to − 1.84; temp: estimate = 1.13, 95% CI 2.15 to 0.20), suggesting that downstream movements of obstacles were more likely under lower flow and higher temperatures. Reproductive status had a strong positive effect (repro: estimate = 4.13, OR = 52.2, 95% CI 1.99 to 6.87), indicating that individuals were much more likely to move downstream an obstacle during the spawning period. The effect of body condition (K) also showed a significant positive association

Table 2 Summary of individual movement metrics for barbel (B) and chub (C) tracked at the Coo and Lorcé sites

ID	Site	Days of tracking	TU (%)	HR (km)	Min (km)	Max (km)	MND (km)	TND (km)	MedND (km)	Cross obstacles Yes/No (number)
B1	Coo	1142	93.3	3.17	− 1.01	2.16	0.11	36.42	0.09	Y (1)
B2	Coo	1140	0.9	0.93	− 0.72	0.21	0.01	3.04	0.01	Y (1)
B3	Coo	1133	0.3	3.75	− 3.75	0.00	0.03	9.41	0.04	Y (1)
B4	Coo	1133	0.3–18.6 *	4.65	− 2.73	1.92	0.07	22.25	0.03	Y (1)*
B5	Coo	1123	100	8.91	− 0.21	8.70	0.16	50.18	0.06	N
B6	Coo	1123	62.3	2.97	− 2.84	0.13	0.01	4.64	0.04	Y (1)
B7	Coo	445	0.9	4.09	− 2.82	1.27	0.05	14.50	0.04	Y (1)
B8	Coo	1109	100	0.46	− 0.07	0.39	0.01	1.95	0.02	N
B9	Coo	1109	52.7	2.39	− 1.65	0.74	0.04	11.15	0.03	Y (1)
B10	Coo	1105	100	4.50	− 0.49	4.01	0.13	40.45	0.05	N
B11	Coo	586	33.4	4.81	− 2.75	2.06	0.05	15.21	0.02	Y (1)
B12	Coo	406	23.4	2.99	− 1.73	1.26	0.07	7.84	0.26	Y (1)
B13	Coo	406	1.2	25.76	− 24.74	1.02	0.24	27.44	0.80	Y (2)
B14	Coo	406	1.7	9.18	− 8.88	0.30	0.16	18.33	0.44	Y (1)
B15	Lorcé	393	100	10.40	− 0.09	10.31	0.21	22.88	0.62	N
B16	Coo	385	4.7	6.27	− 4.33	1.94	0.12	12.79	0.20	Y (1)
B17	Coo	372	27.9	20.70	− 16.85	3.85	0.32	32.17	0.74	Y (1)
B18	Coo	363	100	2.38	− 0.41	1.97	0.10	9.38	0.32	N
B19	Coo	338	27.8	4.54	− 4.39	0.15	0.07	6.15	0.31	Y (1)
B20	Lorcé	329	100	2.09	− 0.07	2.02	0.11	9.68	0.35	N
B21	Lorcé	329	100	1.53	− 0.07	1.46	0.14	11.98	0.57	N
C1	Coo	209	3.3	0.72	− 0.64	0.08	0.03	2.66	0.03	Y (1)
C2	Coo	714	100	1.77	− 0.07	1.70	0.07	14.86	0.05	N
C3	Coo	656	100	2.50	0.00	2.50	0.06	12.12	0.09	N
C4	Coo	656	100	0.66	− 0.50	0.16	0.02	2.88	0.03	N
C5	Coo	123	29.3	4.27	− 4.02	0.25	0.05	6.28	0.23	Y (1)
C6	Coo	375	100	2.52	− 0.02	2.50	0.07	8.61	0.20	N
C7	Coo	375	100	0.51	− 0.21	0.30	0.03	2.97	0.21	N
C8	Coo	374	100	1.01	− 0.25	0.76	0.04	4.91	0.15	N
C9	Coo	336	100	1.57	− 0.33	1.24	0.05	4.43	0.14	N
C10	Coo	313	100	1.08	− 0.01	1.07	0.02	1.46	0.04	N

Variables include number of tracking days, time spent upstream (TU), home range (HR), minimum and maximum longitudinal positions (Min, Max), mean net distance (MND), total net distance (TND), and median net distance (MedND). The last column indicates whether individuals moved downstream of at least one obstacle during the tracking period ("Y") or not ("N"), with the number of crossings in parentheses. An asterisk (*) indicates that the individual re-used the fishway after an initial crossing (estimate = 1.25, OR = 3.49, 95% CI 0.21 to 2.35), suggesting that individuals with a higher condition factor are more likely to move downstream an obstacle. Regarding species, chub were significantly less likely to move downstream an obstacle than barbel (estimate = − 3.95, OR = 0.02, 95% CI − 6.36 to − 1.73). Random effect estimates revealed substantial inter-individual variability (estimate = 2.21, 95% CI 0.96 to 3.71) and moderate variability between dates (estimate = 0.83, 95% CI 0.03 to 2.27), supporting the inclusion of these random effects in the model (Table 4).

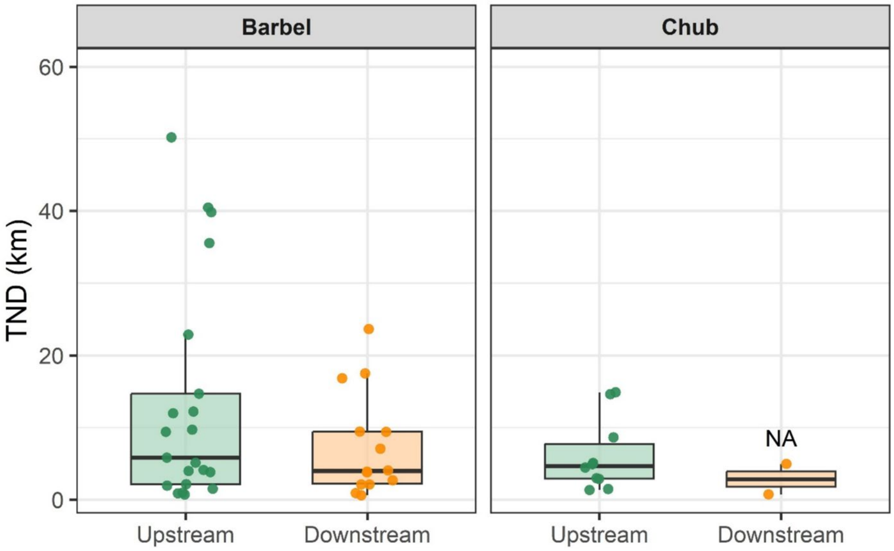

Fig. 5 Boxplots of total net distance (TND, in km) travelled by individual barbel and chub upstream and downstream of an obstacle. Each point represents one individual. For chub downstream, the "NA" label indicates that data from only two individuals were available, preventing meaningful boxplot representation

Table 3 Model ranking based on PSIS-LOO

Rank	Model formula	ELPD	ΔELPD	Stacking weight	Number of predictors
1	dev~flow + temp + k + sp + repro + (1|id) + (1|date)	− 61,85	0.00	0.37	5
2	dev~flow + dj + temp + k + sp + repro + (1|id) + (1|date)	− 62,37	0.52	0.22	6
3	dev~flow + dj + k + sp + repro + (1|id) + (1|date)	− 63,32	1,47	0.08	5

Table 4 Posterior summary statistics of fixed and random effects from the final Bayesian logistic regression model

Random effects	Estimate	Std. Error	95% CI	OR	$\hat{R}$	Bulk ESS
sd(Intercept) date	0.83	0.61	[0.03, 2.27]	–	1.00	3003
sd(Intercept) id	2.21	0.69	[0.96, 3.71]	–	1.00	3517
Fixed effects	Estimate	Std. Error	95% CI	OR	$\hat{R}$	Bulk ESS
Intercept	− 9.88	1.70	[− 13.59, − 6.96]	–	1.00	7095
flow	− 3.99	1.22	[− 6.59, − 1.84]	0.02	1.00	12,702
temp	1.13	0.49	[2.15, 0.20]	0.32	1.00	11,854
k	1,25	0.54	[0.21, 2.35]	3.49	1.00	11,512
repro1	4,13	1.26	[1.99, 6.87]	52.2	1.00	12,156
spChub	− 3,95	1.17	[− 6.36, − 1.73]	0.02	1.00	9886

The final model explained 17.7% of the variance in downstream migration through fixed effects alone (marginal $R^2 = 0.177$, 95% CI [0.004; 0.321]), and 37.1% when including individual- and date-level random effects (conditional $R^2 = 0.371$, 95% CI [0.111; 0.492]). Posterior predictive checks indicated that the final model adequately captured the observed distribution of passage outcomes, supporting its overall goodness-of-fit.

Discussion

Although substantial efforts have been made to restore river connectivity, most studies still focus primarily on whether fish are able to pass barriers, often treating successful passage as an end in itself. Yet what happens to an individual once it has passed through a fishway remains largely unknown. Does it settle immediately upstream? Continue migrating? Return downstream? These questions are crucial for assessing the broader ecological impact of defragmentation, yet they remain poorly documented. Our study helps fill this gap by tracking, over three consecutive years, the movements of individuals that successfully crossed one of two major obstacles (a waterfall and or a dam). This multi-year approach allowed us to generate novel insights into post-passage behaviour, revealing not only whether fish use upstream habitats, but also how this use varies among individuals. The individual movements examined in this study revealed a wide range of post-passage behaviours which can be categorised into three distinct profiles: (i) prospective exploration, with individuals spending months or years upstream before moving downstream of an obstacle; (ii) immediate descent, with individuals that moved downstream within days or weeks; and (iii) permanent residency upstream throughout the three-year study. This variability shows that, once they have overcome an obstacle, fish do not all behave in the same way. However, our results revealed that every instance of large-scale upstream movement occurred between April and June, when temperatures exceeded 13.5 °C and flows were moderate, consistent with the spawning migrations of barbel and chub (Ovidio et al., 2007; De Leeuw & Winter, 2008; Britton & Pegg, 2011; Benitez & Ovidio, 2018).

Several barbel returned to the same upstream location during successive spawning seasons, including one individual repeatedly detected in the Salm tributary alongside conspecifics. Although we lack direct evidence of successful spawning, this spatio-temporal fidelity strongly implies spawning-related behaviour (Baras, 1998; Lucas & Baras, 2001; Britton & Pegg, 2011; Panchan et al., 2022; Gelder et al., 2024b). Such behaviour is well documented in the literature, as barbel are known for their fidelity to habitats (Baras, 1998; De Vocht & Baras, 2003; Ovidio et al., 2007; Britton & Pegg, 2011; Panchan et al., 2022). It is therefore also plausible that some individuals that moved downstream of an obstacle early, or after an exploratory phase may have returned to their original site, potentially after having spawned. Interestingly, several individuals were observed making repeated upstream movements to the foot of the waterfall during the spawning period. These movements could reflect a drive to return to known spawning habitats upstream, consistent with site fidelity, or attempts to locate new spawning sites. Moreover, our results showed that one individual reused the fishway, outside the spawning period, while numerous upstream movements to the foot of the waterfall were recorded. However, as highlighted by Gelder et al. (2024a, b) the low attractiveness of the Coo fishway likely prevents individuals from locating its entrance, which may ultimately result in failed upstream migration attempts. Chub, although less studied in this regard, have also been reported to exhibit site fidelity (Allouche et al., 1999; Fredrich et al., 2003; Capra et al., 2018). However, our study did not reveal clear patterns of such behaviour. Most chub remained in the same area for a time before moving on without returning to previous locations. This suggests more variable or less site-specific use of habitat, at least during the study period.

In terms of movement distances, some barbel displayed home ranges exceeding 20 km, demonstrating that potamodromous species can undertake substantial movements (De Leeuw & Winter, 2008; Baudoin et al., 2015; Panchan et al., 2022; Ovidio et al., 2023; Ordeix & Casals, 2024). Other studies have reported a wide range of maximum home ranges for barbel, reflecting variable movement patterns across systems. For example, Ovidio et al. (2007) and Popp et al. (2024) observed more restricted values, up to 12.8 km and 2.1 km respectively, while Panchan et al. (2022) documented larger home ranges, reaching up to 47 km. This diversity highlights the behavioural plasticity of barbel and suggests that environmental context and habitat availability play key roles in shaping individual movement strategies. Although no statistically significant difference was detected between upstream and downstream net distances travelled, upstream movements tended to be greater. This trend likely reflects an ecological mechanism: fish encountering unfamiliar upstream environments may explore more extensively, while downstream movements more often represent returns to previously occupied, familiar habitats. To robustly confirm these hypotheses, the study would need to be extended to a larger sample of individuals. In contrast, chub exhibited much more restricted mobility. Most individuals remained upstream of the obstacle, with movements typically confined to a few kilometres, in contrast with previous studies reporting movements exceeding 10 km (De Leeuw & Winter, 2008; Capra et al., 2018; Tétard et al., 2025). This interspecific difference likely reflects divergent ecological strategies which may be explained by differences in habitat specificity: barbel are known to be more selective in their environmental requirements, while chub are generally considered more ubiquitous and less demanding (Arlinghaus & Wolter, 2003; Fredrich et al., 2003; Pander et al., 2015; Benitez & Ovidio, 2018). As a result, chub may more readily find suitable habitats in newly accessed areas, reducing the need for extensive exploration.

Our research also set out, for the first time, to identify the factors influencing individual downstream movement at obstacles devoid of any downstream passage facilities. This entirely novel approach provides new insights into post-passage behaviour and helps to better understand the mechanisms underlying individual decision-making process. While Rato et al. (2024) also investigated the environmental drivers of downstream movements of Iberian barbel [*Luciobarbus bocagei* (Steindachner, 1864)] within a fishway, their study did not address individual-level behavioural processes and was conducted in the context of a downstream passage facility. The mixed-effects Bayesian model showed that the probability of downstream migration increases during the spawning period, while high discharges and low temperatures reduce it. These environmental conditions align well with those typically encountered during the spawning period, particularly between April and June, when temperatures rise and discharge levels tend to decrease. Barbel are known to exhibit post-spawning homing behaviour, moving downstream after spawning in order to return to their original habitat (Lucas & Batley, 1996; Lucas & Baras, 2001; Ovidio et al., 2007; Gelder et al., 2024b). Although less well documented in chub, similar movements have also been observed for this species (Lucas et al., 2000; Fredrich et al., 2003). This pattern likely reflects a post-spawning homing movement, whereby individuals moved downstream the obstacle shortly after spawning, still within the spawning period, to return to their original habitat. The stronger homing behaviour described in barbel may also explain the species effect observed in our model, with chub being significantly less likely to move downstream an obstacle than barbel. Individuals in better body condition were more likely to move downstream an obstacle, suggesting that fish with greater energy reserves may be better able to undertake energetically demanding movements. Several studies have shown that home range size tends to increase with individual size and/or weight, which may reflect a greater capacity for movement in larger individuals (Minns, 1995; Woolnough et al., 2009; Nash et al., 2015; Burbank et al., 2023). As condition factor was measured at tagging, its correspondence with the individual's state at the moment of downstream movement over an obstacle may vary, and estimating condition closer to the event would help refine these interpretations. However, our model revealed that inter-individual variability was the most influential factor in explaining whether or not a fish moved downstream an obstacle. This suggests it is primarily driven by intrinsic individual differences rather than by environmental or morphological factors alone. In this context, moving downstream an obstacle, appears to be a voluntary behavioural decision rather than a passive response to external conditions. Such variability may reflect underlying behavioural traits, with some individuals exhibiting a more migratory or risk-prone temperament, while others adopt more resident or cautious strategies (Webster et al., 2007; Harcourt et al., 2009; Conrad et al., 2011; Nakayama et al., 2012; Mittelbach et al., 2014; Polverino et al., 2016; Elias et al., 2018; Fudali & Pietrzak, 2024). Chapman et al. (2012) noted that fish populations often contain both migrant and resident individuals, and that switches between these strategies can occur over an individual's lifetime and/or in response to environmental conditions, which could help explain the high inter-individual variability observed in our study.

This study provides new insights into the long-term post-passage behaviour of potamodromous fish showing that movements vary greatly between individuals and species. By going beyond the traditional focus on successful transition, this study provides a better understanding of defragmentation and the behavioural mechanisms underlying it. Our results show that potamodromous fish make use of habitats both upstream and downstream of obstacles, moving between them throughout the year. Many individuals demonstrated a clear willingness to return upstream after moving downstream an obstacle, indicating that passage is not a one-way event but part of a dynamic movement pattern. This underscores the critical importance of maintaining year-round connectivity, so that fish can access and benefit from the full range of habitats they require. Ensuring that fishways remain fully functional year-round, and assessing their effectiveness, is therefore essential to allow fish to exploit the entire mosaic of habitats available to them and to maximise the ecological return of connectivity restoration efforts.

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

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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