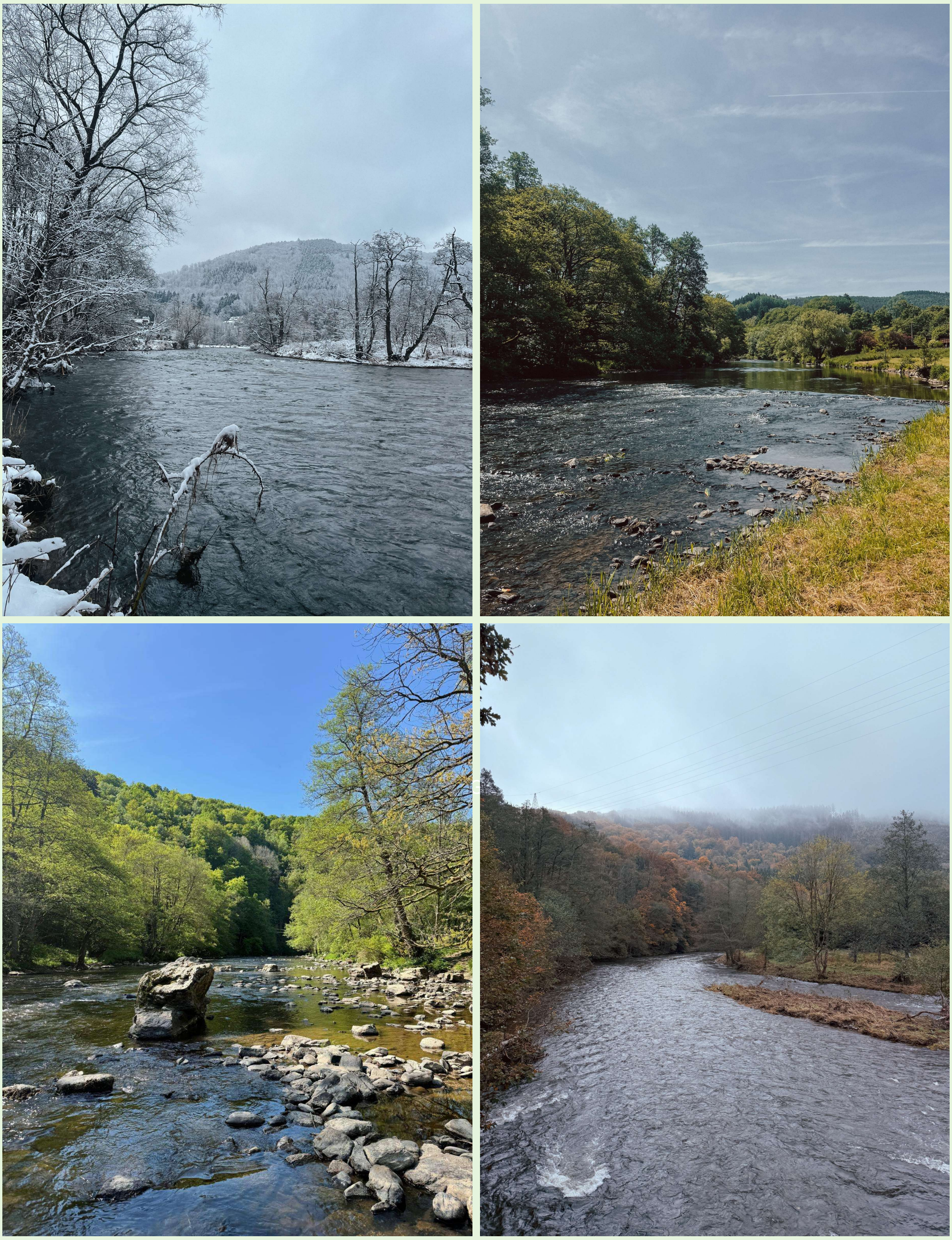

From barriers to reopening : an integrated study of river defragmentation process. How do fish respond to river connectivity restoration?

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Dissertation for the degree of Doctor in Science
at the University of Liège

Academic year 2025-2026

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Acknowledgment

I would like to express my most sincere thanks to my thesis promoter, Prof. Dr. Michaël Ovidio, for giving me the opportunity to carry out this thesis and for having ensured its funding. Thank you for your availability, your always insightful advice and your guidance throughout these years. I am also very grateful to you for allowing me to work in the idyllic setting of the Amblève valley.

I sincerely thank the members of my thesis committee, Jean-Philippe Benitez, Célia Joaquim-Justo and Bruno Frederich, for their numerous pieces of advice during our meetings, as well as for the kindness and constructiveness of their comments, which always enabled me to move forward with confidence in my work. I also wish to express my deep gratitude to the members of my jury who agreed to read and evaluate this work: Bruno Frederich (President), Loïc Michel (Secretary), Gilles Lepoint, Laurane Winandy, Céline Le Pichon, Ine Pauwels and Michaël Ovidio (Promoter).

I would also like to warmly thank my colleagues, for having been such a wonderful team throughout this thesis: the *fish team*. Thank you to Jean-Philippe for his countless pieces of advice and for the field trips that very often turned into expeditions: you know when you leave, but never when you come back. Thank you to Arnaud for his countless helping hands in the field, and whose endless chatter made it impossible ever to be bored. Thank you to Chloé and Émilie for their support, especially during the final stages of this work, and for our precious tea breaks, sources of comfort and good humour. Finally, thank you to Séverine for welcoming me when I first arrived at the lab and for all our moments of escape spent talking about travels. A big thank you also to the students who, as part of their Master’s thesis or internship, contributed to data collection. Thank you for accompanying me in the field and for agreeing to follow me into some rather crazy ideas, such as regular tracking over a full 24-hour cycle.

A huge thank you to my family and friends for their support throughout this adventure. Although my explanations were sometimes complex, and what remained most of all was the idea that I was working with fish, you always showed interest in my work. Thank you also for your many supportive and encouraging messages, which were particularly precious to me.

Finally, I could not conclude these acknowledgements without mentioning Arthur, my life partner, whose support was unwavering throughout this thesis. Thank you for your reassuring presence, your patience in moments of doubt or stress, and for always believing in me, sometimes, indeed often, even more than I did myself. Thank you also for your curiosity, your constant desire to understand my work, but above all for all those times when you made me laugh and helped me to take my mind off things. None of this would have been the same without you.

Summary

Rivers contain a mosaic of functional habitats suitable for numerous species, particularly fish. These exploit different habitats continuously in order to satisfy their vital needs such as feeding, spawning or refuge. However, these movements are strongly constrained by the longitudinal fragmentation of watercourses, caused in particular by dams and various obstacles, which limit the free movement of individuals and affect fish fauna. In this context, river defragmentation represents a major challenge for maintaining fish biodiversity, as it contributes to restoring ecological connectivity through the removal of obstacles or by equipping them with fishway facilities. Defragmentation nevertheless represents a complex process that must be addressed in its entirety. Numerous studies have focused on defragmentation, mainly by evaluating the efficiency of fishways and their use by fish. By contrast, studies addressing defragmentation as a whole, integrating what happens before, during and after the restoration of connectivity, remain non-existent, even though such an approach is essential for fully assessing the real ecological benefits.

This thesis proposes an integrated approach to the process of habitat defragmentation in rivers for holobiotic potamodromous species, considering both the scale of the individual and that of populations. The originality of the work lies in a complete analysis of the temporal continuum “before – during – after” connectivity restoration. To this end, several sites equipped with fishways in Belgium, and complementary methodologies, were mobilised: fish community surveys by electrofishing, multi-annual monitoring of capture devices installed in fishways (from 3 to 8 consecutive years), and telemetry devices (radio and RFID) allowing detailed and continuous behavioural monitoring of individuals over 3 consecutive years.

The results first show the initial state of fish communities upstream and downstream of an impassable obstacle, revealing the structuring effect of barriers on species composition and distribution. The opening of new migratory axes then induced progressive colonisation dynamics, differentiated according to species but also according to sites. Some species showed a marked opening effect, with early colonisation of fishways, whereas others took longer before colonising new habitats. Multi-annual monitoring thus confirms the necessity of long-term data to characterise these processes, owing to strong interannual, interspecific and spatial variabilities.

The evaluation of the efficiency of the Coo fishway on the Amblève River (Belgium), based on the analysis of behavioural metrics, revealed a lack of attractiveness. Although the fishway was used by a wide diversity of species, this reflected only part of the real potential use of such device. These studies are therefore essential in order to identify existing limitations and to optimise fishway design so as to improve their efficiency.

The study of post-passage movements constitutes a major contribution of this work, owing to its multi-annual character (three consecutive years) and the implementation of mobile radio-tracking. Continuous monitoring revealed that individuals effectively used newly accessible habitats, with residence or dispersal behaviours varying

according to species and periods. The monitoring revealed great variability in behaviours, both interspecific and interindividual: some individuals remained upstream after passage, indicating a shift in functional habitats, others exploited accessible habitats before moving back downstream, while some moved downstream directly. Certain individuals also showed interannual fidelity by exploiting the same upstream sites for several consecutive years during spawning period. The use of tributaries was also demonstrated, underlining the importance of lateral connections in colonisation dynamics. A striking result is that many individuals expressed a will to migrate upstream or downstream but found themselves either blocked by an obstacle or unable to locate the entrance of a fishway. This highlights the importance of restoring free movement along the entire length of a watercourse. Moreover, this work shows that passage upstream of an obstacle does not constitute an end in itself: individuals do not always remain confined upstream but exploit upstream and downstream jointly, by reusing fishways.

Finally, the tracking data collected over several consecutive years made it possible to explore the factors influencing downstream passage at obstacles. The results suggest that the spawning season, the increase in temperature, the decrease in discharge or even an increase in condition factor exert an influence on the probability of moving downstream of an obstacle, but above all highlight the predominant role of interindividual variability in the decision to do so or not. These observations strongly suggest that downstream passage choices could be linked to differences in personality traits, with some individuals being more prone to risk-taking than others.

Taken together, the findings of this thesis provide essential scientific insights for understanding the process of habitat defragmentation. They show that defragmentation is not limited to reopening access upstream, but corresponds to the restoration of a continuum where fish exploit upstream and downstream freely according to their ecological needs. By improving our knowledge of the behavioural ecology of individuals as well as the use of fishways, this thesis also provides concrete recommendations to managers in order to optimise connectivity restoration actions and ensure the sustainability of fish communities in fragmented rivers.

Résumé

Les rivières possèdent une mosaïque d'habitats fonctionnels propices à de nombreuses espèces, notamment aux poissons. Ceux-ci exploitent en permanence différents habitats afin de satisfaire leurs besoins vitaux tels que l'alimentation, la reproduction ou encore le refuge. Cependant, ces déplacements sont fortement contraints par la fragmentation longitudinale des cours d'eau, due notamment aux barrages et différents obstacles, qui limite la libre circulation des individus et affecte la faune piscicole. Dans ce contexte, la défragmentation des cours d'eau constitue un enjeu majeur pour le maintien de la biodiversité piscicole, dans la mesure où elle contribue à rétablir la connectivité écologique par l'arasement d'obstacles ou leur aménagement avec des dispositifs de franchissement. La défragmentation constitue toutefois un processus complexe qu'il convient d'aborder dans sa globalité. De nombreuses études se sont intéressées à la défragmentation, principalement en évaluant l'efficacité des dispositifs de franchissement et leur utilisation par les poissons. En revanche, les études abordant la défragmentation dans son ensemble, en intégrant ce qui se passe avant, pendant et après la restauration de la connectivité, demeurent inexistantes, alors qu'une telle approche est essentielle pour évaluer pleinement les bénéfices écologiques réels.

Cette thèse propose une approche intégrée du processus de défragmentation de l'habitat en rivière chez les espèces holobiotiques potamodromes, en considérant l'échelle de l'individu comme celle des populations. L'originalité du travail repose sur une analyse complète du continuum temporel « avant – pendant – après » la restauration de la connectivité. Pour ce faire, plusieurs sites équipés de passes à poissons en Belgique, et des méthodologies complémentaires ont été mobilisées : inventaires piscicoles par pêche électrique, suivis multi-annuels de dispositifs de capture installés dans les passes à poissons (de 3 à 8 années consécutives), et dispositifs de télémétrie (radio et RFID) permettant un suivi comportemental fin et continu des individus durant 3 années consécutives.

Les résultats montrent d'abord l'état initial des communautés piscicoles en amont et en aval d'un obstacle infranchissable, révélant l'effet structurant des barrières sur la composition et la distribution des espèces. L'ouverture de nouveaux axes migratoires induit ensuite des dynamiques de colonisation progressives, différenciées selon les espèces mais également selon les sites. Certaines espèces présentent un effet d'ouverture marqué, avec une colonisation précoce des passes à poissons, tandis que d'autres mettent plus de temps avant de coloniser les nouveaux habitats. Les suivis multi-annuels confirment ainsi la nécessité de données de long terme pour caractériser ces processus, en raison de fortes variabilités interannuelles, interspécifiques et spatiales.

L'évaluation de l'efficacité de la passe à poissons de Coo sur l'Amblève (Belgique), basée sur l'analyse de métriques comportementales, a permis de mettre en évidence un manque d'attractivité du dispositif de franchissement. Bien que la passe à poissons soit utilisé par une grande diversité d'espèce, ceci ne reflète qu'une partie du potentiel réel

d'utilisation de ce dispositif. Ces études sont donc essentielles afin d'identifier les limites existantes et d'optimiser la conception des passes pour améliorer leur efficacité.

L'étude des déplacements post-franchissement constitue une contribution majeure de ce travail, de par son caractère pluriannuel (trois années consécutives) et la mise en œuvre d'un pistage radio mobile. Les suivis continus révèlent que les individus utilisent effectivement les habitats nouvellement accessibles, avec des comportements de résidence ou de dispersion variables selon les espèces et les périodes. Les suivis ont révélé une grande variabilité des comportements, à la fois interspécifiques et interindividuels : certains individus restaient en amont après le franchissement, traduisant un changement d'habitats fonctionnels, d'autres exploitaient les habitats accessibles avant de dévaler, tandis que certains dévalaient directement. Certains individus ont également montré une fidélité interannuelle en exploitant plusieurs années de suite les mêmes sites, situés en amont, lors de la reproduction. L'utilisation d'affluents a également été mise en évidence, soulignant l'importance des connexions latérales dans la dynamique de colonisation. Un résultat marquant est que de nombreux individus ont manifesté une volonté de migrer vers l'amont ou l'aval mais se sont retrouvés soit bloqués par un obstacle, soit incapables de localiser l'entrée d'un dispositif de franchissement. Cela souligne l'importance de restaurer une libre circulation sur l'entièreté d'un linéaire de cours d'eau. Plus encore, ce travail montre que le passage en amont d'un obstacle ne constitue pas une fin en soi : les individus ne se cantonnent pas toujours à l'amont mais exploitent conjointement l'amont et l'aval, en réutilisant les dispositifs de franchissement.

Enfin, les données de pistage collectées sur plusieurs années consécutives ont permis d'explorer les facteurs influençant la dévalaison au niveau des obstacles. Les résultats suggèrent que la saison de reproduction, l'augmentation de température, la diminution du débit ou encore l'augmentation du facteur de condition exercent une influence sur la probabilité de dévaler, mais mettent surtout en évidence le rôle prépondérant de la variabilité interindividuelle dans la décision de dévaler ou non. Ces observations laissent fortement penser que les choix de dévalaison pourraient être liés à des différences de personnalité, certains individus étant plus enclins à prendre des risques que d'autres.

Dans l'ensemble, les résultats de cette thèse apportent des éléments scientifiques essentiels pour comprendre le processus de défragmentation de l'habitat. Ils montrent que la défragmentation ne se limite pas à l'ouverture vers l'amont, mais correspond à la restauration d'un continuum où les poissons exploitent librement l'amont et l'aval selon leurs besoins écologiques. En améliorant nos connaissances sur l'écologie comportementale des individus ainsi que sur l'utilisation des passes à poissons, cette thèse fournit également des recommandations concrètes aux gestionnaires afin d'optimiser les actions de restauration de la connectivité et de garantir la pérennité des communautés piscicoles dans les cours d'eau fragmentés.

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Chapter 1. General Introduction

River ecosystem and fish populations

Ecological continuity

The ecological continuity of rivers refers to the conditions that allow aquatic organisms to move freely and access habitats necessary for performing their biological functions, as well as facilitating sediment transport along the river (Baudoin et al., 2015; Gelder et al., 2024a; Pachla et al., 2022; Rincón et al., 2017). The River Continuum Concept (RCC) proposes that the conditions necessary for the proper functioning of aquatic ecosystems vary continuously along the river, from source to mouth, influencing the structure and function of different biological communities present (Vannote et al., 1980). The functioning of river ecosystems is based on a complex set of physical and biological interactions that influence their structure, productivity, and biodiversity (Kondolf et al., 2006). Furthermore, habitat plays a key role in determining the availability of resources necessary for the biological functions (e.g. feed, reproduce, disperse) of organisms (Baldan et al., 2023; Benitez & Ovidio, 2018; Branco et al., 2014).

Rivers are composed of habitats in "dynamic mosaics" (Keeley et al., 2022; Stanford et al., 2005; Wiens, 2002), characterised by spatial heterogeneity and temporal variability, and structured across four dimensions: longitudinal, vertical, transversal, and temporal (Felin et al., 2025; Keeley et al., 2022; Ward, 1989; Figure 1). Each dimension exhibits distinct physical conditions, allowing for the formation of multiple ecological niches (Stanford et al., 2005; Zeni et al., 2015). Longitudinally, the river is divided into morphologically homogeneous sections, each with varying conditions such as water temperature, vegetation, oxygen, current speed, and substrate (Keeley et al., 2022; Wiens, 2002). This dimension is segmented into four distinct fish zones, as defined by Huet (1949), from upstream to downstream : the "trout zone," "grayling zone," "barbel zone," and "bream zone". Each of these zones is characterised by specific features, such as fast currents and coarse substrates in the upstream trout zone, and calmer currents with abundant vegetation in the downstream bream zone. These conditions influence the distribution of fish species, as temperature and current speed directly impact their presence, as well as the availability of resources for spawning and survival (Huet, 1949). The lateral dimension of a river extends from the minor bed to the major bed. This dimension is crucial for habitat diversity, as it allows the creation of spawning and refuge habitats, particularly during floods, when the floodplain is inundated and can serve as a spawning area for photophilic species (Keeley et al., 2022; Kondolf et al., 2006). The vertical dimension extends from the surface to the riverbed, presenting a gradient of physical conditions such as substrate and current speed (Kondolf et al., 2006; Wiens, 2002). These characteristics and interconnections evolve over time according to variations in the hydrological regime, thus forming the fourth dimension, the temporal dimension (Felin et al., 2025; Keeley et al., 2022; Kondolf et al., 2006; Wiens, 2002). As a result, these dimensions describe the ecosystem as variable and heterogeneous, promoting the creation of multiple ecological niches that enable a high diversity of fish species to establish (Ovidio et al., 2020; Townsend, 1989).

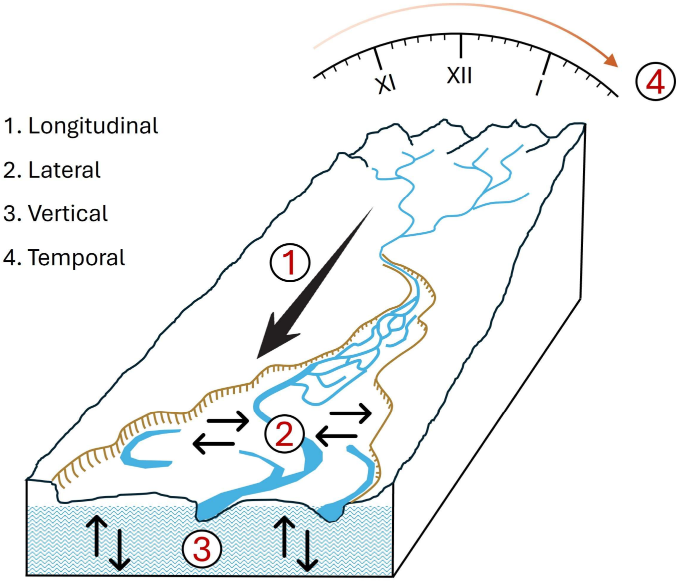

Figure 1. The four dimensions of rivers: (1) longitudinal, (2) lateral, (3) vertical and (4) temporal. Modified from Amoros and Petts (1993).

Types of movement and migration patterns in fish

Among aquatic organisms, fish are in constant movement to meet their vital needs, which change over time according to their life cycle, resulting in continuous movements between different habitats (Baudoin et al., 2015, Dodd et al., 2024; Pachla et al., 2022; Pander et al., 2013). Therefore, river connectivity is essential to ensure the dynamics and resilience of aquatic populations, while maintaining the ecological health of rivers (Ovidio et al., 2023). The area that the fish occupies throughout its life to fulfil all its biological functions is referred to as its home range (Gelder et al., 2024b; Panchan et al., 2022; Woolnough et al., 2009). This home range can be determined in different temporal or biological ways, for instance, based on the season or the specific life stage (Lucas & Baras, 2001; Woolnough et al., 2009), as physiological needs change during the fish’s development (larvae, fry, juvenile, adult) (Baudoin et al., 2015). Consequently, the functional habitats used may vary according to the life stage of the fish (Benitez et al., 2015; Ovidio et al., 2023; Woolnough et al., 2009). Fish undertake movements between different habitats, with the timing, distances, and directions varying depending on the specific needs of each function (Capra et al., 2018; Ovidio et al., 2007). These movements can be daily (e.g., between feeding and refuge areas), seasonal (such as during spawning migrations), or occur at other temporal scales. The extent of these movements can vary greatly, ranging from a few metres to several hundred or even thousands of kilometres (Capra et al., 2018; Davies et al., 2024; De Leeuw & Winter, 2008; García-Vega et al., 2018; Gelder et al., 2024b; Ovidio et al., 2007).

Fish movements can be broadly classified into two categories: active movements, which require energy expenditure, and passive movements, where the surrounding environment transports the fish (Baudoin et al., 2015; Sonny et al., 2006). Passive movements refer to downstream displacements that occur when fish are unable to withstand the current velocity during major flood events. Two main types can be identified: (i) passive displacement, where the individual is completely carried away by the current, and (ii) semi-active displacement, where the individual attempts to swim against the current but fails to exceed its velocity. Once conditions improve, the fish typically swim back upstream to return to their initial habitat (Baudoin et al., 2015). Among passive movements, the drift of fry or young-of-the-year is a key mechanism for individual dispersion, thereby promoting genetic exchange and population expansion. This phenomenon occurs when specific environmental conditions, unique to each species, are met, resulting in a deliberate drift of the fry (Baudoin et al., 2015; Reichard et al., 2002; Sonny et al., 2006). Active fish movements can be triggered by their biological needs or changes in their environment, occurring both upstream and downstream, regardless of the individual's developmental stage (Benitez et al., 2015). These movements are categorised into three types: non-periodic, ontogenetic, and periodic movements (Baudoin et al., 2015; Lucas & Baras, 2001; Ovidio et al., 2020).

- **Non-periodic movements**, also referred to as acyclic movements, occur in response to significant environmental disturbances, such as pollution events or droughts, compelling fish to temporarily leave their habitat in order to survive. When conditions improve, fish often return to their original habitat. These movements are irregular and not part of the natural life cycles of the species, as they are primarily driven by unpredictable environmental changes.

- **Ontogenetic movements** are linked to changes in the ecological, physiological, and biological needs of fish, often driven by shifts in their physiology or developmental stage. These movements occur as fish transition between habitats corresponding to their life stage.

- **Periodic active movements** refer to repetitive and regular displacements over time, which meet their needs in terms of rest, feeding, or activity. These movements are closely influenced by environmental factors such as photoperiod, temperature, or resource availability. They can be divided into two types: daily and seasonal movements.

    - **Daily movements** take place within the fish's home range and involve transitions between distinct areas, such as resting zones and feeding zones, which differ in their hydromorphological characteristics (e.g., calm areas versus fast-flowing waters).

    - **Seasonal movements**, also known as migration movements, involve a distance significantly greater than usual, are predictable and triggered by environmental conditions, affect a large portion of the population, and include, most of the time, a return trip. These migrations span long distances between functional habitats and are regular events that occur at specific points in the fish's life cycle, often driven by the need to find suitable spawning sites.

Migration strategies and ecological groups of fish

Spawning migrations, which involve periodic seasonal movements of mature adult individuals, enable them to reach habitats with specific characteristics suitable for spawning. For example, trout (*Salmo trutta*) are known to migrate to tributaries and sub-tributaries to spawn (Ovidio et al., 1998; Piecuch & Lojkásek, 2007). Moreover, some species, such as the barbel (*Barbus barbus*), remain faithful to their spawning site year after year (Gelder et al., 2024b; Ovidio et al., 2007). Therefore, spawning adults travel long distances (in comparison to their typical daily movements) to locate suitable spawning habitats that also have the characteristics necessary for the development of juveniles (Baudoin et al., 2015; Ordeix & Casals, 2024). These migrations, typically longitudinal, can occur in two directions: upstream or downstream (Silva et al., 2018). Note that some species undertake both longitudinal and transversal migrations, such as the pike (*Esox lucius*), which moves laterally to flooded areas to reproduce on submerged vegetation (Cittadino et al., 2024). Several patterns of spawning migratory behaviours can be observed within rivers. The literature generally distinguishes three main types of migration in freshwater fish (Alvarez-Vázquez et al., 2008; Baudoin et al., 2015; Lucas & Baras, 2001; Ordeix & Casals, 2024):

- **Amphibiotic migration** pertains to species that complete part of their life cycle in saltwater and another part in freshwater. These species are commonly known as diadromous, and travel distances of up to thousands of kilometres:

  - **Anadromous species** spawn in freshwater, with the rest of their life cycle spent in salt water (e.g., Atlantic salmon (*Salmo salar*), sea trout (*Salmo trutta*)).

  - **Catadromous species** spawn in salt water and growth in freshwater (e.g., European eel (*Anguilla anguilla*)).

- **Amphidromous species** move between fresh and salt water without any link to spawning (e.g., Gobies (*Gobius sp*)).

- **Holobiotic potamodromous migration** refers to species whose entire life cycle occurs exclusively in freshwater. Examples include the chub (*Leuciscus cephalus*), the barbel, and the nase (*Chondrostoma nasus*).

Although less well documented in the literature than diadromous species, holobiotic potamodromous species move from a few metres to several tens of kilometres, generally in search of refuge, food or spawning sites (Capra et al., 2018; De Leeuw & Winter, 2008; Ovidio et al., 2023). There are three categories of freshwater fish, depending on their habitat preferences and preferred substrate for laying eggs (Philippart, 2007; Schiemer & Spindler, 1989).

- **Rheophilic species** prefer areas with strong currents and a well-oxygenated water. These species are litophilic and lay their eggs in and/or on a stony substrate (e.g., barbel and chub).

- **Limnophilic species** like areas of stagnant water with a relatively weak current and are phytophilic laying their eggs on subaquatic vegetation, roots or branches (e.g., pike and perch (*Perca fluviatilis*))

- **Eurytopic species** are tolerant with no requirements in terms of egg-laying substrate (litho-phytophilic) and can exploit both types of habitat which allows them to adapt more easily to environmental changes (e.g., roach (*Rutilus rutilus*) and gudgeon (*Gobio gobio*)).

Depending on these ecological preferences, the species will group together and form distinct communities that will be found along the length of the watercourse within the different fish zones.

River fragmentation and impacts

Fragmentation of freshwater ecosystems is widely consider as a major threat to aquatic resources, disrupting habitat connectivity and endangering the abundance, distribution, and diversity of aquatic species (Belletti et al., 2020; Felin et al., 2025; Tummers et al., 2016a). Indeed, 40% of global fish diversity is found in freshwater, but this diversity is largely threatened (Dudgeon et al., 2006). In Europe, 93% of migratory freshwater fish species have declined since the 1970s while the number of artificial barriers along river continues to rise (Deinet et al., 2020). Today, more than 1.2 million obstacles such as dams, weirs, navigation infrastructure or power plants fragment Europe's rivers and more than 4 800 in Wallonia-Belgium (Figure 2). Although installed to provide services to societies such as reducing flooding, producing water reserves, enabling irrigation for agriculture or even producing energy, these obstacles have also had an impact on watercourses by disturbing the water regime, the flow velocities, the depth of the water, modifying water temperature and disrupting connectivity (Deinet et al., 2020; Duarte et al., 2021; Dudgeon et al., 2006; Nilsson et al., 2005).

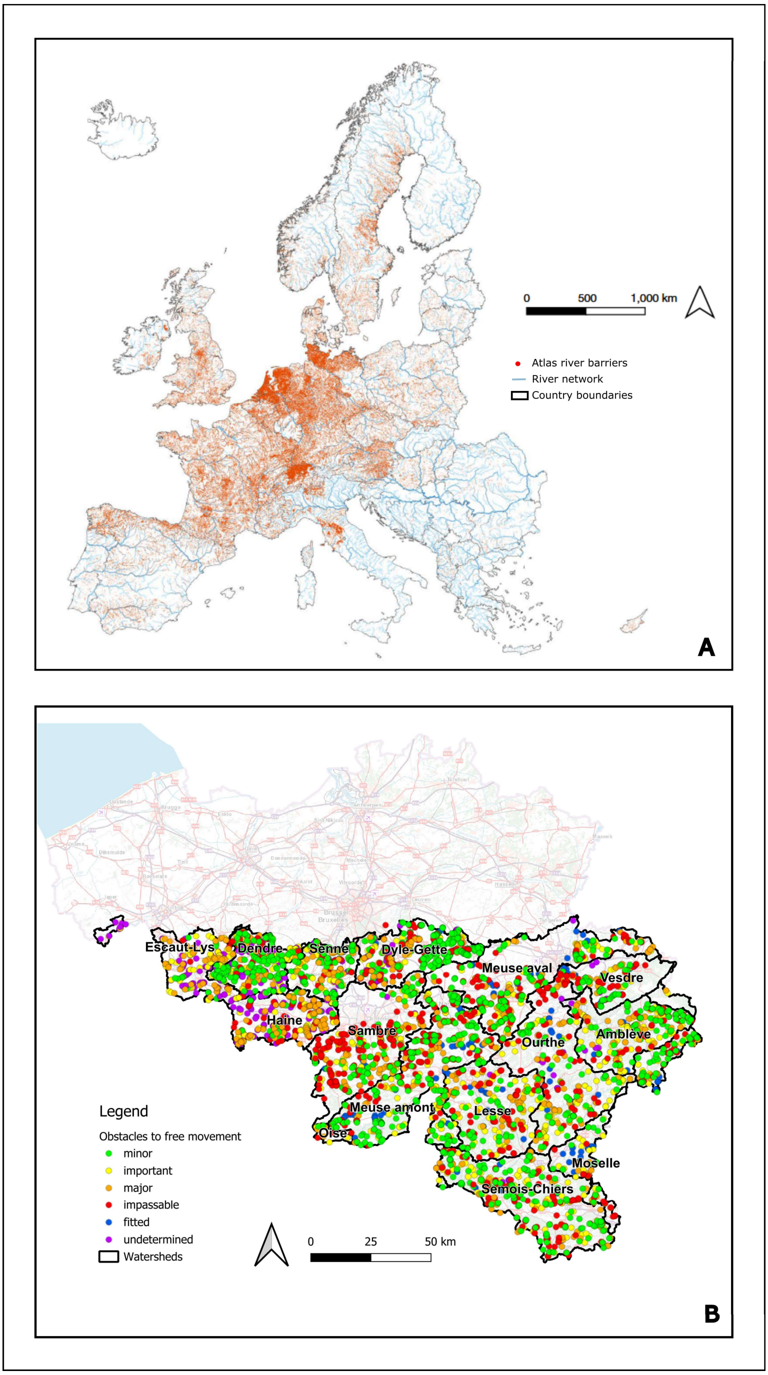

Figure 2. Maps showing (A) the distribution of obstacles to free movement in Europe and (B) the distribution of obstacles in Belgium-Wallonia according to their degree of importance

As a result, these various factors will have an impact on fish fauna. Throughout their life cycle, individuals utilise different habitats, access to which can be significantly restricted by these physical barriers. These obstacles, when impassable, can hinder or even prevent migrations necessary for spawning (Dean et al., 2023; Ovidio et al., 2007). Moreover, the accumulation of obstacles along a watercourse exacerbates these effects (Consuegra et al., 2021; Dean et al., 2023; Yokouchi et al., 2022) by significantly reducing spawning success and imposing increased energetic costs on individuals, potentially leading to their mortality (Nyqvist et al., 2017; Scruton et al., 2008). The isolation of populations located upstream and downstream, caused by an impassable barrier, can also result in a reduction of genetic diversity. This loss compromises the resilience of communities to climate change, limiting their capacity to adapt to environmental disturbances (Baldan et al., 2023; Lange et al., 2018). Beyond their role as physical barriers, dams also profoundly modify riverine environments. By interrupting the natural transport of sediments, they cause sediment accumulation upstream and a deficit downstream, which increases erosion and alters the riverbed. These changes modify the substrate and, consequently, the spawning habitats, particularly affecting species with strict ecological requirements regarding granulometry (Baird et al., 2024; Wang et al., 2024). Additionally, dams can transform lotic into lentic environments, fundamentally altering habitat conditions. Such modifications disrupt natural flow regimes and may lead to a decline in species adapted to lotic environments, favouring instead species that are more typical of lentic habitats (Bower et al., 2024). Hydroelectric power stations induce hydropeaking, which corresponds to discontinuous releases of turbined water downstream of the dam, causing sudden changes in flow rates. These variations in flow can cause a rapid drying of the banks, leading to the trapping and mortality of individuals. Additionally, hydropeaking alters water temperatures downstream of the structure, increasing the average temperature. These thermal conditions promote the establishment of non-native species, often to the detriment of native species (Baird et al., 2024; Cavallaro & Schumann, 2024; Insulaire et al., 2024). In the context of downstream migration, fish can be injured or killed when passing through turbines, due to impacts, pressure changes, or shear forces (Fu et al., 2016; Mueller et al., 2020; Trumbo et al., 2014) or passing over spillway gates (Larinier & Travade, 2002). Without a dedicated downstream bypass, individuals may become trapped upstream of the dam and exhaust themselves while attempting to find a passage (Larinier & Travade, 2002; Nyqvist et al., 2017; Renardy et al., 2020). These disturbances act synergistically, thereby amplifying their impact on fish populations, contributing to their decline, and, in some cases, potentially leading to the extinction of species.

Restoration of ecological continuity

Restoration methods

Restoring longitudinal connectivity to ensure access to functional habitats is a key priority in river restoration projects and management plans (Roni et al., 2002; Silva et al., 2018). Dams are often old and can become obsolete over time, often leading to high restoration costs. River managers assess the costs of both repairing a defective dam and removing it, and in some cases, removal is found to be the more cost-effective solution. While the ideal solution is to remove the obstacle to fully restore the river to its natural state, this approach is not always feasible due to various constraints (Bellmore et al., 2019; Bower et al., 2024; Tummers et al., 2016a). For example, economic constraints arise when dams are used for hydroelectric power generation, hydrological constraints relate to the management of flow regimes, technical constraints are associated with sediment management and social constraints emerge when dams are perceived as a heritage to be preserved (Bellmore et al., 2019).

An alternative to removing the dam is to install crossing devices, known as fishways, at the obstacles. Over the last few decades, numerous fishways have been installed to restore connectivity and allow fish populations to access the various functional habitats (Mameri et al., 2019; Ovidio et al., 2023; Roscoe & Hinch, 2010). The choice of fishways depends on a number of factors, such as the infrastructure and constraints of the site, the target species, the size of the individuals and the hydraulic conditions of the section (Lothian et al., 2019; Ovidio et al., 2017; Romão et al., 2019). The ability of fish to use a fishway depends on their species, life stage, and swimming capabilities. Consequently, fishway designs must be designed to accommodate the specific needs of the target species (Noonan et al., 2012; Silva et al., 2018). Initially designed primarily for diadromous species, due to their economic interest, these devices have evolved to become multi-species, enabling all species to use them (Alvarez-Vázquez et al., 2008; Benitez et al., 2015; Grimardias et al., 2022; Nunn & Cowx, 2012). The restoration of upstream connectivity is the most common restoration measure, as upstream migration for spawning is often considered a priority for fish species (Bunt et al., 2012; Noonan et al., 2012; Roscoe & Hinch, 2010). These are mainly structures located either on the banks or in the centre of the obstacle and they can be of different types: bypass channel, fish lift, denil fishway or pool-type fishway. Although less widespread, some devices facilitate the downstream migration of individuals; however, they will not be discussed in this thesis. The most common device is the downstream bypass at the hydroelectric power station which enables fish to move downstream, avoiding any turbines that may be present (Renardy et al., 2020, 2022).

Type of fishways

The complexity of a fishway lies in its ability to guide fish towards its entrance and allow them to pass through the obstacle as quickly as possible. As a result, the location of this entrance is a determining factor (Bunt, 2001; Iaia et al., 2025; Katopodis & Williams, 2012). To maximise the attractiveness of the fishway, an attraction current is generally set up near the entrance. This directed flow of water simulates the natural conditions of the main current and encourages fish to swim upstream towards the fishway (Bunt, 2001; Cooke & Hinch, 2013; Noonan et al., 2012). While these general principles apply to all fishways, there are different types, each with its own specific characteristics.

Nature-like fishways

Natural fishways are facilities designed to restore the ecological continuity of rivers while mimicking a natural watercourse. These devices have been designed to imitate the flow conditions of the natural river and to integrate seamlessly into the landscape by using primarily natural materials (Stuart et al., 2024; Zhu et al., 2024). The arrangement of these natural materials, generally blocks, and the creation of a rough substrate dissipates energy, facilitating upstream movement for individuals while also creating resting areas. These structures, which mimic the natural river, can be used by all fish species, regardless of their swimming ability (Baudoin et al., 2015; Larinier, 2008; Santos et al., 2005).

Bypass channels and rock ramps are part of these natural fishways. Bypass channels mimic the watercourse by forming a secondary arm of the main river which can include various habitats. This structure requires a large amount of space along the riverbank. On the other hand, the rock ramp typically requires less space and recreates a natural current by placing blocks in a ramp-like formation to facilitate the movement of fish upstream (Baudoin et al., 2015; Larinier et al., 2002; Stuart et al., 2024; Figure 3).

Fish lifts

In cases where the height of the obstacle makes it difficult or impossible to overcome using conventional devices, the installation of a fish lift is often preferred. These devices consist of attracting fish into a cage at the foot of the obstacle (Figure 3). After a certain period or once a specified number of individuals is reached, the cage is automatically raised upstream, where the fish are then released. Due to the numerous mechanical components involved, these systems are costly to maintain and require more extensive maintenance (Baudoin et al., 2015; Larinier et al., 2002).

Denil fishway

The Denil fishway was the first fish ladder to be installed in Belgium on the Ourthe River in 1909 and adapted afterwards (Figure 3). This is a narrow, steeply sloping channel with a series of U-shaped deflectors installed to slow the current. Due to its configuration, this type of fish ladder is particularly suitable for species with good swimming abilities, such as salmonids (Larinier, 2008; Noonan et al., 2012).

Pool-type fishway

Pool-type fishway are the most common type of obstacle crossing structure. These devices can be adapted according to the height of the obstacle to be crossed or the species targeted.

Pool and weir fishways consist of a series of basins arranged in succession, separated by weirs, with water flowing from one to the next from upstream to downstream, enabling the height of the obstacle to be gradually overcome (Figure 3). This design allows fish to ascend stepwise by swimming or jumping from pool to pool, utilising resting areas between each step. Sometimes an orifice in the weir is also installed to allow a wider range of species to use the device (Baudoin et al., 2015; Ead et al., 2004).

Vertical-slot fishways also consist of a series of successive basins but each separated by a vertical slot through which the water flows (Figure 3). These pools offer potential resting areas for fish while the water flowing through the slots generates a current that stimulates fish movement (Baudoin et al., 2015; Wu et al., 1999). Due to their configuration, these devices have a multi-specific character enabling individuals with lower swimming abilities to successfully move upstream (Bao et al., 2019; Romão et al., 2018; Stuart & Berghuis, 2002).

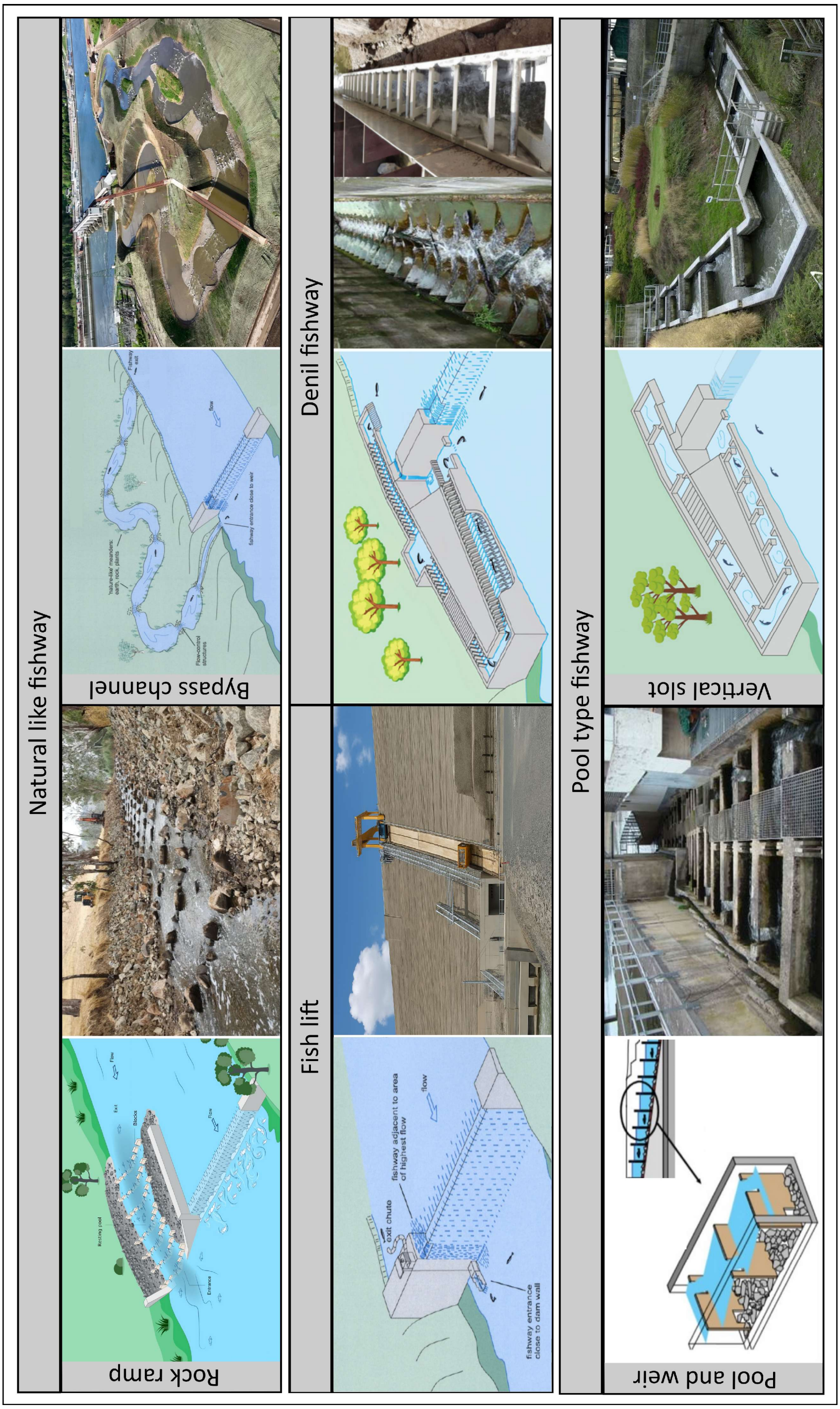

Figure 3. Schemas and photos of the different types of fishway: natural like fishway (rock ramp and bypass channel), fish lift, denil fishway and pool-type fishway (pool and weir and vertical slot).

Evaluating river defragmentation outcomes

Fishway monitoring methodology

Analysing the use of fishways makes it possible to identify the species using these structures, estimate the number of individuals passing through, and collect various biometric data. Different methods, collectively referred to as fishway monitoring, exist with varying levels of accuracy to assess the usage of these devices:

- **Counting individuals**: individuals can be counted automatically or manually. A person can count the number of individuals present in a fishway through a window, trapped in a cage or other capture device, or on the basis of video (Cui et al., 2024; Santos et al., 2002).

- **Video identification**: video surveillance systems installed in the fishways enable the number of individuals to be counted and the species to be identified (video counting) (Bao et al., 2019; Cui et al., 2024; Davies et al., 2007). Species identification can also be carried out during counts by a person trained for this purpose (Cui et al., 2024; Santos et al., 2002)

- **Fishway emptying**: used in fish ladders, draining consists of closing the water inlet of the structure, causing a gradual decrease in the water level. As a result, the individuals move downstream within the structure until they reach the last basin. Once gathered in this area, they can be captured using nets and handled to obtain biometric data such as the size and weight of the individuals, and sex determined when possible (Baras et al., 1994; Kotusz et al., 2006; Prchalová et al., 2011; Slavík et al., 2009).

- **Capture cage monitoring**: this method involves installing a capture cage in the fishway, which is regularly checked. As well as counting and identifying the species present, this monitoring method also enables biometric measurements to be taken (Benitez et al., 2022; García-Vega et al., 2022; Gelder et al., 2023; Ovidio et al., 2023).

Many studies have analysed fish passage through fishways using video surveillance systems (Belo et al., 2021; Cui et al., 2024; Holter et al., 2020; Iaia et al., 2025; Jensen et al., 2024; Mader et al., 2020; Santos et al., 2002, 2007). Automating these monitoring processes saves time and reduces the need for on-site human presence. Additionally, technological advances now allow for the estimation of biological parameters such as the size and weight of individuals based on images (Cui et al., 2024; Santos et al., 2007). However, the lack of direct handling can introduce biases, particularly due to potential errors in species identification (Cooke & Hinch, 2013), for example when high turbidity reduces image quality (Eggers et al., 2024a), and uncertainties in morphometric estimations. The use of capture traps as a monitoring method is demanding, as it requires frequent human intervention. However, it provides accurate and detailed data on fish, including species identification, weight and size measurements, sex determination, and the ability to apply tagging for various scientific purposes (Baek et al., 2021; Benitez et al., 2015, 2022; García-Vega et al., 2018, 2020, 2022; Legrand et al., 2020; Mallen-Cooper & Brand, 2007; Yoon et al., 2016).

Regardless of the monitoring method used, the temporal scope of studies remains a key limitation. In the literature, most fishway monitoring studies are conducted over limited periods, primarily during species migration phases (spawning period) or for a few months (Baek et al., 2021; Cui et al., 2024; Kotusz et al., 2006; Prchalová et al., 2011; Slavík et al., 2009). Long-term studies spanning multiple years remain uncommon due to logistical constraints and the resources required for extended monitoring (Benitez et al., 2015, 2022; Legrand et al., 2020). Additionally, these studies are often monospecific or focus on a few target species, particularly salmonids (Belo et al., 2021; Cooke & Hinch, 2013; García-Vega et al., 2018, 2020, 2022; Holter et al., 2020). Continuous, multi-annual monitoring at a multispecies scale, involving direct handling of individuals for the collection of biometric data, remains particularly rare in the literature (Benitez et al., 2015, 2022; Gelder et al., 2023). This prevalence of short-term and species-specific studies may limit the assessment of interannual variations and long-term trends in fish communities when studying the use of fishways in the context of opening up migratory axis (Iaia et al., 2025; Panagiotopoulos et al., 2024). Long-term fishway monitoring can also highlight species-specific colonisation patterns, providing valuable insights into how different species establish and expand their presence over time.

Effectiveness of fishways

Analysing the use of fishways allows us to identify the species and individuals that use them, but does not allow us to fully determine the effectiveness of the devices (Ovidio et al., 2017; Silva et al., 2012). Assessing the efficiency of a fishway is based on analysing the behaviour of tagged fish as they approach the fishway and pass through it (Dębowski et al., 2022; Hatry et al., 2016; Iaia et al., 2025; Ovidio et al., 2017; Silva et al., 2012; Thiem et al., 2013; Tummers et al., 2016a). This makes it possible to detect any difficulties, such as a passage time that is too long or an inability to locate the entrance to the fishway. According to Baudouin *et al.* (2015), a fishway is considered to be effective if individuals can quickly find the entrance to the device and if these individuals move upstream without difficulty, delay, stress or any other alteration to their physical condition.

The efficiency of a fishway corresponds to the number of individuals successfully passing through the obstacle compared with the number of individuals attempting to pass through it. Assessing the effectiveness of a fishway involves studying the behaviour of marked individuals as they approach the fishway and during their passage through it (Gelder et al., 2024a; Lucas & Baras, 2001; Ovidio et al., 2021, 2023). Various methods can be used to assess the effectiveness of a fishway, each of which involves marking individuals: use of (i) active telemetry with radio transmitter or (ii) passive telemetry with radio frequency identification (RFID). Consequently, these methods require individuals to be captured and marked in order to analyse their behaviour.

Radio transmitters can be used to pinpoint the exact location of individuals when tracking, regardless of their position (Bravo-Córdoba et al., 2023; Calles et al., 2021; Gelder et al., 2024b; Kucukali et al., 2025; Lähteenmäki et al., 2023; Lothian et al., 2019; Ovidio et al., 2020; Sutela et al., 2018; Tummers et al., 2016a; Zampatti et al., 2018). This method allows for precise localisation of individuals at any time, including outside the fishway. However, tracking individuals beyond the range of fixed antennas requires personnel on-site to manually record their positions, which is a resource-intensive and time-consuming task. This is why fixed radio antennas are sometimes preferred or used in conjunction with manual tracking (Belo et al., 2021; Bravo-Córdoba et al., 2023; Calles et al., 2021; De Leeuw & Winter, 2008; Grimardias et al., 2022; Havn et al., 2017; Keefer et al., 2021; Lähteenmäki et al., 2023; Pereira et al., 2017; Sullivan et al., 2019; Thorstad et al., 2017; Weaver et al., 2019; Zampatti et al., 2018). In addition, the monitoring period is constrained by the lifespan of the transmitters, and signal detection can be influenced by environmental characteristics (Lucas & Baras, 2001). There are also acoustic transmitters used mainly in deep water environments. These transmitters emit sound waves that are picked up by hydrophones (Bett et al., 2022; Roscoe et al., 2011; Tétard et al., 2019; Twardek et al., 2023).

Radio frequency identification commonly used is the passive integrated transponder tag (PIT tag), which enables individuals to be located as they pass through specific points, equipped with detection antennae (Benitez et al., 2018; Bett et al., 2022; Bravo-Córdoba et al., 2023; Dębowski et al., 2022; Grimardias et al., 2022; Ke et al., 2024; Keefer et al., 2021; Lothian et al., 2019; Ovidio et al., 2021; Tomanova et al., 2025; Tummers et al., 2016a; Twardek et al., 2023).

This method has the advantage of a theoretically unlimited lifespan, as RFID tags operate without a battery. However, since their detection range is limited to a few metres, individuals are only recorded when they pass near the antennas, with no possibility of tracking their movements between detection points (Lucas & Baras, 2001).

Each of these methods has its advantages and disadvantages. The choice of method will depend on the study objectives as well as constraints related to human resources, available budget, and site characteristics. Based on the data obtained, several metrics can then be studied, such as arrival delay at the entrance of the fishway, rate of attraction or fishway transit time, ultimately allowing for an assessment of the crossing device's effectiveness (Bunt et al., 2012; Gelder et al., 2024a; Hatry et al., 2016; Ovidio et al., 2017; Thiem et al., 2013; White et al., 2011). Furthermore, they provide managers with essential information to adjust and optimise fishways, improving their design and operation to maximise their performance and attractiveness for target species. As demonstrated, the combination of monitoring and individual tagging allows for a comprehensive analysis of fishway use and effectiveness. Most studies related to habitat defragmentation have primarily focused on the performance of passage devices by examining individual movements and behaviours near fishways, often within a restricted area. By using a systematic combination of passive and active monitoring methods, observations can be significantly extended beyond the immediate vicinity of the fishways. This combined approach enables detailed analysis of individual fish behaviour not only close to the fishway but also during the approach phase at a further distance. It allows us to identify behaviours such as repeated approaches without passing or staying near fishways outside the detection zone of the automatic antennae. This, combined with continuous monitoring of the use of the fishway, enables a complete assessment of the effectiveness of the fishways.

However, while assessing the efficiency of a fishway in terms of its ability to facilitate upstream migration is crucial, it is also important to consider what happens after individuals have crossed the obstacle.

What happens after individuals have passed through a fishway?

Despite the proliferation of fishways and studies linked to crossing devices, few studies have investigated the ecological benefits of re-establishing migratory axis for the species concerned. To assess these effects, it is necessary to monitor the evolution of fish over short or long periods, at an individual or population scale, in order to observe adjustments in the new accessible sections of the river. Numerous studies published in the scientific literature have explored the behaviour of individuals in their natural environment in order to analyse their ecology

(Armstrong & Herbert, 1997; Baras & Cherry, 1990; Britton & Pegg, 2011; Capra et al., 2018; Cittadino et al., 2024; Glowa et al., 2024; Jackson et al., 2024; Lucas & Batley, 1996; Ovidio, 1999; Ovidio et al., 1998, 2007; Panchan et al., 2022; Piecuch & Lojkásek, 2007; Zimmer et al., 2010). These studies have provided a comprehensive knowledge of the habits and needs of several species. However, there remains a significant gap in understanding how individuals respond once they have passed upstream of an obstacle following habitat defragmentation. Very few studies have specifically investigated this aspect, and those that do are often limited in scope. Existing research primarily relies on fixed antennas (RFID, radio or acoustic) to detect individuals at successive fishways (Benitez et al., 2018; Błońska et al., 2025; De Leeuw & Winter, 2008; Tétard et al., 2025; Tummers et al., 2016a), or it focuses on a restricted area near the fishway (Tummers et al., 2016a). As a result, our knowledge of the use of newly accessible habitats, behavioural strategies, and the establishment of fish upstream remains incomplete.

To thoroughly analyse post-passage behaviours, it is essential to study the fine-scale movements of individuals with precision and over multiple consecutive years without interruption. This approach ensures a comprehensive understanding of the full range of possible behaviours, encompassing both spawning and non-spawning periods. Moreover, continuous tracking enhances the repeatability of observations, enabling the validation and confirmation of behavioural patterns. Such a methodology relies on intensive and regular tracking, requiring constant surveillance of individuals after they have passed through the fishways. This enables the collection of crucial data on the habitats used, the assessment of their ability to spawn in newly opened areas and the evaluation of whether the observed behaviours correspond to ‘normal’ behaviours described in the literature. While manual radio telemetry is resource-intensive, it remains an effective method for tracking fish movements at all times.

Objectives of the thesis

To fully understand the process of habitat defragmentation in river systems, it is essential to study not only fish passage through fishways but also the dynamics before, during, and after connectivity restoration. This study is the first to integrate a multi-year, continuous approach combining pre-defragmentation population assessments, long-term fishway monitoring with biometric data collection across multiple species, and unprecedented post-passage tracking over consecutive years using radiotelemetry. By covering the entire defragmentation process, this research provides a comprehensive and novel perspective on habitat reconnection and its ecological outcomes.

To thoroughly analyse and understand this habitat defragmentation process, this thesis is structured around several key objectives:

(1) Assessment of the initial fish population structure upstream and downstream of an impassable barrier before connectivity restoration.
(2) Evaluating the representativeness of fishway use by fish species compared to downstream and upstream populations.
(3) Analysis of fish colonisation dynamics and interannual variations in fish passage over multiple consecutive years following the opening of the migratory axis.
(4) Evaluation of the efficiency and attractiveness of a fishway installed near an impassable barrier.
(5) Investigation of fish behaviour and movements after passing through a fishway at a multi-year level, by analysing various behavioural metrics.
(6) Highlighting the use of spawning habitats by fish released upstream of a fishway.

Thesis structure and publication strategy

In order to address the defined objectives, this thesis is structured into different chapters. It begins with a general introduction that outlines the conceptual and scientific framework of the work, followed by a chapter dedicated to the presentation of the study sites and the methodology used. The central part of the thesis consists of five results chapters, each corresponding to a scientific article published or submitted as first author (four accepted and one currently under submission). Finally, a concluding chapter is devoted to the general discussion and the broader interpretation of the findings.

The structure of the thesis was designed to follow the chronological logic of the defragmentation process in a riverine habitat. The first results chapters thus address the dynamics observed before and during defragmentation (community structure, colonisation dynamics, and fishway efficiency), while the subsequent chapters focus on what occurs after defragmentation (post-passage behaviours, use of newly accessible habitats, and site fidelity). This organisation allows for a stepwise exploration of the different phases of ecological response to the restoration of longitudinal connectivity.

Chapter 1 provides a general introduction to the ecological context of river fragmentation and connectivity restoration. It outlines the impacts of barriers on fish populations, the types of fish movements and fishways, and the methods used to evaluate defragmentation outcomes. The chapter concludes with the objectives of the thesis and a presentation of its structure.

Chapter 2 presents the methodological framework of the thesis. It details the study sites, the different methodologies used, and the biological models selected.

Chapter 3 examines the initial state of fish communities upstream and downstream of an obstacle and their response to the opening of a migratory axis on the Amblève River. Using a multi-year monitoring approach combining electrofishing and fishway data, the study assesses changes in fish communities and documents early colonisation dynamics following restoration.

Chapter 4 explores the temporal dynamics of fish colonisation following the opening of migratory axis. Based on multi-year monitoring of three fishways, the study reveals delayed responses, interspecific differences in migration timing, and the importance of long-term data to understand colonisation patterns.

Chapter 5 focuses on the evaluation of a fishway installed at the Coo site, using a combined radio telemetry and RFID monitoring protocol. Through double tagging of individuals and the use of both automatic and manual tracking methods, the study aims to assess fishway performance, device attractiveness, and individual behavioural responses when approaching the structure.

Chapter 6 investigates the short-term post-passage movement and habitat use by fish following the restoration of connectivity on the Amblève River. Manual radio telemetry was used to monitor four potamodromous species upstream of two obstacles, in order to characterise individual behaviours and spatial trajectories within newly accessible habitats.

Chapter 7 analyses post-passage behaviour of two potamodromous species after crossing one of two major obstacles on the Amblève River. Using continuous, three-year manual radiotelemetry monitoring. The study aims to characterise spatial behaviour, mobility indicators, and the factors influencing whether individuals remain upstream or return downstream of an obstacle.

Chapter 8 presents the general discussion of the thesis. It integrates the main findings from the different studies, and concludes with perspectives for future research and river restoration practices.

Chapter 2. Presentation of study sites and methodologies used

Main study site: the Amblève River

General characteristics

The Amblève is a river located in the south-east of Belgium, within the Meuse river basin (Figure 1). It rises at an altitude of 586 metres and flows for 88.4 kilometres before joining the Ourthe River at Comblain-au-Pont (102 metres above sea level). With a catchment area of 1,076.8 km^2, an average natural slope estimated at 5.48 ‰, and a median discharge of 14.2 m^3/s, it is the main tributary of the Ourthe.

The principal tributaries of the Amblève, from upstream to downstream, are the Warche, which flows into the Amblève near Malmedy and drains a basin of 190 km^2; the Salm, which joins the river at Trois-Ponts and has a basin of 243 km^2; and the Lienne, whose confluence is located at Lorcé and which drains an area of 149 km^2. In addition to these major tributaries, the Amblève also receives several smaller watercourses, such as the Möderscheider Bach at Amel, the Emmel at Monteneau, the Recht stream at Bellevaux-Ligneuville, the Roannay at La Gleize, and the Fond d'Harzé stream at Aywaille.

According to Huet's (1949) classification, the Amblève is characterised as a trout zone upstream of its confluence with the Warche, and becomes a grayling/barbel zone downstream of the Warche. Its ecological status is considered good, according to the Public Service of Wallonia (Department of Environmental Studies – DEE), with a total of 23 fish species present in the river. However, the river's original longitudinal profile has been altered by the presence of several barriers, which cause significant fluctuations in water levels (hydropeaking) and hinder the free movement of fish. The Amblève River in Belgium currently contains nine barriers, four of which are hydroelectric dams. In this thesis, we focus specifically on the Coo waterfall and the Lorcé hydroelectric dam, which are considered major obstacles to free fish movement.

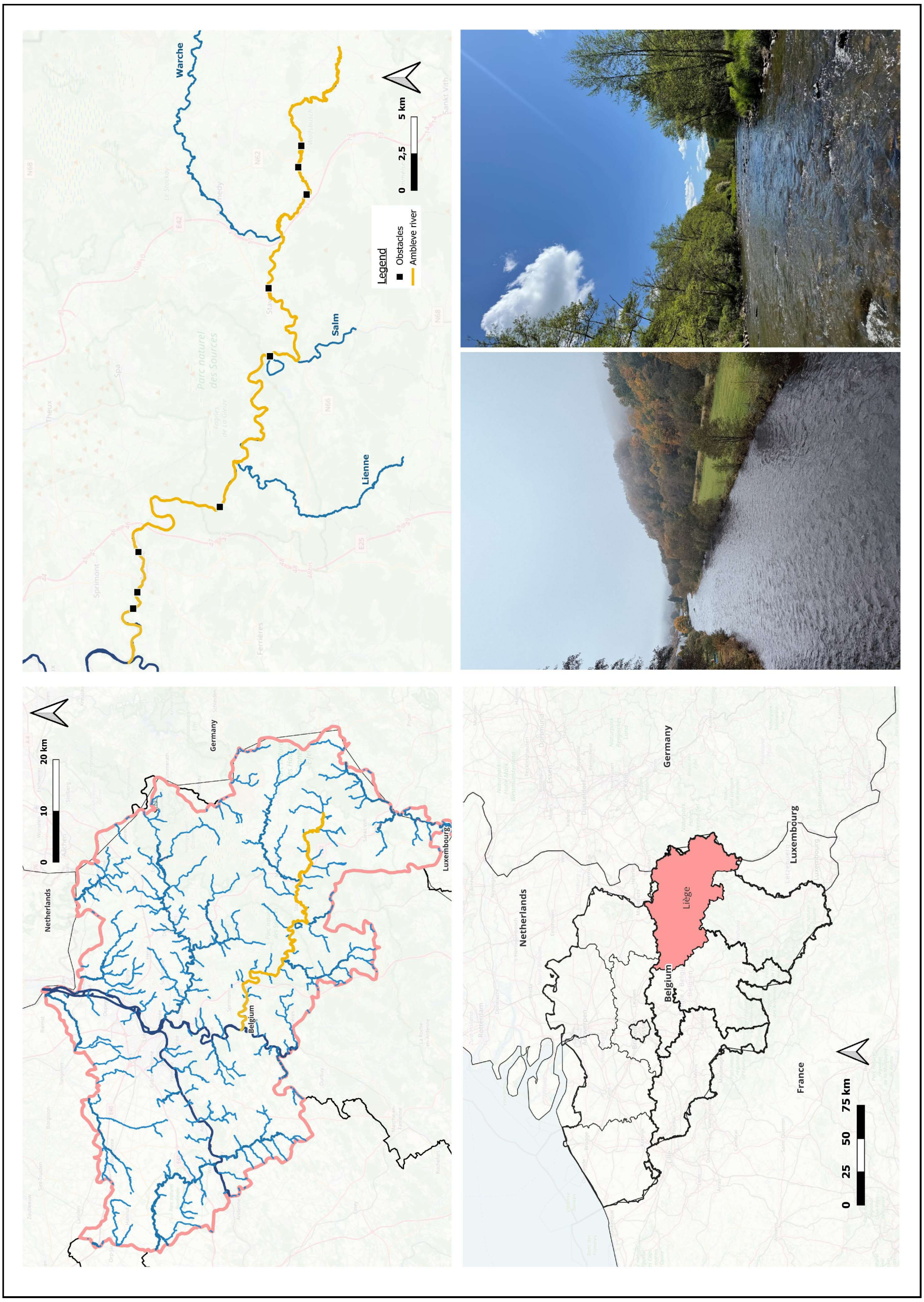

Figure 1. Map of Belgium and the Province of Liège showing the hydrographic network, the Amblève River with its main tributaries, obstacles, and photos of the river.

Coo waterfall

The Coo waterfall is situated 39.7 km upstream from the confluence of the Amblève River with the Ourthe River, downstream of its junction with the Salm River. This semi-artificial barrier was created during the Middle Ages through the artificial cutoff of a meander. The waterfall, divided into two separate drops, has a total height of approximately 11.8 metres (Figure 2), preventing any upstream fish migration at this point.

Until 1970, a natural meander on the left bank of the river functioned as an alternative route, allowing fish to bypass the obstacle. However, in 1970, the construction of the Coo pumped-storage hydropower plant transformed this meander into a water reservoir, and the corresponding section of the Amblève River was bypassed, rendering the waterfall completely impassable for upstream fish migration. In addition, a small hydroelectric power plant, known as the Coo Dérivation Plant, diverts part of the Amblève's flow upstream of the waterfall through a restitution channel and discharges it downstream, further altering the river's hydrological continuity. Consequently, since then, the Coo waterfall has become a major impassable barrier to upstream fish migration, although downstream passage remains possible over the waterfall. This site has been designated as a priority by the "programme for prioritising the restoration of free fish movement in non-navigable waterways of Wallonia (Benelux Decision, 2009)" concerning the restoration of fish continuity. In 2021, to re-establish connectivity, a fishway system was installed within the restitution channel located on the left bank of the Coo waterfall. Given the significant constraints related to the considerable height of the waterfall as well as the site's tourist importance, a capture-transport type system, unique in Belgium, was chosen to effectively address the site's specific requirements.

In order to optimise the placement of the fishway entrance, preliminary studies were conducted. Between 2010 and 2013, a radio telemetry study carried out by our laboratory demonstrated that individuals exclusively used the left bank of the site. These findings initially supported the selection of the left bank for the installation of the fishway. As the restitution channel of the Coo-Dérivation hydroelectric power plant is located on this bank, an additional study was conducted between 2013 and 2014 to determine the most suitable location for the fishway entrance within the channel. Using RFID antennas deployed along the restitution canal, the study revealed that individuals were predominantly detected along the right bank of this channel. As a result, these complementary studies led to the decision to install the fishway on the right bank of the restitution channel, approximately 45 metres upstream of its outlet, with the channel itself located on the left bank of the waterfall. The system comprises two basins of the type vertical slots: one forming the entrance to the fishway and the other serving as the access point to the capture cage. This facility operates on a capture-transport basis: fish entering the fishway are captured in a cage (dimensions: 2.8 × 1.9 × 1.8 m ; length x width x height), which is manually lifted one to three times per week since the fishway was opened. After monitoring, individuals are then transported by vehicle to a release site located 450 metres upstream of the waterfall. It should be noted that, prior to the July 2021 floods, an eroded section along the right bank of the restitution channel formed a current that provided attraction flow to the fishway. This section was silted up and blocked as a result of the flood event, and no longer exists today.

The fishway became operational in 2021, restoring upstream fish migration at this previously impassable site. As a result, the Coo waterfall provides an ideal setting to investigate the full process of habitat defragmentation including conditions prior to, during, and following the restoration of longitudinal connectivity. This makes it the pilot site of the present thesis (See Chapter 3 and 5-7).

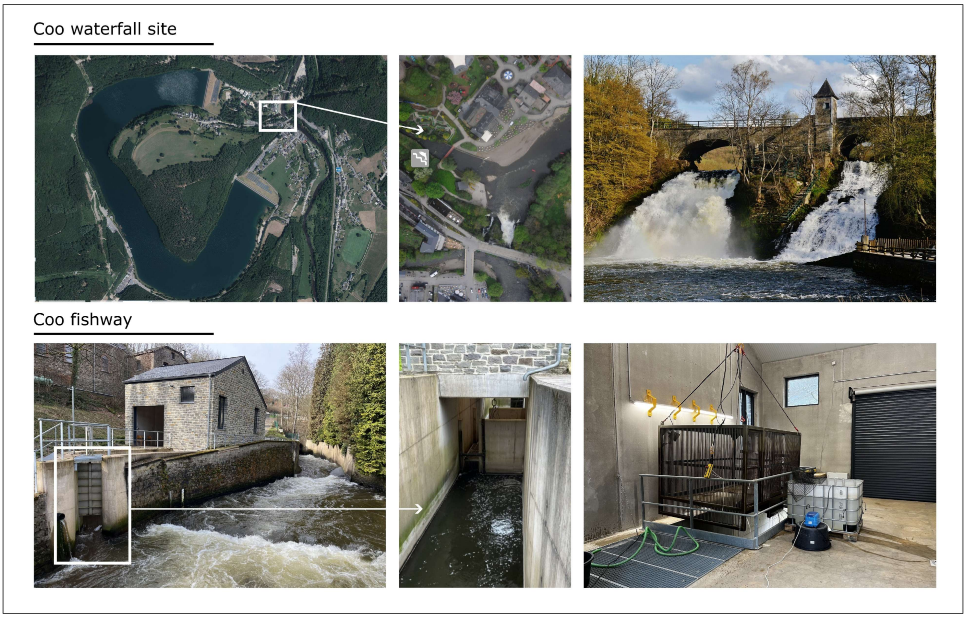

Figure 2. Overview of the Coo site with aerial views (the fishway is indicated by a grey symbol with a white fish), a view of the waterfall, and detailed images showing the entrance of the fishway and the capture cage.

Lorcé hydroelectric dam

The Lorcé dam is located 22.9 km from the confluence of the Amblève River with the Ourthe (Figure 3). It creates a reservoir with a storage capacity of approximately 50,000 m^3, which feeds a penstock situated on the left bank. This penstock supplies water to the Heid de Goreux hydroelectric power plant, located 8 km downstream from the dam and 14.9 km upstream of the Amblève–Ourthe confluence. Downstream of the dam, the Amblève flows with a minimum ecological flow of 3 m^3/s up to the Heid de Goreux hydroelectric power plant.

The Lorcé dam is composed of two mobile gates, 17 metres in length, creating a drop of delta height of 3.3 m (Figure 3). Adjacent to these regulation gates is a 3-metre-wide sector gate used for reservoir drawdown and to increase flow discharge in the event of high water or flooding. In 2007, a fishway was installed on the left bank of the Lorcé dam. The structure is a pool-type vertical slot fishway, with a total length of 67 metres and an operational discharge of 5 m^3/s. It comprises 15 pools, each separated by a water drop of approximately 0.25 m.

A capture cage (dimensions: 1.7 × 1.1 × 1.5 m ; length x width x height) is installed at the upstream end of the fishway. The cage was manually lifted one to three times per week between 2007 and 2015, with the captured fish released immediately upstream. From 2015 to 2022, the fishway was non-operational. It was returned to service in November 2022, at which point monitoring activities resumed.

The reopening of the fishway in November 2022 marked the reopening of a migratory axis that had remained closed for seven years. This site will therefore be included in the thesis for the study of certain aspects of the habitat defragmentation process (See Chapter 4 and 6-7).

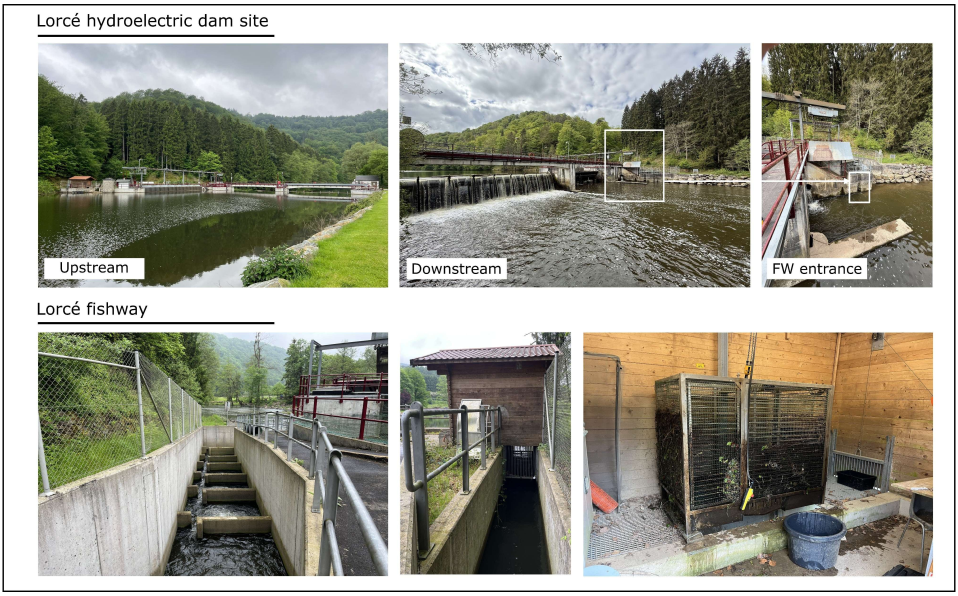

Figure 3. Lorcé hydroelectric dam site with upstream and downstream view of the dam, the fishway (FW) entrance and images showing the fishway and the capture cage.

Supplementary study sites

In addition to the sites located on the Amblève River, two additional sites situated on other rivers are also included in this thesis. Although they are not located on the same river as the pilot site, these sites offer complementary contexts in which specific components of the habitat defragmentation process can be investigated.

Berneau dam

The Berneau dam is located on the Berwinne River, a tributary of the Meuse River. The Berwinne originates near Henri-Chapelle at an altitude of 270 metres, flows over a distance of 29 km, drains a catchment area of 130.9 km^2, and has an average annual discharge of 1.9 m^3/s. The river is affected by four dams, including the one at Berneau.

The Berneau dam is a 15-metre-long concrete ramp-type structure, with a height of 1.4 metres, situated 6 km upstream from the confluence with the Meuse. It was originally built to supply water to a former mill. A pool-type vertical slot fishway was installed in 2002, with an operational discharge of 0.3 m^3/s. The structure consists of four pools, each separated by a water drop of 0.3 m. Monitoring was carried out two to three times per week between 2002 and 2008 using the upstream-most pool of the fishway, which was equipped with a cone entrance, as a capture basin (Figure 4). The data collected through this monitoring since the reopening of the migratory axis in 2002 provide valuable insights into specific aspects of the habitat defragmentation process (See Chapter 4).

Grosses-Battes

The Grosses-Battes dam is located on the Ourthe, the main tributary of the Meuse. The Ourthe originates at an altitude of 266 metres, at the confluence of the Eastern and Western Ourthe, and flows over a distance of 130 km. It drains a catchment area of 3,620 km^2 and has an average annual discharge of 67.4 m^3/s. The river is fragmented by numerous dams, including the Grosses-Battes dam, situated approximately 2.2 km upstream from its confluence with the Meuse.

The Grosses-Battes dam is a 90-metre-long ramp-type structure with a height of 4 metres. On the left bank, two mobile gates allow for flow regulation. In 2009, a fishway was installed on the left bank, replacing a previously existing Denil fishway, which had shown poor functionality. The new structure is a pool-type vertical slot fishway with an operational discharge of 0.5 m^3/s. It comprises 16 pools, each separated by a water drop of 0.25 m, and is equipped with a capture cage (Figure 4). Based on the same monitoring protocol used at other sites, capture data were collected from the opening of the fishway in 2009 until 2012. The fishway was then non-operational between 2012 and 2015, before resuming activity until the July 2021 floods, which rendered it inoperative. Monitoring was reinstated at the end of 2022 and has been ongoing since.

A second fishway was installed on the right bank in 2020, as part of the construction of a hydroelectric power plant equipped with two Kaplan-VLH turbines. This structure is also a pool-type vertical slot pass and includes a capture trap, which has been monitored since its commissioning. In this thesis, only the left-bank fishway, installed in 2009, is considered for the study of selected aspects of the habitat defragmentation process (See Chapter 4).

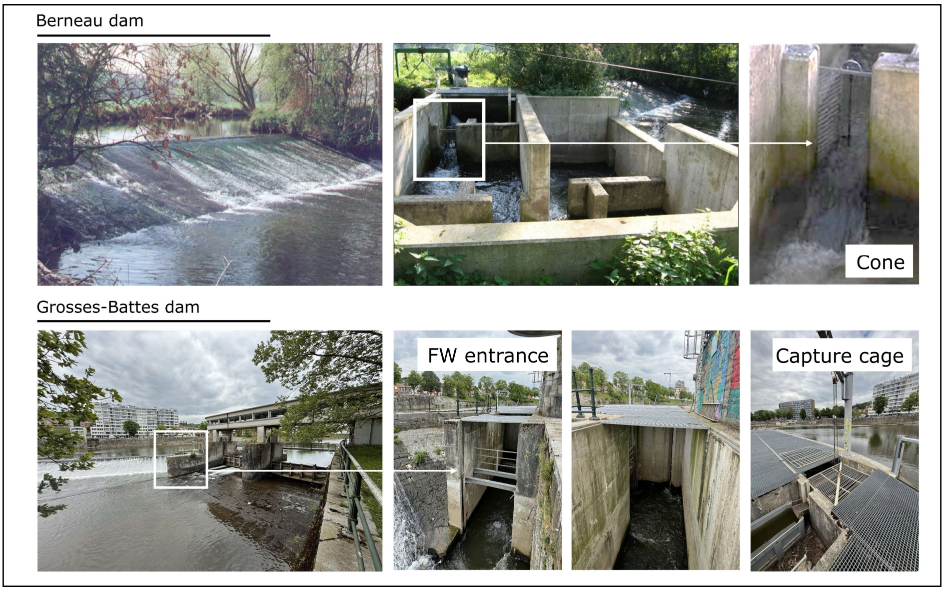

Figure 4. Berneau dam and Grosses-Battes dam site with the fishways and capture systems (basin with cone and cage).

Methodologies used

Fishway monitoring

As part of this thesis, the use of fishways at the different study sites was assessed through capture trap monitoring. Two types of methodologies were implemented for fish capture: the use of a capture cage, or the adaptation of the upstream-most pool of the fishway into a capture basin.

At the fishway of Berneau (Berwinne), the uppermost pool of the fishway was used as a capture basin. In this configuration, a mesh screen was installed at the upstream outlet of the pool to prevent fish from progressing further, while a cone was placed at the downstream end to stop them from swimming back. During monitoring operations, the water level in the fishway was lowered, allowing fish to be captured using a landing net (See Chapter 4).

In the other sites, the method involved the use of a capture cage (Figure 5), placed in the upstream-most pool of the fishway. The cage was fitted with a downstream-facing cone at its entrance to prevent fish from escaping once inside. During monitoring operations, a grid was lowered downstream of the cage to prevent new individuals from entering while the cage was being handled. The cage was then lifted using a hoist, either manually or electrically operated. Fish were removed from the cage either with a landing net through the access door or by opening the evacuation hatch. This method was used at the sites of Coo, Lorcé, and Grosses-Battes (See Chapter 3-4 and 6-7).

All captured fish were first placed in a holding tank before being transferred to an anaesthetic bath containing eugenol (0.2 mL/L). After species identification, biometric data were recorded for each individual, including weight (g), fork length (mm), and sex. The fish were then placed in a recovery tank filled with river water before being released upstream of the obstacle.

Electrofishing surveys

Electrofishing is a method used for various purposes, including fish population surveys and the targeted capture of individuals belonging to one or more specific species.

This technique can be conducted either on foot or from a boat (Figure 5), depending on the characteristics of the river section to be surveyed. It is based on the generation of an electric current by a fixed generator installed on the riverbank or mounted on a boat. A cathode, connected to the generator, is immersed in the water, while an anode, also submerged, is manually operated to close the electric circuit. The anode produces a low-range electric field (a few metres), which induces forced swimming behaviour in fish towards the anode. Once within a few centimetres of the anode, the fish enter a state of electronarcosis and are then caught with a landing net and placed in holding tanks filled with fresh water.

For inventory by electrofishing, all individuals encountered are captured. A 150-metre stretch of river is surveyed twice. Fish captured during the first passage are kept in holding tanks to avoid recapture during the second passage. All individuals are then anaesthetised using eugenol (0.2 mL/L), identified, sexed, weighed (g), and measured for fork length (mm). After these procedures, the fish are transferred to a recovery tank containing river water before being released back into the surveyed section. This protocol provides insight into fish biodiversity and population status within the river.

It is also possible to carry out targeted electrofishing, aimed at capturing only individuals belonging to specific species. In such cases, the length of the surveyed section varies depending on the number of individuals needed, although the general methodology remains the same. Only the targeted individuals are captured and processed according to the same protocol.

Both approaches were implemented at the Coo site (See Chapter 3 and 5).

Biotelemetry

Biotelemetry encompasses all techniques used to monitor living organisms, in this case, fish, based on the use of implanted electronic devices. These devices, whether active (transmitters) or passive (transponders), emit a radio, acoustic, or electromagnetic signal that can be detected remotely by fixed or mobile receivers, thereby allowing the individual to be located or detected without direct disturbance. In the context of this thesis, fish were first captured either by electrofishing or using a capture cage installed within a fishway. Two types of biotelemetry devices were used: a passive RFID device (PIT tag) and an active device emitting radio signals.

Passive RFID

Passive RFID biotelemetry involves the use of transponders (Texas Instruments PIT tags) measuring 23 × 3 mm and weighing 0.7 g, with an unlimited lifespan (Figure 5). These tags are classified as passive devices, meaning they are only activated in the presence of a magnetic field that is originating from an antenna or a mobile detector. Upon activation, the transponder transmits its unique identification code, and the date and time of detection are also recorded. These data are automatically sent to a recording unit connected to the antenna, enabling continuous monitoring 24 hours a day, 7 days a week. Data can then be downloaded via USB. Detection antennas vary in size depending on site configuration, and may be positioned either vertically or horizontally on the riverbed. However, due to the limited detection range of passive RFID systems (typically 0.1 to 1 metre), individuals must pass in close proximity to the antenna to be detected. Prior to tagging, individuals are anaesthetised using eugenol (0.2 mL/L). A 5 mm incision is made with a scalpel in the intraperitoneal cavity to insert the transponder (Ovidio et al., 2017). This procedure does not require sutures, and fish are directly released, after the recovery phase in an oxygenated water tank (See Chapter 3).

Radio telemetry

Radio telemetry is an active biotelemetry method involving the surgical implantation of a radio transmitter equipped with an electronic circuit, a battery and an antenna into the body cavity of fish. The size of the transmitter depends on the target species and the duration of the study, with larger transmitters offering a longer battery life and a wider detection range (Figure 5). To minimise potential impact on the fish, the transmitter weight must not exceed 2.5% of the fish's total body weight (Ovidio et al., 2020). Fish are first anaesthetised using Eugenol (0.2 mL/L) in a water tank and then placed in a tagging cone. An incision of 0.8 to 2 cm is made in the intraperitoneal cavity, just behind the pelvic fins, using a scalpel. The external antenna is guided out laterally through a cannula. The incision is then closed with two to three absorbable sutures (Vicryl) and disinfected with Isobetadine. Fish are subsequently placed in a recovery tank for approximately 20 minutes before being released.

Once tagged, individuals can be tracked using their specific transmission frequency (in this study: 40.000–41.999 MHz and 48.000–49.999 MHz). The radio signals emitted propagate through the aquatic environment and are detected using a receiver connected either to a fixed automatic antenna (submerged or aerial) or to a handheld mobile antenna. Fixed antennas, installed at strategic locations, automatically record the identity of detected individuals along with the date and time of detection. Mobile antennas are used during manual tracking campaigns to precisely localise individuals through point-based detections. Two types are used: (i) whip antennas, mounted on vehicles for long-range detection; and (ii) directional antennas, operated on foot, which enable precise localisation through biangulation or triangulation based on two or three location taken along the riverbank (Figure 5). The intersection of these location indicates the estimated position of the fish, with signal intensity increasing as the receiver approaches the individual.

In the case of manual mobile tracking, each individual was located the day after release and subsequently tracked at a frequency of 2 to 7 times per week, depending on the time of year. During the winter period, tracking was reduced due to limited fish movement. In contrast, during the spring, particularly the spawning period, tracking effort was increased to account for greater mobility.

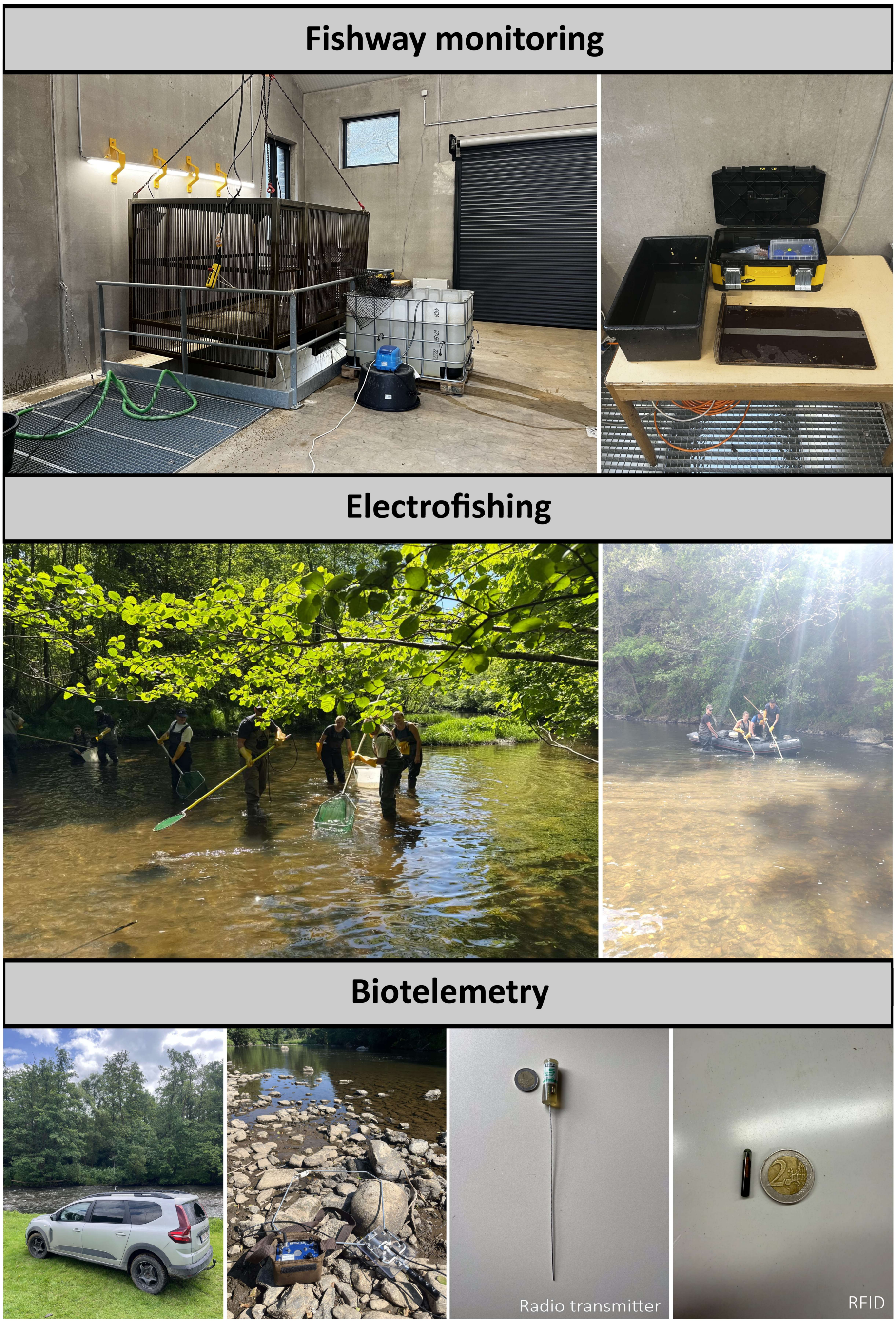

Figure 5. Methodologies used : Fishway monitoring (capture cage and biometric measurement equipment), electrofishing surveys (on foot and from a boat) and biotelemetry (radio transmitters and RFID tags with whip and directional antennas).

In this thesis, individuals were double-tagged during :

- Electrofishing campaigns conducted upstream of the Coo site. Fish were double-tagged with passive RFID and radio transmitters, enabling automated detection via fixed antennas (both radio and RFID) and manual tracking using handheld directional antennas two to third time per weeks (See Chapter 5).

- Capture-trap monitoring at the Coo and Lorcé sites. The individuals were double-tagged with both a passive RFID tag and a radio transmitter, allowing for automated detection via fixed antennas and manual tracking with handheld directional antennas. Manual tracking was conducted between two and seven times per week (See Chapter 6 and 7).

Species as ecological models of movement behaviour and ecology

Barbel (Barbus barbus)

The barbel (*Barbus barbus*) is a cyprinid rheophilic species (Figure 6), exhibiting a marked preference for moderately fast-flowing river sections with coarse substrates such as gravel and cobbles. It inhabits well-oxygenated waters and avoid both stagnant or low-flowing areas and torrent-like sections characteristic of trout zones. Barbel typically occur in flows ranging from 3 to 110 cm/s and depths from 0.17 m to over 1 m (Baras, 1992; Lamouroux et al., 1999), with a preference for depths between 0.05 and 0.8 m and flow velocities below 40 cm/s (Boavida et al., 2013; Capra et al., 2012). Juveniles generally use habitats with lower current velocities and shallower depths (Bischoff & Freyhof, 1999). This species is omnivorous and gregarious, with adult individuals typically measuring between 400 and 600 mm and weighing between one and three kilograms. Adult females tend to reach larger sizes and greater body mass than males (Baras, 1998; Gelder et al., 2024b; Panchan et al., 2022). The species is considered adult from a size exceeding 250 mm and has an estimated lifespan of 20 to 25 years.

The barbel's daily home range generally extends between 0.5 and 5 km (Baras, 1997; Gelder et al., 2024b; Popp et al., 2024). However, this range can expand substantially during spawning migrations, with individuals covering distances of several tens or even hundreds of kilometres. Notably, studies have documented upstream movements ranging from 20 to 40 km (Capra et al., 2018; De Leeuw & Winter, 2008; Ovidio et al., 2007; Panchan et al., 2022), and in some cases, migrations can even reach up to 155 km (Tétard et al., 2025). These findings highlight the species' capacity for long-distance movements.

As a lithophilic species, barbel spawn on shallow areas and well-oxygenated coarse substrates (such as cobbles and gravel), where non-adhesive eggs are buried in the substrate. The spawning period extends from April to June, when water temperatures exceed 14 °C and photoperiod increases (Baras et al., 1994; Benitez & Ovidio, 2018; Lucas & Baras, 2001; Ovidio et al., 2007; Pelz et al., 2025). During this period, individuals undertake upstream spawning migrations. These movements are often pronounced and involve an increase in displacement range. After spawning, individuals migrate downstream to return to their previous habitats, exhibiting a homing behaviour. Males tend to remain longer on the spawning grounds than females, likely to maximise mating opportunities (Lucas & Batley, 1996)

Barbel are well known for their site fidelity. Some studies have also reported interannual fidelity to specific spawning sites, although this behaviour is not consistent across all individuals (Baras & Cherry, 1990; Gelder et al., 2024b; Lucas & Baras, 2001; Ovidio et al., 2007; Panchan et al., 2022; Pelz et al., 2025). A second migratory phase occurs in autumn, when temperatures and photoperiod decrease. This movement leads individuals to overwintering habitats, typically located in deeper areas (Benitez & Ovidio, 2018; Gelder et al., 2024b; Lucas & Baras, 2001).

Due to its ecological preferences matching the typical habitats of the Amblève River in the studied sections, its mobility, the extensive knowledge available on its behaviour in natural conditions, its size reducing predation risk, and its sensitivity to habitat quality, the barbel represents a relevant biological model for the present study (See Chapter 5-7).

Chub (Squalius cephalus)

The chub (*Squalius cephalus*) is a gregarious, omnivorous cyprinid species, eurytopic with a tendency towards rheophilic (Figure 6). It selects moderately flowing, well-oxygenated river sections and is mainly found in the grayling and barbel zones. It can also occur, though less abundantly, in the lower part of the trout zone and the upper part of the bream zone, reflecting its broad habitat tolerance. Chub prefer depths ranging from 0.05 to 0.8 m and flow velocities below 35 cm/s, although they can also occasionally be found in areas with current velocities exceeding 80 cm/s, with juveniles generally using even shallower areas with lower current velocities (Arlinghaus & Wolter, 2003; Capra et al., 2012; Fredrich et al., 2003; Lamouroux et al., 1999). Adult individuals generally measure between 300 and 500 mm in length and weigh between 0.5 and 2 kg. The species is considered adult from a size exceeding 160 mm and can reach a lifespan of 15 to 20 years.

Spawning takes place in spring, generally from April to June, when water temperatures exceed 14°C and photoperiod increases (Benitez & Ovidio, 2018; Gutmann Roberts & Britton, 2020; Lucas & Baras, 2001; Prchalová et al., 2011). The chub is a lithophilic species, depositing its slightly adhesive eggs, without burying them, on coarse substrates (gravel, pebbles) in well-oxygenated shallow areas. It therefore uses spawning habitats similar to those of the barbel. Spawning can be fractional, meaning that females release their eggs over several episodes rather than all at once (Benitez et al., 2015; Fredrich et al., 2003; Gutmann Roberts & Britton, 2020). During the spawning season, individuals undertake upstream spawning migrations, sometimes covering distances of around ten kilometres to reach spawning sites (Fredrich et al., 2003). After spawning, adults return to their original habitats, exhibiting homing behaviour comparable to that observed in barbel (Allouche et al., 1999; Capra et al., 2018; Fredrich et al., 2003). The chub is, however, less demanding in terms of habitat conditions and displays a degree of ecological plasticity (Benitez et al., 2018; Fredrich et al., 2003; Pander et al., 2015).

The chub has a median home range of 2.3 km (Capra et al., 2018), typically ranging from 0 to 15 km (De Leeuw & Winter, 2008; Fredrich et al., 2003), with daily movements between 0 and 0.5 km (Allouche et al., 1999; Fredrich et al., 2003). However, movements exceeding 25 km have also been reported (De Leeuw & Winter, 2008; Tétard et al., 2025).

For these reasons, similar to those outlined for the barbel, such as its mobility and ecological characteristics suited to the conditions of the Amblève River, the chub also represents a relevant biological model for studying habitat defragmentation processes in the present thesis (See Chapter 6 and 7).

Grayling (Thymallus thymalllus)

The grayling (*Thymallus thymallus*) is a rheophilic, carnivorous salmonid species with gregarious behaviour, feeding primarily on invertebrates (Figure 6). It inhabits well-oxygenated rivers with moderately fast currents, generally ranging from 20 to 110 cm/s, and water depths varying between 0.08 and 4 m with adults typically occupying deeper and faster-flowing areas compared to juveniles (Mallet et al., 2000; Nykänen et al., 2001, 2004; Riley & Pawson, 2010; Vom Berge et al., 2025). Grayling are typically found in the grayling zone, as well as in the lower part of the trout zone and the upper part of the barbel zone. They favour substrates composed of stones and gravel. Individuals are considered adult once they exceed a length of 240 mm. On average, adults measure between 300 and 400 mm and weigh between 0.5 and 1 kg. In Belgium, the species has a lifespan of up to six years.

Spawning takes place between March and April, when water temperatures reach approximately 8 °C. During this period, individuals migrate upstream to reach their spawning sites (Benitez et al., 2015; Kodela et al., 2023). The grayling is a lithophilic species, reproducing in shallow areas with coarse substrates, where eggs are buried in the substrate. Once spawning is complete, individuals return to their original habitats, exhibiting homing behaviour similar to that observed in chub and barbel (Ovidio et al., 2004; Parkinson et al., 1999).

The grayling has a median home range of around 8 km (Junge et al., 2014), with average daily movements generally below 0.2 km. During the spawning period, individuals generally move less than 5 km (Gelder et al., 2024b; Ovidio et al., 2004; Parkinson et al., 1999), although movements ranging from 5 to 15 km have also been reported (Jungwirth et al., 2000; Nykänen et al., 2001). However, some studies have documented individuals with home ranges exceeding 60 km (Junge et al., 2014).

Classified as highly vulnerable during the 1970s and subject to a fishing ban since 2021 under a decree by the Walloon Government, the European grayling is currently listed as “Endangered” on the IUCN Red List for Wallonia. Although still classified as “Least Concern” on the global IUCN Red List, the species is in decline across Europe. For this reason, the grayling represents a species of particular interest for the study of habitat defragmentation processes (See Chapter 5-6).

Brown trout (Salmo trutta)

The brown trout (*Salmo trutta*) is a rheophilic salmonid species with solitary behaviour (Figure 6). Its diet is carnivorous, with invertebrates as its primary food source. It shows a strong preference for well-oxygenated habitats, typically found in the trout and grayling zones. Although most abundant in fast-flowing, oxygen-rich environments, it can inhabit a wide range of watercourses, from mountain torrents to larger rivers. Brown trout generally occur at depths ranging from 0.3 to 0.9 m, although they have been observed at depths exceeding 2 m (Schneider, 2000), and at flow velocities typically from 20 to 100 cm/s (Vismara et al., 2001). Juveniles tend to prefer shallower areas with lower current velocities compared to adults (Greenberg et al., 1996; Vismara et al., 2001). Adults typically measure between 250 and 500 mm in length and weigh between 0.2 and 1 kg. The species is considered mature from a size of approximately 250 mm and can live for 4 to 6 years in natural environments.

Spawning takes place in autumn, generally from November to January, when water temperatures range between 6 and 8 °C and photoperiod decreases (García-Vega et al., 2018, 2022). The brown trout is a lithophilic species that reproduces by burying its eggs in well-oxygenated, gravelly, fast-flowing areas. It is also known to use tributaries and sub-tributaries of main rivers as spawning habitats

(Ovidio et al., 1998; Piecuch & Lojkásek, 2007). After spawning, individuals generally return to their original habitats, exhibiting homing behaviour similar to that observed in the previously described species (Ovidio, 1999).

Brown trout exhibit average daily movements ranging from 0.2 to 4 km (Armstrong & Herbert, 1997; Heggenes et al., 2007; Höjesjö et al., 2007; Ovidio, 1999) and while movements exceeding 15 km are typically associated with the spawning period (Gelder et al., 2024b; Ovidio, 1999; Ovidio et al., 1998; Ovidio & Philippart, 2002; Zimmer et al., 2010), they may also occur outside of spawning, as highlighted by Ovidio and Philippart (2002).

Due to its use of tributaries and sub-tributaries for spawning and its well-documented migratory behaviour, the brown trout represents a relevant biological model for the present study (See Chapter 5-6).

Nase (Chondrostoma nasus)

The nase (*Chondrostoma nasus*) is a rheophilic cyprinid species (Figure 6), with a mainly herbivorous diet, feeding primarily on algae together with the insects associated with them (Nelva, 1997). This species is found in the barbel and grayling zones (Rakowitz et al., 2008), but can also occur in the bream zone (Benitez et al., 2022; Ovidio et al., 2023), inhabiting preferably areas with current velocities ranging from 50 to >100 cm/s, depths greater than 2 m, and substrates composed of gravel and stones (Ovidio & Nzau Matondo, 2024). Juveniles are generally found in habitats with weaker currents and shallower depths. Adults reach an average size of 400 mm, with some individuals growing up to 600 mm and living up to 25 years (Ovidio & Nzau Matondo, 2024; Philippart, 1980).

Its spawning period takes place in spring, between March and May, when flow decreases and water temperature rises to between 7.5 and 12.5 °C (Ovidio & Philippart, 2008; Rakowitz et al., 2008). The nase is a lithophilic species without egg burial, with females laying their eggs directly on the substrate, preferably in well-oxygenated areas with coarse materials (7–10 cm in diameter). Before spawning, adults undertake large upstream movements, and a post-spawning behaviour is also observed as they return to their original habitats afterwards (Gelder et al., 2024b; Panchan et al., 2022).

The nase has a home range of around ten kilometres on average (Gelder et al., 2024b; Ovidio & Philippart, 2008; Panchan et al., 2022), but can also travel much longer distances, with movements of more than 25 km (De Leeuw & Winter, 2008), and up to 140 km reported in the literature (Ovidio & Nzau Matondo, 2024), including exchanges between the main river and its tributaries (Panchan et al., 2022).

Due to its characteristics, this species is considered a good indicator of habitat quality and a species of interest (Ovidio & Philippart, 2008). Furthermore, its long-distance movements reported in the literature may be impacted by the various obstacles present in rivers, making it a suitable biological model for this study (See Chapter 6).

Figure 6. Fish species studied for movement behaviour : brown trout, grayling, nase, barbel and chub. (Photo: Jean-Philippe Benitez-UGERAA ULiège)

Chapter 3. Initial state of fish communities prior to the opening of a migratory axis and their response to defragmentation

JOURNAL OF ECOHYDRAULICS
https://doi.org/10.1080/24705357.2025.2523799

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

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Abstract

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

Keywords: defragmentation; fishway; potamodromous species; electrofishing; monitoring

Introduction

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

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

Although many watercourses have been defragmented, relatively few studies have been conducted following this defragmentation (Poff & Hart 2002; Jones et al. 2022; Gelder et al. 2024b). Most studies have focused on the physical aspects (e.g., flow, temperature, sediment) or on the effectiveness of the fishway, with few studies concentrating on the ecological aspect, taking into account changes in fish communities (Bellmore et al. 2017; Cook & Sullivan 2018; Romão et al. 2018; Dębowski et al. 2022; Gelder et al. 2024a). In addition, few studies include data on the initial state of fish populations prior to site defragmentation, which would enable a complete before and after analysis of habitat defragmentation

(Bower et al., 2024; Jones et al., 2022; Tummers et al., 2016a). When installing a fishway, it is interesting to include monitoring of individuals using a telemetry device (Panagiotopoulos et al., 2024). Several studies have highlighted the use of the fishway and the dynamics of individual colonisation towards newly available habitats (Benitez et al., 2022; Gelder et al., 2023; Legrand et al., 2020). However, the performance of these facilities requires rigorous evaluation. With the increasing number of crossing devices being installed, it seems important to have an overall view of fish population evolution compared to the initial state in order to determine the impact of defragmentation on fish populations.

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

Materials and Methods

Study area and monitoring

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

Monitoring of the capture cage started on 15 March 2021 and continued at intervals of one to four times per week. The monitoring frequency increased during periods of intense migration and decreased during periods of low captures. Fish captured in the cage were identified at the species level, weighed (± 1 g) and measured (± 1 mm, fork length) after anaesthesia (Eugenol, 0.1 mL L^{-1}). Non-chipped individuals over 200 mm in length were marked with a radio frequency identification (RFID) tag in the intraperitoneal cavity in order to identify them for potential recaptures. The individuals were then placed in a tank of water with oxygen to recover (+/- 20 min). After recovery, the fish were manually transported in oxygenated tanks using a vehicle and released into the main river channel with a tank, 500 m upstream of the waterfall, at a sufficient distance from the inlet channel to ensure they remained in the natural river flow. The release site provides sufficient depth, moderate current, and the presence of rocks offering shelter. All fish were released the day of capture, with no holding period beyond recovery. This protocol ensured a rapid release to minimise stress.

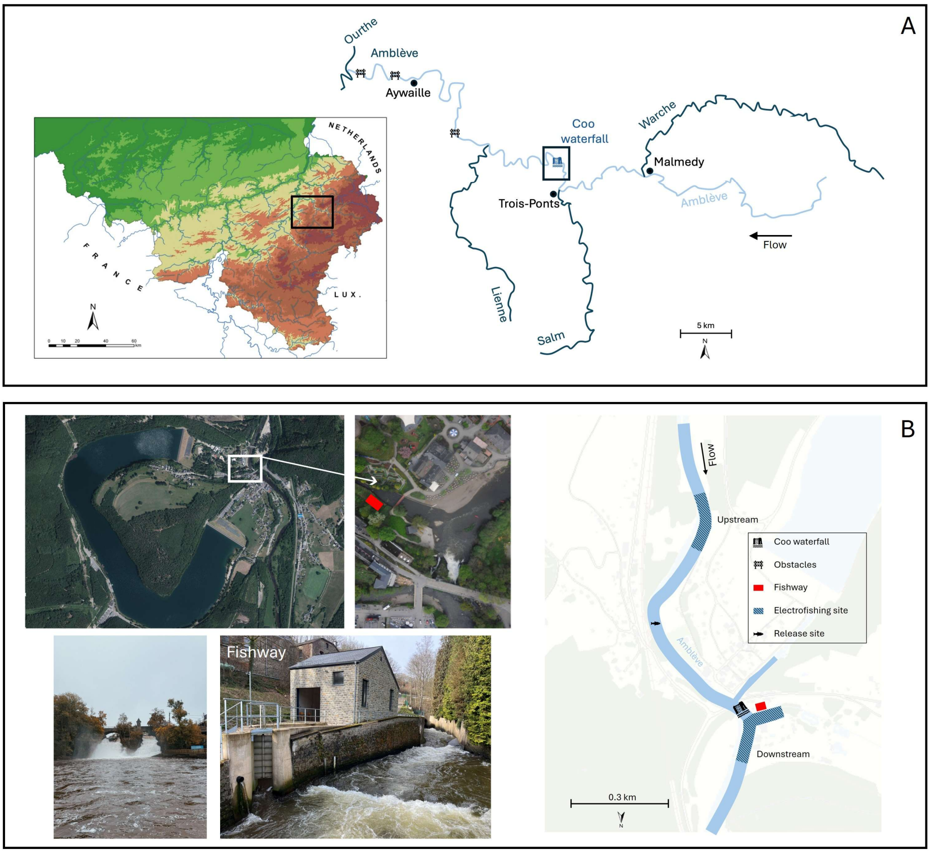

Figure 1. Maps of the Amblève River with the Coo waterfall (A). Pictures showing aerial views of the Coo site, the waterfall, the fishway, and schematic representation of the electrofishing sites and the fish release point upstream (B).

Electrofishing and fish inventories

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

Data analysis

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

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

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

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

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

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

Results

Initial status of populations upstream/downstream

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

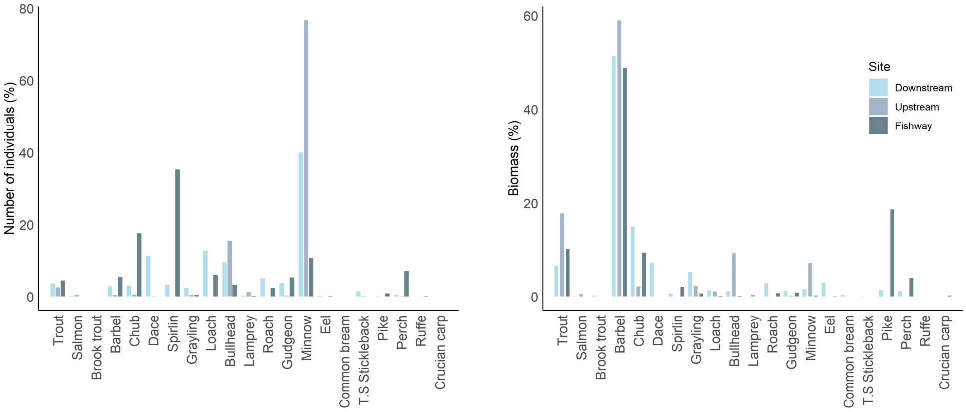

Figure 2. Proportion of the number of individuals captured and the biomass by species (%) upstream and downstream of the waterfall before the opening of the migratory axis and in the fishway.

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

Table 1. Alpha diversity index with species richness (S), Shannon–Wiener diversity index (H'), Simpson's diversity index (Ds), Pielou's index (J) and beta diversity with Bray–Curtis dissimilarity index (DBC) for upstream, downstream and fishway populations. Ds, J and DBC ranged from 0 to 1. ^{a}After the opening of the migratory axis.

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

Use of the fishway and comparison with downstream populations

Since the opening of the fishway on 15 March 2021, 17 species and 2,328 individuals have been captured in the capture cage for a total biomass of 333.7 kg. The fishway was used by a diverse and equitably distributed community (H' = 2.02, D_s = 0.81 and J = 0.71; Table 1). Over the three years, the community was consistently dominated by rheophilic species, which represented more than 70% of the total individuals captured each year (82.7% between 2021 and 2022, 72.4% between 2022 and 2023 and 72.7% between 2023 and 2024). The most abundant species was the barbel between 2021 and 2022 (n = 69), the spirlin between 2022 and 2023 (n = 766), and the loach between 2023 and 2024 (n = 89).

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

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

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

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

The cumulative frequency of fish captured during the three consecutive years of monitoring showed that trout was homogeneously captured over the monitoring period (Chi^2 test, $p > .05$). The other species had a heterogeneous capture distribution: barbel, chub, spirlin, grayling, loach, bullhead, roach, gudgeon, minnow, pike and perch (Chi^2 test, $p < .05$). Pike and barbel reached 50% of their capture in the first year of monitoring, after 17 and 42 days of monitoring, respectively. Several species reached 50% of their capture during the second year of monitoring: the grayling (after 83 days), the trout (after 115 days of monitoring), the chub (after 144 days), the spirlin (after 128 days), the bullhead (after 105 days), the roach (after 151 days), the gudgeon (after 123 days), the minnow (after 92 days) and the perch (after 144 days). The loach had 50% of their capture in the last year of monitoring, after 188 days of monitoring (Figure 3).

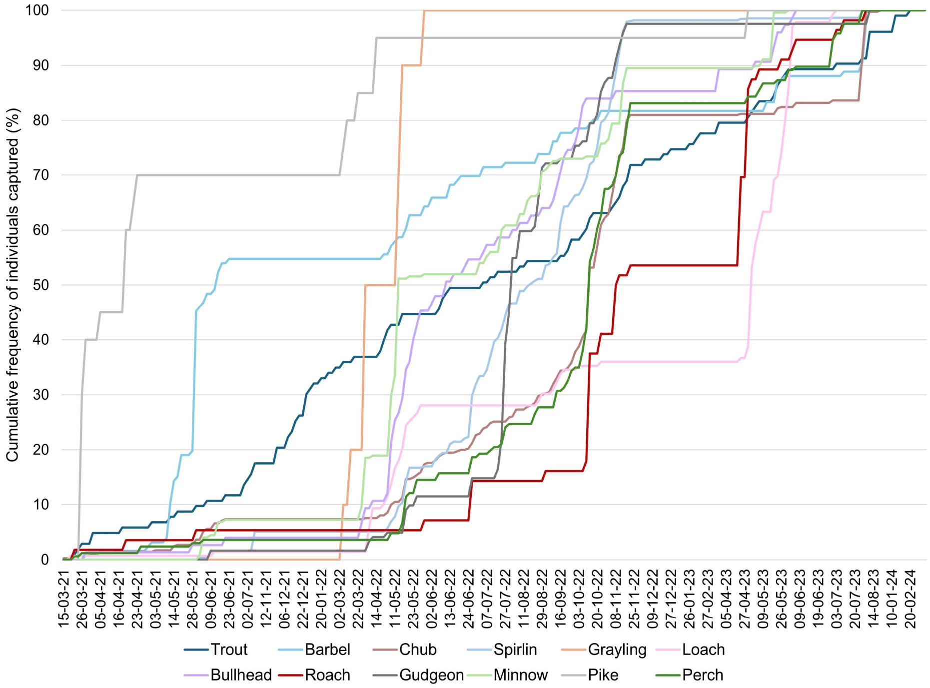

Figure 3. Cumulative frequency of individuals captured (%) per species according to the monitoring days during three consecutive years.

The periodicity of fish captured showed that some species were captured evenly throughout the year, while other species had peaks at specific times. Trout were captured throughout the year, with the highest capture rate in May (n = 16.5%). Some species (chub, spirlin, perch, roach and gudgeon) were not or poorly captured during the winter (December, January and February) but were captured during the rest of the year with the highest capture rates in July (spirlin = 18.1% and gudgeon = 30.3%) and October (chub = 25.1%, roach = 25% and perch = 32.5%). We observed that other species had capture peaks at specific times of the year, like the barbel, the loach, the bullhead and the minnow, with 57.1%, 61.1%, 44% and 43.1%, respectively, of the capture rate in May. The pike was mainly captured in March and April, with 55% and 40%, respectively, of captures, and only adults were captured.

The periodicity with which juveniles were captured was significantly different from that of adults for the barbel, the chub, the grayling, the bullhead, the minnow and the perch (Mann–Whitney test, p < .05). The highest captured rate of juveniles occurred during the autumn for chub (n = 21.2% in October), spirlin (n = 16.8% in November), gudgeon (n = 9.8% in November) and minnow (n = 12.9% in November). The barbel and the grayling had their highest number of juvenile captures in summer, with 12.7% in August and 40.0% in May, respectively. Most of the roach captured were juveniles, with the highest captured rate in May (n = 21.4%; Figure 4).

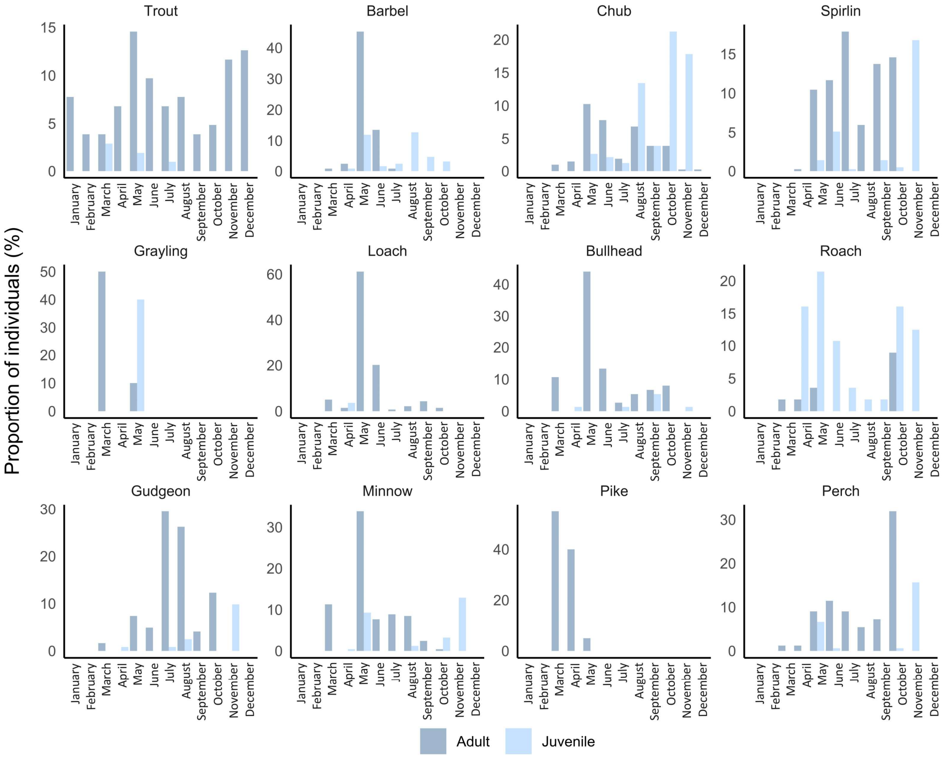

Figure 4. Histograms of the periodicity of captures throughout the year (by months) expressed as a percentage of individuals captured for each species (trout, barbel, chub, spirlin, grayling, loach, bullhead, roach, gudgeon, minnow, pike and perch) with a distinction between adults and juveniles.

Analysis of the sizes of the individuals captured showed that the median size of the individuals captured during the first year of monitoring (2021–2022) after the opening of the migratory axis was very significantly greater than the median size of the individuals present downstream for all species (Dunn test, $p < .001$): the barbel, 494 mm and 372 mm; the chub, 222 mm and 115 mm; and the trou,t 324 mm and 197 mm, respectively. The median size of individuals for barbel and chub was also significantly greater in 2021–2022 than in the following two years (2022–2023 and 2023–2024), with 208 mm for barbel and 146 mm for chub in 2022–2023 and 117 mm for babel and 148 mm for chub in 2023–2024. Although the median sizes of the trout were smaller in 2022–2023 (263 mm) and 2023–2024 (225 mm) compared to the first year, a significant difference was only observed between 2021–2022 and 2023–2024 (Dunn test, $p < .01$; Figure 5).

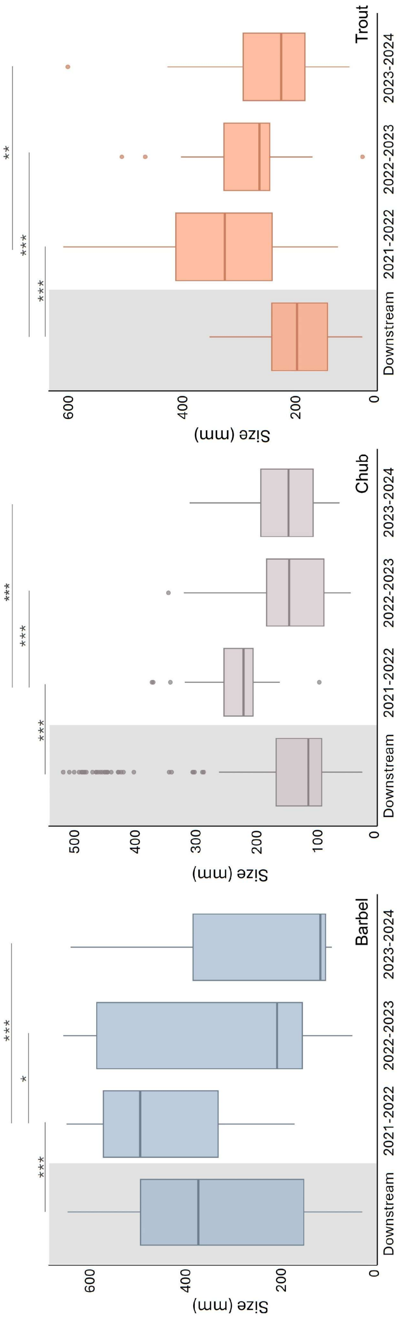

*Figure 5. Size distribution of individuals captured downstream of the waterfall before the opening of the migratory axis (grey background) and individuals captured within the fishway during the three years following the opening of the migratory axis. The horizontal line inside the triangle is the median,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

Discussion

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

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

As upstream migration was previously impossible, the recolonisation of species absent upstream and present downstream could not occur. Given that the removal of the Coo waterfall is not an option, recolonisation was only achievable through the installation of a crossing device. The installation of the fishway has enabled upstream movements to be re-established. Ideally, the entrance to the fishway would be located directly adjacent to the obstacle. However, due to topographic and landscape constraints, it was positioned 100 m away on the left bank of the waterfall. Despite this suboptimal placement, results demonstrated that more than 2,000 individuals from 17 of the 20 downstream species used the fishway and used new habitats available upstream, as shown by the four individuals recaptured upstream during electrofishing. However, a complementary study by Gelder *et al.* (2024a) estimated the efficiency of the fishway at 7.9%, suggesting that the quantity of fish using the fishway underrepresents the real number of fish attempting to migrate upstream. Nevertheless, the structure is used by a wide range of species, confirming its multi-species functionality, and discussions are ongoing to improve its overall efficiency. In addition, the populations using the fishway were significantly correlated with those downstream, confirming that the fishway effectively facilitates upstream migration of the established population (Tan et al., 2024). The fishway was mainly used by rheophilic species, which is consistent with the habitat characteristics of this sector of the Amblève River.

The results also showed that the spirlin was the most abundant species captured during the second year of monitoring, with 766 individuals. This capture peak could potentially reflect the capture of a migrating school of this gregarious species, which may contribute to interannual variation in fishway use (Prchalová et al. 2011; Benitez et al. 2015). No spirlin were captured during electrofishing upstream of the waterfall prior to the opening of the migratory axis, underscoring the fishway's role in enabling the recolonisation of species previously absent upstream (Kiffney et al., 2018; Tummers et al., 2016a). In terms of biomass, total biomass decreased from year to year, with the highest total biomass during the year following the opening of the migratory axis, which suggests an opening effect (Benitez et al. 2015). Although spirlin and loach were captured in much higher numbers over the last two years of monitoring compared to barbel (766 spirlin vs. 34 barbel between 2022 and 2023 and 89 loach vs. 23 barbel between 2023 and 2024), underlining the importance of the multi-species nature of the fishway, barbel accounted for the highest biomass each year due to their larger size. Chub were also captured in large numbers, but the average size of these individuals indicated that they were mostly juveniles (mean size ≤ 160 mm), while the barbel were, on average, adults (mean size ≥ 250 mm). The abundance and biomass of some species decreased over the monitoring period, while for others, the biomass and abundance fluctuated from year to year. This trend was also shown by the cumulative frequency of individuals captured which showed that for some species an opening effect has been visible, such as for barbel and pike, which reached 50% of their captures in the first year. The barbel is a species known in the literature to move regularly and over great distances (Ovidio et al. 2007; Le Pichon et al. 2016). What we observed for pike can be associated with quick colonisation, with 17 individuals captured in the first year of monitoring, followed by a large decrease in the number of individuals captured in the next two years (Gelder et al., 2023). The majority of species (grayling, trout, chub, spirlin, bullhead, roach, gudgeon and minnow) reached 50% of their captures during the second year, and the loach reached this during the last year of monitoring. Except for trout, which were homogeneously captured throughout the year, the other species showed notable variations in their captures from one year to the next. Captures can fluctuate based on environmental conditions. Although we did not analyse the temperature and flow data as part of this study, it is likely that environmental conditions during 2022–2023 and 2023–2024 were favourable for stimulating the migration of these species and consequently increased the number of fish captured. Fishway monitoring over several consecutive years has enabled us to analyse in greater detail the colonisation dynamics of fish populations on a multi-annual scale, as well as on a seasonal scale.

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

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

Chapter 4. What happens when a migratory axis is opened? Colonisation dynamics of fish populations

Knowl. Manag. Aquat. Ecosyst. 2023, 424, 12
© J. Gelder *et al.*, Published by EDP Sciences 2023
https://doi.org/10.1051/kmae/2023009

www.kmae-journal.org

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Journal fully supported by Office
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Multi-year analysis of the fish colonisation dynamic in three newly installed fishways in medium sized Belgian rivers

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Received: 6 January 2023 / Accepted: 18 April 2023

Abstract

The temporal dynamic use of newly installed fishways after a reopening event is not well known as most studies are not performed just after the opening and are generally limited to a single season or year. We carried out monitoring of three fishways for several consecutive years on three rivers in Belgium from the date of their opening. To identify the colonisation dynamics of fish species, we analysed temporal patterns in specific diversity, abundance, biomass, and associated environmental conditions. We detected different capture peaks and the appearance of new species several years after opening the migratory axis (up to 8 years post-opening). The dynamic of colonization showed that the same species may migrate earlier or later depending on the river. The analysis of the periodicity of capture indicated that some species made movements throughout the year while others at more precise periods. Moreover, the periodicity of movements was either stable or fluctuating over the year of monitoring, depending on the species. Our results highlight the importance of long-term monitoring to detect temporal dynamics in fish colonisation, allowing to improve our understanding of the opening effect of a migratory axis.

Keywords: monitoring; fishes; river; restored connectivity; temporal trend; migratory axis

Introduction

Freshwater ecosystem fragmentation is recognised as one of the most impactful on the aquatic resources, affecting habitat connectivity on multiple spatial and temporal scales and leading to reduced species geographical distribution and/ or communities and populations isolation (Carpenter et al., 2011; Consuegra, 2021; Legrand et al., 2020; Ovidio et al., 2020; Romão et al., 2018). As freshwater fish must disperse or migrate throughout the year to access breeding, feeding and refuge habitats, populations are largely impacted in terms of their structure, migration, recruitment or spawning success by physical obstructions (Benitez et al., 2022; Grimardias et al., 2022; Mameri et al., 2019; Ovidio et al., 2021; Weibel & Peter, 2013). Spawning activity is one of the most common motivators for long-distance migration, but other movements may occur outside the spawning period for ontogenetic and trophic reasons (Benitez et al., 2015, 2018). Therefore, the restoration of river longitudinal connectivity is a management restoration action that has to be associated with the presence of qualitative functional habitats and a sufficient physicochemical water quality (Bernhardt & Palmer, 2007; Fullerton et al., 2010; Ovidio et al., 2020, 2023; Tummers et al., 2016a).

Scientists and river managers have succeeded in facilitating the passage of fish around or through obstructions using fishways, bypass channels and fish elevators. The ability to use fishways depends on the species and their life stage but also their ability to swim; consequently, fishways designs may vary depending on the target species (Grimardias et al., 2022; Noonan et al., 2012; Silva et al., 2018). Over the last years, progress has been made to improve fishway access and performance, combining knowledges of hydraulics and fish ecology. Fishways design tend to become predominantly adapted to different species, sizes and migratory strategies (Benitez et al., 2015; Grimardias et al., 2022; Ovidio et al., 2017, 2020; Romão et al., 2019).

When new fishways are installed in rivers, there is also a real interest to perform a monitoring programme to evaluate their seasonal use by different species and to quantitatively evaluate the extent to which fish will have access to newly opened river sections. As humanely and/or logistically costly, very few studies on the use of fishways have been done during several consecutive years (Benitez et al., 2022; Grimardias et al., 2022; Legrand et al., 2020; Tummers et al., 2016a). Such long-term monitoring is, however, interesting to highlight the between years variability in the use of the fishways for different species under fluctuating environmental conditions (Belliard et al., 2018; Benitez et al., 2022). The use of capture traps as a monitoring method is relatively fastidious because it requires regular human passage. However, this method makes it possible to obtain precise and qualitative information on fish such as species taxonomic determination, individuals weight, size or sex, and to employ tagging for different scientific purposes (Benitez et al., 2022; Prchalová et al., 2011). Moreover, monitoring during several consecutive years since the opening of the migratory axis allows to analyse the temporal processes of colonisation of newly re-opened habitats by fish communities, which is an important, but yet purely informed, scientific key-point for following restoration of longitudinal continuity.

In order to restore connectivity, multi-species vertical slot fishways were installed in three medium size rivers in the south of Belgium. Theses fishways were intensively monitored by capture traps during several consecutive years after setup to obtain data on their use by different fish species and on the evolution and changes of fish species using the fishways over time. Such long-term monitoring is particularly adapted to analyse the colonization dynamic of migratory axes, just after the reestablishment of rivers longitudinal connectivity. In order to meet these objectives, we analysed: (1) the diversity, abundance, biomass and size of species captured in the three fishways; (2) the evolution of the dynamic pattern of capture over consecutive years, at species and ecological guild levels; (3) the periodicity of capture and its variation over years of monitoring; and (4) the environmental conditions (water temperature and flow conditions) associated with species capture.

Material and Methods

Study site and fishways characteristics

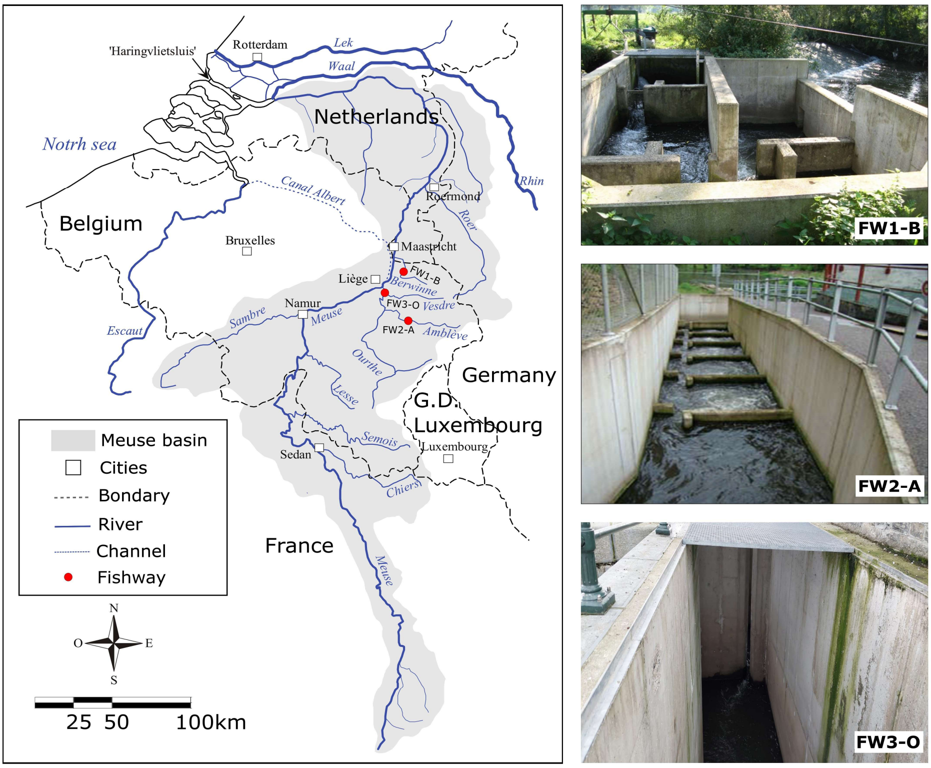


Figure 1. Locations of the Berneau fishway in the Berwinne (FW1-B), the Lorcé fishway in the Amblève (FW2-A) and the Grosses-Battes fishway in the Ourthe River (FW3-O) and pictures showing fishway configurations.

The study was conducted on three rivers belonging to the Belgian Meuse River basin: the Berwinne, a tributary of the Meuse; the Amblève a tributary of the Ourthe; and the Ourthe (Figure 1). Each of these rivers have a fishway (FW) built in 2002 (Berwinne River: FW1-B), 2007 (Ambleve River: FW2-A) and 2009 (Ourthe River: FW3-O) to restore connectivity. Before that, no device was present at these physical barriers (concrete ramp dam at FW1-B and FW3-O and hydropower dam at FW2-A). The average annual discharge is 1.9 m^3/s for the Berwinne, 19.3 m^3/s for the Amblève and 67.4 m^3/s for the Ourthe. The ecological status of rivers as defined by biological, physicochemical and hydro morphological indicators is medium for the Berwinne and good for the Amblève and Ourthe Rivers (*i.e.* Public Service of Wallonia — DEE). According to Huet (1949), the downstream parts of the Berwinne and Amblève Rivers belong to the grayling/barbel fish zone and the Ourthe river is characterised as a barbel fish zone (Huet, 1949). In total, 23 species are potentially present in the

Berwinne and Amblève Rivers and 24 species in the Ourthe River (Electrofishing data, University of Liège). All fishways are vertical-slot pool multi-specific types (height between pools ≤0.3 m) equipped with 4 (FW1-B), 15 (FW2-A) and 16 (FW3-O) pools. The three fishways have a constant operating flow and are not influenced significantly by river flow fluctuations. In addition, a capture trap was installed in the three fishways. The first one (FW1-B) was equipped with a grid located in the upper pool with 3 cm of space in the upstream opening and a cone in the downstream opening. The second (FW2-A) and the last one (FW3-O) had a cage in the upstream pool with a grid of 1 × 1 × 1 cm and 5 × 5 × 5 cm, respectively (Table 1). The minimum capture size is 50 mm (FW1-B), 25 mm (FW2-A) and 150 mm (FW3-O).

Table 1. Characteristics of the Berneau (FW1-B), Lorcé (FW2-A) and Grosses-Battes (FW3-O) fishways.

Characteristics	Berneau (FW1-B)	Lorcé (FW2-A)	Grosse-Battes (FW3-O)
Fishway type	Pool type, vertical slot	Pool type, vertical slot	Pool type, vertical slot
Construction year	2002	2007	2009
Period of monitoring	Oct 2002–Oct 2008	Oct 2007–Oct 2015	Sept 2009–Sept 2012
Delta height of dam (m)	1.4	3.3	4
Attraction flow (m^3/s)	–	–	1.5
Total length of fishway (m)	16	67	73
Number of pools	4	15	16
Pool size of fishway (m)	4.2–3 long × 3–1.8 wide	2.8–5.2 long × 2.7 wide	3.5–5.6 long × 2 wide
Height between pools (m)	0.3	0.25	0.25
Water depth of slot (m)	0.7	1	1.2
Slot width (m)	0.2	0.25	0.3

Fish capture and environmental variables

The three fishways (FW) were monitored for several consecutive years: from October 2002 to October 2008 for FW1-B, from October 2007 to October 2015 for FW2-A and from September 2009 to September 2012 for FW3-O. The monitoring period ranged from 2 to 5 times per week, depending on the capture intensity with a total of 730 monitoring events at FW1-B, 1311 at FW2-A and 286 at FW3-O. Individuals in the capture trap were caught with a dip net after placing a grid just downstream, which prevents the passage of other individuals during the monitoring.

Captured fishes were anesthetised in a solution of 4-allyl-2- methoxyphenol (Eugenol: 0.1 ml/L), identified at the species level, counted, measured (±1 mm, fork length) and weighed (±1 g). Following biometric analyses, fish were released upstream of the dam after a recuperation period of a few minutes. Fish caught were grouped into different guilds according to their ecological preferences (Benitez et al., 2022):

- Rheophilic species: trout (*Salmo trutta)*, sea trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), barbel (*Barbus barbus*), chub (*Squalius cephalus*), nase (*Chondrostoma nasus*), spirlin (*Alburnoides bipunctatus*), asp (*Aspius aspius*), dace (*Leuciscus leuciscus*), grayling (*Thymallus thymallus*), loach (*Barbatula barbatula*) and bullhead (*Cottus rhenanus*).
- Eurytopic species: common bleak (*Alburnus alburnus*), common bream (*Abramis brama*), silver bream (*Blicca bjoerkna*), roach (*Rutilus rutilus*), gudgeon (*Gobio gobio*), european catfish (*Silurus glanis*), minnow (*Phoxinus phoxinus*), European eel (*Anguilla Anguilla*) and three- spined stickleback (*Gasterosteus aculeatus*).
- Limnophilic species: pike (*Esox lucius*), perch (*Perca* fl*uviatilis*), tench (*Tinca tinca*), ide (*Leuciscus idus*), common rudd (*Scardinius erythrophthalmus*), koi (*Cyprinus rubrofuscus*), common carp (*Cyprinus carpio*) and leather carp (*Cyprinus carpio nudus*).

This separation in ecological guilds allows to have a more synthetic view of the colonisation process for species having closer habitat preference.

Environmental variables were continuously recorded (every hour) during the monitoring of the fishways. Data on water temperature (°C) were recorded by data loggers (Tidbit Onset) installed at the inlet of the fishways, and the flow data (m^3/s) were granted by SETHY (Wallonia Public Service of Hydrological Studies) located 3 km downstream of the FW1-B, 16 km downstream of the FW2-A and 0.2 km of the FW3-O.

Data and statistical analysis

Firstly, we produced a global view of the fish diversity (*i.e.* by species and by ecological guild and in terms of abundance, biomass and size) observed in each FW. We presented the results by year of monitoring in order to take in account the spawning periods. It should be noted that some species were not present every year in the different fishways. For species with at least 5 individuals captured per year of monitoring, we compared the sizes of individuals between the different monitoring years for the three FW with non-parametric Kruskal-Wallis test.

We investigated dynamic patterns of capture per year of monitoring for each FW, using cumulative curves for the three ecological groups (including all individuals) and for species with a minimum of 10 captured individuals. The number of captures was computed as a percentage, with 100% corresponding to the total number of individuals captured during the entire monitoring, namely during 6 years at FW1-B, 8 years at FW2-A and 3 years at FW3-O. We used the chi^2 test to determine if the observed distribution of captures during each year of monitoring for each FW was homogeneous or heterogeneous compared to a theoretical number of captures (corresponding to the total capture divided by the number of years of monitoring). We also used chi^2 test to compare (i) the number of captures between rheophilic and eurytopic guilds during the first three years of monitoring for each fishways and between the three fishways since the lowest monitoring time is 3 years at FW1-B; (ii) the number of captures of rheophilic and eurytopic guilds during the first year compared to the sum of captures in the second and third year. Only species with at least 5 individuals captured per year were considered for these tests. This last constrain excluded the limnophilic guild from these tests.

We analysed the periodicity of capture (by month) per year of monitoring for species with at least 5 individuals captured for each year of monitoring using violinplots. We compared temporal trends in capture periodicity between the years of monitoring with non-parametric Kruskal-Wallis tests. The post hoc pairwise comparison of the Mann-Whitney (*U*) test was used when the Kruskal-Wallis test was significant.

The environmental values were transformed into daily data, and each fish captured was linked with the environmental data of the previous day's capture (Benitez et al., 2015). The temperature and flow data were analysed by species with a minimum of 3 individuals for each fishway. Since the rivers have different sizes, the flow values were divided by the average flow of each river. We calculated the 25 and 75 percentiles of index flow values during capture (*i.e.* river flow the day before the capture divided by the average annual flow) to determine 3 migration flow categories:

- Low flow migration: < percentile 25.
- Mean flow migration: between percentile 25 and percentile 75.
- High flow migration: > percentile 75.

The proportion of individuals (%) per species captured for each category was further calculated at the three FW.

The significance level was set at $p < 0.05$ for all statistical tests (chi^2 test, Kruskal-Wallis and Mann-Whitney) and was performed using a R statistical program.

Results

Capture diversity (abundance, biomass and size)

A total of $n = 1506$ individuals from 13 different fish species were captured in the FW1-B from October 2002 to October 2008. In the FW2-A, $n = 4507$ individuals belonging to 23 species were monitored from October 2007 to October 2015. In the FW3-O, $n = 1403$ fish from 21 species were captured from September 2009 to September 2012 (Table 2). The most abundant ecological guild at the FW1-B and FW2-A in terms of number of individuals was the rheophilic guild with 82% and 53% of individuals captured, respectively, and the eurytopic guild in FW3-O with 63% of individuals captured. At FW2-A and FW1-B, eurytopic species were the second most abundant guild with 47% and 18% of individuals captured, respectively, and the rheophilic guild with 35% in FW3-O (Table 2).

During the first year of monitoring, 399 individuals were captured at FW1-B, 540 at FW2-A and 898 at FW3-O. The number of individuals over the monitoring time varied from 163 to 399 in the FW1-B, from 161 to 1333 in the FW2-A and from 117 to 898 in the FW3-O. This represents 5–10 species, 11–17 species and 11–18 species, respectively. At FW1-B, the greatest number of species was captured between 2004 and 2005 with 10 species, between 2012 and 2013 at FW2-A with 17 species, between 2009–2010 and 2011–2012 at FW3-O with 18 species captured. New species were still captured during the fourth and fifth years of monitoring at FW1-B, during the second, fifth, sixth and eight years at FW2-A and during the second year of monitoring at FW3-O (Figure 2). In terms of number of individuals per species, the spirlin (rheophilic) was the most abundant at FW1-B ($n = 548$ individuals), the minnow (eurytopic) at FW2-A ($n = 1837$) and the bream (eurytopic) at FW3-O ($n = 833$) (Table 2). Regarding the biomass, rheophilic species were dominant at FW1-B and FW2-A, representing 95% (139 kg) and 96% (608 kg), respectively, of the total biomass and eurytopic species at the FW3-O with 52% (1275 kg) of the total biomass. The most represented species in terms of biomass was the trout at FW1-B (97 kg), the barbel at FW2-A (276 kg) and the bream at FW3-O (1038 kg). The biomass over year of monitoring varied from 14 to 53 kg at FW1-B, from 32 to 161 kg at FW2-A and from 197 to 1778 kg at FW3-O (Table 2). The largest and smallest individuals captured at FW1-B were an eel (765 mm) during the first year and a minnow (31 mm) during the fourth year of monitoring, respectively; a barbel (640 mm) during the last year and a minnow (39 mm) during the first year of monitoring at FW2-A; an European catfish (1160 mm) during the last year and a spirlin (46 mm) during the first year of monitoring at FW3-O (Table 2). The KW statistical test showed no trend between the different monitoring year regarding the size of individuals captured in the three FW (KW test, all $p > 0.05$).

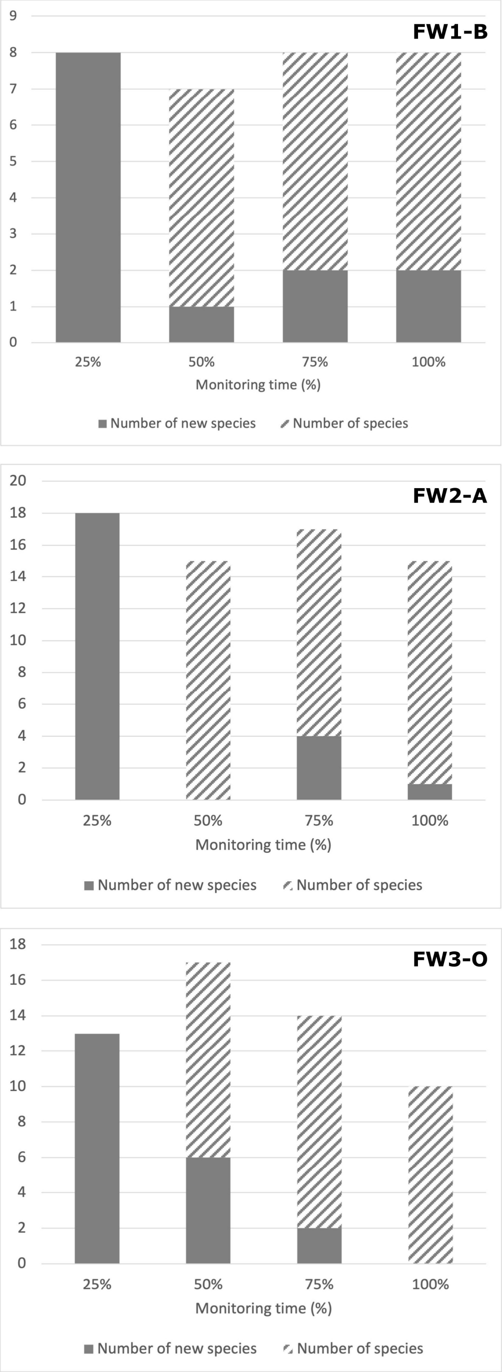


Figure 2. Histograms of the number of species and new species in the Berwinne (FW1-B), the Amblève (FW2-A) and the Ourthe River (FW3-O), depending on the year of monitoring.

Table 2. Number of individuals (n), biomass (g) and range size (mm) of captured fishes for the Berneau (FW1-B), Lorcé (FW2-A) and Grosse-Battes (FW3-O) fishways.

Species	FW1-B																	
	2002-2003			2003-2004			2004-2005			2005-2006			2006-2007			2007-2008		
	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm
Rheophilic species	336	48236	-	167	22250	-	168	22258	-	203	12124	-	217	19052	-	149	15163	-
Trout	74	30305	225-575	53	18152	96-590	43	15177	129-458	31	9463	109-382	40	13088	75-472	23	10868	130-510
Rainbow trout	-	-	-	1	229	283	-	-	-	-	-	-	1	320	294	2	504	270-317
Barbel	7	13697	370-606	-	-	-	1	1150	458	1	353	312	1	1248	467	1	8	87
Chub	52	2670	64-362	93	3591	60-410	111	5776	78-415	43	1606	49-288	73	3389	57-370	38	2683	70-414
Nase	-	-	-	-	-	-	-	-	-	1	4	72	-	-	-	-	-	-
Spirlin	201	1564	62-116	20	278	83-102	13	155	78-108	127	698	57-740	102	1007	71-129	85	1100	71-129
Eurytopic species	62	2516	-	13	186	-	7	40	-	165	1733	-	3	11	-	14	50	-
Roach	2	152	135-192	1	129	96	-	-	-	-	-	-	-	-	-	-	-	-
Gudgeon	-	-	-	-	-	-	-	-	-	3	65	108-130	-	-	-	-	-	-
Minnow	57	177	50-80	12	57	55-80	7	40	61-92	160	348	31-84	2	10	64-77	11	47	57-83
Eel	3	2187	720-765	-	-	-	-	-	-	2	1320	686-740	-	-	-	-	-	-
T.S stickleback	-	-	-	-	-	-	-	-	-	-	-	-	1	1	41	3	3	40-46
Limnophilic species	1	2498	-	-	-	-	-	-	-	-	-	-	1	15	105	-	-	-
Perch	-	-	-	-	-	-	-	-	-	-	-	-	1	15	105	-	-	-
Carp	1	2498	427	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	399	53250	-	180	22436	-	175	22298	-	368	13857	-	221	19078	-	163	15213	-

Species	FW2-A																							
	2007-2008			2008-2009			2009-2010			2010-2011			2011-2012			2012-2013			2013-2014			2014-2015		
	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm
Rheophilic species	392	153722	-	121	40343	-	199	70013	-	666	64733	-	152	88110	-	113	26822	-	324	57634	-	420	107103	-
Trout	219	40285	62-439	72	11101	78-379	79	15362	11-343	63	12966	41-354	59	25635	83-417	51	8246	92-453	138	26098	84-606	179	33860	84-505
Rainbow trout	3	391	133-256	13	5098	210-478	25	12650	276-499	21	11123	235-540	8	14567	180-464	12	4304	202-394	14	10835	307-464	54	22839	187-492
Brook trout	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1272	319-335
Barbel	62	97910	131-595	6	9532	259-554	30	39345	54-575	23	27579	55-620	6	35464	54-544	5	8634	418-558	9	15036	427-580	32	42366	52-640
Chub	12	6166	106-465	9	10572	123-510	3	1374	85-463	35	7475	115-510	8	7641	72-140	11	2976	83-506	2	171	119-220	4	190	136-186
Nase	2	3269	490-500	-	-	-	-	-	-	1	13	108	-	-	-	1	27	125	-	-	-	-	-	-
Spirlin	56	565	74-102	3	34	92-99	49	291	53-105	472	3137	61-121	52	1206	61-115	22	129	66-98	117	2145	58-115	125	2909	54-112
Dace	8	243	103-177	-	-	-	4	42	82-127	33	451	78-188	6	488	76-97	1	76	184	16	333	83-210	5	303	66-250
Grayling	26	4880	173-425	13	3987	179-438	8	945	176-296	10	1934	168-349	11	3041	178-282	10	2430	176-305	25	2991	154-338	16	3340	110-375
Loach	2	2	55-59	3	11	63-90	1	4	80	5	24	42-86	1	26	79	-	-	-	3	25	98-105	1	5	89
Bullhead	2	11	77-85	2	8	62-63	-	-	-	3	31	36-81	1	42	69	-	-	-	-	-	-	1	19	106

Table 2. (continued)

Species	FW2-A																							
	2007-2008			2008-2009			2009-2010			2010-2011			2011-2012			2012-2013			2013-2014			2014-2015		
	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm	n	g	mm
Eurytopic species	147	3926	-	145	1108	-	1134	2707	-	535	2019	-	8	561	-	47	452	-	28	631	-	68	3410	-
Common bleak	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	15	72-94	-	-	-	-	-	-
Bream	1	1528	456	-	-	-	1	6	69	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Silver bream	-	-	-	1	58	144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roach	-	-	-	2	61	110-140	-	-	-	3	43	74-109	-	-	-	1	80	171	4	79	103-114	7	164	84-180
Gudgeon	118	2175	88-150	23	561	100-138	12	271	76-141	34	390	71-124	8	561	94-136	16	276	93-231	23	516	101-145	14	288	100-140
Minnow	26	79	39-74	118	426	52-69	1121	2430	44-87	497	1585	55-82	-	-	-	28	81	56-78	-	-	-	47	2958	52-86
Eel	1	143	469	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	36	296	-	-	-
T.S stickleback	1	1	50	1	2	52	-	-	-	1	1	46	-	-	-	-	-	-	-	-	-	-	-	-
Limnophilic species	1	3828	-	-	-	-	-	-	-	-	-	-	1	2006	-	3	4376	-	3	301	-	-	-	-
Pike	-	-	-	-	-	-	-	-	-	-	-	-	1	2006	612	-	-	-	-	-	-	-	-	-
Perch	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	226	170-220	3	301	158-216	-	-	-
Carp	1	3828	570	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leather carp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4150	560	-	-	-	-	-	-
Total	540	161476	-	266	41451	-	1333	72720	-	1201	66752	-	161	90677	-	163	31650	-	355	58566	-	488	110513	-

Species	FW3-O								
	2009-2010			2010-2011			2011-2012		
	n	g	mm	n	g	mm	n	g	mm
Rheophilic species	381	769401	-	47	72186	-	66	159982	-
Trout	8	12301	249-624	5	4388	254-536	6	6298	362-578
Sea trout	5	10287	499-640	3	4907	472-571	2	6302	561-760
Rainbow trout	4	7688	492-581	1	2206	580	8	20991	492-635
Barbel	170	481573	102-704	13	35380	175-681	29	83956	440-689
Chub	41	60924	184-528	12	14965	373-503	16	35308	421-529
Nase	138	195456	138-512	11	7099	109-422	5	7127	364-479
Spirlin	13	66	46-91	-	-	-	-	-	-
Asp	-	-	-	1	2228	601	-	-	-
Grayling	2	1106	327-398	1	1013	451	-	-	-
Eurytopic species	497	926537	-	69	121606	-	313	227274	-
Common bleak	-	-	-	3	97	133-147	-	-	-
Bream	479	903047	315-575	58	107943	401-550	296	27168	373-590
Silver bream	4	1587	241-276	1	261	237	-	-	-
Roach	9	3095	168-328	5	1809	177-300	8	1856	180-275
Gudgeon	1	24	121	-	-	-	-	-	-
European catfish	4	18784	880-950	2	11496	876-1070	9	198250	920-1160
Limnophilic species	20	82480	-	1	2975	-	11	89717	-
Pike	5	12542	590-761	-	-	-	1	1377	555
Tench	3	4810	432-475	-	-	-	-	-	-
Ide	1	426	295	-	-	-	1	1220	398
Common rudd	1	1528	389	-	-	-	-	-	-
Koï	2	9361	521-671	-	-	-	-	-	-
Carp	8	53813	540-723	1	2975	505	9	87120	674-858
Total	898	1778418	-	117	196767	-	390	476973	-

Dynamic pattern of capture over consecutive years

The rheophilic species were the first to be captured in the three fishways. Species of this guild were captured regularly throughout the year of monitoring at FW1-B and FW2-A, with 50% of individuals captured during the third and fourth years of monitoring, respectively. At FW3-O, rheophilic species showed an earlier capture with 50% of the capture rate during the first year of monitoring; the same trend was observed for the eurytopic species. At FW1-B, the eurytopic species reached 50% of capture rate during the fourth year of monitoring, and during the third year at FW2-A. We observed 50% of capture rate of limnophilic species during the first year of monitoring at FW1-B and FW3-O, and during year sixth at FW2-A (Figure 3).

The cumulative frequency of fish capture during years of monitoring changed according to the species (Figure 4). The grayling at FW2-A and the trout at FW3-O showed a homogeneous distribution of captures throughout the entire monitoring period (Chi^2 test, $p > 0.05$). The trout at FW1-B and FW2-A; the chub at FW1-B and FW3-O; the barbel at FW2-A and FW3-O; the spirlin at FW1-B; the gudgeon at FW2-A; and the nase and the bream at FW3-O had heterogeneous capture frequencies (Chi^2 test, all $p < 0.05$). The distribution of the number of captures of rheophilic and eurytopic guilds is significantly different between the first 3 years for the three fishways (Chi^2 test, all $p < 0.05$). The number of captures of rheophilic species in the first year was significantly greater than the number of captures of eurytopic species at FW1-B and FW2-A and the reverse trend was observed at FW3-O (Chi^2 test, $p < 0.05$). Moreover, the number of captures of rheophilic species during the first year was significantly greater than the sum of the second and third year captures at FW2-A and FW3-O. The same trend was observed for the eurytopic species at FW1-B and FW3-O (Chi^2 test, $p < 0.05$) (Figure 4). Some species were quickly captured: the barbel at FW1-B and FW3-O, for which 54% and 50% of individuals were captured after 30 and 34 days of monitoring respectively, the sea trout (50% of individuals after 60 days), the chub (51% of individuals after 57 days), the nase (72% of individuals after 24 days), the spirlin (69% of individuals after 6 days) and the bream (51% of individuals after 46 days) at FW3-O (Figure 4).

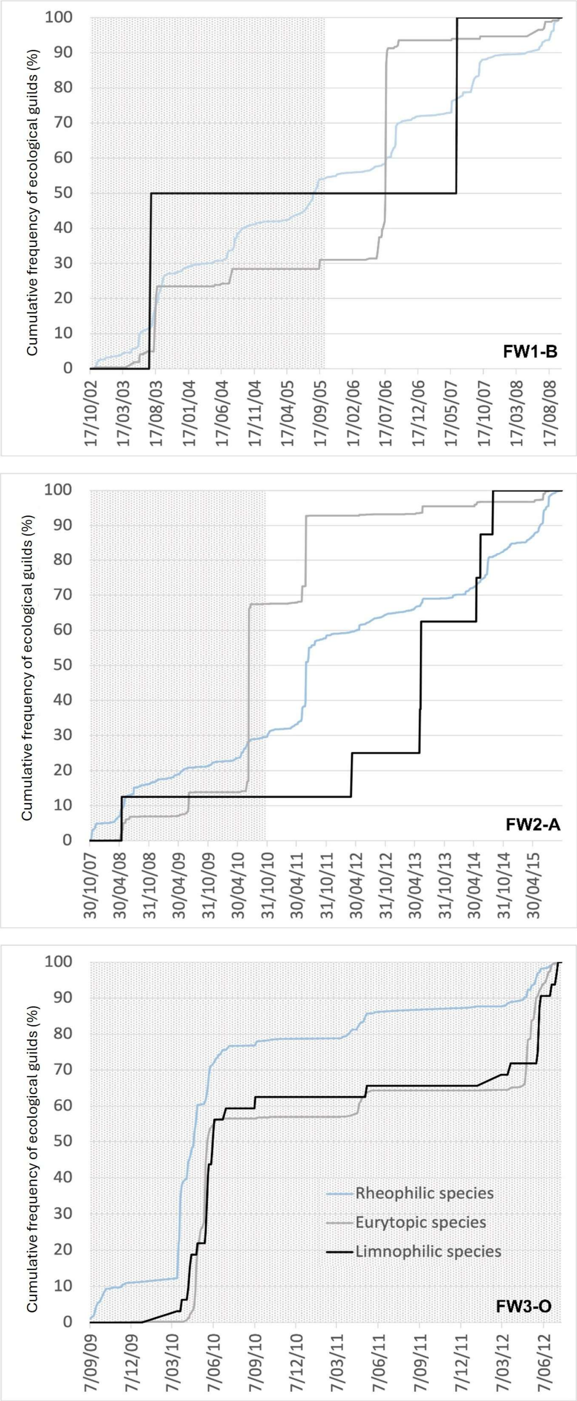


Figure 3. Cumulative frequency of the three ecological guilds with the shaded area corresponding to the first three years of monitoring common to the three FW

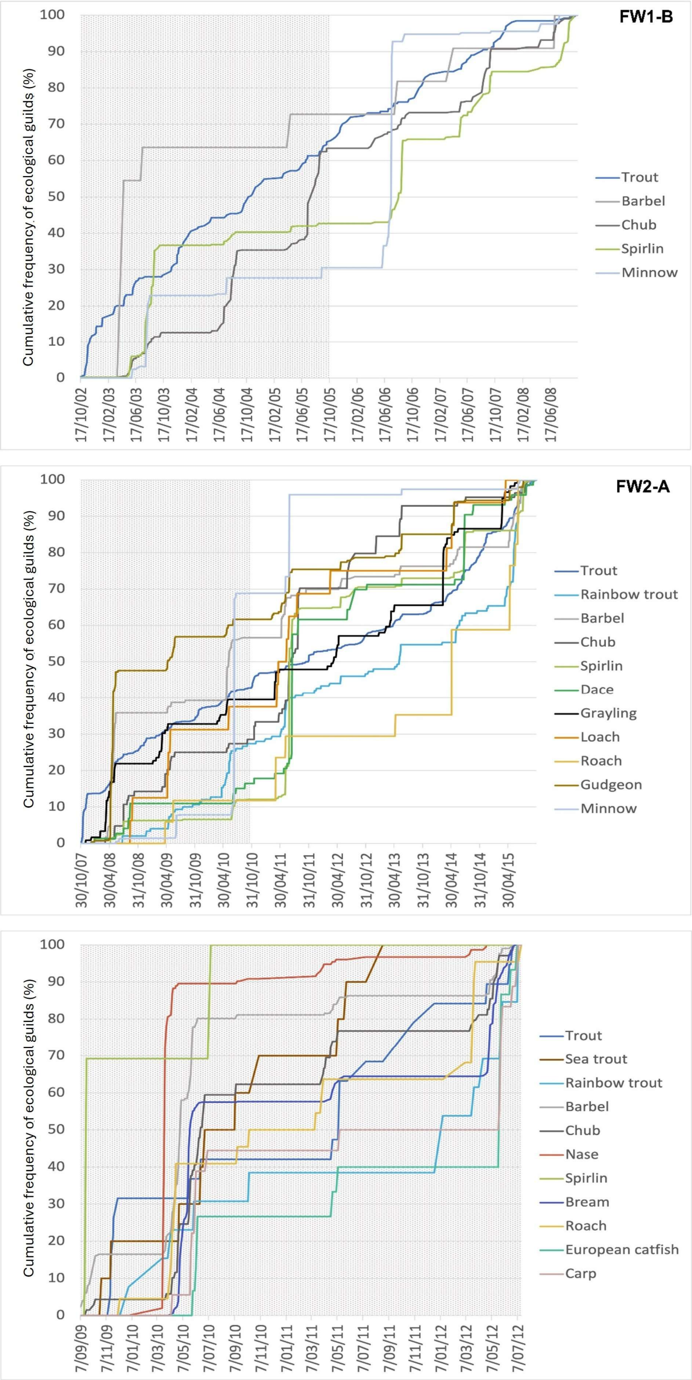


Figure 4. Cumulative frequency of captured individuals per species (belonging to the three guilds only) in the Berwinne (FW1-B), Amblève (FW2-A) and Ourthe River (FW3-O) according to the monitoring days.

Periodicity of capture

The periodicity of capture for the trout at FW1-B, the barbel and the chub at FW3-O showed no significant difference between years of monitoring (KW test, $p > 0.05$). The periodicity was significantly different between years for the other species: the chub and the spirlin at FW1-B, the trout at FW2-A and FW3-O, the barbel, the gudgeon and the grayling at FW2-A, and the bream, the roach and the nase at FW3-O (KW test, all $p < 0.05$). The bream at FW3-O showed a significant difference in the periodicity of capture between all the years of monitoring. Some species had only two years with a different periodicity: the barbel at FW2-A (2007–2008 and 2014–2015) and the trout and the nase at FW3-O (2009–2010 and 2011–2012). The chub and the spirlin at FW1-B had a similar periodicity between years 2005–2006 and 2006–2007 and between years 2005–2006 and 2007–2008. The trout, the gudgeon and the grayling at FW2-A had at least 3 years of similar capture periodicity (Figure 5).

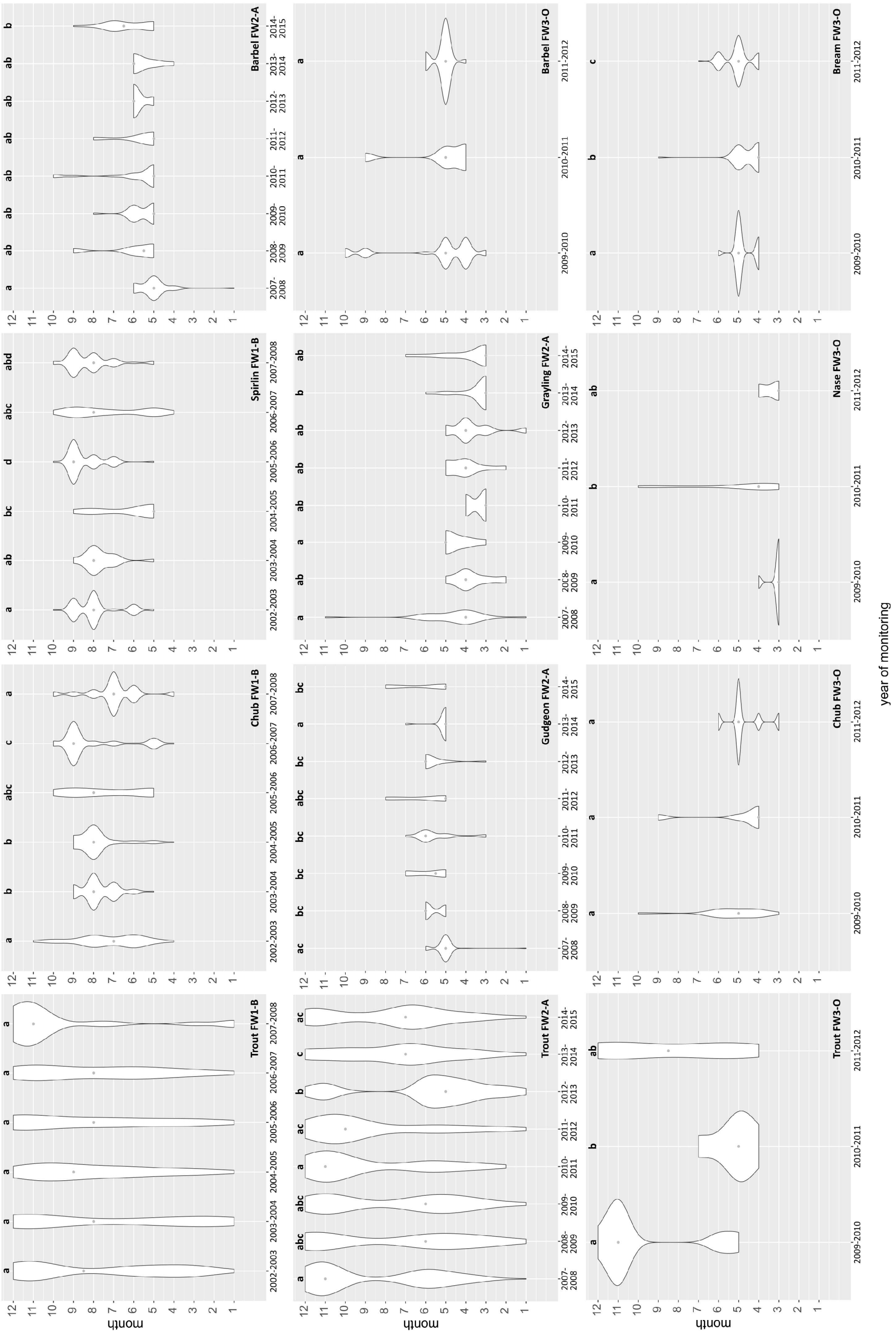


Figure 5. Violin plots of the periodicity of capture (month) by year of monitoring, and the median represented by a point in the Berwinne (FW1-B), the Amblève (FW2-A) and the Ourthe (FW3-O) River. Species sharing at least one common letter (above each violin plot) did not differ at the 0.05 level of significance.

Environmental factors

Temperature and flow values during individuals captures varied by species and by FW. The median capture temperature varied from 10 °C (trout) to 22.1 °C (minnow) for the FW1-B, from 7.4 °C (stickleback) to 25.8 °C (minnow) for FW2-A and from 7.9 °C (grayling) to 19.2 °C (common carp) for FW3-O. The river median index flow at which individuals were captured varied from 0.26 (gudgeon) to 1.3 (eel) for FW1-B, from 0.16 (spirlin) to 2.03 (stickleback) for FW2-A and from 0.15 (spirlin) to 1.08 (nase) for FW3-O. The trout was the species captured at the highest water flow index value for the three fishways, with 6 at FW1-B, 5.1 at FW2-A and 3.4 at FW3-O. The minimum water flow index value was 0.10 (minnow) at FW1-B, 0.08 (spirlin) at FW2-A and 0.13 (trout) at FW3-O (Table 3).

Table 3. Temperature and flow index (i.e. river flow the day before the capture divided by the average annual flow) values (median, minimum and maximum values) per species having at least 3 individuals captured, at the Bewinne (FW1-B), the Amblève (FW2-A) and the Ourthe (FW3-O) rivers.

	Temperature (°C)			Flow index		
Species	FW1–B Median (Min.–Max.)	FW2–A Median (Min.–Max.)	FW3-O Median (Min.–Max.)	FW1-B Median (Min.–Max.)	FW2-A Median (Min.–Max.)	FW3-O Median (Min.–Max.)
Trout	10.0 (4.5–23.3)	10.3 (1.4–25.9)	11.0 (6.9–18.3)	0.82 (0.14–7.99)	0.60 (0.10–6.89)	0.40 (0.13–3.37)
Sea trout	–	–	16.2 (9.5–24.1)	–	–	0.27 (0.13–0.47)
Rainbow trout	12.0 (9.7–16.6)	14.3 (3.3–25.9)	10.4 (5.6–19.8)	0.50 (0.14–4.61)	0.33 (0.10–2.86)	0.38 (0.30–2.07)
Brook trout	–	14.2 (12.6–16.5)	–	–	0.24 (0.23–0.46)	–
Barbel	12.6 (12.6–19.5)	17.0 (6.4–25.9)	14.4 (7.8–20.4)	1.33 (0.26–1.38)	0.33 (0.10–2.36)	0.40 (0.14–1.55)
Chub	17.4 (11.4–23.3)	18.7 (6.6–20.9)	15.3 (8.1–24.1)	0.57 (0.14–4.39)	0.30 (0.11–3.73)	0.39 (0.13–1.20)
Nase	–	10.5 (7.3–18.0)	10.2 (7.5–17.6)	–	1.24 (0.21–2.20)	1.08 (0.13–1.55)
Spirlin	17.9 (11.9–23.3)	20.9 (8.1–25.9)	18.0 (16.0–25.6)	0.37 (0.11–2.44)	0.16 (0.09–1.68)	0.15 (0.14–0.79)
Dace	–	18.0 (5.8–23.4)	–	–	0.21 (0.12–3.73)	–
Grayling	–	8.9 (2.6–25.9)	7.9 (7.5–25.6)	–	0.46 (0.11–2.40)	0.44 (0.14–0.79)
Loach	–	13.9 (7.8–20.1)	–	–	0.32 (0.16–1.37)	–
Bullhead	–	13.0 (5.8–13.9)	–	–	1.21 (0.26–3.46)	–
Common bleak	–	–	17.6 (17.6–17.6)	–	–	0.22 (0.22–0.22)
Bream	–	–	14.8 (8.4–20.4)	–	–	0.37 (0.16–1.08)
Silver bream	–	–	16.7 (12.7–24.1)	–	–	0.30 (0.13–0.37)
Roach	16.0 (14.3–16.0)	14.4 (8.4–25.9)	10.5 (7.4–18.3)	0.95 (0.29–1.21)	0.22 (0.11–1.32)	0.45 (0.19–1.53)
Gudgeon	19.3 (15.7–20.5)	16.3 (4.6–25.9)	–	0.26 (0.22–0.45)	0.31 (0.09–1.74)	–
Minnow	22.1 (12.8–23.3)	25.8 (11.5–25.9)	–	0.37 (0.11–1.27)	0.17 (0.15–1.75)	–
Eel	14.3 (10.0–20.5)	–	–	1.22 (0.45–4.37)	–	–
Stickleback	13.7 (12.0–16.3)	7.4 (7.3–18.1)	–	0.47 (0.25–1.27)	2.03 (0.31–2.20)	–
European catfish	–	–	18.9 (14.9–20.7)	–	–	0.35 (0.17–0.49)
Pike	–	–	10.2 (7.9–11.9)	–	–	0.70 (0.39–1.20)
Tench	–	–	16.4 (12.0–19.1)	–	–	0.28 (0.25–0.40)
Common carp	–	–	19.2 (15.4–22.8)	–	–	0.35 (0.16–0.77)
Perch	–	14.3 (11.5–25.9)	–	–	0.47 (0.28–1.62)	–

Most of captures took place at mean flow (flow index values between 0.17 and 0.64) for all FW with 53% of captures at FW1-B, 58% at FW2-A and 73% at FW3-O. The spirlin was the only species that had most of its individuals captured at low flow index values (flow index <0.17) at FW2-A (63.4%) and FW3-O (92.3%). However, at FW1-B 54.7 % of individuals were captured at mean flow index value. The gudgeon at FW1- B, the brook trout at FW2-A, the common bleak and the European catfish at FW2-0 had 100 % of their capture at mean flow index. Other species had most individuals that were captured under different flow index conditions depending on the river (Table 4).

Table 4. Proportion of capture per species (%) by index flow category; low flow migration (< percentile 25), mean flow migration (between percentile 25 and percentile 75), high flow migration (> percentile 75) with percentile 25 = 0.17 and percentile 75 = 0.64.

Species	**FW1–B**			**FW2–A**			**FW3–O**		
	<P25	[P25–P75]	>P75	<P25	[P25-P75]	>P75	<P25	[P25-P75]	>P75
Trout	1.5	37.7	60.8	9.4	44	46.6	14.3	66.7	19
Sea trout	–	–	–	–	–	–	10	90	0
Rainbow trout	25	25	50	24.3	53.1	22.6	0	64.3	35.7
Brook trout	–	–	–	0	100	0	–	–	–
Barbel	0	27.3	72.7	13.8	77.6	8.6	2.4	78.8	18.9
Chub	2.2	52.9	44.9	7.1	64.3	28.6	9.6	75.3	15.1
Nase	–	–	–	0	50	50	0.6	12.2	87.2
Spirlin	4.9	54.7	40.3	63.4	29	7.6	92.3	7.7	0
Dace	–	–	–	14.9	77	8.1	–	–	–
Grayling	–	–	–	2.5	61.5	36.1	33.3	33.3	33.3
Loach	–	–	–	5.9	70.6	23.5	–	–	–
Bullhead	–	–	–	0	20	80	–	–	–
Common bleak	–	–	–	–	–	–	0	100	0
Bream	–	–	–	–	–	–	0.2	84.3	15.5
Silver bream	–	–	–	–	–	–	20	80	0
Roach	0	33.3	66.7	27.8	61.1	11.1	0	65.2	34.8
Gudgeon	0	100	0	10.9	85.9	3.2	–	–	–
Minnow	11.2	68.3	20.5	5.8	92.7	1.5	–	–	–
Eel	0	20	80	–	–	–	–	–	–
Stickleback	0	75	25	0	33.3	66.7	–	–	–
European catfish	–	–	–	–	–	–	0	100	0
Pike	–	–	–	–	–	–	0	33.3	66.7
Tench	–	–	–	–	–	–	0	100	0
Common carp	–	–	–	–	–	–	5.6	88.9	5.6
Perch	–	–	–	0	80	20	–	–	–

Discussion

Measures to restore the free movement of fish at physical barriers are generally based on the installation of fishways, as the full removal of these barriers is most often not possible (Silva et al., 2018). Long-term scientific monitoring of fishways is not frequent, and most studies focus on the spawning period of a few target species or during a limited time period (synthesis in Noonan et al., 2012 and Benitez et al., 2022). In this study, we performed long-term manual monitoring of three multi-species fishways equipped with capture devices as soon as they were installed in order to analyse their progressive use by fish and to perform analysis on the dynamic of colonisation of the re-opened migratory axis, at a multi-species level and over a long period of time.

Our results show that the three fishways were used by a wide diversity of fish species, as the number of species captured represents 58% of the species potentially present in the Berwinne (species absent: the grayling, the dace, the stone loach, the bullhead, the common bleak, the bream, the pike, the tench and the common rudd), 100% of species in the Amblève and 70% in the Ourthe River (species absent: the loach, the bullhead and the minnow). In terms of representativeness of captures in the fishways, the dominant ecological guild was the rheophilic guild in the Berwinne (FW1-B) and in the Amblève (FW2-A) Rivers. These rivers have low mean annual temperatures, coarse substrate and a high current velocity which correspond to rheophilic preferences in terms of habitats (Huet, 1949). The captures in the lower Ourthe River (FW3-O), with higher mean temperature, higher flow and finer substrate, were dominated by the eurytopic species. The important fish diversity sampled in the three fishways attests of their proper functioning through their use by fish species presenting different ecological exigences (Benitez et al., 2015; Epler et al., 2004; Thiem et al., 2013) and swimming capacities (Baudoin et al., 2015). We observed that the number of new fish species captured in the three fishways was variable and gradual from the beginning (axis opening) to the end of the monitoring. Indeed, new species were still captured after 5 years of monitoring at FW1-B, 8 years at FW2-A and 2 years at FW3-O. To obtain 100% of the species captured in the fishways, it took 220 days of monitoring at FW1-B, 935 days at FW2-A and 87 days at FW3-O. Therefore, while lengthening the monitoring time, we succeeded in detecting species which would have been considered absent on a shorter timescale. This underlines the pertinence of long-term monitoring to have a complete view of the fishway use after the opening of a migratory axis as the migratory impulse may vary depending on the species, their functional habitat requirements, or the environment. Lamouroux *et al.* (2006) observed in a fishway of the Rhône River that the number of species varied from 16 to 26 over the 9 years of monitoring while 32 species were counted in total. The variations in terms of species presence over time between the different rivers could originate from potential seasonal biotic and abiotic variations such as environmental factors that may or may not trigger movements, or pressures present in the rivers that will impact movements in fish populations (Costa et al., 2007; De Leeuw & Winter, 2008; Veiga et al., 2006). As the main goal of installing a fishway is to allow species to move through newly opened habitats, our results underline that the colonisation may be a long process in some instances for some species. But, the important point is that in the long term, the connectivity between river stretches is restored.

The greatest number of individuals were captured during the first year of monitoring at FW1-B (*n* = 399 individuals) and FW3-O (*n* = 897 individuals), and during the third year at FW2-A (*n* = 1333 individuals). Results at FW2-A suggest that even if the fishway was used by fishes just after its opening, the fish capture peaks take some time to appear. Sun *et al.* (2022) showed a marked increase in trout abundance 4 years after restoration of a migratory axis in the river Deerness in England. The maximum fish biomass was observed during the first year of monitoring for the three fishways. During the first year of monitoring, larger species identified as roach, barbel, grayling or common carp, increased the biomass despite a small number of individuals. Concerning the Ourthe River, a larger number of bream (*n* = 479) were captured during the first year for a weight of 903 kg with a strong influence on the repartition of the biomass. When assessing the effect of the reopening of a migratory axis by means of fishway monitoring, it is, therefore, important not to extrapolate trends of a single year of monitoring. The size diversity of individuals captured showed that the three fishways are used by individuals of different age classes, both juveniles and adults (Benitez et al., 2015; Prchalová et al., 2011).

Our results on the dynamic pattern showed that the rheophilic species were the first to be captured at the three fishways. These species are very exigent in terms of habitats suggesting that they migrate first in order to find new suitable habitats for their needs (Benitez & Ovidio, 2018; De Leeuw & Winter, 2008; Pander et al., 2015). In addition, as rheophilic species tend to be attracted by higher flows, it is possible that they found the input of fishways more easily (Benitez & Ovidio, 2018; Benitez et al., 2018; Britton & Pegg, 2011). Rheophilic species were regularly captured at FW1-B and FW2-A throughout the year of monitoring and had an early capture peak at FW3-O, while the eurytopic species showed later peaks for the first two fishways and an earlier peak for FW3-O. In addition, our results showed that the number of captures during the first year of opening of the migratory axis was overall higher than the total captures during the second and third years after opening suggesting post-opening effect of migratory axis. We observed that the same species may colonise fishways at different time steps, depending on the river. For example, the barbel migrated at FW1-B and FW3-O (with 50% of the individuals captured during the first year after opening), while much later at FW2-A (50% of the individuals having been captured during the third year of monitoring). This species is known for its important mobility, moving regularly between its resting and feeding habitats but also at the time of the spawning period (Baras et al., 1994; Le Pichon et al., 2016; Ovidio et al., 2007). The sea trout, the chub, the nase, the spirling and the bream at FW3-O migrated early at FW3-O (with 50% of the individuals captured during the first year of monitoring). This tendency may be associated with a quick colonisation process of the migratory axis since, subsequently, the number and biomass of individuals captured for these species decreased (Benitez et al., 2015). Other species reached

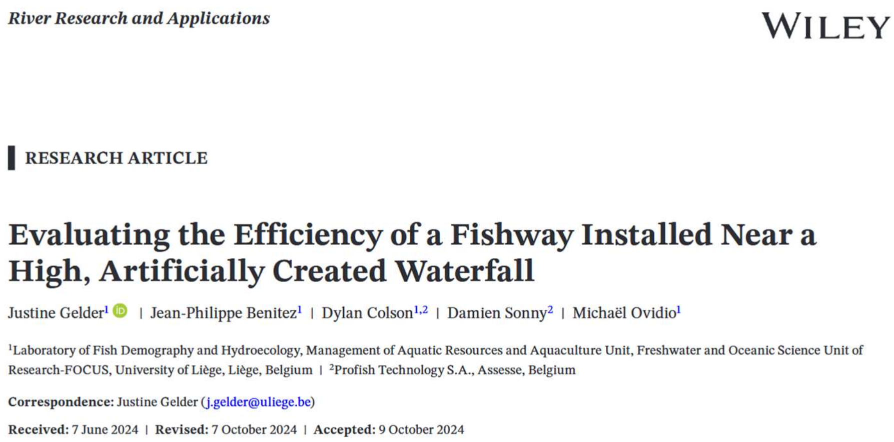
50% of capture rate after more than two years of monitoring like the minnow at FW1-B and FW2-A or the roach and the dace at FW2-A with strong variations between years, as previously shown in the Elbe River in Czech Republic (medium flow conditions = 160 m^3/s) where the abundance of captures varied from one year to another depending on temperature and flow conditions (Prchalová et al., 2011). These results underline that the temporal dynamic of colonisation of a newly opened river stretch is quite variable between species but also for the same species living in different habitats, and that a complete vision of the process requires multi-year monitoring from the opening.

In terms of periodicity of movements between monitoring periods, we observed that the majority of species (except the trout at FW1-B, the barbel and the dace at FW3-O) had a trend of periodicity that varied over time. Variations of recruitment rates and differences in terms of environmental conditions over monitoring time are important factors that influence movement periodicity over time (Ovidio & Philippart, 2008; Pachla et al., 2022; Tummers et al., 2016a). In addition, it could also be expected that movement of individuals from downstream areas to the newly open upstream river stretch may influence the population dynamic and define new biological exchanges that influence mobility patterns of the different size classes in the river (Roscoe & Hinch, 2010). Despite variations of movement periodicity over time, the main peaks were observed during spawning periods for the barbel, the gudgeon, the nase, the grayling, the chub and the bream, which is consistent with the literature (Benitez et al., 2015; Epler et al., 2004; Fredrich et al., 2003; Lucas & Batley, 1996; Ovidio et al., 2007; Ovidio & Philippart, 2008; Philippart, 1989; Romão et al., 2019; Winter et al., 2021). The spirlin at FW1-B showed main peaks outside of its migration period, as also observed by Benitez *et al.* (2015).

Most of the captures were observed above 8 degrees for the three fishways, although some captures of individuals took place at lower temperatures (*e.g.* trout captures between 5 and 7 °C or the grayling captures at FW2-A and FW3-O between 6 and 7 °C). In the Odra River in Poland (mean annual flow = 168 m^3/s), similar results were obtained with fish captures starting/ increasing when temperature reached 8 °C (Kotusz et al., 2006). Temperature ranges of captures for a single species was variable between fishways but with close median values. Some species had wide temperature capture ranges in some fishways and limited in others like the roach with temperatures ranging from 14 to 16 °C at FW1-B (median = 16), 8 to 26 °C at FW2-A (median = 14) and 7 to 18 °C at FW3-O (median = 10.5). The spawning period strongly influenced the temperatures at which individuals of most species were captured (Benitez & Ovidio, 2018; Prchalová et al., 2011). In addition, movement of individuals of a species can vary not only with temperature but also with flow, and sometimes both together (Boavida et al., 2018; Ovidio et al., 1998; Slavík et al., 2009). As for temperature, the flow rate at capture was very variable from one fishway to another as observed by Benitez and Ovidio (2018). The trout was captured at both low and high flow index values. Salmonids are known for their great swimming ability to cope with higher flow conditions (Slavík et al., 2009). The large difference in flow at which trout were captured could be explained by different types of movements (spawning, habitat change). We observed that during some peaks of flow index values, large rheophilic species were captured (trout, rainbow trout, barbel, chub and nase) while small species were preferentially captured at relatively lower flow values like the minnow and the spirlin (Prchalová et al., 2011). Since the ability to swim against current velocity is related to the size of the individuals, large species would be more adapted to move during important flows, contrary to smaller individuals (Mameri et al., 2019; Rasmussen & Belk, 2017; Stoffers et al., 2022). These differences in the influence of environmental factors on the period of movement must be considered when assessing the effect of river connectivity restoration.

Our study based on multi-annual multi-species analysis of the dynamics of fish colonisation of three fishways in three rivers in Belgium showed a wide temporal diversity of species moving upstream through the devices. We detected the presence of different capture peaks and the arrival of new species, sometimes long time after the opening of the migratory axis. The dynamic of captures varied according to the year of monitoring showing that periodicity may fluctuate over time and depending on the river for some species. In the future, to determine the ecological benefit of the opening of new axis for fish populations, it would be interesting to (i) realize an exhaustive fish sampling downstream of the obstacle (before the opening of the migratory axis) in order to obtain information on the species likely to migrate; (ii) incorporate active telemetry monitoring data of individuals that crossed fishways to analyse their capacity to reproduce and to develop adapted behavioural tactics to exploit new habitats.

Chapter 5. Evaluation of the efficiency of a fishway using behavioural metrics



River Research and Applications

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RESEARCH ARTICLE

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

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Received: 7 June 2024 | **Revised:** 7 October 2024 | **Accepted:** 9 October 2024

Abstract

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

Keywords: telemetry; defragmentation; potamodromous species; attractiveness; migratory axis

Introduction

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

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

Today, there are over 4,800 obstacles on Belgian rivers, of which approximately 2,700 are potentially impassable (unpublished data from SPW's Walloon region). The Amblève River has seven main obstacles to fish mobility, including the Coo waterfall, an 11.8 m high obstacle, which has been an impassable barrier for 50 years (Gelder et al., 2024b; Ovidio & Philippart, 2007). In 2021, a fishway was installed on this particular site to restore connectivity, and 21 fish species have been captured, but quantitatively, some species are poorly represented (Gelder et al., 2023). We hypothesised that the presence of the waterfall may attract fish in the wrong direction and prevent them from heading towards the fishway. The objective of this study was to evaluate the fishway performance using the following combination of telemetry: (i) automatic telemetry via integrated transponder tag Radio Frequency IDentification (RFID) and (ii) manual radiotelemetry using a radio transmitter in order to determine the pre-crossing behaviour of individuals through the fishway. To meet this objective, individuals belonging to three fish species were tagged: the barbel (*Barbus barbus*), the trout (*Salmo trutta*) and the grayling (*Thymallus thymallus*).

Material and Methods

Study area and fishway monitoring

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

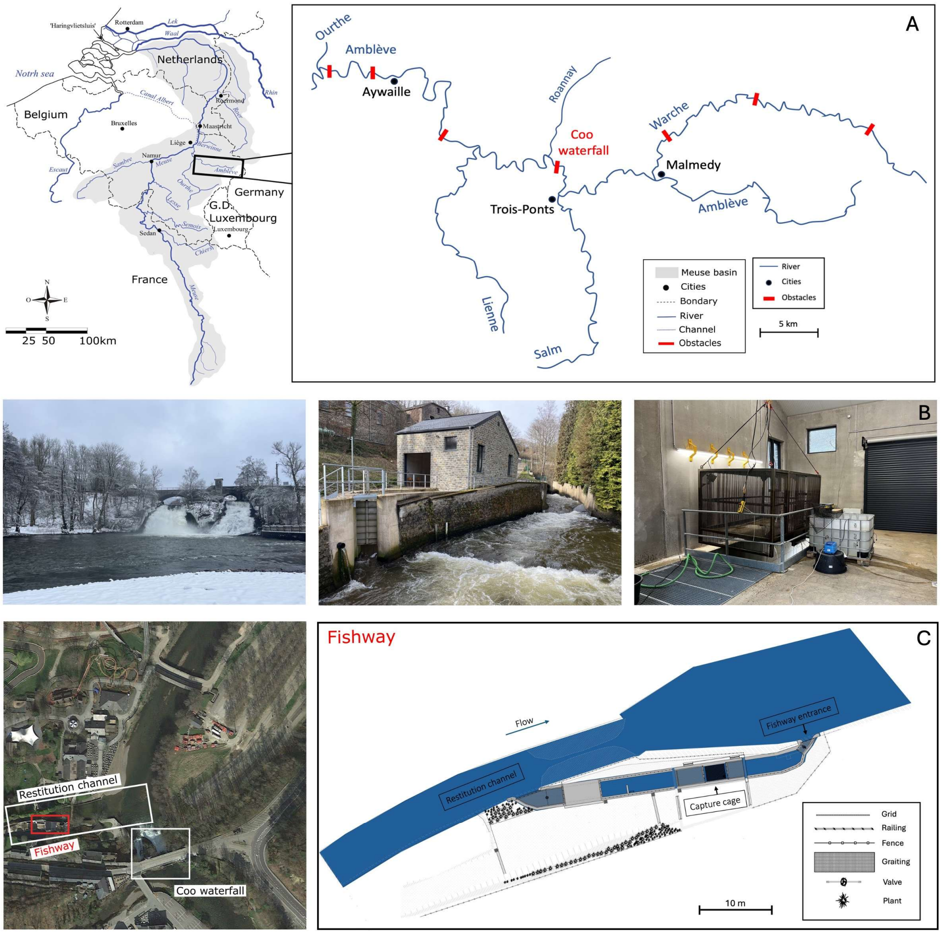

Figure 1. Map of the Amblève River with its seven dams (A) with pictures showing the waterfall, the fishway and the capture cage (B) and an aerial view of the site with the schematic plan of the fishway (C).

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

Electrofishing and fish tagging

The study was carried out from 23 March 2022 to 10 January 2023. Electrofishing (Elektrofischfanggeräte EFKO 7000) was used at four different sites (S) upstream of the waterfall. S1 (23 March 2022), S2 (23 March 2022), S3 (14 April 2022) and S4 (11 October 2022) are 10.3 km, 4 km, 0.47 km and 4.7 km upstream, respectively. Electrofishing captured 38 individuals belonging to three different rheophilic species (grayling, n = 6; barbel, n = 16; trout, n = 16). We chose species known in the literature for their mobility and/or their upstream migration during the spawning period and their homing behaviour so that they would want to return to their capture site (García-Vega et al., 2022; Ovidio et al., 2004, 2007). The date of the electrofishing was chosen to precede the spawning period of the species. However, no grayling of sufficient size was caught in the pre-spawning period (early March). Consequently, a second sample was obtained at the end of March (Table 1; Figure 2A). The grayling is a species known to reproduce from March to May when the temperature rises to 7-11°c (Ovidio et al., 2004; Parkinson et al., 1999). These conditions had not yet been reached before the start of the study, so we assumed that the individuals had not yet reproduced. Captured individuals were anaesthetised (0.2 mL/L of 2-phenoxy-ethanol), weighed, measured and sexed. Only individuals whose weight/transmitter index did not exceed 2.5% were tagged (Ovidio et al., 2020). Two types of tags were implanted in all individuals in their intraperitoneal cavity according to the method used by Gelder *et al.* (2024b): a radio frequency identification (RFID) tag (134.2 kHz, 23 × 3 mm, 0.7 g) and a radio transmitter (Sigma Eight® MST-930, 30 × 8 mm, 3.7 g, 235 mm antenna, 150.34 MHz, pulse rate 1.5 s). In order to match the weight/transmitter index ≤ 2.5%, individuals had to weigh at least ≤ 150g. The fish were then transported, on the same day as the electrofishing, in a 600 litre tank with a bubbler system in a vehicle for 1.2 km downstream of the waterfall, where they were released.

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

Species	***N***	**Mean size ± SD (mm)**	**Mean weight ± SD (g)**	**Sex**	**Capture site**	**Date of capture**
Grayling	6	302.7 ± 17.7	323.7 ± 51.7	4 M/2 F+	S1, S2, S3	23/03/2022 and 14/04/2022
Barbel	16	561.6 ± 74.0	2810.6 ± 1130.5	5 M/9 F/2 I	S2, S3	23/03/2022 and 14/04/2022
Trout	16	275.1 ± 40.2	240.9 ± 105.2	7 M+/5 F/4 I	S4	11-10-22

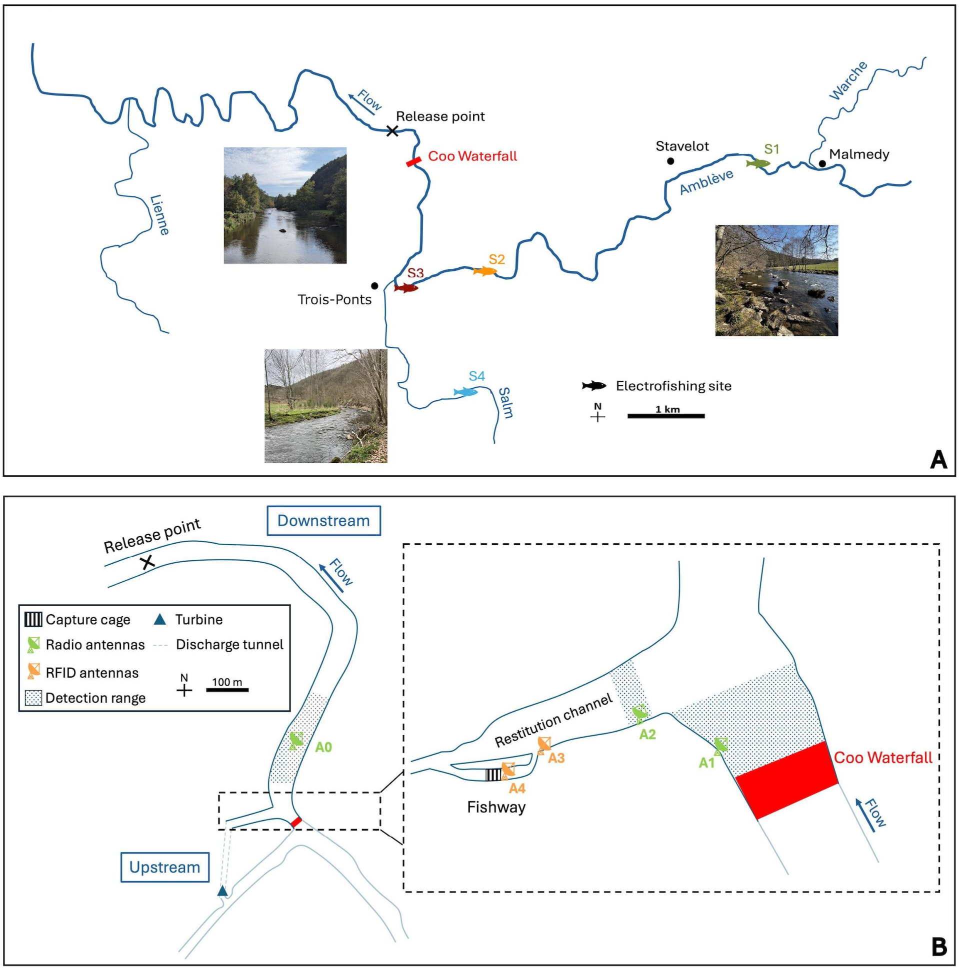

Figure 2. (A) Map showing the electrofishing sites (S1, S2, S3 and S4) upstream of the Coo waterfall, the release point downstream and images illustrating the different environments along the river, and (B) diagram showing the layout of radio (A0, A1 and A2) and RFID (A3 and A4) antennas and their range of detection within the study site (waterfall and fishway).

System for fish detection and environmental variables

A total of three radio antennas and two RFID antennas were installed on the Coo waterfall site to analyse the movements of individuals as they approached the waterfall and fishway. Around the waterfall, two aerial radio antennas and one underwater antenna were installed. One of these aerial antennas was installed at the entrance of the site 160 m downstream of the waterfall (A0). The second antenna was located 10 m downstream of the waterfall (A1) to detect fish approaching the waterfall. The underwater antenna was located at the entrance to the hydroelectric power station's restitution canal (A2) throughout the width of the canal 36 m downstream of the fishway. Around the fishway, two RFID antennas were placed: one at the entrance of the fishway (A3) and a second antenna at the entrance of the capture cage 10 m upstream of the entrance (A4) to confirm the passage of individuals in the fishway (Figure 2B). The RFID and radio antenna stations were operational from the start of the study (March 2022). Radio antennas were used to analyse the approaching behaviour of individuals within the site. RFID antennas were used to analyse the movements of individuals in a narrower zone, the fishway and determine the performance of the crossing device. The selected orientation and spacing of these antennas were specifically configured to prevent any overlapping in their respective detection ranges.

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

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

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

Statistical analyses

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

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

The movements made by each individual were represented for each species using a movement curve graph with a distinction made between individuals that passed through the fishway and were released upstream and those that remained downstream. Water temperature, flow rate and waterfall position were integrated. The flow and temperature values correspond to the average temperature and flow values of the day before tracking. The graphs represent the distances travelled by each individual from their release point (represented by a fish) between two manual radiotracking.

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

Results

Study site approach rate: attraction and efficiency of fishway

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

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

*Table 2. Number and proportion of fish detected by fixed antennas at the system entrance (A0), at the foot of the waterfall (A1), at the restitution channel (A2), at the fishway entrance (A3), at the fishway capture cage entrance (A4), with approach rate and attraction rate and number and proportion of fish discharged upstream of the waterfall with fishway efficiency and adjusted efficiency. *: total taking into account the detection of minimum 1 to maximum 2 trout in A3 and A4.*

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

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

Arrival delay at the antennas and fishway entrance search/transit time

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

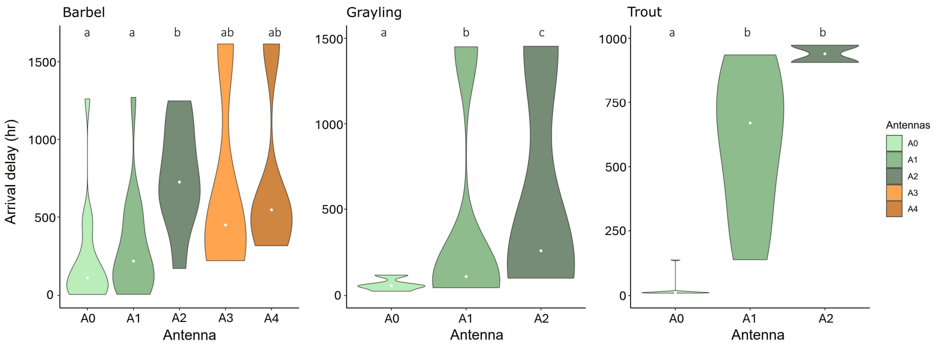

Figure 3. Arrival delay (hr) of individuals grouped by species at each antenna. The white point represents the median arrival delay per antenna. Species sharing at least one common letter (above each violin plot) did not differ at the 0.05 level of significance.

Significant differences in arrival delay were observed in barbel (Kruskal–Wallis, $p = 0.002$) and trout (Kruskal–Wallis, $p < 0.001$) between antennas A1 and A2 (Dunn's test, $p = 0.02$) and between A0 and A2 (Dunn's test, $p < 0.001$) for barbel and between antennas A0 and A1 (Dunn's test, $p = 0.001$) and between A0 and A2 for trout (Dunn's test, $p = 0.007$; Figure 3). Of the five individuals that reached the fishway (detected in A3), grayling (O6) had the shortest searching delay of around 2 days and 10 h (Table 3). Searching delay for the four barbel ranged from 4 days and 20 hr to 66 days and 23 hr, with an overall average of 25 days (± 20 days and 22 hr). Only barbel showed a fishway transit time, with an average of 3 days (± 4 days and 21hr) and times ranging from 28 seconds to 12 days and 23 hr (Table 3).

Table 3. Fishway entrance searching delay and fishway transit time by individuals having reached RFID antennas (A3 and/or A4) and their averages for barbel. Delays are expressed in days (hours:minutes:seconds)

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

Cumulative time spent at the antennas

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

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

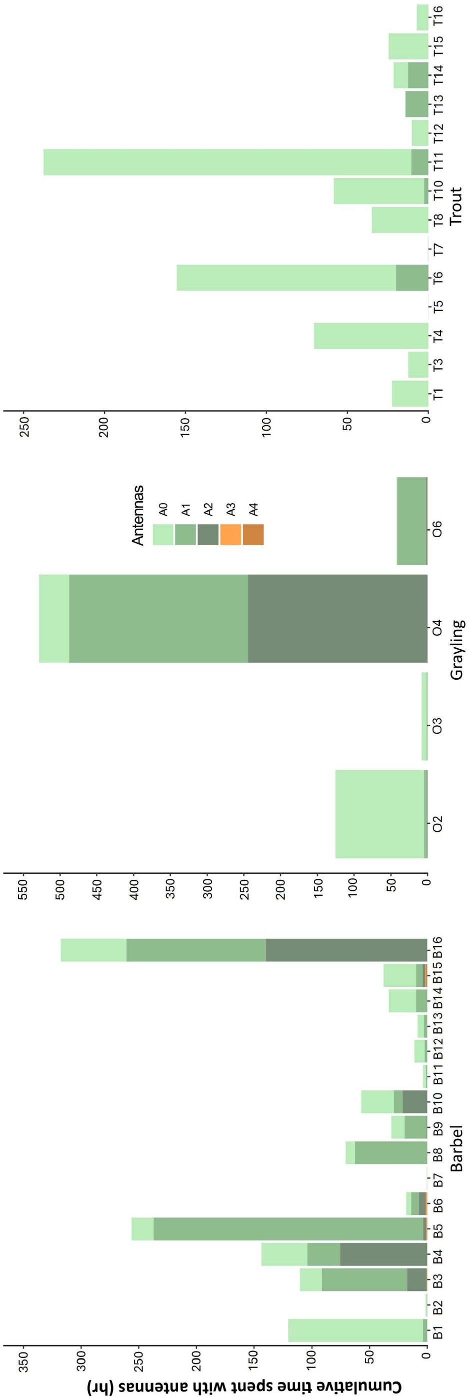

Figure 4. Cumulative time (hr) spent at each antenna (A0, A1, A2, A3 and A4) per individual/species.

Movements of individuals via manual radiotelemetry

Manual radiotelemetry showed that individuals O2, O3 and O4, released on 23 March 2022, remained at the entrance of the study site until early April. O2 and O4 then moved 4 km and 1.2 km downstream, respectively, from the fishway. Individual O6 was released on 14 April 2022 and was detected at the system entrance two days later and moved downstream three days later up to 5.1 km downstream of the fishway. Grayling O2, O4 and O6 then remained stable in their movements, with the exception of individual O4, which made exploratory movements with an amplitude of around 1 km around the released point. Individual O3 was last located 322 m downstream of the fishway approximately one month after its release (Figure 5A).

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

B14 made a major downstream migration of around 6.7 km downstream of the waterfall during the first fortnight of May before returning to the study site. A few days later, it made a second downstream movement of 2.3 km before returning to the study site, where it remained. Individual B16, initially stationary, moved 4.2 km downstream of the fishway on 30 May and remained stationary thereafter. B11 made numerous round trips two days after reaching the waterfall, finally descending 4.2 km. B1, B2, B7 and B12 moved downstream from 19 April to end up around 2.3 km downstream of the fishway. On 11 May, B2, B7 and B12 were found together, and B2 was found dead on 18 May. The other three individuals moved back and forth over an amplitude of around 500 m. Individuals B3, B5, B9, B10, B14 and B13 moved upstream and downstream for two weeks (from 20 April to 4 May). On 9 May, B5, B10, B14 and B3 stabilised at the released point with B8 (1.2 km downstream of the fishway) and B13 moved downstream up to 2.4 km. On 23 May, all the individuals (except B13) were located 1.3 km downstream of the fishway. B9 and B10 remained static for one month. From 31 May onwards, the other individuals made numerous movements between the fishway and 1.2 km downstream (Figure 6).

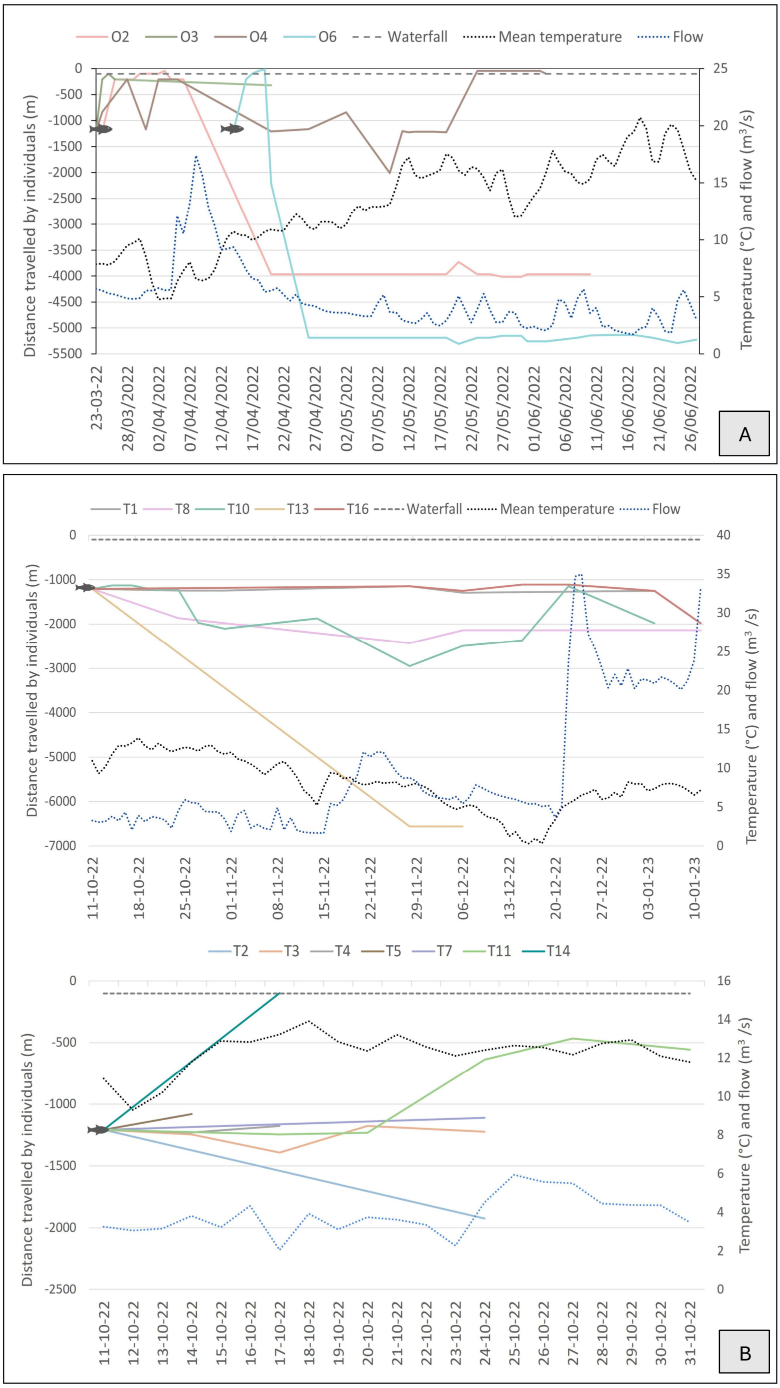

Figure 5. Locations of grayling (A) and trout (B), which stayed downstream of the waterfall, in relation to the Coo fishway capture cage, as a function of time and associated mean temperature (°C) and flow rate (m³/s). The day of release is marked by a fish symbol.

Figure 6. Locations of barbel, which stayed downstream of the waterfall, in relation to the Coo fishway capture cage, as a function of time and associated mean temperature (°C) and flow rate (m^3/s). The day of release is marked by a fish symbol.

Of all the individuals tracked, three individuals (B6, B15 and T6) reached the capture cage and were discharged upstream of the waterfall. After reaching the study site, B6 and B15 moved back and forth for around 20 days before being detected at the entrance to the capture cage. The two individuals were released upstream of the cascade on 9 May. Individual B15 was lost following its release and was not detected by the fixed antennas, suggesting that the individual had remained upstream. Individual B6 was found on 11 May, 2.5 km upstream of the waterfall, in a confluence of the Amblève (Salm River) and spawned with other barbel. B6 was located for the last time on 24 June, which was the last location before the end of the transmitter's life, 1 km upstream of the waterfall. T6 moved between A0, A1 and A2 for four days before being captured and released upstream of the waterfall on 22 November. On 23 November, it was located at A0, but it was not detected at A2; it appears that it tumbled down the discharge tunnel. It was last located on 22 December downstream of the confluence with the Roannay River (approximatively 2.5 km downstream of the waterfall; Figure 7).

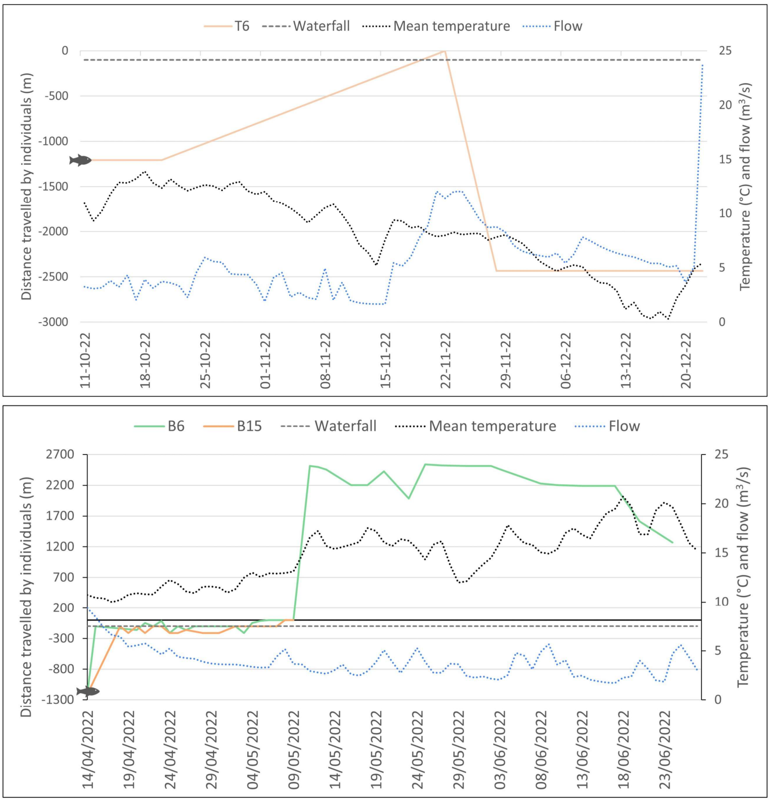

Figure 7. Location of barbel B6 and B15 released on 14 April 2022 and trout T6 released on 11 October 2022 that had passed through the fishway, in relation to the Coo fishway capture cage, as a function of time and associated mean temperature (°C) and flow rate (m^3/s). The day of release is marked by a fish symbol.

Discussion

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

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

Our results showed that the median arrival delay in the system for the three species was similar to data obtained in previous studies involving barbel, trout and grayling, ranging from one to four days (Dębowski et al., 2022; Ovidio et al., 2017). The numerous back-and-forth movements made by individuals suggests intensive habitat search behaviour to find spawning habitats (Gelder et al., 2024b; Panchan et al., 2022). The cumulative time spent at the antennas showed that the restitution channel (A2) was less attractive than the waterfall (A1) for the three species. In addition, all individuals detected in the restitution channel (A2) were first detected at the waterfall, demonstrating its greatest attractiveness. In their meta-analysis, Sun *et al.* (2023) obtained a fishway attraction rate of 49% for non-salmonids and 63% for salmonids. Ovidio *et al.* (2017) showed an attraction rate of 20.5% for grayling, 48.9% for trout and 41% for barbel on the Bocq River (Belgium). David *et al.* (2022) obtained the same rates as Ovidio *et al.* (2017) for barbel on the Rhône River (France). Our results indicate an overall attraction rate of 25% for barbel (non-salmonids) and grayling (salmonids) and an attraction rate of 7.2-14.3% for the trout (salmonids), corresponding to a total attraction rate of 17.6-20.6%. By compiling data from 29 vertical slot fishways, Bunt *et al.* (2012) deduced that the average attraction rate for a vertical slot type fishway was 63% by combining salmonids and non-salmonids. We can reasonably think that low or medium passage performances constitute an improvement (i.e., for gene flow effects and metapopulation reconnection) compared to the absence of connections. However, it is still complicated to assess the demographic gain for a population from fishway improvement or restoration (Ovidio et al., 2020). Some studies have shown that the factor limiting the effectiveness of fishways is their attractiveness (David et al., 2022; Ovidio et al., 2017; Roscoe & Hinch, 2010). Therefore, the location of the fishway entrance is crucial to its success (Bunt, 2001; Katopodis & Williams, 2012). An attraction flow is necessary to increase the water current at the entrance of the fishway (Cooke & Hinch, 2013; Noonan et al., 2012; Romão et al., 2018).

The lack of attractiveness of the restitution channel, where the entrance of the fishway is located, can be explained by the flow at the time of the study, which was particularly low. Moreover, the turbine was not operating, which may have had an impact on the motivation of individuals to use this way (Bao et al., 2019). During the spawning period, fish are stimulated to migrate against the current (Bunt, 2001; Prchalová et al., 2011). However, a flow that is too low can slow down this stimulation and stop individuals from migrating to spawn (Bunt et al., 2012; Maynard et al., 2017; Sprankle, 2005). In addition, prior to the study, a current flow was present on the right bank of the restitution channel, which attracted fish to the entrance of the fishway (Benitez et al., 2015). However, the floods in July 2021 (the year before this study) resulted in the clogging of the right bank, consequently eliminating the current flow that was present prior to this study. This lack of flow may have affected the attractiveness (Laine et al., 2002), as observed by Calles and Greenberg (2005) in Sweden where a low flow at the entrance to the fishway compared with other years resulted in a lower number of individuals reaching the fishway. This lack of attractiveness is linked to the movements detected during manual telemetry. The numerous movements of the individuals, particularly the back-and-forth movements made by the barbel between the fishway site and downstream, suggest that the individuals were unable to quickly find the entrance to the fishway despite the motivation to migrate upstream and therefore reflect the search for a potential new spawning area. In their study in the United Kingdom, Gutmann Roberts *et al.* (2019) showed that dams had an impacted on the upstream migration of barbels, which alternately found spawning habitats within 1 km downstream of the dam. Although other individuals were detected at the entrance to the site (A0), they were only found to be located downstream of the site with telemetry. For these individuals, it is possible that they found alternative suitable spawning habitats because there are many habitats available spawning site downstream of the obstacle. It is likely that these individuals discovered new habitats to which they did not previously have access and settled there, because they not found the entrance to the fishway and had to remain downstream (Calles & Greenberg, 2005, 2007; De Leeuw & Winter, 2008). The fact that there were detections at the antennas (A0 and A1) would suggest this hypothesis.

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

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

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

Chapter 6. What do fish do right after passage of a fishway?

Received: 11 October 2023 | Revised: 13 March 2024 | Accepted: 15 March 2024
DOI: 10.1111/eff.12782

ORIGINAL ARTICLE

Ecology of FRESHWATER FISH WILEY

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

Justine Gelder | Jean-Philippe Benitez | Michaël Ovidio

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, that 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; migratory axis; telemetry; ecological benefit; potamodrous species

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 et al., 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 in addition 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 et al., 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 by means of 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 of a migratory axis for different species (Tummers et al., 2016a). This type of study can be realised on a short or long-time scale 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 the 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 habitat 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.

Material and methods

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 et al., 2023), and the fish are manually released upstream after biometric analyses.

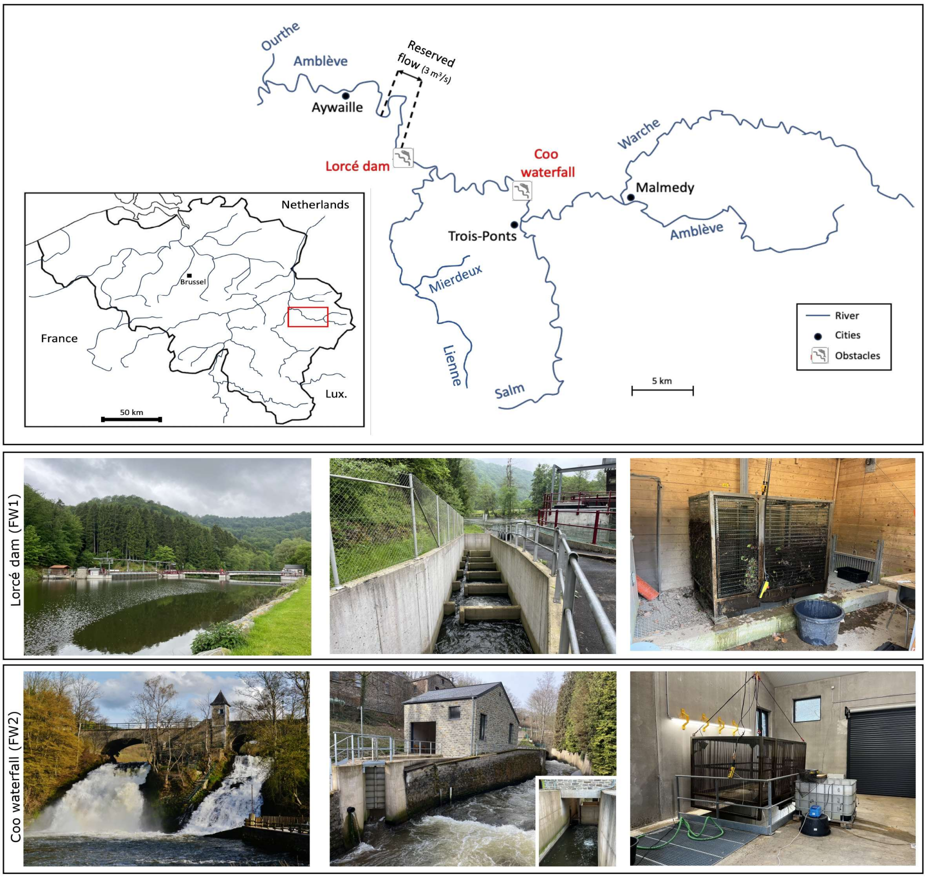

Figure 1. Location of study sites: the Lorcé dam (FW1) with the minimum flow of 3 m3/s over 8 km downstream of the dam and the Coo waterfall (FW2) in the Amblève River in the south of Belgium, and pictures showing obstacles, fishway configurations and capture cages of each site.

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 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 trashrack 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) multi-specific types fishway. A capture cage with dimensions of 1.7 x 1.1 x 1.5 m and a grid of 1 x 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 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 x 1.9 x 1.8 m.

Both capture cages were monitored on average 1 to 3 times per week (Figure 1). Between 2007 and 2016, 23 different species used the Lorcé fishway (FW1) (Gelder et al., 2023) and 21 species between 2021 and 2022 used the Coo fishway (FW2) (Gelder et al., 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.

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 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 anaesthestised 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 ease of access at FW2.

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.

N° 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	04-12-07	20-08-08
G2	306	328	3.8	1.2	F	FW1	05-03-08	07-03-08	16-07-08
G3	308	262	3.8	1.5	M	FW1	05-03-08	07-03-08	11-07-08
B1	488	1423	13.3	0.9	M	FW1	04-04-08	04-04-08	06-07-09
B2	525	1806	13.3	0.7	F	FW1	21-04-08	23-04-08	06-07-09
B3	480	1436	13.3	0.9	F	FW1	21-04-08	23-04-08	02-01-09
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	04-04-08	04-04-08	08-04-09
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	02-06-22	02-06-22	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	04-07-22	04-07-22	29-09-22

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 three to seven days a week, those from FW2 were tracked for two to four days a week, depending on 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 to 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).

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 (Capra et al., 2018; Ovidio et al., 2007; Table 2). 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. This species are known in the literature to travel centers 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).

Table 2. Spatial indicators of fish mobility and their definitions.

Spatial indicators	**Definitions**
Longitudinal home range (HR)	Corresponding to the distance between the mos 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. Expressec 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 absolute value of the travelled dist
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 i downstream direction.

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. 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 study. The most parsimonious model was selected after calculating Akaike information criterium (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 as equal (Zuur, 2009). We have calculated the conditional and marginal R2 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%.

Results

Behaviours upstream of the FW1

Trout 1 (T1) and T2 swiftly ascended the Amblève River after their 28 November 2007, release. They were found in the Lienne River, a tributary, 11.8 km 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 m^3/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 m^3/s) and 23 January (5.8°C, 47.6 m^3/s) and then probably died (transmitter found on the bank on 21 February) (Figure 2A).

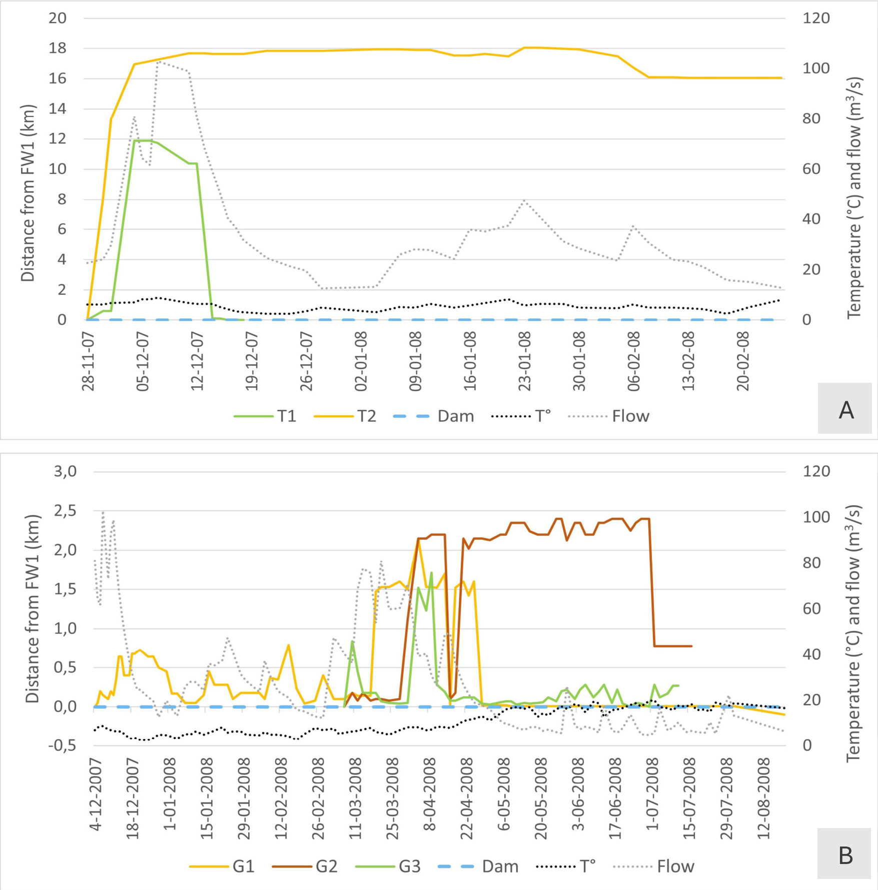

Figure 2. Variations of mean water flow (m^3/s) and mean water temperature (°C) in the Amblève River and the position (km) of the radio-tagged trout T1 and T2 (A), grayling G1, G2 and G3 (B) relative to the discharge point: FW1 during the 2007-009 study with X-axes that differ depending on the time and date of tracking.

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 m^3/s), it migrated toward 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 m^3/s) and 4 April (8.2°C, 39.2 m^3/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 m^3/s), remaining 0.8 km upstream from the Lorce dam. G1 began post-spawning downstream migration in late April (13.1°C, 17.8 m^3/s) and stabilised near the dam, crossing it on 20 August 2008 (16.6°C, 6.6 m^3/s) (Figure 2B).

Five days after tagging, Nase 1 (N1) rapidly migrated upstream on 21 April 2008 (11.0°C, 26.7 m^3/s), reaching the foot of the impassable 11.8 metres Coo waterfall, 16.9 km from the Lorcé dam. It stayed there until 25 April and then returned downstream, where it was located 2.6 km from the dam on 28 April (13.1°C, 17.8 m^3/s). It moved upstream, reaching 13.6 km from the dam on 5 May (14.4°C, 11.1 m^3/s) and stayed until 11 May. After spawning, it migrated downstream (16.3°C, 7 m^3/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 3A).

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 May 30. After spawning, B1, B2 and B4 moved downstream on 2 June (18.3°C, 9 m^3/s), 4 June (17.6°C, 7.4 m^3/s), 13 June (12.8°C, 18 m^3/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 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 dam) and then settled 0.02 km upstream, where tracking ended (Figure 3B).

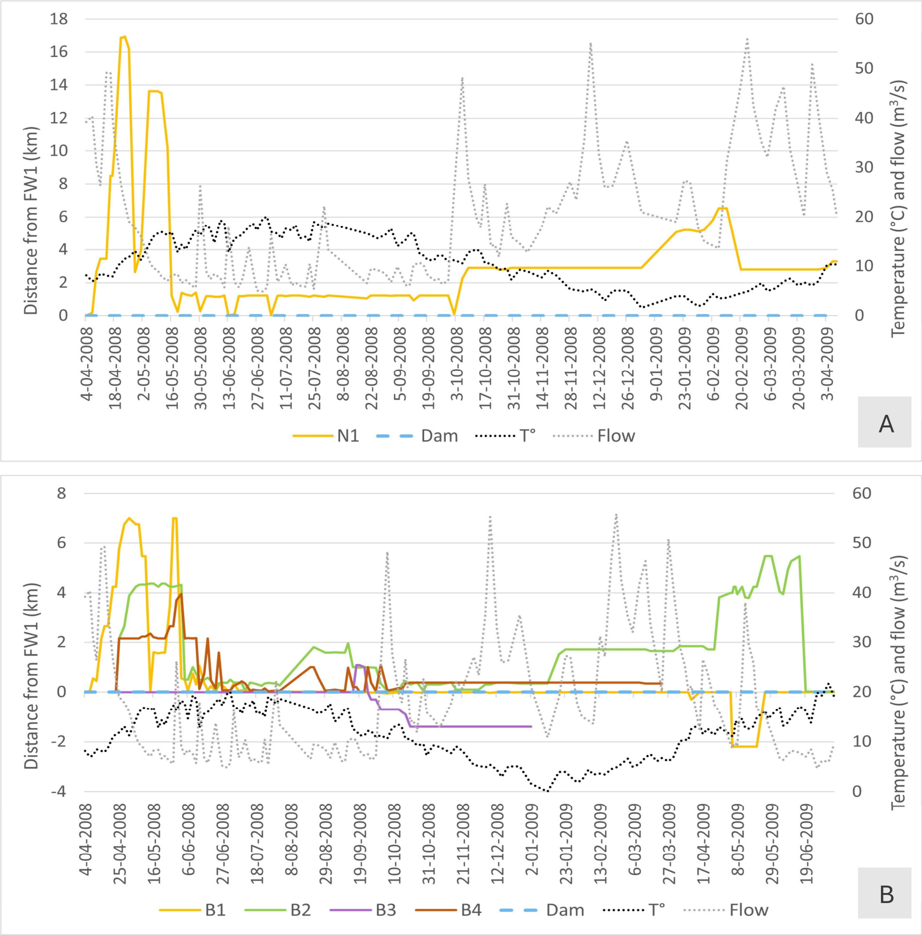

Figure 3. Variations of mean water flow (m³/s) and mean water temperature (°C) in the Amblève River and the position (km) of the radio-tagged nase N1 (A) and barbel B1, B2, B3 and B4 (B) relative to the discharge point: FW1 during the 2007-009 study with X-axes that differ depending on the time and date of tracking.

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 m^3/s) from 20 May to 23 May. It then moved downstream on 25 May (14.3°C and 4 m^3/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 m^3/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 m^3/s) before moving downstream on 17 October (13.2°C and 2 m^3/s), 0.3 km upstream from the release point. B10 was situated downstream of the waterfall on 6 June (16°C and 4.5 m^3/s), where it stayed until 14 June (16.5°C and 2.3 m^3/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 m^3/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 m^3/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 4).

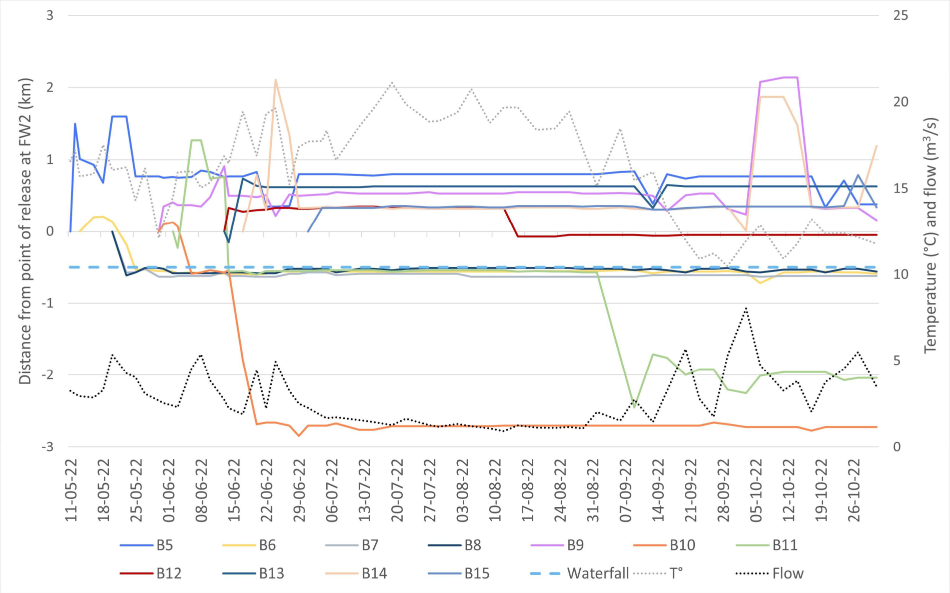

Figure 4. Variations of mean water flow (m^3/s) and mean water temperature (°C) in the Amblève River and the position (km) of the radio-tagged barbels B5 to B15 relative to the discharge point: 500 m upstream of FW2 during the 2022 study.

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, $p < 0.05$; Figure 5). 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, $p < 0.05$). 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 5 barbels moved down the waterfall (B6, B7, B8, B10 and B12; Table 3).

*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. *Corresponding to individuals found downstream of a physical barrier.*

N° 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*	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*	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*	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*	0.9	−0.7	0.2	1.6	−0.6	0.0
B7*	0.6	−0.6	0.0	1.1	−0.6	0.0
B8*	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*	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*	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

The TND was significantly greater for individuals tracked from FW1 (U test, $p < 0.05$) 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, $p > 0.05$) 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 5).

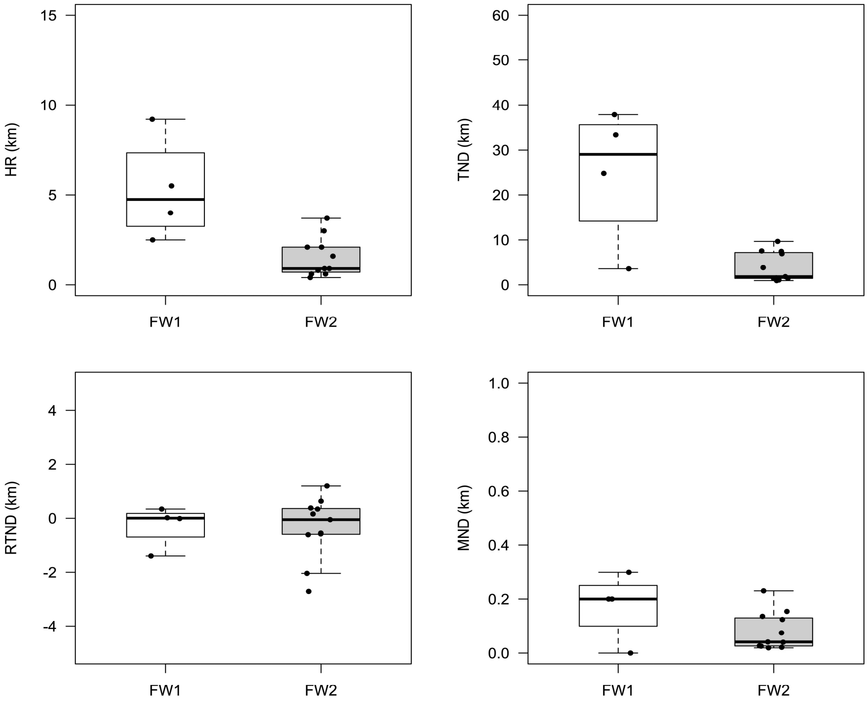

Figure 5. Boxplots of the four spatial indicators (HR, TND, TRD and MND) with barbels combined per site (FW1 and FW2). The end of the whiskers corresponds to the extreme values, and individuals were represented by a dot.

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 R2 = 0.022) and 7.7% at FW2 (marginal R2 = 0.077) of the model's total variance. Allowing for random effects, the model explained 8.4% (conditional R2 = 0.084) of the variance at FW1 and 14.4% at FW2 (conditional R2 = 0.144).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 to 0.048 and 0.004 to 0.013, respectively) and FW2 (95% CI: 0.007 to 0.049 and 0.106 to 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) and depending on the individual, the greatest distance was travelled at low (12.8 km above 74.5 m^3/s) or high flow rates (15.3 km under 34.3 m^3/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 m^3/s; Table 5). The model confirmed the effect of temperature (95% CI: 0.027 to 0.067) on displacement but not flow (95% CI: -0.006 to 0.011).

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. The table include 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 95% confident interval (CI).*

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	Std. Dev.	
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	Std. Error	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 to 0.048]
Flow	0.0081	0.0023	3.516	[0.004 to 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 to 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 to 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	Std. Dev.	
Ind	(Intercept)	0.0238	0.1543	
Residual		0.3057	0.5529	
Number of obs: 545, groups: ind, 11				
Fixed effects : barbel				
	Estimate	Std. Error	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 to 0.049]
Flow	0.1535	0.0239	6.400	[0.106 to 0.200]

Nase covered greater distances at average flow rates (47.1 km between 8 and 26.7 m^3/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 a 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 m^3/s and 23.3 m^3/s), and other (B3) covered a greater distance at low flow rates (under 7.6 m^3/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 m^3/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 (Table 4 and 5, Figure 6).

Table 5. Total net distance travelled (TND) per individual per site by category of flow percentile (m^3/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

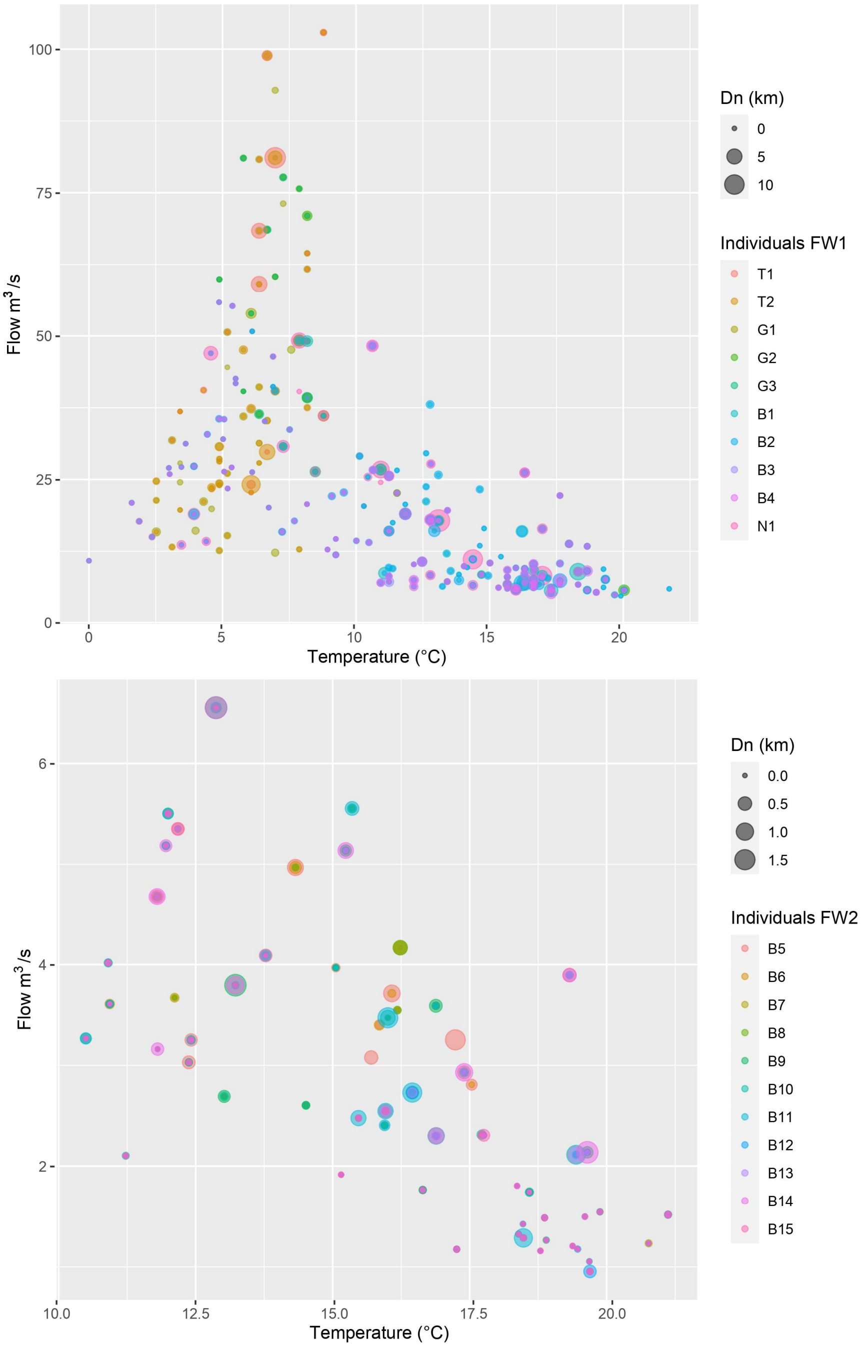

Figure 6. Bubble charts of the net distance travelled (Dn) by individuals between two subsequent locations depending on temperature (°C) and flow (m3/s) at FW1 and FW2 (x = temperature (°C), y = flow (m3/s), z = Dn (size of the circle) and colours = individuals).

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., 2013b). 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.* (2016a) 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 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 et al., 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 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 a mainsteam 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 reached 10°C (Ovidio & Philippart, 2008; Ovidio et al., 2016) 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 2.5 km 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 Ovidio et al., 2007; Benitez & Ovidio, 2017). 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 20 km (Ovidio et al., 2007), but the distance covered by our barbel upstream of FW1 and FW2 reached up to 6 and 2 km, 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 et al., 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. 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 to 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 also the two other barbels, and were blocked several times at FW1, since the dam was impassable when the gates are 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 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, that 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. But, 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, but with precision in terms of tracking, our results encourage the importance of restoring free circulation both upstream and downstream in order 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 toward 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.

Chapter 7. Long-term monitoring of post-passage fish behaviour by telemetry

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

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Hydrobiologia (submitted)

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 of 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 of an obstacle (67% vs. 20%). Moving downstream of an obstacle increased significatively during the spawning period (estimate = 4.13, 95% CI: 1.99 to 6.87) and with higher factor condition (estimate = 1.25, 95% CI: 0.21 to 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 (Baird et al., 2024; Duarte et al., 2021; Dudgeon et al., 2006; Nilsson et al., 2005). For migratory fish species, in particular, such disruptions can have profound consequences on population dynamics, spawning success, and genetic connectivity (Baldan et al., 2023; Dean et al., 2023; Lange et al., 2018; Scruton et al., 2008).

In response to these challenges, river restoration initiatives have increasingly focused on improving 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 (Bellmore et al., 2019; Bower et al., 2024; Dodd et al., 2017; Tummers et al., 2016a). 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 (Barbarossa & Schmitt, 2024; Bellmore et al., 2019). 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 (Lothian et al., 2020; Mameri et al., 2019; Marques et al., 2018; Ovidio et al., 2023; Roscoe & Hinch, 2010). 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 (Bao et al., 2019; Cooke & Hinch, 2013; Dębowski et al., 2022; Gelder et al., 2024a; Iaia et al., 2025; Noonan et al., 2012; Romão et al., 2018; Silva et al., 2012; Stuart & Mallen-Cooper, 1999; Tummers et al., 2016a; Weibel & Peter, 2013).

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; Gelder et al., 2023, 2025; Marques et al., 2018; Sun et al., 2022; 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 (Bravo-Córdoba et al., 2023; Calles et al., 2021; Gelder et al., 2024b; Huber & Kirchhofer, 1998; Kucukali et al., 2025; Ovidio, 1999; Ovidio et al., 2020; Popp et al., 2024; Renardy et al., 2023). 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 including the Coo waterfall and the Lorcé hydroelectric dam. Both of these major obstacles have been equipped with fishways, 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*) and barbel (*Barbus barbus*). 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 behaviours, a component still largely overlooked, yet crucial for assessing the real outcomes of river defragmentation.

Material 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 1,077 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 well-oxygenated waters with current, perfectly suited to rheophilic 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 (Figure 1).

The Lorcé hydroelectric 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 was installed in 2007, it 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.

The Coo waterfall, located 17km upstream of Lorcé dam, has a drop of 11.8m. 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, 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.

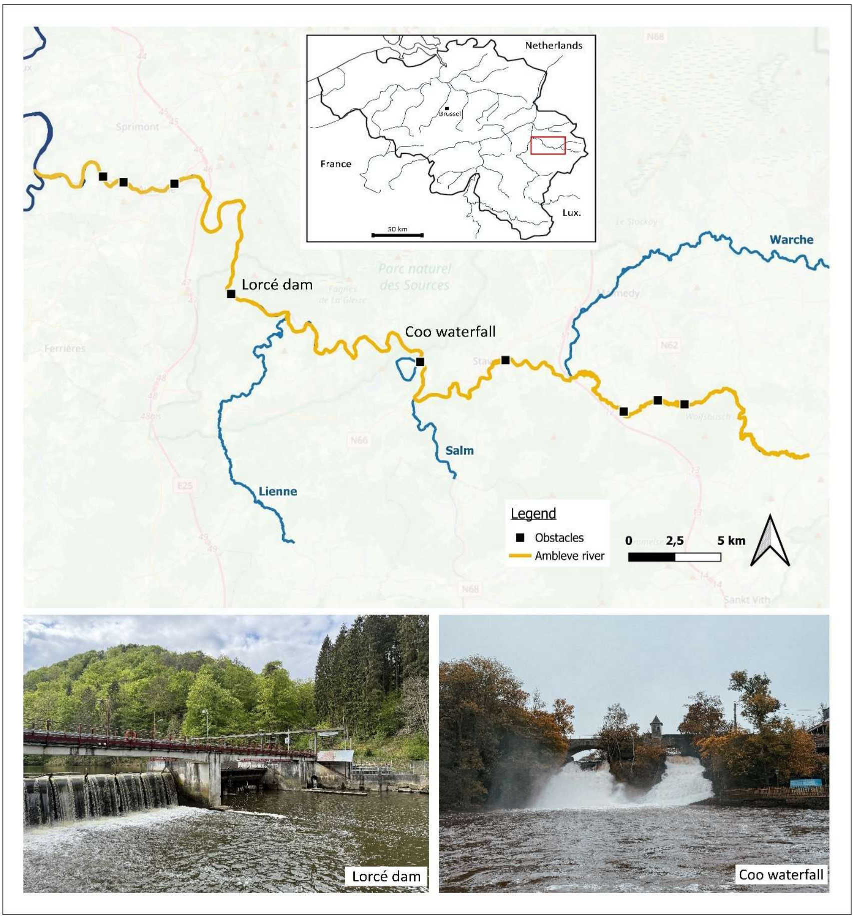

Figure 1. Map of the Amblève River and its nine barriers to longitudinal connectivity. The two study sites, Lorcé hydroelectric dam and Coo waterfall, are indicated and illustrated on the map.

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 captured 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. 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 (Gelder et al., 2024a, 2024b; Ovidio et al., 2020). 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 minutes). Once recovered, individuals were transported in oxygenated tanks and released approximately 500 metres 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 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 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 1,142 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. 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.

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	11-05-22	Coo	20	3160	0,6	620	F	26-06-25
Barbel	B2	13-05-22	Coo	20	3340	0,6	655	F	26-06-25
Barbel	B3	20-05-22	Coo	20	832	2,4	397	F+	26-06-25
Barbel	B4	20-05-22	Coo	20	3670	0,5	620	F	26-06-25
Barbel	B5	30-05-22	Coo	20	2004	1,0	527	M+	26-06-25
Barbel	B6	30-05-22	Coo	20	2674	0,7	615	F+	26-06-25
Barbel	B7	02-06-22	Coo	20	2478	0,8	568	M+	21-08-23
Barbel	B8	13-06-22	Coo	20	2622	0,8	635	M?	26-06-25
Barbel	B9	13-06-22	Coo	20	3662	0,5	644	F+	26-06-25
Barbel	B10	17-06-22	Coo	20	2542	0,8	586	F+	26-06-25
Barbel	B11	04-07-22	Coo	20	2260	0,9	582	M?	24-01-24
Barbel	B12	16-05-24	Coo	14	1664	0,8	501	I	26-06-25
Barbel	B13	16-05-24	Coo	14	1468	1,0	536	F+	26-06-25
Barbel	B14	16-05-24	Coo	14	3780	0,4	632	I	26-06-25
Barbel	B15	29-05-24	Lorcé	14	1056	1,3	440	F+	26-06-25
Barbel	B16	06-06-24	Coo	14	2668	0,5	575	F	26-06-25
Barbel	B17	19-06-24	Coo	14	3550	0,4	668	F	26-06-25
Barbel	B18	28-06-24	Coo	14	2350	0,6	582	F+	26-06-25
Barbel	B19	23-07-24	Coo	14	1940	0,7	550	F	26-06-25
Barbel	B20	01-08-24	Lorcé	14	2246	0,6	570	F	26-06-25
Barbel	B21	01-08-24	Lorcé	14	2420	0,6	590	I	26-06-25
Chub	C1	23-05-23	Coo	3.6	150	2,4	220	M+	30-05-23
Chub	C2	12-06-23	Coo	3.6	2040	0,2	531	F?	26-06-25
Chub	C3	09-08-23	Coo	3.6	278	1,3	269	I	26-06-25
Chub	C4	09-08-23	Coo	3.6	302	1,2	271	I	26-06-25
Chub	C5	16-05-24	Coo	3.6	258	1,4	269	M+	21-06-24
Chub	C6	16-05-24	Coo	3.6	236	1,5	259	M+	26-06-25
Chub	C7	16-05-24	Coo	3.6	236	1,5	260	I	26-06-25
Chub	C8	17-05-24	Coo	3.6	232	1,6	288	I	26-06-25
Chub	C9	24-06-24	Coo	3.6	332	1,1	287	I	26-06-25
Chub	C10	17-07-24	Coo	3.6	300	1,2	270	I	26-06-25

Data processing

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: individuals that remained upstream or individuals that moved downstream of the obstacle. For barbel, 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, (v) and individuals tagged at Lorcé.

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

- **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, Mann–Whitney (U tests) were performed: (i) within barbel, to statistically assess whether significant differences existed between upstream and downstream TND, and (ii) between species, to compare upstream TND of barbel with those of chub.

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' spawning period. Sex was not included as a covariate in the model due to an unbalanced number of males compared to females within 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 4,000 iterations (1,000 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 tests were performed using the R Studio statistical programme version 4.4.2 packages dplyr, lubridate, brms, loo, performance, caret, tidyr and ggplot2 and 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 (Figure 2A–B). After moving downstream of the obstacle, 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 (Figure 3A). 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 moving downstream of the waterfall, B9, B11, and B12 first settled just below the waterfall before progressively moving downstream, reaching maximum distances of 1.7 km (B9 and B12) and 2.8 km (B11). They each briefly returned to the waterfall between early May and early June (>13.5 °C; <3.7 m^3/s). 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 $m^3 s^{-1}$; 9.4 °C). In addition, B1 twice explored a tributary of the Amblève, the Salm, covering approximately 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 in the Amblève.

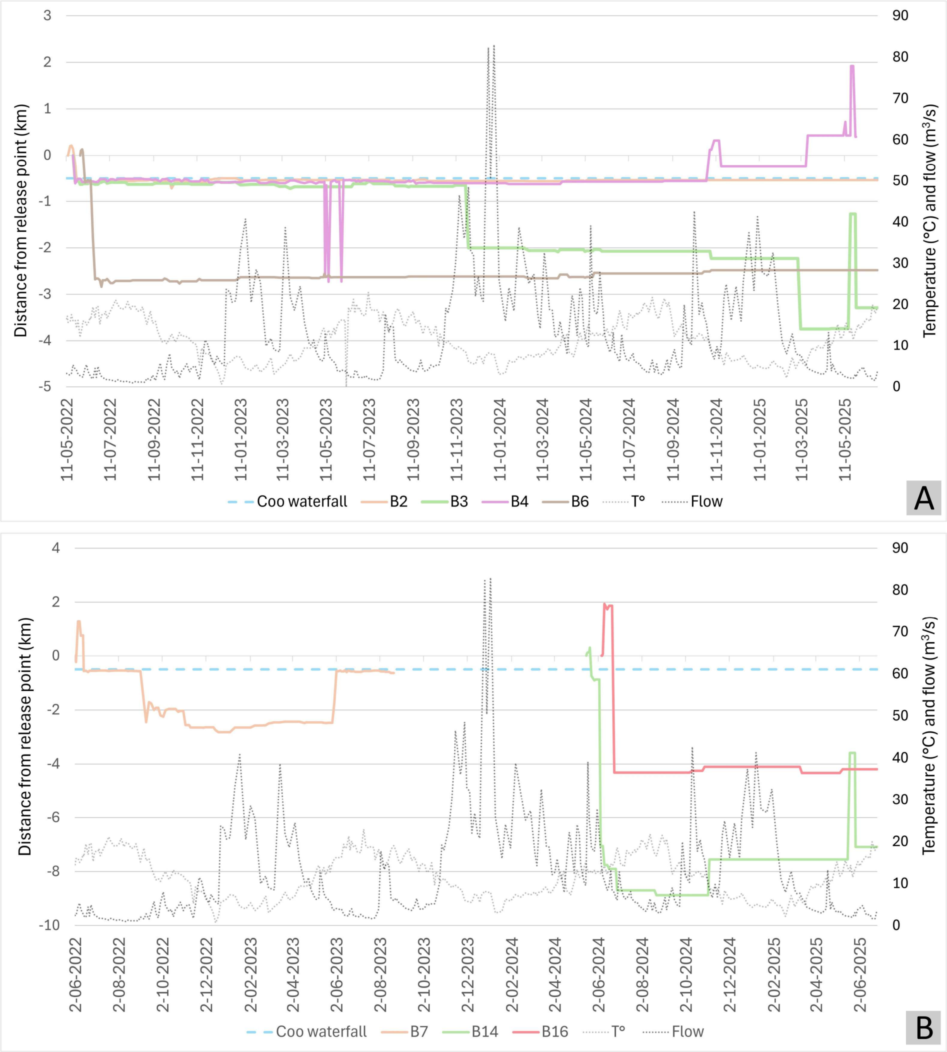

Figure 2. Positions of tagged barbel at the Coo waterfall recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the waterfall), along with water temperature (°C) and flow (m^3/s) variations over the study period.

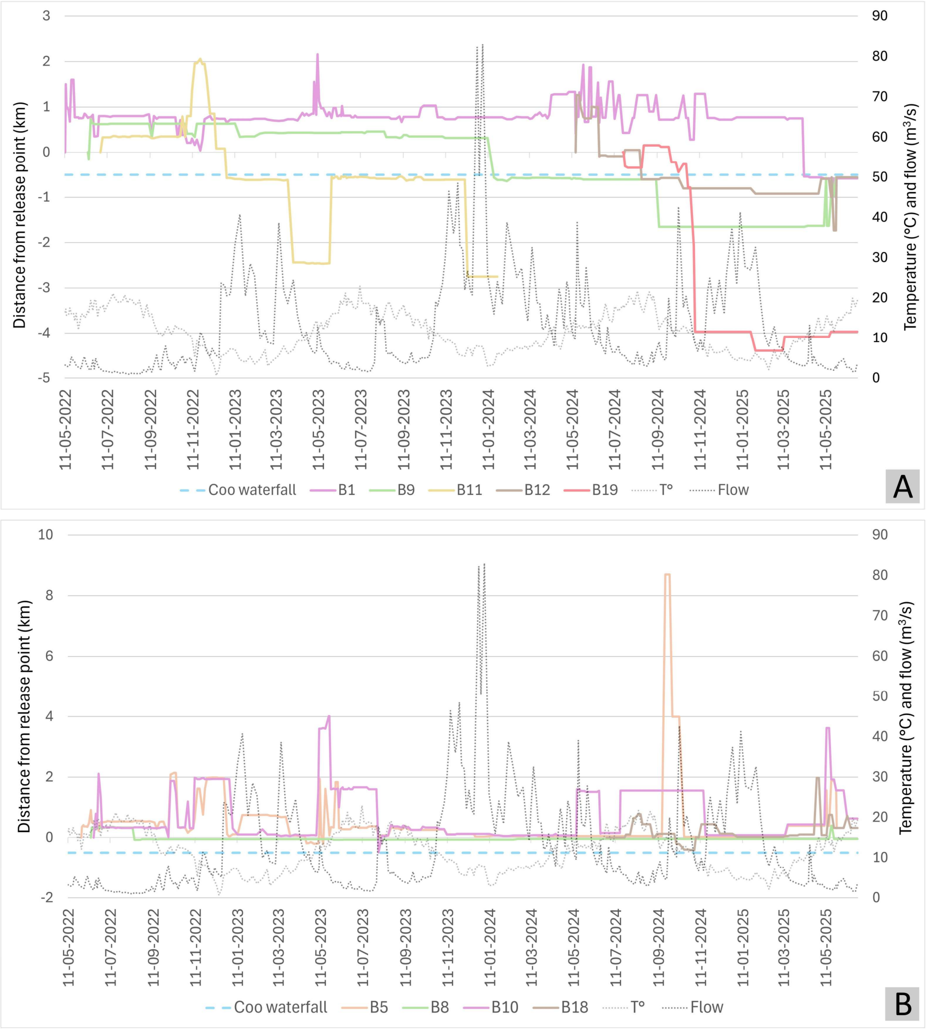

Figure 3. Positions of tagged barbel at the Coo waterfall recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the waterfall), along with water temperature (°C) and flow (m^3/s) variations over the study period.

Among individuals that remained upstream of the Coo waterfall (B5, B8, B10, B18; Figure 3B), 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 (Figure 4A). 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 moving 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 (Figure 4B), except B15, which made a brief 10.3 km upstream excursion in May 2025 (2.1 m^3/s, 14.4 °C) before returning.

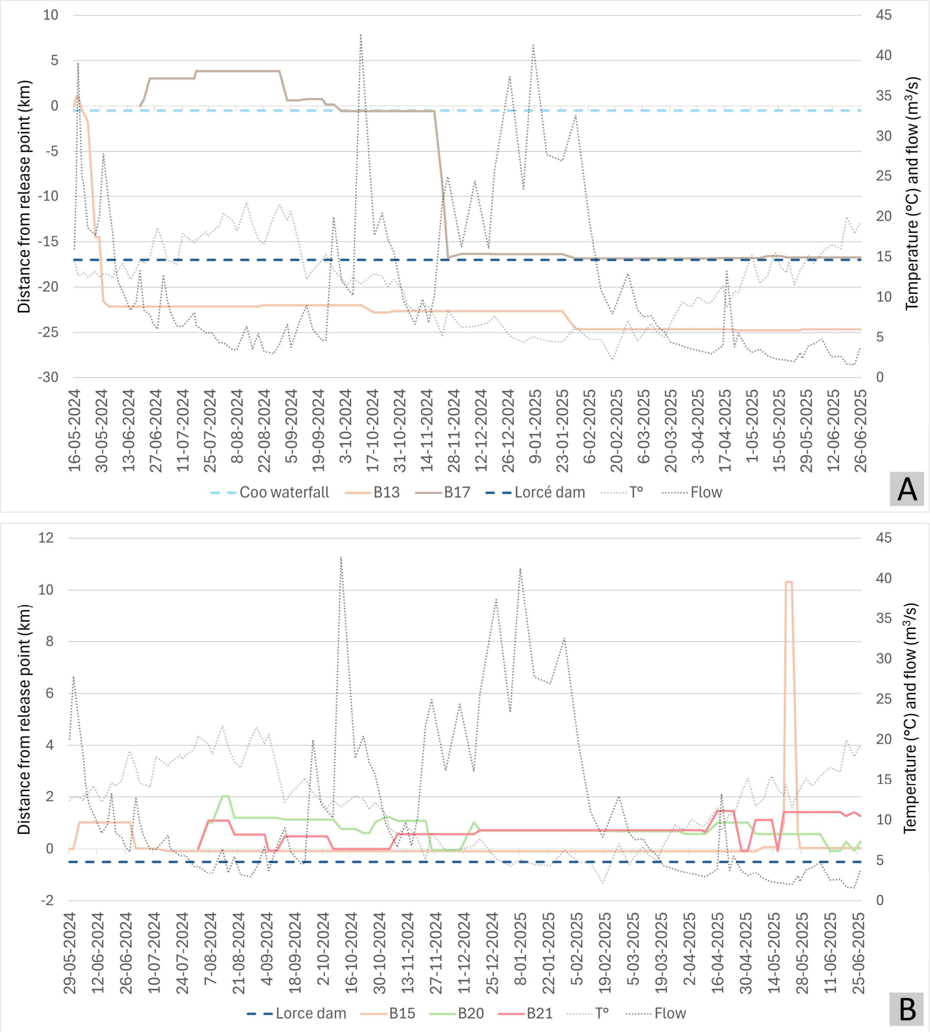

Figure 4. Positions of tagged barbel at the Coo waterfall (A) and the Lorcé dam (B) recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the obstacle), along with water temperature (°C) and flow (m^3/s) variations over the study period.

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 (Figure 5A). 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, 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 (Figure 5B). C1 moved downstream of the waterfall shortly (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.

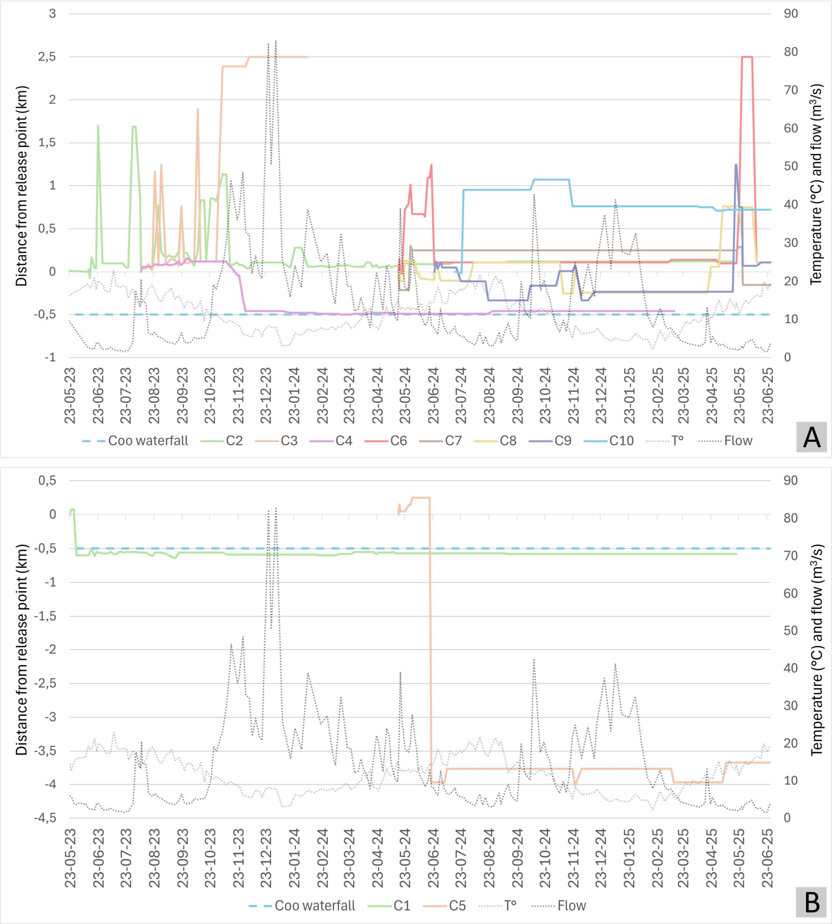

Figure 5. Positions of tagged chub at the Coo waterfall recorded during each tracking session, shown as distance (km) from the release point (0.5 km upstream of the waterfall), along with water temperature (°C) and flow (m^3/s) variations over the study period.

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 between 0.3% (B3) and 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 km 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 hydroelectric dam. The results also showed an event of fishway reuse with 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 12.12 km for C3, that is approximately 3.5 times lower than those observed for 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).

Table 2. Summary of individual movement metrics for barbel (B) and chub (C) tracked at the Coo and Lorcé sites. 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 at least one obstacle during the tracking period ("Y") or not ("N"), with the number of descents in parentheses. An asterisk (*) indicates that the individual re-used the fishway after an initial crossing.

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

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 (Figure 6).

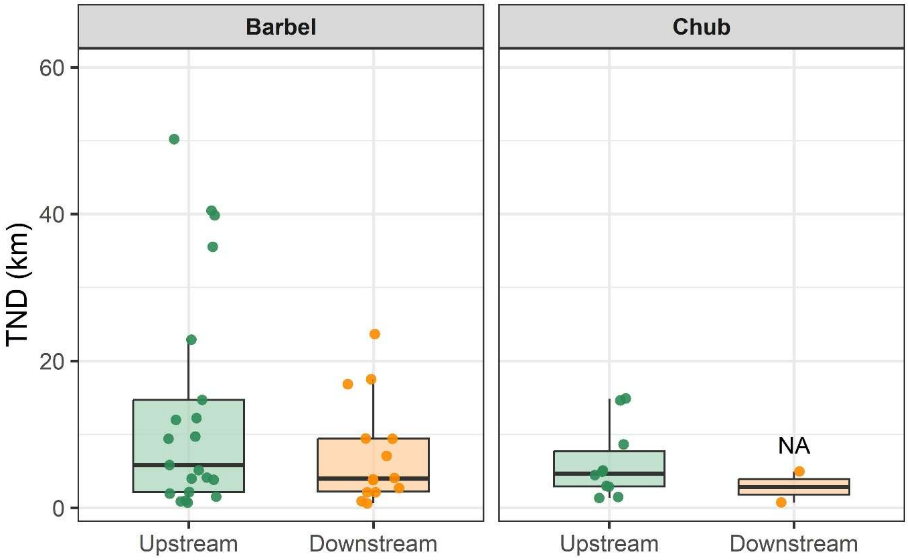

Figure 6. Boxplots of total net distance (TND, in km) travelled by individual barbel and chub upstream and downstream of an obstacle. Each point represents one individual. For chub downstream, the "NA" label indicates that data from only two individuals were available, preventing meaningful boxplot representation.

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 spawning period (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).

Table 3. Model ranking based on PSIS-LOO.

Rank	Model Formula	ELPD	ΔELPD	Stacking Weight	Number of Predictors
1	dev~deb+temp+k+sp+repro+(1|id)+(1|date)	-61,85	0.00	0.3658	5
2	dev~deb+dj+temp+k+sp+repro+(1|id)+(1|date)	-62,37	0.52	0.2184	6
3	dev~deb+dj+k+sp+repro+(1|id)+(1|date)	-63,32	1,47	0.0845	5

Posterior summaries of the final model showed that daily discharge (flow), daily temperature (temp), condition factor (K), the spawning period (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. Spawning period 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 (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; Table 4).

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.

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	R̂	Bulk ESS
sd(Intercept) date	0.83	0.61	[0.03, 2.27]	-	1.00	3 003
sd(Intercept) id	2.21	0.69	[0.96, 3.71]	-	1.00	3 517
Fixed Effects	**Estimate**	**Std. Error**	**95% CI**	**OR**	**R̂**	**Bulk ESS**
Intercept	–9.88	1.70	[–13.59, –6.96]	—	1.00	7 095
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	9 886

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 stay immediately upstream? Continue migrating? Return downstream? These questions are crucial for assessing the broader ecological impact of defragmentation. 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 exhibit the same behaviour. 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 (Benitez & Ovidio, 2018; Britton & Pegg, 2011; De Leeuw & Winter, 2008; Ovidio et al., 2007).

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; Britton & Pegg, 2011; Gelder et al., 2024b; Lucas & Baras, 2001; Panchan et al., 2022). Such behaviour is well documented in the literature, as barbel are known for their fidelity to habitats (Baras, 1998; Britton & Pegg, 2011; De Vocht & Baras, 2003; Ovidio et al., 2007; 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), 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; Capra et al., 2018; Fredrich et al., 2003). 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 (Baudoin et al., 2015; De Leeuw & Winter, 2008; Ordeix & Casals, 2024; Ovidio et al., 2023; Panchan et al., 2022), challenging the prevailing perception of limited mobility in non-salmonid freshwater fish. 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 (Capra et al., 2018; De Leeuw & Winter, 2008; 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; Benitez & Ovidio, 2018; Fredrich et al., 2003; Pander et al., 2015). 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. This entirely novel approach provides new insights into post-passage behaviour and helps to better understand the mechanisms underlying individual decision-making process. 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 (Gelder et al., 2024b; Lucas & Baras, 2001; Lucas & Batley, 1996; Ovidio et al., 2007). Although less well documented in chub, similar movements have also been observed for this species (Fredrich et al., 2003; Lucas et al., 2000). 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 (Burbank et al., 2023; Minns, 1995; Nash et al., 2015; Woolnough et al., 2009). 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 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 (Conrad et al., 2011; Elias et al., 2018; Fudali & Pietrzak, 2024; Harcourt et al., 2009; Mittelbach et al., 2014; Nakayama et al., 2012; Polverino et al., 2016; Webster et al., 2007). 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 passage, 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.

Chapter 8. General discussion

Scientific contribution and novelty of the approach

This thesis makes a significant contribution to the understanding of river habitat defragmentation processes. This research stands out through the comprehensive integration of the various phases involved in restoring connectivity, from the initial state of fish communities prior to habitat defragmentation to the behavioural responses of individuals following reconnection. While the restoration of ecological continuity has become an increasingly prominent area of study, most existing research focuses either on the performance of fishways devices or on short-term analyses of colonisation dynamics. No study has yet adopt an integrated approach encompassing the entire defragmentation process within a temporal framework as extensive and rigorous as the one employed here.

The originality of this work lies in an integrated approach, combining the analysis of fish community structure upstream and downstream of an impassable barrier, multi-year monitoring of fishway usage, and detailed study of individual behaviour following passage. While evaluating the performance of a fishway remains a central issue for validating its effectiveness, this research goes beyond this purely technical dimension by addressing the broader ecological response to the opening of a migratory axis.

Another major contribution of this thesis lies in the attention given to holobiotic potamodromous species, which are often underrepresented in the literature despite constituting a significant component of the biodiversity of European river systems. Furthermore, by adopting a multi-species approach, this research highlights both common patterns and marked contrasts between species and ecological guilds. Such a level of detail in the analysis of colonisation and passage processes remains rare, as most studies tend to focus on a limited number of target species during a single year.

Based on a unique multi-year dataset, this thesis brings to light temporal dynamics that are seldom documented in habitat defragmentation studies. Observing the processes of recolonisation and fishway use over several consecutive years reveals patterns that typically go unnoticed in short-term investigations. In this respect, the interannual dimension of the monitoring framework proves essential for understanding the actual dynamics of ecological restoration, beyond the immediate effects following the implementation of a passage structure.

These contributions strengthen the scientific foundations necessary for evaluating habitat defragmentation in river systems and offer concrete perspectives for river management and restoration. Ultimately, this thesis addresses an important gap in the literature by providing an integrated view of the defragmentation process. By focusing on the post-passage behaviour of individuals, it delivers novel and essential insights for assessing the ecological significance of restoration efforts.

Methodological choices

The methodological framework developed in this thesis was designed to understand the complexity of ecological responses to the restoration of longitudinal connectivity.

Fixed detection systems, using radio and RFID telemetry, are standard tools for quantifying fishway efficiency. They allow for the automatic detection of individual movements via antennas (located within and/or outside the fishway) and enable the calculation of key metrics such as passage success rates, transit times, or delays in locating the fishway entrance (Dębowski et al., 2022; Hatry et al., 2016; Lucas & Baras, 2001; Ovidio et al., 2017, 2023; Silva et al., 2018; Thiem et al., 2013; Tummers et al., 2016a). However, their spatial coverage is limited to the detection zone, restricted to the fishway and its immediate surroundings, and they do not provide information on individual behaviours beyond zones equipped with detection antennas. To overcome this spatial limitation and access more fine-scale behavioural information, manual radio telemetry was used as a complementary approach (Bravo-Córdoba et al., 2023; Gosset et al., 2006; Grimardias et al., 2022; Keefer et al., 2021; Lothian et al., 2020; Zampatti et al., 2018). Although still rarely employed in studies assessing the restoration of longitudinal connectivity, this method offers a major methodological advantage: it enables precise localisation of individuals in any environmental conditions and provides detailed behavioural data on dispersion, stationarity and potential movements downstream of an obstacle. These elements are essential for assessing the true ecological value of defragmentation, beyond the sole technical validation of the structure.

However, manual radio telemetry presents several operational constraints. It requires significant human effort, with regular tracking campaigns, often over extended daily timeframes and under varying field conditions. It also limits the number of individuals that can be monitored simultaneously due to its time-consuming nature (Brownscombe et al., 2019). In this study, these constraints resulted in the tracking of 37 tagged individuals over three years. This limited sample size is largely compensated by the high precision of the data collected and by the implementation of a continuous three-year monitoring effort, still uncommon, which provides essential temporal depth for analysing recolonisation dynamics.

Manual radio telemetry enabled the fine-scale characterisation of post-passage behaviours, which remain no documented in the current literature. As such, this approach represents an original and relevant methodological contribution to the evaluation of ecological connectivity restoration.

As part of this work, the status of fish populations before and after the opening of the migratory axis was assessed through electrofishing surveys. This well-established and widely used method remains a reference approach for generating quantitative fish inventories and characterising community structure (Bower et al., 2024; Cancel Villamil & Locke, 2022; Da Silva Córdova Junior et al., 2025; Gelder et al., 2025; Jones et al., 2022; Kukuła & Bylak, 2022; Tummers et al., 2016a; Whittum et al., 2023). It provided a robust baseline of fish assemblages upstream and downstream of the barrier prior to defragmentation.

Finally, the choice of a fishway monitoring based on the capture of individuals was motivated by the possibility of directly handling individuals (Benitez et al., 2015, 2018; García-Vega et al., 2022; Kotusz et al., 2006; Ovidio et al., 2023; Prchalová et al., 2011). This approach enables the collection of biometric data (length, weight and sex) and also allows the individual marking of fish. Captured individuals can also be scanned with an RFID reader to identify potential recaptures, thereby providing valuable information on individual development and on the repeated use of the fishway. It thus provides an essential complement to the study of passage dynamics by yielding more detailed information on the structure of populations using the fishway (e.g. differences between juveniles and adults), as well as on the maturity status of individuals at the time of passage. Such information provides a more precise understanding of the range of individuals and life-history stages making use of the fishway in the context of habitat defragmentation.

What happens before the defragmentation?

The defragmentation of watercourses is a gradual process aimed at restoring ecological continuity disrupted by the presence of barriers. It goes beyond the implementation of a fishway, forming part of a broader ecological dynamic that involves delayed responses from both communities and individuals. Understanding this process requires approaching it in several stages: before, during, and after defragmentation. In this context, characterising the initial state of fish communities represents a fundamental step. Documenting the structure of populations upstream and downstream of a barrier, prior to any intervention, provides a reference point, a time zero, essential for subsequent evaluation. This approach also makes it possible to measure the historical impact of fragmentation on communities, by identifying any imbalances in terms of species richness, abundance or the composition of communities between upstream and downstream of an obstacle.

Several studies focusing on habitat defragmentation have reported marked differences between upstream and downstream communities. Downstream sections tend to host more abundant, diverse, and evenly distributed assemblages, while upstream reaches are often characterised by a subset of the downstream, with a few species tending to dominate the assemblage (Anderson et al., 2006; Cancel Villamil & Locke, 2022; Da Silva Córdova Junior et al., 2025; Ding et al., 2019; Dodd et al., 2003; Gardner et al., 2013a; Jones et al., 2022; Stoller et al., 2016; Tan et al., 2024; Watson et al., 2018). For example, Stoller *et al.* (2016) recorded 37 species immediately below a low-head dam compared with 27 above it, and, on a rock-ramp fishway, richness fell from 34 species downstream to 29 upstream. Gardner *et al*. (2013a) observed the same discontinuity at a dam, species richness downstream was 9-14 species (Shannon diversity index (H') = 1.18-1.63) and 5-6 species (H' = 0.66-1.03) just upstream. At a natural barrier they found that 4 to 6 species (H' = 1.15 to 1.40) persisted above the falls, whereas 8 to 11 (H' = 1.06 to 1.41) were present below. In our study in the Amblève River, at the Coo waterfall results have likewise revealed the absence of seven species in the reach upstream of the waterfall (H’ = 1.21 upstream and 2.93 downstream). Dodd *et al.* (2003) generalised this trend across several low-head barriers, estimating an average loss of 4.1 species between downstream and upstream segments. This imbalance reflects the consequences of fragmentation on ecological connectivity, as barriers reduce access to habitats and constrain the natural structuring of communities and the gene flow that supports long-term population viability. The Coo waterfall on the Amblève River, for example, had remained impassable to upstream migration for almost 50 years, which for several species represents multiple generations of isolation. Restricted dispersal means that upstream reaches not only host fewer species but also harbour smaller, more isolated demes prone to inbreeding and the erosion of genetic diversity. Describing this initial state provides the essential baseline for assessing the impact of any future habitat defragmentation. But once the migratory axis has been reopened, what happens next? How, and at what pace, do fish communities recolonise the environment? It is precisely this defragmentation dynamic that will now be examined.

What happens during the defragmentation?

Colonisation dynamics and fishway use

Once longitudinal connectivity has been restored, it is essential to examine how fish communities respond to this reconnection. The opening of a migratory axis through the installation of a fishway provides an opportunity to observe how individuals make use of this renewed access to upstream habitats. Analysing passage dynamics such as timing, frequency of use, and species composition offers valuable insight into the underlying mechanisms of recolonisation. Analysing colonisation dynamics demands dedicated monitoring of the fishway from the moment of installation, followed by regular sampling thereafter. A multi-annual survey design is particularly valuable, although few studies have attempted it, precisely because it is time-consuming and resource-intensive, it captures year-to-year trends and covers all seasons (Iaia et al., 2025), rather than focusing solely on the main spawning period. Moreover, although multi-species studies are becoming more common and interest in potamodromous species is gradually increasing (Benitez et al., 2015, 2022; Iaia et al., 2025; Mader et al., 2020; Mallen-Cooper & Brand, 2007; Santos et al., 2007), the literature remains largely dominated by research focused on salmonids, anadromous or diadromous species (Belo et al., 2021; García-Vega et al., 2018, 2020, 2022; Hiebert et al., 2000; Legrand et al., 2020; Noonan et al., 2012; Roscoe & Hinch, 2010; Sun et al., 2023). This has resulted in a continued lack of knowledge regarding non-salmonid species.

In this thesis, we conducted multi-species monitoring in the Meuse River basin (Belgium) at four fishways, Berneau, Grosses-Battes, Lorcé and Coo over periods of six, three, eight and three years respectively. Monitoring throughout the entire year quickly showed that all fishways are used in all seasons (Benitez et al., 2015, 2022; Prchalová et al., 2011). Although captures outside the spawning months are lower, the fact that movements never truly cease underlines the need to keep fishways operational all year, rather than targeting the spawning period.

At Coo, the reopening of the migratory axis produced an additional outcome, the spirlin, a species never previously recorded upstream of the waterfall, was detected in the fishway during the first year of monitoring and increased markedly during the second. Similarly, Kiffney *et al.* (2018) showed on the Cedar River that restoring longitudinal connectivity enabled a species previously considered absent, because it had never been visually detected upstream, to recolonise that reach. In our study, pre-opening electrofishing surveys provided a comprehensive baseline of the upstream and downstream fish communities: they confirmed that spirlin were indeed absent above the waterfall and, together with subsequent fishway monitoring, allowed us to compare the river's overall assemblage with the full set of species actually using the fishway. This example demonstrates how restoring connectivity allows species that were formerly excluded to extend their distribution, exploit new habitats, and ultimately enrich the upstream community.

Extending the survey over multiple years brought other insights that a single-season study would have missed (Panagiotopoulos et al., 2024; Roscoe & Hinch, 2010). At Lorcé, for example, new species were still being captured eight years after the migratory axis was opened. Interestingly, the highest number of individuals was recorded in the first year at both Berneau and Grosses-Battes, whereas peak numbers were only observed in the third year at Lorcé and the second year at Coo. The opening effect can therefore be almost immediate, but may also appear with a delay of several years. Such lags may reflect site-specific hydraulic conditions, site design, or episodic events (for example, an entire shoal of spirlin at Coo substantially increased year-2 totals) (Benitez et al., 2015; Prchalová et al., 2011). Capture periodicity differed between sites, confirming that each operates in a distinct hydro-geomorphological and ecological context, it is essential to study each site individually, attempting to generalise across systems risks obscuring important site-specific responses. Long-term data also revealed contrasting colonisation patterns among species: some recolonised upstream habitats as early as the first year, while others required several seasons, or even several years, before their numbers began to rise. For example, at Berneau, 54% of all barbel individuals were recorded within 30 days of the migratory axis opening, whereas at Lorcé, 50% of all grayling captures occurred more than three years after the axis had been opened. These findings reinforce the importance of multi-annual monitoring to detect both immediate and delayed ecological responses following the reopening of migratory axis. Studies on fishway use are often restricted either to the spawning period or to monitoring campaigns of fewer than two years (Cui et al., 2024; Kotusz et al., 2006; Prchalová et al., 2011; Santos et al., 2002; Slavík et al., 2009). Such work provides valuable snapshots of the early stages of colonisation dynamics, yet, as demonstrated in this thesis, it can overlook slower or inter-annual processes. By contrast, multi-year surveys, such as those of Benitez *et al.* (2015, 2022), reveal both recurring year-to-year patterns (for instance, the increase in captures during the spawning season) and variations linked to environmental or physiological conditions that change from one season to the next. Having several years of data thus captures this natural variability and provides the most accurate possible understanding of the colonisation dynamics that unfold once a migratory axis has been opened.

Monitoring based on the systematic handling of individuals requires a considerable investment: several visits per week, along with the handling and measuring of each fish. For this reason, many studies today favour less time-consuming approaches such as video monitoring or automatic counters (Belo et al., 2021; Cui et al., 2024; Hiebert et al., 2000; Iaia et al., 2025; Jensen et al., 2024; Kiffney et al., 2018; Mader et al., 2020; Santos et al., 2007; Wang et al., 2025), which allow for fish passage to be recorded without the need for constant staff presence. However, direct handling provides irreplaceable added value, offering precise data on weight, length, sex, and physiological condition. It also makes it possible to mark fish with a unique PIT tag for each individual, thereby enabling the identification of potential fish re-using the fishway. Several fish previously tagged in the fishway were later recaptured, demonstrating that they were making use of the newly accessible upstream habitats and were capable of moving back downstream and returning upstream again. These recaptures therefore confirm the effective restoration of bidirectional movement between upstream and downstream sections.

Although several studies have already analysed the size of fish observed inside fishways (Benitez et al., 2015, 2022; Cui et al., 2024; Dodd et al., 2017; Eggers et al., 2024b; Iaia et al., 2025; Kotusz et al., 2006; Laine et al., 2002; Lothian et al., 2020; Mallen-Cooper & Stuart, 2007; Mameri et al., 2019; Prchalová et al., 2011; Stuart & Berghuis, 2002; Stuart & Mallen-Cooper, 1999; Weibel & Peter, 2013), ours is the first investigation carried out immediately after the reopening of a migration axis to establish which size class colonises first. By comparing these pioneer fish (i) with individuals recorded downstream before defragmentation and (ii) with those using the fishway in later years, we show that they are larger. It is therefore the migratory contingent, rather than the smaller, “resident” fish, that exploits the fishway from the outset to meet its ecological requirements (Burbank et al., 2023; Griffiths, 2006; Woolnough et al., 2009).

Three years after the migratory axis was reopened, the upstream reach already shows encouraging signs of change: alpha-diversity has increased and the assemblage is more evenly balanced. Shannon’s index has risen from 1.21 to 1.71, Simpson’s dominance from 0.39 to 0.76, and Pielou’s evenness from 0.47 to 0.71. Nevertheless, the post-opening upstream fish community remains distinct from that recorded in the fishway itself (Bray–Curtis dissimilarity index = 0.7). Alpha-diversity can respond quickly to restored connectivity through the arrival of new individuals or species upstream. Cancel Villamil and Locke (2022) observed that species richness increased markedly upstream just three months after dam removal. In contrast, a reduction in β-diversity is likely to require more time, as it depends on the progressive establishment and homogenisation of communities between upstream and downstream reaches and consequently between these reaches and the assemblages recorded in the fishway. Comparative studies of complete barrier removals often report a rapid ecological rebound, with upstream species richness increasing rapidly and β-diversity dropping gradually as upstream and downstream fish assemblages converge (Cancel Villamil & Locke, 2022; Whittum et al., 2023).

In our site, by contrast, fish must first find the fishway entrance before exploiting the upstream reach, a behavioural that can temper or delay the response and may also act as a filter, since not all individuals succeed in finding the entrance. Marques *et al.* (2018) also investigated β-diversity in the context of a fishway, analysing dissimilarity between upstream and downstream reaches. Within four years post-opening, they reported a reduction from 0.57 to 0.47, suggesting an incipient convergence. At Coo, prolonged monitoring and post-opening downstream fish surveys are therefore essential to determine whether the communities on either side of the waterfall will eventually converge.

Ultimately, reopening migratory axis triggers complex recolonisation dynamics processes that unfold on differing timescales. Yet, before we can conclude that these structures truly achieve river defragmentation, their effectiveness must be rigorously evaluated.

Effectiveness of the fishway device

Evaluating the effectiveness of a fishway facility is a crucial step in any river defragmentation process involving the installation of a fishway. Verifying whether a structure truly enables upstream migration is essential not only to validate its technical operation, but also to assess the extent to which it genuinely restores connectivity for target species. Although such evaluations are increasingly represented in the scientific literature (Bao et al., 2019; Dębowski et al., 2022; Dodd et al., 2017; Ke et al., 2024; Knaepkens et al., 2006; Ovidio et al., 2017; Romão et al., 2018; Silva et al., 2012; Stuart & Mallen-Cooper, 1999; Sun et al., 2023; Tomanova et al., 2025; Tummers et al., 2016b), their importance remains central, as they help to identify potential design limitations and guide necessary technical adjustments. In parallel, several recent meta-analyses have broadened our understanding of attraction and passage rates and now increasingly include non-salmonid species (Bunt et al., 2012; Hershey, 2021; Noonan et al., 2012; Roscoe & Hinch, 2010). However, these evaluations remain highly site-specific, and results are rarely transferable from one location to another, since fishway performance depends on numerous local factors, including hydraulic configuration, channel morphology, flow regime, and technical constraints. Consequently, a design that proves effective in one river may be entirely unsuitable in another, underscoring the need for each site and its associated fishway to be assessed within its own ecological and technical context (Martino et al., 2025).

In the literature, certain *trap-and-transport* or *trap-and-haul* systems have been described, notably in the United Kingdom and Canada, but these rely on capture methods external to a fishway structure, such as the use of nets (McDougall et al., 2013; Piper et al., 2020). They are therefore not integrated into a dedicated fishway. Additionally, other studies conducted in Australia, Canada and North America have evaluated integrated capture-and-transport systems, but these have mainly been implemented at large dams (Harris et al., 2019), or within a single-species context, most commonly for the transport of salmon, even when installed at natural barriers such as waterfalls (Hill et al., 2025; Kock et al., 2021). Such systems, however, are generally associated with significant energetic and logistical constraints, as they require sustained human intervention for their operation. In this context, the device implemented at Coo is particularly distinctive. To our knowledge, it is the only capture-and-transport fishway device to have been studied in Europe. At the global scale, the site stands out through a unique combination of characteristics: the type of device used (capture-transport consisting of two vertical slot pools), the nature of the barrier, and the multi-species design of the fishway. This work therefore represents an original and novel contribution to the scientific literature on fish passage solutions and strategies for restoring ecological connectivity.

At the Coo site, the study revealed a low fishway efficiency (7.9 %), primarily due to insufficient attraction flow. The results showed that the low current attraction in the restitution channel failed to guide individuals towards the fishway entrance, leading most fish to orient themselves instead towards the waterfall. However, despite the limited efficiency, the study highlighted actual use of the fishway by numerous species and individuals, with 21 species recorded and over 2,000 individuals captured since it was opened. These findings suggest that the observed usage reflects only a limited fraction of the fishway's true passage potential, as its functionality is currently constrained by poor attractivity. Improving these conditions would likely result in an increase in passage rates. Thus, while the measured performance remains low, the fishway can already be considered a functioning multispecies passage route, albeit underutilised.

Importantly, this work also enabled a clear identification of the fishway's limitations and led to the development of targeted recommendations aimed at improving its attractiveness. These recommendations led to work being carried out in 2024, including measures to increase the attraction flow on the bank where the fishway entrance is located, in order to recreate the attraction current that was present prior to the July 2021 floods. A new efficiency assessment is currently underway to evaluate the effectiveness of these modifications.

Having examined the effectiveness of the fishway and gained insight into the mechanisms at play during the opening of a migratory route, the next step is to focus on what happens beyond the obstacle.

What happens after the defragmentation?

Post-passage behaviour of individuals

Assessments of river defragmentation have predominantly concentrated on quantifying passage success at fishways and other connectivity restoration structures. While such evaluations are essential, they provide little information on the subsequent behaviours of individuals once upstream of a formerly impassable obstacle. Understanding post-passage behaviour, including habitat use, movement strategies, and potential return downstream, is critical for evaluating the full ecological benefits of connectivity restoration. To our knowledge, this aspect has not previously been examined in a systematic, long-term framework. This thesis addresses this knowledge gap by providing a detailed, multi-year analysis of fish behaviour following upstream passage, thereby extending the scope of defragmentation assessments beyond the point of passage itself. Continuous manual radiotelemetry proved particularly well suited for investigating post-passage behaviour, as it allows for the precise localisation of individuals and the detailed characterisation of their movements once upstream of an obstacle. Furthermore, its application over several consecutive years provided, complete monitoring records spanning up to three years, for some individuals, and three spawning seasons. Such temporal continuity is rare in fish movement studies and offers a unique opportunity to examine the recurrence of certain behaviours from year to year, reactions to environmental conditions, and long-term behavioural strategies following obstacle passage.

The multi-year radiotelemetry monitoring of five holobiotic potamodromous species revealed clear inter-individual variability in post-passage strategies. Some individuals colonised upstream habitats and remained there for extended periods, whereas others eventually moved back downstream, either immediately after passage or following an exploratory phase upstream. This pattern is consistent with homing behaviour, which is particularly well documented in barbel, a species known to return to its original habitat (Baras, 1998; Britton & Pegg, 2011; Ovidio et al., 2007; Panchan et al., 2022; Pelz et al., 2025). Repeated use of the same habitats over several consecutive spawning seasons by certain individuals further reflects strong site fidelity (De Vocht & Baras, 2003; Ovidio et al., 2007; Panchan et al., 2022) and it is plausible that some fish spawned upstream before moving back downstream of an obstacle, and subsequently attempted to return to the same spawning sites.

However, we also observed individuals that remained upstream after passage for extended periods, suggesting a functional habitat shift. This indicates that some fish found suitable habitats upstream in which to establish themselves and fulfil all of their ecological requirements. Such observations highlight the importance of maintaining complete longitudinal connectivity.

Some studies investigated fish movements following fishway passage, but with different scopes and methodological constraints, often restricted to detections at the fishway itself using fixed RFID antenna systems (Benitez et al., 2018; Ovidio et al., 2023; Tétard et al., 2025; Tummers et al., 2016a). Tétard *et al.* (2025) described several behavioural patterns, including individuals that passed through a fishway and were later detected downstream, either successfully reascending or failing to do so. However, their fixed RFID antenna system, installed exclusively at the fishway, could not determine the behaviour of individuals once passage had occurred, without additional detection points upstream or downstream, it is impossible to know whether a fish remained upstream or moved back downstream. Similarly, Tummers *et al.* (2016a) tracked trout for 63 days after passing a series of obstacles, but focused on quantifying passage success and identifying bottlenecks rather than analysing fine-scale post-passage movements or the behaviours of individuals. Together, these studies highlight that, despite valuable insights into passage efficiency, most monitoring designs still overlook the detailed behavioural dynamics occurring once fish have gained upstream access. In our study, the use of radiotelemetry overcame this limitation by revealing what happens outside the detection range of antennas, identifying in detail back-and-forth movements in front of an obstacle, indicative of active searching for a passage route, and determining whether an individual moved downstream of an obstacle or remained upstream after passage. Moreover, long-term monitoring data from the Coo fishway showed that some individuals were recaptured, sometimes repeatedly, within the fishway. In particular, one brown trout was recaptured three times over a three-month period, clearly illustrating recurrent movements between upstream and downstream sectors. This capacity to move freely between upstream and downstream habitats could promote population regulation through dispersal, reduce density-dependent pressures, and facilitate gene flow (Anderson et al., 2006; Baldan et al., 2023; Ding et al., 2019; Lange et al., 2018; Tummers et al., 2016a; Van Leeuwen et al., 2016). These findings emphasise that passage over an obstacle does not imply that individuals will remain confined upstream. Instead, they underline that river connectivity should not be viewed solely as providing access to upstream habitats, but rather as restoring the opportunity for individuals to move freely along the entire river continuum.

Beyond these behavioural patterns, movement metrics emphasise the mobility potential of potamodromous species. Home ranges could exceeded 10–20 km, with some individuals covering net distances greater than 30 km, including one nase that travelled 78 km. These findings confirm the capacity of potamodromous fish to undertake substantial movements within river systems (Baudoin et al., 2015; Ordeix & Casals, 2024; Ovidio et al., 2023; Panchan et al., 2022; Tétard et al., 2025). In addition, several individuals used tributaries of the mainstem during the spawning period, underscoring the importance of lateral connectivity for accessing suitable spawning habitats (Gosset et al., 2006; Ovidio et al., 1998; Pachla et al., 2022; Panchan et al., 2022; Popp et al., 2024).

Behavioural observations also revealed that some individuals attempted to move upstream or downstream but were blocked by impassable barriers or were unable to find the entrance to the fishway (Tétard et al., 2025; Tummers et al., 2016a). These constraints induced repeated back-and-forth movements, upstream or downstream in search of a passage, ultimately forcing individuals to abandon migration attempts and to utilise habitats within the accessible river sections. Such situations may be energetically costly, potentially leading to exhaustion and increased mortality risk (Lucas et al., 2000; Nyqvist et al., 2017; Scruton et al., 2008; Van Leeuwen et al., 2016). Repeated inter-annual use of potential spawning sites by certain individuals further suggests that restored connectivity enables fish to locate and repeatedly exploit new suitable habitats, potentially with successful spawning. Together, these results underline the ecological value of restoring and maintaining functional connectivity, not only to enable upstream access, but also to support the full range of movement strategies expressed after passage.

Factors influencing movement and downstream passage

In general terms, our results indicate that environmental variables, particularly water temperature and discharge, exert a clear influence on movement patterns. Large-scale displacements were recorded under a range of environmental conditions, yet net movements tended to be greater during periods of rising temperature and increasing discharge, supporting the view, well established in the literature, that such changes can act as stimuli for movement initiation (Britton & Pegg, 2011; Epple et al., 2022; García-Vega et al., 2022; Lucas et al., 2000; Ovidio & Philippart, 2002; Piecuch & Lojkásek, 2007). The present study, however, goes further by addressing a question never previously explored in the literature, specifically investigating the factors influencing downstream passage at obstacles. Multi-year tracking revealed that many individuals, at some stage, moved downstream of an obstacle. While downstream movements often coincided with environmental contexts linked to the spawning period (rising temperatures combined with declining discharge), consistent with post-spawning homing behaviour whereby individuals return to their original habitats. Such movements may also be influenced by physical factors such as body condition. However, our observations suggest that individual behavioural variability plays a more prominent role. This finding corroborates the idea that fish exhibit differing temperaments or behavioural types, which may shift across an individual's lifespan or in response to prevailing environmental conditions (Conrad et al., 2011; Fudali & Pietrzak, 2024; Harcourt et al., 2009; Mensinger et al., 2021; Mittelbach et al., 2014; Nakayama et al., 2012; Polverino et al., 2016). For example, Mesinger *et al.* (2021) observed in laboratory trials that eels with more exploratory tendencies were more likely to initiate an attempt to enter a fishway, although this trend was not statistically significant. Similarly, Jones *et al.* (2021) found that, in brown trout, passage success was significantly associated with the trait of boldness, suggesting that individual motivation can influence passage outcomes. In a lake in Sweden, Chapman *et al.* (2011) reported that bolder roach were significantly more likely to migrate from a lake to connected streams, independent of body size, supporting the view that more risk-prone and exploratory individuals are more inclined to undertake large-scale movements. Conversely, Lothian *et al.* (2021), after conducting laboratory personality tests to characterise individuals prior to releasing them downstream of a dam equipped with a fishway, found no significant effect of boldness on being among the first to attempt passage, instead, their results were more closely linked to discharge and body size. These differences highlight the heterogeneity of findings in the literature and the difficulty of assessing personality, particularly under natural conditions, while still suggesting that individual motivation may play a role in passage decisions and success.

In our case, the focus was on downstream movement past an obstacle rather than upstream passage. The strong influence of inter-individual variability suggests that, as in studies of upstream passage, such decisions may be influenced by personality traits. Such inter-individual differences in risk-taking or exploratory tendency are likely to shape not only the decision to move downstream of an obstacle, but also the overall movement behaviours adopted. A second hypothesis arises from the observation that moving downstream of an obstacle was positively associated with the spawning period, and that barbel in particular is known to exhibit strong post-spawning homing behaviour (Baras & Cherry, 1990; Ovidio et al., 2007). Given that barbel was the species most frequently observed moving downstream of an obstacle, it is plausible that some individuals express a more pronounced homing behaviour tendency than others. Consequently, certain fish may actively seek to return downstream to their original habitat shortly after spawning, whereas others may establish themselves upstream or move downstream of the obstacle later.

Management implications of the findings

This thesis highlights several key elements for optimising river management and the planning of defragmentation projects. It showed that, to accurately assess the real benefits of ecological continuity restoration, it is important to move beyond short-term or single-aspect evaluations. This calls for multi-annual monitoring and jointly considering both upstream and downstream movements. Multi-annual monitoring is necessary because ecological responses to restored connectivity often unfold gradually and are not always visible after a single year. Moreover, this approach allows for interannual comparisons, which are essential to distinguish long-term trends from short-term fluctuations. Similarly, considering both directions of movement is essential, since connectivity does not merely provide access to upstream habitats, but also enables individuals to return downstream and repeatedly exploit habitats along the continuum. It is also important to recognise the site-specific nature of ecological responses, results from one site cannot be directly extrapolated to others, since each site has its own topographical, hydrological and environmental particularities. Together, these recommendations already offer a more realistic and ecologically relevant assessment of restoration outcomes, helping to avoid conclusions biased by too restricted monitoring.

The results shows that fishways are used throughout the year, including outside spawning periods. From a management perspective, this strongly argues for keeping fishways operational year-round, rather than limiting their functioning to spawning migration periods only. Similarly, fishways are used by a wide diversity of species with different swimming capacities, which supports a multi-species design rather than one targeted at certain species, in order to maximise the ecological benefits of restored connectivity.

It is equally important to rigorously evaluate the effectiveness of fishways. Without assessment, facilities may be operational but fail to fulfil their ecological function, either because passage success is not optimal or because only certain species or size classes succeed to pass. Evaluating efficiency through monitoring programmes is therefore essential, both to verify that the objectives of restored connectivity are achieved and to identify potential adjustments. Such evaluations also provide critical feedback for improving future designs. For instance, the capture–transport fishway at the Coo waterfall, unique in Belgium, has demonstrated the constraints of such a system: it requires human intervention to capture and transport fish upstream, which entails heavy logistical demands. In such cases, it would be more easy at long term to envisage automated solutions, designed in coherence with the site’s typology, to ensure functionality and sustainability.

Furthermore, post-passage behavioural revealed that individuals do not necessarily remain upstream after passing an obstacle, but move between upstream and downstream, sometimes on multiple occasions, by moving downstream of the obstacle and reusing the fishway. This finding has two major implications for management: on the one hand, mitigation measures must not only facilitate upstream migration, but also include the development of safe and effective downstream passage facilities, designed not only for diadromous migrants but also for potamodromous species; on the other hand, the efficiency of these facilities must be evaluated and, if necessary, optimised to ensure their functionality.

Finally, the fact that some individuals also use tributaries to access key habitats, particularly during the spawning period, reinforces the importance of management that is not limited to the main channel of a watercourse. Restoring or maintaining ecological continuity at the scale of the entire river network, mainstems and tributaries, appears to be an essential condition for ensuring the freedom of fish movement and the full expression of their natural behaviours, even if its implementation remains complex.

Conclusion and perspectives

Beyond the results presented in this thesis, several research avenues appear particularly relevant for further assessing the benefits of defragmentation. First, it would be necessary to extend fish surveys upstream and downstream of the restored obstacles, notably through electrofishing campaigns carried out several years after the opening of the fishways, or through the use of environmental DNA (eDNA). Recently, environmental DNA has emerged as a promising tool for assessing fish communities. Initially used to detect species presence or absence (Curto et al., 2025; Daun et al., 2025; Duda et al., 2021; Griffiths et al., 2024; Yamanaka & Minamoto, 2016), this method has benefited from recent advances that move toward estimating relative abundance and even biomass of detected species (Lacoursière-Roussel et al., 2016a, 2016b; Liu et al., 2025; Muha et al., 2021). However, these quantitative applications still require further refinement and must account for confounding factors such as water temperature, discharge, species-specific shedding rates, individual body size and DNA degradation processes (Curto et al., 2025; Daun et al., 2025; Lacoursière-Roussel et al., 2016a). In the future, eDNA could offer a relevant non-invasive complementary method for monitoring changes in upstream and downstream communities following barrier removal, several years after habitat defragmentation. The monitoring already conducted upstream in this study has made it possible to highlight certain trends, but its duration still remains too short to reveal significant changes at the population level.

Prolonged monitoring upstream and downstream would provide the opportunity to quantify more precisely the evolution of fish assemblages and to establish a comprehensive link between the use of fishways by individuals and the changes observed in these communities.

Furthermore, increasing the number of tagged individuals would represent a considerable asset, despite the logistical and technical constraints this implies. A larger sample would provide more robust data, allowing a better understanding of the variability of individual behaviours and a finer comprehension of post-passage behaviours. This effort could be further enhanced by combining manual radio telemetry with automated monitoring technologies, thereby reducing the workload and time demands while maintaining detailed and reliable behavioural information. In addition, diversifying the species tagged by including smaller-bodied fishes would make it possible to obtain a more comprehensive view of how different species respond to defragmentation. Although this would require the use of smaller transmitters, implying shorter monitoring durations and weaker signal detection, it would nevertheless provide valuable insights into the reactions of a wider range of species, rather than being limited to larger-bodied individuals.

Next, innovative DNA-based approaches could offer complementary insights. The collection of DNA samples from individuals using the fishways, followed by comparisons with the genomes of juveniles or adults captured upstream in subsequent years, would make it possible to verify whether individuals actually passing the obstacle contribute to the recruitment of populations upstream. Such an approach would thus provide insight into the spawning success and allow the direct quantification of the ecological added value of fishways in terms of genetic input to upstream populations.

Finally, this thesis has shown that individuals do not necessarily remain upstream after passage, but instead carry out recurrent movements between upstream and downstream, sometimes moving downstream of obstacles on several occasions. Although in our case the individuals survived these passages, including at the Coo waterfall despite a 12 m drop, it is important to note that downstream passage can be energetically costly, or even fatal. This risk is particularly critical in hydroelectric contexts, where turbines represent a major risk. It therefore appears essential that future studies focus on downstream movements not only in diadromous species, but also in potamodromous or even multi-species contexts. Such investigations would make it possible to better assess the consequences of downstream passage at obstacles that are not yet equipped with specific facilities, particularly in terms of energetic costs or survival. This knowledge would provide valuable insights into the real impacts on individuals and could ultimately guide the implementation and improvement of downstream passage devices.

In summary, this thesis shows that river defragmentation is a broad and multidimensional process, going beyond the simple technical validation of fishways. By documenting how upstream reaches are recolonised, how fishways are used year-round by a diversity of species, and how individuals develop complex movement behaviours over multiple years, this work provides a rare, integrated view of the full defragmentation process. These findings emphasise that the ecological benefits of connectivity restoration cannot be assessed solely at the point of upstream passage. Equally critical are the range of movement strategies, the potential for downstream return, and the capacity to repeatedly exploit habitats along the river continuum. Defragmentation should therefore not be understood as a one-way opening towards upstream habitats, but as the restoration of a continuum where individuals can move freely according to their ecological needs with behavioural responses shaped by inter-individual variability. By adopting an integrated, multi-year and multi-species approach, this study offers a more comprehensive understanding of how defragmentation translates into tangible ecological benefits for fish populations, and provides a model for future restoration projects.

Chapter 9. Bibliography

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