Journal of Environmental Management 377 (2025) 124646

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Restoration of river connectivity enables long-distance spawning migrations in a potamodromous fish

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ARTICLE INFO

Keywords:
Fish pass
Weir modification
European barbel
Stable isotope analysis
Acoustic telemetry
Movement ecology

ABSTRACT

Rivers across the world are increasingly fragmented due to anthropogenic barriers, with the restoration of connectivity often using fish passes. Fish passes are, however, usually designed for anadromous species, despite ecologically important non-anadromous species being present in the communities impacted by fragmentation. To assess the outcomes for non-anadromous fishes of the installation of multiple fish passes and weir modifications, the movements of the potamodromous European barbel *Barbus barbus* were evaluated in the lower River Severn basin, western Britain, which was fragmented by six weirs (two on a tributary, four on the Severn mainstem). Movements of individual fish were measured using long-life acoustic transmitters, with stable isotope analysis assisting the assessment of individual variability in movements. The movements of three tagging groups were measured: barbel tagged in 2015 ($n = 19$; no fish passes/modifications), 2018 ($n = 19$; tributary weirs modified), and 2020/21 ($n = 20$; all Severn mainstem weirs fitted with fish passes). No fish in the 2015 group passed the weirs on the Severn mainstem, despite approaches, and only one fish in the 2018 group passed the most downstream weir during high water conditions in winter. Following the opening of all fish passes in early 2021, individuals in the 2020/21 group moved above all the weirs via the fish passes between April and June (the spawning season). These fish then moved upstream for up to 110 km, and some were detected returning downstream. These spawning migrations potentially have high ecological and evolutionary significance, indicating that reconnection schemes designed for anadromous fishes also benefit potamodromous fishes.

1. Introduction

Anthropogenic barriers in rivers, such as weirs and dams, interact with geomorphological and climatic factors to shape river dynamics, with basin morphology, sediment load, and water temperature gradients significantly influencing the impacts of the resulting river fragmentation (Valjarević, 2024). Low-head barriers (weirs, culverts, ramps and dams with head-heights of less than 2 m) are particularly common in rivers, with one barrier present every 0.74 km of river length in Europe (Belletti et al., 2020). The disruption of hydrological, geomorphological and ecological processes by these structures significantly alters the habitats available for fish with, for example, the river upstream of the barrier being impounded and characterized by reaches that are deeper, slower flowing and relatively homogeneous (e.g. Birnie-Gauvin et al., 2017; Belletti et al., 2020; Duda et al., 2021). The loss of longitudinal connectivity then severely disrupts fish movements and migrations, with

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https://doi.org/10.1016/j.jenvman.2025.124646
Received 16 December 2024; Received in revised form 5 February 2025; Accepted 17 February 2025

this considered a major threat to the populations of diadromous and potamodromous fish populations (Su et al., 2021).

Restoring habitat connectivity in highly fragmented rivers includes removing these anthropogenic barriers (Thieme et al., 2024). Barrier removal restores the natural flow regime and longitudinal connectivity, enabling the swift recovery of freshwater biodiversity and ecosystem functioning (e.g. Catalano et al., 2007; Pess et al., 2014; Ding et al., 2019). However, the societal function of many barriers (e.g. flood defences, hydropower generation) often means these structures cannot be removed and so the restoration of river connectivity requires alternative methods, such as installing fish passes (fish ladders/fish ways) on the barriers (Silva et al., 2018; Birnie-Gauvin et al., 2019). Fish pass designs can be generally classified as technical (e.g. pool-type, vertical slot), nature-like (e.g. bypass channels, rock-ramps) and special-purpose (e.g. fish lifts) (Silva et al., 2018). Designs at specific barriers are then a function of the most suitable design for that location, where the focus is usually aimed at providing passage solutions to anadromous salmonids, despite other fish species with differing traits and behaviours also potentially benefitting from the increased river connectivity (Wilkes et al., 2019).

Most fish pass studies focus on fish pass performance, where the passage rates and efficiencies are calculated (Błońska et al., 2024; Sun et al., 2023). A recent review on the use of fish passes by species of the Cyprinidae family indicated their overall passage rates can be at least comparable to anadromous salmonids, including through vertical slot passes (Błońska et al., 2024). However, knowledge on the subsequent movement and dispersal of fish using passes is also important for understanding the wider benefits of pass installation. For example, Rourke et al. (2019) demonstrated an increase in species richness and a wider distribution of fish populations only two years after the fish pass installation on a coastal river in southeast Australia. However, Kiffney et al. (2023) revealed that the recolonization of upstream reaches by three vagile fish species required at least a decade following fish pass installation on a barrier.

Although the selection pressures caused by barriers are alleviated by fish pass installation, the passes can also impose their own directional intra-specific selection pressures (Gelder et al., 2024). Many non-diadromous fish species are phenotypically diverse, with experimental studies indicating that inter-individual variability in behavioural traits is often structured on a proactive-reactive axis (Baker et al., 2018; Amat-Trigo et al., 2024a). Although selection at fish passes can be for proactive phenotypes, whose traits include boldness, high activity and large home ranges (Lothian and Lucas, 2021), evidence remains equivocal on the general direction of fish pass selection pressures (Landsman et al., 2017), especially in non-diadromous fishes. This knowledge gap occurs despite many non-diadromous and phenotypically diverse species expressing behaviours that enable some individuals to occupy large home ranges in the absence of fragmentation, including some individuals undertaking relatively long-distance migrations to specific spawning areas (Winter et al., 2021).

The aim of this study was to assess how a phenotypically diverse fish population responds to the restoration of river connectivity in a lowland river that was fragmented by multiple weirs. The focal species was European barbel *Barbus barbus* ("barbel") and the study area was the lowland reaches of the River Severn catchment that was impacted by six weirs. Three time periods were used: before, during and after the restoration of river connectivity, which was achieved via weir modifications (e.g. to a rock-ramp design) and fish pass construction (vertical slot passes and a bypass channel). Barbel is highly suited to testing the outcomes of river reconnection schemes as they are a rheophilic and potamodromous species encountered in the middle and lower reaches of many temperate rivers in Europe (Britton and Pegg, 2011). Individuals can reach lengths of 0.9 m and mass to 11 kg, and are popular for angling (Antognazza et al., 2016). Individual variability in their movements and behavioural traits is often apparent, with populations generally composed of fish with relatively small home ranges (<5 km) but with a small proportion of individuals being highly vagile with relatively large home ranges (>10 km) (Gutmann Roberts et al., 2019), with these individuals capable of making relatively large spawning migrations (Britton and Pegg, 2011). Where catch and release angling pressure is relatively high on populations, some individual barbel have diets comprising largely of angling baits, whereas others continue to mainly consume natural prey, suggesting some phenotypic diversity in their foraging that might also relate to individual differences in their movement ecology (De Santis et al., 2019; Gutmann Roberts et al., 2017). Several studies have shown that barbel can use fish passes to move upstream, primarily during the spring and summer, but with varying efficiency (Benitez et al., 2018; Lothian et al., 2019; Grimardias et al., 2022; Ovidio et al., 2017, 2020, 2023). However, these studies have not measured the effect of reconnection on the wider movements of these barbel.

2. Materials and methods

2.1. Study area

The study area covered the River Severn and its tributary, the River Teme (Fig. 1). The focal area of the River Severn was the lower, non-tidal sections, characterised by impoundment from four major weirs (downstream to upstream: Diglis, Bevere, Holt and Lincomb; Supplementary material, Fig. S1). Constructed in the 1850s, these weirs were built to make the river navigable through creating impoundments that would always be sufficiently deep for navigation and also be less prone to the effects of low summer flows. This impoundment was achieved through the construction of these concrete weirs with head-heights of at least 2 m under typical river levels. These weir head-heights, however, presented a major obstacle to the migrations of anadromous species (Antognazza et al., 2021; Davies et al., 2021). Accordingly, to facilitate the upstream passage of anadromous twaite shad *Alosa fallax* during their annual spawning seasons, each weir had a fish pass fitted recently: the Diglis fish pass (deep vertical slot, DVS) opened in April 2021, Bevere in September 2020 (bypass channel), Holt in January 2022 (DVS) and Lincomb in June 2021 (DVS) (https://unlockingthesevern.co.uk/our-fish-passes/; Table S1). The anadromous and iteroparous twaite shad enters the river in late April and May, moves considerable distances upstream to access suitable spawning areas, before moving downstream and emigrating back to the sea between June and August (Davies et al., 2021). As the presence of the weirs has severely impeded their spawning migrations and driven their population declines (Antognazza et al., 2021), river reconnection was considered necessary for their population restoration. While the passes and modification thus potentially provide twaite shad passage for up four months of the year, river resident species might benefit from the passes throughout the year.

Compared to the River Severn mainstem, the River Teme tributary provided a shallower, cooler habitat (Amat-Trigo et al., 2024b). It had two weirs in its lower reaches (Powick and Knightwick) that were obstacles to fish movements; both were highly modified in summer 2018 to facilitate passage for shad. The height of Powick Weir was lowered and the weir face removed and replaced with a rock-ramp design, with Knightwick Weir having a low gradient rock ramp constructed up to the original crest (Antognazza et al., 2021).

2.2. Fish sampling and tagging periods

Barbel is non-indigenous to the River Severn, with the population founded from approximately 500 adult fish released into the middle reaches in 1956, which established a population and then dispersed throughout the catchment (Antognazza et al., 2016). Here, all of the barbel that were tagged were captured from the contiguous river section downstream of Diglis and Powick Weirs in the lower river (Fig. 1). There were three time periods when barbel were tagged: (1) tagging year group 2015; (2) tagging year group 2018; and (3) tagging year group

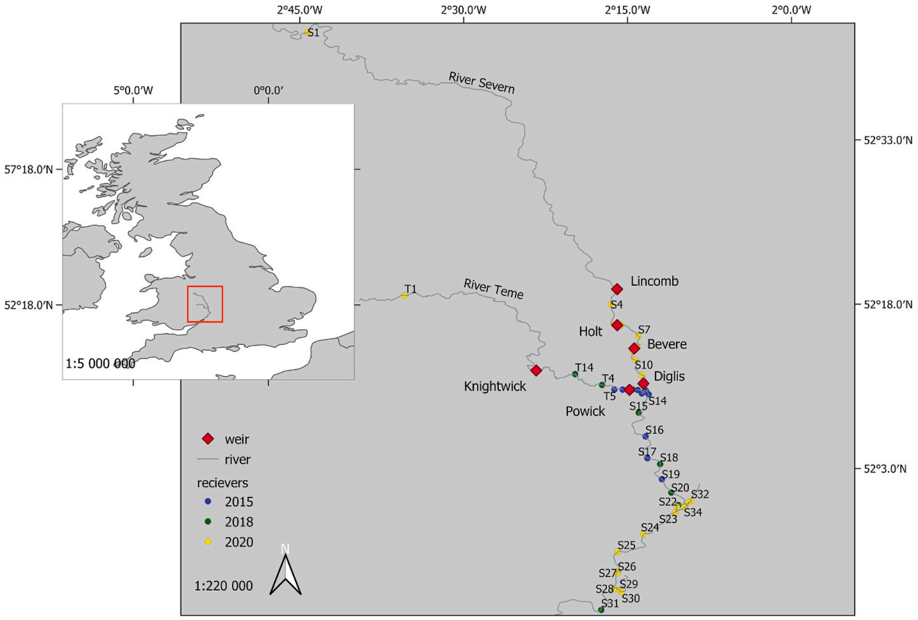

Fig. 1. Maps showing the (a) study area within Great Britain, and (b) the core research area in the Rivers Teme and Severn. The Teme flows from west to east, while the Severn flows from north to south. Due to the high density of receivers at the lower end of the River Teme and near its confluence with the Severn, some receiver positions are obscured, for more clarity on receiver number and location, see Fig. S1 and Table S3.

2020/2021 (“2020” hereafter for brevity). These tagging groups corresponded with the major stages of the restoration of river connectivity, where 2015: the collection of baseline data in the highly fragmented conditions with no weir modifications; 2018: partial reconnection achieved through the Teme weir modifications only; and 2020/2021: completion of the reconnection programme, with all Severn fish passes opened within the lifespan of the acoustic transmitters implanted into barbel. Therefore, the three tagging groups enabled the temporal and spatial assessment of the progressive effects of river reconnection for barbel.

A proportion of the barbel that were tagged were captured by electric fishing from a boat in the lower River Teme downstream of Powick Weir in September 2015, 2018 and 2020. The remaining barbel were sampled by rod-and-line angling; in the 2015 and 2018 group, the fish were angled from the lower River Teme at the same time as electric fishing. In September 2020, however, insufficient barbel were captured, so angling was repeated in March 2021 in the lower River Severn (all in the section of river located downstream of Diglis Weir) (Table S2). During angling, captured fish were unhooked on a foam mat to prevent damage and their air exposure time was minimised to reduce stress responses; no fish that were tagged subsequently were considered as being impaired by their capture by either angling or electric fishing. Across the three tagging groups, there were 58 barbel detected for at least one day across the entire study period, of which 26 were sampled by angling and 32 by electric fishing (Table S2). Their fork lengths were 295–838 mm, with those from electric fishing (EF) being significantly smaller than those angled (A) (mean fork length: 543 ± 34 mm; EF: 464 ± 37 mm; A: 639 ± 35 mm; $t_{56} = 6.97$, $p < 0.001$). The lengths of barbel across the three tagging groups (2015, 2018, 2020) were, however, similar (Fig. 2), with the differences not significant ($F_{2,\,55} = 1.57$, $p = 0.22$).

2.3. *Acoustic transmitter implantation*

Following their capture, the barbel were transferred to holding tanks (1000 l) containing aerated river water before being implanted with a Vemco V9 acoustic transmitter (“acoustic tag”). The acoustic tags were 9 × 37.5 mm, approximate weight 5 g, and operated on 69 kHz (Vemco, 2017), and coded for individual fish identification. Tag pulse delay was 60 s, providing a battery life of approximately 22 months for 2015 and 2018 fish, and at least 13 months for the 2020 fish (these tags had a temperature sensor fitted, reducing battery life). The acoustic tags were inserted into the peritoneal cavity of the barbel via a mid-ventral incision and closed with a single suture, with the fish under general anaesthesia (tricaine methanesulfonate; 0.8 g/10 L water) throughout. A 23 mm passive integrated transponder (PIT) tag was also inserted. Each fish was transferred to a recovery tank containing aerated river water, held until returning to normal swimming behaviour and then returned to the river within 500 m of their capture site. All fish were observed to swim away from the release area and were detected subsequently on at least one receiver. Information recorded for each fish was fork length (nearest mm) and method of capture (electric fishing/angling), with scale samples collected (3–5 scales collected from below the dorsal fin but above the lateral line) (Table S2). All surgical procedures were completed following ethical approval and were licenced under the U.K. Animals (Scientific Procedures) Act (1986) (project licence numbers: 70/8063 (2015), PD6C17B56 (2018, 2020).

2.4. *Acoustic receiver array*

Barbel movements were tracked through the river via detections of their acoustic tag on VR2 receivers, where the detection identified the tag number by its unique coded transmission pattern and recorded its date and time of detection. Following detection distance trials, a standard detection distance of 100 m was utilised in subsequent analyses, with the detection distances always exceeding the river width (Gutmann Roberts et al., 2019; Amat-Trigo et al., 2024b).

As all barbel were captured downstream of Powick and Diglis Weirs, the receiver arrays were designed to: (i) track movements in this river section; (ii) detect any individuals moving upstream of these weirs (ascending), and (iii) identify the extent to which they moved upstream. Across the three tagging groups, there were differences in the extent of the river covered by the array, with more receivers used in 2018 than 2015, and more in 2020 versus 2018. This related to the increased river connectivity between these groups, with more receivers deployed in upstream areas as the weirs were modified/fish passes installed. Within the focus area of each tagging group, receivers were placed upstream and downstream of each weir. Locations for receivers placed along the free-flowing stretches were chosen for regular spacing and accessibility.

Receivers were placed in deeper, slow flowing sections where appropriate to maximise detection efficiencies. Downstream of weirs, the receivers were located approximately 100–300 m away from the weir, where water turbulence and associated noise levels enabled adequate detection range. Importantly, in the 2015 and 2018 tagging groups, the most upstream receiver on the River Severn never detected a tagged barbel and so the different spatial extent of the arrays between the groups did not affect the barbel total range estimates (*cf*. Results). For the 2015 tagging group, 15 receivers were deployed through the lower River Severn and Teme, with three of these upstream of Powick Weir on the River Teme and one upstream of Diglis Weir on the River Severn and no receivers further upstream. For the 2018 tagging group, the number of receivers was increased (22) as it took advantage of tracking studies in the river on anadromous species (e.g. Davies et al., 2021). Nevertheless, the main array largely mirrored that of the 2015 fish, with additional receivers providing increased spatial resolution in the lower Severn and greater spatial coverage in upstream areas (downstream and upstream of all navigation weirs, and upstream of Knightwick Weir) (Fig. 1, Fig. S1). The receiver array for the 2020 fish was similar to 2018, but with a further increase in receiver number (46), including a receiver located approximately 100 km upstream from the fish tagging in the main River Severn, being located just downstream of the next upstream weir on the river at Shrewsbury (Fig. 1, Fig. S1).

Following installation of the Diglis fish pass, PIT tag detection equipment was immediately installed throughout the pass, primarily for the purposes of an alternative study tracking twaite shad *Alosa fallax* (J. Dodd unpublished data). The presence of this detection equipment thus also provided the opportunity to detect (via their PIT tag) whether any of the tagged barbel entered and moved through the fish pass at Diglis Weir.

2.5. *Stable isotope analysis*

The behavioural and physiological phenotypic diversity of the barbel could not be measured directly and so trait differences were inferred from their trophic ecology (stable isotope analysis, SIA). At the same time as the electric fishing, a macroinvertebrate sample was collected using kick-sampling, with *Gammarus* spp. present in all samples in high abundances. Samples of *Gammarus* spp. (minimum three replicates) were collected for stable isotope analysis (SIA), where a sample was 3–5 individuals to provide sufficient mass for analysis. As some barbel in the river have diets comprising of high proportions of angling bait (mainly pelletised fishmeal, which is isotopically distinct from macroinvertebrate prey resources through significantly higher δ^{13}C and lower δ^{15}N), samples of the pellets commonly used by anglers were also analysed (Gutmann Roberts et al., 2017; Nolan et al., 2019).

For the SIA, all the fish scale, *Gammarus* spp. and angling bait samples were dried to constant mass at 60 °C before analysis at the Cornell University Stable Isotope Laboratory (New York, USA) for δ^{13}C and δ^{15}N in a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, USA) interfaced to a NC2500 elemental analyser (CE Elantach Inc., USA). Calibration of the equipment was against international reference materials provided by the International Atomic Energy Association, with analytical precision of the δ^{13}C and δ^{15}N sample runs estimated against an internal standard sample of animal (deer) material every 10 samples, with the overall standard deviation estimated at 0.08 and 0.04 ‰ respectively. Ratios of C:N indicated no requirement for lipid normalisation (generally 3.5 to 3.9) (Winter and Britton, 2021). Due to differences in the δ^{13}C of *Gammarus* spp. between the sampling periods, barbel δ^{13}C data were converted to corrected carbon ($\delta^{13}C_{corr}$) (Olsson et al., 2009):

$$\delta^{13}C_{corr} = \left(\delta^{13}C_{fish} - \delta^{13}C_{meanMI}\right) \ / \ CR_{MI}$$

wherein $\delta^{13}C_{fish}$ is the δ^{13}C of each fish, $\delta^{13}C_{meanMI}$ is the mean δ^{13}C of the *Gammarus* spp. and CR_{MI} is their carbon range ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$)

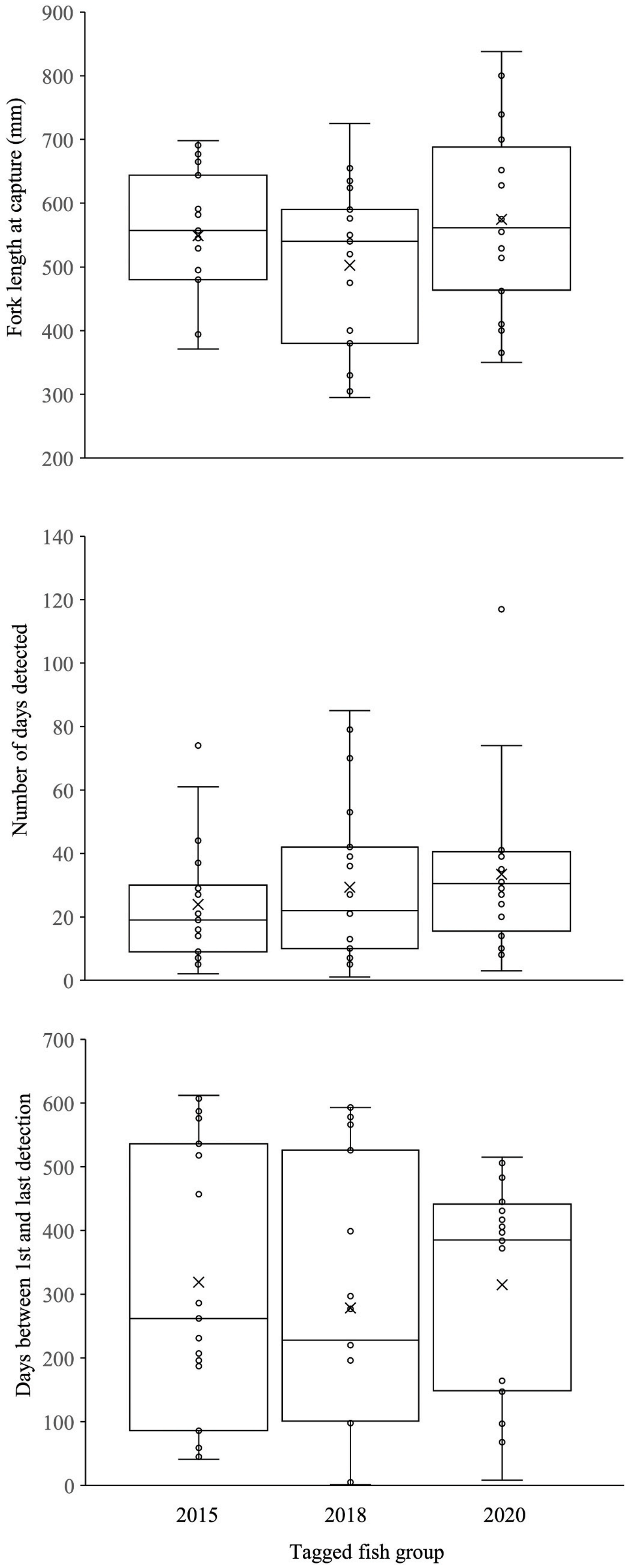

Fig. 2. Box plots of European barbel *Barbus barbus* lengths, number of detection days and the number of days between first and last detection for the three groups of tagged fish (2015/2018/2020). Horizontal lines denote the 10th, 25th, 50th, 75th and 90th percentiles, x is the mean and clear circles are the individual fish.

(Olsson et al., 2009). Discrimination factors of $\delta^{13}C$ between prey and fish consumers are generally 1–2 ‰ but can be higher for fin (e.g. up to 4 ‰ on invertebrate based diets; Busst and Britton, 2016). To provide an ecologically relevant metric based on $\delta^{15}N$, these data were converted to trophic position (TP) (Olsson et al., 2009):

$$TP = \left(\delta^{15}N_{fish} - \delta^{15}N_{prey} \ / \ 3.4\right) + 2$$

where TP and $\delta^{15}N_{fish}$ are the trophic positions and the nitrogen ratios of each barbel, $\delta^{15}N_{prey}$ is the mean nitrogen ratio of the *Gammarus* spp. and 2 is their trophic position, and 3.4 is the generally accepted fractionation factor between adjacent trophic levels (Post, 2002). Both the uncorrected and corrected stable isotope data revealed high variability between individual barbel (uncorrected: $\delta^{13}C$ range: 8.05 ‰, $\delta^{15}N$ range 4.52 ‰; corrected: $^{13}C_{corr}$ range: 1.91–17.65 ‰; trophic position range: 2.11–3.42). Individuals of lower $\delta^{13}C_{corr}$ were of significantly higher trophic position compared to fish of higher $\delta^{13}C_{corr}$ values (linear regression: $R^2 = 0.49$; $F_{1,56} = 53.41$, $p < 0.001$) (Fig. 3). This variability in the corrected SI data was important for their inclusion in statistical models on barbel movements. This is because $\delta^{13}C_{corr}$ values > 4 ‰ indicate that the individual was consuming higher proportions of allochthonous food resources – angling baits – where higher values of $\delta^{13}C_{corr}$ indicate increasing proportions of angling bait in their diet (De Santis et al., 2019). This SI individual variability was considered as potentially being driven by differences in barbel movement ecology, where fish of smaller total ranges potentially have greater proportions of angling bait in their diet due to their higher spatial encounters with anglers (Gutmann Roberts et al., 2019).

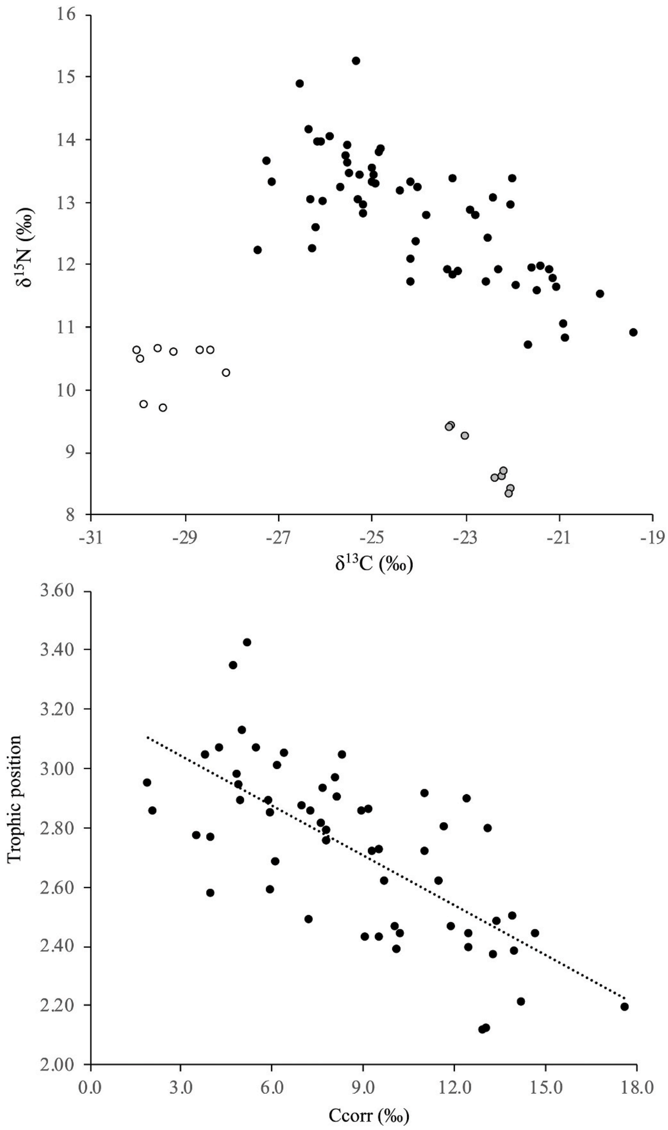

Fig. 3. Stable isotope bi-plots of European barbel *Barbus barbus* in the lower River Severn, 2015 to 2020. Top: Uncorrected stable isotope data of barbel (black circle), macroinvertebrate prey (clear circle) and angling bait (grey circle); bottom: Corrected stable isotope data (as corrected carbon and trophic position) of barbel where the dashed line is the significant relationship according to linear regression.

2.6. Fish movement metrics and analysis

The detection data downloaded from the receivers was initially checked in the *explore* function of the actel R package to remove false detections (e.g. transmitter code errors caused by code collisions) (Flávio and Baktoft, 2021). Each tagging period was analysed separately due to differences in the array receiver number. In contrast to previous studies that only used 12 months of detection data (2015 tagging group; Gutmann Roberts et al., 2019) and movement data from summer periods only (2020 tagging group; Amat-Trigo et al., 2024b), the analyses here incorporated all true detections (i.e. from tagging until expiry of the tag) (Table S2). These detection data were processed with the *detectionSummary* function from the `Vtrack` package, which integrates the detection data from across all receivers (Udyawer et al., 2018). This enabled a suite of movement metrics to be calculated for each tagged fish per tagging group (including number of days of detection, total range, total distance moved), with these metrics based on Gutmann Roberts et al. (2019) (Table S2). The distances between the receivers were computed in QGIS and given as the length of river centreline split into sections perpendicular to the deployed receivers (Pursche et al., 2013; QGIS, 2024). The river centrelines were based on Environment Agency (2024) and were extended manually based on satellite image overlay where these were incomplete. The calculated distances between receivers differed from a previous study based on the 2015 tagged fish (Gutmann Roberts et al., 2019), so there are differences in the calculated distances moved by the fish in that tagging group. The total range for each fish was calculated as the sum of the river length (main channel and tributary) it used, based on the distance between the upstream and downstream receivers where detections occurred. The total distance travelled by each fish was determined by summing all movement distances between receivers, regardless of direction.

To visualize the spatial distribution of barbel within the study area, the point density method was applied (Silverman, 1986) to plot heat maps of receiver detections for each tagging group. Each plot was developed using only locations of the receivers used for the 2015 tagging group in the areas below Powick and Diglis Weirs due to the additional number of receivers used in the 2018 and 2020 groups that would otherwise inhibit comparisons. The method specifically used kernel density to calculate point density within a set bandwidth radius (Aksu et al., 2021; Amat-Trigo et al., 2024b), with kernel density estimation (KDE) used to calculate intensity based on the distance between grid cells and the event centre (Hart and Zandbergen, 2013). This non-parametric method, which requires few assumptions about data structure, generated a density surface based on the receiver network (Silverman, 1986; Worton, 1989; O'Brien et al., 2012). The density in each cell was determined by counting the detections within the neighbourhood and calculating the point density as a ratio of detections to neighbourhood area, all using ArcMap version 10.8.2. Where flow data were used in the Results, they were used as daily mean values derived from a gauging station in the section of the river located downstream of Diglis Weir (CEH, 2024).

Differences in barbel lengths between sampling methods and tagging groups were evaluated using t-tests and ANOVA. Differences between tagging groups in days of detection and the number of receivers detecting tagged fish were assessed using Kruskal-Wallis tests due to non-normality of data. All analyses were preceded by the Shapiro-Wilk test for normality. To evaluate how river reconnection influenced the total ranges of the barbel tagging groups and to test the effect of other variables on the individual variability in movement apparent in the data (Table S2), generalized linear mixed models (GLMMs; gamma distribution) with negative binomial distribution (due to overdispersion) were used. Total distance moved was not tested in models as it was significantly and positively related to total range (linear regression $R^2 = 0.38$, $F_{1,56} = 34.05$, $P < 0.001$; Table S2). Total distance moved could also be influenced by differences in receiver density between the tagging groups, but with this not an issue for total range. Before model fitting, data exploration used the protocol of Zuur et al. (2010), which included checking for missing data, outliers in the response and explanatory variables, homogeneity, collinearity among explanatory variables, balance of categorical variables, and the nature of relationships between the response and predictors. Outliers were checked in each tagging group and removed if they were statistically significant, as tested using the Grubbs' test from the `outliers` R package, reducing the total range dataset from 19 to 5 and 7 individuals in 2015 and 2018, respectively and from 20 to 12 in 2020. Also, $\delta^{13}C_{corr}$ and $\delta^{13}C_{corr}$ TP were highly correlated ($r = 0.7$), with $\delta^{13}C_{corr}$ retained in the models. The retained fixed factors were tagging group, $\delta^{13}C_{corr}$, fork length, and sampling method (angling/electric fishing), with FishID as a random factor to account for individual variability. All candidate models were subsequently validated using the `DHARMa` package in R (Hartig and Lohse, 2022), with the *simulateResiduals* function used to simulate standardized residuals for each fitted model, enabling diagnostic checks of model assumptions. For model validation, the residuals were plotted against fitted values to assess whether they showed any systematic deviations, indicating potential misspecifications in the model structure. Additionally, the *plotQQunif* function generated a Q-Q plot, allowing evaluation of the normality of residuals. Tests for model dispersion and the presence of outliers were also conducted during this step.

In all cases, where variation is expressed around the mean, it represents 95% CI unless otherwise stated. Where median values are provided, variation is expressed as the interquartile range.

3. Results

3.1. Barbel detections and movement metrics

The barbel were detected for periods of 1–612 days, with the number of days that each fish was detected being 1–117 days (Fig. 2). The differences in the detection periods and number of detection days were not significantly different between the tagging groups ($\chi^2 = 2.17$, df = 2, $p = 0.34$). Barbel total range (TR) increased from a maximum of approximately 15 km in the 2015 group to 110 km in the 2020 group, with some increases in total distance moved (TDM) also apparent (Fig. 4). The best fitting GLMM revealed TR was significantly and positively influenced by the tagging year group and significantly and negatively influenced by $\delta^{13}C_{corr}$ (Table 1; Fig. 5). Fish length and sampling method were included in the final model but were not significant (Table 1).

3.2. Spatial occupancy and timing of weir passage

The increased TR of barbel across the tagging groups was also reflected in their spatial occupancy, with some individuals in the 2020 tagging group present much further upstream in both the River Severn and Teme (Fig. 6). Prior to the fish pass being installed on Diglis Weir, 11 individual barbel (6 from 2015 to 5 from 2018 tagging groups) had approached this weir. Only one in the 2018 group ascended the weir (Fish 11180; Table S2), doing so on three occasions in winter 2019/20 during flows of 218–402 $m^3 s^{-1}$ (Q_{50}: 53.5 $m^3 s^{-1}$; Q_{10}: 227 $m^3 s^{-1}$) but did not move any further upstream. The increased TR of the 2020 tagging group was due to three barbel ascending Diglis Weir through the newly installed fish pass (from 9 individuals that approached the weir). PIT tag detection data revealed Fish 15520 ascended through the fish pass on April 21, 2021 (mean flow: 26.9 $m^3 s^{-1}$), 15484 on May 31, 2021 (66.0 $m^3 s^{-1}$) and 15488 on June 7, 2021 (37.1 $m^3 s^{-1}$). All three fish then went onto pass the remaining upstream weirs within the study reach. The ability of these barbel to now pass Diglis Weir during relatively low flows and in their spawning period had a marked effect on TR;

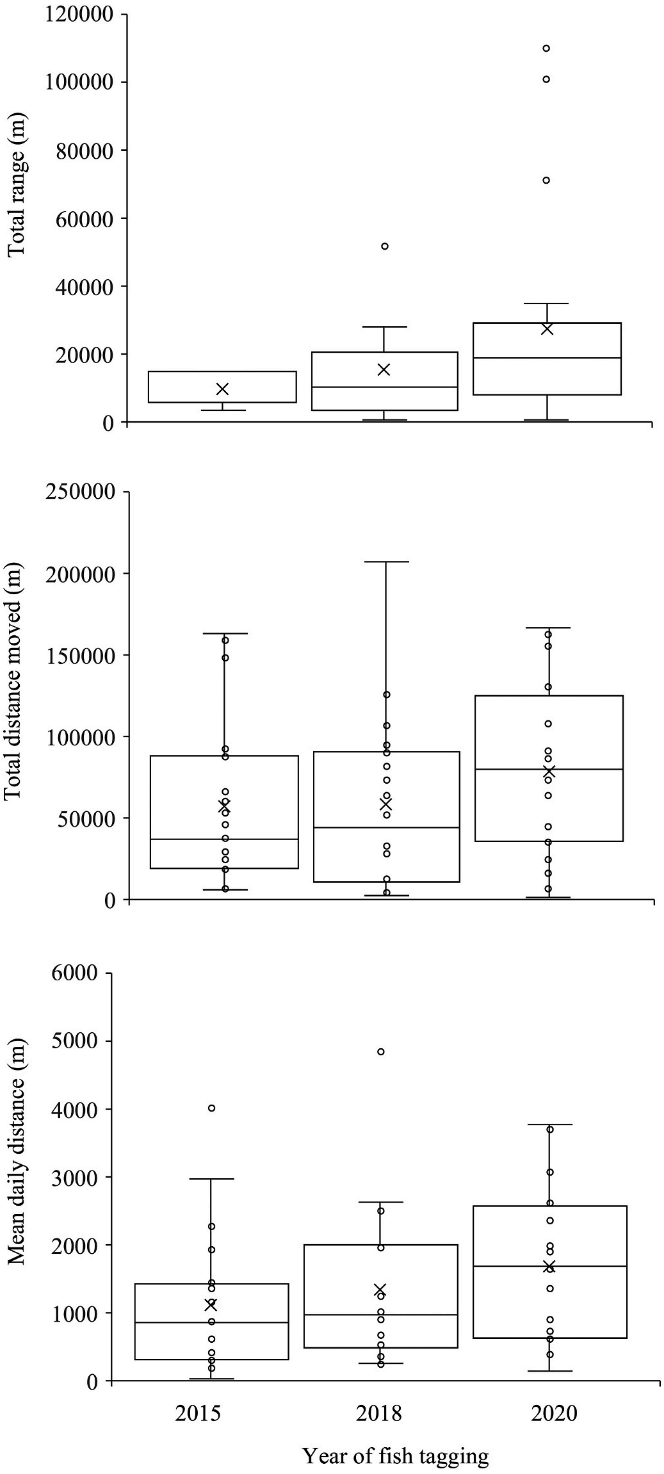

Fig. 4. Box plots of European barbel *Barbus barbus* total range and total distance moved across the three tagging groups, where horizontal lines represent to 10th, 25th, 50th, 75th and 90th percentiles, x is the mean and clear circles are individual data points.

Table 1
Results of best fitting general linear mixed models (GLMM) testing individual European barbel movement metric total ranges versus fork length (FL), corrected carbon ($\delta^{13}C_{corr}$), barbel tagging group (2015/2018/2020) and sampling method (SM), with fish identification number (N_{fishID}) included as a random variable. Significant *P* values are indicated in bold.

Coefficient	Estimates	Conf. Int (95%)	P-value
(Intercept)	10.43	8.47–12.12	**<0.001**
FL	−0.01	−0.01 – 0.01	0.581
$\delta^{13}C_{corr}$	−0.14	−0.26–−0.02	**0.019**
2018 group	0.91	0.13–1.69	**0.022**
2020 group	1.18	0.20–2.17	**0.019**
SM (EF)	−0.22	−0.96 – 0.53	0.563

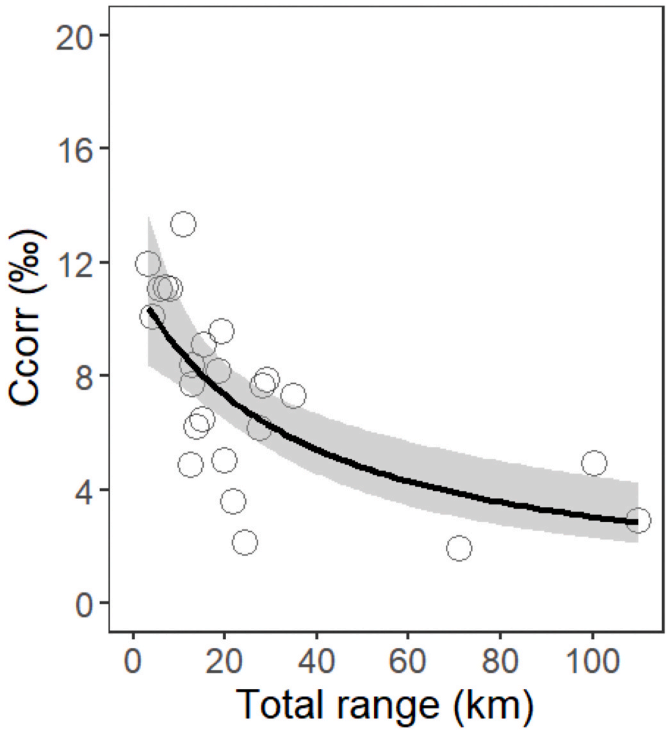

Fig. 5. The significant and negative relationships revealed by GLMM between the total range of European barbel and their corrected carbon stable isotope data (C_{corr}). The solid black line is the significant non-linear relationship and the grey shading the 95% confidence limits.

individuals that approached Diglis Weir but did not ascend had a mean TR of 14.9 ± 9.7 km (n = 12) versus those that ascended in their spawning season having a mean TR of 79.1 ± 33.1 km (n = 3). Fish 15520 and 15488 were also both recorded moving upstream through the fish pass weir in subsequent years, indicating these fish had returned back downstream of Diglis Weir after their 2021 upstream movement. The modified River Teme weirs also enabled more individuals to pass upstream (passed/approached: 2015: 3/6, 2018: 3/9, 2020; 6/7). However, the effect of weir passage on TR was less marked than for Diglis Weir (approached but not ascended Powick Weir: 9.8 ± 3.4 km, n = 10; ascended Powick Weir: 19 ± 10 km, n = 12).

4. Discussion

The impacts of habitat fragmentation can be partially alleviated through barrier modifications that help restore riverine connectivity, where modifications include reducing weir head heights and installing fish passes. Both reconnection methods were used across six weirs here to restore riverine connectivity in the lower River Severn basin. It was apparent that compared to tagged barbel in the pre-reconnection period, some of the tagged barbel in the reconnected period had substantially higher total ranges, with the largest total ranges increasing from a maximum of 15 km to over 100 km between the 2015 and 2020 tagging groups. These larger total ranges in the 2020 tagging group were due to some fish completing relatively long spawning migrations (3 individuals) that were only possible due to installation of the fish pass on Diglis Weir as it enabled weir passage during flows that were less than Q_{50}. While these fish then also moved across three more weirs upstream, the lack of PIT tag detection equipment in these passes means it can only be speculated that these barbel also ascended these weirs via the new passes rather than over the weirs. As the head height of these weirs is at least 2m, it is considered unlikely these fish ascended directly over them. Moreover, two of the fish that completed these long-distance upstream movements were subsequently detected as being back downstream of Diglis Weir through their use of the fish pass in subsequent years. Although previous studies have demonstrated barbel using fish passes (e.g. Benitez et al., 2018; Lothian et al., 2019; Grimardias et al., 2022; Ovidio et al., 2017, 2020, 2023), the novelty and significance of this study is its demonstration of how newly constructed fish passes immediately enable some individual potamodromous fish to undertake long-distance spawning migrations that previously were never recorded.

Understanding the use of fish passes can be complex given that unsuccessful passage attempts may result from various factors, including the passage design failing to meet the species' needs, lack of motivation in individuals, and/or species-specific traits that predispose them to failure (Castro-Santos and Haro, 2010). Moreover, the linear water flow

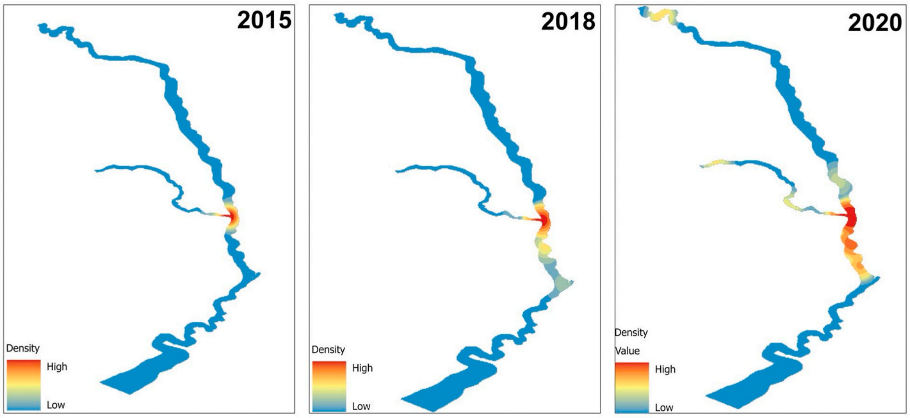

Fig. 6. Heat maps of European barbel *Barbus barbus* probability of river occupancy according to receiver detections across the three tagging groups, from blue (0) to red (1). For receivers downstream of Powick and Diglis Weirs, only receivers used in 2015 were included in plot construction.

of rivers restricts aquatic animals to movement in only two major directions, leaving no alternative routes around obstacles (Lothian and Lucas, 2021). Fish pass efficiency studies have generally focused on migratory anadromous species, which exhibit highly directed passage motivations and greater capacity to navigate hydraulically demanding environments when compared to many other species (Birnie-Gauvin et al., 2019). Much less attention has been given to non-diadromous species, despite these species needing to access spatially discrete habitats for reproduction, foraging and refuge (Birnie-Gauvin et al., 2019; Wilkes et al., 2019). Some of these species express movement patterns that are seasonally variable, with the longest distances travelled being during the pre-spawning and spawning periods (Fredrich et al., 2003; Britton and Pegg, 2011). Although it was only a small proportion of barbel that made the long-distance migrations following fish pass installation in our study, these fish potentially have high ecological and evolutionary significance. As Allgayer et al. (2021) predicted, in the absence of the upstream migration, the emigration probability of riverine fish from upstream to downstream areas is much reduced, resulting in strong patterns of spatial sorting, coupled with high philopatry in upstream areas. Thus, enabling at least some long-distance upstream dispersal enables the evolution of higher emigration probabilities to emerge in the population (Allgayer et al., 2021). Consequently, the upstream migration detected in barbel here following the installation of the fish passes could be a process that enables gene flow across their entire population, reducing spatial sorting.

European barbel populations express considerable inter-individual variability in their behaviour, with a relatively high proportion of fish being relatively sedentary, but with the remainder often being highly vagile (Britton and Pegg, 2011). For example, a tagging study on barbel in the middle reaches of the River Severn completed in the early 1970s revealed that 86 % of fish were recaptured within 5 km of their tagging site, but the remainder were recaptured up to 34 km away (Hunt and Jones, 1974). This individual variability in movement is considered to relate to the presence of a proactive-reactive axis in populations, with behavioural experiments in aquaria suggesting a range of exploratory, social and foraging behaviours across individuals that are correlated and repeatable (Amat-Trigo et al., 2024a). Consequently, we suggest that the long-distance spawning migrations detected in the 2020 tagging group and made possible by fish pass installation was at least partially related to the presence of a proactive-reactive axis in the population, where the long-distance migrants were strongly proactive individuals (high exploratory behaviours). Barbel that did not even approach Diglis Weir to attempt to move upstream would then be more reactive individuals that lacked motivation to undertake large upstream spawning migrations (Amat-Trigo et al., 2024a).

The individuals making these spawning migrations were predictable according to their stable isotope ecology at their time of tagging, but not by their length or the sampling method used to capture them. The carbon stable isotope (as $\delta^{13}C_{corr}$) indicated that the barbel that made the long-distance movements had diets based primarily on natural prey, whereas those less vagile had diets strongly influenced by angling bait. Previous studies have indicated that there is considerable variability between individual barbel in the proportions of angling bait in their diets in rivers where catch-and-release angling is practised (De Santis et al., 2019; Gutmann Roberts et al., 2019). Some barbel have diets composed almost entirely by these baits, resulting in the $\delta^{13}C$ values being similar to marine fishes due to the high fishmeal content of baits, but with other fish of similar sizes having negligible proportions, resulting in their $\delta^{13}C$ values being strongly freshwater based (Gutmann Roberts et al., 2017; De Santis et al., 2019). We suggest that the less exploratory barbel would have more spatial encounters with anglers and angling baits due to their daytime refuge areas being more easily targeted by anglers who then introduce relatively large amounts of bait to increase their catch probability (Arlinghaus et al., 2017; Monk and Arlinghaus, 2017). Conversely, barbel that are highly exploratory might have fewer angler interactions and so rarely encounter angling baits to consume. Thus, barbel stable isotope values can provide a proxy measure of their behavioural phenotype and thus their probability of making long distance movements, including for spawning.

The management programme to restore river connectivity in the lower River Severn basin through fish pass installation and weir modifications had a major effect on the movements of some barbel. Prior to these river management works commencing, the total range of river used by individuals never exceeded 15 km. Following their completion, while many barbel remained relatively sedentary and did not pass upstream, a small proportion now made movements upstream of over 100 km, with their subsequent return to their original reach of river. This research is important in its demonstration of how non-target fishes can benefit from river reconnection programmes by enabling individuals to complete volitionary long-distance spawning migrations in reaches where fragmentation previously made this largely impossible. Thus, river reconnection programmes aimed at improving the passage of anadromous species can deliver ecological benefits across the wider fish community. Although barbel have been recorded using fish passes before (e.g. Lothian et al., 2019; Ovidio et al., 2020), a novel insight provided by this study is its demonstration that the long distance migrations of the barbel were made possible only by the installation of the fish passes. These results thus emphasise that fish pass installation remains an important management tool for restoring river connectivity in highly fragmented rivers that can benefit non-target species.

CRediT authorship contribution statement

Dagmara Błońska: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Ali Serhan Tarkan:** Writing – review & editing, Writing – original draft, Formal analysis. **Demetra Andreou:** Writing – review & editing, Investigation, Conceptualization. **Jonathan D. Bolland:** Writing – review & editing, Investigation. **Peter Davies:** Writing – review & editing, Investigation. **Jamie R. Dodd:** Writing – review & editing, Investigation. **Phillipa Gillingham:** Writing – review & editing, Conceptualization. **Catherine Gutmann Roberts:** Writing – review & editing, Investigation. **Fatima Amat-Trigo:** Writing – review & editing, Investigation, Conceptualization. **Sadi Aksu:** Writing – review & editing, Investigation. **Andrew Hindes:** Writing – review & editing, Investigation. **O. Jonas Palder:** Writing – review & editing, Formal analysis. **Mark Yeldham:** Writing – review & editing, Investigation. **J. Robert Britton:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Błońska was supported by a Marie Curie Individual Fellowship HORIZON-MSCA-2022-PF-01 (project 101105250 - PROSPER) within the European Union's Horizon 2022 research and innovation programme, funded by UKRI. Tarkan was supported by TÜBITAK BIDEB (2219 Program). Amat Trigo was supported by a Marie Curie Individual Fellowship (H2020-MSCA-IF-2019) within the European Union's Horizon 2020 research and innovation programme. Yeldham was supported by a PhD studentship awarded by Bournemouth University and the Fishmongers' Company. Gutmann Roberts was supported by a PhD studentship awarded by Bournemouth University and the Severn Rivers Trust. The authors would like to thank Bartosz Janic for his help with Fig. 1. We thank all the anglers who participated in fish capture, Shaun Nurse for his organisation and all land-owners and angling clubs for access permissions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.124646.

Data availability statement

Data are available from the corresponding author on reasonable request.

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