

RESEARCH ARTICLE

Bidirectional connectivity in fishways: A mitigation for impacts on fish migration of small hydropower facilities

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Abstract

1. Most freshwater fish need to move freely through rivers to complete their life cycles. Thus, river barriers (e.g. dams, culverts and gauging stations) may delay, hinder or even block their longitudinal movements, affecting fish conservation. The most widespread solution to allow upstream fish migration are fishways, whereas downstream migration is basically facilitated through spillways, turbines or specific solutions such as bypass systems.
2. So far, studies and scientific discussions concerning bidirectional movements through fishways are scarce and focused on large dams and reservoirs, mainly with large migratory species such as salmonids, rather than smaller facilities and lesser known species.
3. This study investigated bidirectional movements through a small run-of-the-river hydropower plant with a pool-and-orifice type fishway, using the Iberian barbel (*Luciobarbus bocagei*), a potamodromous cyprinid, as the target species. Passive integrated transponder and radio tracking data were collected over 4 years and combined to characterize upstream and downstream movements. The study focused primarily on fish movements through the fishway, but also estimated the multiple associated routes of passage.
4. The results show diverse fish movements with inter- and intra-annual variability, with several individuals performing bidirectional movements and even some fish returning over the years.
5. The documented movements and observations indicate that fishways can serve as an effective bidirectional migration corridor for fish, potentially enhancing the conservation efforts for potamodromous species. This study supports the decision to use fishways as an overall mitigation tool to reduce the impact of small hydropower facilities on fish.

KEYWORDS

downstream migration, fish conservation, fish passage, PIT-telemetry, radio-telemetry, river management, upstream migration

1 | INTRODUCTION

Many freshwater fish rely on the ability to move freely through rivers to complete their life cycles, especially migratory fish that require long-, medium- or short-distance movements (Thurrow, 2016). Therefore, river barriers may delay, hinder or even block the longitudinal movements of migratory fish. This impact directly affects their reproduction, feeding and habitat use (Lucas et al., 2001; Nilsson et al., 2005). Among all the possible threats to fish, the installation of dams and weirs is known to have the most severe consequences. Dams and weirs generate a barrier effect, as well as creating a flooded area that transforms lotic to lentic habitats (Larinier, 2001). Depending on the dimensions of the flooded area and the water reservoir residence time, many fish species may not find the trophic and environmental resources to which they are adapted or require (Santos et al., 2018). Flooded areas can act as mazes where fish have few chances to find the exit to continue their way (Pelicice, Pompeu & Agostinho, 2015; Lopes et al., 2021). A holistic solution to these impacts would need to allow safe, directed, undistracted and bidirectional fish migration between different habitats (Lucas et al., 2001; Makrakis et al., 2007; Tamario et al., 2019); that is to say, it would need to allow a complete two-way migration (Calles & Greenberg, 2009; Fjeldstad, Pulg & Forseth, 2018), enabling fish to move safely both downstream and upstream of the barriers (Katopodis & Williams, 2016; Silva et al., 2018). However, despite the existence of mitigation measures at dams and weirs, they may have further implications (e.g. phenotypic selection, stress, energy expenditure or accumulative efforts) with long-term effects on communities of native fish populations (Birnie-Gauvin et al., 2017; Lothian et al., 2020; Sánchez-González et al., 2022).

The most common effort related to fish conservation in fragmented rivers is to allow upstream fish migration through fish passes (or fishways), which include various designs and devices such as technical fishways, fish lifts, nature-like channels and ramps, culverts, and mixed systems (Larinier, 2002; Makrakis et al., 2019). Technical fishways are an interesting design choice because they have shown to be a simple and functional solution for maintaining the migratory flow of fishes (Godinho & Kynard, 2008; Gutfreund et al., 2018; Bravo-Córdoba et al., 2018a). These structures consist of low-slope channels that divide the total height of a barrier in smaller water drops or reduce the velocity of water flowing through them using baffles or roughness. Numerous studies have investigated the efficiency of fishways as upstream fish passage mitigation measures, by observing the proportion of fish that pass upstream (Bunt, Castro-Santos & Haro, 2012; Noonan, Grant & Jackson, 2012; Bravo-Córdoba et al., 2021b). However, downstream efficiency of fishways has received comparatively little research attention, with most studies

focused on anadromous salmonids (Calles & Greenberg, 2009; Havn et al., 2017) and only a small number examining potamodromous fish (Gutfreund et al., 2018; Celestino et al., 2019; Sanz-Ronda et al., 2021). For downstream migration, apart from fishways, fish have other alternative routes such as spillways, turbines or specific bypass systems (Antonio et al., 2007; Celestino et al., 2019; Algera et al., 2020).

In recent years, the usefulness of fishways as two-way migration routes has been called into question, as it seems that, in some cases, they allow the bidirectional movement of fish (Makrakis et al., 2007; Celestino et al., 2020). Bidirectional fish movements are defined as successful upstream or downstream movements through the fishway, coming back to the starting point after spending a period of time on the other side of the dam (Silva et al., 2018; Celestino et al., 2019). The possibility of these movements ensures that fish, especially iteroparous species, are free to choose the better habitat (upstream or downstream) over time for feeding, shelter or even reproduction (Celestino et al., 2020).

The lack of research on bidirectional connectivity in fishways, particularly downstream movements, can be attributed to several factors, including: (i) the complexity of the problem and data analysis; (ii) the inter-annual time required for experiments; (iii) the need for fine-tuning of equipment owing to the faster downstream movements that require higher sampling rates (Castro-Santos, Haro & Walk, 1996; Gutfreund et al., 2018; Celestino et al., 2019); (iv) the resulting higher costs; and (v) the premise that fishways are designed for upstream passage, assuming that downstream migration through them is unusual (Makrakis et al., 2011; Fontes et al., 2012; Bravo-Córdoba et al., 2018a; Birnie-Gauvin et al., 2019; Geist, 2021). This argument is often reinforced by concerns about fish disorientation in reservoirs. The physical characteristics of reservoirs (e.g. extension, low visibility or flow conditions) can make it difficult for fish to find the way out upstream from the reservoir or the fishway entrance when migrating downstream (Kraabøl et al., 2009; Pelicice, Pompeu & Agostinho, 2015; Williams & Katopodis, 2016; Li et al., 2020; Lopes et al., 2021).

Although there has been some discussion and research into bidirectional movements through fishways in large dams and reservoirs, particularly in the Neotropical region (Celestino et al., 2020), it is difficult to extrapolate these findings to other studies owing to differences in region, size of the facilities and species composition and their physiological characteristics. For instance, in smaller dams and weirs (with lower reservoir residence time), which represent the larger proportion of longitudinal barriers all over the world (Makrakis et al., 2019; Belletti et al., 2020; Brewitt & Colwyn, 2020), it is possible to hypothesize that the smaller spatial dimensions of the dams could trigger bidirectional movements more

easily, thus contributing significantly to fish conservation (Santos et al., 2006). Therefore, confirming or refuting safe bidirectional connectivity in these facilities is essential.

Considering the above, this study aimed to analyse the longitudinal connectivity in a small hydropower plant (HPP) facility. The specific objectives were: (i) to study bidirectional movements through the fishway (fine spatial resolution of fish movements); (ii) to evaluate fish movements through alternative routes in the area influenced by the HPP (coarse resolution); and (iii) to consider the implications for fish conservation. For this, passive integrated transponder (PIT) and radio tracking data collected over 4 years were combined to characterize fish movements in an HPP facility located in the Duero River (Spain). The Iberian barbel *Luciobarbus bocagei* (hereafter referred to as barbel), a potamodromous cyprinid, was selected as the target species. The selection of this species was motivated by its strong migratory behaviour and the available information about its home range (Alexandre et al., 2016; Branco et al., 2017), as well as its known fishway passage performance (Sanz-Ronda et al., 2021; Bravo-Córdoba et al., 2021b). This species may be considered a representative of several medium-sized potamodromous cyprinids in the Iberian Peninsula and circum-Mediterranean region (Sanz-Ronda et al., 2019). Assessing and understanding the contribution of a fishway to bidirectional connectivity, as well as determining its limitations, is vital for identifying the need for further fish migration mitigation measures at river barriers. This, in turn, may help to define more precise conservation strategies to promote the long-term survival and sustainability of fish species.

2 | MATERIAL AND METHODS

2.1 | Study site

The HPP facility studied is located in the mainstream of the Duero River, between Guma and Vadocondes villages (Burgos) in the north-west part of Spain (41°38'13.9" N, 3°32'36.9" W; Figure 1). The river reach is limited by two dams, one 16 km downstream of the HPP facility (Aranda village) and the other 4 km upstream (Guma village), both with unfavourable fishways (Valbuena-Castro et al., 2020), thus representing the potential limits for fish dispersal. This river section is characterized by low flows in summer (4–5 m³ s⁻¹) and medium to high flows in winter and early spring (30–45 m³ s⁻¹). The fish assemblage is composed mainly of native cyprinids (*L. bocagei*, *Pseudochondrostoma duriense*, *Squalius carolitertii* and *Gobio lozanoi*) and the increasing presence of the invasive alien species *Alburnus alburnus*.

The HPP facility has an influence of approximately 3,000 m upstream of the dam (the reservoir length). The downstream direct influence extends only 300 m below the dam until the union between the tailrace channel and the natural river channel, where the river flows freely again with full discharge (Figure 1). The HPP is a run-of-the-river type with a total water height of 8.85 m and two Kaplan S

Voith turbines (total installed capacity of 2.25 MW and maximum flow discharge of each turbine of 7 and 25 m³ s⁻¹). The powerhouse is located on the left river bank, whereas on the right bank there is a pool-and-orifice type fishway. This fishway is composed of 36 cross-walls with notches and submerged orifices (FAO/DVWK, 2002) (notch width = 0.3 m; sill height = 0.8 m; orifice size = 0.175 m × 0.175 m) and 35 pools (length = 2.6 m; width = 1.6 m; slope = 8.8%) with mean water drops of 0.25 m, mean water depth in the pools of 1.2 m, mean volumetric power dissipation of 121 ± 10 W m⁻³ and total fishway length of 101 m (3D scheme in Figure 1). More details about the study site, fishway geometrical characteristics and previous fishway efficiency studies can be found in Bravo-Córdoba et al. (2018b) and Sanz-Ronda et al. (2021).

2.2 | Fish collection and tagging

Barbel were captured by electrofishing (Hans-Grassl ELT60II backpack equipment; 180–250 V and 1.5–2.5 A) downstream and upstream of the dam as well as by landing nets into the fishway between May and October of 2018 and 2019 (27 tagging events in total, Table 1). All fish were anaesthetized with eugenol (50 mg L⁻¹ diluted in ethanol in proportion 1:10, exposure time between 1 and 2 min), measured (fork length, ±0.1 cm) and intraperitoneally tagged with an HDX PIT tag (Oregon RFID®) by an incision posterior to the left pectoral fin. Tags measured 12 or 23 mm long by 2.12 or 3.65 mm diameter and 0.1 or 0.6 g (in all cases respecting the relationship of tag weight lower than 2% of fish weight). Fish were held in aerated recovery tanks (80 × 80 × 60 cm; 15–20 fish per tank) at ambient temperatures and with water supplied directly from the river. After visual evidence of recovery from anaesthetic and tagging effects (minimum recovery time of 2 h), fish were released in two locations: 700 m upstream from the dam for those fish captured downstream or 400 m downstream from the dam for those fish captured upstream (Table 1 and Figure 1). This procedure of translocation was followed to increase the probability of fish moving as a consequence of possible homing behaviour (Wagner et al., 2012; Alexandre et al., 2016; Branco et al., 2017; Bravo-Córdoba et al., 2018a; Celestino et al., 2019).

In addition, 20 barbel were double-tagged with radio transmitters (radio tags) and PIT tags: 10 in 2018 (TXC007I Scubla S.R.L.®) and 10 in 2019 (NTF-6-1 Lotek®; Table 1), half captured upstream and the other half downstream of the dam. The Scubla model has an internal coil antenna, whereas the Lotek model has an external antenna, both with a size of 19 × 10 mm (length × diameter) and a weight of 2.9 and 2.5 g, respectively. Their theoretical battery life is about 4 months (20–40 pulses per minute) and their frequency is between 151.0 and 164.2 MHz. The radio tags were implanted in the intraperitoneal cavity through an incision of about 1.5 cm (deep anaesthesia with eugenol 80 mg L⁻¹ diluted in ethanol in proportion 1:10). The wound was closed with three absorbant stitches and a liquid cutaneous suture (Wagner et al., 2011). The external antenna stood out of the body via a small incision of about 3 mm between the pelvic and anal

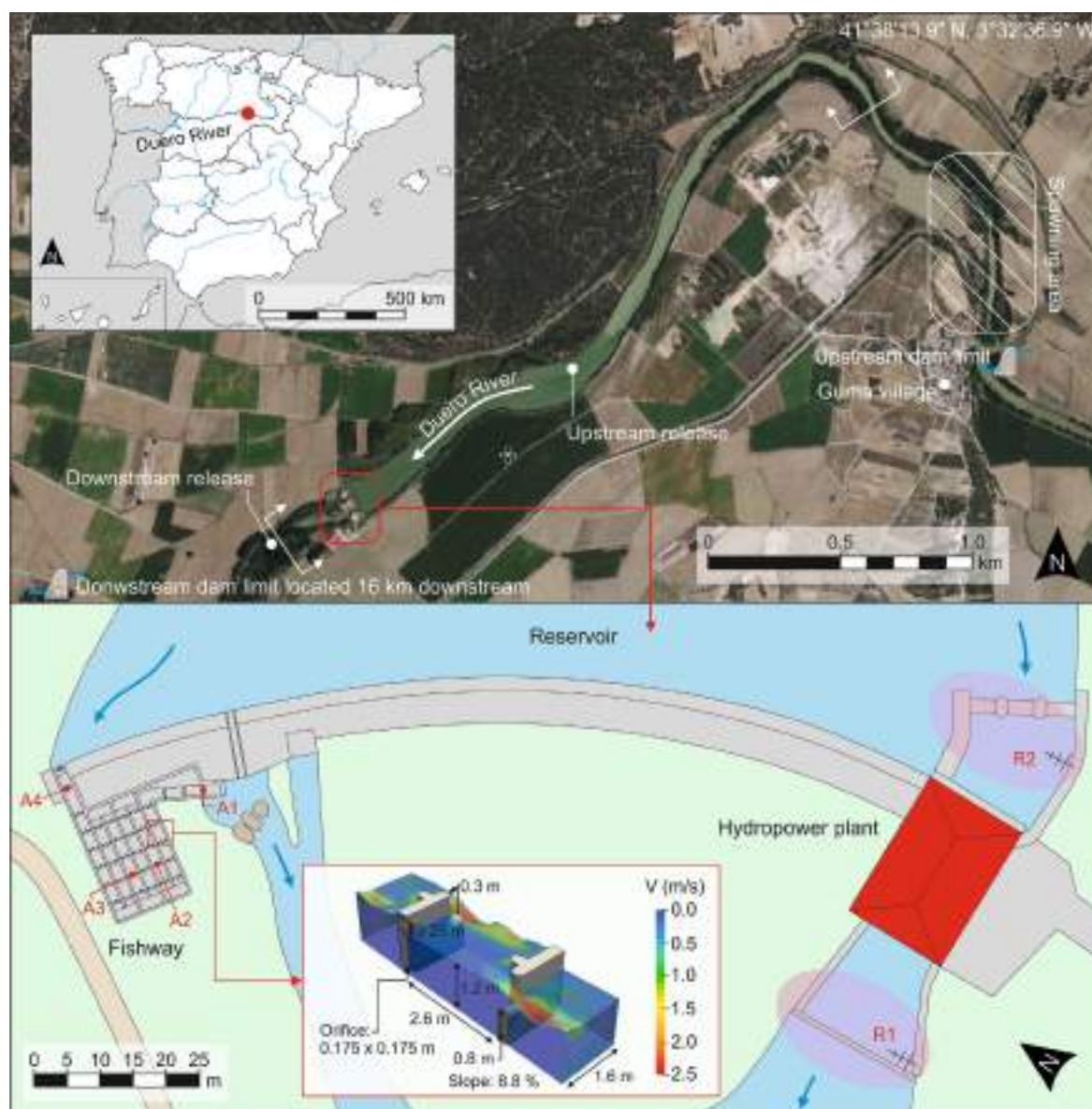


FIGURE 1 Location of the hydropower plant (HPP) complex. Upper part: orthoimage of the HPP complex, its influence area (delimited by square brackets) and the upstream and downstream fish release points. Bottom part: plan view of the HPP complex with passive integrated transponder antennas (A) and fixed radio antennas (R) location; accompanied by the scheme of the Computational Fluid Dynamic model for a straight section of the fishway (more details in Bravo-Córdoba et al., 2021a).

fins, using a catheter as a guide (this incision was without a suture because of its small size). The surgical processes were performed in a portable fish surgery box, where barbel could stay in a fixed position, with the gills completely submerged in fresh water and with continuous water oxygenation with maintenance doses of anaesthetic (eugenol 50 mg L⁻¹). The mean time of fish surgery was approximately 5 min. After surgery, the recovery of fish was confirmed and they were released following the same procedure and locations as for the PIT-tagged fish (Figure 1 and Table 1).

All experiments were performed following European Union ethical guidelines (Directive 2010/63/UE) and Spanish Act RD 53/2013, with the approval of the competent authorities (Regional Government on Natural Resources and Water Management Authority).

2.3 | Monitoring

Barbel movements were monitored from 24 May 2018 to 23 May 2021. A PIT tag antenna system was used to detect and record fish movements through the fishway (fine spatial resolution approach). Four pass-through antennas were installed in four cross-walls of the fishway, covering both the notch and the orifice. Two were located at the most downstream (A1) and upstream (A4) pools, covering the downstream and upstream fishway entrances respectively, and the others were halfway up the fishway (antenna A2 and A3; Figure 1). Antennas were connected to a reader (Half Duplex multiplexer reader, Oregon RFID®) programmed to send and receive information at 14 Hz (3.5 Hz or 0.29 s per antenna). The reader was supplied with solar

TABLE 1 Fish sample characteristics.

Month	Tag	Release place	N	Fork length (mm)	
				Mean $\pm$ SD	Range
May	Only PIT	Downstream	66	140 $\pm$ 10	88–236
		Upstream	-	-	-
	Radio and PIT	Downstream	3	248 $\pm$ 69	229–280
		Upstream	-	-	-
June	Only PIT	Downstream	142	144 $\pm$ 6	91–260
		Upstream	21	146 $\pm$ 20	77–243
	Radio and PIT	Downstream	7	224 $\pm$ 20	200–250
		Upstream	5	334 $\pm$ 93	241–420
July	Only PIT	Downstream	73	136 $\pm$ 10	92–320
		Upstream	71	132 $\pm$ 8	85–249
	Radio and PIT	Downstream	-	-	-
		Upstream	5	233 $\pm$ 29	200–255
August	Only PIT	Downstream	1	288	-
		Upstream	24	147 $\pm$ 12	112–245
	Radio and PIT	Downstream	-	-	-
		Upstream	-	-	-
September	Only PIT	Downstream	37	146 $\pm$ 11	98–210
		Upstream	125	141 $\pm$ 6	93–265
	Radio and PIT	Downstream	-	-	-
		Upstream	-	-	-
October	Only PIT	Downstream	26	126 $\pm$ 10	93–189
		Upstream	21	142 $\pm$ 16	99–229
	Radio and PIT	Downstream	-	-	-
		Upstream	-	-	-
GLOBAL	Only PIT ^{a,c}	Downstream	345	141 $\pm$ 4	88–320
		Upstream	262	140 $\pm$ 4	77–265
	Radio and PIT ^{b,c}	Downstream	10	231 $\pm$ 18	200–280
		Upstream	10	283 $\pm$ 54	202–420

Note: Tag: type of tag used for fish monitoring. Release place: release location relative to the dam location. N: number of available fish. Range: minimum–maximum.

Abbreviations: PIT, passive integrated transponder; SD, standard deviation

^aThere were no significant differences in fork length between release places for the PIT-tagged fish ($P = 0.706$).

^bThere were marginal significant differences in fork length between release places for the radio-tagged fish ($P = 0.052$).

^cThere were significant differences in fork length between fish tagged with PIT and radio ($P < 0.001$).

power and lead-acid batteries connected via a charge controller (power of solar panel of 140 W and capacity of the battery of 110 Ah), allowing continuous operation throughout the year, except for some night hours from mid-November to mid-February (approximately between 2:00 and 8:00 AM depending on how sunny the day was), and during January and February 2020 (as a result of extraordinary flood events). The system was functional for about 98% of the study period.

In addition, radiotracking was used to detect other possible migration routes (coarse spatial resolution approach). From June to October (2018 and 2019), mobile radiotracking (walking near the river bank) was carried out once or twice a week with a three-fold element Yagi antenna and a VHF portable receiver (Telenax[®] R-1000) in the

river reach located 4,000 m upstream and 3,000 m downstream from the HPP. From 17 May to 5 November 2019, two stationary radiotracking stations (Datasika SRX400 Lotek[®]) were also used to monitor possible passes through the turbines, one installed just downstream (antenna R1) and the other one upstream (antenna R2) of the turbines of the HPP (Figure 1).

2.4 | Data processing

Data recorded by antennas were classified considering the following criteria for the different metrics used:

1. 'Fishway downstream or upstream location' was assigned to those fish with at least one record at the uppermost antenna (A4; fishway location during the downstream passage) or the lowermost antenna (A1; fishway location during the upstream passage), respectively.
2. 'Fishway downstream or upstream entry' was assigned to those fish with records in A4 and A3 (and/or A2) during the downstream passage or in A1 and A2 (and/or A3) during the upstream passage, respectively.
3. 'Successful fishway downstream or upstream passage' was assigned to fish with records in A1 and A4, and at least one in A2 or A3 (if upstream the sequence was A1-A2-A3-A4 and if downstream A4-A3-A2-A1, respectively). To ensure a successful passage, those fish that passed the last antenna but turned back in less than 2 h were excluded (failed passage attempt), according to the criterion used in Celestino et al. (2019). This conservative calculation aimed to ensure that no fish remained in the first or last pool of the fishway after passing the first or last antenna.
4. 'Fishway bidirectional movements' were assigned to those fish that completed an upstream or downstream passage through the fishway and returned at an interval greater than 7 days completing again the inverse upstream or downstream passage of the fishway. This period of 7 days was established according to the criterion used in Celestino et al. (2019) and Frechette, Goerig & Bergeron (2020), so as not to account for possible fallbacks (successful fishway passages with returns between 2 h and 7 days). This criterion aimed to minimize the allocation of bidirectional movements to fish that successfully passed upstream and downstream of the fishway but were unable to leave the area of influence of the HPP facility and reach the natural sections of the river and thus have the choice of completing their life cycles. It is worth mentioning that 7 days were considered for conservative and comparative reasons, as different HPP facilities may have different fallback limits, depending on their spatial influence (see Section 2.5).
5. 'Record in another year' was assigned to those fish with any record at any antenna in more than one calendar year.
6. 'Downstream passage through the turbines-spillway' was defined using several criteria:
 - For radio-tagged fish: it was assigned to those fish with detections first in R2 and then in R1 or A1.
 - For PIT-tagged fish it was assigned to:
 - Those fish that were released upstream of the dam and had the first record in A1.
 - Those fish with previous records in A4 and subsequent records in A1, without records in A2 and A3, and with an elapsed time between them of at least 24 h (this time is above the 90th percentile of the transit time of the downstream passage for this fishway; Sanz-Ronda et al., 2021). It was considered for conservative and comparative reasons.

It is important to note that not all downstream movements could be identified. As PIT antennas were in the fishway, some barbel

could have descended through the turbines or spillways, but if they neither approached nor entered the fishway, they could not be accounted for as downstream passage events.

7. 'Location time of the fishway' was calculated based on the elapsed time between the release and the first detection at A1 (upstream passage) or A4 (downstream passage). Therefore, location time refers only to the closest fishway location event from the release.
8. 'Return time for those fish with fishway bidirectional movements' was obtained as the difference from the time between the last record of a successful downstream or upstream passage event and the first record of the next successful upstream or downstream passage event, respectively (considering the return interval criterion of at least 7 days). This metric was subdivided as:
 - 'Intra-annual': those that happened in the same year.
 - 'Inter-annual': those that happened between different years.

2.5 | Data analysis

To check possible differences in the proportion metrics (fishway location, fishway entry, successful fishway passage, fishway bidirectional movements, record in another year, downstream passage through turbines-spillway) between release zones (upstream vs. downstream) and/or tag type (only PIT vs. radio and PIT) the chi-square test of independence was used.

In addition, a Mann-Whitney *U* test was used (owing to the non-normality of the data) to evaluate if there were any significant differences in time-related metrics (location time of the fishway, return time for fishway bidirectional movements, both intra-annual and inter-annual), selecting one event per fish (the first event). For avoiding the possible bias resulting from the date of fish release in the analysis of location time, when comparing PIT-tagged fish to radio-tagged fish only fish released in the same period (from May to July) were considered.

To evaluate the potential impact of selecting different time periods for defining fallbacks (e.g. 7 days) on the number of counted bidirectional movements, a frequency distribution curve was used. This analysis examined the evolution of the number of bidirectional movements in relation to various possible time periods.

All data analyses were performed in Statgraphics Centurion statistical software (Statgraphics Technologies, Inc., The Plains, Virginia, USA; Version 19).

3 | RESULTS

In total, 627 barbel were captured and tagged (607 with only PIT and 20 double-tagged with PIT and radio tags; Table 1). During the monitoring period, 55.5% of those fish released below the dam located the fishway via the downstream route, whereas 41.2% of those fish released above the dam located it via the upstream route (Table 2; metrics related to fishway location). Most of them, as well as

locating the fishway, managed to enter it (95.4% for downstream and 86.4% for upstream), and more than half performed successful passages (50.4% for upstream passage and 61.0% for downstream passage; Table 2; metrics related to fishway entry and successful passage). In addition, fishway bidirectional movements were confirmed for the 7.7% of fish that made any movement registered by the antennas (33/(260 + 169); Figure 2), and evidence of fish returning to the fishway another year was also found (9.6% of the total fish tagged; Table 2).

There were no significant differences by tag type for most proportion metrics, except for the successful fishway upstream passage and the passage through turbines–spillways, where, despite the lower number, the proportion of radio-tagged fish was significantly greater. In addition, and as expected, for both tag types the fishway downstream location was significantly greater for those fish released downstream, whereas the upstream location and entry were significantly greater for those fish released upstream (Table 2). The diversity and complexity of the barbel movements observed in the HPP facility are shown in Figure 3 (focus on fish tagged only with PIT), separately for those released downstream and upstream of the dam, shown diagrammatically.

Owing to limitations in the monitoring system, it is possible that passage through the turbines–spillways was underestimated. If a fish tagged only with PIT descended through these routes and did not return to the fishway afterwards, then it could not be taken into account as there were no records that would allow its passage to be confirmed. However, the following estimation could be made. Considering a similar probability (P) of fishway location after a descent event for those fish moving through turbines–spillways and through the fishway (i.e. $P(\text{Fishway location after fishway downstream passage}/\text{Fishway downstream passage}) \approx P(\text{Fishway location after turbine–spillway downstream passage}/\text{Turbine–spillway downstream passage}) \rightarrow (16 + 41)/(66 + 36) \approx (32/\text{Turbine–spillway downstream passage})$). If the unknown quantity is solved, potentially 57 fish could descend through the turbines–spillways route. This would represent 36% of the total downstream passage ($57 * 100/(102 + 57)$).

Regarding metrics related to time (Table 3), there were no differences in the location time of the fishway by tag type. Nevertheless, significant differences were observed depending on the release zone for PIT-tagged fish. Fish released upstream needed 2 days to locate the fishway, being significantly lower than the location time for fish released downstream of the dam, which needed 9 days. Regarding bidirectional movements through the fishway, radio-tagged fish did not provide information. PIT-tagged fish took a median of 17.7 days in returning to the fishway in the same year and 218.9 days (≈ 7.7 months) between different years, with no significant differences between fish that remained in the upstream or downstream zone during the no-detection period. In this regard, most fish remained downstream of the dam in this inter-year period (Figure 2), mainly coinciding with the winter season, whereas more variability in the area where they remained was observed within the same year (Figure 2).

Regarding the time criteria used for the definition of bidirectional movements and the passage through the turbines–spillway, Figure 4

shows the frequency distribution of all these possible movements. Specifically, Figure 4a represents the probability of fish to stay upstream or downstream of the fishway for a certain number of days between successful fishway passages. They are related to bidirectional movements and their link to the possible fallbacks, probably caused by behaviour in response to the new environment or a mechanism of homing (Frank et al., 2009). As can be seen, there is an initial accelerated decrease in the curve until a first probability plateau is reached from 3.5 to 7 days, being the criterion adopted for assigning bidirectional movements (7 days) in the upper limit and therefore being conservative. By contrast, Figure 4b represents the probability associated with the transit time of all the fishway downstream passages. Again, there is a clear initial decrease in the curve with a significant change in slope and beginning of the plateau before 24 h (coinciding with criterion 6 of data processing for assigning passage through turbines–spillway for fish with records in the uppermost and the lowermost fishway antennas). These curves give a unique and study site-dependent signature of their metrics and their relationships with time variables that define them.

The results of distance travelled by fish (assessed via mobile radiotracking; Figure 5) showed that 35% (7/20) crossed the reservoir and reached the spawning areas just below an impassable dam located 4,000 m upstream from the HPP facility, spending a median time of less than 7 days in performing this migration, whereas 45% (9/20) moved 500 m downstream from the dam. However, most of the fish that approached the dam from downstream (six out of seven fish) did it by the fishway branch instead of the turbine outlet (Figure 1).

4 | DISCUSSION

Fishways are one of the most common tools for mitigating impacts on longitudinal connectivity. Most studies related to fishway effectiveness have focused on upstream pre-reproductive movements (Noonan, Grant & Jackson, 2012; Bunt, Castro-Santos & Haro, 2016; Hershey, 2021; Bravo-Córdoba et al., 2021b), while downstream migration remains almost unexplored and mainly focused on anadromous salmonids or large dams in Neotropical rivers (Pelicice, Pompeu & Agostinho, 2015; Havn et al., 2017; Havn et al., 2020). The number of studies on bidirectional connectivity in the same stream is decreasing and continues to focus on the same type of location or species (Calles & Greenberg, 2007; Reischel & Bjornn, 2011; Celestino et al., 2019; Snow & Goodman, 2021). However, this does not stop researchers from hypothesizing about two-way connectivity and it is possible to find many current works discussing the phenomenon (Katopodis & Williams, 2016; Fjeldstad, Pulg & Forseth, 2018; Silva et al., 2018; Pelicice, Pompeu & Agostinho, 2020), illustrating its interest and importance. On this basis, the overall aim of this study was to analyse bidirectional movements in the framework of a small HPP and, more specifically, to show the relevant role that fishways can play in mitigating the impacts of hydropower. The results show a variety of barbel

TABLE 2 Results of metrics (shown as a proportion, with the detail of the individuals taken into account for the calculation between brackets) by tagging type and release zone (downstream and upstream takes as reference the location of the hydropower plant facility under study).

Metric	Total	Release zone				
		Radio and PIT			Radio and PIT	
		Global - Only PIT (N = 607)	Global - Radio and PIT (N = 20)	Only PIT	Downstream (N = 345)	Upstream (N = 262)
Fishway downstream location	41.5% (260/627)	42.0% (255/607) P = 0.132	25.0% (5/20)	55.9% (193/345) P < 0.001	40.0% (4/10) P = 0.029	10.0% (1/10)
Fishway upstream location	27.0% (169/627)	27.2% (165/607) P = 0.467	20.0% (4/20)	16.5% (57/345) P < 0.001	0.0% (0/10) P = 0.025	40.0% (4/10)
Fishway downstream entry	95.4% (248/260)	95.3% (243/255) P = 0.634	100% (5/5)	95.9% (185/193) P = 0.345	100% (4/4) P > 0.999	100% (1/1)
Fishway upstream entry	86.4% (146/169)	86.7% (143/165) P = 0.527	75% (3/4)	73.4% (42/57) P = 0.002	NA (0/0) NA	75.0% (3/4)
Successful fishway upstream passage	50.4% (131/260)	49.4% (126/255) P = 0.026	100% (5/5)	47.7% (92/193) P = 0.343	100% (4/4) P > 0.999	100% (1/1)
Successful fishway downstream passage	61.0% (103/169)	61.8% (102/165) P = 0.141	25.0% (1/4)	63.2% (36/57) P = 0.904	NA (0/0) NA	25.0% (1/4)
Fishway bidirectional movement	5.3% (33/627)	5.4% (33/607) P = 0.284	0.0% (0/20)	4.6% (16/345) P = 0.319	0.0% (0/10) P > 0.999	0.0% (0/10)
Record in another year ^a	9.6% (60/627)	9.7% (59/607) P = 0.480	5.0% (1/20)	7.8% (27/345) P = 0.071	0.0% (0/10) P = 0.305	10.0% (1/10)
Passage through turbines-spillway	5.9% (37/627)	5.3% (32/607) P < 0.001	25.0% (5/20)	4.1% (14/345) P = 0.123	20.0% (2/10) P = 0.606	30.0% (3/10)

Note: See Section 2.4. Data processing: for the details related to the selection criteria on each metric. P corresponds to the P-value of the tests for the comparisons of proportions (χ^2 test of independence); P in bold for significant comparisons ($\alpha = 0.05$). N: number of fish.

Abbreviations: NA, not applicable; PIT, passive integrated transponder.

^a32 barbel were recorded in 2 consecutive years, 20 during 3 consecutive years, three during the 4 years of study and five in alternate years.

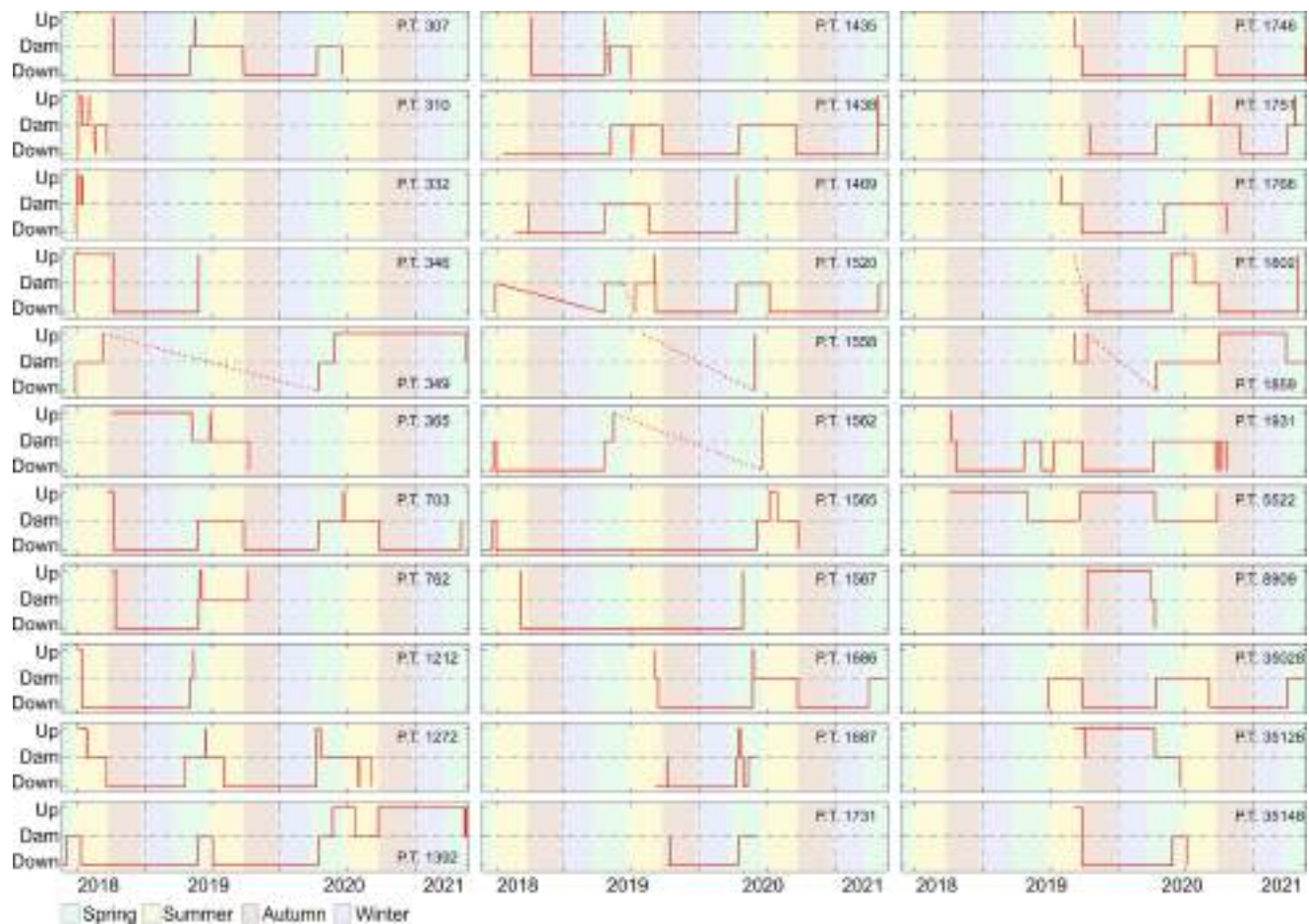


FIGURE 2 Schemes of the 33 bidirectional movements performed by barbel along the different years of tracking. Grey dashed line represents the dam location. Movements above this dashed line represent upstream migration and movements below represent downstream migration. Red dashed line refers to descending movements through routes different from the fishway (spillway or turbines). Coloured bars represent the seasons of the year: blue: winter; green: spring; yellow: summer; brown: autumn. Abbreviations and numbers on the right side of each scheme represent passive integrated transponder (P.T.) tag numbers.

movements upstream and downstream through the facility, with different intra-annual and inter-annual migration patterns, confirming the existence of a two-way migration corridor through the HPP facility and demonstrating that a fishway can act as a key bidirectional route.

4.1 | Bidirectional movements

Bidirectional movements through the fishway were confirmed in several individuals ($\geq 7.7\%$). However, it should be noted that the minimum return period (7 days) used to quantify bidirectional movements was the same established by Celestino et al. (2019) and Frechette, Goerig & Bergeron (2020). This value serves as a breakpoint to separate reproductive migration from fallback events, and it is expected to be unique for each study site and species. Considering the small size of the HPP complex, together with the evolution of the probability curve of barbels to stay upstream or downstream between successful fishway passages, it seems that, in

this study site, the return period may have been lower. Indeed, from 3.5 to 7 days, the value of the probability curve is quite similar; however, it was decided to follow the criterion of previous studies so as not to overestimate bidirectional movements and to make easier comparisons. Considering this, radiotracking records reveal that fish need less than 7 days to surpass the reservoir and return to the fishway.

Intra-annual bidirectional movements were completed within the range of 11–36 days (median 18 days), mainly in the spring–summer period, with no differences regarding the release area. This suggests that barbel can use downstream and upstream zones interchangeably as refuge, feeding or spawning areas. Similarly, a low fidelity of seasonal habitats and spatiotemporal variability has also been observed in partial migrators (Philippart & Baras, 1996; Penaz et al., 2002; Benitez & Ovidio, 2018). Inter-annual bidirectional movements (last successful passage of the year until the first of the next year) lie between 6 and 9 months (median 7 months), coinciding with the autumn–winter period, preferring the downstream zone during this period. Although some studies have related cyprinid

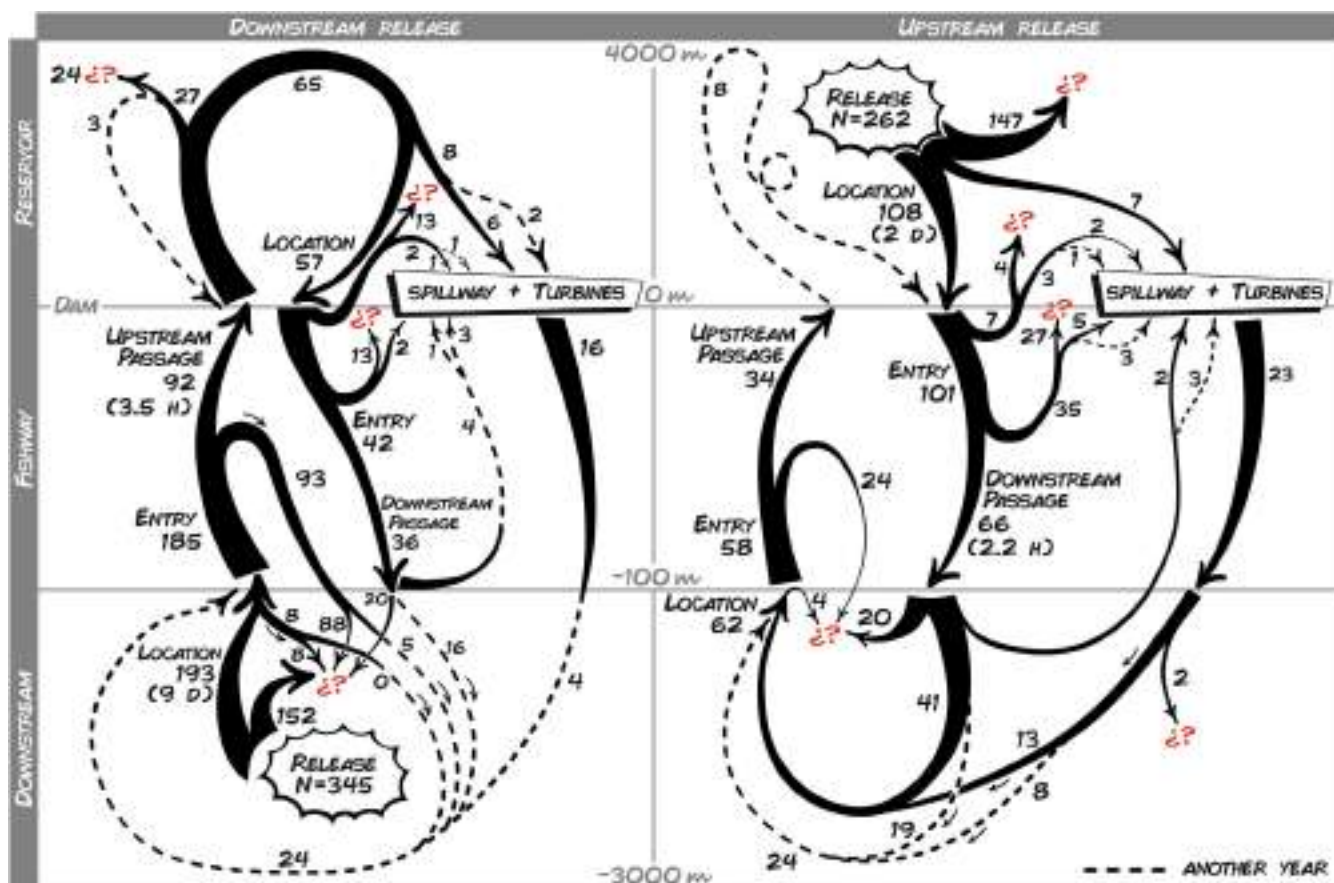


FIGURE 3 Scheme of the main movements made by fish tagged only with passive integrated transponders. Left: fish released downstream of the dam. Right: fish released upstream of the dam. Y-axis represents the longitudinal distance of the river reach under study (not to scale). Question marks mean fish with unknown paths. The median movement times in hours (H) or days (D) are shown in brackets. Fish with downstream passage via spillway + turbines are necessarily those that have been able to locate the fishway afterwards (for more details see Section 2.4).

TABLE 3 Results of time metrics (in days) by tag type and release zone (downstream and upstream takes as reference the location of the hydropower plant facility under study; median and interquartile range in brackets).

Metric	Global - Only PIT	Global - Radio and PIT	Release zone			
			Only PIT		Radio and PIT	
			Downstream	Upstream	Downstream	Upstream
Location time of the fishway	8.0 (3.0–16.5)	12.0 (2.0–17.5)	9.0 (5.0–18.0)	2.0 (1.0–5.0)	12.5 (12.0–17.5)	2.0 (1.0–14.0)
	$P = 0.646$		$P < 0.001$		$P = 0.211$	
Return time for those fish with bidirectional fishway movements (Intra-annual)	17.7 (11.4–35.5)	–	16.3 (14.1–25.5)	19.9 (10.8–46.2)	–	–
	NA		$P = 0.858$		NA	
Return time for those fish with bidirectional fishway movements (Inter-annual)	218.9 (197.8–286.0)	–	221.8 (198.4–286.0)	209.4 (184.1–260.4)	–	–
	NA		$P = 0.457$		NA	

Note: See Section 2.4. Data processing: for the details related to the selection criteria on each metric. P corresponds to the P -value of the Mann–Whitney test between groups; P in bold for significant comparisons ($\alpha = 0.05$). –No data available.

Abbreviations: NA, not applicable; PIT, passive integrated transponder.

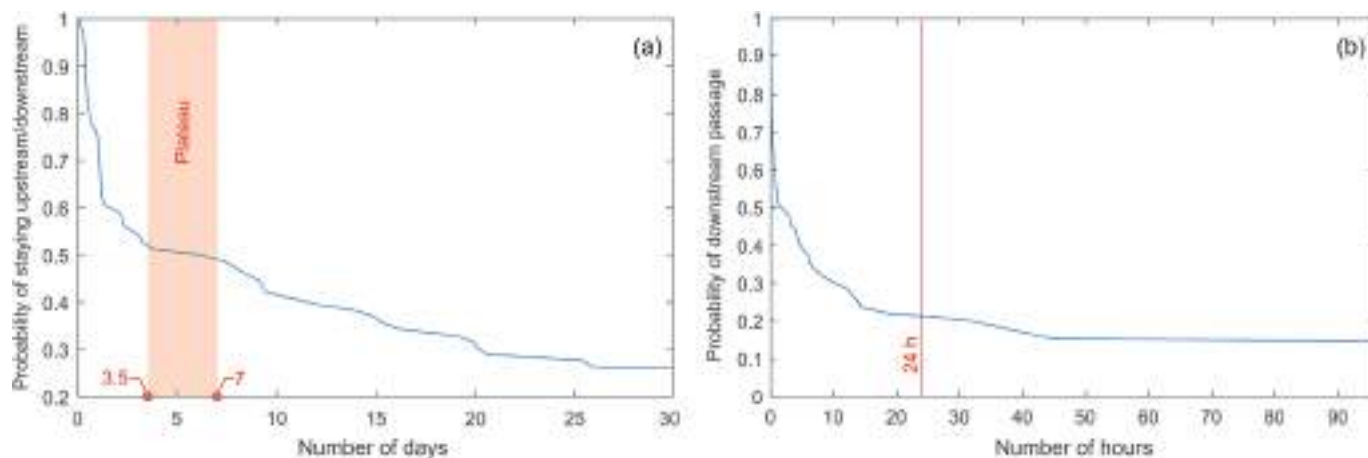


FIGURE 4 (a) Probability curve of passive integrated transponder-tagged fish to stay upstream or downstream between fishway successful passages, for a certain number of days. The vertical line represents the threshold of 7 days adopted here and according to the literature (Celestino et al., 2019; Frechette, Goerig & Bergeron, 2020). (b) Probability curve of passive integrated transponder-tagged fish for fishway downstream passage transit time (in hours). The vertical line represents the threshold taken in this study.

upstream movements to the pre-spawning season, and downstream movements to the post-spawning season (summer/winter habitats) (Ovidio et al., 2007; Britton & Pegg, 2011), depending on river reach and habitat availability they can move both upstream or downstream searching for spawning and refuge habitats (Aparicio & De Sostoa, 1999; Lucas et al., 2001).

4.2 | The variety of movements

Several movement patterns were observed throughout the monitoring period. The variety of movements registered, and their repetition inter- and intra-annually, shows the extensive use of fishways by potamodromous fish. All movements recorded are part of the normal behaviour of some species; for instance, exploration or habitat selection (Frank et al., 2009). These movements require further investigation to recognize their diversity and ecological relevance (Birnie-Gauvin et al., 2019; Sánchez-Pérez et al., 2022), as it has even been suggested that pool-type fishways can serve as spawning areas in the gravel piles that are naturally formed within the pools (based on the authors' observations in a nearby and similar pool-type fishway, and the evidence shown in nature-like fishways (Nagel et al., 2021)).

Barbel showed upstream and downstream movements of up to 4 km, in line with the usual home range of this species (Alexandre et al., 2016; Branco et al., 2017); however, this distance may be greater owing to the constraints imposed by the dam at that point (several radio-tagged fish were detected at the foot of the dam). Considering the minor influence of the reservoir, barbel could easily leave the affected area in a short time (mean water velocity is below 0.01 m s^{-1} (Sanz-Ronda et al., 2021)), without disorientation. Moreover, in contrast to larger reservoirs (Lopes et al., 2021), a generalized fallback phenomenon was not observed and most of the bidirectional movements were for long periods (consecutive or

subsequent years) coinciding with the seasonality of this species. This seems to confirm the hypothesis that fishways serve as a route for complementing annual fish cycles, which is in agreement with the results presented for Neotropical rivers or other small HPPs (Havn et al., 2017; Celestino et al., 2019; Celestino et al., 2020). Nevertheless, fishway effectiveness is mainly related to its attraction, i.e. competing discharge and proximity to bulk flow and shoreline; therefore, general conclusions and extrapolation of the results should be made with caution.

4.3 | Alternative routes for downstream migration

Bidirectional movements through fishways are not essential for ensuring the completion of fish life cycles, as there are alternative routes for downstream migration (e.g. spillways and turbines). However, bidirectional movements through fishways prove to be a safer downstream route than spillways or turbines as they avoid the possibility of barotrauma or mechanical shock (Larinier & Dartiguelongue, 1989; Felizardo et al., 2010; Wilkes et al., 2018). In this study, the possible spillway passage was dismissed as the pre-analysis revealed that flow through the spillway was a low probability event. Spillway overflow only happened for a few days in the entire study period (about 20 days) coinciding with the cycle of the least movement of fish (December–March). Without a bypass and no discharge through the spillway, the most probable downstream passage route (together with the fishway) was the turbines. Many authors have confirmed that downstream movements through turbines are a common route for many fish species (Antonio et al., 2007; Pracheil et al., 2016; Mueller, Pander & Geist, 2017; Celestino et al., 2019). In the present study, a rough estimation of 36% of fish moved downstream through turbines. This percentage may have been higher as fish might suffer disorientation (Coutant & Whitney, 2000; Pracheil et al., 2016) or even lack of motivation due

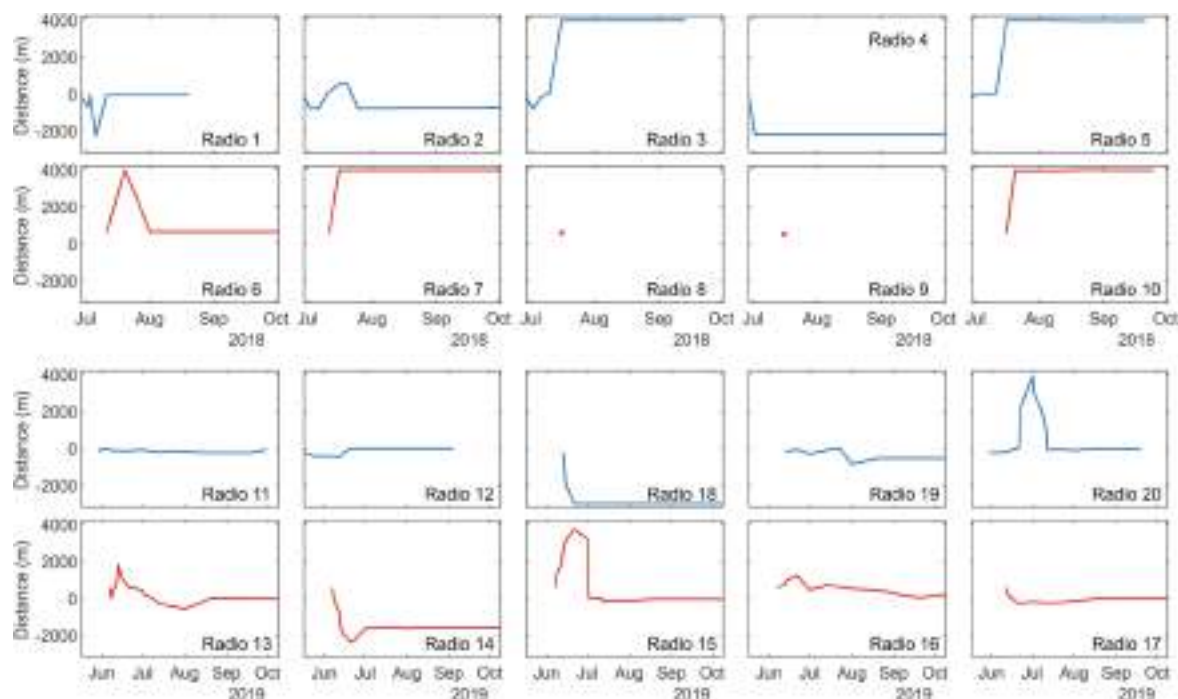


FIGURE 5 Ascending and descending movements of radio-tagged fish. Distance 0 represents the location of the hydropower plant complex. In red: fish released upstream of the dam; in blue: fish released downstream of the dam. Points represent fish that were impossible to locate after release.

to stress, making it difficult for them to locate the fishway afterwards (and therefore be recorded). In addition, confirmed turbine passage events appeared to be harmless or at least without severe injuries, as many fish were recorded with normal activity after those events. This is in accordance with Pracheil et al. (2016), who classified Kaplan-type turbines as the least harmful for fish.

4.4 | Aspects to take into account in monitoring bidirectional movements

An analysis of bidirectional connectivity should consider factors such as the number of fish and seasonality during the monitoring period. Short monitoring periods and the use of a low number of fish can influence results owing to the seasonal changes in river discharge (García-Vega, Sanz-Ronda & Fuentes-Pérez, 2017; García-Vega et al., 2021), the partial migration behaviour of some species (Alexandre et al., 2016; Branco et al., 2017; Bravo-Córdoba et al., 2018a), the handling and tagging effect (Thiem et al., 2011; Radinger et al., 2019; Davies et al., 2023) or other factors such as fish mortality during the monitoring period. For instance, 27 barbel started providing data 1 year after their tagging. Thus, in this study, to absorb the effect of uncontrollable factors, several years have been considered in the analysis. The challenge of considering monitoring over long periods is that the efficiency of the antennas could be compromised during high flow, although in the present study this only happened for a few days, coinciding with the winter, which is the season with lower fish activity (Sanz-Ronda et al., 2021). In addition, a

reduction in the PIT-tagged fish population over years might be expected as a result of tag losses and natural mortality (Grieve et al., 2018), which reinforces the need for tagged fish supplementation over time. However, the response of long-term monitoring using PIT technology can reveal bidirectional movements and provides a better understanding of the ecology of migratory fish (Gutfreund et al., 2018; Celestino et al., 2019; Celestino et al., 2020). It is also important to note that regular maintenance of the structure is crucial for this type of fishway, as orifices and notches often become clogged and can disrupt fish movements and their monitoring.

4.5 | Relevance to fish conservation

Fish conservation is undoubtedly associated with the recovery of longitudinal connectivity in rivers (Roscoe & Hinch, 2010). The need to maintain and restore river connectivity is an urgent challenge around the world, especially in Europe, where there are at least 1.2 million instream barriers over 36 European countries, representing a mean of 0.74 barriers per kilometre of river network, 68% of which are structures less than 2 m high that are often overlooked (Belletti et al., 2020). Dam removal and fishway construction have been the main strategies to restore the connectivity where there are existing barriers. In contrast, in other regions where a large number of new dams are planned, such as Africa, Asia and South America, the challenge is still to find the best way to provide bidirectional connectivity (Winemiller et al., 2016; Makrakis et al., 2019).

The importance of detecting bidirectional movement lies not only in quantifying passages through the facility but also in ensuring a minimum gene flow to secure a diverse fish population between fragmented river sections and access to critical habitats on both sides of the barrier (Pompeu, Agostinho & Pelicice, 2012; Gouskov et al., 2016; Ferreira et al., 2017; Tamario et al., 2019). For instance, gene flow contributes to maintaining potamodromous cyprinid populations that show partial migration in fragmented rivers (De Leeuw & Winter, 2008; Chapman et al., 2012; Branco et al., 2017). That is to say, fish metapopulations with mobile and resident individuals can show a shift between population percentages from mobile to resident ones in fragmented rivers (Branco et al., 2017; Jones et al., 2021a). One of the findings in the present study was the confirmation of multiple upstream and downstream passage events through different routes, including the fishway, turbines and spillways. This indicates the presence of a mobile proportion of the fish population that needs to migrate over the dam throughout its life cycle. However, a potential drawback of improving longitudinal connectivity is that in some rivers fishways may serve as routes for the spread of alien species. To confirm the magnitude of this drawback, specific studies of these species at the study site are necessary. Previous research has already suggested this possibility (Castro-Santos, Shi & Haro, 2016; Rahel & McLaughlin, 2018; Zielinski et al., 2020). For example, the controversial construction of the Canal da Piracema, at the Itaipu Dam (Makrakis et al., 2007), led to *Hemiodus orthonops*, which, until recently, was absent from the Upper Paraná River basin but is now invading of the new environment, notable both for its rapid colonization of the new environment and for its abundance (authors' observations). For this reason, it is necessary to assess the presence of natural barriers, such as large waterfalls, which may make the installation of fishways unjustifiable. Recent studies have proposed that flow velocities inside the fishways could act as a physical barrier to avoid non-native species dispersal (Morán-López & Uceda Tolosa, 2016; Jones et al., 2021b). Although it seems an interesting option, there would need to be an important leap in fishway science to meet this challenge.

The aim of this article is not to underestimate or ignore the variety and severity of impacts associated with HPPs or dams, particularly the fragmentation of critical habitats and migration routes, well reviewed in the scientific literature. The better solution for the maintenance of fish populations is to preserve free-flowing rivers (Sun, Galib & Lucas, 2021). However, it is crucial to for researchers not to start from the premise that fishways are unidirectional and to apply the broad package of technical solutions available to maintain fish populations present in fragmented rivers. It is necessary to strike a balance between the 'green' and 'red' aspects of hydropower (Geist, 2021), especially critical in the current energy crisis, at least until the services provided by dams are no longer needed (Celestino et al., 2019). Therefore, it is relevant to highlight the existence of bidirectional movements in fishways and their surroundings in some cases, scarcely analysed to date, but with the potential of contributing to the conservation of fish populations. This study has shown a feasible route both for downstream and upstream movements of a

potamodromous fish (the Iberian barbel) in a small HPP facility. Although fishways cannot by themselves restore river connectivity, they can play an important role as an element in a broader conservation strategy for migratory fish.

AUTHOR CONTRIBUTIONS

Conceptualization and developing methods: Francisco Javier Bravo-Córdoba, Leandro Fernandes-Celestino, Sergio Makrakis and Francisco Javier Sanz-Ronda. *Conducting the research:* Francisco Javier Bravo-Córdoba, Ana García-Vega, Juan Francisco Fuentes-Pérez and Francisco Javier Sanz-Ronda. *Data analysis:* Francisco Javier Bravo-Córdoba and Francisco Javier Sanz-Ronda. *Data interpretation:* Francisco Javier Bravo-Córdoba, Ana García-Vega, Juan Francisco Fuentes-Pérez and Francisco Javier Sanz-Ronda. *Preparation of figures and tables:* Francisco Javier Bravo-Córdoba, Juan Francisco Fuentes-Pérez and Francisco Javier Sanz-Ronda. *Writing:* Francisco Javier Bravo-Córdoba, Ana García-Vega, Juan Francisco Fuentes-Pérez, Leandro Fernandes-Celestino, Sergio Makrakis and Francisco Javier Sanz-Ronda.

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CONFLICT OF INTEREST STATEMENT

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

DATA AVAILABILITY STATEMENT

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

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