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River Research and Applications

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Fish Behaviour in a Vertical Slot Fishway: Multi-Species Upstream Passage Success, Size Selectivity and Diel Passage Patterns in a Large Italian River

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Received: 3 May 2024 | **Revised:** 18 November 2024 | **Accepted:** 19 November 2024

Funding: F.E. and A.S. have received funding from the European Union Horizon 2020 Research and Innovation Programme under the Marie Sklodowska-Curie Actions, Grant Agreement No. 860800.

Keywords: barbel | bleak | carp | chub | fishway | gudgeon | upstream fish passage

ABSTRACT

Hydropower dams come with high ecological and social costs, not least concerning longitudinal connectivity in rivers, which causes declines and sometimes local extinctions of fish species. Fishways are widely used to allow fish to pass dams, but their efficiency is highly variable between species and sites. Many species, and at places entire fish communities, remain understudied, likely hindering the implementation of effective remedial measures. Here, we studied fish passage behaviour in a vertical slot fishway in the Po River, Italy. Almost 1000 individual fish of nine species, representing the local fish community, were tagged and released within and downstream of the fishway. The only species passing the fishway at relatively high numbers were potamodromous barbel and Italian chub, and for these species passage success was positively related to fish size. Passage was more likely to occur at night than during the day for barbel, but not for chub. In relation to the dispersal of invasive species, it is noteworthy that a few individuals of wels catfish and common carp passed the fishway.

1 | Introduction

Hydropower is an important renewable energy source representing about 16% of the global electricity production (IHA 2023). It is expected to increase in importance with at least 3700 major dams planned or under construction worldwide (Zarfl et al. 2015). Hydropower dams, however, come with high ecological and social costs (Olden 2015), not least concerning longitudinal connectivity in rivers, causing declines and sometimes local extinctions of migratory fish species (Jonsson, Waples, and Friedland 1999; Lenders et al. 2016). Maintaining open migratory routes is therefore an important aspect of safeguarding ecological connectivity and conserving migratory fish species (McIntyre et al. 2015; Schiavon et al. 2024). Ideally, migrating as well as non-migrating fish should be allowed to pass dams to maintain genetic diversity and dispersal in the river system (Jones et al. 2021). In face of this, fishways and other fish passage solutions are used to restore longitudinal connectivity at hydropower dams (Noonan, Grant, and Jackson 2012).

Fish passage solutions must ensure safe passage routes for a substantial portion of the migrating fish. The functioning of a fishway depends on local conditions (e.g., operation, discharge, temperature, physical structures) as well as fish characteristics (species, size, life stage, motivation) (Silva et al. 2018). Although interspecific differences in swimming capability and behaviour are widely acknowledged (Katopodis and Williams 2012; Williams et al. 2011), fishway design, monitoring, and research have long focused on strong swimmers, such as salmonids (Katopodis and Williams 2012; Mallen-Cooper 1999). Thus, knowledge about other species is often lacking, resulting in variable or low fish passage performance for many fish species (Bunt, Castro-Santos, and Haro 2012, 2016; Hershey 2021; Noonan, Grant, and Jackson 2012; Sun et al. 2023). As for fish ecology and management in general, knowledge is particularly lacking for small-sized species with little commercial interest (Silva et al. 2018; Smialek et al. 2019; Vøllestad 2023).

Evaluations of existing fish passage solutions, as well as the behaviour of target species, are key to ensure the restoration of longitudinal connectivity (Benoit et al. 2023; Roscoe and Hinch 2010). Fish counters (Pereira et al. 2021) or large sampling efforts (Panagiotopoulos et al. 2024) can give valuable information on understudied species. One drawback of these methods, however, is that they do not account for the fish (individuals or species) that fail to pass the fishway, and they typically yield only low spatial and temporal resolution on behaviour in the fishway (Eggers et al. 2024). To quantify fine-scale behaviour of fish in fishways, tracking of individual fish by telemetry is needed (CEN 2021; Eggers et al. 2024; Hershey 2021; Sun et al. 2023).

The composition of species and size of successfully and unsuccessfully passing fish are straightforward study outcomes from tagging-based fishway evaluations. For example, specific passage efficiencies are standard evaluation metrics (Bravo-Córdoba et al. 2021; CEN 2021) and commonly used in meta-analyses of fish passage performance (Bunt, Castro-Santos, and Haro 2012, 2016; Hershey 2021; Noonan, Grant, and Jackson 2012; Sun et al. 2023). Size-selective passage is a common issue in fish passage management (Haugen et al. 2008; Maynard, Kinnison, and Zydlewski 2017; Sullivan, Bailey, and Berlinsky 2023), and long durations to overcome migratory barriers—consisting of the time to enter and the transit time through a fishway—are associated with excessive energy expenditure, migration failure and predation mortality (Agostinho et al. 2012; Baktoft et al. 2020; Castro-Santos, Cotel, and Webb 2009; Thorstad et al. 2008). In addition, diel movement dynamics may influence time-specific passage performance because many species are either diurnally or nocturnally active (Benoit et al. 2023; Jones and Hale 2020). Diel patterns in activity, although often neglected, may also be limited or shaped by the specific conditions of the fishway (Nyqvist et al. 2017). Diel passage patterns are particularly relevant in face of the increase in, and disruptive potential of, artificial light illuminating rivers at nights (Tarena et al. 2023; Vega et al. 2024).

In this study, we evaluated fish passage behaviour in a recently constructed vertical slot fishway at a dam in the Po River, the largest river in Italy, by tracking multiple understudied species of the local fish community using PIT telemetry. With a focus on small-sized species and size classes, we investigated species-specific (1) passage success and fishway transit time, (2) potential size selection on successful passers and (3) diel passage patterns. In addition, we used radio telemetry on a subset of large individuals (barbel and common carp) to detect fish movements in the vicinity of the dam and to describe large-scale behaviour around the fishway.

2 | Methods

2.1 | Study Site

The study was carried out at the hydropower plant Casale Monferrato (45°08′44.8″N 8°27′15.4″E) on the Po River, in the Piedmont Region, NW Italy (Figure 1). Since 2020, the Casale Monferrato Dam is the second obstacle along the Po River, 468 km from the Adriatic Sea. The first barrier, the Isola Serafini Dam, is located 168 river km downstream (at river km 300) and is equipped with a pool-weir fish passage solution, whereas the Canale Lanza Dam, located 3.4 km (at river km 471) upstream from the Casale Monferrato Dam, constitutes an unpassable obstacle for upstream-migrating fish. The Po River near Casale Monferrato has a mean annual discharge of about 260 m^3/s. River reaches upstream and downstream of the dam are part of the high-plain section of the Po, characterised by a low mean slope (0.08% around Casale Monferrato), a bottom substrate of mainly coarse gravel, and a general warming of the water (ADBPO 2009). The fish community is heavily impacted by non-native species (Bianco 2014), whose occurrence exceeds 50% (Abbà et al. 2024; Castaldelli et al. 2013; Puzzi et al. 2010). A systematic electrofishing campaign found 16 native and seven non-native species in this section in 2007 (ADBPO 2009).

The Casale Monferrato hydropower plant has been in operation since 2020 using a run-of-river hydropower scheme. A 192-m-long weir with an inflatable rubber dam regulates the upstream water level at 105.55 m a.s.l., creating an average head of 4.05 m. The mean annual abstracted discharge for hydropower generation is 72.1 m^3/s (about 28% of the mean annual river discharge) which is passed through an intake channel to an adjoining powerhouse equipped with four Kaplan turbines (installed capacity 4.4 MW). A vertical slot fishway (Figure 2) is located between the rubber dam and the intake channel, connecting the powerhouse tailrace to the upstream end of the intake channel. The fishway is approximately 85.5 m long (linear distance entrance to exit) and contains 26 large compartments (5.2–6.7 long × 3.0 m wide) with every second compartment divided by a 1.9 m wide deflector wall into two smaller pools to further dissipate energy and orient the stream flow. The pools are connected by 1.10-m-wide, full-depth vertical slots with a head drop of 0.15 m. The design discharge in the fishway is 0.8 m^3/s, with a maximum water velocity in the slots estimated to be 1.72 m/s, and a mean water velocity in the pools of approximately 0.35 m/s. Under these conditions, power dissipations in the differently sized pools are 76 W/m^3 in the large pools and around 153 W/m^3 in the small pools. The upstream water level is kept ca. constant by operating the rubber dam inflation and the hydropower turbines. The mean daily discharge of the fishway ranged from 0.60 to 0.76 m^3/s in the survey period.

Temperature was continuously recorded in the intake channel upstream the dam using a HOBO MX-2202 data logger (HOBO,

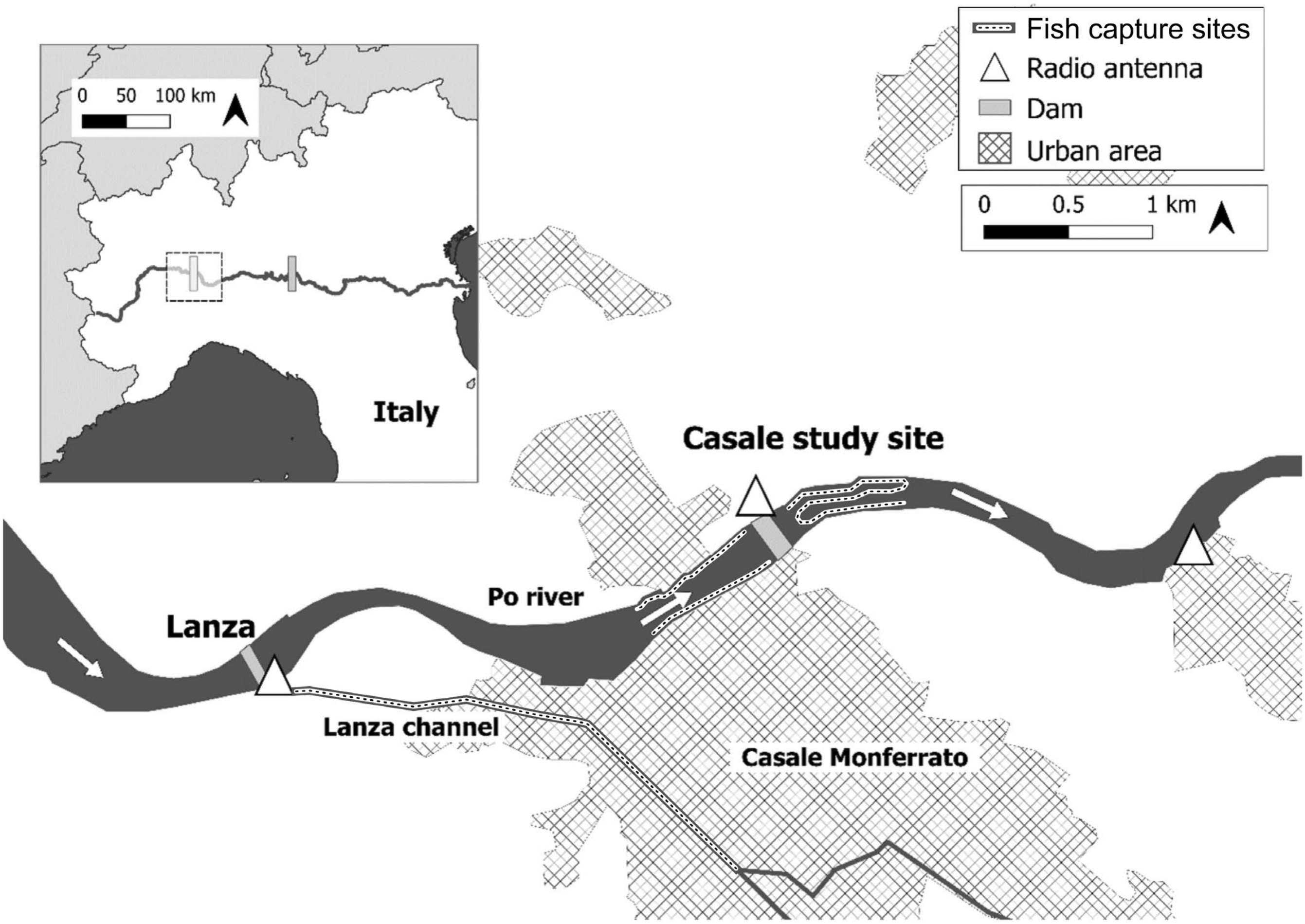

FIGURE 1 | The Casale Monferrato hydropower dam, with radio telemetry stations, Lanza Channel and Lanza dam without fish passage facilities. The smaller map shows the position of the Po River with Isola Serafini dam (grey) and study reach (light grey) in Northern Italy.

USA; Figure 3). Hourly discharge data including flow over the weir, through the fishway and through the turbines, was obtained from Idrobaveno Srl.

2.2 | Fish Capture

Fishes were caught by electrofishing in the Lanza Channel (an artificial channel originating at the upstream part of the Canale Lanza Dam; Figure 1) between 26 October and 2 November 2021 and upstream and downstream of the Casale hydropower dam on 7–8 April, 2022. A boat was used for electrofishing in the river itself and most fish were captured near the riverbanks and around shallows (Figure 2). After capture, fishes were held in fyke nets for up to 24 h near the riverbank at the dam until tagging.

2.3 | PIT Tagging and Telemetry

Before tagging, fish were anesthetised in clove oil (Aromalabs, USA; approximately 0.2 mL clove oil/L water). Fish longer than 6 cm were tagged (Table 1) with 12 mm PIT tags (Biomark, USA; 12 × 2.1 mm, 0.10 g) using a gun injector. The needle of the injector was inserted at a 45° angle at the ventral side of the fish anterior of the pelvic fins, followed by a full insertion of the tag, almost parallel to the fish body, into the abdominal cavity (Schiavon et al. 2023). Fork length (to the nearest 0.5 cm) and body mass (to the nearest g) were measured (Table S1), and the fish were left to recover in tanks filled with regularly changed river water (between 20 min and 3 h). All fish recovered in a span of 5 min and no tag loss or mortality was observed before release of fish into the river. Fishes were released at three sites (Figure 2): (1) in the middle of the fishway (release site: fishway), (2) 11.5 m downstream of the fishway entrance (release site: downstream) and (3) near the tailrace 85 m downstream (release site: tailrace). Small fish were gently released from buckets inside and downstream of the fishway in similar numbers, whereas large fish (> 30–45 cm, depending on species) could not be released from buckets, and were instead released from the riverbank into the tailrace (Figure 2). For the inferential analyses, only the 942 small sized fish released in and downstream of the fishway were used (Table 1).

Nine species or taxonomic groups of fish were tagged (Table S1) and seven of those in sufficient numbers to be included in the analyses (Table 1). All seven analysed species have been reported to be potamodromous, and flow preferences of these species reach from lentic environments to rheophilic (Table S2). *Alburnus arborella* (alborella) and *Squalius squalus* (Italian chub) are native to the Po catchment. *Barbus*

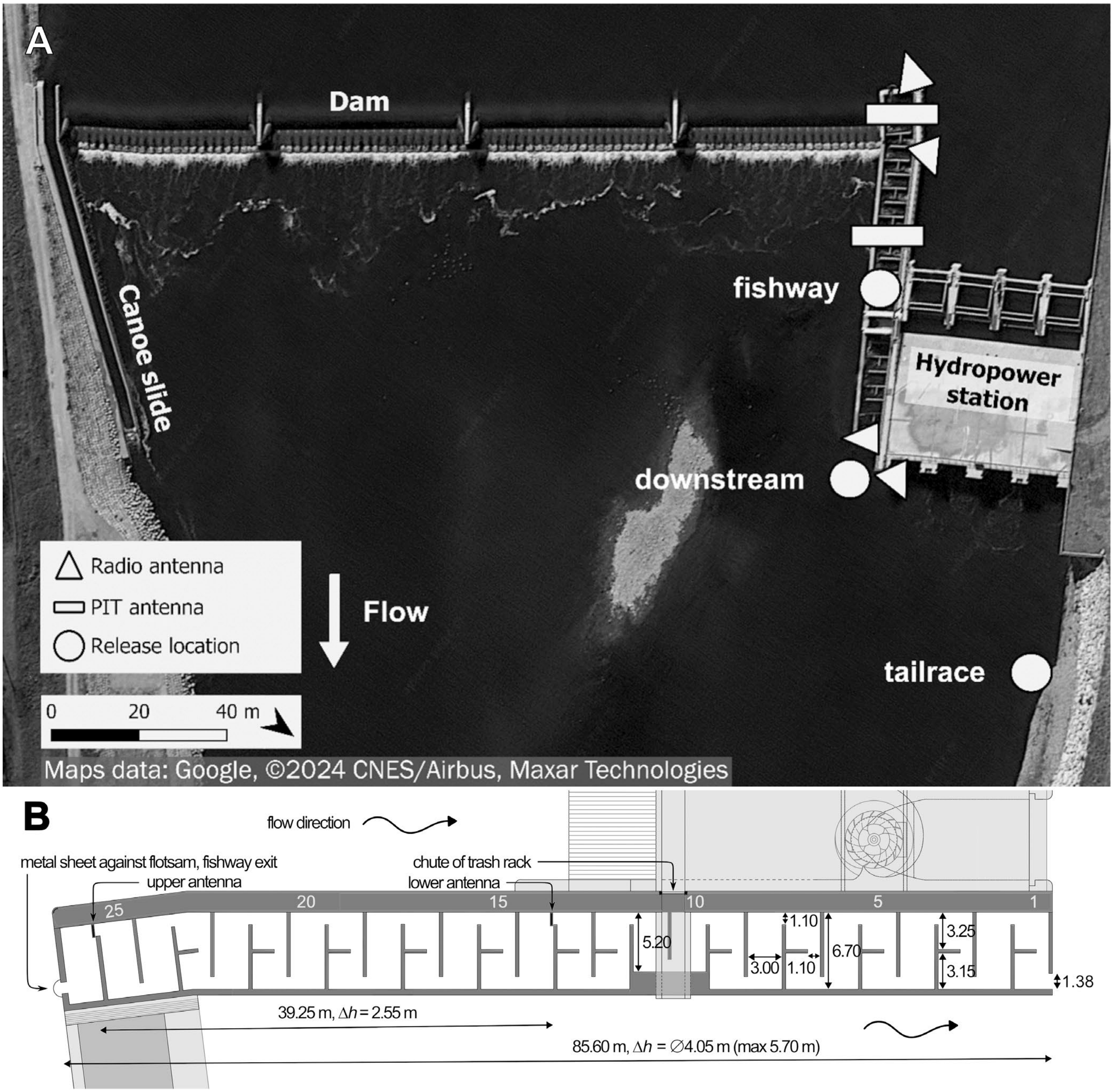

FIGURE 2 | (A) An aerial photo of the fishway at the Casale Monferrato hydropower facility on the Po River, with the evaluated vertical slot fishway and the position of PIT- and radio antennas and the release sites of tagged fish. (B) Scheme of the vertical slot fishway (top view).

spp. (barbel) are hybrid populations formed by non-native and now dominant *Barbus barbus* and native *Barbus plebejus* (Meraner et al. 2013). *Cyprinus carpio* (common carp) is an historical introduction in this catchment, but more recently introduced and spreading in other freshwater systems globally (Badiou, Goldsborough, and Wrubleski 2011). The non-native *Carassius* spp. (carassius) is most likely dominated by *Carassius auratus*, but intrusion of *Carassius gibelio* and *Carassius carassius* cannot be excluded (Fortini 2016). *Silurus glanis* (wels catfish) and *Gobio gobio* (gudgeon) are also non-native (Abbà et al. 2024; Bianco and Ketmaier 2005; Nyqvist et al. 2024). All nine species are part of the larger fish community in the high-plain section of the river Po and five species have been observed in this stretch before the dam was constructed (ADBPO 2009).

Two PIT antennas (Model "Cord Antenna System", Biomark, USA) were placed in the fishway, each encircling a vertical slot. One antenna was placed in the last slot before the exit of the fishway (the upper antenna), whereas the other antenna was placed in the middle of the fishway (hereafter called the lower antenna; Figure 2). The variable water levels downstream the dam prevented the positioning of an antenna close to the fishway entrance. Detection ranges of both antennas covered the full width of the slots and about 30 cm in an up- and downstream direction, and were regularly tested using a PIT tag identical to those

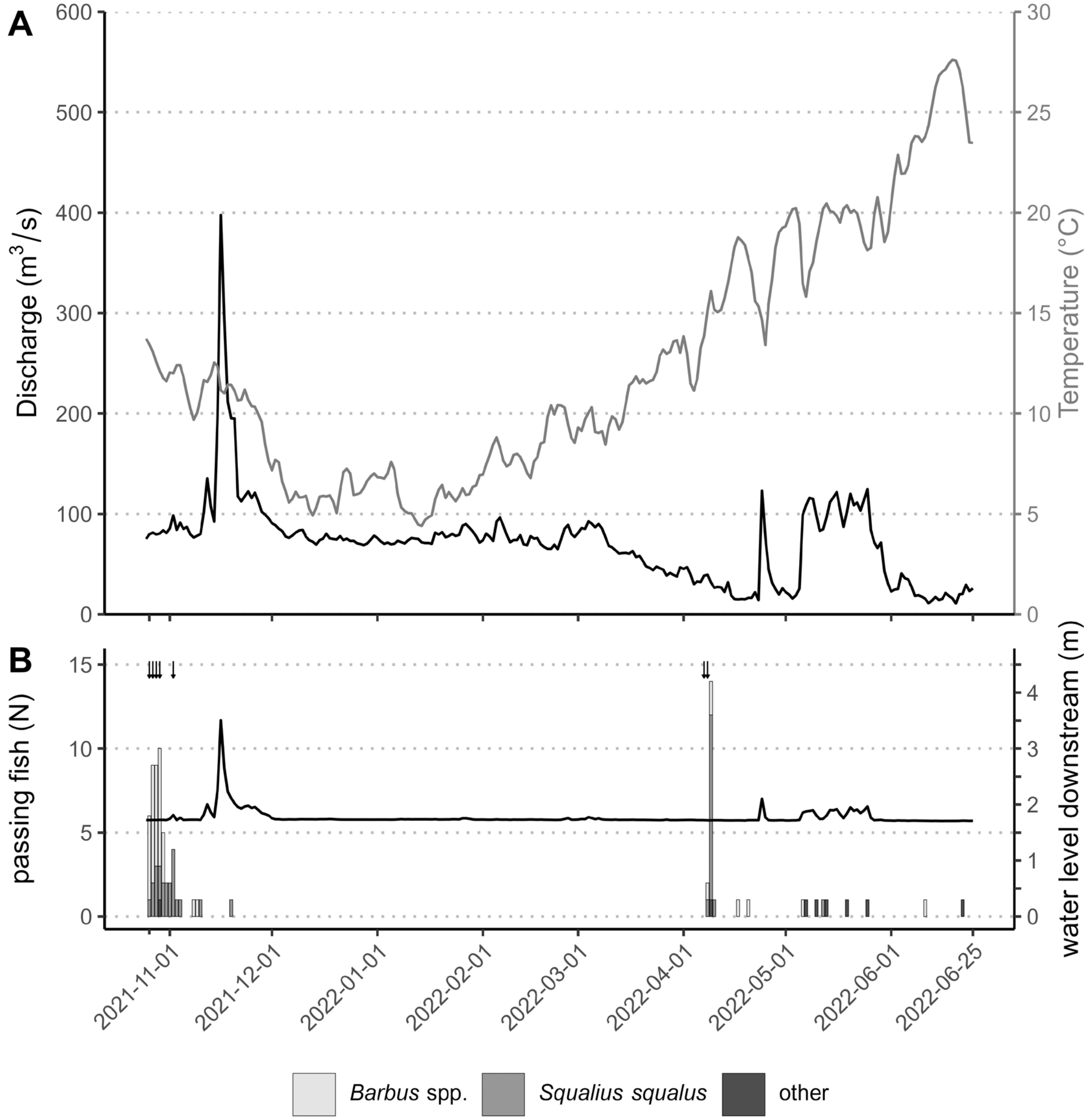

FIGURE 3 | Daily mean total discharge (black line) and daily mean water temperature (grey line) at the Casale Monferrato hydropower plant over the observation period (26/10/2021 to 25/06/2022).

in the tagged fish. No change in detection range over time and no downtime was observed for any of the antennas. The tag detection probability (sensu CEN 2021) of the lower antenna was estimated from individual fish detections at the upper antenna missing at the lower antenna. It detected 71 of 81 detections, equalling a tag detection probability of 88%.

PIT detections on the two antennas were used to quantify fish behaviour in the fishway. We defined *passage success* as detection of a fish at the upper antenna and *overall passage success* as the proportion of successful fish of all fish released (overall FPS efficiency in CEN 2021; per cent passage in Silva et al. 2018). *Entrance time* was the time from release to first detection in the fishway (at the lower antenna). As the lower antenna was positioned mid-way up the fishway this time includes both entry and initiation of ascent and care should be exercised when comparing with other studies. Fishway *transit time* was the time from the last detection at the lower antenna to the first detection at the upper antenna. In case of multiple transits of an individual between lower and upper antenna, only the first successful attempt was analysed. To quantify diel activity patterns, times of detection were transformed from standard time to their relative positions between either sunrise and sunset (day) or astronomical evening twilight and morning twilight (night) with the help of a daytime calendar. An average day was then calculated for the observation period (26/10/2021 to 26/06/2022) with mean values of sunrise, sunset and (astronomical) twilights. Times of detections were then transformed into times on the average day by using their relative position between either sunrise and sunset (day) or evening and morning twilight (night). First detections at the upper antenna were used to assign passage at either day or night (including twilight). Their corresponding times on the average day were used for plotting (Figure 6). In case of multiple upstream movements by a single individual over the observation period, we only used the first passage in the analyses.

TABLE 1 | PIT-tagged fishes used in the study. Small sized fish ($n = 954$) were released in or just downstream the vertical slot fishway, while large sized fish ($n = 42$) were released in the tailrace of the hydropower plant.

Release	Species	English name	N	Length (cm)		
				Median	Min.	Max.
Fishway and downstream	*Alburnus arborella*	Alborella	100	7.3	6.0	9.5
	Barbus spp.	Barbel	235	12.5	6.8	38.5
	Carassius spp.	Carassius	40	20.5	12.0	28
	Cyprinus carpio	Common carp	139	22.0	15.0	39.5
	Gobio gobio	European gudgeon	111	9.2	7.1	13.0
	Silurus glanis	Wels catfish	41	30.5	6.9	59.0
	Squalius squalus	Italian chub	276	15.9	6.2	34.5
Tail-race	*Barbus* spp.	Barbel	9[a]	58.0	53.0	75.0
	Cyprinus carpio	Common carp	15[a]	63.0	30.5	77.0
	Silurus glanis	Wels catfish	18	82.0	73.0	116.0

[a]Of the large fish, 9 barbel and 15 common carp were also radio-tagged.

2.4 | Statistical Methods

Species with at least 150 released and at least 10 detected individuals were considered for inferential analyses, based on a power analysis of simulated Fisher's exact tests ($\alpha = 0.05$, $\beta = 0.20$, first group proportion = 0.05 and second group proportion to be compared = 0.20). Effects of fish length, release site, capture location and season of release were tested using logistic regression. The Akaike Information Criterion (AIC) was used to select the best model among all candidate models (Bolker 2008). All combinations of the covariates were included among candidate models. Models with an AIC-value of −2 or lower from the null ($\Delta\ AIC_{null} < -2$) model and within 2 AIC units from the best model ($\Delta\ AIC_{min} > 2$) were considered good models (Bolker 2008), and we considered the model with the fewest parameters among the good models to be the best. Mann–Whitney *U*-tests were used to test if release location affected entrance and transit times. We used Fisher's exact tests to test for differences between groups of fish (release sites and day/night). We used R (version 4.3.1), with dplyr for data management, lme4 for logistic regression modelling and ggplot2 for plotting data.

2.5 | Large Fish and Radiotelemetry

Large fish (barbel and carp ≥40 cm, wels catfish ≥60 cm) could not be released within the fishway. To complement the small-sized fish data and describe large-scale behaviour downstream and upstream of the fishway, large fish taggable with external radio tags were tagged and tracked. Due to tag weight, size, and attachment position, radio tags were only attached to fish with a broad dorsal fin and a weight of 600 g and above, equalling up to 2.5% of body weight (Chittenden et al. 2009; Jepsen et al. 2005). Only large common carp ($N = 15$) and barbel ($n = 9$) fulfilled this criterion. These fishes (Table 1) were tagged on October 26–27 and November 2, 2021 (13 carp) and April 8, 2022 (two carp and nine barbel) with external radio transmitters (model F2120; 16 g; 21 × 52 × 11 mm; 55 ppm; Advanced Telemetry System ATS, USA), each transmitting on a unique frequency (151.000–151.640 MHz) and two different pulse rates indicating an active (55 ppm) or a passive/dead (30 ppm after 8 h without movement) fish. The tags were attached below the dorsal fin, using wires inserted horizontally through the upper part of the musculature (Nyqvist et al. 2019). Large wels catfish were not taggable with external radio tags and were therefore only PIT-tagged ($n = 19$). After tagging, fish were let to recover in tanks before being released in the tailrace (Figure 2).

The movement of the radio-tagged fish were tracked using an array of stationary automatic receivers (model R4500S; ATS, USA), connected to a unidirectional antenna. One radio receiver was positioned 2.6 km downstream and one 3.4 km upstream at the Canale Lanza Dam (Figure 1), whereas four receivers were positioned at the Casale Monferrato Dam (Figure 2).

Passage success was inferred from the relative signal strength (upstream/downstream antennas) recorded on the receivers at the Casale Monferrato Dam. Presence at this dam was defined by detections above a signal strength of 120 on the dam receivers before passage. Detections by the antenna at the upstream Canale Lanza Dam indicated continued upstream movement after passage. Fishes were also regularly manually tracked in the river reach between the fixed downstream and upstream receivers using a handheld antenna and receiver (R4000 and R410, ATS, USA).

2.6 | Ethics Statement

The study was performed in accordance with Ufficio Tecnico Faunistico e Ittiofauna della Provincia di Alessandria (authorization DDAP2-867, dated October 10, 2021), Ente di Gestione delle Aree Protette del Po Piemontese and ISPRA (prot.51778 dated October 1, 2021).

3 | Results

Detections of 99 of 988 (10%) PIT-tagged fishes (470 small fish released in the fishway, 472 small fish downstream of the fishway, 46 large-bodied in the tailrace) belonging to five of seven species were recorded by the two PIT antennas over the whole observation period of 8 months (Tables S3 and S6). The majority of detections were recorded shortly after release, both in autumn and spring. Of the 99 detected fishes, 80 individuals successfully passed the fishway. Among the successfully passing small fish, barbel ($n = 36$) and Italian chub ($n = 36$) were the dominating species, but single individuals of alborella and common carp also passed (Table 2). No carassius or gudgeon were detected. Among the catfish, no small fish, but a few large fish passed the fishway. A small number of fish passing the upper antenna turned around and returned downstream in the fishway (one barbel and four chubs). Only barbel and Italian chub passed in sufficient numbers to allow for quantitative analysis (Table S3).

3.1 | Passage Success

For both species, body size and release location significantly affected passage success, and passage of Italian chub was also affected by season (Tables 3, S4, and S5). Longer fish were more likely to pass than short fish. On average, each additional cm in body length increased passage success by 1.5% for barbel and 2% for Italian chub (logistic regression; Table 3). The median fork length of barbel successfully passing the fishway was 23 cm (min. 8, max. 36), whereas it was 12 cm (min. 6.8, max. 38.5) for barbel not passing (Figure 4). For Italian chub the corresponding lengths were 20 cm (min. 10.8, max. 34) and 15.2 cm (min. 6.2, max. 34.5). Passage success of Italian chub was affected by season. Chubs released in spring had an on average 22% higher probability of passage than those released in autumn (Table 3).

3.2 | Differences Between Release Locations

Overall passage success was significantly higher for fish released in the fishway (barbel 22.6%; Italian chub 17.6%) than for those released downstream (7.2% and 8.2%; Table 2; logistic regression; barbel, $p = < 0.001$; chub, $p = 0.016$; Table 3). Taking other factors into account, this corresponds to an average decrease of 16% for barbel when being released downstream instead of inside the fishway, and a decrease of 10% for Italian chub. The proportions of individuals passing successfully from the lower to the upper antenna (36 of 39 = 92.3% for barbel and 36 of 47 = 76.6% for chub) did not differ significantly between the release groups for any of the two species (Fisher's exact test, $p > 0.05$).

3.3 | Entrance and Transit Times

Entrance and transit times were variable for both barbel and chub (Figure 5).

Barbel released in the fishway were detected significantly earlier after release (median 7.5 h, min. 0.7 h, max. 162 days; Figure 5A) than individuals released downstream of the fishway (median 13.1 h, min. 7.0 h, max. 174 days), as indicated by a Mann–Whitney U-test ($U = 42$, $Z = 2.236$, $p = 0.025$). Barbel from the fishway release group had a longer transit time (median 2.1 h, min. 0.2 h, max. 22.1 h) than those released downstream (median 0.5 h, min. 0.3, max. 2.2; Figure 5B; $U = 44$, $Z = 2.541$, $p = 0.011$).

For Italian chub, there was no difference between release groups in entrance time (fishway release: median 17.1 h, min. 0.9 h, max. 196 days; downstream release: median 82.1 h, min. 1.7 h, max. 21 days; Figure 5A; $U = 134$, $Z = 1.85$, $p = 0.064$) or transit time (fishway release: median 0.7 h, min. 0.3 h, max. 13.8 h; downstream release: median 1.1 h, min. 0.2 h, max. 23.1 h; Figure 5B; $U = 89$, $Z = 1.380$, $p = 0.167$). A single passing alborella was detected 27 h after release at the lower antenna and needed 1.7 h for transit. A single carp was detected after 3.6 h and had a transit time of 8.3 h.

3.4 | Timing of Passage

The majority of successful barbel (84%, 31 of 37) and Italian chub (92%, 33 of 36) passed the fishway within a week after release under similar environmental conditions, respectively (Figure 3B). Daily mean discharge ranged from 15 to 195 m^3/s and water temperature from 9.7°C to 26.3°C at days of passage (Figure 3A). On a scale of 24 h, passages were not equally distributed between day and night (Figure 6). The first detection at the upper antenna was more likely to occur at night for barbel ($n_{day} = 6$, $n_{night} = 31$, $p = 0.006$), but not for Italian chub ($n_{day} = 10$, $n_{night} = 26$, $p > 0.05$).

TABLE 2 | Detections of small-bodied PIT-tagged individuals of four fish species released inside, and downstream of, a vertical slot fishway at the Casale Monferrato hydropower station.

	Released in fishway				Released downstream			
	Released	Detected			Released	Detected		
Species	N_{tot}	N_{lower}	N_{upper}	$\%_{tot}$	N_{tot}	N_{lower}	N_{upper}	$\%_{tot}$
Alburnus arborella	47	2	1	2.1	53	0	0	0
Barbus spp.	124	31	28	22.6	111	8	8	7.2
Cyprinus carpio	63	4	1	1.6	76	0	0	0
Squalius squalus	142	34	25	17.6	134	13	11	8.2

Note: The number of individuals released (N_{tot}), detections by the lower (N_{lower}) and upper (N_{upper}) antennas, and the overall passage efficiency ($\%_{tot}$) are provided separately for the two release sites (fishway and downstream). Info on other species in Table S3.

TABLE 3 | Binary logistic regression results for passage success of small-bodied barbel and Italian chub (released either in or downstream of the fishway).

Dependent variable/regressors	Coefficient	SE	z	p	AME	95% CI Lower	95% CI Upper
Passage success of barbel (*Barbus* spp.; model $\rho^2 = 0.25$, df = 232)							
Intercept	4.57	0.58	−7.86	< 0.001	—	—	—
Fork length (cm)	0.15	0.03	5.72	< 0.001	0.015	0.01	0.02
Release location (downstream)	−1.26	0.36	−3.54	< 0.001	−0.16	−0.24	−0.08
Passage success of Italian chub (*Squalius squalus*; model $\rho^2 = 0.14$, df = 270)							
Intercept	−5.00	0.76	−6.58	< 0.001	—	—	
Fork length (cm)	0.18	0.04	4.50	< 0.001	0.02	0.01	0.03
Release location (downstream)	−0.69	0.29	−2.41	0.016	−0.10	−0.17	−0.02
Season (spring 2022)	1.35	0.42	3.17	0.002	0.22	0.09	0.35

Abbreviations: 95% CI = 95% confidence interval; AME = average marginal effect; df = degrees of freedom; ρ^2 = peudo-R^2 (McFadden).

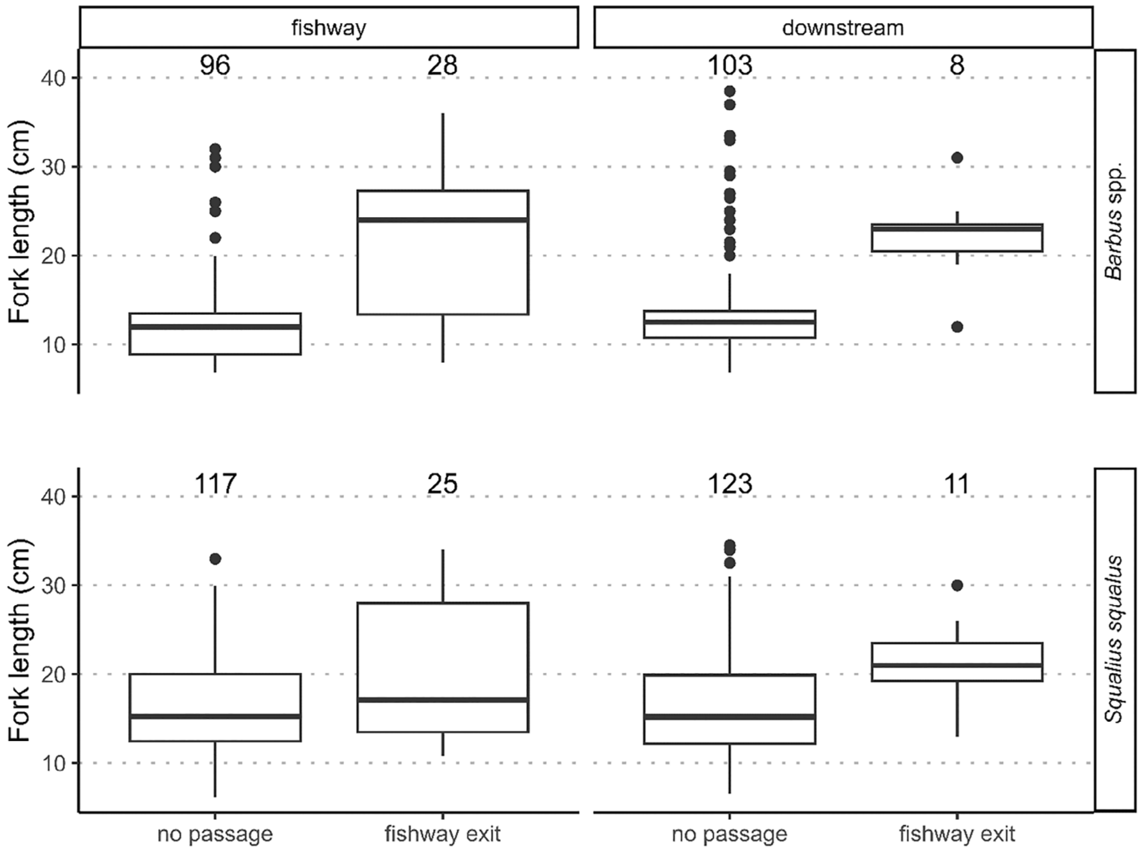

FIGURE 4 | Boxplots of fork lengths of *Barbus* spp. or *Squalius squalus* released inside the vertical slot fishway (fishway), or downstream of the fishway (downstream). Data divided between fish that successfully passed (detected at the upper PIT antenna, i.e., fishway exit) and those that did not pass. Boxes show median with interquartile ranges, whiskers show the 1.5-fold interquartile range, dots represent outliers. Numbers of observations (n) written above each boxplot.

3.5 | Large Fish

Among the large fish released within the tailrace of the hydropower station, passage success was 9% (1 of 11) for barbel, 27% (4 of 15) for common carp, and 16% (3 of 19), for wels catfish (Table S6). All eight fish passed in late spring or in summer. Among the common carps, three left in a downstream direction immediately after tagging (all in autumn) and were never seen again. The other carps were present by the dam from 15 h to 42 days (median = 9 days), distributed over 2–41 visits (median = 12 visits). Although carps were present at the dam for an extended period in autumn ($n = 10$), no fish passed upstream.

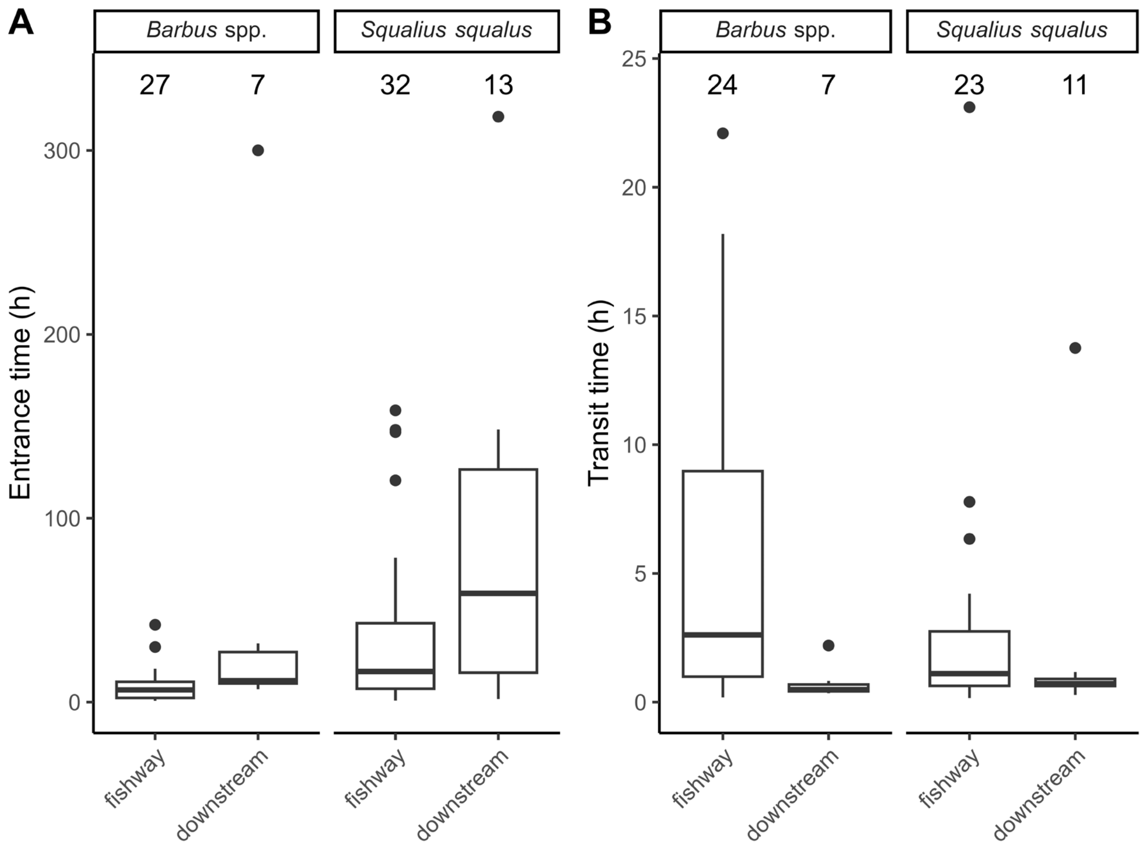

FIGURE 5 | Boxplots of (A) times towards the entry (entrance time) and (B) transit times between the lower and upper antenna inside the fishway for *Barbus* spp. and *Squalius squalus* released either inside (fishway) or downstream of the fishway (downstream). Three entrance times of *Barbus* spp. (161.7, 173.6, 196.7 days) and two values of *S. squalus* (197.9, 21.6 days) not shown in panel A. Boxes show median with interquartile ranges, whiskers show the 1.5-fold interquartile range, dots represent outliers.

After repeated visits, all of these carps left the dam in a downstream direction during October–November to overwinter in a deep slow flowing river reach 1–2 km downstream. Nine carp returned to the dam in April–May the following year. In spring, four of eleven carps (36%) present downstream of the dam successfully passed the fishway. Fish passing did so from 1 to 25 May after 9–32 visits to the dam. The final visit lasted 1.5–44 h before passage. Transit times from the lower to upper antenna inside the fishway were 17–28 min ($n = 2$). All four carp continued to move upstream until reaching the next dam in the system (Canale Lanza Dam).

Barbel were tagged only in spring 2022. Two barbel moved downstream immediately after tagging, seven individuals were present 6–104 days downstream of the dam, distributed over 2–44 visits. No radio-tagged barbel passed in the observation period. For the barbel tracked at least twice, the median linear home range was 880 m (min.–max. = 400–1800 m). Four barbel and four carps started registering dead/inactive signals during the study, which was attributed to tag loss or mortality. Fishing is relatively intense in the area and may have contributed to this result.

The three passing wels catfish had transit times between 38 and 51 min. One wels catfish moved up and down in the fishway twice in 1 day.

4 | Discussion

We studied fish passage behaviour in a vertical slot fishway in the Po River, Italy. Almost 1000 individual fish of 10 species, representing the local fish community, were tagged and released within or downstream of the fishway. The only species passing the fishway at relatively high numbers were barbel and Italian chub, and for these species passage success was positively related to fish size. Passage was more likely to occur at night than during the day for barbel, but not for chub. In relation to the dispersal of invasive species, it is noteworthy that a few large individuals of wels catfish and common carp pass the fishway during spring and early summer.

Barbel and Italian chub had higher detection probabilities than the other surveyed species but still relatively low overall passage success (7% and 8% for the downstream group, respectively). From other studies in vertical slot fishways, however, both lower and higher overall passage success have been reported for species of the same genera. For barbel, overall passage efficiencies of 2%–29% (Benitez et al. 2018; Grimardias et al. 2022; Ovidio et al. 2017; Ovidio, Dierckx, and Benitez 2023), but also 80%–83% (Ovidio et al. 2017; Sanz-Ronda et al. 2019) have been reported. For chub, overall passage efficiencies of 5%–16% (Grimardias et al. 2022; Lothian et al. 2019), but also 48% (Benitez et al. 2018) and 73% (Ovidio,

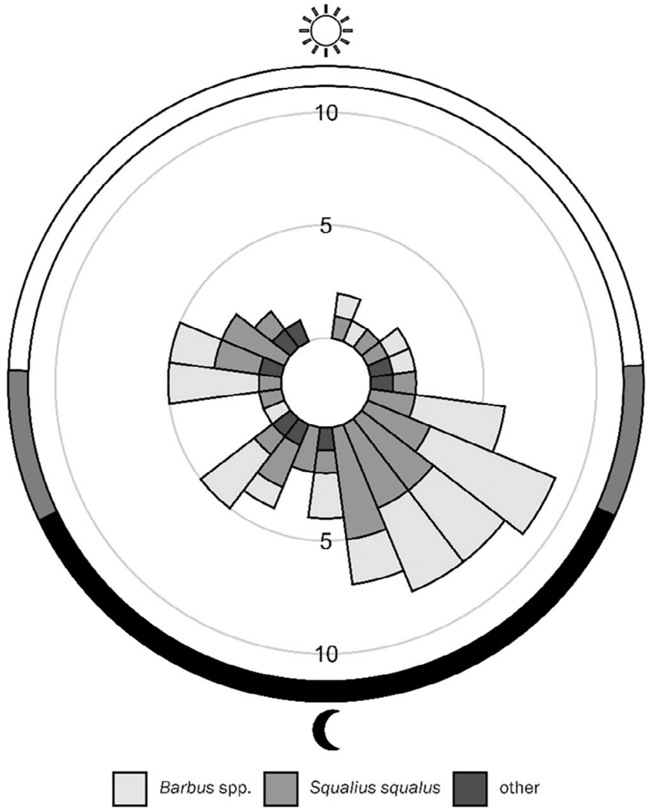

FIGURE 6 | Number of first detections at the upper antenna in the fishway at hours of the day. The outer ring shows daylight (white) and night (black) including twilight (grey). Depicted are times on the average day of the observation period (26/10/2021 to 26/06/2022) due to changing daytime lengths over time. Calculation of the average day and times on the average day in methods section.

Dierckx, and Benitez 2023) have been observed. Proportions of passage from the lower to the upper antenna, on the other hand, were relatively high for both species (92% for barbel, 77% for chub). They were also comparable to those described elsewhere. Passage efficiencies from entry to exit of a vertical slot fishway were observed to be 63%–95% for barbel (Benitez et al. 2018; Grimardias et al. 2022; Ovidio et al. 2020; Ovidio, Dierckx, and Benitez 2023; Sanz-Ronda et al. 2019) and 45%–94% for chub (Benitez et al. 2018; Grimardias et al. 2022; Lothian et al. 2019; Ovidio, Dierckx, and Benitez 2023). The median transit times of 0.5–2 h for a height difference of 2.55 m were also likely not long enough that they negatively affected fitness (Bravo-Córdoba et al. 2021; Sanz-Ronda et al. 2019). These results imply that the reasons for the low overall passage efficiencies stem from further downstream: possible reasons could be low attraction towards or entering of the fishway, and low motivation to move upstream (Cooke and Hinch 2013; Hershey 2021; Kemp 2016; Ovidio et al. 2017). Potentially, the large proportion of barbel and chub that did not pass could also reflect behavioural variability within the respective populations, in interaction with motivation. In large-scale observations, only 3%–20% of barbel and 10% of chub showed migratory behaviour, while the larger fraction remained within a few kilometre of their release locations (Branco et al. 2017; de Leeuw and Winter 2008). Both chub and barbel migrate towards spawning grounds in spring (Fortini 2016). Barbel has also been observed to migrate in autumn as well (Benitez and Ovidio 2018; Epler et al. 2004), possibly driven by dispersal towards wintering habitats. In fact, in this study chub were more likely to pass in spring while no difference was seen between autumn and spring in barbel.

Despite a high number of fish tagged, only a relatively low number was detected in the fishway. The overall low proportion of fish detected (10%) across all species is heavily influenced by several species with very low or no detections. To be detected, fish needed to ascend to the lower antenna, placed mid-way up the fishway. Entry into the study area hence include also some ascent in the fishway, regardless of release group. As many studies place the lower antenna at the entrance of the fishway (Benitez et al. 2018; Grimardias et al. 2022; Lothian et al. 2019; Sanz-Ronda et al. 2019; Ovidio, Dierckx, and Benitez 2023), one can expect lower number detection and longer entrance times compared to these studies. Only a few alborella and small carp were detected by any antenna while no carassius, gudgeon or small wels catfish ascended far enough to be detected by the lower antenna. This led to overall low numbers of detected fish. The reasons for the passage failure of these species remain unknown and warrant further studies, but may include lack of motivation (Chapman et al. 2012; Cooke and Hinch 2013; Kemp 2016), stress from handling (Portz, Woodley, and Cech 2006; Sullivan, Bailey, and Berlinsky 2023) or low swimming performance (Jones et al. 2020). Nevertheless, individual alborella, common carp and wels catfish were detected at the fishway exit, albeit in low numbers. This demonstrates that the fishway was passable and may have offered longitudinal connectivity to some extent for these species, allowing genetic transfer from downstream to upstream of the dam (Jones et al. 2021; Tamario et al. 2019; Wilkes et al. 2019).

European gudgeon and carassius, however, were released and never detected again. While carassius is a rather lentic fish species, with limited fish swimming capacity (Yan et al. 2012), the lack of passage events for gudgeon may be interpreted as a warning that the fishway may not function well for this species. Gudgeon showed a strong tendency to move upstream against a current and over a relatively modest hydrodynamic obstacle in flume experiments (Tarena et al. 2023) and are commonly observed passing various fishway designs in the Netherlands (Panagiotopoulos et al. 2024), accentuating this warning. Swimming capacity is often considered a key characteristic to determine passage performance in fishways (Castro-Santos et al. 2022; Katopodis and Gervais 2012). The maximum flow velocities downstream of the slots in the studied fishway is about 1.7 m/s. In the literature, the average maximum swimming speed for gudgeon has been estimated to 9.8–13.3 BL/s (Nyqvist et al. 2024; Tudorache et al. 2008). For our gudgeon this corresponds to sufficient swimming capability only for the largest and/or best performing individuals (range: 1.02–1.73 m/s). The same species, however, has been observed to pass a pool-type fishway with submerged orifices in Poland with flow velocities of up to 2.3 m/s (Kotusz et al. 2006) and in a vertical slot fishway in Belgium with flow velocities of up to 2.2 m/s (Benitez et al. 2015). Fish that volitionally swim against strong currents could outperform fish in forced swimming performance tests (Castro-Santos, Sanz-Ronda, and Ruiz-Legazpi 2013).

In addition, tagging is unlikely to substantially have reduced swimming performance (Ficke, Myrick, and Kondratieff 2012; Nyqvist et al. 2022, 2024; Schiavon et al. 2023). As the vertical slot fishway in Casale Monferrato solely relies on substrate provided by the surrounding river and flow velocities do not change much from top to bottom (Katopodis, Kells, and Acharya 2001), the fishway likely lacks substrate and with it surface roughness around the slots. Small, bottom-oriented species such as gudgeon could therefore profit from arranged, stable substrate within the fishway (Muraoka, Nakanishi, and Kayaba 2017; Rodgers et al. 2017).

Some fishways select against small fish (Volpato et al. 2009). Also in our study, body size was positively related to passage success for barbel and chub. This is likely an effect of a positive relationship between size and swimming ability (Castro-Santos 2005; Videler 1993). Larger fish are also likely more motivated to swim through fishways (Goerig and Castro-Santos 2017) and less prone to predation (Christensen 1996; but see Boulêtreau et al. 2018, for exclusive predation on large fish by wels catfish). Nevertheless, a large range of sizes passed in our study. Of relevance to the functionality of the fishway, barbel and chub are both expected to migrate upstream mainly in relation to spawning, at sizes larger than most fish that failed to pass in our study (Britton and Pegg 2011; de Leeuw and Winter 2008; Fredrich et al. 2003). Consequently, size selection might not be an important problem for the longitudinal connectivity at the study site for these species.

Not only the fishway itself, but also the motivation of fish to swim through the fishway and its interplay with environmental conditions may have played a role for our results (Cooke and Hinch 2013; Dodd et al. 2023; Goerig and Castro-Santos 2017). Although releasing fish in or close to fishways or culverts is a commonly used method to study fish passage behaviour (Goerig and Castro-Santos 2017; Sanz-Ronda et al. 2019; Silva et al. 2020), one important caveat for our study is that fish were largely tagged and released outside the migratory season. In addition, the fish in our study were not enclosed, could leave and most likely had suitable spawning and feeding habitat available also downstream (ADBPO 2009). Hence, our evaluation of fish passage success is relying on the tendency of fish to return upstream and to swim against the current (Dodd et al. 2023; Lucas and Baras 2001). The overall results are therefore not directly comparable with those of spawning and volitionally passing fish. The importance of motivation for fish passage is corroborated by the radio-tagged common carp being present by the dam for extended periods of time also during autumn but only passing the dam as part of a potential spring spawning migration (Fortini 2016; Finger et al. 2020; Banet, Fieberg, and Sorensen 2022).

Passage of non-native species may facilitate invasions and be detrimental for the local upstream fish community (Zaccara et al. 2021). Barbel, consisting mainly of the non-native European barbel, were the most successful in passing the fishway, but have already been dominant in the Po River basin before this fishway was built (Antognazza et al. 2023; Meraner et al. 2013). The successful passage of large individuals of common carp and wels catfish (although previously present upstream; Nyqvist et al. 2022) show the potential of similar fishways offering colonisation pathways in other systems. Particularly, wels catfish is a large-sized voracious predator, sometimes even exploiting fishways themselves as feeding grounds (Boulêtreau et al. 2018; Copp et al. 2009; Cucherousset et al. 2018). Although the potential of selective fish passage solutions that pass native fish but stop non-native fish is being discussed (Benoit et al. 2023), proposed solutions affect non-target species as well (Rahel and McLaughlin 2018; Vélez-Espino et al. 2011) and no good practises for the management of non-native species in fishways exist to our knowledge. Caution is warranted when building fishways connecting isolated native species with downstream non-native or invasive populations (Antognazza et al. 2023).

Barbel were more likely to pass the fishway at night than during the day, and a similar but not statistically significant tendency was seen in Italian chub. This is in line with diel fish passage patterns described for barbel and chub elsewhere (Ovidio et al. 2020). Sometimes, hydrodynamically difficult passage routes may require visual cues and daytime passage (Nyqvist et al. 2017; Stuart 1962). Most fish species, however, display diel changes in behaviour, such as movement and migration, activity, anti-predator responses and habitat use (Helfman 1986). In relation to fish passage, for example, wels catfish, European eel (*Anguilla anguilla*), grayling (*Thymallus arcticus*) and a range of Iberian cyprinids have been observed to predominantly pass fishways at night (Ovidio, Dierckx, and Benitez 2023; Plymesser et al. 2024; Santos et al. 2005). The preference for diurnal vs. nocturnal passage proportions should be taken into account when designing the fishway. Particularly, light sources in the vicinity of the fishway should be avoided to prevent artificial light from disturbing passage behaviour (Hadderingh et al. 1999; Tarena et al. 2023; Vega et al. 2024).

A small number of large carps and barbel were radio tagged to provide data on fish behaviour relevant to fish passage dynamics beyond the reach of the PIT-antennas. Interestingly, although radio-tagged carps were present at the dam for an extended time in autumn, no fish passed upstream. In spring, on the other hand, four of eleven carps present downstream of the dam successfully passed the fishway. No radio-tagged barbel passed, whereas many small barbel released in the fishway (only PIT tagged) successfully passed the fishway. The larger radio-tagged individuals should have a substantially higher swimming ability, and thus a higher physical capability to ascend the fishway, than their smaller conspecifics (Castro-Santos 2005). Fish released in the tailrace also lacked the direct current that likely served as the main motivator for upstream movement for fish released in the fishway (Lucas and Baras 2001). Similarly, the other large fish released in the tailrace mainly passed after a long time, with upstream movements likely related to a seasonal migratory or dispersal motivation. Also, all radio-tagged barbel were initially captured in the downstream area of the dam and might have simply lacked incitement to move away from their original home range. These results, again, emphasise the importance of understanding the motivation of fish in relation to passage performance (Dodd et al. 2023; Goerig and Castro-Santos 2017), and underscore that the absence of passage does not necessarily imply the lack of ability.

Related to the fish passage solution as a whole, it is important to remember that successful passage is not only about successfully moving upstream a fishway, but a series of events including approach, entering, passing through and exiting the fishway (Castro-Santos, Cotel, and Webb 2009). Each event is affected by local conditions and designs and may constitute a bottleneck for successful passage, leading to passage failure or substantial delays (McLaughlin et al. 2013; Nyqvist et al. 2017). Here we mainly studied the ability of fish to enter (downstream release group) and ascend the fishway (all groups). Lower passage success in the downstream release group indicates issues with locating and/or entering the fishway—but this could also be related to the lack of immediate exposure to a current enticing rheotactic upstream movement through the fishway (Lucas and Baras 2001). The upstream movement of fish released in the tailrace, although in low numbers, demonstrate the ability of fish to approach, enter and pass the fishway. Systematic telemetry studies are needed to pinpoint fish passage bottlenecks to truly evaluate passage efficiencies and thereby contribute to the development of fish pass design (CEN 2021).

5 | Conclusion

Knowledge of fish behaviour in fishways is critical to preserve fish communities in fragmented rivers. The need for community level conservation efforts is widely acknowledged; yet many species remain understudied, likely hindering the implementation of effective remedial measures (Vøllestad 2023). We evaluated fish passage behaviour for a range of species representative of the local fish community at a vertical slot fishway in a large Italian river. We demonstrate successful passage of some species (chub and barbel), but failures of others (carassius and gudgeon). Fish size was positively related to passage success in both chubs and barbel, and a tendency of nocturnal passage was observed in both species. Additionally, caution is warranted in relation to fishways that are facilitating the spread of invasive species.

Acknowledgements

We want to acknowledge Michele Spairani, Tiziano Bo, Fabio Tarena and Claudio Ganora for assistance in the field. Thanks to Martin Österling for the helpful comments on some aspects of the manuscript and statistical analysis. We thank Idrobaveno Srl, Consorzio Irriguo Coutenza Canali Lanza e Mellana and Allara S.p.A for access to facilities to deploy the upstream and downstream antenna. F.E. and A.S. have received funding from the European Union Horizon 2020 Research and Innovation Programme under the Marie Sklodowska-Curie Actions, Grant Agreement No. 860800. We are grateful to three anonymous reviewers providing extensive comments and perspectives that helped to improve the initial manuscript.

Data Availability Statement

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

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.