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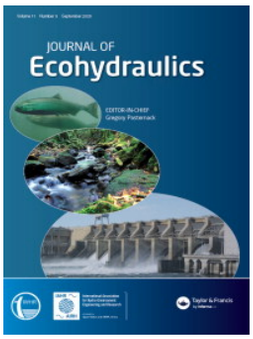
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Multi-species assessment of fish passage success and behaviour in a Larinier super-active baffle fishway

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ABSTRACT

River fragmentation caused by low-head barriers represents a threat to longitudinal connectivity in freshwater ecosystems. Technical fishways are implemented to mitigate these impacts, yet their effectiveness for small-bodied non-salmonid species remains understudied under demanding hydraulic conditions. In this study, we evaluated fish passage performance in a Larinier super-active baffle fishway operating at a 15% slope, corresponding to the upper limit of recommended design criteria. Using PIT telemetry, we quantified upstream passage success, passage rate, and transit time for five non-salmonid species inhabiting the upper Tanaro River (NW Italy). Passage success was species-specific, ranging from 56.8% in Italian chub (*Squalius squalus*)to 47.0% in barbel (*Barbus* spp.), while Italian riffle dace (*Telestes muticellus*), European bullhead (*Cottus gobio*), and minnow (*Phoxinus* sp.) exhibited no upstream passage. Within species, body size emerged as a key driver of passage success, with a positive effect of larger body size on upstream passage rate. Transit time differed between species, with Italian chub traversing the fishway rapidly and barbel exhibiting prolonged and variable ascent times, reflecting contrasting behavioral strategies. Our results indicate that 15% slope Larinier fishways impose hydraulic selectivity and may disproportionately limit passage for small-bodied species, highlighting the need for species-specific considerations when designing fishways.

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1. Introduction

Worldwide, river networks are increasingly fragmented by millions of anthropogenic barriers, including dams, weirs, and culverts (Belletti et al. 2020). These structures profoundly alter freshwater ecosystems by disrupting longitudinal connectivity and impairing the biological, hydrological, and hydro-geomorphological processes that characterize free-flowing rivers (Dudgeon et al. 2006; Nyqvist et al. 2025). Loss of connectivity is widely recognized as one of the primary drivers of freshwater biodiversity decline (Reid et al. 2019; Sayer et al. 2025), contributing to the status of fishes as the most threatened vertebrate taxon globally. Fish are particularly sensitive to river fragmentation because many species depend on longitudinal connectivity to complete key life-history processes (Fullerton et al. 2010). Diadromous and potamodromous species rely on river corridors for migration between feeding, spawning, and refuge habitats (McIntyre et al. 2015). However, barriers also strongly affect non-migratory species by restricting access to essential habitats, fragmenting populations, and reducing dispersal and gene flow, thereby increasing local extinction risk (Jones et al. 2021). Consequently, restoring longitudinal connectivity has become a central objective in river management and conservation. To reduce the ecological impacts of anthropogenic barriers, a wide range of fish passage solutions has been developed, including technical fish passes designed to facilitate upstream movement (Larinier et al. 2002; Nyqvist et al. 2025). Despite the diversity of fishway designs, their effectiveness has been disproportionately evaluated for charismatic, economically valuable, or large-bodied species, particularly salmonids, while non-charismatic taxa remain poorly studied (Smialek et al. 2019; Vøllestad 2023). This knowledge gap is problematic from a conservation perspective, as these species often dominate fish assemblages and play key functional roles in river ecosystems.

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Among technical fish passes, the Larinier super-active bottom baffle fishway (Larinier fishway), developed in France in 1981 (Larinier et al. 2002), is one of the most widely implemented designs in the UK and is gaining increasing interest as a fish passage solution retrofitted to existing low-head barriers (Armstrong et al. 2010; Tummers et al. 2016). In fact, this fishway, consisting of a straight, sloping rectangular channel equipped with a herringbone pattern of thin metallic bottom deflectors to dissipate energy and reduce flow velocity (Larinier et al. 2002), operates on steep slopes (10–15%), requiring limited space and offering advantages in terms of cost, ease of construction and maintenance, and resistance to debris accumulation (Armstrong et al. 2010). Although initially designed for salmonids, this type of fishway is promoted as suitable for a wide range of species, including low-performance cypriniform fish (Armstrong et al. 2010). Empirical evidence supporting its effectiveness for small- and medium-sized, non-salmonid fishes, however, remains limited.

While studies on nature-like and vertical-slot fishways have reported moderate to high passage efficiencies for some cyprinid species such as *Barbus* spp. and *Squalius* spp. (Benitez et al. 2018; Tarena et al. 2025), comparable data for baffled fishways are scarce (Tummers et al. 2016; Piper et al. 2018; Lothian et al. 2020). Among salmonids, brown trout, Atlantic salmon, and grayling have been reported to ascend Larinier fishways at medium or high efficiencies (Peirson et al. 2013; Noble et al. 2016), whereas among other fish species only chub and dace have displayed a comparable performance (Piper et al. 2018). Moreover, available evidence suggests that Larinier fishways may be ineffective for certain taxa, including European river lamprey, highlighting the potential for strong species-specific responses to hydraulic conditions within fishways (Tummers et al. 2016; Lothian et al. 2020). Given that small- to medium-sized species often exhibit diverse swimming capacities, behavioral strategies, and habitat preferences, their passage performance can vary substantially among species and fishway designs. Yet, these differences are rarely quantified, particularly under challenging hydraulic conditions such as steep slopes approaching the upper operational limits of technical fish passes.

In this field study, we evaluated the upstream passage performance of adult individuals of five fish taxa inhabiting the upper Tanaro River (Italy) to assess the effectiveness of a single ramp of a Larinier fishway operating at a 15% slope. Specifically, we aimed to determine whether the hydraulic conditions within the fishway allow successful passage across the size range of small- to medium-sized South European species of different swimming behavior guilds. We further investigated whether transit time and time to passage differed between species. Within species, we quantified the effects of fish body length, water temperature, time of day, and water level on upstream passage rate.

2. Material and methods

2.1. Study area and studied species

The field experiment was conducted on a Larinier fishway installed at a low-head weir in Trappa, Garessio (NW Italy; 44°10′58.0″ N, 7°59′25.4″ E), in the Tanaro River (Figure 1a). The Tanaro River originates in the Ligurian Alps and is, in its upper reaches, characterized by an alpine hydrological regime. The fish community is dominated by rheophilic species typical of the upper cyprinid zone of the Po River Basin. The fish assemblage is predominantly composed by Italian riffle dace (*Telestes muticellus*); minnow (*Phoxinus* sp.), not identified to species level; and two demersal taxa: barbels (*Barbus* spp.) and European bullhead (*Cottus gobio*). The barbel group comprised individuals of brook barbel (*Barbus caninus*) and Italian barbel (*Barbus plebejus*), as well as putative hybrids between these taxa. Italian chub (*Squalius squalus*) is also present but occurs in lower abundance. Non-native fish species, brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), occur at low abundances within the study reach as a result of past stocking activities (Candiotto, pers. obs.).

The studied species span a broad ecological gradient and differ in migratory behavior and diel activity patterns, though comprehensive knowledge remains incomplete for some taxa as data on endemic species with limited distributions are often fragmentary or derived from congeners. Among barbels, some *Barbus* species undertake upstream spawning migrations in spring with predominantly crepuscular to nocturnal activity (Benitez et al. 2018; Ovidio et al. 2023; Eggers et al. 2025; Santos et al. 2005). Importantly, barbels have also been reported to pass fishways without a clear diel pattern (Ovidio et al. 2023), and *Barbus caninus* in small streams did not show any clear spawning migration or strong diel activity pattern (Schiavon et al. 2025b). Among leuciscids, Italian chub has been observed traversing fishways during the spawning season with no strong diel pattern detected (Eggers et al. 2025), consistent with reproductive movements described for the congener *Squalius cephalus* (Fredrich et al. 2003; Ovidio et al. 2023). Italian riffle dace is reported to undertake spawning migrations (Kottelat and Freyhof 2007), though in small streams rather limited movements have been documented (Schiavon et al. 2025a).

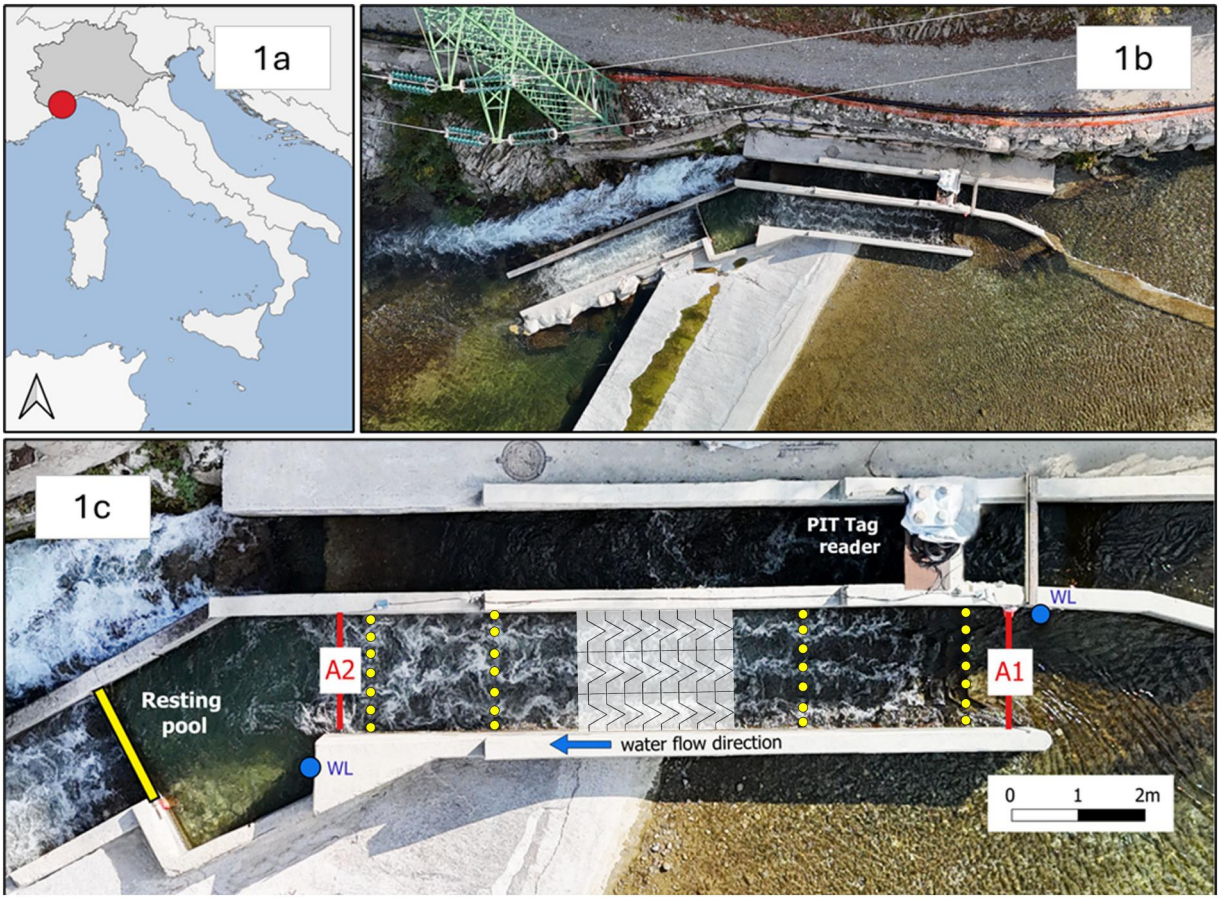


Figure 1. Study area and experiment. (a) Location of the study site along the Tanaro River at the Garessio fishway (NW Italy) is indicated by the red dot within the Po River basin in grey. (b) Aerial view of the study reach, highlighting the weir, the environmental-flow channels, the two ramps, and the resting pool of the Larinier fishway. (c) Detailed view of the investigated fishway section: showing the position of the downstream net blocking the resting pool where fish were released (yellow line); the positions of the downstream (A2) and upstream (A1) PIT-tag antennas (red lines); the temperature and water level (WL) monitoring points (blue dots), the location of the 28 water velocity measurement points (yellow dots); the flow direction; and the characteristic hydrodynamic pattern generated by the super-active baffles (a schematic representation of their herringbone pattern is superimposed on the central portion of the fishway).

Fishway studies indicate higher passage activity under daytime or lit conditions for Italian riffle dace, despite the fish being active both during the day and at night (Tarena et al. 2025). Minnow undertakes short upstream spawning migrations (Froese and Pauly 2026), though available data remain limited. The European bullhead is a small benthic and largely sedentary species with no directed spawning migration and no clear diel difference in passage behavior (Knaepkens et al. 2005; Tarena et al. 2025). Despite this ecological and behavioral diversity, all target genera have been recorded using fishways (Panagiotopoulos et al. 2024; Eggers et al. 2025; Schlautmann et al. 2026).

2.2. Larinier fishway design and hydraulic parameters

The studied Larinier fishway consists of two straight ramps, each 10 m long and 1.8 m wide, with a longitudinal slope of 15%, separated by a resting pool. Each ramp has a hydraulic head drop of 1.5 m, resulting in a total head drop of 3.0 m across the entire structure. The resting pool measures 3.35 m in length, 2.80 m in width, and 1.0 m in depth, with an approximate volume of 9 m^3. Each ramp is equipped with three 0.60 m wide units of super-active metallic baffles with a thickness of 8–10 mm and a uniform height of 0.10 m. The baffles are regularly spaced at 0.26 m intervals along the ramps, resulting in 39 baffles per ramp. The fishway is located on the hydrographic right bank of the Tanaro River and is bordered by additional environmental-flow channels (Figure 1b, c). During the study period, water temperature and water level were continuously monitored using two HOBO MX2001 data loggers (Figure 1c, 3). Water level data were subsequently used to calculate discharge following ISO 748:2021 (International Organization for Standardization [ISO], 2021), resulting in an experimental discharge range of 0.3–0.4 m^3 s^{-1}. Hydraulic conditions within the studied fishway ramp were assessed by measuring local flow velocities using an electromagnetic flowmeter (Seba

Hydrometrie FlowSens) at four longitudinal cross-sections along the ramp (located at 0.5, 2.5, 7.5, and 10 m upstream from the lowermost baffle; Figure 1c), under both minimum and maximum operational discharges. To capture the dominant hydrodynamic patterns between baffles, flow velocities were measured at seven points equally spaced along the cross-section at two vertical positions: (i) at half baffle depth (approximately 5 cm below the top of the baffles), representative of near-bed conditions within the baffle zone, and (ii) at the mid-water column above the baffles, representative of the main flow. A total of 112 velocity measurements were collected. Across the tested discharge range, mean velocities at the mid-water column above the baffles were 1.1 m s^{-1}, whereas substantially lower velocities were observed within the baffle zone, with mean values of 0.4 m s^{-1} (Table 1).

This clear differentiation between near-bed baffle regions and the overlying water column, together with a marked horizontal heterogeneity of the velocity values sampled across the fishway cross-sections, highlights a strongly heterogeneous hydraulic environment. The vertical shear (dV/dz), estimated at each sampling point as a finite-difference approximation between mid-water column and half-baffle velocities, ranges from 0.45 to 16.4 s^{-1}, reflecting strong vertical velocity gradients and marked spatial variability along the channel. Reynolds numbers, computed from depth-averaged velocity and flow depth at each measurement point, range from approximately 2.7×10^4 to 2.6×10^5, indicating fully developed turbulent open-channel flow throughout the domain. Section-averaged Reynolds numbers, ranging from 7.5×10^4 to 1.8×10^5, further confirm consistently turbulent conditions across all cross-sections and discharge scenarios (Chow 1959; Nezu and Rodi 1986).

2.3. Fish sampling, tagging, and experimental design

The five selected fish taxa were barbels, Italian chub, minnow, bullhead, and Italian riffle dace; fish were collected by electrofishing in the vicinity of the weir, within approximately 100 m upstream and downstream of the structure. Following capture, individuals were immediately transferred to aerated holding tanks supplied with flowing river water to maintain adequate oxygen levels and minimize handling stress. All fish were tagged on the day of capture (26 September). Prior to tagging, individuals were anaesthetized using a clove oil solution (Aromlabs, USA; approximately 0.05 mL L^{-1}). Tagging was performed directly on the riverbank following well-tested procedures (Schiavon et al. 2023; Nyqvist et al. 2024a). A small ventral incision was made, and a passive integrated transponder (PIT tag; Oregon RFID, USA; 12 × 2.1 mm; 0.10 g) was inserted. After tagging, fish were transferred to four perforated circular holding tanks (500 L each) to recuperate after tagging and handling for 5–7 days before entering the experimental trials. The holding tanks were positioned in the Tanaro River downstream of the weir, along the left riverbank within a natural deep-water pool. Each species was maintained in a separate tank, with the exception of barbels and Italian chub, which were kept together due to the low number of chub individuals and the low risk of interspecific predation or aggressive interactions between these taxa. The tanks were covered with nets and securely anchored to the riverbank to prevent escape and predation by ichthyophagous birds. Perforated bricks were added to provide shelter during the holding period. Continuous exchange of river water through the perforated tank walls ensured adequate circulation and stable water temperature.

At the start of the experiment, fish were released into the resting pool of the fishway, which was enclosed with fine-meshed nets (0.5 × 0.5 cm) to prevent downstream exit (Figure 1c; Tarena et al. 2025). A total of 523 fish divided into six groups were released over three consecutive days (1–3 October) at midday (mean = 12:05) and sunset (mean = 18:56) (Table 2, Table S1). Downstream nets were inspected and cleaned twice daily to remove accumulated leaves and floating debris.

Table 2. Summary of biometric measurements (fork length and wet mass) reported as median, range, and interquartile range (IQR) for the 523 individuals from five species included in the experiment.

		Fork length (cm)			Wet mass (g)		
Species	n	Median	Range	IQR	Median	Range	IQR
Barbels	115	17	8.2–33	14.9–19	67	8–426	45–90
Italian chub	37	16.3	9.8–20.5	11.3–18.2	50	9–120	17–79
Minnow	106	7.5	6.3–9	7.2–7.9	5	3–10	4–6
Bullhead	116	10.0	7.6–14	8.7–10.6	11	4–32	7–14
Italian riffle dace	149	10	7.2–14.8	8.6–12	10	6–45	8–23

Table 1. Flow velocity statistics (mean, standard deviation, minimum, and maximum) were measured at two vertical positions within the baffle fishway at half baffle depth and at the mid-water column above the baffles under minimum and maximum discharge conditions ($Q = 0.3$ and 0.4 m^3 s^{-1}).

	$Q = 0.3$ m^3 s^{-1}				$Q = 0.4$ m^3 s^{-1}			
Measurement height	Vmean (m s^{-1})	SD	Vmin	Vmax	Vmean (m s^{-1})	SD	Vmin	Vmax
Half baffle depth	0.31	0.10	0.07	0.47	0.40	0.22	0.16	0.94
Mid-water column above baffle	1.00	0.33	0.58	1.55	1.14	0.39	0.54	1.86

After release, fish movements were continuously monitored using the RFID antenna system installed within the fishway (Figure 1c), allowing detection of individual fish at both the downstream and upstream sections of the ramp. During the early morning of 4 October, windy conditions caused leaf accumulation against the downstream net enclosing the resting pool and the formation of a small opening (diameter = 1 cm), potentially allowing smaller individuals to exit the resting pool. The experiment finally ended at midday on 6 October. The downstream net was removed, and fish were allowed to freely disperse in both directions.

The study was performed in accordance with the Ufficio Caccia e Pesca of the Provincia di Cuneo (n.76798 of 2 September 2025), under the provisions of art.2 of the national Decree n.26/2014 (implementation of Dir. 2010/63/EU).

2.4. RFID-antenna configuration and operational performance

Fish movements were continuously monitored using two RFID antenna systems installed within the fishway, one close to the exit and one just upstream of the release pool (Figure 1). The RFID antennas were vertical loop antennas with a width of 180 cm and a height of 55 cm. Prior to the study, antenna performance was tested and revealed no detection gaps within the loop and a lateral detection range of approximately 10 cm. Operation efficiency was then assessed throughout the study using reference marker tags installed in proximity of each antenna and calculated as the ratio between detected and expected detections. The PIT system operated continuously from 11:30 on 1 October to 11:30 on 6 October with a 100% operation efficiency for both antennas.

2.5. Data interpretation and statistical analysis

PIT-tag detection records were integrated with biometric measurements and release-group data for descriptive and statistical analyses. Detection at the downstream antenna (A2) confirmed movement activity at the fishway entrance. Successful passage was defined by detections at the upstream antenna (A1). Passage success was calculated as the proportion of fish successfully passing out of those displaying movement activity. Time to passage was calculated as the time elapsed between release and first detection at the upstream antenna. Fishway transit time (i.e. the time required to traverse the fishway ramp structure) was quantified as the time between the last detection at the downstream antenna and the subsequent detection at the upstream antenna. The transit speed was calculated as the linear distance between the antennas divided by the median transit time for each species. A swimming speed was estimated by adding the mean water velocity at the mid-water column above the baffles, associated with the water level recorded at the time of the passage event, to the transit speed. As fish may have tracked a non-linear route or exhibited stop-and-go progression within the fishway, estimated swimming speeds should be interpreted with caution. Swimming speed was additionally normalized and expressed in body lengths per second ($BL \cdot s^{-1}$).

The effect of body length on passage success was assessed for each species using binomial generalized linear mixed models (GLMMs), with release group included as a random effect to account for variation among groups. To identify factors influencing the rate of upstream passage, we used Cox proportional hazards models to assess how fish characteristics and environmental conditions affected the probability of passage over time within species. Time of day (day/night), water temperature, and water level (proxy of discharge) were included as time-varying covariates (within 1h slots for continuous variables), and fish length was included as a time-invariant covariate among the candidate models (Castro-Santos and Perry 2012; Abd ElHafeez et al. 2021; Nyqvist et al. 2024b). Time to passage was defined as the interval from release until successful passage. Fish that did not complete passage until 4 October were right-censored, as they may have escaped downstream and hence possibly not be available to pass. The release group was included as a frailty term in the model to account for potential effects related to the release procedures. The proportional hazards assumption was evaluated for all covariates using Schoenfeld residual tests (Zhang et al. 2018), and correlations between covariates were assessed. To select the best model among candidate models, minimization of the Akaike information criterion (AIC) was used. As time of day and temperature correlated ($r = 0.40$), these two covariates were not allowed to co-occur in the same model. Models with an AIC value of 2 or lower from the null model and within 2 AIC units from the best model were considered good models (Burnham and Anderson 2002). Only the most parsimonious model was explored in detail if more than one competing model fulfilled these criteria (Harbicht et al. 2022). Species differences in time to passage and transit time were tested using a Mann-Whitney U test, as the data violated parametric test assumptions. The effects of body length on transit time were assessed using Spearman's rank correlation for each species separately. One Italian chub exhibiting an anomalously long transit time (>20 h) was

excluded from these analyses. All statistical analyses were performed in R (2024) using RStudio version 2025.05.1 + 513 (Posit, 2025). Data handling and visualization were conducted using the *dplyr*, *tidyverse*, and *ggplot2* packages. Mixed-effects Cox proportional hazards models were fitted using the *coxme* package.

3. Results

Across all species, most released individuals were detected at the downstream antenna located at the base of the fishway, indicating movement activity following release (Table 3). Detection rates at the downstream antenna exceeded 97% for all species, reaching 100% for barbel (*Barbus spp.*), Italian chub (*Squalius squalus*), and Italian riffle dace (*Telestes muticellus*), 95.7% for European bullhead (*Cottus gobio*), and 94.3% for minnow (*Phoxinus sp.*). The time elapsed between release and first detection at the downstream antenna varied markedly among species (Fig. S1). Italian chub reached the fishway entrance most rapidly (median = 0.31 h, IQR: 0.15–0.80 h, range: 0.02–3.42 h), whereas bullhead exhibited the longest delays (median = 4.48 h, IQR: 1.53–9.38 h, range: 0.29–31.85 h). Intermediate arrival times were observed for barbel (median = 0.63 h, IQR: 0.32–1.51 h, range: 0.02–33.43 h), Italian riffle dace (median = 0.45 h, IQR: 0.25–0.85 h, range: 0.01–55.06 h), and minnow (median = 1.24 h, IQR: 0.68–2.01 h, range: 0.15–44.60 h).

3.1. Passage success

Despite the high proportion of individuals detected at the downstream antenna, successful upstream passage was limited and strongly species-dependent (Table 3). Only barbel and Italian chub completed upstream passage during the entire study period, with 47.0% and 56.8% of released individuals, respectively, successfully passing. No upstream passage was recorded for minnow, bullhead, or Italian riffle dace (Table 3). Body length was a significant positive predictor of passage success in both species (barbel: $\beta = 0.36 \pm 0.09$, $p < 0.001$; Italian chub: $\beta = 0.80 \pm 0.23$, $p < 0.001$), with complete passage failure occurring below a species-specific size threshold. In barbel, all individuals below 14.0 cm failed to pass ($n = 23$), whereas passage success increased above this threshold, with 59.8% of individuals $\geq$14.0 cm successfully passing (54 of 92). Similarly, in Italian chubs, no upstream passage was recorded for individuals shorter than 13.2 cm ($n = 12$), while passage success above this length reached 84.0% (21 of 25).

Among individuals that successfully passed the fishway, time to passage was significantly different (Mann-Whitney U test: $W = 228$, $p < 0.001$) with median values of 3.77 h (IQR: 1.98–8.83 h) for barbel and 21.6 h (IQR: 6.50–25.1 h) for Italian chub (Figure 2).

3.2. Passage rate

Fish length exerted a strong positive effect on passage rate in both species (Table 4). For barbel, the selected good model included only fish length, while for Italian chub, the selected good models included fish length and temperature as well as fish length and time of day. Indeed, graphical scrutinizing of the data confirms that fish passed at higher rates during the day and under higher temperatures (Figure 3). Water level was not included among the good models for any of the two species.

3.3. Transit time

Barbel and Italian chub exhibited markedly different fishway passage durations (Mann-Whitney U test: $W = 1019$, $p < 0.001$). Italian chub crossed the fishway rapidly, with a median transit time of 17 s (IQR: 14–23 s; range: 10–1108s; Figure 4) and a median transit speed of 0.60 $m \cdot s^{-1}$. The fastest individual clocked a swimming speed of 2.15 $m \cdot s^{-1}$ (10.61 $BL \cdot s^{-1}$). In contrast, barbel displayed substantially longer and more variable passage durations, with a median of 1265s (IQR: 334–2205s; range: 33–9816s; Figure 4) and a median transit speed of 0.01 $m \cdot s^{-1}$. For barbel, transit time decreased significantly with increasing body length (Spearman's $\rho = -0.37$, $p = 0.007$) indicating that larger individuals passed more rapidly. In contrast, no significant effect of body length was detected in Italian chub (Spearman's $\rho = -0.12$, $p = 0.617$, $n = 20$).

Table 3. Number of fish released and detection outcomes.

Scientific name	English name	Released (*n*)	Detected at downstream antenna A2, n (%)	Detected at upstream antenna A1, *n* (%)
Barbus spp.	Barbel	115	115 (100.0)	54 (47.0)
Squalius squalus	Italian chub	37	37 (100.0)	21 (56.8)
Phoxinus sp.	Minnow	106	100 (94.3)	0 (0.0)
Cottus gobio	Bullhead	116	111 (95.7)	0 (0.0)
Telestes muticellus	Italian riffle dace	149	149 (100.0)	0 (0.0)
		Total 523	512 (97.9)	75 (14.6)

Detection at A2 indicates presence in the downstream section of the fishway, whereas detection at A1 indicates successful upstream passage. Values are reported as counts (*n*) and percentages. Percentages for A2 are calculated relative to the number of fish released per species. Percentages for A1 represent adjusted passage success and are calculated relative to the number of fish detected at A2.

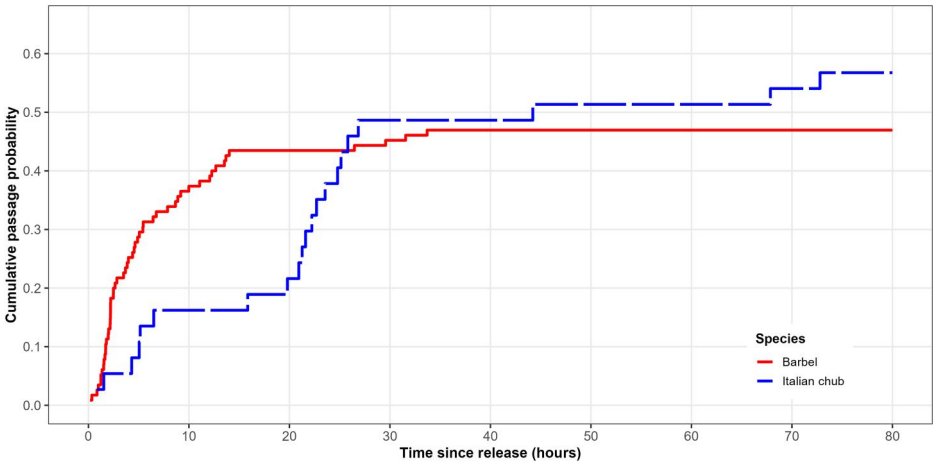


Figure 2. Cumulative passage probability observed during the studied period through the super-active baffle fishway for barbel ($n = 115$, solid red) and italian chub ($n = 37$, dashed blue) over time since release.

Table 4. Model coefficients for the most parsimonious Cox-regression models for passage rate of Barbel and Italian chub in the Larinier super-baffled-fishway.

Species	Model	Variable	$\beta \pm$ SE	*p*-value
Barbus spp.	Length	Length	0.18 ± 0.04	<0.01
Squalius squalus	Length + Daynight	Length	0.42 ± 0.15	<0.01
		Night	-2.91 ± 1.2	0.02
	Length + Temperature	Length	0.32 ± 0.12	0.12
		Temperature	0.82 ± 0.33	0.01

Time since release was right censored at 00:00 on 4 October 2025. For each covariate included in the most parsimonious models, $\beta \pm$ SE and *p*-value are reported.

4. Discussion

This study assessed fish passage performance at a Larinier fishway operating at a 15% slope, focusing on the ability of five non-salmonid small- to medium-bodied fish species to overcome a technical fishway operating at the upper limit of its recommended operational range design (Larinier et al. 2002). Passage success varied markedly among species: Italian chub and barbel showed moderate passage success (57% and 47%, respectively), whereas no upstream passage was recorded for Italian riffle dace, European bullhead, or minnow. Within both Italian chub and barbel, longer fish passed at higher rates than shorter fish. Despite similar overall passage success, the two species exhibited markedly different passage behaviors: Italian chub traversed the fishway rapidly in a single continuous ascent, whereas Barbel displayed substantially longer and more variable transit times, consistent with a stepwise ascent.

Overall, these results are consistent with previous studies reporting low passage success for non-salmonid and weaker-swimming species in Larinier fishways (Tummers et al. 2016; Piper et al. 2018, Lothian et al. 2020). Among the species that did pass, both barbel and Italian chub exhibited moderate passage success, with approximately half of the released individuals successfully completing the upstream passage. For barbel, this moderate performance contrasts with studies reporting relatively high, and in some cases near-complete, passage success in technical fishways (Benitez et al. 2018; ; Ovidio et al. 2020; Eggers et al. 2025; Tarena et al. 2025). For Italian chub, the results are consistent with results reported for its sister species, *Squalius cephalus*, in another Larinier fishway (Piper et al. 2018) and place the performance of this fishway typology within the wide range of passage success documented for chub across various technical fishway designs (e.g. Benitez et al. 2018; Lothian et al. 2020; Ovidio et al. 2020). Taken together, these patterns suggest that the steep slope and complex hydrodynamics of the Larinier fishway represent a limiting factor even for relatively strong swimmers.

Among Italian riffle dace, bullhead, and minnow, not a single fish passed. Although the experiment was conducted outside the spawning season, this timing is unlikely to explain the observed patterns. Autumn water temperatures in the study reach can be similar to those occurring in spring and partially overlap with temperatures experienced during the spawning period of the studied species (Fortini 2016). Moreover, upstream movements of Italian riffle dace and European bullhead have been documented outside the reproductive period (Tarena et al. 2025; Schiavon et al. 2025a). In fact, in a similar study in a vertical slot fishway, also outside of the spawning season, both Italian riffle dace and bullhead passed with high or relatively high passage success, (Tarena et al. 2025). The very high proportion of fish detected at the downstream antenna confirms that fish were displaying active swimming behavior and were present at the fishway entrance for upstream movement. Although these detections do not necessarily reflect passage attempts, they do show that fish were able to locate and approach the structure and that they were very likely to do so.

The complete absence of successful passage by Italian riffle dace is noteworthy. This species has

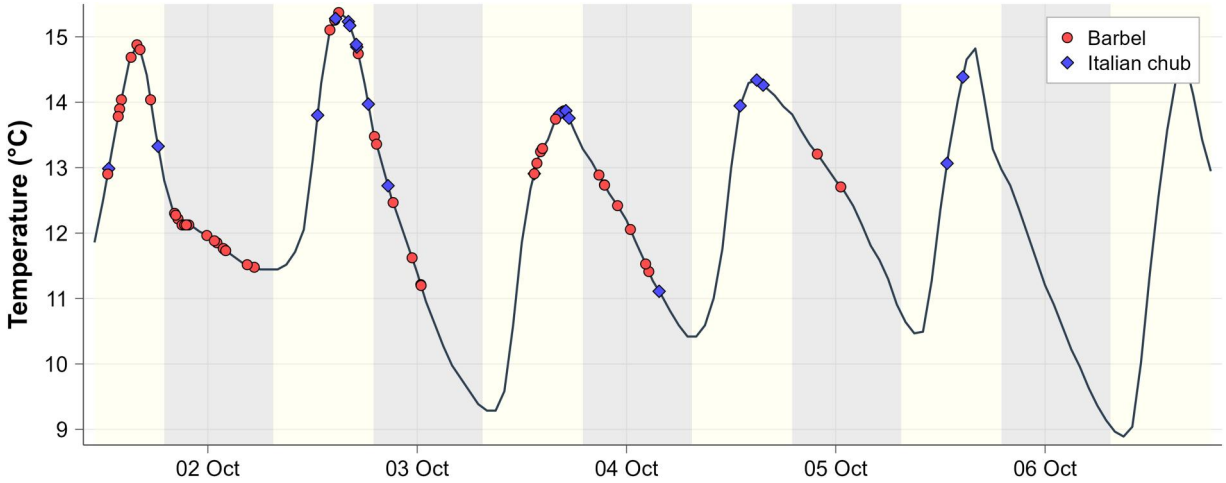


Figure 3. Passage timing (first detection on upstream antenna) in relation to photoperiod and temperature during 1–6 October 2025. Barbel passages are shown as red circles and Italian chub passages as blue diamonds. Background shading denotes photoperiod based on local sunrise and sunset times (yellow: daylight; grey: darkness).

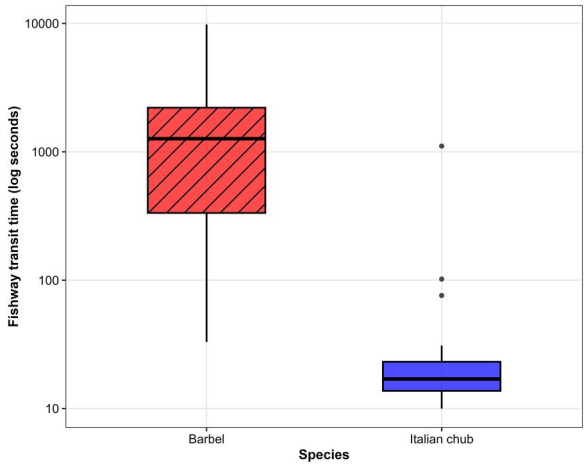


Figure 4. Boxplot of fishway transit time (log seconds) for Barbel in dashed red ($n = 53$) and Italian chub in solid blue ($n = 20$). Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers extend to values within 1.5 × IQR. One Italian chub, transiting for > 20 h is excluded from the figure.

previously been reported to pass vertical-slot fishways at high passage efficiencies (Tarena et al. 2025). For European bullhead, on the other hand, the results align well with existing literature. This benthic species frequently exhibits very low passage ability across a wide range of fishway types and barrier configurations. Several field and experimental studies have reported 0% passage efficiency for bullhead in pool-and-weir fish passes (Knaepkens et al. 2006), block ramps (Weibel and Peter 2013), and step-pool and vertical-slot fishways (Iaia et al. 2025). Although cases of relatively high passage success have been documented in a vertical-slot fishway (Tarena et al. 2025). Here, passage may have been particularly difficult for bullhead, as they would need to pass above flow barriers created by strong vertical velocity gradients above the baffles to ascend the structure (Tarena et al. 2025). Minnow are poorly represented in fish passage studies but even if high numbers of minnows have been observed in fishways (Benitez et al. 2015), experimental studies have documented 0% passage of *Phoxinus phoxinus* both across small vertical drops (Jones et al. 2021) and through block ramps (Weibel and Peter 2013). Together with previous work, the complete failure to pass for Italian riffle dace, European bullhead, and minnows underlines the difficulty and attention to hydrodynamic conditions necessary to pass the whole fish community, especially small-sized species (Marsden and Stuart 2019). The low-velocity pathways potentially provided by the marked spatial heterogeneity of the flow along Larinier fishways here resulted likely fragmented and unstable under the fully turbulent conditions and pronounced vertical shear due to the high slope of this structure. Under these challenging conditions, only stronger swimmers seem to have managed to cope with elevated velocity gradients and effectively exploit available flow pathways.

Body size seemed to have both a direct and indirect effect on passage success in the Larinier fishway. Among the barbel and Italian chub, larger individuals demonstrated higher passage rates and passage success probabilities, with the smallest tested individuals all failing to pass. Fishways are known to sometimes select against small fish (Volpato et al. 2009), often explained by a lower swimming capability in smaller compared to larger fish (Videler 1993; Katopodis and Gervais 2012). Indeed, a similar-sized related passage probability was observed for the same species in a vertical slot fishway (Eggers et al. 2025). The size range of the three fish species that did not pass were close to or below the minimum passage threshold where all Barbel and Italian chub failed to pass (13.2–14.0 cm). This suggests swimming performance-related selection may

have occurred over multiple scales, as larger individuals as well as particular species may have been better suited to negotiate the hydraulically demanding conditions.

For Italian chub, passage rate increased with temperature and daylight, two factors impossible to fully tease apart in this dataset. Indeed, this species tended to pass during the day when temperatures were higher. Higher passage rates at higher temperatures may reflect increased swimming performance at higher temperatures (Ficke et al. 2011; Sobenes et al. 2024), translating into higher passage performance (Rodríguez et al. 2006). Daylight, on the other hand, may reflect the need to use visual cues while negotiating a turbulent and hydrodynamically demanding environment (Nyqvist et al. 2017) or natural diurnal behavioral patterns (Tarena et al. 2025). In addition, high turbulence in the Larinier design likely reduces visibility for ichthyophagous predators (Higham et al. 2015) and predation related to passage (Boulêtreau et al. 2018), potentially increasing passage activity in daylight.

While having similar passage success, barbel and Italian chub displayed markedly different passage behaviors. Among individuals that successfully passed the fishway, Italian chub transitioned the ramp substantially faster than barbel, indicating contrasting passage strategies. Barbel, a rheophilic benthic species, relies on substrate contact and prolonged use of low-velocity refuges within fast-flowing habitats (Schiavon et al. 2025b), possibly including hydrodynamic shelters formed by bottom baffles. This likely makes it move upstream in steps, resting between baffles, resulting in slower net upstream movement. In contrast, Italian chub, being a more pelagic species, may be less prone to use benthic hydrodynamic refuges between baffles and may instead minimize energetic costs by reducing transit time, using a combination of burst and prolonged swimming (Beamish 1978). The body size further modulated these patterns, with larger barbels transitioning the fishway faster than smaller ones. Smaller barbel are likely able to occupy narrow inter-baffle spaces, whereas larger individuals may be less able or less inclined to do so. At the same time, the larger barbel can be expected to be a better swimmers and hence more able to negotiate the fishway with less rest compared to the smaller barbel (Katopodis and Gervais 2012). In Italian chub, no significant size-related effect on transit time was detected, potentially due to the limited sample size and the size range tested but probably reflecting their behavioral strategy of rapid ascent with minimal or null use of inter-baffle refuges.

The interspecific difference in transition times contrasts with a reversed pattern for the time from release to passage. It took Italian chub substantially longer than the barbel to pass the fishway when also time spent in the release pool was taken into account. This could be due to the two species preferring different river habitats even when co-occurring in the same river reach. Barbels have a natural preference for relatively fast-flowing water, often negotiating the flow by being bottom-oriented (Britton and Pegg 2011; Schiavon et al. 2025b). This may have made them perceive the fast-flowing turbulent fishway environment as a relatively familiar habitat, resulting in a fairly fast habituation followed by attempted passage. The more water-column-oriented Italian chub, on the other hand, seems to have taken longer to habituate to the experimental environment. Despite the wide ecological valence of Italian chub (Fortini 2016), this species exploits highly demanding hydrodynamic habitats only occasionally, and these conditions may therefore not be perceived as familiar, requiring a longer time to initiate passage attempts compared to the barbels.

A potential factor that could have decreased the swimming performance of the studied species, and consequently their ability to overcome the fishway, is the effect of tagging. Within non-salmonid species, numerous studies have demonstrated high survival and PIT tag retention rates across a wide range of species and size classes (Bolland et al. 2009; Ficke et al. 2011; Nyqvist et al. 2024a). For *Cottus gobio*, *Barbus caninus*, and *Telestes muticellus*, previous studies further reported no behavioral effect of tagging on burst swimming performance (Knaepkens et al. 2007; Schiavon et al. 2023; Nyqvist et al. 2024a). No data are currently available for *Squalius* and *Phoxinus*, and although Leuciscidae as a family generally show no behavioral effects following tagging (Ficke et al. 2011; Nyqvist et al. 2024a), this extrapolation should be treated with caution for *Phoxinus*, whose small body size may increase susceptibility to tagging effects. Overall, while tagging effects cannot be entirely excluded, the available evidence suggests they were likely minimal across the studied species and are therefore unlikely to have substantially influenced fishway ascent success.

5. Conclusion

This study shows that a Larinier fishway operating at a 15% slope does not allow passage for several small-sized fish species while displaying moderate passage performance for others. Italian chub and barbel achieved moderate passage success while subject to size selection. The minnows, Italian riffle dace, and bullhead, on the other hand, did not pass at all. Overall, the findings demonstrate that fishway

passage performance is strongly shaped by species-specific characteristics, including swimming capacity, size, environmental conditions, and behavioral strategies (Williams et al. 2012; Silva et al. 2018), underscoring the need for fishway designs that explicitly account for ecological and functional diversity. Future studies may evaluate the functionality of a lower gradient version of this technical fish passage solution to assess if the advantages in terms of cost, ease of construction, and maintenance compared to other technical fishways can be coupled with an adequate passage success. Until then, it should be applied with caution or complemented by alternative solutions if the fish community, including weak-swimming species, should be allowed passage.

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CRediT: **Alfredo Schiavon**: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing; **Ambra Alderighi**: Data curation, Investigation, Methodology; **Michele Spairani**: Investigation, Methodology, Resources; **Alessandro Candiotto**: Investigation, Methodology, Resources; **Daniel Nyqvist**: Conceptualization, Formal analysis, Methodology, Supervision, Validation, Visualization, Writing – review & editing; **Claudio Comoglio**: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

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Data availability statement

Data will be made available on request.

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