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Passage performance of three small-sized fish species in a Vertical Slot Fishway with and without overhead cover

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A R T I C L E I N F O

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A B S T R A C T

Hydropower dams block fish movement, cause river fragmentation, and constitute a threat to biodiversity worldwide. Vertical Slot Fishways (VSF) are a widespread solution to mitigate these effects by enabling fish passage at obstacles. In the past, fish passage research has focused mainly on strong swimming salmonids, often resulting in knowledge gaps and low passage success for other fish species, especially small-sized ones. In addition, although hydrodynamics is fundamental to assess the functionality of a fishway, other environmental factors can impact passage success. Light can affect several behaviors in fish and often plays a role in fish migration and movement. At fishways, light can both promote and hinder passage, with highly species-specific effects remaining underexplored for many species. Here we study the passage performance in an alternatingly open and covered VSF of three small-sized fish species: brook barbel (*Barbus caninus*), European bullhead (*Cottus gobio*), and Italian riffle dace (*Telestes muticellus*). Passage success was very high for brook barbel (100 %) and Italian riffle dace (95.2 %) while fewer European bullhead (46.4 %) successfully passed the fishway. Fish showed a preference for passage without overhead cover: both brook barbel and Italian riffle dace displayed lower overall passage rates under covered compared to open conditions, and entry rates were lower with cover for all three species.

1. Introduction

The global increase in renewable energy demand has increased the importance of hydropower in human society (Brown et al., 2011; Kaygusuz, 2004). A large number of dams are built every year (Zarfl et al., 2015), affecting aquatic ecosystems globally (Dudgeon et al., 2006). Despite the several benefits provided by hydropower at a societal level, the damming and regulation of rivers pose a notable threat to freshwater ecosystems, with river fragmentation and habitat deterioration being among the main causes of biodiversity loss (Allan and Flecker, 1993; Reid et al., 2019). Obstructions of longitudinal movements can block important fish migrations, but also negatively affect resident communities as foraging for resources, demographic exchanges, and gene flow between populations may be limited if not impeded (Agostinho et al., 2005; Antonio et al., 2007; Cosgrove et al., 2018).

Given the several negative effects of dams on freshwater ecosystems, an holistic ecological approach would be to restore the conditions prior to the dam construction by the direct removal of the barrier (Katopodis and Williams, 2012; Silva et al., 2018). This is, however, most often unfeasible and a widespread solution to mitigate the impact of river fragmentation is the construction of fishways to allow the passage of fish over the artificial barriers (Katopodis and Williams, 2012; Larinier, 2002). Fishways can have a large variety of designs and geometries, from technical to nature-like types. A common type of technical fishway

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is the Vertical Slot Fishway (VSF): the height of the dam is split in smaller drops through a series of basins (pools) interconnected by a slot allowing fish to move upstream. VSFs can accommodate different water levels, allow the fish to pass at the preferred depth, and have been used to pass a wide diversity of fish species (Marriner et al., 2016; Silva et al., 2018). However, like all fishways, VSFs functionality varies depending on sites and species (Bunt et al., 2012; Noonan et al., 2012).

Historically, fish passage research and management have been focused on strong swimming salmonid species (Bunt et al., 2012; Katopodis and Williams, 2012; Noonan et al., 2012). As for their ecology in general (Smialek et al., 2019; Vøllestad, 2023), there are large knowledge gaps on the passage performance and behavior of many fish species (Leng and Chanson, 2020; Zhang et al., 2023). Something that is reflected in variable, and often low, passage efficiencies. During the last decades, however, the need to pass the whole fish community has been widely acknowledged (Castro-Santos and Haro, 2010; Larinier, 2002; Silva et al., 2018), and research efforts have been accompanied by improved functionality (Marsden and Stuart, 2019). Typically, the need to pass also small sized fish is reflected in fish passage guidelines in the form of lowered slopes or drops in the fishway, reducing the swimming capacity required to ascend the fishway (Katopodis and Williams, 2012; Schmutz and Mielach, 2013). In practice, however, these design guidelines remain largely untested for most fish species.

Although fish swimming performance is important for predicting fish passage performance (Goodwin et al., 2006; Tan et al., 2018), successful passage is not a simple function of swimming capacity and water velocity (Jones and Hale, 2020; Vowles and Kemp, 2012; Williams et al., 2012). Fish behavior plays a crucial role for fish passage success (Williams et al., 2012) as motivation (Dodd et al., 2024), experience (Hagelin et al., 2021), presence of conspecifics (Nyqvist et al., 2024) as well other hydraulic, visual and acoustic cues affect passage success (Ericsson et al., 2024). Light seems to be a particular important factor influencing fish passage behavior with different fish species primarily passing fishways at night, while others predominately during the day (Ovidio et al., 2023; Santos et al., 2005). Artificial light at night has been seen to both promote and prevent fish passage (Tarena et al., 2023). At the same time, light can be a necessary condition for fish to be able to negotiate the complex hydraulic environment of a fishway (Jones et al., 2017; Nyqvist et al., 2017). Often, the transition between light and darkness seems to be particularly likely to affect fish behavior (Jones and Hale, 2020; Tétard et al., 2019), with both transition to light (Vowles and Kemp, 2021) and shade (Ono and Simenstad, 2014) constituting obstacles to movement. For example, in a fish passage setting, shade from overhead cover resulted in avoidance and guidance in salmonids (Greenberg et al., 2012; Kemp et al., 2005, 2008). For most species, the effect of shading on passage performance remains unknown, a knowledge gap particularly relevant considering the frequent presence of bridges and boardwalks on the top of fishways, as well as in relation to culverted river reaches (Jones and Hale, 2020; Keep et al., 2021; Stuart et al., 2007).

Brook barbel (*Barbus caninus* Bonaparte, 1839), European bullhead (*Cottus gobio* Linnaeus, 1758) and Italian riffle dace (*Telestes muticellus* Bonaparte, 1837) are small-bodied (typically <20 cm), rheophilic fish that represent diverse swimming behaviors. Brook barbel is a free swimming fish typically associated with the river bed, Italian riffle dace typically lives in the water column, and European bullhead is a fully benthic species mainly resting on the bottom (Fortini, 2016; Knaepkens and Eens, 2005). While the former two are found on the Italian peninsula, but also in neighboring areas such as southern France and Switzerland, the latter is native to wider parts of central Europe (Abbà et al., 2024; Fortini, 2016). Although all three species are considered relatively stationary, they do partake in dispersal movements (Bianco and Delmastro, 2004; Knaepkens et al., 2004; Schiavon et al., 2025) or move in response to shifting environmental conditions (Schiavon et al., 2024), and both European bullhead and Italian riffle dace has been observed to use fishways (Iaia et al., 2025; Panagiotopoulos et al., 2024). European bullhead, when studied, has shown very low passage efficiencies (Knaepkens et al., 2006, 2007), while the passage behavior of brook barbel and Italian riffle dace remains largely unknown for the scientific community.

To reduce the scarcity of knowledge on passage behavior of small-sized fish species, we tested the passage performance of brook barbel, European bullhead and Italian riffle dace through a VSF. In addition, the impact of different light conditions on the passage performance was tested by interchangeably covering and uncovering the fishway. In this way, we quantified the passability of the fishway, as well as the effect of overhead cover on entry-, transition-, exit-, and overall passage rates. We hypothesized that all three fish species would be able to pass, with lower upstream passage success for European bullhead, but that overhead cover would reduce the rate of passage.

2. Material and methods

A field experiment was conducted to test for passage performance and impact of overhead cover on fish passage rates in a vertical slot fishway for brook barbel, European bullhead and Italian riffle dace. The hydrodynamic conditions of the VSF were defined at the beginning of the experiment and kept constant throughout. The total days of experiment were 9, from July 8th to July 17th 2024.

2.1. Experimental site and fishway

The study area is located in the downstream part of the Casotto river, a small stream in Piedmont Region (NW Italy), tributary to the Corsaglia river and part of the Po river system. The stream is characterized by a nivo-pluvial hydrological regime, typical for small torrential watercourses of the Alpine region of Italy, and has a total catchment area of 77.4 km^2, a total reach length of 23.8 km and a mean annual discharge of 3 m^3/s. The coarse bed granulometries, low water temperatures and relatively high slopes typical of rivers in the southern alpine hydro-ecoregion constitute suitable habitat conditions for fish families of cyprinids, cottids and salmonids (Comoglio et al., 2012; Fortini, 2016).

The experiments were carried out in a VSF (Fig. 1) located in the downstream section of the Casotto river (44°19′20.4“ N, 7°55’45.5” E) at a Tyrolean transversal weir with a small hydropower plant located on the right bank. The internal geometry of the fishway is aligned with VSF *Design 1* of Rajaratnam et al. (1992) and it is composed by nine consecutive pools (2 m long and 1.6 m wide), mutually interconnected with a rectangular slot with a width of 0.20 m and height of 1 m (Fig. 1). Additionally, the pools are preceded by a non-sloping rectilinear headrace channel 4.2 m long and followed by a squared 1.2 m long tailrace turning 90° to connect the structure to the downstream riverbed. On the left side wall of the last downstream pool, a 1 m wide lateral weir keeps the VSF discharge regulated below a value of 0.15 m^3/s.

The slope of the fishway is 9 %, which is a value usually adopted to limit construction costs and at the same time guarantee a suitable flow – although generally a slope of 5–7 % is recommended for the passage of multiple species (Marriner et al., 2016; Quaranta et al., 2019). The concrete bottom was covered by differently sized loose gravel material transported by the river. The fishway was cleaned from boulders and larger cobbles while gravel material was left to support the ascent of bullhead through the structure, mimicking an ideal management of the fishway (Egger et al., 2021). For the experiments, water inflow at the entrance was partially blocked (with a rectangular wooden sluice gate) to achieve a relatively constant discharge within the fishway (0.13 m^3/s), independent of river level fluctuations. The lowermost slot, the lateral weir and the rest of the perimeter of pool 1 were enclosed with fine-meshed nets, preventing fish from exiting the fishway in the downstream direction (Fig. 1). The nets were cleaned twice per day (morning and evening) from accumulating leaves and other floating debris.

Velocities and water levels inside the VSF were measured daily at

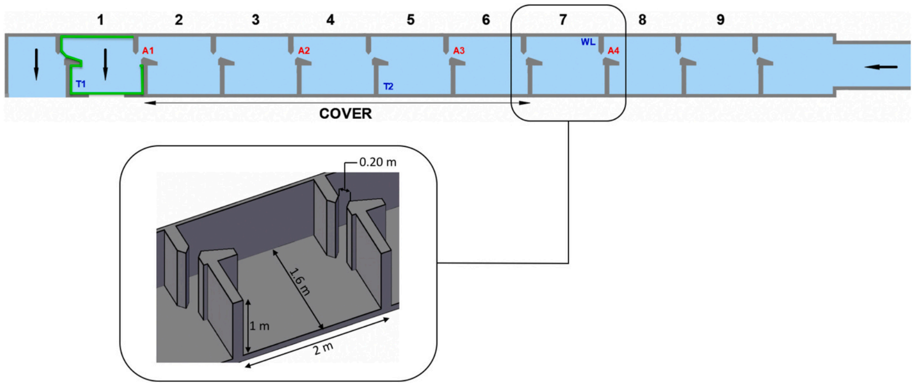

Fig. 1. Vertical slot fishway (VSF) and experimental setup. A top view of the experimental arena inside the VSF is reported showing the position of the different elements of the setup: antennas A1-A4 (red), temperature and light loggers (T1, T2), water level logger (WL) and downstream nets in pool 1 (green). The pools numbers are reported, together with the indication of the ones (2–6) interested by the overhead cover treatment. Fish were manually inserted in pool 1 at the start of each trial. The direction of flow is marked by the black arrows. Additionally, a three-dimensional view of a pool is reported with geometrical measures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reference points using a portable flowmeter (Flow-Probe, SCUBLA, Italy) and were stable over the study period (velocities never varied more than 0.05 m/s within a slot). The volumetric power dissipation inside the pools was calculated as $P_V = \frac{\rho g Q \delta h}{V}$ (where ρ is water density, g is gravity, Q is the flow rate, δ_H is the head difference at the upstream slot and V the volume of water in the pool). The complete range of the hydraulic condition in the VSF is reported in Table 1. The partial obstruction to flow due to the downstream nets in pool 1 created an M1 backwater surface profile (Fuentes-Pérez et al., 2024), with a consequent uneven distribution of the water levels along the fishway, with drops at each slot increasing from 5 (downstream) to 15 cm (upstream).

For the overhead cover treatment, two thick black polyester tarps (3x5m) covered the fishway from pool 2 to pool 6 (Fig. 2). First and last pool (pool 1 and 7) were always left open to test for the effects of shading on entry and exit. In the open conditions, the tarps were completely overturned to the right side of the fishway, leaving the channel top fully open (Fig. 2).

To monitor fish movements in the fishway four PIT-antennas (ORMR; Oregon RFID, USA) were installed in the fishway (Fig. 1). The wire loops of the antennas were attached around the upstream exit slots of pool 1 (A1), pool 3 (A2), pool 5 (A3) and pool 7 (A4), and used to record entry (A2), transition (A2-A3) and exit (A4) along the covered or open fishway. Two stationary test-tags (Oregon RFID, USA) were positioned in correspondence of A2 and A4 to continuously monitor the functionality of the antennas. The PIT-system was powered by a solar panel connected to a battery. Fish behavior was quantified only in the first seven pools (Fig. 1).

Temperature and light intensity within the experimental pools were monitored throughout the experiment using two sensor-loggers (MX2202, HOBO) fastened to rocks and placed inside pool 1 and pool 5 (obtaining a measure for both a pool that was always open, and one with alternated treatments). Water temperature was relatively stable during the experiment, averaging 19.2 ± 2.1 °C (mean ± SD) in open conditions and 19.1 ± 2 °C in covered conditions. In open conditions, light intensity was 13,967 ± 19,151.1 lx during the day and 2.1 ± 8.4 lx at night, while the corresponding values for covered conditions were 2.5 ± 66.5 lx (day) and 0 lx (night). Water level, monitored by a datalogger (MX2001, HOBO) in pool 7, ranged between 0.28 m and 0.41 m throughout the experiment (Table 1).

Table 1
Range of the hydraulic values for the studied VSF: water level inside the pools (WL), mean discharge (Q_m), velocity at the slots (v_{slot}), water level drop at the slots (drop) and volumetric power dissipation (P_V).

Parameter	Values range
WL	28–41 cm
Q_m	0.13 m^3/s
v_{slot}	1–1.5 m/s
drop	5–15 cm
P_v	50–150 W/m^3

2.2. Fish

All three species were collected with electrofishing on 1–2 July 2024. Brook barbel and Italian riffle dace were all caught upstream and downstream of the experimental site, while European bullhead, found to be scarcely present within Casotto river at the time of the experiment, were also caught in Corsaglia river upstream the confluence with Casotto river (44°16′53.3” N, 7°49′46.9″ E).

All fish were PIT-tagged on the same day as caught, following anaesthetization with clove oil (Aromlabs, USA; approximately 0.05 mL clove oil/L water). A small incision of 2–4 mm was made on the ventral side of the fish and a Passive Integrated Transponder (PIT-tag; Oregon, USA; 12 × 2.1 mm; 0.10 g) was applied within the incision, pushing forward inside the abdominal cavity parallel to the fish body (Nyqvist et al., 2023; Schiavon et al., 2023). Tag-to-weight ratios were 1.4 % (± 1.1 %) for brook barbel, 1.5 % (± 1 %) for Italian riffle dace and 0.6 % (± 0.4 %) for European bullhead, within the tag-fish-weight ratios typically used to avoid tagging effects (Brown et al., 1999).

After measuring for length and weight, fish were left to recover for at least 6 days before the start of the experiment. Fish were held in three perforated circular water tanks (500 L each) placed on the left bank of the river, inside a natural pool with deep water. The tanks were covered with nets and anchored to the river banks. A continuous exchange of water was provided by three flexible plastic pipes bringing water from upstream of the weir to each tank (continuous flow was ensured by gravity) and small holes drilled into the tank walls. Rocks and bricks were put inside the tanks to provide shelter for the fish. Water temperature (as well as light intensity) within the tanks was monitored through a sensor-logger (MX2202, HOBO). Fish in the tanks were fed every evening with commercial dry shrimps (Royal Fish, Italy).

2.3. Experimental procedure

In total, 42 brook barbel (mean fork length [FL] ± standard deviation [SD] = 9.8 ± 2.5 cm; mean weight [W] ± SD = 13.9 ± 10.5 g), 61 European bullhead (FL ± SD = 11.7 ± 1.8 cm; W ± SD = 21.6 ± 9.9 g) and 86 Italian riffle dace (FL ± SD = 8.6 ± 1.8 cm; W ± SD = 9.5 ± 5.5

Fig. 2. The vertical slot fishway in covered (left) and open (right) conditions. In the foreground the uppermost antenna (A4) and test tag are visible on both photos. The position of the four antennas (A1-A4) is indicated in red on the right. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

g) were tested over 12 trials.

Before the start of each trial, the four antennas were checked and leaves clogging the downstream nets in pool 1 were removed. Fish were then gently netted from the holding tanks, scanned for PIT-ID (HPR Plus PIT Tag handheld reader, Biomark, USA), carried to the fishway inside a water bucket, and gently released in pool 1. In each trial 1–4 brook barbel, 4–6 European bullhead and 6–9 Italian riffle dace were released. Six trials started in the morning (8–9 am) and six in the evening (19,30–20:30 pm). Cover condition (covered or open) was changed every evening just before the release of fish (taking 3–13 min). After the release of the last group of fish (14 July, trial 12), fish were given three additional days to pass the fishway (also during these days the cover conditions were changed every evening). Therefore, fish released in the VSF during the experiment faced a change of cover condition approximately 12-24 h after release (depending on release group) and then every 24 h.

After the end of the experiment, the fishway was manually checked for the presence of fish remaining using a mobile backpack PIT-antenna (Mobile HDX Long Range PIT Tag Reader Kit, Oregon, USA). Two European bullhead were found dead (impinged against the nets in the downstream pool) and were, hence, excluded from the analysis.

2.4. Data interpretation

The efficiency of each antenna was evaluated by computing the ratio between the number of fish whose passage was detected by the antenna and the number of fish detected upstream of the antenna (or assumed to have passed upstream antennas without detection). Based on observed detection efficiencies at the different antennas, overall passage success was defined by assuming fish last detected at A2, A3 or A4 and not found in the fishway by the end of the experiment as having successfully passed. Fish without their last detection upstream of A1 and that were not found in the fishway at the end of the study were assumed to have exited the fishway in the downstream direction passing through the small space between nets and concrete. These fish were excluded from event rate analysis after their last detection at A1 and from the quantification of passage success.

PIT-detections were used to define passage times and behavior inside the fishway. A series of events was defined: entry (detection at A2), transition (detection at A3) and exit as well as overall passage of the fishway (detection at A4). Cox-regression, a type of time-to-event analysis, allows to model effects of fixed and time-varying covariates on passage rates (Castro-Santos and Haro, 2003; Castro-Santos and Perry, 2012; Hosmer et al., 2008), and was applied to test for covariate effects on the series of events (Castro-Santos et al., 2009; Silva et al., 2018). Fish were considered available to enter the fishway from release to first detection at A2, to transition in the fishway from having entered the fishway to first detection at A3, and to exit the fishway (detection at A4) after having transitioned the fishway. Fish returning downstream in the fishway (detection on the downstream antenna), also temporarily left the pool of fish available for the event. Subsequent returns upstream were considered as subsequent attempts. Only data until the first successful attempt was included in the analysis. For overall passage, fish were considered available to pass from release to exit. The effect of fishway cover condition (open/covered) and fish length on event rates was tested using a mixed effects Cox-regression (Abd ElHafeez et al., 2021). As the effect of cover could be different according to the external luminosity (day or night), day/night and an interaction term between day/night and cover condition was included in the model. Since fish were released in trial groups and some fish made repeated attempts, potential non-independencies between attempts and groups were accounted for by adding a random effect term of individual nested in group. Each covariate was considered significant in the model for *p*-values lower than 0.05. All models were tested for the assumption of proportionality of hazards (Kuitunen et al., 2021).

Data analysis, plotting and statistical tests were performed in *R* (ver. 4.2.2), involving the following packages: *ggplot2* (ver. 3.4.0) and *plotly* (ver. 4.10.1) for plots and visual analysis, *dplyr* (ver. 1.0.10) and *sqldf* (ver. 0.4.11) for data management, and *coxme* (ver. 2.2.18.1) for time-to-event analysis.

2.5. Ethical statement

The study was performed in accordance with the Ufficio Caccia e Pesca of the Provincia di Cuneo (n.43719 of 24 May 2024), under the provisions of art.2 of the national Decree n.26/2014 (implementation of Dir. 2010/63/EU).

3. Results

Estimated detection efficiencies were 98.9 %, 97.2 %, 97.4 %, and 78.4 % for A1, A2, A3, and A4 respectively. 147 fish were last detected on A4 or on A2-A3 and not found in the fishway by the end of the study and assumed to have successfully passed. 34 fish were found in the fishway at the end of the experiment. Finally, 8 fish (6 European bullhead and 2 Italian riffle dace) were not found in the fishway at the end of the study and did not have their last detections upstream of A1, and therefore were assumed to have exited the fishway in the downstream direction. These fish were included in the event rate analysis until the time of their last detection at A1 but excluded from the quantification of the passage success.

Overall passage success was 100 % for brook barbel, 46.4 % for European bullhead and 95.2 % for Italian riffle dace, with all the fish being ascending to A2 or beyond, indicating initiation of ascent (access to pool 2) by all three species (Table 2). Moreover, more than 90 % of all three species reached A3 (pool 5; Table 2).

3.1. Brook barbel

All brook barbel passed through the fishway, after a median time of 2.1 h (IQR = 4.8 h) following their release. Overhead cover reduced overall passage rates (i.e. fish had higher passage times), as well as entry and transition rates (Fig. 3, Table 3). Larger fish had a higher overall passage rate as well as higher entry and exit rates (Table 3). No effect of day/night and interaction between time of the day and cover was observed for brook barbel (Table 3).

3.2. European bullhead

Only 46.4 % of European bullhead successfully passed the fishway. Time to passage was also relatively long, with a median of 37.1 h (IQR = 51 h). Only 19.2% passed within 12 h and one-third (34.6 %) within 1 day.

In European bullhead, there was a lower entry and transition rate, as well as a non-significant tendency of lower overall passage rate, under covered conditions (Table 4, Fig. 4). European bullhead was also less likely to exit the fishway at night. An effect of fish length was detected, with bigger fish entering, transitioning and passing slower than smaller ones (Table 4).

3.3. Italian riffle dace

Among Italian riffle dace, 95.2 % passed the fishway with a median passage time of 7.6 h (IQR = 20.1 h). More than one half of the passing Italian riffle dace (54.4 %) passed in the first 12 h and four-fifths (78.5 %) within one day.

For Italian riffle dace, overall passage rate as well as entry rate was lower under covered conditions than compared to open ones, while the exit rate was higher in covered conditions (Table 5). Additionally, Italian riffle dace entered the fishway substantially faster during the day (Fig. 5). There was also a significant effect of the interaction between day/night and cover condition on transition rate: Italian riffle dace passed substantially slower at night under cover than under other conditions (Fig. 5). Bigger fish also passed the fishway at higher rates than smaller fish – including higher entry, exit and overall passage rates (Table 5). For transition and overall rates, a model including all the covariates did not fulfill the assumptions of proportionality of hazards and was hence run without the inclusion of length (for transition) and with a stratification on day-night (for overall passage).

Table 2
Proportion of brook barbel ($n = 42$), European bullhead ($n = 56$) and Italian riffle dace ($n = 83$) ascending to A1, A2, A3 or exiting the fishway, and the minimum negotiated drop required. The 8 fish leaving the fishway from downstream were not included in the count.

	Drop (cm)	brook barbel (%)	European bullhead (%)	Italian riffle dace (%)
A1	5	100	100	100
A2	10	100	100	100
A3	11	100	91.1	98.8
A4 (Exit)	15	100	46.4	95.2

4. Discussion

In this experiment, we studied the passage performance of three small-sized fish species inside a VSF and evaluated the effect of overhead cover on fish entering, transitioning and exiting the structure. Estimated passage success was very high for brook barbel (100 %) and Italian riffle dace (95 %) while European bullhead passed at lower proportions (46 %). Under the alternatingly open and covered VSF, fish showed a general preference for passage without overhead cover. Both brook barbel and Italian riffle dace displayed lower overall passage rates under covered compared to open conditions, and entry rates were lower with cover for all three species. Brook barbel and European bullhead also ascended the covered fishway at a slower rate than the open fishway.

Brook barbel showed the highest passage efficiency among the three species with all fish successfully passing the fishway. Median passage time was 2.1 h. The majority of brook barbel overcame the structure within 12 h from the release into the VSF, showing high passage motivation and capability. Based on results from studies on larger sized barbel species this outcome was not surprising. Large barbels have been reported to pass technical fishways at high efficiencies and with short passage times. Southern Iberian barbel (*Luciobarbus sclateri* Günther, 1868) has displayed high motivation to pass and high passage performance (80 %) in a VSF (Sanz-Ronda et al., 2019). Iberian barbel (*Luciobarbus bocagei* Steindachner, 1864) passed with 100 % of success inside an experimental VSF specifically set to exceed the recommendations for recommended hydraulic parameters for cyprinids (Romão et al., 2024), and with short passage times (0.5 h) in a prototype VSF (Romão et al., 2018). The same species also showed relatively high passage efficiency in both a surface-notch and bottom-orifice (60 %; Santos et al., 2013) and bottom-orifice (67 %; Alexandre et al., 2013) experimental fishways. Also, in our study, and similar to brook barbel, Italian riffle dace showed a high passage success. Altogether, this underlines previous work highlighting the high passage performance of rheophilic cyprinids in correctly constructed fishways (e.g. Branco et al., 2013b; Branco et al., 2013a; Sanz-Ronda et al., 2019).

European bullhead, instead, had the lowest passage success among the three species, with less than half of the individuals overcoming the fishway and median passage time of 37.1 h. A possible explanation for this lack of passage success can be the similarity between the natural habitat of European bullhead and the internal pools of the fishway (Knaepkens et al., 2006). The presence of coarse substrate together with the low velocities at the bottom may have constituted a suitable habitat for the bullheads, making them reluctant to leave. On the other hand, our bullhead passed at substantially higher proportions than previously reported for the species, and 91.1 % of the fish successfully reached pool 5 (A3). Previous studies on European bullhead passage have reported very low passage success in technical fishways, where no fish at all passed a pool-and-weir (Knaepkens et al., 2006, 2007) or very few fish passed a VSF (Egger et al., 2021). The higher passage success displayed by European bullhead in our study could be due to the fishway typology. Pool-and-weir fishways do not allow the passage at the bottom and often require jumping (Ficke et al., 2011). Compared to bare concrete or just the addition of large stones (Egger et al., 2021), the presence of differently-sized natural granulometry over the concrete in our study creates a more complex hydrodynamic environment. Lower velocity pockets at the slots bottom then likely facilitated upstream movement of

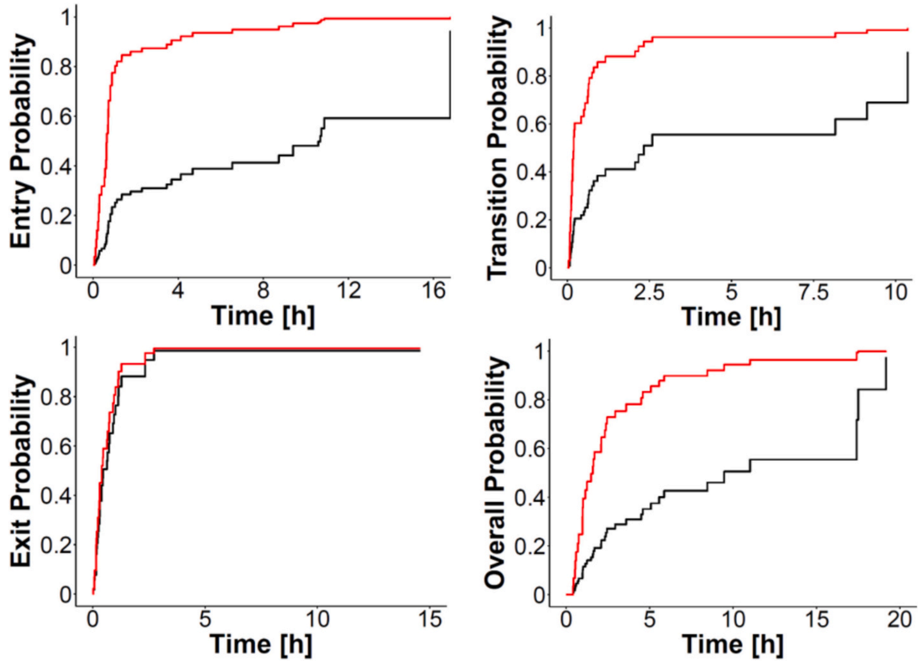

Fig. 3. Time-to-event plots for brook barbel. The different events probability for the treatments open (red) and cover (black) is reported in function of time: entry, transition, exit and overall passage. The model is plotted for day time conditions and mean fish length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Time-to-event analysis for brook barbel for the four tested events: Entry, Transition, Exit and Overall. The variables included in the statistical models are: Cover treatment (Cover), Time of the day (Night), Fish length (Length) and Interaction term (Cover/Night). The number of fish included in each model (n) is reported, together with the statistical parameters of Cox regression for each variable: regression coefficient (β), Hazard Risk (HR), Standard Error (SE), z-value (z) and p-value (p). The rows of covariates with a statistically significant effect are highlighted in bold.

		β	HR	SE	z	p
Entry (n = 41)	**Cover**	**−1.77**	**0.17**	**0.46**	**−3.87**	**$1.1 \bullet 10^{-4}$**
	Night	0.56	1.75	0.92	0.61	0.54
	Length	**0.02**	**1.02**	**0.01**	**2.66**	**0.01**
	Cover/ Night	1.52	4.56	0.97	1.56	0.12
Transition (n = 39)	**Cover**	**−1.39**	**0.25**	**0.47**	**−2.94**	**$3.3 \bullet 10^{-3}$**
	Night	−0.35	0.71	0.76	−0.46	0.65
	Length	$4.7 \bullet 10^{-4}$	1.00	0.01	0.67	0.50
	Cover/ Night	1.38	3.98	0.99	1.39	0.16
Exit (n = 36)	**Cover**	−0.23	0.79	0.47	−0.49	0.62
	Night	−0.24	0.78	0.52	−0.46	0.64
	Length	**0.03**	**1.03**	**0.01**	**3.56**	**$3.7 \bullet 10^{-4}$**
	Cover/ Night	−0.49	0.61	0.83	−0.59	0.55
Overall (n = 42)	**Cover**	**−1.56**	**0.21**	**0.52**	**−3.02**	**$2.5 \bullet 10^{-3}$**
	Night	−0.06	0.94	0.62	−0.10	0.92
	Length	**0.02**	**1.02**	**0.01**	**2.69**	**0.01**
	Cover/ Night	0.61	1.83	0.89	0.68	0.50

Table 4
Time-to-event analysis for European bullhead for the four tested events: Entry, Transition, Exit and Overall. The variables included in the statistical models are: Cover treatment (Cover), Time of the day (Night), Fish length (Length) and Interaction term (Cover/Night). The number of fish included in each model (n) is reported, together with the statistical parameters of Cox regression for each variable: regression coefficient (β), Hazard Risk (HR), Standard Error (SE), z-value (z) and *p*-value (p). The rows of covariates with a statistically significant effect are highlighted in bold.

		β	HR	SE	z	p
Entry (n = 61)	**Cover**	**−1.06**	**0.35**	**0.44**	**−2.39**	**0.02**
	Night	0.69	2.00	0.42	1.65	0.10
	Length	**−0.04**	**0.96**	**0.01**	**−4.05**	**$5.2 \bullet 10^{-5}$**
	Cover/ Night	−0.63	0.53	0.78	−0.81	0.42
Transition (n = 58)	**Cover**	**−0.94**	**0.39**	**0.41**	**−2.32**	**0.02**
	Night	−0.30	0.74	0.38	−0.80	0.42
	Length	−0.01	0.99	0.01	−0.59	0.56
	Cover/ Night	−0.51	0.60	0.77	−0.67	0.51
Exit (n = 53)	**Cover**	−1.11	0.33	0.59	−1.87	0.06
	Night	**−1.23**	**0.29**	**0.58**	**−2.11**	**0.04**
	Length	**−0.05**	**0.95**	**0.02**	**−3.44**	**$5.7 \bullet 10^{-4}$**
	Cover/ Night	1.38	3.97	1.07	1.29	0.20
Overall (n = 61)	**Cover**	−0.99	0.37	0.54	−1.81	0.07
	Night	−0.76	0.47	0.61	−1.25	0.21
	Length	**−0.04**	**0.96**	**0.01**	**−3.16**	**$1.6 \bullet 10^{-3}$**
	Cover/ Night	0.28	1.32	1.03	0.27	0.79

European bullhead (Hoover et al., 2003; Tudorache et al., 2008). In general, holding-station onto the substrate, interchanged with short bursts, rather than actively swimming, is a strategy commonly used by benthic species (Egger et al., 2021; Langerhans and Reznick, 2010).

Overall passage rates were lower under covered conditions than under open conditions for both brook barbel and Italian riffle dace. In fact, covering the fishway reduced passage rates with 4.8-times for brook barbel (Table 3) and 7.1-times for Italian riffle dace (Table 5). No effect of overhead cover on overall passage rates was detected in European bullhead. This species, however, also passed in substantially lower numbers regardless of cover condition, indicating that other behavioral factors governed bullhead overall passage rates (see paragraph above). Looking at just the lower part of the fishway (entry rates), that a substantial portion of the European bullhead reached, this species follows the same pattern. Importantly, upstream movement in fishways is not a standalone process but it encompasses a series of successive

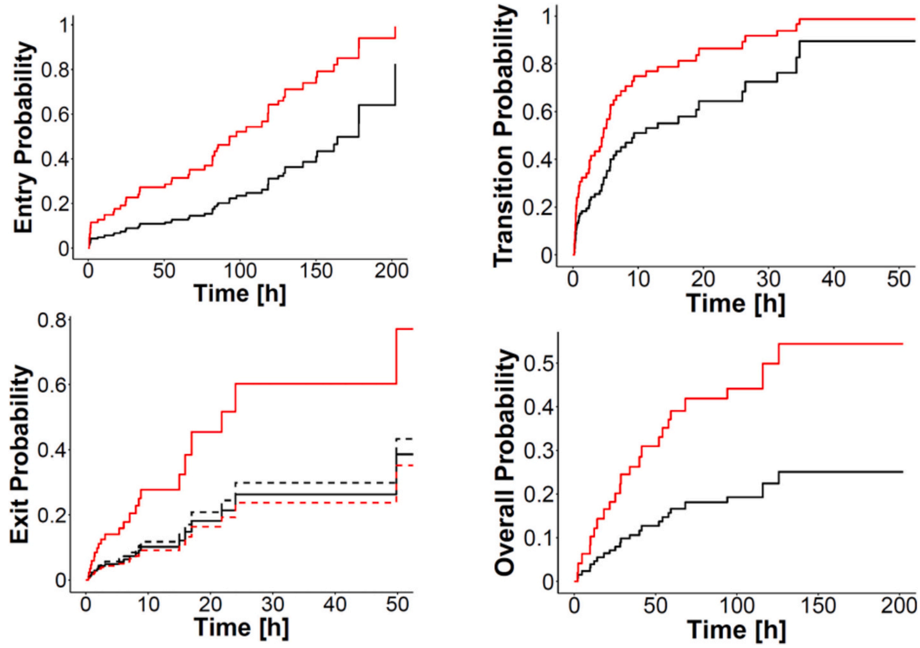

Fig. 4. Time-to-event plots for European bullhead. The different events probability for the treatments open (red) and cover (black) is reported in function of time: entry, transition, exit and overall passage. Models are plotted for mean fish length. When covariate day/night or interaction day/night – cover was significant the curve corresponding to each condition is reported: open-day (red solid), open-night (red dashed), cover-day (black solid), cover-night (black dashed), otherwise the model is plotted based on day conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
Time-to-event analysis for Italian riffle dace for the four tested events: Entry, Transition, Exit and Overall. The variables included in the statistical models are: Cover treatment (Cover), Time of the day (Night), Fish length (Length) and Interaction term (Cover/Night). The number of fish included in each model (n) is reported, together with the statistical parameters of Cox regression for each variable: regression coefficient (β), Hazard Risk (HR), Standard Error (SE), z-value (z) and *p*-value (p). Transition and Overall models were run without the inclusion of variable length and with a stratification on day/night, respectively. The rows of covariates with a statistically significant effect are highlighted in bold.

		β	HR	SE	z	p
Entry ($n = 86$)	**Cover**	**−2.54**	**0.08**	**0.40**	**−6.39**	**$1.6{\bullet}10^{-10}$**
	Night	**−1.25**	**0.29**	**0.47**	**−2.68**	**0.01**
	Length	**0.02**	**1.02**	**0.01**	**2.28**	**0.02**
	Cover/ Night	−22.83	1.2E-10	$7{\bullet}10^{4}$	0.00	1.00
Transition ($n = 81$)	**Cover**	0.09	1.10	0.44	0.21	0.83
	Night	0.32	1.37	0.41	0.78	0.44
	Cover/ Night	**−3.00**	**0.05**	**1.20**	**−2.50**	**0.01**
Exit ($n = 73$)	**Cover**	**0.92**	**2.51**	**0.41**	**2.23**	**0.03**
	Night	−0.18	0.84	0.42	−0.43	0.67
	Length	**0.02**	**1.02**	**0.01**	**2.97**	**$2.9{\bullet}10^{-3}$**
	Cover/ Night	−0.25	0.78	1.16	−0.22	0.83
Overall (n = 86)	**Cover**	**−2.02**	**0.14**	**0.45**	**−4.53**	**$6{\bullet}10^{-6}$**
	Length	**0.02**	**1.03**	**0.01**	**2.67**	**$7.6{\bullet}10^{-3}$**

events (Castro-Santos et al., 2009; Nyqvist et al., 2016) and light conditions might impact each one differently. In our study, covered or open conditions constituted ascent in close to total darkness or in partially lit (depending on time of day) conditions, while the presence of the cover generated sudden shifts from light to darkness at both entrance and exit of the fishway.

Abrupt changes in light intensity, in particular, are known to affect fish trajectories and behavior in relation to both downstream and upstream passage (Greenberg et al., 2012; Keep et al., 2021). In our experiment, overhead cover - the transition into the shaded part of the fishway - reduced entry rates for all three species. A reluctance to enter shaded areas has also been seen in small-sized Australian species passing through culverts (Jones et al., 2017; Jones and Hale, 2020), and in American shad (*Alosa sapidissima* Wilson, 1811) and sea lamprey (*Petromyzon marinus* Linnaeus, 1758) when passing through an Ice-Harbor type fishway (Hard and Kynard, 1997). Surprisingly, a similar effect was not seen for exit rates where no delaying effect of the presence of cover - and hence the change in light conditions - on passage rates was detected. Instead, Italian riffle dace exited at a higher rate in presence of the overhead cover.

While fish were exposed to a change in light condition at the entrance and exit, the transition of the fishway took place either under the cover (darkness) or in open conditions (light). Both brook barbel and European bullhead transitioned the fishway at lower rates under covered than under open conditions, while Italian riffle dace did not display a clear effect (but showed the lowest transition rate during covered nights). The lower transition rates under darker conditions may be a result of lowered ability to negotiate the fishway without visual cues. Loss of orientation in darkness (Kemp and Williams, 2009) and need for visual cues to overcome challenging turbulent flows (Jones et al., 2017; Nyqvist et al., 2017) has been reported for other fish species. It is also possible that fish felt less stressed under the protection of overhead cover, making them more likely to remain in the fishway (Hair et al., 1994; Watz et al., 2015).

In our experiment, fish were tested continuously both day and night, and fish movements as well as effect of cover could have been different according to the time of the day or the external solar illuminance. Actually, migration times and daily movements in fish are often regulated by natural light conditions (Hölker et al., 2010), with different species exhibiting distinct diel activity patterns in approaching and overcoming fishways (Ovidio et al., 2023; Prchalová et al., 2006). Brook barbel did not show a day/night preference in passage which is in line with what has been observed for Iberian babel and common barbel (*Barbus barbus* Linnaeus, 1758) (Ovidio et al., 2023; Rato et al., 2025). The same species have, however, also been observed to pass a flat-V flow gauging weir (Lucas and Frear, 1997), a pool-type fishway (Prchalová et al., 2006) and a nature-like fishway (Santos et al., 2005) primarily at

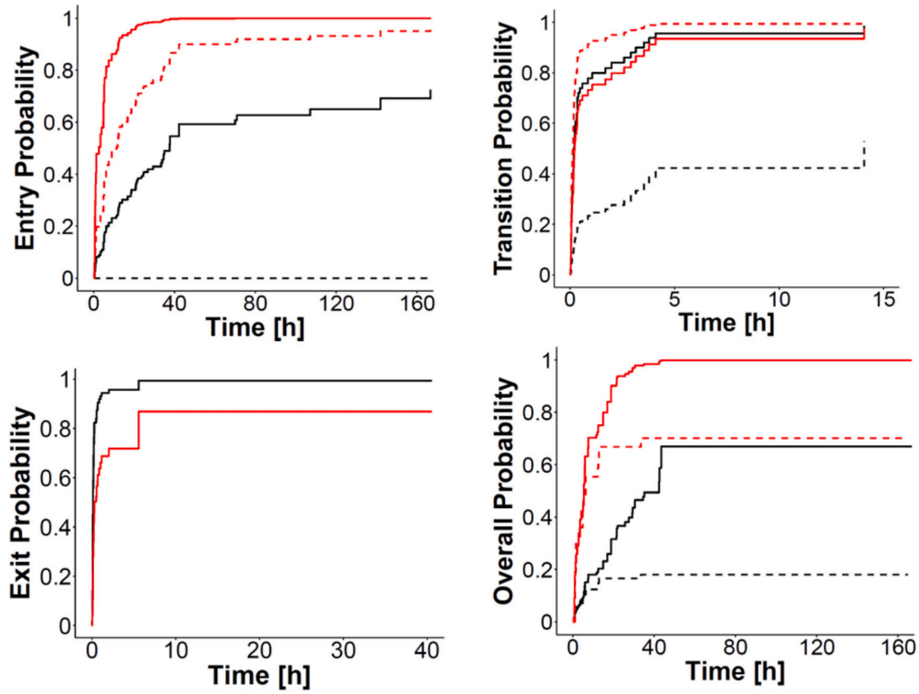

Fig. 5. Time-to-event plots for Italian riffle dace. The different events probability for the treatments open (red) and cover (black) is reported in function of time: entry, transition, exit and overall passage. When covariate day/night or interaction day/night – cover was significant the curve corresponding to each condition is reported: open-day (red solid), open-night (red dashed), cover-day (black solid), cover-night (black dashed). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

night showing high variability between sites. European bullhead and Italian riffle dace both displayed higher movement rates during the day regardless of cover treatment. Whereas European bullhead has been described as more active in darkened hours (Andreasson, 1973; Smyly, 1957), in our study it was more likely to exit the fishway during the day. Italian riffle dace, on the other hand, showed preference in entering the fishway in daytime. Importantly, even if we quantify changes in event rates over day and night, all trials started during daytime (in the morning or in the evening) and we most likely fail to capture the full extent of the species diurnal rhythms.

In the larger picture, this study contributes to the rare pool of data on the passage performance of small sized fish (Marsden and Stuart, 2019). Over the years, fish passage guidelines increasingly underline the need to allow passage of a wider range of species, with a particular attention to weaker swimmers (Mallen-Cooper and Brand, 2007; Schmutz and Mielach, 2013). The very high passage performance of brook barbel and Italian riffle dace, and the (compared to literature) relatively high passage success of European bullhead, despite some differences between our VSF and technical guidelines, is encouraging. The 9–10 % slope in our experiment is often considered to be a good compromise between non-selectiveness of passage and construction costs, although even lower values are recommended in specific cases (Marriner et al., 2016; Quaranta et al., 2019). The design of the pools is in line with Rajaratnam et al. (1992) and provided an adequate dissipation of the flow energy for passage keeping the power dissipation within the pools in the range 50–150 W/m^3 (Schmutz and Mielach, 2013), but larger dimensions of the pools are often recommended for passage of multiple species (Marriner et al., 2014, 2016). Hydraulic parameters like slot velocities of 1.5 m/s and 15 cm drops, although exceeding suggested reference values for small-sized species as 1–1.2 m/s and 5–7.5 cm (Marsden and Stuart, 2019; Schmutz and Mielach, 2013), still allowed passage at high efficiency. This shows, in accordance with Romão et al. (2024), that non-standard VSF designs can still be suitable for passage of strong swimming cypriniforms. Passage of small-sized rheophilic species may have been facilitated by the presence of a coarse substrate creating a more functional vertical velocity profiles (Clay and Eng, 1995; Egger et al., 2021).

Importantly, in our experiment fish were tested after being released in the fishway and prevented from moving downstream. Although this approach is not uncommon in fish passage studies (e.g. Bunt, 2001; Katopodis and Williams, 2016; Xu et al., 2024), and does demonstrate the capability of the fish to ascend the fishway, it tests only a part of the fish passage process. In nature fish would first have to locate the entrance of the fishway and consequently decide to enter the structure (Castro-Santos et al., 2009; Silva et al., 2018). Indeed, the attraction phase in fish passage is particularly challenging, requiring sufficient attraction flow, and often associated with delays and low efficiencies (Cooke and Hinch, 2013; Gisen et al., 2017; Ovidio et al., 2017). In relation to effects of overhead cover, it cannot be excluded that the interaction with the hydrodynamics of the fishway entrance, or the possibility to search for another way upstream, can exacerbate the delay observed in our study. More research is also needed concerning the approach behavior and efficiencies of small sized riverine fish in relation to fishways.

5. Conclusions

In an alternatingly open and covered vertical slot fishway, three small-sized Italian species were tested for passage performance under different light conditions. Regardless of the cover treatment, very high passage success was displayed for brook barbel and Italian riffle dace, while a relatively high passage success was revealed also for European bullhead. The presence of a differently-sized coarse substrate may have improved passage conditions for the tested species. Although interspecific difference occurred, overhead cover tended to reduce passage rates, with a particular influence on entrance and transition rates. In light of our findings, keeping fishway environments open and exposed to natural light conditions might prevent passage failures and unnecessary delays.

CRediT authorship contribution statement

Fabio Tarena: Writing – review & editing, Writing – original draft, Software, Investigation, Data curation, Conceptualization. **Claudio Comoglio:** Visualization, Supervision, Methodology, Conceptualization. **Michele Spairani:** Methodology, Investigation. **Alessandro Candiotto:** Methodology, Investigation. **Muhammad Usama Ashraf:** Methodology, Investigation. **Margherita Abbà:** Investigation. **Carlo Ruffino:** Investigation. **Daniel Nyqvist:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

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Data availability

Data will be made available on request.

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