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Individual activity levels and presence of conspecifics affect fish passage rates over an in-flume barrier

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Abstract

Dams and other in-stream obstacles disrupt longitudinal connectivity and hinder fish from moving between habitats. Fishways and other fish passage solutions are used to pass fish over these artificial migration barriers. Fish passage functionality, however, varies greatly with fish passage design and environmental conditions and depends on fish species and characteristics. In particular, swimming performance and fish behaviour are considered key characteristics to predict fish passage performance. It is also well known, but not well quantified, that the presence of conspecifics affects fish passage behaviour. In this study, we quantified individual passage rates of PIT-tagged gudgeons (*Gobio gobio*) over a scaled deep side notch weir in an hydraulic flume. We then quantified individual swimming capability (time to fatigue) and activity level (distance moved in an open field test) for the same individual fish and tested for potential effects on fish passage rate. To check for potential group effects, we then repeated the passage experiment for fish individually or in groups of five. More active fish displayed higher passage rates compared to less active fish, and fish passed the obstacle at higher rates in groups of five compared to alone. No effect of fish swimming capability on passage rates was detected. This result highlights the need to take both individual variation as well as the presence and behaviour of conspecifics into account in fish passage studies and evaluations. Doing so has the potential to improve the understanding of fish behaviour, and in the end, the design of fish passage solutions. Future studies should explore these results on free ranging fish and in relation to in-situ fish passage solutions.

KEYWORDS

behavioural type, fish swimming performance, gudgeon, personality, social facilitation

1 | INTRODUCTION

Fish migrate for feeding, reproduction and refuge, and in response to environmental or developmental changes (Lucas et al., 2001). Fish migrate in the marine environment, between freshwaters and the sea, or exclusively in freshwater (Morais & Daverat, 2016). Even within rivers the scale of fish migration varies from meters to thousands

of kilometres (Herrera-R et al., 2024; Lucas et al., 2001; Schiavon et al., 2024). For riverine fish, the presence of dams and other in-stream obstacles hinder fish from migrating between habitats and has caused declines and sometimes even local extinctions of migratory species (Jonsson et al., 1999; Lenders et al., 2016). Maintaining open migratory routes in river systems is an important aspect of safeguarding ecological connectivity and conserving migratory fish

species (McIntyre et al., 2015). Ideally, non-migrating fish should also be able to pass dams to maintain genetic diversity and fish dispersal in rivers (De Fries et al., 2023; Jones et al., 2021). In face of this, fishways and other fish passage solutions (e.g., eel ladders, fish lifts, trap-and-transport solutions, low-sloping racks) are used to pass fish over migration barriers (Katopodis & Williams, 2012; Noonan et al., 2012; Silva et al., 2018).

The need for fishways and other passage solutions to facilitate two way fish passage at migration barriers has been acknowledged for hundreds of years (Calles et al., 2013; Katopodis & Williams, 2012), but their functionality remains variable, and is often low (e.g., passage efficiency and attraction efficiency; Bunt et al., 2012; Noonan et al., 2012). Passage performance of fish varies with fish passage design and environmental conditions, but also between species and related to fish characteristics (Nyqvist et al., 2018; Silva et al., 2018). Swimming performance is considered a key characteristic to predict fish passage performance (Katopodis & Gervais, 2012), and fish behaviour in relation to local conditions is central to successful passage (Mawer et al., 2023; Williams et al., 2011). Importantly, swimming performance and behaviour differ between, but also within species, something that contributes to the high variability in fish passage functionality (Fraser et al., 2001; Katopodis & Gervais, 2012; Silva et al., 2018).

Fish swimming performance is crucial for dispersal, migration, and predator–prey interactions (Katopodis & Gervais, 2012; Tudorache et al., 2013), and fish swimming capabilities are tested explicitly to contribute to fish passage design (Castro-Santos et al., 2022; Peake et al., 1997; Romão et al., 2012). Low swimming capabilities compared to prevailing hydrodynamic conditions are often the reason for low fish passage performance for weak swimmers and small-sized fishes (Marsden & Stuart, 2019a; Volpato et al., 2009). Fish swimming performance varies with species and sizes (Katopodis & Gervais, 2012), but also between individuals (Hechter & Hasler, 2019; Oufiero & Garland Jr, 2009), potentially modulating selection in fish populations having to pass velocity barriers (Haugen et al., 2008; Volpato et al., 2009).

Fish behaviour in relation to its environment is determines how and if fish approach, enter, ascend, and exit the fishway (Nyqvist et al., 2017; Williams et al., 2011). Fish can be guided or repelled by hydrodynamic cues such as absolute or changing water velocities (Kemp et al., 2005, 2008), but also react to light (Hansen et al., 2019; Tétard et al., 2019) and sound (Heath et al., 2021), or their combinations (Miller et al., 2022). In addition, consistent inter-individual differences in activity, such as exploration or boldness can influence animal movement patterns (Wu & Seebacher, 2022). For example, both in killifishes (*Rivulus hartii*) and salmonids (*Salmo trutta*), activity in the laboratory correlates with dispersal in nature (Fraser et al., 2001; Watz, 2019). Related to fish passage, activity levels have been observed to correlate with bypass passage in Atlantic salmon smolts (*Salmo salar*; Haraldstad et al., 2021). There are also indications of fish with higher boldness score to be better upstream passers (Hirsch et al., 2017; Lothian & Lucas, 2021), although not always (Landsman et al., 2017). Even if not conclusive in the literature, high

activity and exploratory behaviour should, intuitively, be conducive to finding and navigating fishways.

Contrary to most models on fish passage behaviour, many fish in nature do not pass through fishways individually, but in groups (Mawer et al., 2023). The presence and behaviour of conspecifics are therefore likely to affect the passage behaviour of fish. Fish in larger groups can be more exploratory and bolder than single or few fish, covering more ground and exploring a greater portion of the test arena (Ward, 2012), locating food faster (Pitcher et al., 1982), and feeding more efficiently and for longer periods of time (Magurran & Pitcher, 1983). Fish can also learn from observing other fish (Johnsson & Åkerman, 1998), and fish more prone to move may be followed by more shy fish, increasing overall movement rates for fish in groups compared isolated fish (Cote et al., 2011; Harcourt et al., 2009). Related to fish passage, experiments on barbel (*Barbus barbus*) and trout (*Salmo trutta*) show an increased motivation to pass in groups (Albayrak et al., 2020) compared to alone, while salmon densities downstream of dams have been observed to correlate with rates of passage (Okasaki et al., 2020). Still, although many species are known to migrate and pass fishways in groups, little is known about actual group effects on fish passage rates (De Bie et al., 2020; Mawer et al., 2023).

Gudgeon (*Gobio gobio*) is a small-sized riverine and lake-dwelling fish species native to temperate Europe. Its range extends from France in the south to Southern Finland in the north, and Eastern United Kingdom in the west, while its eastern distribution is still unclear (Freyhof & Kottelat, 2007; IUCN, 2010). The species is introduced in Italy, where it is of particular interest as a direct competitor to the threatened Italian gudgeon (Bianco & Ketmaier, 2005). Gudgeon is a gregarious species (Fortini, 2016; Freyhof & Kottelat, 2007), with group sizes ranging from single fish or a few individuals to more than 20 fish (personal observation) and most likely varying over time and between sites (Hoare et al., 2000; Svensson et al., 2000). It spawns from April–August in temperatures above 12°C and in shallow water (Freyhof & Kottelat, 2007). Although typically relatively resident, it can partake in substantial dispersal movements (Stott, 1967). While little is known about its fish passage behaviour, it has, at places, been frequently observed in fishways (Panagiotopoulos et al., 2024).

Individual passage performance over a scaled deep side notch weir, corresponding to the passage environment of a pool-and-weir fishway, had previously been estimated for PIT-tagged gudgeons in groups of 10, in an hydraulic flume experiment (Tarena et al., 2024). In this study, we quantified individual swimming performance (time to fatigue) and activity (distance moved in an open field test) for the same PIT-tagged gudgeons, and tested for effects of individual swimming performance and activity on fish passage rates. To investigate potentially modulating effects of the presence of conspecifics, we repeated the original passage experiment but in trials involving a single fish or a group of five fish. Passage rates were then compared between gudgeons in single fish treatments and gudgeons in group treatments. We hypothesized that higher swimming performance and higher activity levels are associated with higher passage rates, and that fish pass at higher rates in groups compared to alone.

2 | MATERIALS AND METHODS

2.1 | Fish and tagging

Gudgeons were caught backpack electrofishing (direct current; ELT60IIGI, Scubla, Italy) in the Rocca Grimalda Channel (44°39'47" N, 8°49'51.5" E), a tributary to Orba River (Italy) and brought to the Alessandria Province hatchery in Predosa (Italy) on 19 September 2022. The fish were PIT-tagged (Oregon, USA; 12 mm × 2.1 mm; 0.10 g) in two batches on 20 September ($n=14$) and 4 November ($n=46$).

Before tagging, fish were anaesthetised in clove oil (Aromlabs, USA; approximately 0.05 mL clove oil / L water). A 2–4 mm ventral incision was made anterior of the pelvic fin, slightly offset from the centre. The tag was then inserted through the incision and pushed forward in the abdominal cavity to align with the fish body (e.g., Bolland et al., 2009; Schiavon et al., 2023). Fish were measured for fork length (mean ± standard deviation = 10 ± 0.6 cm) and weighed (11.3 ± 2.2 g). Tag-to-fish weight ratios were 1% ($\pm 0.2\%$), lower than recommended in telemetry literature (Brown et al., 1999; Jepsen et al., 2005). PIT-tags have been seen not to affect burst swimming ability or volitional swimming performance in similar sized cypriniformes (Nyqvist, Schiavon, Candiotti, Tarena, et al., 2024; Schiavon et al., 2023), even just 1 day after tagging (Ficke et al., 2012). Tagged fish were left to recover in an aerated water tank for at least 20 min, before being transferred to spring fed flow-through tanks ($59 \times 150 \times 20$ cm) and left to recover for at least 3 days before starting of the experiments. All fish remained healthy looking and active after tagging. Fish were held in standing water, under a natural photoperiod and semi-natural light conditions (windows and artificial lights during daytime, darkness at night), had access to perforated brick shelters in the tanks, and were fed commercial fish pellets (Tetra, TabiMin, Germany) regularly. Water temperature was stable at $13 \pm 1^\circ\text{C}$.

2.2 | Passage experiment I

Passage experiments I and II were conducted in a recirculating open channel flume ($30 \times 30 \times 140$ cm) made of plexiglass (Figure 1). Temperature was kept constant (mean ± SD = $13.15 \pm 0.02^\circ\text{C}$, aligned with the temperature in the holding tanks), switching on and off a chiller to counter heating from the action of the pump when needed.

A deep side notch weir (Larinier, 2002), consisting of a grey-painted plexiglass panel with a gum gasket to prevent leaks from the side of the weir, was fitted to the flume dimensions (Figure 1). A flow straightener delimited the experimental arena in an upstream direction while a fine meshed rack prevented fish from going downstream. The weir divided the experimental arena in an upstream (46 cm) and downstream part (94 cm). Experimental conditions consisted of a total discharge of 4.44 L/s that created an upstream water depth of 20 cm, a downstream water depth of 12 cm, and a streaming flow drop of 8 cm over the 5 cm wide weir slot. The drop and the downstream arena dimensions correspond to recommendation for small-sized fish in fish passage guidelines (Marsden & Stuart, 2019b; Schmutz & Mielach, 2013), resulting in a maximum water velocity of 1.25 m/s (Larinier, 2002). A solid brick in the downstream part of the experimental arena offered fish shelter from the flow (Figure 1), while a perforated brick in the upstream area constituted both shelter from the flow and a structural shelter to discourage downstream movements of fish.

Two synced PIT-antennas (ORSR; Oregon, USA), attached to the external wall of the flume, were used to track the movement of the fish in the flume (Figure 1). Presence within detection range (a few cm) resulted in detection. The downstream antenna detected fish when they approached the weir, and the upstream antenna detected fish when passing. The experiments were also video recorded (Sony 4K, FDR-AX43, 100fps) from the long side of the flume. In darkness, an IR-camera (Survey3, Mapir, USA) was supported by an IR-lamp (DOME 5 MPX, Proxe, Italy).

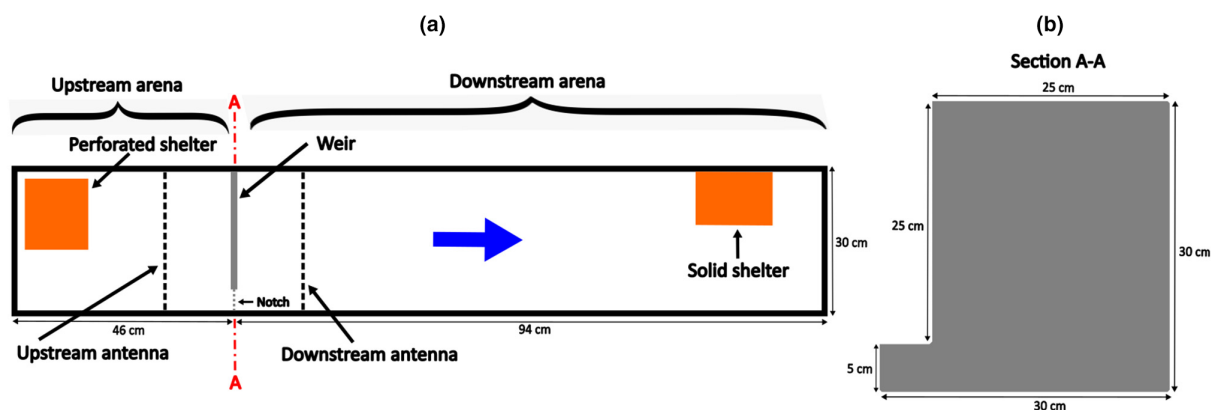


FIGURE 1 A scaled drawing of the experimental arena: (a) top view of the experimental arena inside the flume (the large arrow indicates the flow direction), (b) front view (section A-A) of the deep side notch weir. The upstream end of the flume is delimited by a flow straightener, and the downstream end by a fine meshed rack (Figure adopted from Tarena et al., 2024).

For passage experiment I, fish were randomly divided into 6 groups of 10 fish each and left to recuperate from handling for 3 days in perforated boxes (37×54×13 cm) within larger flow-through tanks. To initiate the trial, a group of fish was netted from the holding box, placed in a small bucket and gently released into the flume on the downstream side of the weir. Fish were given 90 min to pass before the experiment was ended and fish captured and returned to the flow-through tanks.

PIT-data were then used to assign passage success (yes/no) and passage time (time since start of the trial) for each fish. Single detections were not used as proof of passage (to avoid occasional false positives) and video recordings were scrutinised to confirm each passage event. For some fish, PIT-detection data did not allow a direct assignment of passage time (e.g., when many fish upstream the weir caused tag collisions). In such cases video recordings were also used to extract passage time. Although some fish passed the weir several times, only the time of first passage was used in the analyses.

The 60 gudgeons were tested in a series of passage tests under three different light conditions (daylight, darkness at night, low light at night) in the period 9–11 November 2022. The light treatments were part of another study (see Tarena et al., 2024 for details and results of the light experiment). Here the passage data from these trials were used while taking the effect of light into account in the statistical modelling. Only the first passage trial for each fish was included to avoid learning effects, and repeated measures on the same individual. This means that, in passage experiment I, 20 fish were tested in darkness ($LI=0lx$) at night, 20 fish in lit conditions during daytime ($=6\pm 0.7lx$), and 20 fish in lit conditions during night ($4\pm 0.17lx$).

2.3 | Fish swimming performance

Individual swimming trials for the 60 gudgeons were conducted on 23 November 2022 in the same open channel flume as the passage experiment I, following Schiavon et al. (2023). The swimming arena was 97 cm long, delimited by the flow straightener in the upstream direction and the fine meshed rack in the downstream direction. An individual fish was netted, gently released in the swimming arena, and given 5 min to habituate to the flume at a low flow velocity of 18–20 cm/s (Ashraf et al., 2024). At the start of the swimming trial, water velocity was increased to 60 cm/s. This velocity was based on pilot trials to achieve fatigue times in the range of seconds to around a minute; relevant in a fish passage context (Katopodis et al., 2019; Starrs et al., 2011). Water depth during the swimming trial was 9.4 cm. When the fish rested on the downstream grid, it was gently encouraged (poked with a stick) from the downstream side of the downstream grid. The fish sensed the poke but the poke could not displace the fish. A fish was considered fatigued after resting on the grid despite poking or after resting again after the third poke, and the time from the start of the swimming trial constituted the time to fatigue (Ashraf et al., 2024). After the swimming trial, the fish was scanned for PIT-ID and returned to a separate holding tank.

2.4 | Open field test

On 24 November, the 60 gudgeons were subject to an open field test to score their movement activity (Miklósi et al., 1992; Nyqvist et al., 2023; Watz, 2019). Without eliciting an escape response, an individual fish was randomly netted from the holding tank, placed in a small bucket and gently released into an arena (length×width×depth = 56.5×36.5×10.0 cm). Water in the test tanks was changed regularly to maintain a stable temperature across trials. Temperature was measured continuously in a separate tank, subject to identical conditions as the test tanks. The fish was left in the arena for 10 min: 5 min to habituate to the new environment and 5 min for the open field test (Miklósi et al., 1992; Nyqvist et al., 2023; Watz, 2019). Two trials were run in parallel. The arena was filmed with an overhead video camera (Sony 4K, FDR-AX43, 50fps). After the open field test, the fish was scanned for PIT-ID and placed in an aerated tank. When all fish had been tested and recovered, they were returned to the holding tank. Using the video recordings and a custom-made MATLAB script (<https://github.com/SilverFox275/manual-point-tracking>; R2021b The MathWorks Inc, Natick, Massachusetts, USA), fish positions (centre of mass) were manually tracked at one frame per second. Distances in pixels were translated to distance in meters based on known dimensions of the arena (Nyqvist et al., 2023). From the series of positions, a total distance moved was quantified for each fish (e.g., Haraldstad et al., 2021; Nyqvist et al., 2023; Watz, 2019).

2.5 | Passage experiment II—Groups versus individuals

To test for effects of the presence of conspecifics on individual passage rates, passage trials were repeated on 14–15 December using the same experimental design of experiment I and a subset of fish ($n=40$). This resulted in 20 trials with one fish, and four trials with groups of five fish. One or five fish were randomly netted from the holding tank and placed in the downstream part of the experimental arena. Fish were given 60 min to pass the weir, before the experiment was aborted and fish returned to a separate holding tank. Individual passage success and times (20 per treatment) were assessed using PIT-data and videos as for the original passage experiment. The experiments were conducted under a randomised block design (1 group trial, 5 single fish trials) and in lit conditions during daytime and evenings. One fish (in a five fish treatment) had lost its tag and was therefore excluded from the analysis. After finalising the experiments, the fish were released in an isolated pond at the hatchery premises.

2.6 | Statistical analysis

Time-to-event analysis (also called survival analysis) is suitable for fish passage data, taking into account both the proportion of fish passing and the time it takes for them to pass (Castro-Santos &

Haro, 2003; Castro-Santos & Perry, 2012; Hosmer et al., 2008). It is widely applied in medical research, but during the last decades also increasingly in behavioural ecology and fish passage research (Bravo-Córdoba et al., 2021; Silva et al., 2018). Cox-regression, a type of time-to-event analysis, was used to model effects of the categorical variable light condition (daylight, artificial light at night, darkness at night) and the continuous variables swimming capability (time to fatigue) and activity score (distance moved in the open field test) on passage rate in the first trials for each fish in experiment I. Fish were defined as available to pass from the time of release into the downstream experimental arena. Fish not passing were censored at the end of the experiment (that is after 90 min) but considered available to pass until this time (i.e., included in the analysis as fish failing to pass after 90 minutes of having be possibility to do so). All combinations of light treatment, activity score, and swimming capability were included among the candidate models. The interaction between light treatment and activity score was included among the candidate models to check for context dependent effects. For the follow up experiment investigating group effects (passage experiment II), all combinations of group treatment (one or five fish), swimming capability (time to fatigue) and activity score (distance moved), as well as the interaction between activity score and group treatment, were included among the candidate models. The tested fish were relatively uniform in length and hence this variable was not included among the candidate model. To account for non-independence of observations from the same trial/group, all models were clustered on trial (Kelly, 2004; Therneau & Grambsch, 2000; Therneau & Lumley, 2017). Clustering is used to deal with correlated or grouped data, allowing the use of individual event times for subjects within groups. It has, for example, been used to handle non-independence in spatially autocorrelated field data (Binning et al., 2018; Stelbrink et al., 2019), among chicks from the same nest (Christensen-Dalsgaard et al., 2018), and between multiple animals in experimental trials (Harbicht et al., 2022; Nyqvist, Schiavon, Candioto, Tarena, et al., 2024). To select the best model among candidate models, minimisation of Akaike information criterion (AIC) was used. 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 & Anderson, 2003). If more than one competing model fulfilled these criteria, all were presented and used to describe the effects of covariates. For all good models, the assumption of proportionality of hazard was explicitly tested (Fox & Weisber, 2002). The analysis was performed in R, and packages survival (Therneau & Lumley, 2017) and mass (Ripley et al., 2013), and plotted with ggplot (Wickham, 2016) and survminer (Kassambara et al., 2017).

2.7 | Ethics statement

The study was performed in accordance with the Ufficio Tecnico Faunistico e Ittiofauna of the Provincia di Alessandria (n.50338 of 20 September 2022), under the provisions of art.2 of the national Decree n.26/2014 (implementation of Dir. 2010/63/EU).

3 | RESULTS

In all tests, fish exhibited normal swimming behaviour. Gudgeons displayed a high inter-individual variation in swimming performance and activity in the open field test, with no correlation between the two traits (Spearman rank test, $p = .23$; Figure 2).

3.1 | Passage experiment I

In total, 46 out of 60 fish (77%) successfully passed the barrier. Higher activity in the open field test (distance moved) corresponded to higher passage rates, taking effects of the light treatment into account. No interaction between light conditions and activity score, nor fish swimming capability, affected passage rates (Table 1a). Light treatment also affected passage rates (see Tarena et al., 2024; Table 1a).

3.2 | Passage experiment II—group versus individuals

The proportion of successful passages was 94% (18/19) among the fish in groups and 75% (15/20) among single fish. Fish in groups passed at a higher rate than single fish (Figure 3; Table 1b). No effect of activity (distance moved in the open field test) or swimming capability—or their interaction with group treatment was detected (Table 1b).

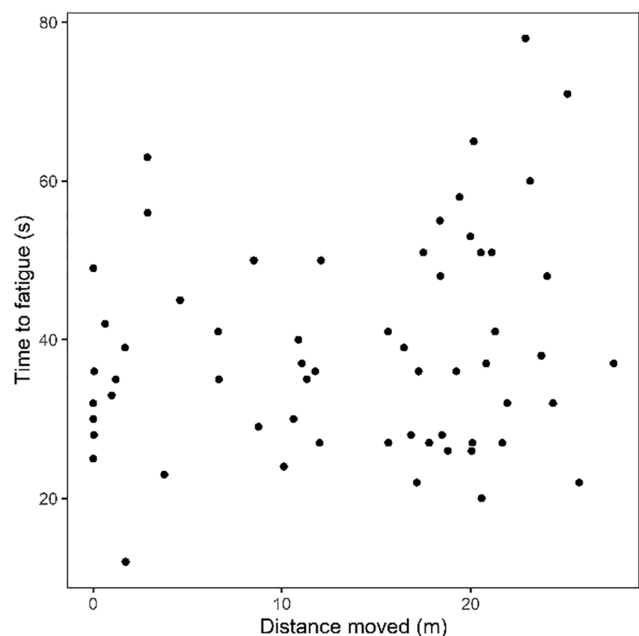


FIGURE 2 Time to fatigue (s) in swimming performance test at a constant velocity of 0.6 m/s on the x-axis, and total distance moved (m) during 5 min in an open field test for the tested gudgeons ($n = 60$). No correlation between the two traits (Spearman rank test, $p = .23$, $\rho = 0.15$).

TABLE 1 List of good models based on the Akaike information criterion (AIC; an AIC-value of 2 or lower from the null model, and within 2 AIC units from the best model).

	AIC without covariates	AIC with covariates	Delta AIC (null)	Delta AIC (min)	Variable	Coefficient	Robust SE	p-value
A. Groups under different light conditions								
Treatment + activity	326.9	316.7	-10.1	0	Treatment-Day	-1.45	0.39	<.01
					Treatment-ALAN	-0.73	0.34	.05
Treatment	326.9	317.6	-9.3	0.85	Activity	0.03	0.02	.04
					Treatment-Day	-1.39	0.39	.02
Treatment + Activity + Time to fatigue	326.9	318.5	-8.4	1.74	Treatment-ALAN	-0.65	0.34	.09
					Treatment-Day	-1.48	0.4	<.01
					Treatment-ALAN	-0.73	0.34	.04
					Activity	0.03	0.02	.03
					Time to fatigue	0.01	0.01	.68
B. Groups versus individuals								
Group	200.1	196.9	-3.17	0	Group	0.81	0.36	<.01
Group + Activity	200.1	197	-3.14	0.03	Group	0.88	0.36	<.01
					Activity	0.03	0.02	.12
Group + TF	200.1	197.5	-2.56	0.61	Group	0.84	0.36	<.01
					TF	0.02	0.01	.27
Group + Activity + Time to fatigue	200.1	197.8	-2.32	0.84	Group	0.90	0.36	<.01
					Activity	0.03	0.02	.12
					TF	0.02	0.01	.35

Note: Delta AIC (null) is the difference between the AIC of the model and AIC of the null model (without covariates). Delta AIC (min) is the difference between AIC of the model and AIC of the best model. (a) Passage experiment I (different light conditions); darkness at night as baseline for treatment. (b) Passage experiment II (single fish vs. groups of five); single fish as baseline in the group variable.

4 | DISCUSSION

Fish passage performance, even at the same site, varies between but also within species. Using repeated tests on individually tagged fish, we explored the effect of fish swimming capability (time to fatigue at a fixed velocity), activity level (distance moved in an open field test), and the presence of conspecifics on individual fish passage rate over an in-flume weir. More active fish displayed higher passage rates compared to less active fish, and fish also passed the obstacle at higher rates in groups of five compared to alone. No effect of fish swimming capability on passage rates was detected.

Fish behavioural types scored in the laboratory are known to correlate with a range of natural behaviours, making up behavioural syndromes when displaying behavioural consistency within and between individuals and contexts (Sih et al., 2004), and could help explain individual variability in fish passage performance. We demonstrate an effect of activity score in an open field test on fish passage rates over a model fishway weir. Similar results are reported for Atlantic salmon smolts passing downstream over a bypass (Haraldstad et al., 2021), and swimming speed in open field tests predicted the likelihood of juvenile American eel (*Anguilla rostrata*) passing an eel ladder (Mensing et al., 2021). For brown trout (*Salmo trutta*) and rainbow smelts (*Osmerus mordax*), however, no correlation between behavioural test scores and passage success through nature-like fishways was seen (Landsman et al., 2017; Lothian & Lucas, 2021). In situation where, for example, more active fish pass at higher rates than less active fish, fish passage may exert a selective pressure on activity in affected fish populations (Wolf & Weissing, 2012) similar to what has been observed for length selective fish passage solutions (Haugen et al., 2008; Maynard et al., 2017; Volpato et al., 2009). Especially if the selected trait is

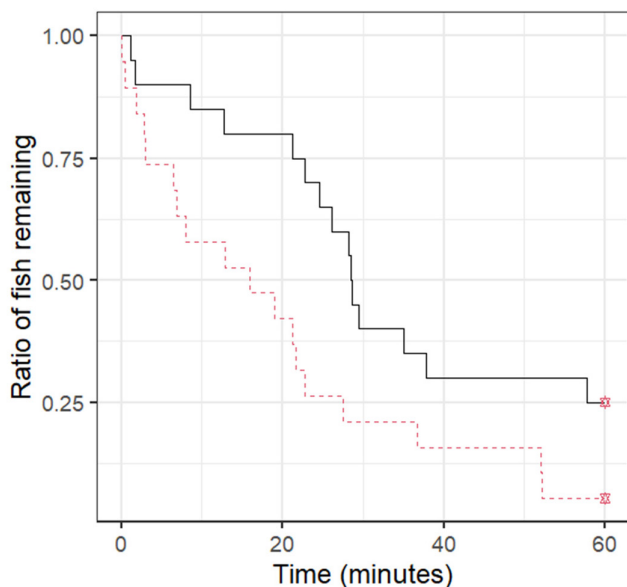


FIGURE 3 Kaplan–Meier curve representing the ratio of single fish (solid line) and fish in the group treatment (dashed line) remaining downstream the barrier over time.

heritable (Brown et al., 2007). With activity level also correlating with, for example, dispersal (Fraser et al., 2001; Watz, 2019), diurnal behaviour (Závorka et al., 2016), and feeding behaviour (Nannini et al., 2012) there is a risk of this selection affecting a wider repertoire of fish behaviours within the population, and in the end the whole ecosystem (Raffard et al., 2017; Wilson & McLaughlin, 2007).

Fish in groups of five passed the barrier at higher rates compared to fish exposed to the weir in solitude. The presence of conspecifics can increase activity levels of individual fish, increasing both feeding efficiencies and exploration (Magnhagen & Bunnefeld, 2009; Magurran & Pitcher, 1983; Ward, 2012), and, as shown in our study, also passage rates. Mechanisms behind this social facilitation can be manifold, including reduced perceived predation risk (Lima & Dill, 1990) and related calming effects (reduction in metabolic rates; Nadler et al., 2016; Parker Jr, 1973), observation of other fish passing (Ryer & Olla, 1991; Sundström & Johnsson, 2001), and individual fish more inclined to pass increasing passage and activity rates also for others (Cote et al., 2011; Harcourt et al., 2009). Although, increased passage rates under higher densities downstream fishways have been reported (Okasaki et al., 2020), and it is well known that many fish species preferably pass in groups (Albayrak et al., 2020; Mawer et al., 2023), the topic has so far received little attention in the scientific literature. Previously, to our knowledge, not quantified, our results highlight the importance for social behaviour in fish passage. This, in turn, underscores the need to accommodate groups of fish in designing fish passage solutions.

Fish swimming capability is often deemed instrumental in the design of fishways (Castro-Santos et al., 2022; Katopodis & Gervais, 2012) but did not affect passage rates in our experiment. This is likely because the passage was relatively undemanding and within the performance range of the whole group of fish. Our barrier was modelled after a deep side notch weir fishway with drop and water velocity values in line with recommendations for small-sized fish in fish passage literature (Marsden & Stuart, 2019a; Schmutz & Mielach, 2013), and hence expected to allow passage at high rates. In provoked swimming trials, however, maximum swimming speed for gudgeon has been estimated to 9.8–13.3 BL/s (average; Nyqvist, Schiavon, Candiotta, & Comoglio, 2024; Tudorache et al., 2008), which for our gudgeons would predict a sufficient swimming capability to pass for only a portion of the fish (0%–80% above 1.25 m/s). Interestingly, the very high passage performance observed could be due to our volitionally passing fish outperforming the fish in the provoked swimming trials cited (Castro-Santos et al., 2013). Regardless, under more demanding passage conditions, as in the passage at real fishways with a long series of (not seldom higher) drops, it must be deemed likely that fish swimming capability affects individual variability in passage success.

The behaviour of fish of different behavioural types have previously been found to be modulated by light conditions (Závorka et al., 2016), and the presence of conspecifics (Harcourt et al., 2009; Magnhagen & Bunnefeld, 2009; Webster et al., 2007). For example, high and low activity scored brown trout display different diel activity patterns in streams (Závorka et al., 2016), and it is known that

the presence conspecifics may shape the behaviour of individual fish (Harcourt et al., 2009; Magnhagen, 2012). In our study, we did not find any effect of the interaction between activity level and light treatment or group size on passage rates. It is, however, important to keep in mind that our sample sizes were relatively low, potentially preventing us from detecting weaker effects on fish passage rates. Future, dedicated experiments need to further explore these potential interactions in more depth.

In real fish passage situation, fish need to approach, enter, transition several compartments, exit and continue their upstream movement, with potential effects of activity type and presence of conspecifics on the whole series of events (Castro-Santos et al., 2009; Nyqvist et al., 2017). This study was performed in a relatively small flume where small-sized gregarious fish was exposed to a deep side notch weir, modelled after a technical fishway. Future studies need to further explore these dynamics in relation to real fishways and free ranging fish, studying also other species. In particular, video data, telemetry and machine learning technologies could be useful tools for these purposes (Couzin & Heins, 2023). In transparent waters, video data could be used to understand the behaviour of individuals and groups downstream, in, and upstream fishways (Zhang et al., 2022). Data from fish counters (Pereira et al., 2021), although currently underutilised, could provide important data on the passage of groups of fish (and group sizes) in relation to fishway type for a range of species. Telemetry techniques can be used to study the movement of tagged individuals in relation to the movement of other tagged conspecifics (Monk et al., 2023), but also the behaviour of the fish after or before passage (Burnett et al., 2017; Hagelin et al., 2016). The latter can be used to test for correlations between passage behaviour or success and other behaviours. This, like in our experiment, through standardised arena trials (Haraldstad et al., 2021; Lothian & Lucas, 2021), or also based on behaviour (e.g., movement rates, habitat choice, spawning behaviour) in nature (Sih et al., 2004).

To conclude, using an in-flume barrier corresponding to a deep side notch weir fishway, we demonstrate effects of individual differences in activity level on fish passage rate and that fish in groups passed at higher rates than isolated individuals. These result highlights the need to take into account both individual variation as well as the presence and behaviour of conspecifics in fish passage studies and evaluation, and may help explain variation in fish passage behaviour (Bunt et al., 2012; Noonan et al., 2012). Designing fishways that allows fish to pass in groups, may increase fishway functionality. Fishways as a potential selection mechanism on fish behavioural types, highlights a potential hidden ecological cost of impounded rivers (Mensingher et al., 2021). Future studies should explore these dynamics on free ranging fish and in relation to real fish passage solutions.

AUTHOR CONTRIBUTIONS

Fabio Tarena, Claudio Comoglio and Daniel Nyqvist conceived of the presented idea. Fabio Tarena, Daniel Nyqvist and Alessandro

Candiotta ran the experiments. Daniel Nyqvist wrote the manuscript with final edits from Claudio Comoglio and Fabio Tarena. All authors discussed the results and contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data will be made available upon a reasonable request.

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