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

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

Daniel Nyqvist[1*], Fabio Tarena[1], Alessandro Candiotto[2], and Claudio Comoglio[1]

[1] Department of Environment, Land and Infrastructure Engineering, Politecnico di Torino, Italy

[2] Ittiologo libero professionista, Predosa, Italy

*Corresponding author. DIATI, Corso Duca degli Abruzzi, 24, Torino, 10129, Italy. +46701756369

Emails and ORCID:

Daniel Nyqvist: daniel.nyqvist@polito.it; 0000-0002-3098-0594

Fabio Tarena: fabio.tarena@polito.it; 0009-0004-4465-3537

Alessandro Candiotto: ale.candiotto@libero.it

Claudio Comoglio: claudio.comoglio@polito.it; 0000-0002-7962-0653

Short running title: Activity levels and presence of conspecifics affect fish passage rates

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 behavior 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 behavior. 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 PIT-tagged gudgeons (*Gobio gobio*) 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 behavior of conspecifics into account in fish passage studies and evaluations. Doing so has the potential to improve the understanding of fish behavior, 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: fish swimming performance, behavioral type, personality, social facilitation, gudgeon

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 kilometers (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 behavior in relation to local conditions is central to successful passage (Mawer *et al.*, 2023; Williams *et al.*, 2011). Importantly, swimming performance and behavior 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, 2019; 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 behavior in relation to its environment is crucial for the fish to approach, enter, ascend, and exit the fishway (Nyqvist *et al.*, 2016; 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 behavior should, intuitively, be conductive to finding and navigating fishways.

Contrary to most models on fish passage behavior, many fish in nature do not pass through fishways individually, but in groups (Mawer *et al.*, 2023). The presence and behavior of conspecifics are therefore likely to affect the passage behavior of fish. Fish in larger groups can be more exploratory and bolder than single or few fish, covering more groundexploring 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 in temperate Europe. Its range extend 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; Schiavon *et al.*, 2024). 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 behavior, 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 ten, 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.

MATERIAL AND METHODS

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 anesthetized 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 (eg. 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% (± 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 *et al.*, 2024; Schiavon *et al.*, 2023), even just one 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 (59x150x20 cm) and left to recover for at least three 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±1°C.

Passage experiment I

Passage experiments I and II were conducted in a recirculating open channel flume (30x30x140 cm) made of plexiglass (Fig. 1). Temperature was kept constant (mean ± SD = 13.15 ± 0.02 °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.

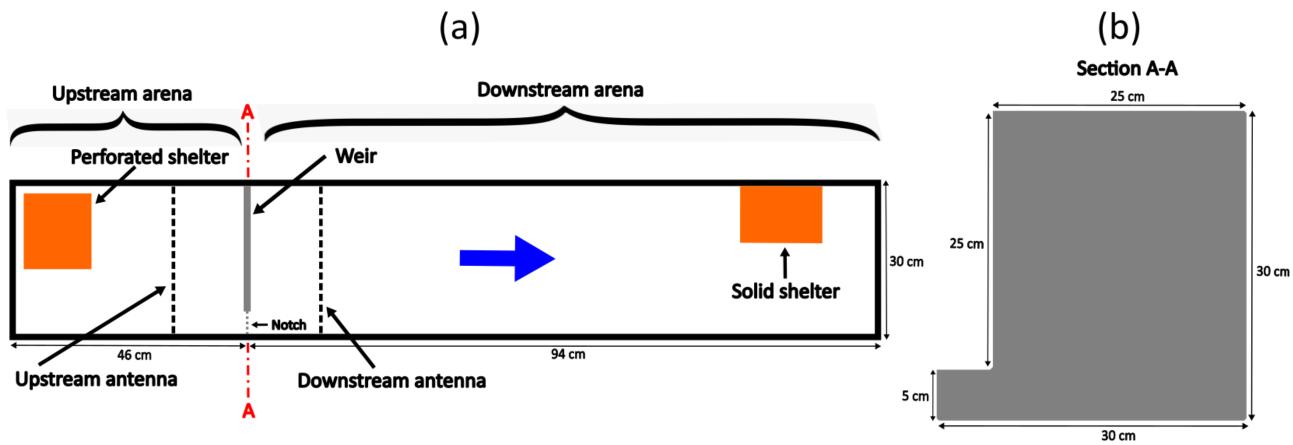

Figure. 1 – A scaled drawing of the experimental arena: (a) top view of the experimental arena inside the flume (the large arrow indicates the flow direction), (b) front view (section A-A) of the deep side notch weir. The upstream end of the flume is delimited by a flow straightener, and the downstream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

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 (Fig. 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 (Fig 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 (Fig. 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).

For passage experiment I, fish were randomly divided into 6 groups of 10 fish each and left to recuperate from handling for three days in perforated boxes (37 x 54 x 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 scrutinized to confirm each passage event. For some fish, PIT-detection data did not allow a direct assignment of passage time (for example 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 sixty 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 only 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 = 0 lx) at night, 20 fish in lit conditions during daytime (= 6 ± 0.7 lx), and 20 fish in lit conditions during night (4 ± 0.17 lx).

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 a 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.

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 minutes: 5 minutes to habituate to the new environment and 5 minutes 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 (center 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 (eg. Haraldstad et al., 2021; Watz, 2019; Nyqvist et al. 2023).

Passage experiment II – groups vs 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 randomized 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 finalizing the experiments, the fish were released in an isolated pond at the hatchery premises.

Statistical analysis

Time-to-event analysis (also called survival analysis) is suitable for fish passage data, taking in to 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 behavioral 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 *et al.*, 2024). To select the best model among candidate models, minimization 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 and 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, 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).

Ethical 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).

RESULTS

In all tests, fish exhibited normal swimming behavior. 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 = 0.23; Fig. 2).

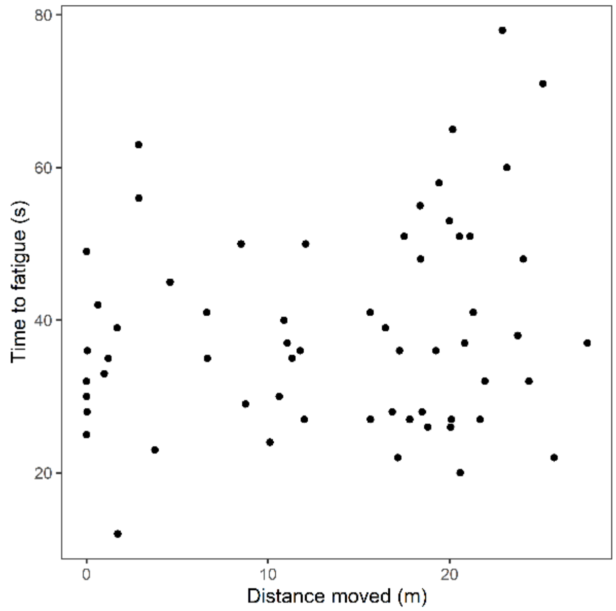

Figure 2. Time to fatigue (s) in swimming performance test at a constant velocity of 0.6 m/s on the x-axis, and total distance moved (m) during 5 minutes in an open field test for the tested gudgeons (n=60). No correlation between the two traits (Spearman rank test, p = 0.23, rho = 0.15).

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).

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). 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.

	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	0.49	<0.01
					Treatment-ALAN	-0.73	0.37	0.05
					Activity	0.03	0.01	0.04
Treatment	326.9	317.6	-9.3	0.85	Treatment-Day	-1.39	0.59	0.02
					Treatment-ALAN	-0.65	0.38	0.09
Treatment + Activity + Time to fatigue	326.9	318.5	-8.4	1.74	Treatment-Day	-1.48	0.48	<0.01
					Treatment-ALAN	-0.73	0.36	0.04
					Activity	0.03	0.01	0.03
					Time to fatigue	0.01	0.02	0.68
B. Groups vs individuals								
Group	200.1	196.9	-3.17	0	Group	0.81	0.27	<0.01
Group + Activity	200.1	197	-3.14	0.03	Group	0.88	0.27	<0.01
					Activity	0.03	0.02	0.12
Group + TF	200.1	197.5	-2.56	0.61	Group	0.84	0.29	<0.01
					Time to fatigue	0.02	0.02	0.27
Group + Activity + Time to fatigue	200.1	197.8	-2.32	0.84	Group	0.90	0.29	<0.01
					Activity	0.03	0.02	0.12
					Time to fatigue	0.02	0.02	0.35

Passage experiment II - group vs 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 (Fig. 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).

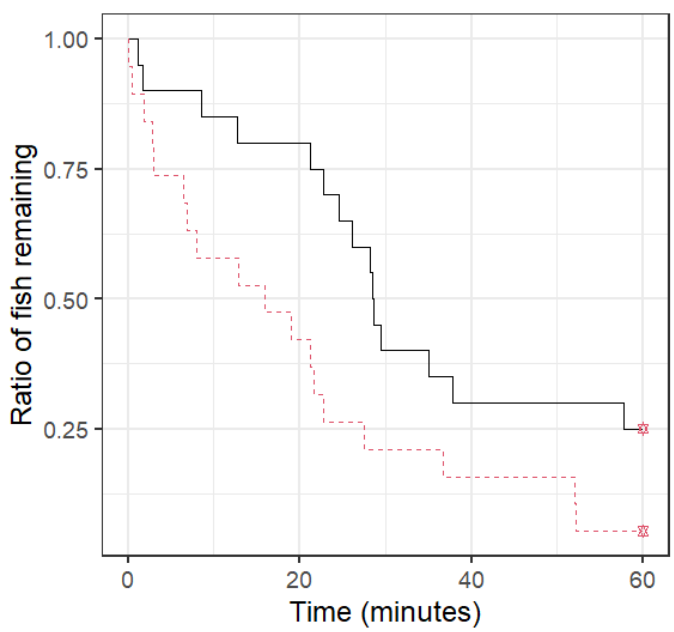

Figure 3. Kaplan-Meier curve representing the ratio of single fish (solid line) and fish in the group treatment (dashed line) remaining downstream the barrier over time.

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 behavioral types scored in the laboratory are known to correlate with a range of natural behaviors, making up behavioral syndromes when displaying behavioral 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 (Mensinger *et al.*, 2021). For brown trout (Salmo trutta) and rainbow smelts (Osmerus mordax), however, no correlation between behavioral 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 heritable (Brown *et al.*, 2007). With activity level also correlating with, for example, dispersal (Fraser *et al.*, 2001; Watz, 2019), diurnal behavior (Závorka *et al.*, 2016), and feeding behavior (Nannini *et al.*, 2012) there is a risk of this selection affecting a wider repertoire of fish behaviors 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 increasing 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 behavior 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 *et al.*, 2024a; 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, nder 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 behavior of fish of different behavioral 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 behavior 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 hindering us to detect 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.*, 2016). 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 behavior of individuals and groups downstream, in, and upstream fishways (Zhang *et al.*, 2022). Data from fish counters (Pereira *et al.*, 2021), although currently underutilized, 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 behavior of the fish after or before passage s(Burnett *et al.*, 2017; Hagelin *et al.*, 2016). The latter can be used to test for correlations between passage behavior or success and other behaviors. This, like in our experiment, through standardized arena trials (Haraldstad *et al.*, 2021; Lothian & Lucas, 2021), or also based on behavior (e.g. movement rates, habitat choice, spawning behavior) 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 behavior of conspecifics in fish passage studies and evaluation, and can help explain variation in fish passage behavior (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 behavioral types, highlights a potential hidden ecological cost of impounded rivers (Mensinger *et al.*, 2021). Future studies should explore these dynamics on free ranging fish and in relation to real fish passage solutions.

ACKNOWLEDGEMENTS

We wish to thank Andrea Cagninei, Usama Ashraf, Luciano Candiotto, Christos Katopodis, Costantino Manes, and Alfredo Schiavon for assistance in the setup and running of the experiment.

AUTHORCONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

Data will be made available upon a reasonable request.

REFERENCES

Albayrak, I., Boes, R. M., Kriewitz-Byun, C. R., Peter, A., & Tullis, B. P. (2020). Fish guidance structures: Hydraulic performance and fish guidance efficiencies. *Journal of Ecohydraulics*, 113–131.

Ashraf, M. U., Nyqvist, D., Comoglio, C., & Manes, C. (2024). The effect of in-flume habituation time and fish behaviour on estimated swimming performance. *Journal of Ecohydraulics*, *0*, 1–9.

Bianco, P. G., & Ketmaier, V. (2005). Will the Italian endemic gudgeon, Gobio benacensis, survive the interaction with the invasive introduced Gobio gobio. *Folia Zool*, *54*, 42–49.

Binning, S. A., Roche, D. G., Grutter, A. S., Colosio, S., Sun, D., Miest, J., & Bshary, R. (2018). Cleaner wrasse indirectly affect the cognitive performance of a damselfish through ectoparasite removal. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20172447.

Bolland, J. D., Cowx, I. G., & Lucas, M. C. (2009). Evaluation of VIE and PIT tagging methods for juvenile cyprinid fishes. *Journal of Applied Ichthyology*, *25*, 381–386.

Bravo-Córdoba, F. J., Valbuena-Castro, J., García-Vega, A., Fuentes-Pérez, J. F., Ruiz-Legazpi, J., & Sanz-Ronda, F. J. (2021). Fish passage assessment in stepped fishways: Passage success and transit time as standardized metrics. *Ecological Engineering*, *162*, 106172.

Brown, C., Burgess, F., & Braithwaite, V. A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. *Behavioral Ecology and Sociobiology*, *62*, 237–243.

Brown, R. S., Cooke, S. J., Anderson, W. G., & McKinley, R. S. (1999). Evidence to challenge the “2% rule” for biotelemetry. *North American Journal of Fisheries Management*, *19*, 867–871.

Bunt, C., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*, 457–478.

Burnett, N. J., Hinch, S. G., Bett, N. N., Braun, D. C., Casselman, M. T., Cooke, S. J., … White, C. F. H. (2017). Reducing Carryover Effects on the Migration and Spawning Success of Sockeye Salmon through a Management Experiment of Dam Flows. *River Research and Applications*, *33*, 3–15.

Calles, O., Rivinoja, P., & Greenberg, L. (2013). A Historical Perspective on Downstream Passage at Hydroelectric Plants in Swedish Rivers. *Ecohydraulics* (pp. 309–322). John Wiley & Sons, Ltd.

Castro-Santos, T., & Haro, A. (2003). Quantifying migratory delay: a new application of survival analysis methods. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 986–996.

Castro-Santos, T., Goerig, E., He, P., & Lauder, G. V. (2022). Applied aspects of locomotion and biomechanics. *Fish Physiol. A*, *39*, 91–140.

Castro-Santos, T., & Perry, R. (2012). Time-to-event analysis as a framework for quantifying fish passage performance. *Telemetry techniques: a user guide for fisheries research. America Fisheries Society, Bethesda, Maryland*, 427–452.

Castro-Santos, T., Sanz-Ronda, F. J., & Ruiz-Legazpi, J. (2013). Breaking the speed limit—comparative sprinting performance of brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 280–293.

Castro-Santos, T., Cotel, A., & Webb, P. (2009). Fishway evaluations for better bioengineering: an integrative approach. (pp. 557–575). Bathesda, MD, USA.

Christensen-Dalsgaard, S., May, R. F., Barrett, R. T., Langset, M., Sandercock, B. K., & Lorentsen, S.-H. (2018). Prevailing weather conditions and diet composition affect chick growth and survival in the black-legged kittiwake. *Marine Ecology Progress Series*, *604*, 237–249.

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K., & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: group composition matters. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1670–1678.

Couzin, I. D., & Heins, C. (2023). Emerging technologies for behavioral research in changing environments. *Trends in Ecology & Evolution*, *38*, 346–354.

De Bie, J., Manes, C., & Kemp, P. S. (2020). Collective behaviour of fish in the presence and absence of flow. *Animal Behaviour*, *167*, 151–159.

De Fries, L., Camana, M., Guimarães, M., & Becker, F. G. (2023). Road crossings hinder the movement of a small non-migratory stream fish. *Environmental Biology of Fishes*, *106*, 1295–1311.

Ficke, A. D., Myrick, C. A., & Kondratieff, M. C. (2012). The effects of PIT tagging on the swimming performance and survival of three nonsalmonid freshwater fishes. *Ecological Engineering*, *48*, 86–91.

Fortini, N. (2016). Nuovo atlante dei pesci delle acque interne italiane: guida completa ai pesci, ciclostomi e crostacei decapodi di acque dolci e salmastre. Aracne.

Fox, J. (2002). Cox proportional-hazards regression for survival data. *An R and S-PLUS companion to applied regression*, 1–18.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist*, *158*, 124–135.

Freyhof, J., & Kottelat, M. (2007). Handbook of European freshwater fishes.

Hagelin, A., Calles, O., Greenberg, L., Nyqvist, D., & Bergman, E. (2016). The Migratory Behaviour and Fallback Rate of Landlocked Atlantic Salmon (Salmo salar) in a Regulated River: does Timing Matter? *River Research and Applications*, *32*, 1402–1409.

Hansen, M. J., Steel, A. E., Cocherell, D. E., Patrick, P. H., Sills, M., Cooke, S. J., … Fangue, N. A. (2019). Experimental evaluation of the effect of a light-emitting diode device on Chinook salmon smolt entrainment in a simulated river. *Hydrobiologia*, *841*, 191–203.

Haraldstad, T., Haugen, T. O., Olsen, E. M., Forseth, T., & Höglund, E. (2021). Hydropower-induced selection of behavioural traits in Atlantic salmon (Salmo salar). *Scientific Reports*, *11*, 16444.

Harbicht, A. B., Watz, J., Nyqvist, D., Virmaja, T., Carlsson, N., Aldvén, D., … Calles, O. (2022). Guiding migrating salmonid smolts: Experimentally assessing the performance of angled and inclined screens with varying gap widths. *Ecological Engineering*, *174*, 106438.

Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., & Manica, A. (2009). Social feedback and the emergence of leaders and followers. *Current Biology*, *19*, 248–252.

Haugen, T. O., Aass, P., Stenseth, N. C., & Vøllestad, L. A. (2008). Changes in selection and evolutionary responses in migratory brown trout following the construction of a fish ladder. *Evolutionary Applications*, *1*, 319–335.

Heath, V. L. S., Miehls, S., Johnson, N., & Higgs, D. M. (2021). Behavioural response of sea lamprey (*Petromyzon marinus*) to acoustic stimuli in a small stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*, 341–348.

Hechter, D. T., & Hasler, C. T. (2019). Repeatability of burst swimming performance in medaka (Oryzias latipes). *Fish physiology and biochemistry*, *45*, 1299–1307.

Herrera-R, G. A., Heilpern, S. A., Couto, T. B. A., Victoria-Lacy, L., Duponchelle, F., Correa, S. B., … Anderson, E. P. (2024). A synthesis of the diversity of freshwater fish migrations in the Amazon basin. *Fish and Fisheries*, *25*, 114–133.

Hirsch, P. E., Thorlacius, M., Brodin, T., & Burkhardt-Holm, P. (2017). An approach to incorporate individual personality in modeling fish dispersal across in-stream barriers. *Ecology and Evolution*, *7*, 720–732.

Hoare, D. J., Ruxton, G. D., Godin, J.-G. J., & Krause, J. (2000). The social organization of free-ranging fish shoals. *Oikos*, *89*, 546–554.

Hosmer, D. W., Lemeshow, S., & May, S. (2008). *Applied Survival Analysis: Regression Modeling of Time-to-Event Data, Second Edition*. John Wiley & Sons, Inc., Hoboken, New Jersey, USA.

IUCN. (2010). Gobio gobio: Freyhof, J.: The IUCN Red List of Threatened Species 2013: e.T184448A8277959, 2010.

Jepsen, N., Schreck, C., Clements, S., & Thorstad, E. B. (2005). A brief discussion on the 2% tag/bodymass rule of thumb. *Aquatic telemetry: advances and applications*, 255–259.

Johnsson, J. I., & Åkerman, A. (1998). Watch and learn: preview of the fighting ability of opponents alters contest behaviour in rainbow trout. *Animal Behaviour*, *56*, 771–776.

Jones, P. E., Champneys, T., Vevers, J., Börger, L., Svendsen, J. C., Consuegra, S., … Garcia de Leaniz, C. (2021). Selective effects of small barriers on river-resident fish. *Journal of Applied Ecology*, *58*, 1487–1498.

Jonsson, B., Waples, R., & Friedland, K. (1999). Extinction considerations for diadromous fishes. *ICES Journal of Marine Science: Journal du Conseil*, *56*, 405–409.

Kassambara, A., Kosinski, M., Biecek, P., & Fabian, S. (2017). Package ‘survminer’. *Drawing Survival Curves using ‘ggplot2’(R package version 03 1)*.

Katopodis, C., & Gervais, R. (2012). ECOHYDRAULIC ANALYSIS OF FISH FATIGUE DATA: ECOHYDRAULIC ANALYSIS OF FISH FATIGUE DATA. *River Research and Applications*, *28*, 444–456.

Katopodis, C., Cai, L., & Johnson, D. (2019). Sturgeon survival: The role of swimming performance and fish passage research. *Fisheries Research*, *212*, 162–171.

Katopodis, C., & Williams, J. G. (2012). The development of fish passage research in a historical context. *Ecological Engineering*, *48*, 8–18.

Kelly, P. J. (2004). A Review of Software Packages for Analyzing Correlated Survival Data. *The American Statistician*, *58*, 337–342.

Kemp, P. S., Gessel, M. H., & Williams, J. G. (2005). Fine-scale behavioral responses of Pacific salmonid smolts as they encounter divergence and acceleration of flow. *Transactions of the American Fisheries Society*, *134*, 390–398.

Kemp, P. S., Gessel, M. H., & Williams, J. G. (2008). Response of downstream migrant juvenile Pacific salmonids to accelerating flow and overhead cover. *Hydrobiologia*, *609*, 205–217.

Landsman, S. J., Wilson, A. D. M., Cooke, S. J., & van den Heuvel, M. R. (2017). Fishway passage success for migratory rainbow smelt Osmerus mordax is not dictated by behavioural type. *River Research and Applications*, *33*, 1257–1267.

Larinier, M. (2002). POOL FISHWAYS, PRE-BARRAGES AND NATURAL BYPASS CHANNELS. *Bulletin Français de la Pêche et de la Pisciculture*, 54–82.

Lenders, H., Chamuleau, T., Hendriks, A., Lauwerier, R., Leuven, R., & Verberk, W. (2016). Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports*, *6*.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.

Lothian, A. J., & Lucas, M. C. (2021). The role of individual behavioral traits on fishway passage attempt behavior. *Ecology and Evolution*, *11*, 11974–11990.

Lucas, M. C., Baras, E., Thom, T. J., Duncan, A., & Slavík, O. (2001). *Migration of freshwater fishes*. Wiley Online Library. Vol. 47.

Magnhagen, C. (2012). Personalities in a crowd: What shapes the behaviour of Eurasian perch and other shoaling fishes? *Current Zoology*, *58*, 35–44.

Magnhagen, C., & Bunnefeld, N. (2009). Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3369–3375.

Magurran, A. E., & Pitcher, T. J. (1983). Foraging, timidity and shoal size in minnows and goldfish. *Behavioral Ecology and Sociobiology*, *12*, 147–152.

Marsden, T., & Stuart, I. (2019a). Fish passage developments for small-bodied tropical fish: field case-studies lead to technology improvements. *Journal of Ecohydraulics*, *4*, 14–26.

Marsden, T., & Stuart, I. (2019b). Fish passage developments for small-bodied tropical fish: field case-studies lead to technology improvements. *Journal of Ecohydraulics*, *4*, 1–13.

Mawer, R., Pauwels, I. S., Bruneel, S. P., Goethals, P. L. M., Kopecki, I., Elings, J., … Schneider, M. (2023). Individual based models for the simulation of fish movement near barriers: Current work and future directions. *Journal of Environmental Management*, *335*, 117538.

Maynard, G. A., Kinnison, M. T., & Zydlewski, J. D. (2017). Size selection from fishways and potential evolutionary responses in a threatened Atlantic salmon population. *River Research and Applications*, *33*, 1004–1015.

McIntyre, P. B., LIERMANN, C. R., CHILDRESS, E., HAMANN, E. J., HOGAN, J. D., JANUCHOWSKI-HARTLEY, S. R., … PRACHEIL, B. M. (2015). Conservation of migratory fishes in freshwater ecosystems. *Conservation of Freshwater Fishes* . Cambridge University Press Cambridge, UK.

Mensinger, M. A., Brehm, A. M., Mortelliti, A., Blomberg, E. J., & Zydlewski, J. D. (2021). American eel personality and body length influence passage success in an experimental fishway. *Journal of Applied Ecology*, *58*, 2760–2769.

Miklósi, A., Topal, J., & Csányi, V. (1992). Development of open-field and social behavior of the paradise fish (Macropodus opercularis L.). *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *25*, 335–344.

Miller, M., Sharkh, S. M., & Kemp, P. S. (2022). Response of upstream migrating juvenile European eel (Anguilla anguilla) to electric fields: Application of the marginal gains concept to fish screening. *PLOS ONE*, *17*, e0270573.

Monk, C. T., Aslak, U., Brockmann, D., & Arlinghaus, R. (2023). Rhythm of relationships in a social fish over the course of a full year in the wild. *Movement Ecology*, *11*, 56.

Morais, P., & Daverat, F. (2016). *An Introduction to Fish Migration*. London, UK: CRC Press.

Nadler, L. E., Killen, S. S., McClure, E. C., Munday, P. L., & McCormick, M. I. (2016). Shoaling reduces metabolic rate in a gregarious coral reef fish species. *Journal of Experimental Biology*, *219*, 2802–2805.

Nannini, M. A., Parkos III, J., & Wahl, D. H. (2012). Do behavioral syndromes affect foraging strategy and risk-taking in a juvenile fish predator? *Transactions of the American Fisheries Society*, *141*, 26–33.

Noonan, M. J., Grant, J. W., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, *13*, 450–464.

Nyqvist, D., Elghagen, J., Heiss, M., & Calles, O. (2018). An angled rack with a bypass and a nature-like fishway pass Atlantic salmon smolts downstream at a hydropower dam. *Marine and Freshwater Research*, *69*, 1894–1904.

Nyqvist, D., Greenberg, L. A., Goerig, E., Calles, O., Bergman, E., Ardren, W. R., & Castro-Santos, T. (2016). Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. *Ecology of Freshwater Fish*, *26*, 707–718.

Nyqvist, D., Schiavon, A., Candiotto, A., Mozzi, G., Eggers, F., & Comoglio, C. (2023). PIT-tagging Italian spined loach (Cobitis bilineata): Methodology, survival and behavioural effects. *Journal of Fish Biology*, *102*, 575–580.

Nyqvist, D., Schiavon, A., Candiotto, A., Tarena, F., & Comoglio, C. (2024). Survival and swimming performance in small-sized South European Cypriniformes tagged with passive integrated transponders. *Journal of Ecohydraulics*.

Okasaki, C., Keefer, M. L., Westley, P. A., & Berdahl, A. M. (2020). Collective navigation can facilitate passage through human-made barriers by homeward migrating Pacific salmon. *Proceedings of the Royal Society B*, *287*, 20202137.

Oufiero, C. E., & Garland Jr, T. (2009). Repeatability and correlation of swimming performances and size over varying time-scales in the guppy (Poecilia reticulata). *Functional Ecology*, *23*, 969–978.

Panagiotopoulos, P., Buijse, A. D., Winter, H. V., & Nagelkerke, L. A. J. (2024). A large-scale passage evaluation for multiple fish species: Lessons from 82 fishways in lowland rivers and brooks. *Ecological Engineering*, *199*, 107158.

Parker Jr, F. R. (1973). Reduced metabolic rates in fishes as a result of induced schooling. *Transactions of the American Fisheries Society*, *102*, 125–131.

Peake, S., McKinley, R., & Scruton, D. (1997). Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *Journal of Fish Biology*, *51*, 710–723.

Pereira, E., Quintella, B. R., Lança, M. J., Alexandre, C. M., Mateus, C. S., Pedro, S., … Telhado, A. (2021). Temporal patterns of the catadromous thinlip grey mullet migration in freshwater. *Ecohydrology*, e2345.

Pitcher, T. J., Magurran, A. E., & Winfield, I. J. (1982). Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, *10*, 149–151.

Raffard, A., Lecerf, A., Cote, J., Buoro, M., Lassus, R., & Cucherousset, J. (2017). The functional syndrome: linking individual trait variability to ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171893.

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass'. *Cran r*, *538*, 113–120.

Romão, F., Quintella, B., Pereira, T., & Almeida, P. (2012). Swimming performance of two Iberian cyprinids: the Tagus nase Pseudochondrostoma polylepis (Steindachner, 1864) and the bordallo Squalius carolitertii (Doadrio, 1988). *Journal of Applied Ichthyology*, *28*, 26–30.

Ryer, C. H., & Olla, B. L. (1991). Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Environmental Biology of Fishes*, *30*, 317–323.

Schiavon, A., Comoglio, C., Candiotto, A., Hölker, F., Ashraf, M. U., & Nyqvist, D. (2023). Survival and swimming performance of a small-sized Cypriniformes (Telestes muticellus) tagged with passive integrated transponders. *Journal of Limnology*, *82*.

Schiavon, A., Comoglio, C., Candiotto, A., Spairani, M., Hölker, F., Tarena, F., … Nyqvist, D. (2024). Navigating the drought: upstream migration of a small-sized Cypriniformes (Telestes muticellus) in response to drying in a partially intermittent mountain stream. *Knowledge & Management of Aquatic Ecosystems*, *https://doi.org/10.1051/kmae/2024003*.

Schmutz, S., & Mielach, C. (2013). Measures for ensuring fish migration at transversal structures. *ICPDR – International Commission for the Protection of the Danube River*. 2013.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*, 372–378.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., … Braun, D. C. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*, 340–362.

Starrs, D., Ebner, B. C., Lintermans, M., & Fulton, C. J. (2011). Using sprint swimming performance to predict upstream passage of the endangered Macquarie perch in a highly regulated river. *Fisheries Management and Ecology*, *18*, 360–374.

Stelbrink, P., Grendelmeier, A., Schabo, D., Arlettaz, R., Hillig, F., & Pasinelli, G. (2019). Does acoustically simulated predation risk affect settlement and reproduction of a migratory passerine? *Ethology*, *125*, 535–547.

Stott, B. (1967). The Movements and Population Densities of Roach (Rutilus rutilus (L.)) and Gudgeon (Gobio gobio (L.)) in the River Mole. *Journal of Animal Ecology*, *36*, 407–423.

Sundström, L. F., & Johnsson, J. I. (2001). Experience and social environment influence the ability of young brown trout to forage on live novel prey. *Animal behaviour*, *61*, 249–255.

Svensson, P. A., Barber, I., & Forsgren, E. (2000). Shoaling behaviour of the two-spotted goby. *Journal of Fish Biology*, *56*, 1477–1487.

Tarena, F., Comoglio, C., Candiotto, A., & Nyqvist, D. (2024). Artificial light at night affects fish passage rates in two small-sized Cypriniformes fish. *Ecology of Freshwater Fish*, *n/a*, e12766.

Tétard, S., Maire, A., Lemaire, M., De Oliveira, E., Martin, P., & Courret, D. (2019). Behaviour of Atlantic salmon smolts approaching a bypass under light and dark conditions: Importance of fish development. *Ecological Engineering*, *131*, 39–52.

Therneau, T. M., & Grambsch, P. M. (2000). *Modeling Survival Data: Extending the Cox Model*. Statistics for Biology and Health. New York, NY: Springer.

Therneau, T. M., & Lumley, T. (2017). Package 'survival'.

Tudorache, C., Viaene, P., Blust, R., Vereecken, H., & De Boeck, G. (2008). A comparison of swimming capacity and energy use in seven European freshwater fish species. *Ecology of freshwater fish*, *17*, 284–291.

Volpato, G. L., Barreto, R. E., Marcondes, A. L., Andrade Moreira, P. S., & de Barros Ferreira, M. F. (2009). Fish ladders select fish traits on migration–still a growing problem for natural fish populations. *Marine and Freshwater Behaviour and Physiology*, *42*, 307–313.

Ward, A. J. W. (2012). Social facilitation of exploration in mosquitofish (Gambusia holbrooki). *Behavioral Ecology and Sociobiology*, *66*, 223–230.

Watz, J. (2019). Structural complexity in the hatchery rearing environment affects activity, resting metabolic rate and post-release behaviour in brown trout *Salmo trutta*. *Journal of Fish Biology*, *95*, 638–641.

Webster, M. M., Ward, A. J. W., & Hart, P. J. B. (2007). Boldness is influenced by social context in threespine sticklebacks (Gasterosteus aculeatus). *Behaviour*, *144*, 351.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer.

Williams, J., Armstrong, G., Katopodis, C., Larinier, M., & Travade, F. (2011). Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. *River Research and Applications*, *28*, 407–417.

Wilson, A. D., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, Salvelinus fontinalis: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, *74*, 689–698.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in ecology & evolution*, *27*, 452–461.

Závorka, L., Aldvén, D., Näslund, J., Höjesjö, J., & Johnsson, J. I. (2016). Inactive trout come out at night: behavioral variation, circadian activity, and fitness in the wild. *Ecology*, *97*, 2223–2231.

Zhang, C., Xu, M., Lei, F., Zhang, J., Kattel, G. R., & Duan, Y. (2022). Spatio-temporal distribution of Gymnocypris przewalskii during migration with UAV-based photogrammetry and deep neural network. *Journal of Ecohydraulics*, *7*, 42–57.