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

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1 # Individual activity levels and presence of

2 # conspecifics affect fish passage rates over

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

16

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

77 also react to light (Hansen *et al.*, 2019; Tétard *et al.*, 2019) and sound (Heath *et al.*, 2021), or their
78 combinations (Miller *et al.*, 2022). In addition, consistent inter-individual differences in activity,
79 such as exploration or boldness can influence animal movement patterns (Wu & Seebacher,
80 2022). For example, both in killifishes (*Rivulus hartii*) and salmonids (*Salmo trutta)*, activity in the
81 laboratory correlates with dispersal in nature (Fraser *et al.*, 2001; Watz, 2019). Related to fish
82 passage, activity levels have been observed to correlate with bypass passage in Atlantic salmon
83 smolts (*Salmo salar;* Haraldstad *et al.*, 2021). There are also indications of fish with higher
84 boldness score to be better upstream passers (Hirsch *et al.*, 2017; Lothian & Lucas, 2021),
85 although not always (Landsman *et al.*, 2017). Even if not conclusive in the literature, high activity
86 and exploratory behavior should, intuitively, be conductive to finding and navigating fishways.

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

101 Gudgeon (*Gobio gobio)* is a small-sized riverine and lake-dwelling fish species native in temperate
102 Europe. Its range extend from France in the south to Southern Finland in the north, and Eastern
103 United Kingdom in the west, while its eastern distribution is still unclear (Freyhof & Kottelat,
104 2007; IUCN, 2010). The species is introduced in Italy, where it is of particular interest as a direct
105 competitor to the threatened Italian gudgeon (Bianco & Ketmaier, 2005; Schiavon *et al.*, 2024).
106 Gudgeon is a gregarious species (Fortini, 2016; Freyhof & Kottelat, 2007), with group sizes ranging
107 from single fish or a few individuals to more than 20 fish (personal observation) and most likely
108 varying over time and between sites (Hoare *et al.*, 2000; Svensson *et al.*, 2000). It spawns from
109 April-August in temperatures above 12°C and in shallow water (Freyhof & Kottelat, 2007).
110 Although typically relatively resident, it can partake in substantial dispersal movements (Stott,
111 1967). While little is known about its fish passage behavior, it has, at places, been frequently
112 observed in fishways (Panagiotopoulos *et al.*, 2024).

113 Individual passage performance over a scaled deep side notch weir, corresponding to the passage
114 environment of a pool-and-weir fishway, had previously been estimated for PIT-tagged gudgeons
115 in groups of ten, in an hydraulic flume experiment (Tarena *et al.*, 2024). In this study, we

116 quantified individual swimming performance (time to fatigue) and activity (distance moved in an
117 open field test) for the same PIT-tagged gudgeons, and tested for effects of individual swimming
118 performance and activity on fish passage rates. To investigate potentially modulating effects of
119 the presence of conspecifics, we repeated the original passage experiment but in trials involving
120 a single fish or a group of five fish. Passage rates were then compared between gudgeons in single
121 fish treatments and gudgeons in group treatments. We hypothesized that higher swimming
122 performance and higher activity levels are associated with higher passage rates, and that fish
123 pass at higher rates in groups compared to alone.

124

MATERIAL AND METHODS

Fish and tagging

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

132 Before tagging, fish were anesthetized in clove oil (Aromlabs, USA; approximately 0.05 ml clove
133 oil / L water). A 2-4 mm ventral incision was made anterior of the pelvic fin, slightly offset from
134 the centre. The tag was then inserted through the incision and pushed forward in the abdominal
135 cavity to align with the fish body (eg. Bolland *et al.*, 2009; Schiavon *et al.*, 2023). Fish were
136 measured for fork length (mean ± standard deviation = 10 ± 0.6 cm) and weighed (11.3 ± 2.2 g).
137 Tag-to-fish weight ratios were 1% (± 0.2%), lower than recommended in telemetry literature
138 (Brown *et al.*, 1999; Jepsen *et al.*, 2005). PIT-tags have been seen not to affect burst swimming
139 ability or volitional swimming performance in similar sized cypriniformes (Nyqvist *et al.*, 2024;
140 Schiavon *et al.*, 2023), even just one day after tagging (Ficke *et al.*, 2012). Tagged fish were left to
141 recover in an aerated water tank for at least 20 min, before being transferred to spring fed flow
142 through tanks (59x150x20 cm) and left to recover for at least three days before starting of the
143 experiments. All fish remained healthy looking and active after tagging. Fish were held in standing
144 water, under a natural photoperiod and semi-natural light conditions (windows and artificial
145 lights during daytime, darkness at night), had access to perforated brick shelters in the tanks, and
146 were fed commercial fish pellets (Tetra, TabiMin, Germany) regularly. Water temperature was
147 stable at 13±1°C.

Passage experiment I

149 Passage experiments I and II were conducted in a recirculating open channel flume (30x30x140
150 cm) made of plexiglass (Fig. 1). Temperature was kept constant (mean ± SD = 13.15 ± 0.02 °C,
151 aligned with the temperature in the holding tanks), switching on and off a chiller to counter
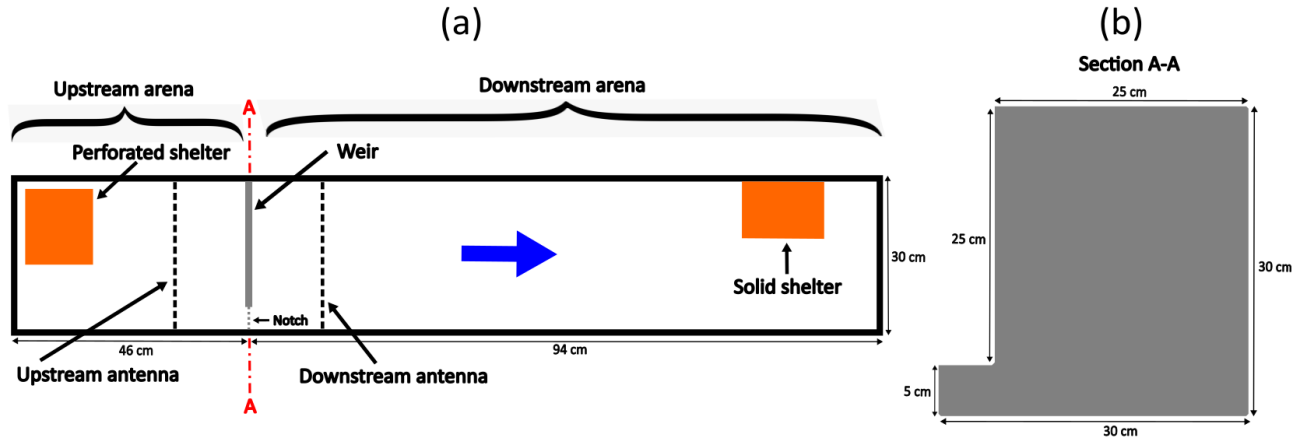152 heating from the action of the pump when needed.

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.

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

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

197 **Fish swimming performance**

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

213 **Open field test**

214 On 24 November, the 60 gudgeons were subject to an open field test to score their movement
215 activity (Miklósi *et al.*, 1992; Nyqvist *et al.*, 2023; Watz, 2019). Without eliciting an escape
216 response, an individual fish was randomly netted from the holding tank, placed in a small bucket
217 and gently released into an arena (length*width*depth = 56.5*36.5*10.0 cm). Water in the test
218 tanks was changed regularly to maintain a stable temperature across trials. Temperature was
219 measured continuously in a separate tank, subject to identical conditions as the test tanks. The

220 fish was left in the arena for 10 minutes: 5 minutes to habituate to the new environment and 5
221 minutes for the open field test (Miklósi *et al.*, 1992; Nyqvist *et al.*, 2023; Watz, 2019). Two trials
222 were run in parallel. The arena was filmed with an overhead video camera (Sony 4K, FDR-AX43 ,
223 50fps). After the open field test, the fish was scanned for PIT-ID and placed in an aerated tank.
224 When all fish had been tested and recovered, they were returned to the holding tank. Using the
225 video recordings and a custom-made MATLAB script (https://github.com/SilverFox275/manual-
226 point-tracking; R2021b The MathWorks Inc, Natick, Massachusetts, USA), fish positions (center
227 of mass) were manually tracked at one frame per second. Distances in pixels were translated to
228 distance in meters based on known dimensions of the arena (Nyqvist *et al.*, 2023). From the series
229 of positions, a total distance moved was quantified for each fish (eg. Haraldstad et al., 2021; Watz,
230 2019; Nyqvist et al. 2023).

Passage experiment II – groups vs individuals

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

Statistical analysis

244 Time-to-event analysis (also called survival analysis) is suitable for fish passage data, taking in to
245 account both the proportion of fish passing and the time it takes for them to pass (Castro-Santos
246 & Haro, 2003; Castro-Santos & Perry, 2012; Hosmer *et al.*, 2008). It is widely applied in medical
247 research, but during the last decades also increasingly in behavioral ecology and fish passage
248 research (Bravo-Córdoba *et al.*, 2021; Silva *et al.*, 2018). Cox-regression, a type of time-to-event
249 analysis, was used to model effects of the categorical variable light condition (daylight, artificial
250 light at night, darkness at night) and the continuous variables swimming capability (time to
251 fatigue) and activity score (distance moved in the open field test) on passage rate in the first trials
252 for each fish in experiment I. Fish were defined as available to pass from the time of release into
253 the downstream experimental arena. Fish not passing were censored at the end of the
254 experiment (that is after 90 min) but considered available to pass until this time (i.e. included in
255 the analysis as fish failing to pass after 90 minutes of having be possibility to do so). All
256 combinations of light treatment, activity score, and swimming capability were included among
257 the candidate models. The interaction between light treatment and activity score was included
258 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).
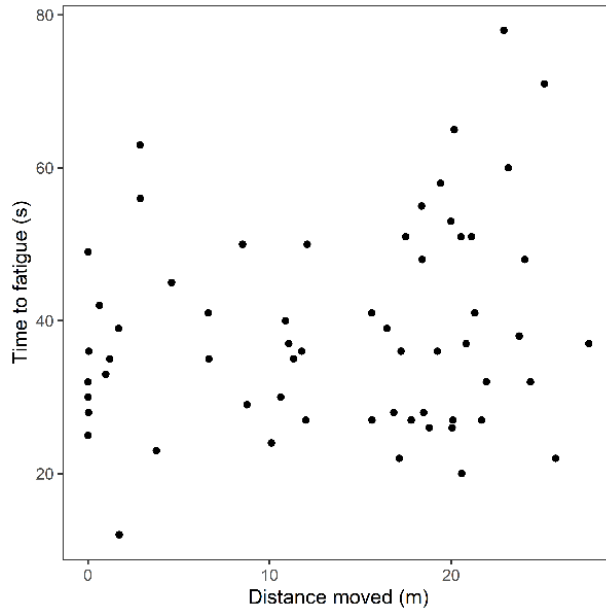
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Figure 2. Time to fatigue (s) in swimming performance test at a constant velocity of 0.6 m/s on the x-axis, and total distance
moved (m) during 5 minutes in an open field test for the tested gudgeons (n=60). No correlation between the two traits
(Spearman 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

	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

302

Passage experiment II - group vs individuals

304 The proportion of successful passages was 94% (18/19) among the fish in groups and 75%
305 (15/20) among single fish. Fish in groups passed at a higher rate than single fish (Fig. 3; Table
306 1b). No effect of activity (distance moved in the open field test) or swimming capability – or
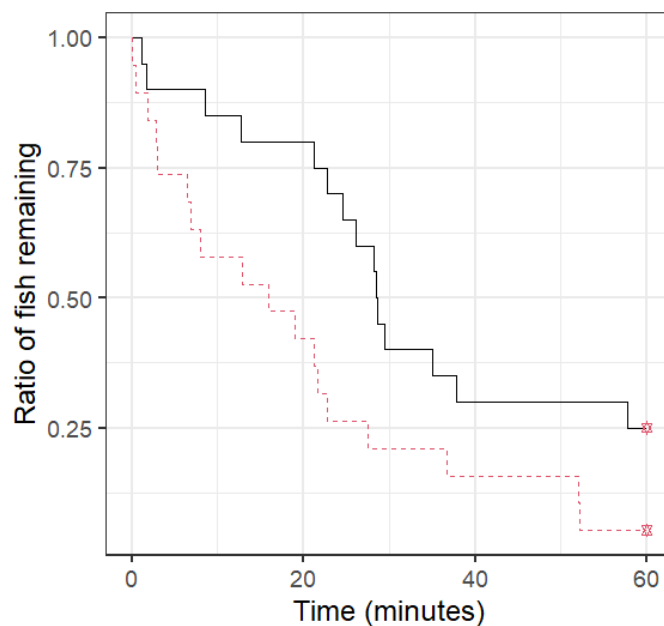307 their interaction with group treatment was detected (Table 1b).

308

309 *Figure 3. Kaplan-Meier curve representing the ratio of single fish (solid line) and fish in the group treatment (dashed line)*
310 *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

349 quantified, our results highlight the importance for social behavior in fish passage. This, in turn,
350 underscores the need to accommodate groups of fish in designing fish passage solutions.

351 Fish swimming capability is often deemed instrumental in the design of fishways (Castro-Santos
352 *et al.*, 2022; Katopodis & Gervais, 2012) but did not affect passage rates in our experiment. This
353 is likely because the passage was relatively undemanding and within the performance range of
354 the whole group of fish. Our barrier was modelled after a deep side notch weir fishway with drop
355 and water velocity values in line with recommendations for small sized fish in fish passage
356 literature (Marsden & Stuart, 2019a; Schmutz & Mielach, 2013), and hence expected to allow
357 passage at high rates. In provoked swimming trials, however, maximum swimming speed for
358 gudgeon has been estimated to 9.8 - 13.3 BL/s (average; Nyqvist *et al.*, 2024a; Tudorache *et al.*,
359 2008), which for our gudgeons would predict a sufficient swimming capability to pass for only a
360 portion of the fish (0-80% above 1.25 m/s). Interestingly, the very high passage performance
361 observed could be due to our volitionally passing fish outperforming the fish in the provoked
362 swimming trials cited (Castro-Santos *et al.*, 2013). Regardless, nder more demanding passage
363 conditions, as in the passage at real fishways with a long series of (not seldom higher) drops, it
364 must be deemed likely that fish swimming capability affects individual variability in passage
365 success.

366 The behavior of fish of different behavioral types have previously been found to be modulated
367 by light conditions (Závorka *et al.*, 2016), and the presence of conspecifics (Harcourt *et al.*, 2009;
368 Magnhagen & Bunnefeld, 2009; Webster *et al.*, 2007). For example, high and low activity scored
369 brown trout display different diel activity patterns in streams (Závorka *et al.*, 2016), and it is
370 known that the presence conspecifics may shape the behavior of individual fish (Harcourt *et al.*,
371 2009; Magnhagen, 2012). In our study, we did not find any effect of the interaction between
372 activity level and light treatment or group size on passage rates. It is, however, important to keep
373 in mind that our sample sizes were relatively low, potentially hindering us to detect weaker
374 effects on fish passage rates. Future, dedicated experiments need to further explore these
375 potential interactions in more depth.

376 In real fish passage situation, fish need to approach, enter, transition several compartments, exit
377 and continue their upstream movement, with potential effects of activity type and presence of
378 conspecifics on the whole series of events (Castro-Santos *et al.*, 2009; Nyqvist *et al.*, 2016). This
379 study was performed in a relatively small flume where small sized gregarious fish was exposed to
380 a deep side notch weir, modelled after a technical fishway. Future studies need to further explore
381 these dynamics in relation to real fishways and free ranging fish, studying also other species. In
382 particular, video data, telemetry and machine learning technologies could be useful tools for
383 these purposes (Couzin & Heins, 2023). In transparent waters, video data could be used to
384 understand the behavior of individuals and groups downstream, in, and upstream fishways
385 (Zhang *et al.*, 2022). Data from fish counters (Pereira *et al.*, 2021), although currently
386 underutilized, could provide important data on the passage of groups of fish (and group sizes) in
387 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.

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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.

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