

Comparative swimming performance and behaviour of three benthic fish species: The invasive round goby (*Neogobius melanostomus*), the native bullhead (*Cottus gobio*), and the native gudgeon (*Gobio gobio*)

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Abstract

Efforts to restore river ecosystem connectivity focus predominantly on diadromous, economically important fish species, and less attention is given to nonmigratory, small-bodied, benthic fish species. Data on benthic fish swimming performance and behaviour in comparison with ecologically similar native species are especially relevant for the study of one of the most successful invaders in the last decades: the Ponto-Caspian gobiid species *Neogobius melanostomus*. To evaluate future measures against its further upstream dispersal, we conducted comparative swimming performance and behaviour experiments with round goby and two native species: the European bullhead (*Cottus gobio*) and the gudgeon (*Gobio gobio*). Experiments in a swim tunnel revealed a high variation in the swimming performance and behaviour within and among the three species. Gudgeon performed best in both U_{crit} and U_{sprint} experiments and displayed a rather continuous, subcarangiform swimming mode, whereas bullhead and round goby displayed a burst-and-hold swimming mode. Experiments in a vertical slot pass model, which contained a hydraulic barrier as a challenge to upstream movement, confirmed the high swimming performance of gudgeon. Gudgeon dispersed upstream even across the hydraulic barrier at the highest flow velocities. Round goby showed a higher capability to disperse upstream than bullhead, but failed to pass the hydraulic barrier. Our results on comparative swimming performance and behaviour can inform predictive distribution modelling and range expansion models, and also inform the design of selective barriers to prevent the round goby from dispersing farther upstream.

KEYWORDS

dispersal, fish pass, habitat fragmentation, swim tunnel, vertical slot

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1 | INTRODUCTION

Fragmentation of river systems due to the presence of artificial structures, such as hydropower dams and weirs, has greatly affected fish migration and dispersal, ultimately restricting the range and abundance of many freshwater fish species (Freyhof & Brooks, 2011; Fullerton et al., 2010; Geist & Hawkins, 2016). Efforts to restore and maintain ecological connectivity in river systems include the construction or the renovation of fish passes—structures created to enable safe and timely fish movement past artificial structures (Silva et al., 2018). In order to ensure the upstream movement of fish, fish pass design requires knowledge about swimming performance and behaviour of the target species. Up to the present day, the focus of fish pass research has traditionally been on economically important fish stocks, which perform long-distance migrations (Birnie-Gauvin et al., 2017; Nieminen et al., 2016; Silva et al., 2018). More recently, the geometry and the hydraulics of fish passes have been conceived to take into account the swimming performance of the complete local fish species community, thus reflecting the growing awareness about impacts of in-stream barriers on small nonmigratory fishes (Branco et al., 2017; Perkin et al., 2015; Wilkes et al., 2018).

The critical swimming speed procedure (U_{crit}) as developed by Brett (1964) is probably the most established measure for the swimming performance. To determine U_{crit} , water flow velocity is increased at specific increments for a defined duration in a water tunnel until the fish is fatigued. U_{crit} has been defined as the maximum prolonged swimming speed using both aerobic and anaerobic metabolism and is thus considered an ecologically relevant measure for migrating and pelagic fish species (Blake, 2004; Plaut, 2001). More recently, Starrs et al. (2011) proposed an incremental swimming speed test that measures sprint speeds (U_{sprint}) attained by fish over shorter periods (20 – 300 s). Given that in fish passes both prolonged and sprint swimming modes are likely to be at play, a combination of U_{crit} and U_{sprint} tests might better inform about the upstream passage capabilities of fish (Starrs et al., 2011).

Swimming performance alone, however, is not enough to describe the factors that determine fish pass success. Ultimately, the behavioural decisions of individual fish determine when and how swimming and dispersal are performed against physical limits. In migratory fish, for example the success rate of ascending a fish pass depends on the attempt rate (Castro-Santos, 2004) and the duration of effort (Silva et al., 2018). Quantifications of these aspects of behaviour ultimately serve as a proxy for how motivated a fish is to ascend a fish pass, although a fish's motivation is no indication of its actual ability to swim upstream (Goerig & Castro-Santos, 2017).

The effects of habitat fragmentation on small benthic fish species across spatial scales have been largely neglected until now. Benthic fish are classically assumed to be inferior swimmers compared with pelagic and migratory fish, because they did not evolve a body shape adapted to minimise drag forces during

prolonged swimming (Langerhans & Reznick, 2010). Instead of swimming steadily against the flow, like pelagic fish, benthic fish display a characteristic burst-and-hold swimming mode (Tierney et al., 2011; Tudorache et al., 2007; Veillard et al., 2017). Whereas the behavioural mechanisms behind prolonged swimming in pelagic fish have been studied in great detail (e.g. Kármán gaiting, an undulatory swimming mode superimposed with translational and rotational motion (Akanyeti & Liao, 2013)), very little is known about the behavioural spectrum displayed by benthic fish, when swimming.

A growing area of research on fish swimming aims to design in-stream barriers, which selectively block invasive species from passing, while allowing the native species to pass (Rahel & McLaughlin, 2018). Such selective barriers have, for example been developed in Europe for invasive signal crayfish (*Pacifastacus leniusculus*: Astacidae; (Frings et al. 2013)), and in North America for sea lampreys (*Petromyzon marinus*: Petromyzontidae) entering the Laurentian Great Lakes (Miehls et al. 2019). There is, however, a need for comparative data on the capabilities of invasive and comparable native species to ascend the barrier (Holthe et al., 2005). The demand for such data is exemplified by the spread of one of the most successful aquatic invaders in the last three decades, the Ponto-Caspian round goby *Neogobius melanostomus*: Gobiidae. Having colonised the Laurentian Great Lakes, the Baltic Sea, and major European river systems, the round goby caused deleterious ecological impacts, such as competition for resources with native species (Kornis et al., 2012). In order to evaluate the suitability of a barrier, which discriminates against the round goby to inhibit its active dispersal into currently unaffected water bodies, knowledge about round goby swimming behaviour and performance is crucial. Ideally, such knowledge is gained by comparative studies including ecologically similar native species. Until now, only a few studies tested the swimming performance of invading round goby from the Laurentian Great Lakes, and none of them compared round goby with native species (Gilbert et al., 2016; Hoover et al., 2003; Pennuto & Rupprecht, 2016). Two of these reported U_{crit} tests, but noted that because round goby tend to hold station against the substrate by using their pectoral fins, U_{crit} does not only represent a pure measure of critical swimming speed, but also includes substrate holding and slipping behaviour (Hoover et al., 2003; Tierney et al., 2011). Here, we focus on the invasive round goby, and compare it with two native benthic species, the European bullhead (*Cottus gobio*: Cottidae) and the gudgeon (*Gobio gobio*: Gobionidae); which are both native to the High River Rhine catchment in Central Europe. Round goby and bullhead both lack a swim bladder and share a similar ecological niche, whereas gudgeon possess a swim bladder and have a more benthopelagic lifestyle.

Research on the success of fish overcoming fish passes is often based on in situ observations or mark-recapture studies, for example (Amtstaetter et al., 2017; Muir et al., 2001; Roscoe et al., 2011). Recent literature has also highlighted that swimming performance estimates derived from laboratory experiments may underestimate actual abilities of free-swimming fish

(Castro-Santos et al., 2013; Peake, 2004; Silva et al., 2018). There is a lack of empirical quantifications for the processes involved in benthic fish species ascending against the flow in a semi-natural setting, such as fish passes, but see Grabowska et al. (2019); Tudorache et al. (2007).

In this study, we aimed to obtain a comprehensive insight into swimming performance, behaviour, and upstream dispersal capability across a vertical fish pass for the three benthic fishes mentioned above. We hypothesised that species would not only show different swimming speeds but also differences in the behaviours displayed during swimming.

Controlled laboratory settings, such as a swim tunnel, enable detailed insight into swimming performance and behaviour, but might underestimate the limits of swimming performance in nature (Peake, 2004; Plaut, 2001). Therefore, we conducted experiments on two scales. Firstly, we developed protocols to determine the swimming performances (U_{crit} and U_{sprint}) of the three species and quantified species-specific swimming behaviours based on published methodology (Brett, 1964; Starrs et al., 2011; Tierney et al., 2011) in a swim tunnel. Video recordings during these experiments enabled retrieval of high-resolution temporal data on the actual behaviours displayed during the unique swimming mode of benthic fish. Secondly, we evaluated the swimming and upstream dispersal performance in a more realistic setting—a model of a vertical slot fish pass. In detail, we calculated the number of approaches towards, and complete and uncompleted passages through an unaltered vertical slot and a prototype of a hydraulic barrier installed in a vertical slot. Here, we hypothesised that differences across species that were measurable in the swim tunnel, would be detectable as differences in the capability to ascend upstream.

2 | MATERIAL AND METHODS

2.1 | Study sites and sampling

2.1.1 | Sampling of fish used in swim tunnel experiments at the University of Basel (2018)

Round goby ($N = 44$) were sampled between May and October 2018 in the High Rhine in Basel, Switzerland, using minnow traps with dry dog food (Frolic) as bait. Fish were anaesthetised using MS222 (Sigma-Aldrich), tagged with glass-encapsulated passive integrated transponder (PIT) tags (MiniHPT8, 8 x 1.4 mm dimensions, Biomark), and transferred to aquaria at the University of Basel. European bullhead ($N = 12$) were caught on 6 June 2018 using scoop nets in both the Maispracherbach and the Wintersingerbach in Magden, Switzerland, and transferred to aquaria at the University of Basel. Gudgeon ($N = 12$) were collected on 27 June 2018 in the Spittelmattbach in Basel, Switzerland, by electrofishing and transferred to aquaria at the University of Basel. Bullhead and gudgeon were also anaesthetised and tagged as described above. For

information on the standard and total length of all experimental animals used in this study see Supplementary Material Figure S1.

2.1.2 | Sampling of fish used in experiments at the Karlsruhe Institute of Technology (KIT) (2019)

During the summer of 2018, it was not possible to sample bullhead and gudgeon in the Maispracherbach, the Wintersingerbach and the Spittelmattbach, as unusually low water levels and exceptionally high water temperatures affected fish stocks of small rivers and creeks. Instead, 45 bullhead and 45 gudgeon were collected from the River Alb in Karlsruhe, Germany, on 14 March 2019, by means of electrofishing and transported directly to the KIT. Round goby were collected between 22 and 29 March 2019, at the same location as in 2018, using minnow traps with dry dog food as bait, transported to aquaria facilities at the University of Basel and on 1 April, transferred to the KIT.

2.2 | Fish maintenance

2.2.1 | University of Basel

Round goby were initially housed in aquaria (60 x 30 x 35 cm) with 3–4 individuals per aquarium and later transferred into a larger aquarium to optimise maintenance effort (100 x 40 x 40 cm) up to 15 individuals per aquarium. All individuals of bullhead, and gudgeon, respectively, were kept in one single aquarium (100 x 60 x 45 and 100 x 40 x 40 cm). Fish were fed twice daily with krill (round goby) and bloodworms (round goby, bullhead, and gudgeon). All aquaria had a flow-through water supply and water temperature ranged between 15.8°C and 18°C; aquaria were illuminated with an overhead white light on a 11:13 hr light : dark cycle.

2.2.2 | Karlsruhe Institute of Technology (KIT)

Fish were kept in six polyethylene tanks (Craemer, Germany, dimensions 91 x 59 x 48 cm) with flow-through water supply, separated by species in densities between 25 and 50 fish per container and fed daily with krill (round goby) and bloodworms (round goby, bullhead, and gudgeon). Temperature ranged between 15.8°C and 22°C.

2.2.3 | Ethical approval and fish welfare

To optimise holding conditions and fish welfare, all aquaria and containers were equipped with more plastic tubes and flower pots than individuals to ensure an oversupply of shelters. All containers also contained natural stones and plastic plants for structural enrichment. Well-being of all individuals was routinely checked by specially trained staff. All experiments were approved by the Swiss cantonal authorities (permits No 2934 and 2846) and by the German regional authorities (permit Nr. G217_17-IWG).

2.3 | Experiments

2.3.1 | Experiment 1: U_{crit}

In a first experiment, prolonged swimming trials (U_{crit}) were performed in a swim tunnel (185 L, 50 Hz, Loligo Systems, Tjele, Denmark) (Figure 1). The swim tunnel included a slippery bottom substrate made of smooth plastic with an estimated absolute roughness coefficient k of $0.0015 - 0.007 \cdot 10^{-3}$ m (<https://www.engineeringtoolbox.com>). The water velocities generated by the swim tunnel's propeller were calibrated using a flow metre ('MiniAir20' Schiltknecht, Gossau, Switzerland), and temperature was kept at 16°C during experiments. Fish were introduced into the swim tunnel and left for 20 min in stagnant water for acclimatisation. Then, water flow speed was set at 0.15 m/s for 10 min and the movements of fish were filmed with two action cameras (Hero 4, GoPro). One camera was placed in the front of the swim tunnel, while the second one was placed above. If fish were reluctant to swim and stayed at the rear-end grid of the swim tunnel within the first minute of the increment, we attempted to set a stimulus for swimming by approaching the fish with the back

of a hand-net until gently touching it. In case this stimulus did not elicit the fish to swim, the experiment was immediately terminated. Experiments were also terminated if we observed indications of stress of the fish, such as continued resting at the grid in a body-posture not normally part of the fish's behavioural repertoire. In case an experiment had to be terminated due to stress, the fish was tested later again, with a minimum of 3 days between experiments. The flow speed was subsequently increased by 0.10 m/s and the stimulus applied after 1 min if fish stayed at the rear-end grid of the swim tunnel. Water flow velocity was increased every 10 min until fish could not hold position at the rear-end grid or showed signs of fatigue.

2.3.2 | Experiment 2: U_{sprint}

In a second experiment, we evaluated sprint speeds (U_{sprint}) of the three study species using an experimental protocol modified after Starrs et al. (2011). Following 5 min acclimation at 0.05 m/s, water flow velocity was increased by 0.05 m/s every 10 s until fish reached fatigue. In contrast to the previous U_{crit} experiment, fish were

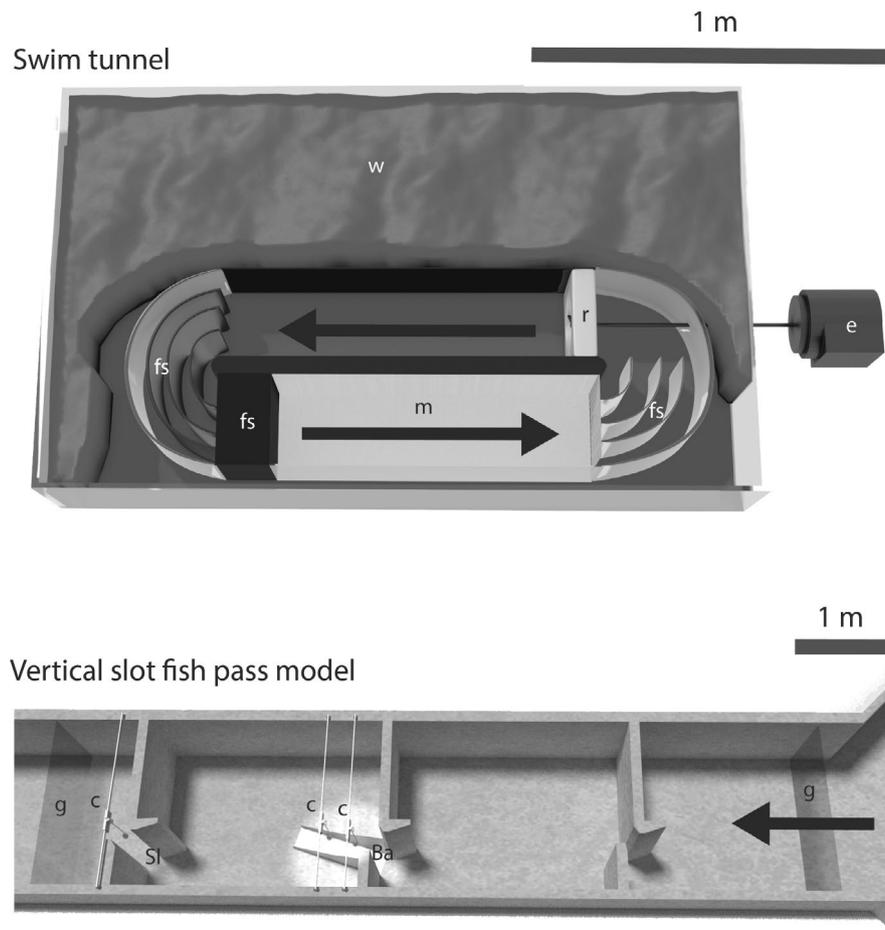


FIGURE 1 Swim tunnel and vertical slot fish pass model used for the experiments. The swim tunnel was completely covered by water (w) during the tests. Water flow velocity was controlled by a rotor (r) connected to an electric engine (e). Flow straighteners (fs) ensured homogenous flow in the measuring chamber (m). Flow direction is indicated by black arrows for both experimental setups. The vertical slot fish pass model was limited by grids (g) in up- and downstream direction to prevent the escape of fish. Cameras (c) were installed over the slot (Sl) and barrier (Ba) to record behaviour of fish

stimulated as soon as they touched the rear-end grid of the swim tunnel; cameras were set-up as described above. The experiment was terminated when the stimulus did not evoke swimming behaviour within 3 s. After termination of the experiment, fish were given a 10 min break in the swim chamber without water flow, after which the experiment was repeated. Experiments were terminated when fish refused to swim, or were unduly stressed; such instances were excluded from further analyses.

2.3.3 | Experiment 3: vertical slot fish pass model

The swimming performance tests described above served as basis for the third experiment in a vertical slot fish pass model at the Karlsruhe Institute for Technology (KIT) in Germany. The vertical slot fish pass was designed to serve as a true-to-scale model of a standard vertical slot fish pass, which is the most common fish pass in Europe (see Figure 1 and DWA (2014); Gebler (2015) for technical details). The basin had a length of 2.39 m and a width of 1.7 m, the slot opening was 0.28 m wide. The vertical slot fish pass had a semi-natural bottom substrate containing pebbles in rough concrete, which has an estimated absolute roughness coefficient k of $0.3 - 5 \cdot 10^{-3}$ m.

The rationale behind these experiments was to assess whether a prototype of a barrier (Figure 1) installed in a fish pass could prevent the passage of round goby, but allow gudgeon and bullhead to ascend. The barrier was designed with the aim to create a more homogeneous water flow in comparison with an unaltered vertical slot and to reduce the substrate holding abilities of round goby. To this end, a stainless-steel panel (100 cm x 24 cm), which has an estimated absolute roughness coefficient k of $0.001 - 0.006 \cdot 10^{-3}$ m was used to provide a slippery bottom-substrate. The steel panel was equipped with sidewalls to prevent fish from entering the barrier sideways (Figure 1). The setting allowed us to evaluate the fishes' capabilities to pass through the slot with the installed barrier (henceforth called barrier slot) in comparison with an unaltered vertical slot at three discharge rates (80 L/s, 105 L/s and 130 L/s). The two lower discharge rates were applied to test the behaviour of the fish under flow velocity conditions that we assumed to not pose a challenge to their swimming capacities. This increased the likelihood of observing upstream movements in all species. The discharge rate of 130 L/s was chosen to be an approximation of real flow velocities occurring in vertical slot passes in the River Rhine catchment. Flow velocity measurements were conducted with the same flow metre as in the swim tunnel. Measurements at nine locations directly above ground revealed flow velocities of $0.47 \text{ m/s} \pm 0.16$ standard deviation (*SD*) at 80 L/s, $0.76 \text{ m/s} \pm 0.13$ *SD* at 105 L/s, and $1.07 \text{ m/s} \pm 0.16$ *SD* during both trials conducted at 130 L/s in the unaltered slot. Flow velocities in the barrier prototype were on average $0.52 \text{ m/s} \pm 0.13$ *SD* at 80 L/s, $0.76 \text{ m/s} \pm 0.17$ *SD* at 105 L/s, and $1.1 \text{ m/s} \pm 0.26$ *SD* at 130 L/s. All velocities are higher than the minimum velocities

recommended to ensure fish orientation in this type of vertical slot fish pass (Gebler, 2015). Velocities at the highest discharge match unpublished measurements conducted in vertical slot fish passes in the High River Rhine and are well in the range of published data from modern fish passes with optimised slot layouts (Bombac et al., 2017).

Experiments were conducted between 4 and 17 April 2019, and each species was tested separately with group sizes between 39 and 45 fish per trial. These group sizes were chosen to reflect natural densities and to account for the fact that fish frequently ascend in groups (Baer et al., 2017). At the start of each experiment, fish were introduced downstream near the outlet of the fish pass (between 'g' and 'c' in Figure 1), and fish movements were monitored and recorded with cameras (Security-Center IR CCTV-Camera, 380 TV-lines, IP 68, Abus, Wetter, Germany). One camera was installed ahead of the first, unaltered slot between outlet and basin 2; two cameras were positioned ahead of the first barrier slot between basin 2 and basin 1; another camera (GoPro Hero 4) was installed at the wall downstream of the barrier, recording the barrier opening (see Figure 1 for camera positions). Due to time constraints, only one experiment per species was performed for discharge rates 80 L/s and 105 L/s, but three experiments per species were conducted at the more realistic discharge conditions of 130 L/s. Each experiment was run for two hours. It should be noted that these experiments were conducted with the same individuals and, therefore, do not constitute independent replicates; to avoid the issue of making false claims based on pseudoreplication, we addressed this issue statistically (see below) and present our results with caution.

2.4 | Data analyses and statistics

2.4.1 | Experiment 1: U_{crit}

The recorded videos filmed from above the swim tunnel were analysed with the software Solomon Coder (vers. beta 17.03.22) to extract the proportions of the following behaviours for each completed velocity step: a) swimming (against water flow); b) station holding (absence of movement on the ground but keeping position), c) sliding backward (absence of movement on the ground leading to a passive rearward slide movement); d) resting at grid (fish keeping its position at the rear-end grid of swim tunnel's swim chamber, see Figure 1).

The critical swimming speed (U_{crit}) was calculated after Brett (1964):

$$U_{\text{crit}} = U_i + (U(t_i/t))$$

where U_i is the penultimate velocity (m/s), t_i is the amount of time the fish swam in the final increment, t is the total time increment (10 min), and U is the water velocity increment (0.10 m/s).

2.4.2 | Experiment 2: U_{sprint}

As with U_{crit} experiments, recorded videos were analysed with the software Solomon Coder (vers. beta 17.03.22). Here, we used recordings from the camera positioned in front of the swim tunnel, which allowed analysing the swimming behaviour in more detail, that is to distinguish between swimming on ground versus swimming (approximately 2 cm) above ground.

U_{sprint} was calculated analogous to U_{crit} :

$$U_{\text{sprint}} = U_i + (U(t_i/t))$$

where U_i is the penultimate velocity (m/s), t_i is the amount of time the fish swam in the final increment, t is the total time increment (10 s), and U is the water velocity increment (0.05 m/s).

2.4.3 | Statistical tests for experiment 1 and experiment 2

To statistically test for differences between species in U_{crit} and U_{sprint} , we used an ANCOVA with species as the categorical predictor variable and the recorded U_{crit} and U_{sprint} for each individual as the response variable. Fish body size was included as a co-variable. To estimate how substantially different the species were in U_{crit} and U_{sprint} , we used Cohen's d as a measure of effect size, with the effect being the species. To statistically test for differences in the swimming behaviour observed during the ramping up of velocities U_{crit} , we used a nested ANCOVA, representing a variance partitioning approach that allowed to account for the repeated measures (same individuals within each species, with repeated observations of their behaviour and within the different velocities). The four different behavioural categories were the response variables. These responses were nested in the different velocity steps, which were in turn nested in species as the categorical predictor variable. At the highest velocities (>0.65 m/s) only gudgeon were still swimming; therefore, statistical analyses were limited to velocity steps below the ">0.65 m/s" step. Statistica™ was used to run the ANCOVAs.

2.4.4 | Experiment 3: Vertical slot fish pass model

Blender (v.79) was used to extract from the videos the number and time of the following behavioural events for both the unaltered slot and the barrier slot.

- "completed upstream passage": the fish entered the field of view of the camera downstream and left it upstream.

- "uncompleted upstream passage": the fish entered the field of view of the camera downstream, crossed the line between either slot or barrier walls (see Figure 1), but did not leave it upstream. Instead, the fish left the field of view in the downstream direction.

- "completed downstream passage": the fish entered the field of view of the camera upstream and left it downstream moving with the flow.

- "uncompleted downstream passage": the fish entered the field of view of the camera upstream, crossed the line between either slot or barrier walls (see Figure 1), but did not leave it downstream. Instead, the fish left the field of view in the upstream direction.

- "upstream approach": the fish entered and left the field of view of the camera downstream and did not cross the line between either slot or barrier walls. No downstream approaches were recorded during experiments.

2.4.5 | Data processing and statistical tests for experiment 3

We computed the frequency of the behavioural events based on the sum of all events to compare the proportion of events: (a) among species, (b) between the unaltered slot and the barrier slot and (c) among different water discharge rates. The upstream passage rate (PR) was computed as:

$$PR = \frac{CP}{AP} \times 100$$

$$AP = CP + UP + APR$$

With the number of completed passages (CP) and approximation to slot or barrier (AP). AP was computed with the number of completed passages (CP), uncompleted passages (UP) and approaches (APR).

To statistically compare the capability of the three species to ascend across the barrier and through the unaltered slot, we performed Chi-squared tests for the passage rate, which was the most important categorical outcome. This allowed us to test the observed passage rates in all three species against a hypothesised equal distribution of passages rates, in which there were no species differences (Hill & Lewicki, 2006). Data processing was performed in Matlab R2019b.

3 | RESULTS

3.1 | Benthic fish swimming performance and behaviour

3.1.1 | Experiment 1: U_{crit}

Gudgeon reached the highest U_{crit} values with 0.72 ± 0.13 m/s ($N = 12$), followed by bullhead (0.55 ± 0.10 m/s; $N = 12$), and round goby (0.54 ± 0.10 m/s; $N = 18$), which performed similarly (Figure 2). The effect sizes showed negligible differences between round goby ($N = 18$) and bullhead ($N = 12$) (Cohen's $d = -0.20$ (Upper and

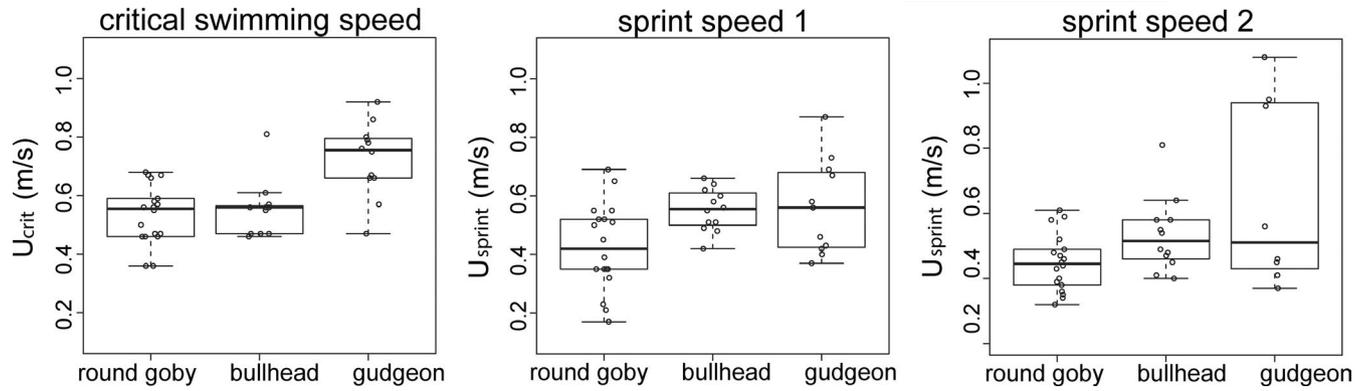


FIGURE 2 Boxplots of critical swimming speed (U_{crit}) and sprint speed (U_{sprint}) for round goby, bullhead, and gudgeon. Sprint speed experiments were repeated (sprint speed 2) 10 min after the initial experiment (sprint speed 1). The boxes represent the interquartile range, the median and the minimum and the maximum in the data

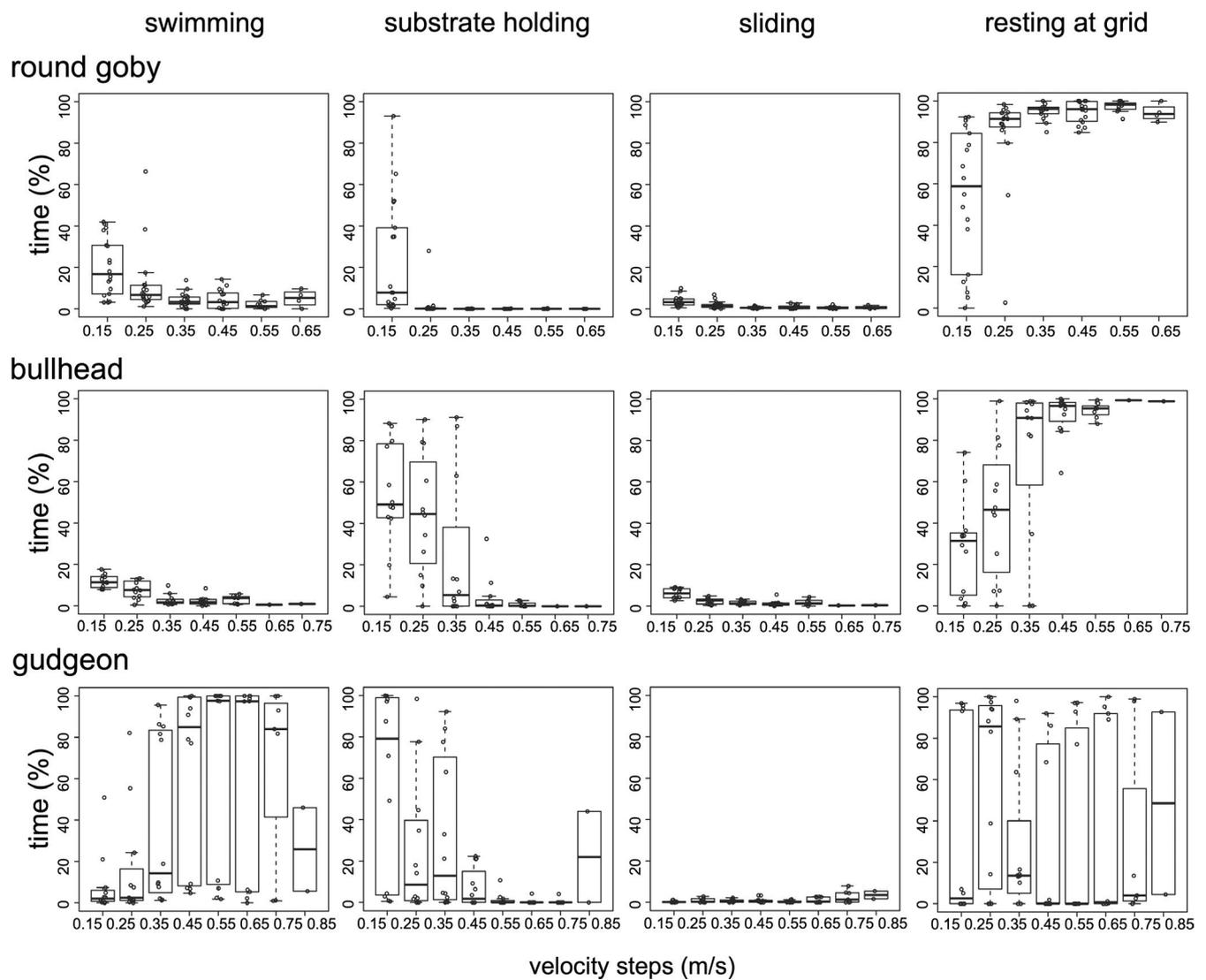


FIGURE 3 Boxplots showing the percentage of time round goby, bullhead and gudgeon spent swimming (against water flow), station holding (absence of movement on the ground but keeping position), sliding (absence of movement on the ground leading to a passive rearward slide movement) and resting (fish keeping its position at the rear-end grid of the swim tunnel's swim chamber during different velocity steps in U_{crit} experiments

lower confidence limits: $-0.97, 0.57$). Substantial differences existed between round goby ($N = 18$) and gudgeon ($N = 12$) ($d = -1.72$ ($-2.60, -0.83$)), and between bullhead ($N = 12$) and gudgeon ($N = 12$) ($d = -1.53$ ($-2.50, -0.57$)). The ANCOVA confirmed that there were differences in U_{crit} between the species ($df = 2, SS = 0.14, MS = 0.01, F = 11.77, p < .001$). The co-variable standard length did not have a statistical effect on the differences between species ($df = 1, SS = 0.01, MS = 0.01, F = 1.26, p = .27$). Accordingly, there was no association between critical swimming performance (U_{crit}) and body size (SL and TL), neither when analysing the whole dataset, nor any of the three species-specific datasets (for all correlations see Supplementary Material Table S1).

Analyses of the recorded videos revealed overall differences between species in each of the observed behavioural categories (nested ANCOVA for fixed effect of species with standard length as a co-variable: $df = 2$; swimming: $MS = 21,057, F = 40.42, p < .001$; station holding: $MS = 8,879.1, F = 17.84, p < .001$; sliding: $MS = 64.95, F = 34.55, p < .001$; resting at grid: $MS = 26,197.96, F = 10.64, p < .001$). The ANCOVA also showed that behaviours differed between velocities, and that the co-variable standard length had a statistical influence on the time spent swimming, and on the time spent resting at the rear-end grid of the swim tunnel (for a table on all statistics see Supplementary Material Table S2).

During U_{crit} trials, all three species spent on average less than 20 % of the time swimming in the first and second velocity increment (0.15 m/s and 0.25 m/s, respectively, see Figure 3). While bullhead and round goby spent even less time swimming with increasing water velocities (≥ 0.25 m/s), gudgeon spent on average more time swimming at higher velocity steps (e.g. over 90 % of the time at 0.55 m/s). The species also differed in their ability to maintain a hold on the substrate: round goby managed to hold onto the substrate on average 23% of the experimental time and only during the first velocity increment (0.15 m/s). Bullhead were able to hold onto the substrate for 44 % and 23 % of the time even at 0.25 m/s and 0.35 m/s, respectively. Gudgeon were best able to hold onto the substrate, with one individual remaining on the substrate for approximately 50 % of the time at the velocity step 0.85 m/s. Both, bullhead and round goby, spent more time at the rear end of the swim tunnel with increasing water velocities, whereas gudgeon individuals spent the majority of time either swimming or resting at the rear grid throughout velocity increments 0.35 m/s to 0.65 m/s (Figure 3). In six of the experiments testing gudgeon and two experiments testing round goby, the termination criteria were met. These fish were tested later again (with a minimum of 3 days between experiments), successfully with the exception of one round goby.

3.1.2 | Experiment 2: U_{sprint}

U_{sprint} trials revealed similar performances of gudgeon and bullhead, with mean U_{sprint} values of 0.56 ± 0.16 m/s ($N = 11$) and 0.55 ± 0.07 m/s ($N = 12$), respectively, and a lower sprint swimming performance for round goby with 0.43 ± 0.14 m/s ($N = 18$).

The effect sizes also confirmed differences between round goby ($N = 18$) and bullhead ($N = 12$) ($d = -1.05$ ($-1.87, -0.23$)), and between round goby ($N = 18$) and gudgeon ($N = 11$) ($d = -0.76$ ($-1.56, 0.04$)), whereas the differences between bullhead ($N = 12$) and gudgeon ($N = 11$) were negligible ($d = 0.09$ ($-0.75, 0.94$)). The ANCOVA for the first trial did not detect statistically significant differences in U_{sprint} between the species ($df = 2, SS = 0.04, MS = 0.02, F = 2.39, p = .11$). In the repetition of the experiment, 10 min after the termination of the first U_{sprint} trials, bullhead and round goby achieved similar mean U_{sprint} values as in the initial experiment (0.53 ± 0.11 and 0.45 ± 0.09 m/s). Nine out of 18 round goby performed better in the rerun than in the initial experiment, seven performed worse and one individual performed similarly. Most bullhead performed worse in the repetition (9 out of 12), but three individuals achieved higher U_{sprint} values. For gudgeon, 4 out of 11 individuals were reluctant to swim in the repetition (representing terminated trials), whereas three performed better and one individual performed equally. The effect sizes of the rerun also confirmed large differences between round goby ($N = 18$) and bullhead ($N = 12$) ($d = -0.87$ ($-1.66, -0.07$)), large differences between round goby ($N = 18$) and gudgeon ($N = 8$) ($d = -1.18$ ($-2.13, -0.25$)) and medium differences between bullhead ($N = 12$) and gudgeon ($N = 11$) ($d = -0.59$ ($-0.15, 0.73$)). The ANCOVA for the rerun detected statistically significant differences in U_{sprint} between the species ($df = 2, SS = 0.10, MS = 0.02, F = 4.07, p = .03$). The effect of body size (SL) was statistically significant in the first trial ($df = 1, SS = 0.13, MS = 0.02, F = 8.28, p = .01$). Body size as a co-variable, however, did not have a statistical effect on the species differences in U_{sprint} in the rerun experiment ($df = 1, SS = 0.02, MS = 1.28, F = 1.28, p = .27$). There was a weak negative correlation between swimming performance in the first U_{sprint} trial and body size (SL) when analysing the whole dataset ($U_{sprint} - SL: cor = -0.40, p = .01; U_{sprint} - W: cor = -0.48, p = .002$). When analysing species-specific subsets, only round goby showed a weak negative correlation between swimming performance and body size or mass ($U_{sprint} - SL: cor = -0.44, p = .07$), for all correlations see Supplementary Materials Table S1). No such correlation was found in the repetition of the experiment.

Results of behavioural analyses from the first U_{sprint} experiment are shown in Figure 4. As we prevented fish from resting at the rear-end grid of the swim tunnel, U_{sprint} represents stimulated swimming performance. Behaviours were quantified from videos recorded in front of the swim tunnel for the whole duration of the experiment (and not for each 10 s velocity step separately). All three species swam both on (touching or partly touching the ground) and above the ground (Figure 4); round goby and bullhead, however, displayed a similar burst-and-hold swimming mode, whereas gudgeon showed a rather continuous swimming mode. With increasing velocities, round goby failed to hold onto the substrate and slid backwards, as evidenced by more time spent sliding than bullhead and gudgeon (Figure 4). Gudgeon spent more time swimming forward (and did so predominantly on the ground) as compared to round goby and bullhead. Bullhead spent more time holding to the substrate than round goby and gudgeon, and both bullhead and gudgeon did not slide backwards, but rather turned and actively swam backwards during experiments (Figure 4).

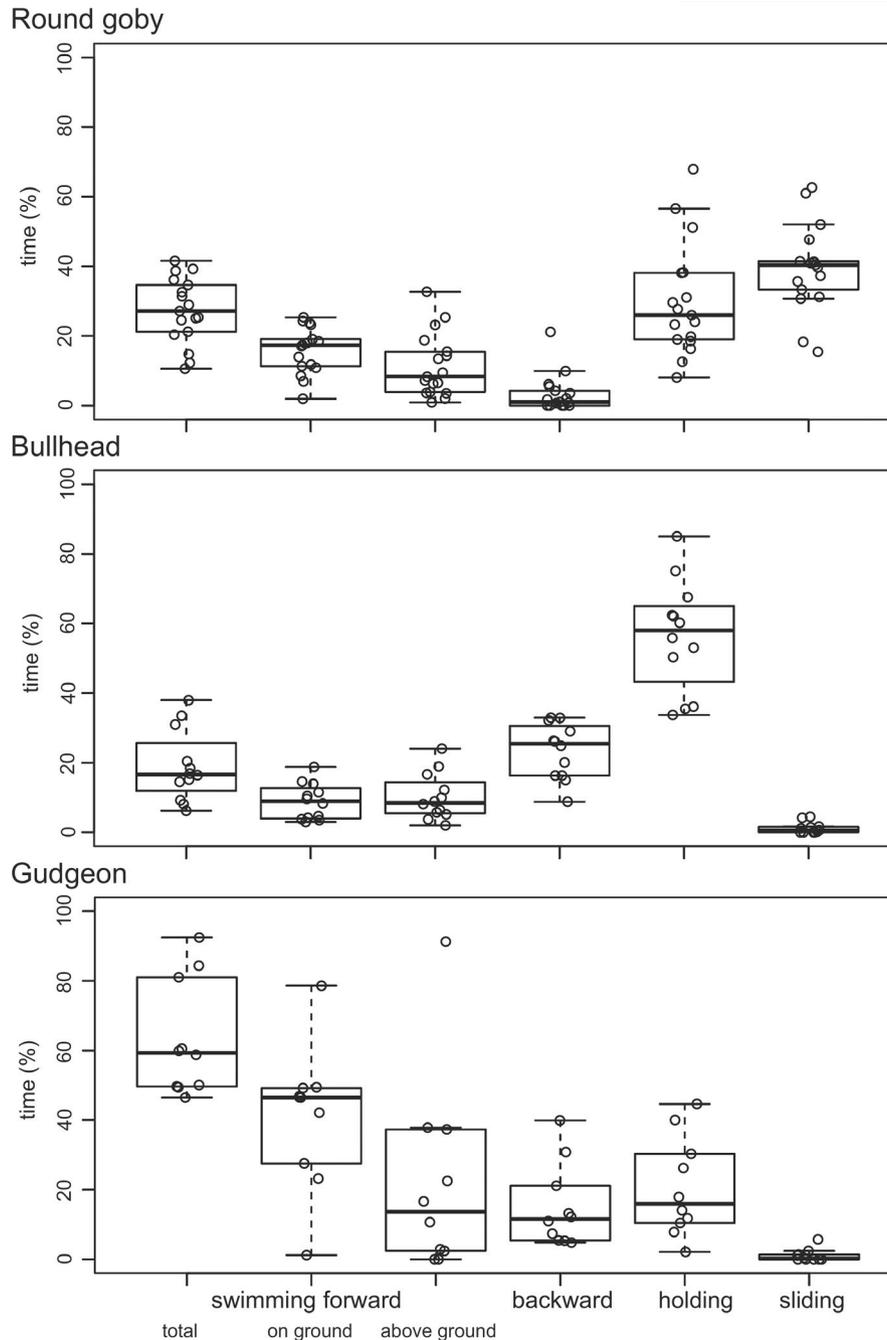


FIGURE 4 Boxplots showing the percentage of time round goby, bullhead and gudgeon spent swimming forward (shown separately as “total” of the time and swimming “on ground” or “above ground”), actively swimming backwards (backward), holding to the substrate (holding) and sliding (absence of movement on the ground leading to a passive rearward slide movement) during U_{sprint} experiments

The ANCOVA detected statistical differences across species in all the recorded behaviours, except for swimming forward above ground and actively swimming backwards (ANCOVA for fixed effect of species with standard length as a co-variable: $df = 2$; swimming forward on the ground: $MS = 3001.81$, $F = 22.25$, $p < .001$; swimming forward above ground: $MS = 451.85$, $F = 1.76$, $p = .19$; backward active swimming: $MS = 64.95$, $F = 0.73$, $p = .49$; backward slide: $MS = 1864.72$, $F = 14.67$, $p < .001$; station holding: $MS = 4030.58$, $F = 16.24$, $p < .001$; see Supplementary Material Table S3 for a summary table of all the statistics of the ANCOVA). The effect of the

standard length as a co-variable was only detected for the behaviour backward active swimming, which did not differ between species.

3.2 | Semi-natural swimming performance assays

3.2.1 | Experiment 3: vertical slot fish pass model

In total, 3979 behavioural events were recorded, with 2307 events observed at the unaltered slot and 1517 events at the barrier slot.

The majority (64 %) of events was recorded for gudgeon, while 28 % of the detected events were recorded for round goby and only 7 % of events were recorded for bullhead. The most frequent events were approaches of fish towards the unaltered slot or the barrier slot (Figure 5). For all three species tested, there was a much higher proportion of complete up- and downstream passages at the unaltered slot than at the barrier slot at all discharge rates (Figure 5).

The Chi-squared test revealed that the completed passage frequencies observed at the unaltered slot and at the barrier showed statistical differences between species at all discharge rates (Table 1). At the highest water discharge rate tested (130 L/s), we detected in total six complete upstream passages and seven uncompleted upstream passages for gudgeon at the barrier (see Supplementary

Material Table S4 for all data). At 130 L/s not a single bullhead completed the upstream passage, but four individuals attempted the upstream passage (uncomplete upstream passage). Round goby approached the barrier slot 91 times, but there was neither an uncomplete nor a complete passage event at a discharge rate of 130 L/s. At 105 L/s discharge rate, gudgeon completed more upstream passages at the unaltered slot (75) and the barrier slot (7) than round goby (56 and 4) and bullhead (26 and 0).

At 80 L/s discharge rate, most complete upstream passages were detected for round goby at the unaltered slot (72) and the barrier slot (11), followed by bullhead (18 and 2) and gudgeon (3 and 0).

Both uncompleted upstream and downstream passage events were generally rather scarce and occurred more frequently at

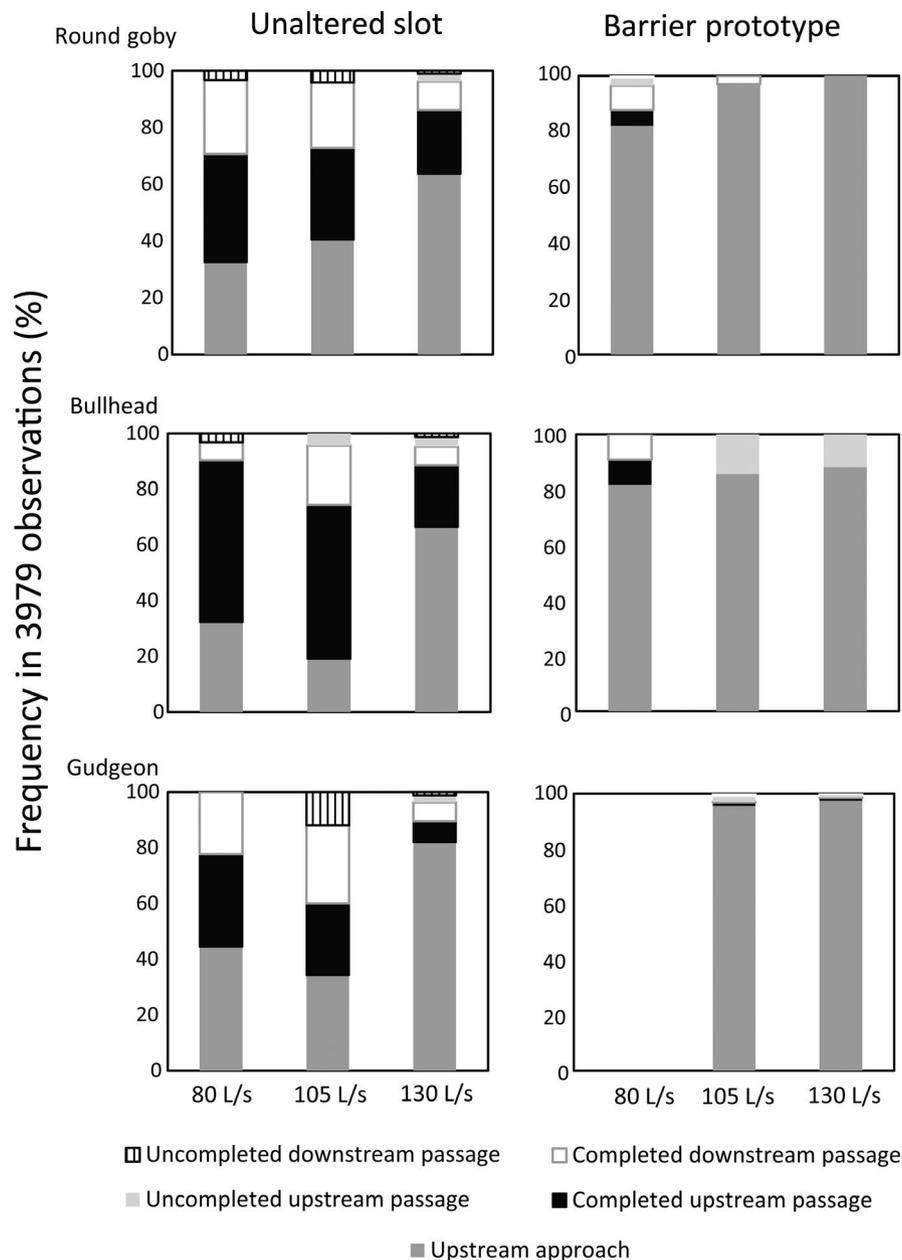


FIGURE 5 The frequency of behavioural events observed for the three species at the unaltered slot and the barrier slot at different water discharge rates (note that at a discharge rate of 80 L/s no events were detected for gudgeon at the slot with the installed barrier prototype)

higher discharge rates (105 L/s and 130 L/s), with gudgeon showing the highest frequencies of these events at the unaltered slot at 105 L/s (Figure 5). Completed downstream passages occurred more frequently, with the highest number performed by gudgeon at the unaltered slot (82). The rate of complete upstream passages at the unaltered slot was highest for bullhead at water discharge rates 80 L/s and 105 L/s and highest at the barrier slot at 80 L/s (Figure 6). Gudgeon displayed the highest number of complete upstream passages overall but showed the lowest rate of completed upstream passages at all discharge rates at the unaltered slot and at 80 L/s

and 115 L/s at the barrier slot. To minimise handling stress, fish were not individually marked for this experiment, and therefore, we could not relate fish size with any measure of swimming performance or behaviour.

4 | DISCUSSION

4.1 | Habitat fragmentation and fish passes—filling the research gap for benthic fish

TABLE 1 The Chi-squared test-statistics for completed passage frequency comparison between tested species

Location	Water discharge (L/s)	<i>p</i>	χ^2	<i>df</i>
Barrier	80	<.01	15.872	2
Barrier	105	.034	6.745	2
Barrier	130	<.01	12.018	2
Slot	80	<.01	85.113	2
Slot	105	<.01	23.466	2
Slot	130	<.01	22.771	2

Anthropogenic ecosystem fragmentation in river systems globally influences the composition, abundance and distribution of fish species (Gardner et al., 2013; Matthews, 2009; Nislow et al., 2011; Perkin & Gido, 2012). Efforts to restore river ecosystem connectivity focus predominantly on diadromous, economically important fish species, although fragmentation is also affecting nonmigratory, small-bodied, benthic fish species (Fuller et al., 2015; Roberts et al., 2013). Several of these species are listed by the International Union for Conservation of Nature (IUCN) for Switzerland, for example bullhead (near threatened) (CSCF-karch Data Server, 2017). Importantly, the consideration of small, benthic fish species in the

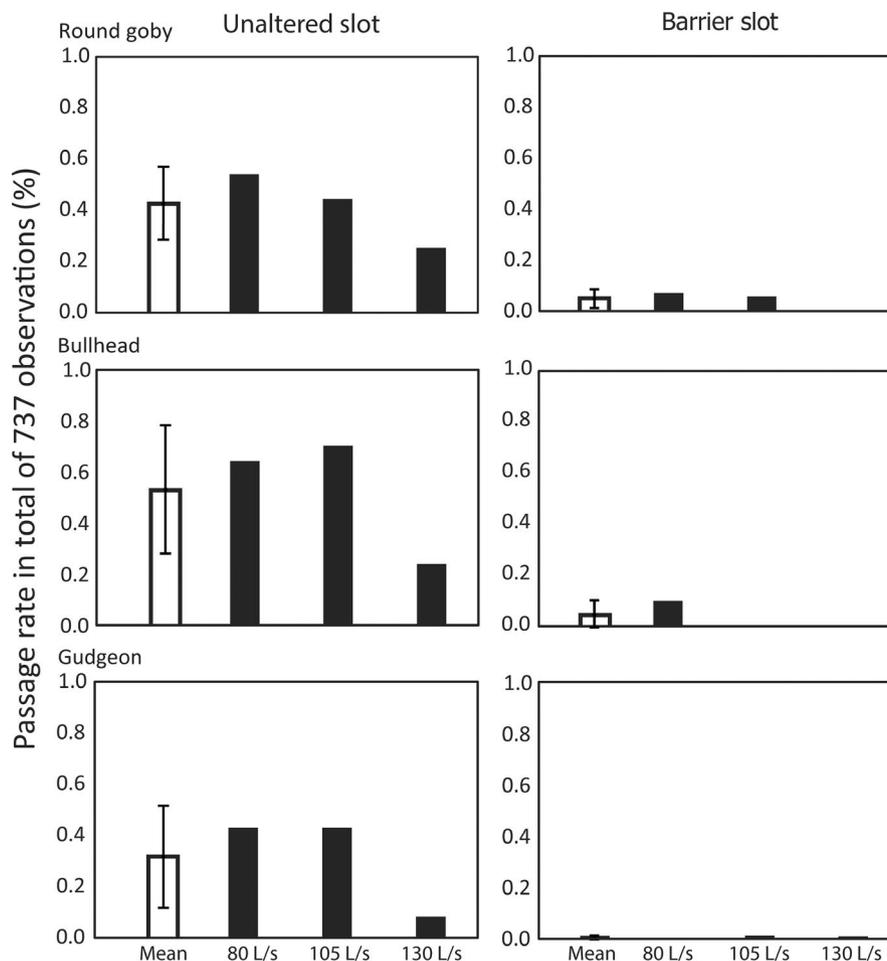


FIGURE 6 Upstream passage rates observed for the three fish species at the unaltered slot and the barrier slot at different water discharge rate and the overall mean with standard deviations

restoration of river environments requires detailed knowledge of their ecological demands and swimming capabilities (Jungwirth et al., 2000). To gain insight into the swimming behaviour and performance of benthic fishes, we conducted both, highly controlled laboratory experiments in a swim tunnel, and experiments in a semi-natural setting—a vertical slot pass model, which represents a more realistic upstream dispersal setting.

4.2 | Species-specific swimming behaviour and performance

Here, we provide the first comparative data on the swimming behaviour and swimming performance of the invasive round goby and two native benthic species that occupy a similar ecological niche, the European bullhead and the gudgeon. Behavioural analyses of swimming performance experiments revealed that bullhead and round goby display a burst-and-hold swimming mode, whereby both species tended to hold onto the substrate until increasing flow velocities forced a transition into bursting and holding to prevent sliding towards the rear grid of the swim tunnel. Such behaviour was previously described for sculpins (*Cottus* spp.) and round goby (Tierney et al., 2011; Tudorache et al., 2007; Veillard et al., 2017). In contrast, gudgeon displayed a more continuous swimming mode, comparable to the subcarangiform swimming mode of salmonids such as several trout species (Lindsey, 1978). The time fish spent swimming during our predominantly volitional U_{crit} experiments was generally low and differed considerably among species and velocity steps. Initially, swimming activity was highest in round goby, but decreased dramatically at relatively moderate velocities (0.25 m/s; Figure 2). Bullhead and gudgeon spent more time holding to the substrate at low flow velocities (0.15 – 0.35 m/s) than round goby, which indicated that round goby did not show superior holding capabilities compared with native species. Such holding capabilities have been attributed to round goby, and their fused, pectoral fin has been speculated to act as a suction cup (e.g. (Tierney et al., 2011); recent research, however, has falsified this assumption (Pennuto & Rupprecht, 2016). Both native species achieved substrate holding at high flow velocities (> 0.35 m/s) by wedging their body against the sidewall of the swim chamber using their pectoral and caudal fins (Bernd Egger, pers. observation). Such a behaviour might indicate that the fish were able to benefit from the hydraulic phenomena of reduced flow velocities that one can expect in boundary layers in the corners. During U_{crit} experiments, all three tested species, especially round goby and bullhead, spent a majority of the experimental time resting at the rear grid of the swim chamber, suggesting a lack of motivation to swim under laboratory settings.

Previous studies that evaluated the swimming performance of round goby reported substantially lower U_{crit} values (0.21 m/s, Hoover et al., 2003; 0.36 m/s, Tierney et al., 2011) than our study (0.54 m/s). Differences in U_{crit} among studies may be attributable to a range of factors, such as experimental protocol, population, sex and seasonal differences (Berli et al., 2014; Downie & Kieffer, 2017;

Hammer, 1995). The primary cause for the higher U_{crit} in our study is likely that, for ethical reasons, we did not stimulate fish to swim via an electrified grid at the end of the swim tunnel as it was done in other studies. As reported above, this allowed the fish to spend experimental time resting at the rear end of swim tunnel. The individuals probably did not fatigue as fast as when an electric grid would prevent them from resting. This could lead to a longer time elapsed at fatigue velocity, which would result in an overestimation of U_{crit} . We would, therefore, like to emphasise that we used the U_{crit} test not as a predictor of the prolonged swimming performance of the three species tested, but mainly to quantify behavioural differences across, and behavioural variation within species. Moreover, previous studies already recognised that due to the burst-and-hold swimming mode of round goby, U_{crit} should be considered as an indicator of swimming and holding abilities (Gilbert et al., 2016; Hoover et al., 2003; Tierney et al., 2011). Our behavioural data indicate that only at very low velocities (0.15 m/s) round goby were able to hold onto the smooth substrate of the swim tunnel; except one individual that successfully held to the substrate at 0.25 m/s for a prolonged period (Figure 2). Our observations confirm the notion that a slippery bottom substrate might indeed pose a challenge for benthic fish in need of friction to hold their position against the flow.

Bullhead performed similarly to round goby, with a mean U_{crit} value of 0.55 m/s. Both species lack a swim bladder and employ a burst-and-hold swimming mode, which might explain the similar performance in the predominantly volitional swimming test. With a mean U_{crit} of 0.72 m/s, gudgeon reached the highest value of the three species tested. Interestingly, whereas roughly half of the tested individuals spent up to 100 % of the incremental period swimming, the other half remained resting at the rear-end grid of the swim tunnel for the majority of the time. Tudorache et al. (2007) reported lower U_{crit} values of 0.54 m/s and 0.60 m/s for two different size classes of gudgeon, but there is no information about individual variation within size classes. As there was no association between U_{crit} and body size in our study, and as we did not measure other factors that might affect swimming performance, the reason for this behavioural variation remains unknown.

In U_{sprint} experiments, fish were restrained from resting at the rear grid of the swim chamber and, therefore, were generally more active as during U_{crit} experiments. Here, gudgeon spent most of the experimental time swimming, whereas bullhead predominantly held to the substrate. Round goby performed less well in substrate holding than bullhead, and repeatedly slid towards the rear grid of the swim chamber until the stimulus induced burst forward swimming of fish. Differences in substrate holding ability best explained the higher U_{sprint} performance of bullhead in comparison with round goby.

4.3 | Semi-natural swimming performance assays

In our vertical slot pass, we were able to test the swimming performances of the three species under more realistic conditions.

Based on camera recordings, we could not only count the number of fish that passed the unaltered slot and the barrier slot, but also the number of uncompleted passages and approaches towards both obstacles. In line with results from our swim tunnel experiments, we found gudgeon to show the best swimming performance among the three species: only gudgeon were able to complete upstream passages at the barrier at the highest discharge rate of 130 L/s. Gudgeon were generally the most active species at higher discharge rates (105 L/s and 130 L/s). This is evidenced by the majority of total events detected, which comprised predominantly approaches towards both, the unaltered slot and the barrier slot. Conversely, most behavioural events for round goby were detected during the lowest discharge rate of 80 L/s, with the highest number of approaches and complete up- and downstream passages among the three species at both the unaltered slot and the barrier slot. Round goby, however, also showed a high frequency of behavioural events at higher discharge rates, but no individual managed to pass the barrier at 130 L/s. This indicates that a hydraulic barrier—in our case, the combination of homogeneous flow velocities and a slippery substrate—may impede upstream dispersal of round goby, as had been suggested in previous studies (Hoover et al., 2003; Tierney et al., 2011).

In contrast to gudgeon and round goby, bullhead generally displayed a rather low number of behavioural events. For example at 105 L/s few bullhead were recorded at both the unaltered slot (e.g. the absolute number of approaches was 9 for bullhead versus 100 and 70 for gudgeon and round goby, respectively). However, at 105 L/s, 26 upstream passages were recorded at the unaltered slot, resulting in the highest passage rate of the three species (Figure 6). Notably, bullhead failed to pass the barrier slot already at 105 L/s and 130 L/s although one individual was recorded conducting an uncompleted passage event. Thus, a hydraulic barrier installed in a fish pass would likely not only prevent the upstream dispersal of round goby, but also prevent other benthic fishes with similar swimming modes, that is burst-and-hold swimming mode, from passing.

At lower discharge rates, round goby and bullhead both displayed a burst-and-hold swimming mode within the unaltered slot during ascent, as video recordings from the exact moment of passage through the unaltered slot showed. The ability to hold position against the flow is most likely increased by the rough bottom substrate. The semi-natural bottom contained pebbles and the individuals seemed to “anchor” themselves between pebbles. This observation again confirms the importance of bottom structure for the ascent of benthic fish species against flow (Hoover et al., 2003; Tudorache et al., 2007). Ecohydraulic studies could be advanced by considering the fish an agent that interacts with the flow and the bottom. This is an important novel perspective, especially for benthic fish species, whose swimming capabilities are still understudied. In contrast to pelagic species, the swimming capability in benthic species can only be understood by studying both the effect of the complex swimming behaviour of the individual and its interaction with the ground. The interaction of flow with objects on the ground leads to a much more complex flow field, compared with flow fields

occurring in the open water. The interaction with the ground is a novel interaction component that is largely absent in studies on pelagic fish.

4.4 | Practical relevance for research into fish swimming and design of fish passes

Generally, applied research needs to inform the design of novel fish passages to guarantee passage success of target species—or alternatively, in the case of invasive species, to create a species-selective barrier. Concerning specific threshold values for swimming performance, our study design mitigates the informative value of U_{crit} , and our results indicate that U_{sprint} might represent the more accurate metric for the swimming performance of the three species. With respect to upstream passage success in fish passes, which requires short but continuous swimming at elevated speeds, U_{sprint} might be more accurate than U_{crit} (Starrs et al., 2011). Importantly, since we aimed to evaluate swimming performances of the three species with respect to a hydraulic barrier preventing the further spread of round goby, consideration of the variation in U_{sprint} within and among species seems more relevant than average values for the species. Ideally, to prevent the farther dispersal of round goby, the most powerful swimmers should be considered when designing a selective barrier, whereas if passage for gudgeon and bullhead was desired, their whole performance range should be taken into account. Mean U_{sprint} values were generally lower than U_{crit} values in all three species—again this is likely due to forced swimming or substrate holding during U_{sprint} versus mostly volitional swimming during U_{crit} experiments. Although mean U_{sprint} values—especially for bullhead and round goby—were similar in the initial test and the respective repetition, there were substantial differences in individual performance of fish. There was no general pattern of fish performing worse in the repetition of U_{sprint} , indicating that the 10 min break between initial test and repetition allowed individual fish to recover fully. Taken together, the results from the controlled swim channel experiments can inform the design of fish passes by providing more complete swimming performance indicators (rather than a single threshold value) for three benthic fish species.

4.5 | Wider ecological relevance of the approach and the results

Research has recently suggested that migration barriers may act as human-made environmental filters (Hale et al., 2016). On the one hand, this filter determines community composition upstream of barriers, that is fast-swimming species can still ascend across a fish pass, whereas slow-swimming species cannot (Rahel & McLaughlin, 2018). On the other hand, this filter also determines the phenotype composition within a single population as faster swimming phenotypes, which are more motivated to ascend, will become

over-represented above the barrier (Hale et al., 2016). Our data suggest that in all three species, the variation in swimming performance and motivation to ascend is substantial. Simple correlations with surrogate performance indicators such as body size could not explain these variations. This underappreciated variation in fish not only highlights how existing barriers might introduce environmental filters, but also emphasises the potential limitations of using newly designed fish passes as selective anthropogenic barriers. Barriers designed to prevent the ascent of a target species might also filter nontarget species. Eventually, this can create a novel anthropogenic selection regime for swimming performance-phenotypes, which should be acknowledged as an ecological factor in the discussion of habitat fragmentation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available in the article's supplementary material.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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