ORIGINAL ARTICLE



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Impact of hydraulic forces on the passage of round goby (Neogobius melanostomus), gudgeon (Gobio gobio) and bullhead (Cottus gobio) in a vertical slot fish pass

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Abstract

Every fish migrating upstream through vertical slot fish passes must swim through slots, where the resistance force of flowing water could affect the passage success. We measured the hydraulic force acting on the body of preserved benthic fish in a vertical slot at different water discharge rates (80 and 130 L/s) to compare the hydraulic burden individual fish species (round goby Neogobius melanostomus Pallas, 1814, gudgeon Gobio gobio L. and bullhead Cottus gobio L.) must overcome. The forces measured in three spatial axes were then compared to acoustic Doppler velocity measurements and the passage probability of 39-45 live fish per species. Passage probability reduction of 28.26% for round goby and 39.29% for bullhead was observed at the higher water discharge. Gudgeon showed increased numbers of passages and approaches when larger hydraulic forces were experienced at 130L/s compared to the lower water discharge. Gudgeon experienced significantly lower hydraulic forces (mean $0.27 \,\text{N} \pm 0.12$ standard deviation) compared to round goby (mean $0.32 \,\text{N} \pm 0.12$ SD) and bullhead ($0.35 N \pm 0.14$ SD). Potentially, the increased hydraulic forces at the higher water discharge contributed to the reduction in passages in round goby and bullhead. That gudgeon behaved differently from the other species illustrates how fish species deal differently with flowing water and the hydraulic forces experienced. Our approach provides a species-oriented assessment of the flow field in ecologically relevant fish passes. These findings represent an important step towards the development of purposeful fish pass designs, which is essential for ecosystem-oriented river connectivity.

KEYWORDS

benthic fish, fish pass, force, hydrodynamics, passage, water discharge

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1 | INTRODUCTION

More than half of the world's largest river systems are fragmented (Nilsson et al., 2005) and there are more than 1.2 million instream barriers in Europe (Belletti et al., 2020). The need to reduce barriers to all species in aquatic ecosystems was anchored in the Convention on Biological Diversity of the United Nations (1992). Fish passes are a well-established management option to enable the passage of fish across fragmenting obstacles (Katopodis & Williams, 2012). Numerous types of fish passes have been developed, with a predominant focus on supporting economically relevant species (Katopodis & Williams, 2012). However, recently, there has been increasing appreciation of the need to provide passage also for other native species that represent important ecosystem components (Silva et al., 2018).

Examples of species that are less economically relevant, but represent important ecosystem components, are gudgeon (Gobio gobio L.) and bullhead (Cottus gobio L.). Indeed, there is little knowledge about the performance of such small-bodied, bottom-dwelling species in fish passes and how they move upstream against the flow (Knaepkens et al., 2007). Some benthic fish possess specialised styles of swimming to resist flow and hold station in microhabitats (Carlson & Lauder, 2011; Gilbert et al., 2016). However, how benthic fish can hold their position against the flow is only partly understood. The creation of negative lift forces through adjusting the pectoral fins has been reported as one mechanism that enables station holding at increased water flow (Carlson & Lauder, 2011). When swimming upstream in a fish pass, benthic fish have to leave the flow-sheltering structures on the riverbed and actively swim in the free water column, where they are exposed to the flow field. How benthic fish experience the flow during passage and their behavioural response to the forces induced by the water on the fish body are presently unknown. This knowledge could enable the design of fish passes adapted to the requirements of specific species relevant to ecosystems.

Commercial shipping has dispersed the round goby (*Neogobius melanostomus* Pallas, 1814) in the Baltic Sea, the Laurentian Great Lakes and European river systems, such as the River Rhine (Kornis et al., 2012). While round goby commonly resides in a local area, some individuals have been reported to disperse upstream via swimming (Bronnenhuber et al., 2011; Šlapanský et al., 2020). Upstream migration of the invasive round goby can extend negative impacts on ecosystems (Hirsch et al., 2016; Kornis et al., 2012; Tierney et al., 2011). Increased effort to restore river connectivity, which may allow unwanted fish species to disperse, leads to trade-offs for stakeholders when they decide about enabling the passage of river obstacles (McLaughlin et al., 2013; Milt et al., 2018).

Rahel and McLaughlin (2018) mentioned the need for integrated interdisciplinary research to implement species-selective fragmentation as a management option for aquatic environments. If impeding the passage of invasive species, fish passes may protect the native aquatic biodiversity (Vélez-Espino et al., 2011). Flow fields within fish passes could be modified by adapting their design to support passage of target species (Puertas et al., 2012). Conversely, flow fields that do not meet the requirements of other fish could be used to hamper the passage of undesired, invasive species.

The variations in body shape among fish species can determine their passage success in fish passes (Castro-Santos et al., 2009), possibly as swimming performance depends on body shape (Ohlberger et al., 2006; Rubio-Gracia et al., 2020; Sagnes & Statzner, 2009). Nevertheless, in order to design fish passes that create flow fields adapted to the requirements of specific species, it is essential to understand the physical impact of flow on the fish body, how this impact differs between species due to their individual shapes and thereby how flow affects the passage success of fish. Several studies have described the flow fields in fish passes (Baki et al., 2017; Larinier, 2008; Liu et al., 2006). However, the direct effects of the flow field on a fish body in a fish pass is, to our knowledge, unknown. Some researchers have measured the direct hydraulic forces of flowing water acting on the bodies of fish under standardised conditions (Barrett et al., 1999; McLetchie, 2003; Quicazan-Rubio et al., 2019; Wiegleb et al., 2020), but there are no data on the hydraulic forces fish encounter during the passage of a real fish pass. Knowledge of how flow differentially affects the swimming behaviour of individual species of invasive and native migrating fish may enable the evaluation of existing fish passes and the adaptation of future fish pass constructions to the requirements of the corresponding ecosystem.

In previous studies, we assessed the performance of a prototype hydraulic barrier for three comparable species, the invasive round goby and the native gudgeon and bullhead (Egger et al., 2020, Wiegleb et al., 2022). These studies compared the swimming capacity among species (Egger et al., 2020) and reported that the hydraulic forces experienced in the barrier flow field differed among species. These differences in the hydraulic forces experienced corresponded to the individual swimming behaviour observed for the species (Wiegleb et al., 2022). In the present study, we questioned how these hydraulic forces affect the passage of live fish differently among species at different flow conditions and focused on the hydraulic forces experienced in the vertical slot downstream of this prototype hydraulic barrier (Wiegleb et al., 2022). We therefore applied a three-step approach by: (i) assessing the flow field, (ii) measuring the forces acting on preserved fish bodies within this flow field and (iii) comparing passage frequencies of live fish among different water discharges and the test species. Based on the assumption that fish migration is hydraulically mediated (Goodwin et al., 2014) and because hydraulic forces experienced by the fish increase with the water velocity (Wiegleb et al., 2020), we expected that higher water discharge would create greater forces for fish moving upstream to overcome. As these hydraulic forces are assumed to vary among species, we expected species that experience a lower hydraulic burden would pass the vertical slot more frequently. Using this three-step approach, we investigated the hypotheses that the forces experienced by preserved fish in the flow field of a vertical slot at different water discharges differ among species (I) and correspond to the passage success of live fish (II).

2 MATERIALS AND METHODS

The live fish observation data were obtained at the downstream vertical slot from the experiment that assessed the prototype hydraulic barrier for invasive gobies in the test rig at the Theodor-Rehbock Hydraulic Laboratory, Karlsruher Institute of Technology (KIT), Germany, reported in Egger et al. (2020) and Wiegleb et al. (2022). The flow measurements were performed using the same acoustic Doppler velocimeter, and the hydraulic forces were measured using preserved fish with the same probe as reported in Wiegleb et al. (2022). A multi-axis-F/T-sensor (Schunk®) represented the core of this probe. A 10-cm-long brass stick connected the preserved fish with the force sensor and functioned as a transducer of the hydraulic forces. The force sensor was sheltered against lateral flow by a polyvinyl chloride hull.

2.1 Flow channel setup

The flow channel experiments were performed in a vertical slot fish pass test rig at the KIT (Figure 1). Vertical slot fish passes are one of the main types of technical passes installed at transverse structures (weirs) to enable upstream passage of fish (Wu et al., 1999). Vertical slot fish passes consist of a rectangular channel with partition walls containing vertical openings that separate the channel into pools. The flow through these slots creates a jet with accelerated water velocity, which has to be passed by the fish migrating upstream (Wu et al., 1999). The test rig consisted of a water channel (width: 1.70 m) with partition walls that formed the vertical slots (width: 28 cm) with a 2.40-m-long pool between the partition walls.

To assess the effect of the water discharge rate on the performance of different species in the vertical slot fish pass, we measured water velocities at three water discharges (80, 105 and 130L/s) and measured the hydraulic forces experienced by preserved fish at two water discharges (80 and 130L/s); 130L/s was assumed to be most representative of the conditions in real fish passes (Bombač et al., 2017). The hydraulic forces experienced by the fish were not measured at 105 L/s to increase the sample sizes for the highest (130L/s) and lowest (80L/s) water discharge rates. The fish pass test rig used in these experiments had a slope of zero degrees and the water discharge rate was adjusted via a recirculation pump. We measured the water depth of the different basins to maintain similar water depths and velocities across trials with a given water discharge. The depth of water downstream of the assessed vertical slot was 38 cm at 130 L/s, 46 cm at 105 L/s and 62 cm at 80 L/s; the water level upstream of the vertical slot was 50 cm at 130 L/s, 51 cm at 105 L/s and 65 cm at 80 L/s.

2.2 Flow measurements

The flow was measured using methods similar to Wiegleb et al. (2022). An acoustic Doppler velocimeter (Vectrino ADV, Nortek

FIGURE 1 The probe (P) used to measure the 3D forces experienced by preserved fish positioned close to the channel bottom was mounted on a carriage (a), which was programmed to adjust the probe position in the x- (green), y- (red) and z-axes (blue) close to the vertical slot in a vertical slot fish pass model (b). The flow direction is indicated by the black arrow. The force sensor (S) was mounted at the lower end of the probe and connected to the fish (F) via a 3-mm-diameter, 10-cm-long, brass stick (c). The force sensor measured the forces in the x-, y- and z-directions; the x-axis was located at angle of 110° relative to the partition wall and

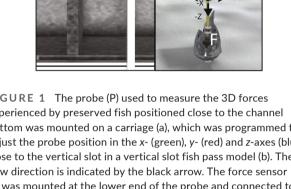
AS) was mounted on an electric carriage (Isel; Figure 1), which was programmed to drive a pattern of 19 measurement points one-byone in the vertical slot (Figure 2). The flow was measured for 1 min at every measurement point and we computed for every measurement point the mean water velocity (v) for this period from the three directional axes (v_x, v_y, v_z) :

parallel to the longitudinal axis of the body of the fish (F).

$$v = \sqrt{v_x^2 + v_y^2 + v_z^2}$$

The measurement points that were included in the flow and the force measurements were labelled 6 d to 9 h, while four measurement points were only included in the flow measurements (1-4) (Figure 2). These four measurement points could not be approached by the force measurement probe due to its shape. The flow was measured as close as possible to the channel bottom (ca. 2cm above channel bottom) for 5 min at every measurement point. The measurement points were evenly distributed above the bottom to give an insight into the spatial distribution of the water velocity. All fish migrating upstream of the vertical slot must pass through the area between the two side walls. We located two measurement points in this area, one in the centre (position g9) and one close to a side wall (position h9; Figure 2).

FRESHWATER FISH -WILEY 3 (a) P



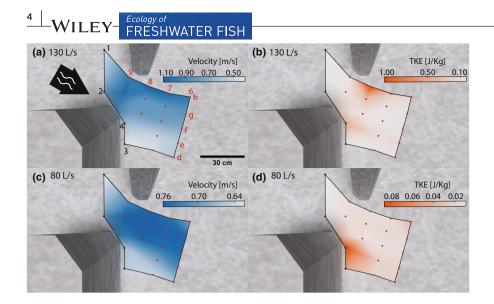


FIGURE 2 Mean water velocity (a, c) and turbulent kinetic energy (TKE) (b, d) for the 130 and 80 L/s water discharge, measured at different measurement points (red dots) close to the vertical slot. The flow measurements included four points (points 1, 2, 3 and 4 in black) that were not included in the force measurements.

The acoustic Doppler probe had a nominal velocity range of 1.0 and 2.5 m/s, measurement volume of 7 mm³ and sampling rate of 25 Hz. The raw flow data were processed using WinADV32 (V.2.031) and MATLAB 2019 to compute mean and standard deviation velocities [m/s], and turbulent kinetic energy (TKE) [J/Kg] as a measure of turbulence in the vertical slot (Quaranta et al., 2017).

2.3 | Fish catch, maintenance and ethical approval

The same fish from the swimming performance experiments reported by Egger et al. (2020) were used in the fish behaviour observations of the present study. Electrofishing was employed to catch bullhead and gudgeon in the River Alb in Karlsruhe (Germany) in March 2019. We caught round gobies in the High Rhine in Basel, Switzerland, using minnow traps. All fish were immediately transported to the KIT, and held in six polyethylene tanks (Craemer, Germany; dimensions $91 \times 59 \times 48$ cm) with flow-through water supply. See Egger et al. (2020) for further details on the fish capture and maintenance. The swimming experiments (Section 2.8) were performed as described in Egger et al. (2020) and Wiegleb et al. (2022), then the fish were euthanised with an overdose of MS-222 and transported on ice to our laboratory in Basel, Switzerland, for preservation in formalin according to Wiegleb et al. (2020) to provide preserved fish for the force measurements. All animal experiments were approved by the Swiss cantonal authorities (permits Nr. 2934 and 2846) and the German regional authorities (permit Nr. G217_17-IWG).

2.4 | Force measurement probe

The force probe consisted of a water-resistant (IP 68) 3D-Force/ Torque sensor (Nano17, ®ATI) within an outer PVC-U hull that protected the sensor against lateral flow. The sensor was installed at the lower end of the probe (Figure 1c), which enabled us to position the force sensor close to the fish. The length of the fixation stick that transduced the forces experienced by the preserved fish to the sensor was 10 cm. A detailed description of the probe is provided in Wiegleb et al. (2022).

The 3D-force measuring probe was mounted on the same electric carriage from the flow measurements (Isel; Figure 1), which was programmed to drive a pattern of 15 measurement points one-byone in the vertical slot (Figure 2; red points). To maintain comparability, the force and flow measurements were measured at the same positions.

As soon as the probe was positioned over a measurement point, we started the measurements manually to record forces and torque in the x-, y- and z-axes simultaneously at a frequency of 1000 Hz over a period of 60s, then manually stopped the measurements and proceeded to the next measurement point.

The preserved fish connected to the sensor mimicked the body postures of fish swimming upstream (straight body posture and pectoral fins attached to the body) and were positioned as close as possible to the channel bottom, ensuring there was no physical contact between the fish and the channel bottom (ca. 2 cm). Physical contact with the channel bottom would induce uncontrolled friction and thereby impact the force measurements. Egger et al. (2020) previously assessed the swimming performance of round goby, gudgeon and bullhead, and observed the fish predominantly swam slightly above channel bottom; hence, we secured the preserved fish at the same distance from the channel bottom during the force measurements in the present study. Further discussion on the force measurements approach is provided in Appendix S1.

2.5 | Measurement of the forces experienced by fish: Experimental run procedure

The preserved fish were perforated in the dorsoventral direction in their assumed centre of gravity, as previously described by Wiegleb et al. (2020) and Sagnes et al. (2000), and fixed on the fixation stick between two nuts (one dorsal and one ventral). We adjusted the fish to an angle of 110° relative to the partition walls (Figure 5d) to approximate the orientation of the fish to the predominant direction of

flow in the vertical slot flow field. We maintained this angle for every measurement point to ensure comparability between the forces experienced at the different measurement points. A wire clamp (ca. 1 cm long) piercing the fish at both sides of the spine was fixed to the fixation stick to prevent lateral rotation of the fish around the *z*-axis.

At the beginning of every experimental run, we reset the offset of the sensor to avoid influence of drift over time at zero water velocity (in a plastic barrel) 10 cm above the actual measurement height (due to the barrel bottom). Because the sensor was reset before measuring every fish, individual vertical bouncy forces were equalised. As a quality control and to determine the forces induced by the fixation stick, we performed a reference run without fish and measured the forces at the 15 measurement positions. The hydraulic forces were measured for every species at 130L/s (n = 7) and 80L/s (n = 5) to compare the forces experienced at different water discharge rates (Table 1).

2.6 | Processing of the raw force data

As the fish were connected to the sensor via a 0.1 m fixation stick (L), we computed the force [N] acting on the fish and the stick (F) from the torque detected by the sensor (M):

$$F = \frac{M}{L}$$

To compare the vectoral size of the forces experienced by the fish, we computed the strength [N] and the direction [°] of the force vectors (F) experienced per time step (n = 60,000 per fish and measurement point) from the three force components detected by the sensor (x-, y- and z-axes) using the Pythagorean theorem (see Wiegleb et al., 2022). These 3D-force vectors represent the forces experienced by the fish at a corresponding time point. The mean 3D-force vectors across the measurement period of 60seconds were then used to compare the forces experienced by preserved fish at the same measurement points at different water discharge rates. In addition, the mean 3D forces were used to test for significant differences in the forces experienced among species. To compare the direction of planar forces (plane

TABLE 1 Mean and standard deviation (SD) of total length (T_L), wet weight (W_W), and sample sizes (*n*) of the fish used for the force measurements at 130 and 80L/s water discharge.

	Mean T _L [cm]	SD T _L [cm]	Mean W _w [g]	SD W _w [g]	n		
130L/s water discharge							
Round goby	10.58	1.08	14.74	5.34	7		
Gudgeon	10.03	0.88	6.44	1.92	7		
Bullhead	8.94	1.16	7.76	2.90	7		
80L/s water discharge							
Round goby	10.98	1.30	17.68	7.06	5		
Gudgeon	12.42	0.77	12.48	2.36	5		
Bullhead	9.64	1.00	9.41	3.14	5		

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2.7 | Live fish passage

To investigate whether a relationship exists between the forces experienced by the fish and their actual passage success, we recorded live fish moving across the vertical slot over time using a video camera. The fish were initially released downstream of the vertical slot at the beginning of the experiment and were free to move through the vertical slot for 2h, unaffected by the presence of humans. Each species was tested separately in groups of 39-45 live fish per experiment (Appendix S2). The mean and standard deviation (SD) of total fish length (T₁) was 10.43 cm ± 1.28 for round goby, 11.46 cm ± 1.13 for gudgeon and 9.91 cm ± 1.22 for bullhead. A Security-Center IR CCTV-Camera (380 TV lines, IP 68, Abus) was positioned above the vertical slot to film the fish passage behaviour during the experiment. We tested every species three times at 130L/s as this water discharge rate was assumed to be representative of real fish passes (Bombač et al., 2017), and once at 80L/s. After the experiment, we viewed the videos and determined how many fish approached the vertical slot from downstream and left the camera view in upstream direction (passage) and how many fish approached the vertical slot from downstream and left the camera view in downstream direction again (approach).

2.8 | Software and statistics

The statistical analyses were performed in R v.4.0.2 using the "stats" package. Mean flow velocities and TKE measured at the 19 measurement points were compared between the different water discharge rates using pairwise *t*-tests. Non-normally distributed data (based on the Shapiro–Wilk test) were compared using pairwise Wilcoxon tests.

To assess the differences in the 3D forces experienced in the vertical slot, we first confirmed that the force data were normally distributed (Shapiro–Wilk test). We then examined the significance of the differences among species using one-way repeated measures ANOVA to account for repeated measurements of the fish at the 15 measurement points. We compared the groups using pairwise *t*-tests to identify whether the forces experienced at the different measurement points in the vertical slot differed among species. The Bonferroni correction was used to correct for alpha error cumulation in multiple comparisons.

Spearman's linear regression was used to test whether there was a linear relationship between water velocity and hydraulic forces measured at the different measurement points. Spearman's linear regression was also applied to test whether there was a linear relationship between the water velocity and TKE measured at the different measurement points. WILEY- FRESHWATER FISH

The lift forces experienced by the fish at the different measurement points in the vertical slot fish pass were compared using repeated measures ANOVA for the vertical force component (z-axis). Pairwise t-tests with the Bonferroni correction were applied for pairwise comparisons. The force vectors were computed in MATLAB (R2019b).

The numbers of observed "passage" and "approach" events per species and water discharge were used to compute the passage probability as the proportion [%] of "passage" per total number of events observed (sum of "passage" and "approach").

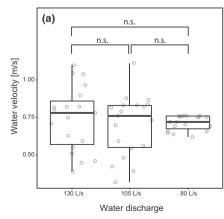
RESULTS 3

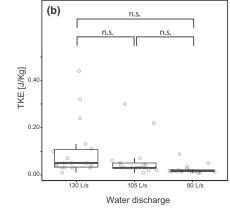
Flow in the vertical slot 3.1

Our experiments revealed that the water velocity was higher in the centre of the slot than at the location close to the side wall across all water discharges investigated (Table 2). In contrast, the TKE was generally higher at the side wall than in the centre of the slot: at 130L/s, the velocity was on average 7.22% faster in the centre (g9) than the vicinity of the side wall. At 105 L/s, the water velocity was 5.06% higher in the centre than at the side wall. Similarly, the velocity was 5.55% higher in the centre than the side wall at 80L/s. In

TABLE 2 Water velocity and turbulent kinetic energy (TKE) at two measurement points laying between the partition walls of the slot in the area that has to be passed by every fish that swims upstream of the slot. One point was in the central position between both partition walls (g9) and one point was next to a side wall (h9).

Water discharge [L/s]		Centre (point g9)	Partition wall (point h9)
130	Water velocity [m/s]:	1.04	0.97
130	TKE [J/Kg]:	0.073	0.052
105	Water velocity [m/s]:	0.83	0.79
105	TKE [J/Kg]:	0.030	0.043
80	Water velocity [m/s]:	0.76	0.72
80	TKE [J/Kg]:	0.013	0.017





contrast to the tendency for higher water velocity in the centre of the slot, the turbulent kinetic energy (TKE) was 40.38% higher close to the side wall than the centre at 130L/s, 43.33% higher at point h9 than point g9 at 105 L/s and 30.77% higher at point h9 than point g9 at 80L/s.

The overall flow field assessed in the vicinity of the vertical slot showed similar mean flow velocities and similar mean TKE across all water discharges, as indicated by the absence of any significant differences in the mean water velocity among water discharges (Figure 3, Table 3) (see Appendix S3 for the mean water velocity and TKE measured at the different measurement points and the different water discharges). Indeed, the SD was smaller at 80L/s compared to the other water discharge rates (see the sample distributions in Figure 3), which suggests that although the mean velocity was not significantly different among water discharges, the velocity was more homogenous across the measurement points at the lower water discharge (80L/s), while the velocity gradient increased among measurement positions at 105 L/s (Appendix S4) and 130 L/s (Figure 2, Table 3). This led to higher flow velocities in the central area of the vertical slot at 130 and 105L/s, whereas the velocity decreased at the outer measurement points (e.g. 3, 4, d6 and d7) at these water discharge rates.

TKE was highest close to the side walls, with a shift observed between 130L/s and 80L/s; the highest TKE was observed at point h8 (1.061 J/kg) at 130 L/s and point h4 (0.088 J/kg) at 80 L/s.

Linear regression did not reveal strong correlation between the water velocity and TKE at 130 L/s (r = .37, p = .099; Appendix S5C) or 80L/s (r = -.36, p = .104; Appendix S5F). This suggests that the flow conditions varied among the measurement points in the vicinity of the vertical slot.

3.2 3D forces experienced by preserved fish in the vertical slot

At 130L/s water discharge, we observed significantly different mean 3D forces among species in the vertical slot: gudgeon $(0.27 \,\text{N} \pm 0.12$ SD) experienced significantly lower mean 3D forces than round goby $(0.32N \pm 0.12 \text{ SD})$ and bullhead $(0.35N \pm 0.14)$ (Figure 4) (see

> FIGURE 3 Water velocity (a) and turbulent kinetic energy (TKE) (b) measured by an acoustic Doppler velocimeter at different measurement points close to the vertical slot in the fish pass model. We did not observe any significant differences (all p > .05; n.s.) between the different water discharge rates. Three outliers (130 L/s: 1.06 J/kg; 105 L/s: 1.52 and 0.53 J/kg) lie outside the ordinate range in B.

Appendix S6 for data of the mean vertical force, mean 3D force and corresponding SD per fish individual, water discharge and measurement position). Larger forces were detected for the reference measurement (the force experienced by the stick only, without fish) than the measurements with fish at 130 L/s (0.41N±0.31 SD), with the largest forces detected at the central locations near the slot (e.g. f6, f7, f8, g6, g7 and g8).

TABLE 3 Mean water velocity and mean turbulent kinetic energy (TKE) with standard deviation (SD) across all measurement points near the vertical slot for the tested water discharges.

Water discharge [L/s]	Water velocity [m/s]	SD water velocity [m/s]	TKE [J/ kg]	SD TKE [J/kg]
130	0.74	0.21	0.151	0.248
105	0.70	0.20	0.163	0.353
80	0.71	0.05	0.022	0.029

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At 80L/s water discharge, bullhead experienced significantly smaller forces ($0.11N\pm0.05$) than round goby ($0.13N\pm0.05$) and gudgeon ($0.13N\pm0.06$) (Figure 4). There were no significant differences between the forces experienced by round goby and gudgeon at 80L/s. The lowest mean 3D force across all treatments and water discharges was detected for the reference at 80L/s ($0.05N\pm0.00$ SD).

The largest change in the mean 3D forces among water discharges was observed for the reference (87.8% reduction at the 80L/s water discharge compared to 130L/s), followed by bullhead (68.6% reduction) and round goby (59.4% reduction). With 51.9% reduction of the mean 3D force at the 80L/s water discharge compared to 130L/s, the smallest difference of the mean 3D force between water discharges was observed for gudgeon (see Appendix S7 for a direct visual comparison of the 3D forces experienced by the fish at the different water discharges).

Comparison of the forces and water velocities measured at the same points revealed not only considerable variation but also significant positive linear correlations between the forces and water

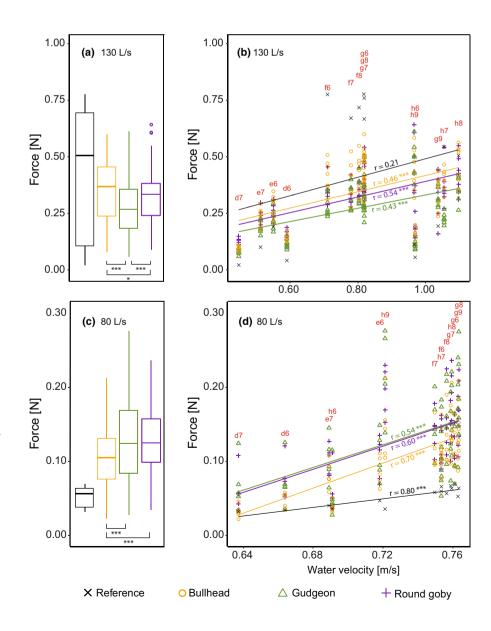


FIGURE 4 3D forces experienced by the fish at 130L/s (a) and 80L/s water discharge (c). Significant differences between species are marked by asterisks (*: *p* < .10; **: *p* < .05; ***: *p* < .01). Correlation of the 3D forces on the water velocity at the different measurement points at 130 L/s (b) and 80 L/s (d). We tested seven fish per species at 130L/s and five fish per species at 80L/s. The black reference markers represent the force measurements recorded for the fixation stick without a fish attached. The asterisks next to the correlation coefficients represent the significance level of the correlations (*: p < .10; **: *p* < .05; ***: *p* < .01).

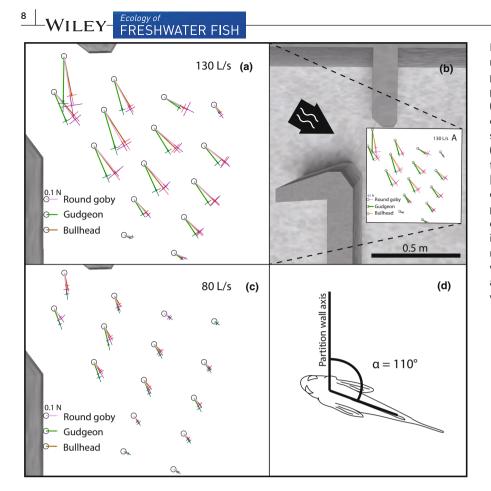


FIGURE 5 Direction and length of mean force vectors experienced by preserved fish at different measurement points close to the vertical slot at 130L/s (a) and 80 L/s (c). The error bars at the end of the vector arrows represent the standard deviation of the vector length (in Newton [N], in direction of the mean force vector) and direction (in degrees [°], represented by the bars in orthogonal direction to the mean force vector). The position of the measurement points (black circles) in the vertical slot fish pass model is indicated in (b) with the flow direction represented by the black arrow. The fish were oriented to the measurement probe at an angle of 110° (α) to the partition walls (d).

velocities for every species and at both water discharge rates tested (Figure 4). This reveals that the fish experienced larger forces at positions with higher water velocities, and smaller forces at locations with lower velocities.

3.3 | Planar forces (x- and y-direction) experienced by the preserved fish above the channel bottom

We observed the fish were predominantly pressed to the left side (from the perspective of the fish) in the vicinity of the vertical slot (Appendix S8). This left-side tendency was highest for gudgeon at both water discharge rates (mean \pm SD angle: 163.15° \pm 18.05 at 130L/s and 164.78° \pm 21.00 at 80L/s), while the angles were similar for round goby (179.09° \pm 19.49 at 130L/s and 168.34° \pm 21.65 SD at 80L/s) and bullhead (174.16° \pm 16.18 at 130L/s and 172.02° \pm 16.20 at 80L/s; Figure 5).

3.4 | Lift forces

The lift forces (vertical force component) differed significantly among all species at 130L/s. Compared to the reference (mean lift force: $-0.09 N \pm 0.06 \text{ SD}$), gudgeon experienced positive lift forces ($-0.04 N \pm 0.07 \text{ SD}$), whereas bullhead experienced negative lift forces ($-0.20 N \pm 0.10 \text{ SD}$) at 130L/s (Figure 6) (Appendix S6). The

lift forces experienced by round goby ($-0.12 N \pm 0.09 SD$) were similar to the reference. Similarly, at 80L/s water discharge, gudgeon experienced significantly higher lift forces ($-0.03 N \pm 0.03 SD$) compared to round goby ($-0.07 N \pm 0.05 SD$) and bullhead ($-0.06 \pm 0.03 SD$) (Figure 6). The reference lift force at 80L/s water discharge was $-0.05 N \pm 0.01 SD$.

3.5 | Live fish passage through the vertical slot

The probability that a fish passed if it approached the slot (passage probability) decreased by 28.26% in round goby and 39.29% by bullhead at the higher water discharge (130L/s), when the fish experienced larger hydraulic forces compared to the lower water discharge (80L/s) (Figure 7). Gudgeon displayed the largest mean number of passages (2.33 ± 6.66 SD) among all species at 130L/s, but had the lowest passage probability among all species at 130L/s ($8.38\% \pm 1.71$ SD). The low mean passage probability of gudgeon at 130L/s was found to result from the high number of both passage (mean 28.33 passages ± 6.67) and approach (mean 306.00 ± 25.71 SD) (Figure 7.) It was not possible to compute a passage probability for gudgeon at 80L/s because neither approaches nor passages were observed for gudgeon at this water discharge.

The largest number of passages was observed for round goby at 80L/s (72 passages). Bullhead showed 18 passages across the vertical slot. At 130L/s, gudgeon showed the largest number of passages

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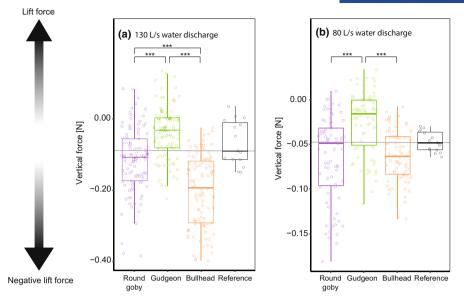


FIGURE 6 Vertical forces (lift force) experienced by preserved fish (n = 7 fish per species at 130L/s and n = 5 fish at 80L/s) at 15 measurement points close to the vertical slot. Please notice the differing ordinate scale on both graphs. The sensor was reset at zero velocity at nearly the measurement depth to equalise bouncy between fish individuals. Significant differences between species are marked with asterisks (***: p < .01). The reference median was slightly smaller than point zero of the force sensor scale (ordinate), which is presumably the result of pressure variation over the measurement points. Therefore, the forces experienced by the fish should be compared to the reference (i.e. the measurements without fish) when discriminating between lift and negative lift forces.

at 130L/s (mean of the three runs performed at 130L/s: 28.33 ± 6.66 SD) compared to round goby (mean 22.33 ± 3.21 SD) and bullhead (mean 11.00 ± 6.56 SD). The largest number of approaches was observed for gudgeon at 130L/s (mean 306.00 ± 25.71 SD), while round goby showed mean 63.00 ± 34.39 SD approaches and bullhead approached the vertical slot the least (mean 33.00 ± 4.58 SD). At 80L/s, the largest number of approaches observed for round goby (61 approaches) with 10 approaches observed for bullhead and no approaches observed for gudgeon.

4 | DISCUSSION

4.1 | The hydraulic burdens experienced by the three species: Filling the research gap

Application of our three-step approach enabled a detailed and species-oriented description of the flow field that benthic fish species encounter when swimming upstream through a vertical slot fish pass. Similar to Wiegleb et al. (2022), we found the forces experienced by the preserved fish differed significantly among the three species and increased with the water discharge rate. Variation in body shape was reported to determine the passage success of fish in fish passes (Castro-Santos et al., 2009) and swimming performance of fish depends on their body shape (Ohlberger et al., 2006; Rubio-Gracia et al., 2020; Sagnes & Statzner, 2009). Considering that fish migration through fish passes is hydraulically mediated (Goodwin et al., 2014), it is likely that the increased hydraulic forces at higher water discharge contributed to the reduced passage probability in round goby and bullhead. Gudgeon behaved differently and showed increased passages and approaches at the higher water discharges, which highlights that fish can respond differently to the hydraulic burden experienced. As the flow conditions and hydraulic forces varied spatially in the vertical slot, it is likely that the fish were able to choose routes whose hydraulic conditions better matched the individual swimming style of the fish. Overall, our results show that besides the hydraulic forces experienced, further factors, such as the individual species' behaviour, are likely involved in determining fish passage.

4.2 | How do the fish experience the flow? Hydraulic forces as a species-oriented measure of the flow field

Numerous parameters affect the swimming behaviour of fish (Cano-Barbacil et al., 2020; Lothian & Lucas, 2021). Besides boldness, exploration or activity (Lothian & Lucas, 2021), such factors as fish condition, temperature or seasonality could affect the migration behaviour of fish. Nevertheless, the usability of the hydraulic characteristics of the flow field determines the effectiveness of the fish pass for the corresponding species (Katopodis & Williams, 2012). Measuring the effect of the flow on the fish body directly can help to understand how the fish actually perceive the flow. This concept was implemented in several studies that aimed to perceive the flow field from the perspective of the fish via artificial lateral line systems (Chambers et al., 2014; Fuentes-Pérez et al., 2015; Venturelli et al., 2012). Such probes are commonly designed using simplified

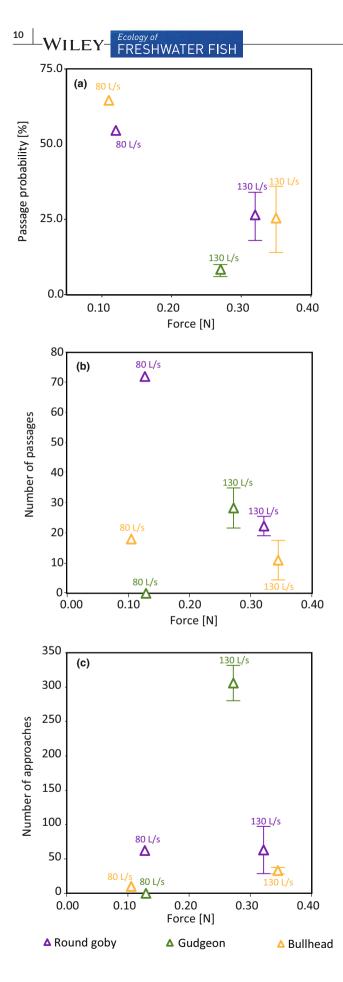


FIGURE 7 Correlation of fish passage probability (a), numbers of passages (b) and numbers of approaches (c) measured at two water discharges [L/s] and the mean hydraulic forces experienced by the three fish species. Error bars indicate the standard deviation for the 130L/s water discharge, where three experimental runs per species were performed.

shapes of fish and do not account for the individual morphological characteristics of specific species. Variations in the morphology of fish have been shown to be directly related to swimming costs (Ohlberger et al., 2006), and several studies reported morphological adaptations in fish from riverine habitats (Dashinov et al., 2020; Franssen et al., 2013; Imre, 2002; Meyers & Belk, 2014). Thus, the force measurements accounted for the individual body shapes and provided a species-oriented assessment of the flow field near a vertical slot. Because of the independence from live fish behaviour, the force measurements can be used to assess flow fields that would be avoided by live fish.

4.3 | Hydraulic forces and their relevance to fish swimming behaviour

To the best of our knowledge, this study provides the first measurements of the hydraulic forces experienced by preserved fish in a realistic environment that replicates the conditions fish encounter in vertical slot fish passes. Indeed, measurements of hydraulic forces do not account for the general swimming behaviour of live fish, which depends on the individual species biology (Blake, 2004; Coombs et al., 2007; Sfakiotakis et al., 1999). For instance, round goby and bullhead have been described to perform predominantly burst-and-hold swimming styles with an increased capability of station holding compared to gudgeon (Egger et al., 2020). When station holding, benthic fish can escape the flow using sheltering regions in the bottom substratum and support station holding by pressing their body onto the channel bottom using specific pectoral fin postures (Carlson & Lauder, 2011). This station holding behaviour was not accounted for in our force measurements because it was important to avoid friction with the channel bottom while measuring the forces. Indeed, we observed stronger 3D forces and negative lift forces for bullhead compared to the other species at the highest water discharge. It is possible that these negative lift forces supported station holding for bullhead (Egger et al., 2020), which might facilitate passage of bullhead at higher water discharge rates.

Compared to bullhead, remarkably more passages were observed for round goby at the lower water discharge. This high number of passages corresponds to studies describing a general upstream tendency for round goby (Tierney et al., 2011), which was indeed only observed for the 80L/s water discharge in the present study. Nevertheless, the passage probability of round goby at 80L/s water discharge was smaller than for bullhead together with a larger number of round goby approaches at 80L/s. Because the round goby vertical forces were similar to the hydraulic forces measured without fish (reference measurement), it is possible that contrary to bullhead, round goby may not profit from vertical forces pressing the fish to the bottom at higher water discharge. This disadvantage for round goby compared to bullhead may have led to reduced passage numbers, while the number of approaches remained similar.

Nevertheless, while bullhead may profit from negative lift forces, the opposite could be the case for gudgeon: increased lift forces at higher water discharge may support their continuous subcarangiform swimming mode above the channel bottom (Egger et al., 2020). Gudgeon is reported to exhibit good swimming performance, as revealed by high U_{crit} values (Tudorache et al., 2008). In direct comparison among the three fish species, Egger et al. (2020) reported that gudgeon can swim faster than round goby or bullhead.

Fish morphology contributes to the net swimming costs (Ohlberger et al., 2006). It is possible that gudgeon experienced reduced hydraulic forces because of a more streamlined body shape, which may provide an energetic advantage compared to the other species. Considering that the physiology among species might be different, this potential hydraulic advantage of gudgeon may explain the higher frequency of gudgeon passages across the vertical slot at higher water discharge, compared to the other species tested.

Besides the general individual swimming styles, Wiegleb et al. (2022) found distinct swimming patterns among the species when overcoming a prototype hydraulic barrier. This finding supports that the fish have individual ways they encounter the flow behaviourally, as reported by Williams et al. (2012). Similar to the present study, Wiegleb et al. (2022) detected significantly smaller hydraulic forces experienced by gudgeon at 130L/s water discharge. These similar results between two measurements at different flow fields (Wiegleb et al., 2022 tested an extended, homogenised flow field) suggest that the detected hydraulic advantage of gudgeon compared to the other species is stable across flow conditions. While it is likely that the fish respond behaviourally to the experienced hydraulic forces in the flow and choose their favoured paths, it is questionable whether the hydraulic forces will enable an assessment of the flow field usability for the fish on a small scale and may enable the prediction of swimming trajectories based on the individual species response on the hydraulic forces in the future. Such an approach would require an assessment of the forces with higher spatial resolution (more measurement points) in combination with high-quality video records of live fish.

Force measurements might be one of the most direct measures to assess the impact of local turbulence on the fish body. Turbulence has been reported to have an important impact on the swimming performance of fish (Lupandin, 2005) and can positively, as well as negatively, impact swimming performance (Beal et al., 2006; Facey & Grossman, 1992). Eddies of similar diameter as fish length can destabilise the fish, which can lead to destabilisation and uncontrolled downstream translocation (Lupandin, 2005; Tritico & Cotel, 2010). The presence of turbulent eddies in the vicinity of fish is reported to affect habitat selection, station holding, migration and the ability to maintain posture in flow (Tritico & Cotel, 2010). Detecting larger

Ecology of FRESHWATER FISH -WILEY eddies of a size that can impact the stability of the fish might not have been possible with the acoustic Doppler because of the measurement volume, which was remarkably smaller than the size of the fish (Wiegleb et al., 2022), while the force measurement was sensitive for flow conditions with higher physical impact on the fish, such as eddies of corresponding size. Following Tritico and Cotel (2010), these were the eddies that led to most of the fish destabilisations in turbulent water. We, therefore, assume that the force measurements are sensitive to flow conditions with increased physical im-

4.4 Evaluation of the force measurement approach

pact on the fish body.

Our results show that measurements of the hydraulic forces acting on preserved fish bodies provide a more species-oriented measure of the flow field than conventional flow measurements to assess the flow field suitability for specific target species. While acoustic Doppler measurements indicated similar mean water velocities at different water discharges, the differences in the forces across different species highlight the discrepancy between unified flow conditions and the actual hydraulic burden at the species level. In addition to the forces acting on the fish in three directions (x-, y- and z-axes), we were able to compute the strength and directions of the 3D forces over the measurement period, and thereby provide a basic description of the physical burden the fish encounter during passage. In addition, the force measurements were generated using preserved fish and are thus independent of various biological factors that influence swimming, such as adaptation to the test facility, feeding, parasite load, fatigue, personality and motivation. Furthermore, it is possible to assess the forces acting on bodies that are specifically tailored to the specific research question (e.g. whether it is possible to adapt fish body shapes using 3D-printing technology; Quicazan-Rubio et al., 2019). We showed that it is possible to assess a flow field independently from live fish swimming behaviour and to estimate the passage probability of specific species. Indeed, differences in the behaviour response to increased hydraulic burden at higher water discharge among species highlight that further research is needed to understand how species deal with the individual hydraulic burden behaviourally.

The force measurements of our study can be seen more as a tool to describe the flow field suitability for general passage than as a method to describe the detailed swimming behaviour of the fish, such as swimming trajectories. The forces measured in the present study are assumed to deviate from the actual forces live fish encounter when swimming upstream through the vertical slot because of various factors. Live fish are able to choose the time of their passage attempt and can thereby wait for favourable conditions and choose routes of their choice. In addition, it may not be possible to measure the direct forces experienced by live and swimming fish, as reported by Drucker and Lauder (2003). Fixation of a live fish to a force sensor would cause a significant amount of pain and the fish would probably not show any natural behaviour under

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these conditions. Therefore, we decided to approximate the swimming conditions of live fish as far as possible by using preserved fish and mimicking swimming fish in the preserved body posture (Wiegleb et al., 2020). These preserved fish were fixed at static position at the measurement points for the force measurements, which increased the comparability between measurements but did not account for the effect of fish motion on the experienced forces.

Another reason why the force measurements are rather a description of the flow suitability for the fish is that the preserved fish were fixed in one standardised direction which led to the observation of increased lateral forces while a live fish might have oriented the head to the flow to reduce the drag forces experienced. In addition, the force measurements required strict avoidance of physical contact between preserved fish and channel bottom or vertical slot side walls. Such contact would have been uncontrollable and would have negatively affected the force measurement due to uncontrolled friction forces. Because of this requirement to avoid uncontrolled friction with the channel bottom, it was required to measure the forces slightly above the bottom and it is probable that the live fish were able to make use of microhabitats closer to the channel bottom and rest in the floe field (Facey & Grossman, 1992; Matthews, 1985). Thereby, the fish may have experienced lower hydraulic forces in the flow field than actually measured with the preserved fish. Indeed, when swimming upstream the vertical slot, the fish must avoid channel bottom contact and thereby leave the sheltering region at the bottom, which might approximate the fish's swimming routes to the level where the hydraulic forces were measured. Nevertheless, by measuring the hydraulic forces in standardised manner, at the same locations as the flow measurements, at the same positions among species and at positions across a defined pattern near the vertical slot, we described the flow field more species specific than it would be possible with conventional flow measurements. By maintaining equal conditions among species (e.g. similar fish size, same measurement positions and same water discharges), we established a promising approach to describe the general burdens fish encounter when challenged with flow. This approach provides the necessary reduction of complexity and deviation from nature required to detect differences across species.

We tested the size of fish that we caught, which we assumed were representative of an adult majority of the populations. Further research would be required to assess the dependency of the hydraulic forces experienced in the vertical slot flow field on fish of different sizes. Lupandin (2005) reported that fish are more affected by turbulence if the vortex size is similar to the body size. This suggests together with our finding that areas of increased TKE can change among water discharges and that preferred regions near the vertical slot may vary between size classes. Indeed, this hypothesis needs to be tested in future experiments.

4.5 | Implementation for future assessment of fish passes and future research

Force measurements have the potential to represent a refinement of the traditional approach, which is to describe the functionality

of fish passes through flow field descriptions and observations of the behaviour of live fish. Therefore, force measurements provide a new, direct way to assess the flow field created within fish passes in the context of the physical requirements of target fish species in a standardised manner. Force measurements have the potential to particularly inform the design of technical fish passes, such as vertical slot designs, as they can be used to assess a defined area of increased flow in the vertical slot that fish must pass through to migrate. For more nature-like fish passes with more diverse flow, it would be challenging to find defined areas that determine passage of fish. As the force measurements do not require live fish, they avoid live animal experiments and make the results more replicable. In addition, the force measurements provide important insights into the hydraulic burden experienced by benthic fish during passage and how these burdens differ among species. This allows quantifications of parameters (forces) that traditionally could only be gleaned from mathematical models with many untested assumptions (e.g. Drucker & Lauder, 1999; Sällström & Ukeiley, 2014). Further research is needed to understand the specialised swimming behaviour of benthic fish and the factors that determine their passage behaviour.

We can now describe one piece of the total puzzle of parameters that determine whether a fish migrates upstream of a vertical slot or not. This puzzle is strongly related to the condition that can be changed by adapting the design of fish passes: the water flow conditions. Thereby, we describe how force measurements represent a valuable measure that enables the assessment of fish pass designs for the suitability of specific target species that can be applied in the laboratory or in the field at existing systems. Future research should focus on refinement of this measurement technique and the relationships between the forces experienced in flow and the behavioural responses of live fish to these forces.

AUTHOR CONTRIBUTIONS

P.B.H. conceived the study. All authors conceptualised the research. G. R. provided the force measurement system and gave instructions in particular for the force measurements. F.S. helped with the analysis of the flow data. J. W. performed the flow and force measurements. J.W. and P.E.H. performed the live fish experiments. J.W. analysed the data, created the figures and wrote the first draft. All authors wrote and edited the manuscript. P.B.H. supervised the study and acquired funding. All authors gave final approval for publication.

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CONFLICT OF INTEREST

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

Data are available in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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