

Hydraulic burden and swimming behaviour of benthic  
fish in a vertical slot fish pass

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Dekan



*“There is time to say ‘Hello’ and ‘Good bye’.*

*And sometimes  
both are very close.”*

*for*

*Johannes 09.03.2018\*†*

*Cornelius 16.02.2019\**

*Martin 10.06.2020†*

*Julius 05.11.2020\**

*and*

*Franzi*



## Summary

The majority of the world's rivers is fragmented and fish passes are frequently installed to enable fish passage across river obstacles. Beside native, also invasive species, such as round goby, can use fish passes to disperse upstream in uninvaded ecosystems. The present study aimed at evaluating a prototype hydraulic barrier in a vertical slot fish pass that impedes passage of the invasive round goby and enables passage of native, comparable species, such as gudgeon and bullhead. In addition, the study was designed to provide basic insight in the differences between the hydraulic forces experienced by the fish species in the flow and their individual behavioural response to different flow conditions.

The barrier was designed to homogenize the flow field over an extended distance to exceed the swimming capability of the round goby and impede resting by station holding due to the smooth bottom. The selective effect was created by the flow field that induced hydraulic burden, varying between species due to the individual body shapes of the fish.

The performance of the hydraulic barrier was assessed using a three step-approach: Flow measurements (Step 1), measurements of the hydraulic forces experienced by preserved fish (Step 2) and live fish swimming behaviour observations in the same flow field (Step 3). This approach was applied in a flow channel study under homogenised flow conditions and in a nearly full-scale vertical slot fish pass model. The purpose of this approach was to evaluate the prototype hydraulic barrier (i), create basic evidence about how flow affects the fish species individually and whether the hydraulic burden experienced in the flow field differ between species (ii), and to assess how the hydraulic burden experienced by benthic fish affect the passage behaviour across the prototype hydraulic barrier and at an unaffected vertical slot (iii).

The results showed: There was a species selective effect of the prototype hydraulic barrier. No round goby passed the barrier at the highest water discharge tested (130 L/s), while six gudgeon passed the barrier and four bullhead attempted passage but immediately returned. This passage behaviour agreed with the hydraulic forces measured as gudgeon experienced significantly lower forces at 130 L/s water discharge compared to the other species. Because the hydraulic forces differed between species and corresponded to the live fish swimming behaviour, and the live fish passage behaviour differed between water discharges, it is probable that the selective effect of the barrier was mediated by the created flow field. Beside this selective effect, the prototype barrier had a general impact on the fish migration behaviour. There were significantly less passages recorded at the prototype hydraulic barrier compared to the downstream untreated slot.

The fish indeed experience hydraulic burden differing between species and these hydraulic burden correspond to the individual swimming styles of the corresponding species. The fish respond to these hydraulic burden individually, depending on their own species biology. Nevertheless, there was a general adaptation of the passage behaviour to increased water discharge: All species swam faster with more speed variation and with straighter paths upstream the barrier.

With providing basic evidence about the individual hydraulic burden an invasive species experiences in comparison to two native, comparable species, this thesis is a further step towards species selective fragmentation of rivers for ecosystem conservation purposes. These findings open an avenue to fish pass design adapted to the fish community of specific ecosystems and will inform fish pass engineers, decision makers and researchers who work about the behavioural response of fish to flowing water.

## Zusammenfassung

Die Mehrzahl der Flüsse auf der Erde sind fragmentiert. Um Fischen die Wanderung stromauf zu ermöglichen, werden häufig Fischpässe an Wanderhindernissen eingesetzt. Neben einheimischen Arten wandern ebenfalls invasive Arten, wie etwa die Schwarzmundgrundel, diese Fischpässe hinauf und bedrohen stromauf gelegene Ökosysteme. Die vorliegende Arbeit beschreibt einen Prototypen einer hydraulischen, selektiven Sperre für den Einsatz in 'Vertical slot' Fischpässen. Diese Sperre soll den Aufstieg der invasiven Schwarzmundgrundel verhindern und gleichzeitig für einheimische und vergleichbare Arten, wie etwa Gründling oder Groppe, durchlässig sein. Zusätzlich soll die Studie Grundlagenwissen über die individuellen hydraulischen Hürden und die Art und Weise, wie die Fische mit Ihrem Schwimmverhalten auf die Hürden umgehen, schaffen.

Das Funktionsprinzip der Sperre ist, dass die Strömung über eine gewisse Distanz homogenisiert wird und die bodenlebenden Fische durch die glatte Oberfläche daran gehindert werden, sich am Boden festzusetzen und auszuruhen. Der selektive Effekt soll durch ein Strömungsfeld erzeugt werden, das aufgrund unterschiedlicher Körperform der Fische unterschiedliche hydraulische Kräfte auf die Fischkörper erzeugt. Damit erzeugt das Strömungsfeld aufgrund der individuellen Körperform der Fischarten unterschiedliche hydraulische Hürden für die Fische bei der Überwindung der Sperre.

Die Sperre wurde in einem dreistufigen Verfahren getestet: Strömungsmessungen (Stufe 1), Messungen der hydraulischen Kräfte, die die Fische in der Strömung erfahren (Stufe 2) und Beobachtungen des Schwimmverhaltens lebender Fische im selben Strömungsfeld (Stufe 3). Dieses Verfahren wurde in Vorversuchen in einem Schwimmkanal unter standardisierten Strömungsverhältnissen und in einem physischen, fast maßstabsgetreuen 'Vertical slot' Fischpass angewendet. Dabei sollte die Funktionalität der hydraulischen Sperre untersucht werden (i), Grundlagenwissen darüber geschaffen werden, wie Strömung die Fischarten unterschiedlich beeinflusst und ob die Fischarten unterschiedliche hydraulische Hürden bei der Passage der Sperre überwinden müssen (ii) und untersucht werden, wie diese hydraulischen Hürden das Schwimmverhalten der Fische unterschiedlich beeinflussen.

Die Ergebnisse zeigen: Die hydraulische Sperre hat eine artselektive Wirkung. Beim höchsten getesteten Wasserabfluss (130 L/s) passierten keine Schwarzmundgrundeln die Barriere, während sechs Gründlinge die Barriere passierten und vier Groppen eine Passage versuchten, jedoch sofort zurückkehrten. Dieses Durchgangsverhalten stimmt mit den gemessenen hydraulischen Kräften insofern überein, dass Gründlinge im Vergleich zu den anderen Arten signifikant geringere Kräfte bei 130 L/s Wasserabfluss erfahren. Da die hydraulischen Kräfte zwischen den Arten unterschiedlich sind, dem Schwimmverhalten der lebenden

Fische entsprechen und das Verhalten der lebenden Fische zwischen den Wassereinleitungen unterschiedlich ist, ist eine selektive Wirkung der Barriere durch das erzeugte Strömungsfeld sehr wahrscheinlich.

Neben diesem selektiven Effekt hatte die Barriere einen generellen Einfluss auf das Fischaufstiegsverhalten. An der hydraulischen Sperre wurden im Vergleich zum stromabwärts gelegenen, unbehandelten Schlitz, deutlich weniger Passagen der Fische aufgezeichnet.

Tatsächlich erfahren die Fische je nach Art unterschiedliche hydraulische Belastungen in der Strömung. Auf diese hydraulische Belastung reagieren die Fische individuell, entsprechend ihrer eigenen Artbiologie. Es wurde allerdings auch eine generelle Anpassung des Schwimmverhaltens an stärkere Strömung bei allen Arten beobachtet: Alle Arten schwammen schneller mit mehr Geschwindigkeitsvariation und mit geraderen Wegen die hydraulische Sperre hinauf.

Diese grundlagenwissenschaftlichen Erkenntnisse über die hydraulischen Hürden in Fischpässen einer invasiven Art im Vergleich zu zwei einheimischen, vergleichbaren Arten, sind ein wichtiger Schritt Richtung artselektive Fragmentierung von Flüssen zum Schutz des Ökosystems.

Diese Thesis bietet Grundlagen für die Gestaltung von Fischaufstiegshilfen, die an die Anforderungen des Ökosystems angepasst sind. Damit hat sie Relevanz für Fischpass-Entwickler, Entscheidungsträger und Wissenschaftler, die über das Verhalten von Fischen in der Strömung forschen.

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## List of papers

- Paper I:** Wiegleb, J., Hirsch, P. E., Egger, B., Seidel, F., & Burkhardt-Holm, P. (2020). Flow field-induced drag forces and swimming behavior of three benthic fish species. *Limnologica*, 84, 125812. <https://doi.org/10.1016/j.limno.2020.125812>
- Paper II:** Egger, B., Wiegleb, J., Seidel, F., Burkhardt-Holm, P., & Hirsch, P. E. (2020). 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*). *Ecology of Freshwater Fish*, 30 (3), 391-405. <https://doi.org/10.1111/eff.12592>
- Paper III:** Wiegleb, J., Hirsch, P. E., Seidel, F., Rauter, G., & Burkhardt-Holm, P. (2021). Flow, force, behaviour: Assessment of a prototype hydraulic barrier for invasive fish. *Hydrobiologia*, accepted.
- Paper IV:** Wiegleb, J., Hirsch, P. E., Seidel, F., Rauter, G., & Burkhardt-Holm, P. (2022). Against the stream: Hydraulic forces and passage behaviour of benthic fish in a vertical slot fish pass. Submittable manuscript.

## Prologue

At the beginning was a fish in my hand. It was a cloudy day at the time when I went to school. I was a passionate angler and loved to fish some great barbels and eels in the lower Rhine near Cologne. I spent numerous hours there, rather than learning for my school exams and it was just a great time. Then came the day when I held this fish in my hand. I caught it in the Rhine some seconds ago and I just wondered. It was a small fish, about 10 cm long, which looked a bit curious. It was hard to identify the species but with my unexperienced view, I identified this fish as a European bullhead. Knowing that bullheads prefer rivers with good water quality, I was very happy, solved the fish from the hook carefully and released it into the river. Indeed, happiness did not stay long. It were only seconds and the small bell on the top of my rod rang again and I caught the next 'bullhead'. This continued until the evening and I packed my stuff and went home. The fishing day was very disappointing because I caught numerous small 'bullheads' but not a single big and strong barbel. At this time, I did not guess that this day would have important impact on my future.

The time of good fishing at the river Rhine was over and I never caught a great barbel again. I still spent years fishing for barbels at the Rhine, but the only fish I caught was this small fish that looked like a bullhead. However, I knew from fishing magazines that it was an invasive species, called round goby. There was hope it might disappear someday, but the round goby stayed.

I finished school, studied Biology in Düsseldorf, and decided to continue my studies in a Masters Program at the University of Rostock. Looking forward to many fishing opportunities in Rostock, I thought to leave the round goby behind –not knowing that round gobies had distributed in the Western Baltic Sea already and became even bigger in brackish environments. I just felt a bit tracked by the round goby but accepted the opportunity to investigate predation of the round goby on Atlantic herring eggs in my Master thesis, which I performed at the Thünen-Institute for Baltic Sea fisheries. Fortunately, this thesis opened the door to Basel for investigating methods to impede the upstream migration of the round goby via active swimming.

This story reports my inner motivation for the following thesis. This story and my personal experience taught me one thing: Every catastrophe provides a chance. It is up to us what we make out of it.

During the work at my dissertation, I experienced two more catastrophes with such a force, that years were required to recognize the chance provided. Shortly after the beginning of my research project, my wife and I said goodbye to our first born son, who died late in pregnancy before giving birth for unknown reasons. About two years later, my younger brother passed away by suicide. After these events, my research project

became least important of everything and it took a lot of mental strength to just keep going. However, much power was provided by my wonderful wife and my fantastic kids. Both living kids were born during my dissertation project. Now, when I am sitting here at my desk and write down my thesis, I can hear them playing in the living room and the chance from the experienced becomes clear to me: It is our responsibility to take care of the younger members of our community and we must provide them with all the tools and advice available to develop themselves, the society, the globe, and science.

## Introduction

### *River fragmentation and fish passage*

Rivers have undergone significant changes in the two past centuries (Habersack & Piégay, 2007). Today, the majority of the world's rivers are fragmented by anthropogenic barriers (Belletti et al., 2020). Indeed, river connectivity has been reported to be important for fish diversity (Shao et al., 2019), which is why diverse passage constructions have been developed (Katopodis & Williams, 2012). Numerous fish pass types were developed following a trial-and-error approach, focusing predominantly on the passage of economically relevant species, such as salmonids (Katopodis & Williams, 2012; Roscoe & Hinch, 2010). Following the application of fish passes that were actually designed for salmonid species for the whole fish community, Mallen-Cooper & Brand (2007) observed a poor performance of these fish passes for native species and even an increase of non-native species. The Convention on Biological Diversity raised the need to adapt fish passes to the requirements of species of relevance for the ecosystems (United Nations, 1992). To develop fish pass structures accounting for the individual differences in swimming performance between species, a combination of research approaches from fluid dynamics, engineering and behavioural ecology is promising (Castro-Santos et al., 2012).

A modern, frequently investigated fish pass type is the vertical slot fish pass, which is commonly installed at transversal structures, such as weirs (Wu et al., 1999). Vertical slot fish passes consist of a rectangular channel with partition walls. These partition walls contain vertical openings which separate the channel into pools. The flow through these slots creates a jet with accelerated flow velocities that has to be passed by the fish migrating upstream (Wu et al., 1999). Due to its construction, vertical slot fish passes are robust against variation in water discharge and maintain steady hydraulic conditions at slots and pools (Katopodis & Williams, 2012).

### *The threat of invasive species*

Invasive species have become a world-wide threat to aquatic ecosystems (Havel et al., 2015). Designing fish passes that support specific species of importance for the ecosystem and hold back undesired species can support species selective fragmentation of the river (Rahel & McLaughlin, 2018). Selective fragmentation is a possible management option to impede the spreading of invasive species (Rahel & McLaughlin, 2018). Ensuring the passage of native species and impeding the passage of invasive species

over river obstacles is a major challenge for decision makers and requires advances in integrated interdisciplinary research (Rahel and McLaughlin, 2018).

One of the 100 worst aquatic invasive species has been reported the round goby (Hirsch et al., 2016). The round goby arrived in Switzerland 2012 (Kalchhauser et al., 2013) and continued to disperse upstream the River Rhine (Lutz et al., 2020). Beside diffusion across short distance, also long distance dispersal via active swimming (approximately 500 m per year) have been reported for round goby (Bronnenhuber et al., 2011). Because of the individual swimming style of the round goby (Tierney et al., 2011), the idea of selective hydraulic barrier seems feasible (Hoover et al., 2003), which is why the round goby swimming performance has been assessed by Tierney et al. (2011) and Hoover et al. (2003). Indeed, to create a hydraulic selective barrier for the round goby that is passable by native species, it must be understood how the round goby swimming response to the flow conditions in the barrier differ between comparable, native species.

### *Swimming in fish*

Fish are generally well adapted to move in their fluid environment (Lauder and Madden 2007). The main properties of water, especially its high density and incompressibility, have played an important role in fish evolution (Sfakiotakis et al., 1999). There are numerous ways fish create vortices in the water body to move in flowing water (Fish & Lauder, 2006; Lauder, 2015; Triantafyllou et al., 2000), which have evolved with time (Sfakiotakis et al., 1999). One specialized swimming style has been reported for benthic fish, such as the round goby: the ability to hold station at the bottom to save energy in flowing water (Gilbert et al., 2016; Tierney et al., 2011). Small body size (7-8 cm length, 1-2 cm height) facilitates station holding by escaping the flow at cobble substrates. In addition, larger pectoral fins enabled a benthic fish, darter (*Etheostoma tetrazonum* Hubbs & Black, 1940), to produce negative lift forces pressing the fish to the bottom (Carlson & Lauder, 2011).

### *Model species*

Such behaviour, to produce downwards directed forces using pectoral fins for station holding and thereby increasing the swimming capacity, has also been reported for the invasive round goby (*Neogobius melanostomus* Pallas, 1814) (Gilbert et al., 2016; Tierney et al., 2011). In addition, (Tierney et al., 2011) reported a general tendency to swim upstream of the round goby at moderate velocities, while it has been reported that the water discharge must be greater than 125 cm/s to prevent round goby upstream migration.

A similar bottom-dwelling fish species is European bullhead (*Cottus gobio* L.), which occupies a similar ecological niche as the round goby (Roje et al., 2021). Bullheads prefer creeks with higher velocities and coarse substrate (Davey et al., 2005; Van Liefferinge et al., 2005), while low swimming capacities have been reported (Tudorache et al., 2008). Indeed, bullheads profit from a similar station holding behaviour based on usage of pectoral fins to ‘anchor’ on the bottom (Tudorache et al., 2008).

Gudgeon (*Gobio gobio* L.) is another bottom-dwelling fish occurring in similar habitats like round goby and bullhead. Contrary to the round goby and bullhead, gudgeon has more a benthopelagic life style and no specialized station holding behaviour has been reported for gudgeon.

Because bullhead and gudgeon are native species of the local fish community in the River Rhine and its tributaries near Basel and the mentioned similarities in their species biology and swimming behaviour, they were selected as representatives for native fish in the present study.

### *How do fish experience the flow?*

To create a hydraulic barrier with a flow field that affects the passage behaviour of fish species differently, it is important to understand how the fish experience the flow differently. Several studies aimed at perceiving the flow field from a fish perspective –for example via artificial lateral line systems (Chambers et al., 2014; Juan Francisco Fuentes-Pérez et al., 2015; Venturelli et al., 2012). There are robots mimicking swimming fish to understand basics in fish kinematics (Thandiackal et al., 2021). Indeed, these studies are commonly based on simplified fish shapes and neglect the effect of the individual body shape of the fish on their hydraulic burden experienced. Fish morphology is directly related to swimming costs (Ohlberger, Staaks, & Hölker, 2006) and several studies showed morphological adaptation in fish from riverine habitats (Dashinov et al., 2020; Franssen et al., 2013; Imre, 2002; Meyers & Belk, 2014). It is possible that these adaptations in body shape in habitats of increased flow occurred to reduce the hydraulic forces experienced.

Mathematical models are commonly used to estimate the hydraulic forces fish bodies experience in flowing water, such as Drucker & Lauder (1999), Sällström & Ukeiley (2014), Van Wassenbergh et al. (2015). Indeed, more direct measurements at real fish would probably provide a more realistic picture of the hydraulic burden. Therefore, (Sagnes et al., 2000) implemented measurements of drag experienced by dead fish, when describing the change in hydraulic drag during ontogenesis of grayling larvae (*Thymallus thymallus* L.). Further studies applying physical force measurements focus on single species and artificial fish (Barrett et al., 1999; Quicazan-Rubio et al., 2019).

Measuring the direct forces experienced and comparing these forces between species might increase the understanding of how flow affects the fish species differently. This can be the key for understanding how flow fields can be changed to induce selective passage of specific fish species corresponding to the ecosystem requirements.

### *Objectives and hypotheses*

One purpose of this study was to provide the fundamentals for a hydraulic barrier that impedes the further upstream migration of the round goby, while maintaining passage of comparable native species, such as bullhead or gudgeon. The prototype barrier was designed and tested based on the idea of a selective, hydraulic barrier that impedes station holding by a smooth surface and homogenous flow conditions over an extended distance, exceeding the swimming performance of the round goby while native species can ascend (Hoover et al., 2003). Nevertheless, to create species selective hydraulic conditions in a fish pass, it is important to understand how the fish species experience the flow differently and how the flow affects the individual swimming behaviour of the fish.

To fill this knowledge gap, a three step-approach is implemented in the present thesis: This approach consisted of flow measurements (1. Step), force measurements on preserved fish (2. Step), and live fish swimming behaviour observations (3. Step). The direct forces experienced by preserved fish in the flow were measured as a proxy for the hydraulic burden live fish encounter when swimming against flow. The hydraulic burden fish experience was defined as the hydraulic force the fish body experiences from the flow field while passage. These hydraulic burden were then compared to live fish observations to describe how hydraulic burden mediate the live fish swimming behaviour. This was done to create evidence about how benthic fish respond behaviourally to flow and how this response differs between species.

The aim of the present thesis was to create basic evidence about how the flow affects the fish species individually and whether the hydraulic burden experienced in the flow differ between species (Paper I, III, IV):

**Hypothesis 1: The hydraulic burden the fish experience while passage differ between species.**

Further, the present thesis aimed at evaluating a prototype, hydraulic, and selective barrier that was designed to impede the passage of the invasive round goby (Paper II, III):

**Hypothesis 2: The hydrodynamics in the barrier prevent the passage of the invasive round goby while native, comparable species can ascend.**

Finally, to assess how the hydraulic burden experienced by the fish affect passage behaviour, the hydraulic burden experienced by the fish were compared with the live fish swimming behaviour (Paper I, III, IV):

**Hypothesis 3: Species with smaller hydraulic burden have increased passage capability.**

Based on the above mentioned hypotheses, four publications were created with individual research questions (Fig. 1):

## Methods

Two experiments (Fig. 1) were performed to fill the knowledge gap. The first experiment focused on the hydraulic burden and the fish behaviour of the three test species (round goby, gudgeon and bullhead) under standardized and homogenous flow conditions in a flow channel in the laboratory at the University of Basel, Switzerland. In the second experiment, the prototype hydraulic barrier, as well as the hydraulic forces, and live fish swimming behaviour of the same species, were assessed in a realistic, full-scale fish pass model (test rig) at the Karlsruher Institute for Technology. To keep both experiments as comparable as possible, the three step-approach was applied in both experiments always with the same test species (round goby, gudgeon, and bullhead). To describe the dependency of the hydraulic forces experienced by the fish and the swimming behaviour from the flow velocity, both experiments were performed for different water discharges.

After the live fish observations in both experiments, the fish were euthanized with an overdose of MS-222 and preserved in formalin. Formalin increased the stiffness of the fish and preserved their body postures in a standardized way. After three days in 4% formalin with straight body postures, the fish were transferred stepwise via 40% ethanol (24 h) and 60% ethanol (24 h) to 75% ethanol solution to reduce toxicity of the fish (Paper I). The preserved fish were then punctuated vertically at the assumed centre of gravity with a needle and connected to the fixation stick. This fixation stick held the fish at position in the flow field and transduced the force experienced to the force sensor. 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).

### *1. Flow channel study (Paper I and II)*

We used a Loligo® flow channel (swim Tunnel Respirometer, 185 L volume, 88 \* 25 \* 25 cm measuring chamber) to describe the flow, the forces and the swimming behaviour of our test species in a rectangular flume that had a shape being representative for our idea of a hydraulic barrier (homogenized flow over a smooth bottom for a distance of 88 cm) for a first quantification of flow conditions, the hydraulic forces and the swimming behaviour of live fish in a rectangular flume.

### *Flow channel study: Flow measurements*

The flow velocity was measured using an acoustic Doppler velocimeter (ADV, Nortek Vectrino®) at 36 positions in the measurement chamber and at three adjusted velocities (0.25, 0.55, and 0.85 m/s) that were considered relevant for swimming in benthic fish (Tierney et al., 2011; Tudorache et al., 2008).

### *Flow channel study: Hydraulic forces*

The hydraulic forces experienced by preserved fish were measured by a Vernier® Go Direct Force and Acceleration Sensor (GDX-100609). The near ground-drag force was measured at 45 measurement points in the measurement chamber and at 0.25, 0.55, and 0.85 m/s flow velocity. This measurement was performed for single individuals of round goby, gudgeon, and bullhead with attached fins to display the spatial distribution of the forces above the bottom in the measurement chamber. In the next step, the hydraulic forces were measured at the central position in the flow channel at different velocity steps to measure the dependency of the hydraulic force from the flow velocity. To determine the effect of the fins on the forces experienced, three fish per species with attached and three fish with completely spread fins were tested in this measurement.

### *Flow channel study: Live fish swimming behaviour*

First, prolonged swimming trials ( $U_{crit}$ ) were performed with 18 round goby, 12 gudgeon, and 12 bullhead. The single fish were released into the measurement chamber and left for 20 min in stagnant water for acclimatisation before the water flow was set to 0.15 m/s for 10 min. In the following, the flow speed was increased by 0.10 m/s every ten minutes until the fish could not hold position or showed signs of fatigue.

Afterwards, sprint speeds ( $U_{sprint}$ ) of the three species were evaluated for 18 round goby, 11 gudgeon and 12 bullhead. After 5 min acclimatisation at 0.05 m/s flow velocity, the flow was increased by 0.05 m/s every 10 s until the fish reached fatigue. Following a 10 min break in the measurement chamber with no flowing water, the experiment was repeated until the fish refused to swim or were unduly stressed. The fish were recorded during both assessments from vertical perspective by Gopro® cameras (Hero 4).

## *2. Fish pass experiment at Karlsruher Institute for Technology (Paper II, III, and IV)*

A nearly full scale test rig (1:1.6 scaled physical model of the fish pass in Koblenz, Germany) at the Theodor-Rehbock Hydraulic Laboratory at Karlsruher Institute for Technology (KIT), Germany (Fig. 1B) was used to assess the prototype hydraulic barrier and to describe the hydraulic burden experienced by preserved fish (round goby, gudgeon, and bullhead) and passage behaviour of live fish under realistic conditions. Water discharges can vary in real vertical slot fish passes, which is why three different water discharges (80, 105 and 130 L/s) were tested in the experiments. The two lower discharge rates were chosen to increase the probability of recording migration behaviour of the live fish, because they did not pose a challenge to the swimming capacities of the tested species as revealed from the flow channel study (Paper II). The 130 L/s water discharge was included in the experiment because we found this discharge led to the most representative flow velocities compared to actual best-practice vertical slot fish passes (Bombač et al., 2017). Flow measurement and live fish observations were performed at 80, 105, and 130 L/s water discharge. The force measurements were performed at 80 and 130 L/s and not at 105 L/s water discharge to increase the sample size of tested fish in the time available.

### *Fish pass experiment: Flow measurements*

The acoustic Doppler (a similar device from the flow channel study) was mounted at an electronic, programmable, carriage (Isel ®) that was first adjusted over the prototype barrier (Fig 1). This carriage positioned the flow measurement probe at predefined measurement points automatically. Flow was measured at 14 measurement points, which were equally distributed over the barrier and ca. 2 cm above the bottom. Subsequently, the electronic carriage was adjusted above the untreated slot and the flow was measured at 19 measurement points which were equally distributed in the vicinity of the slot, ca. 2 cm above the bottom.

### *Fish pass experiment: Hydraulic forces*

The hydraulic forces experienced by seven fish per species at 130 L/s water discharge and five fish per species at 80 L/s water discharge were measured using a water resistant (IP 68) force-torque sensor (Nano 17, ATI ®), which was integrated in a PVC-hull to protect the sensor from disturbing flow. The force measurement probe was adjusted at the same electronic carriage and measurements were performed at the same measurement positions from the flow measurements. Four measurement points at the untreated slot

were excluded from the force measurement because the probe design impeded positioning of the probe above these points.

Similar to the flow channel study, the fish were punctuated and connected to the fixation stick prior the carriage positioned the fish over the first measurement point. At the measurement point, the hydraulic forces in X-, Y-, and Z-direction were recorded for 60 s with a data collection frequency of 1000 Hz. After the period of 60 s, the probe with the fish was positioned over the next measurement point and the data recording was started again.

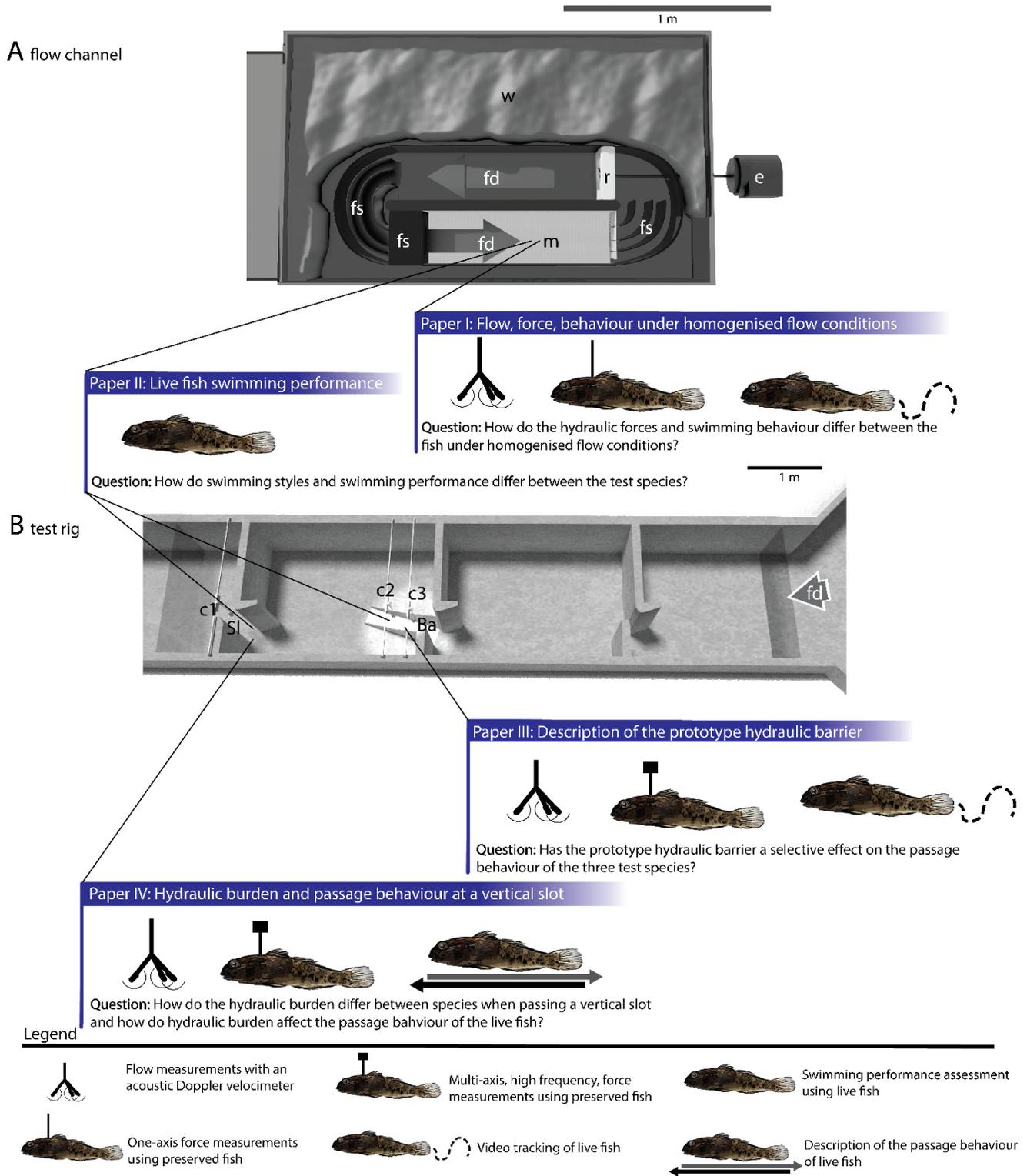
### *Fish pass experiment: Live fish swimming behaviour*

The fish were released downstream the untreated vertical slot and were able to swim freely in the test rig (Fig. 1B) unaffected by human presence for two hours to ensure the fish displayed only voluntary swimming behaviour. Because it was not clear how the fish might behave at the beginning of the experiments, the experimental period of two hours was chosen to increase the probability to observe a meaningful amount of untreated slot and barrier passages. Three cameras (Security-Center IR CCTV-Camera 380 TV-lines, IP 68, Abus ®, Germany) were installed (one above the vertical slot, two above the prototype hydraulic barrier) and recorded the fish while passage. In addition, metal grids were used to block the vertical slot and barrier after the period of 2 h to enable counting the fish that had migrated finally after this period of 2h.

The experiment was performed for three water discharges (80, 105, and 130 L/s). Because 130 L/s was assumed most representative for the conditions in real fish passes (Bombač et al., 2014), the experiment was performed for three times at this water discharge. To increase the number of fish included in the experiments and thereby the probability to record migration behaviour with the cameras, all fish (43 ±4 individuals per species) available were tested in every run. To discriminate between species in the video analysis, species were tested separately.

Following the live fish experiment, the video footage was screened by eye and the time and number of defined events (Appendix 1) was recorded in the program Blender (v. 2.79). Afterwards, the paths of the fish that displayed these events were tracked in X-, Y- coordinates. These trajectories were used to compare the swimming patterns between the species at the different water discharges and to compare the swimming behaviour with the hydraulic burden experienced.

Information about individual contributions of the articles' authors and further supporters is provided in Appendix 2.



**Figure 1:** The experiments were performed in a flow channel at the University of Basel (A) and in a nearly full-sized, physical vertical slot fish pass model at the Karlsruhe Institute for Technology (B). The flow direction is represented by grey arrows (fd). The water (w) in the flow channel was accelerated by a rotor

(r), which was powered by an electric engine (e). Flow straighteners (fs) ensured homogenised flow in the measurement chamber (m), where the measurements were performed. At the test rig, the observations focused on an untreated vertical slot (Sl) and the prototype hydraulic barrier (Ba). Three cameras (c1, c2, c3) were installed above slot and barrier for live fish observations. All experiments were performed for the three test species and at different water discharges to describe how the flow affected the fish species differently.

## Results and Discussion

### *The prototype hydraulic barrier*

The experiments revealed a species selective effect of the prototype hydraulic barrier. No invasive round goby passed the barrier at the highest water discharge tested (130 L/s), while six native gudgeon passed the barrier and four native bullhead attempted passage but immediately returned. That the selective effect was hydraulically mediated is probable because round goby has strongly changed its passage behaviour across the barrier between water discharges. Round goby was the species that passed the barrier most frequently of all tested species (18 times) at the lowest water discharge (80 L/s). In addition, round goby showed a general upstream dispersal tendency at the untreated slot downstream the barrier as indicated by 65 round gobies that passed at 130 L/s water discharge. One further observation supporting that the selective effect was hydraulically mediated was: gudgeon, the species with most passages across the barrier at 130 L/s water discharge, experienced the smallest hydraulic forces on the barrier and might therefore have experienced the lowest hydraulic burden while passage.

Beside the selective effect, the prototype barrier had a general impact on the fish migration behaviour. There were significantly less passages recorded at the prototype hydraulic barrier compared to the downstream untreated slot across all water discharges. This might be explained by the need to overcome the untreated slot prior challenging the prototype barrier in our experiment. It is possible that the fish fatigued after passage of the untreated slot and were physiologically unable to pass the barrier accordingly. However, two hours experimental time may have enabled the fish to recover from the passage of the untreated slot. In addition, the same fish were used for the different experimental runs and the fish were therefore able to assess the flow fields and learn (Kieffer & Colgan, 1992) the energetically favourable routes across barrier and slot. Indeed, that there was no clear change of the fish behaviour between the three runs performed at 130 L/s water discharge (Paper IV), suggests that adaptation and learning across the experiments played rather a minor role. Another important point is that such flow field assessment effects of the fish can, beside in our experiments, also occur in real fish passes. At a barrier installed in a real fish pass, there would also

be untreated slots that have to be overcome by the fish prior challenging the barrier. The experimental setup was as realistic as possible and the study was designed to exclusively record voluntary migration behaviour (the fish were completely unaffected by human presence for the experimental period of 2 h). Under these conditions the results showed: While having a species selective effect at 130 L/s water discharge, the barrier reduced the passage of all species at all water discharges compared to the untreated slot (Paper II).

Hoover et al. (2003) reported that a hydraulic barrier would have to maintain flow velocities greater than 0.75 m/s over an extended distance to exceed the physiological swimming endurance of the round goby. Tierney et al. (2011) mentioned flow speeds > 1.25 m/s without microhabitats, allowing the fish to recover, to be required for withholding the round goby. Our flow measurements reveal that the prototype barrier fulfilled the requirements mentioned by Hoover et al. (2003) but the flow speed was lower than the requirement suggested by (Tierney et al., 2011). The water flow velocity measured on the barrier at 130 L/s water discharge was 0.91 m/s  $\pm$  0.08 SD (Standard deviation). Thereby, the water velocity above the barrier was higher and more homogenous than at the untreated slot (mean velocity of 0.74 m/s  $\pm$  0.21 SD at 130 L/s water discharge). This reveals: The barrier created a near-homogenous jet stream (Liu, Rajaratnam, & Zhu, 2006) over the barrier length which affected the fish body differently, as indicated by force measurements. Thereby, we showed that the flow field created on the barrier primarily explains the differing live fish upstream migration behaviour, as revealed by the varied passage frequencies between untreated slot and barrier observed in the live fish observations (Paper II).

Although the prototype hydraulic barrier performed promisingly in the reported laboratory experiments, the barrier must be assessed in long term field experiments to describe its long term-ecosystem impacts. It is possible that vegetation or debris on the barrier could alter the hydraulics of the barrier over time. In addition, two hours experimental time can be too short when compared to the time available to round gobies challenging the barrier in a real fish pass. It is possible that the fish exercise and learn how to overcome the barrier over time (Kieffer & Colgan, 1992). If then only the most powerful swimmers of the goby population can pass the barrier, it seems possible that these fish found an upstream population with species of increased migration tendency and swimming capability. How these potentially negative effects need to be weighed against the barrier's positive effects has to be assessed in long term-field experiments.

### *The hydraulic burden experienced by the fish*

Based on the referenced literature, the present thesis provides the first experimental comparison of the hydraulic forces experienced between real, preserved benthic fish species, at homogenised flow and in vertical slot fish pass flow fields. The hydraulic burden experienced by the fish in flowing water were

shown to depend on the flow velocity and on the fish body surface exposed to the flow (Paper I). Thereby, the pectoral fin size and position were observed to have important impact on the hydraulic burden experienced by the fish. Especially round goby and bullhead experienced stronger forces when pectoral fins were spread (Paper I), which supports their specialized swimming style. Benthic fish have been described to adjust pectoral fin postures in a way that the forces experienced press the fish to the bottom and support station holding (Coombs et al., 2007). The experiments overall revealed significant differences in the hydraulic burden between fish species with the smallest hydraulic burden experienced by gudgeon, largest vertical force directed to the ground experienced by bullhead and median forces experienced by round goby. Considering that gudgeon is described as a powerful semi-pelagic swimmer (Tudorache et al., 2008, Paper II), that bullhead is highly oriented to the ground and uses flow sheltered regions between rocks to withstand the flow (Gosselin et al., 2010; Tudorache et al., 2008; Van Liefferinge et al., 2005, Paper II), and that round goby has been described a versatile swimmer (Tierney et al., 2011), the results suggest that the hydraulic burden corresponded to the individual swimming styles of the fish.

These hydraulic burdens were recorded for different fish samples at two different positions with different flow fields in our experimental setup: At the barrier and the untreated slot. In both independent measurements, we recorded significantly smaller hydraulic burden for gudgeon at 130 L/s water discharge. This observation supports that the hydraulic burden variation between species remains stable between different flow fields of the untreated slot and the barrier.

The hydraulic forces varied between measurement positions especially at the untreated slot, where we also observed local variation in the flow field. Positive correlation between hydraulic forces and flow velocity suggest that the local flow determines the force the fish experience (Paper III and IV) and thereby facilitated passage, especially at the untreated slot, where the flow field was more diverse. This result was not expected because we observed a strong dependency of the hydraulic forces from the adjusted water flow velocity when measuring at one central point in the measurement chamber (Paper I). In the untreated slot however, we observed this local change in the hydraulic burden across measurement points although the water discharge was fixed to 130 L/s (Paper IV). This finding suggest that local flow conditions (e.g. flow direction, flow velocity or turbulence) determine the local force experienced. This means that fish might be able to reduce their hydraulic burden during passage by choosing swimming routes of reduced hydraulic forces. Thereby, fish passes of diverse flow conditions might favour fish passage and homogenous flow conditions can have selective effects.

### *The effect of the hydraulic burden on the fish swimming behaviour*

The fish varied in their upstream migration behaviour between species at the barrier as revealed by the random forest machine learning approach (Paper III). It was possible to identify round goby and gudgeon with high accuracy, only with information about water discharge and swimming patterns. When predicting the species, the most important predictor variable was the water discharge. This agrees with our observation that round goby showed most passages at lower water discharge, while gudgeon passed most frequently at higher water discharge at the untreated slot (Paper IV) and barrier (Paper III). Because the water discharge was the only varied parameter between the experiments, these findings support, together with the observed reduced hydraulic burden measured for gudgeon at higher water discharge, that hydraulic burden have an important effect on the individual swimming behaviour of the fish. Beside this species specific effect, there was a general adaptation observed in the swimming behaviour of all fish at higher water discharge. All fish increased their mean swimming speed, swam with more variable speed and used straighter paths on their way upstream the barrier; probably to reduce the hydraulic burden when swimming upstream.

The hydraulic forces measured cannot reflect the general swimming behaviour of live fish in a flow field because this depends on the individual species biology (Blake, 2004; Coombs et al., 2007; Sfakiotakis et al., 1999) and individual personality traits (Hirsch et al., 2017; Lothian & Lucas, 2021). However, hydraulic forces can provide evidence of one piece of a puzzle of all determinants of fish swimming behaviour: The physical burden the fish experience in the flow due to their body exposed to the flow. It is known that flow conditions can support swimming or make swimming more difficult. For example, turbulence is reported to have important impact on the swimming performance in fish (Lupandin, 2005) and can have positive, as well as negative impact on fish swimming performance. Fish can make use of areas of reduced vorticity to save energy (Facey & Grossman, 1992) and also experience passive propulsion under specific flow conditions (Beal et al., 2006). Although smaller forces at measurements with fish compared to a reference run without fish were detected at 130 L/s at the untreated slot (Paper IV) and in the flow channel experiment (Paper I), no forces directed against flow direction were revealed by the measurements with the 3D-sensor when a fish was connected to the fixation stick. We do therefore not assume that the fish experienced passive propulsion in our experiments.

Measuring hydraulic forces experienced by the fish can be a refinement of the common approach, which is to assess fish passes by flow characterisation and live fish observations (e.g. Drucker & Lauder, 1999; Porreca et al., 2017; Sagnes & Statzner, 2009). The force measurements provide a new, direct and standardized way to describe how the created flow field, which is determined by the fish pass design, affects the fish physically. This approach does not require the use of live fish and thereby improves fish welfare

by avoiding animal experiments. However, there is more research needed to understand how the species respond to the hydraulic burden individually.

### *Challenges*

The direct forces applied to surrounding water of swimming fish are not directly measurable, which complicates the quantification of their locomotor forces (Drucker & Lauder, 1999). The applied approach to measure the forces by real, preserved fish was an approximation to live fish swimming several millimetres above ground but it did not account for the impact of movement and different body postures on the forces experienced.

The live fish observations of the first experiment revealed that especially round goby and bullhead used flow channel corners and friction forces to withstand the flow (Paper I and II). Because friction was not standardisable with the measuring device applied, it was not possible to account for the usage of friction forces to withstand the flow in benthic fish (Carlson & Lauder, 2011) in the present study. This important question, how benthic fish resist the flow by using friction forces, remains a future challenge.

Prior to testing preserved fish, there was the idea to 3D-scan real fish, print them by a 3D-printer, and measure the forces experienced by 3D-printed fish as a proxy for real fish. Using computer manipulation, it would have been possible to create multiple 3D-models of the same fish with different fin and body postures. This would have enabled to test the effect of fin and body posture on the forces experienced in a more standardized way than it was possible with the preserved fish. Another advantage would have been that the measurements would have been highly replicable because the model could be used several times, the model shape data could be stored and published in a repository and replicates of the model could be printed with a 3D-printer by researchers everywhere in the world. Indeed, it turned out at the beginning of this research project, that the 3D-scan and 3D-print represent two methodological steps adding important inaccuracy to the model due to technical limitations. Because the shape of the 3D-printed models varied obviously from real fish shapes, preserved fish turned out to be best representative for real fish for the experiments. Nevertheless, further development of the 3D-printing technique might enable its application in such studies in future.

## Conclusion

The present work provides a description of the performance of a prototype hydraulic barrier which was designed to impede the upstream migration of the invasive round goby, while enabling passage of native, comparable species. With application of the three step-approach, it was possible to describe the barrier's mechanism, which was based on the creation of flow conditions affecting the swimming behaviour of the fish species differently.

From an applied research perspective, it became evident that the prototype hydraulic barrier had a selective effect at 130 L/s water discharge because no round goby passed the barrier, while gudgeon and bullhead passed. Because the hydraulic forces differed between species and corresponded to the live fish swimming behaviour, and the live fish passage behaviour differed between water discharges, it is highly probable that the selective effect of the barrier was mediated by the created flow field. As this evidence merged from a laboratory experiment, long term field studies are necessary to assess the performance of the barrier in the field and its impact on the ecosystem.

From a basic research perspective, this thesis developed an approach to compare the hydraulic burden comparable benthic fish encounter when swimming in flowing water. In addition, this thesis provides the first empiric assessment of the hydraulic forces that benthic fish experience in flow fields of such ecological importance. An important insight was that the fish indeed experience hydraulic burden differing between species and that these hydraulic burdens correspond to the individual swimming styles of the corresponding species. The fish respond to these hydraulic burden individually, depending on their own species biology. Nevertheless, there was a general adaptation of the passage behaviour to increased water discharge: All species swam faster with more speed variation and with straighter paths upstream the barrier.

This thesis is a further step towards species selective fragmentation of rivers for ecosystem conservation purposes. These findings open an avenue to fish pass design adapted to the fish community of specific ecosystems and will inform fish pass engineers, decision makers and researchers who work about the behavioural response of fish to flowing water.

## Outlook and perspectives

### *Assessment of the barrier for more species*

The barrier performed promising in the experiments and the need to perform field studies to describe the long term effect of the barrier and its ecosystem effects was already mentioned. Indeed, the effect of the barrier on further species is still unknown. Therefore, special attention should be spent on the effect of the barrier on the passage performance of all further species that were not included in the present study to ensure their passage will not be negatively affected by the barrier.

### *Assessment of fish passes for their suitability of target species*

The force measurement enabled a close description of the hydraulic burden the fish have to overcome when swimming upstream a vertical slot fish pass. Thereby, the force measurements provided a more direct flow field assessment for the requirements of the specific species than common flow measurements, such as acoustic Doppler-velocimeter applications. Measuring hydraulic forces provides a valuable technique enabling the assessment of fish pass designs for the suitability for species of relevance for the corresponding ecosystem. This method can be applied in the laboratory at prototype fish pass models or in the field at constructions that exist already. Nevertheless, because it is still not possible to measure the forces fish experience while swimming, future research should focus on the refinement of this measurement technique.

### *Development of the force measuring technique*

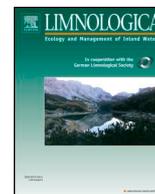
There is potential to further develop and improve the force measurement technique. In the reported approach, the preserved fish were connected to the multi-axis force-torque sensor via a fixation stick. The stick was five times smaller compared to flow channel study (Paper I), which increased the precision of the measurement, but the stick was still exposed to the flow and thereby affected the forces measured. In addition, because the stick represented a lever, it was not possible to account for all measurement channels provided by the sensor because it was not possible to account for the torque experienced by the fish. If integrating the sensor in the fish, these problems would have been avoided and all sensor channels could have been used including force in X-, Y-, Z-direction and torque in X-, Y-, and Z-direction. Indeed, the size of both, fish and sensor impeded an integration of the sensor. With continued development of such sensors to smaller size or testing larger fish, these problems could be solved.

### *Automated fish pass monitoring*

With tracking the live fish and predicting the species based on swimming trajectory features that trained a random forest machine learning approach, this thesis provides the basics for automated fish identification based on swimming patterns. Similar approaches based on automated fish contour recognition (Mandal et al., 2018; Shafait et al., 2016) are already available, but these approaches require high resolution images of the fish contours. When identifying the fish via individual swimming patterns, also poor image quality without sharp contours could be sufficient for species identification because only tracking the trajectories of the fish is required. To further develop this approach, it is promising to replace the supervised random forest machine learning algorithm by an unsupervised approach, such as Convolutional Neural Networks (X. Wang & Gupta, 2015), that account for patterns in the swimming paths that were not accounted by the trajectory features included in the present study. This model could be implemented in a tracking program that automatically records fish trajectories (e. g. Rodríguez et al., 2015) and feeds the trajectories to the fish identification model. All technical tools for such an approach are available. The largest challenge might be to obtain sufficient training data of fish migrating upstream with known identity.

Flow field-induced drag forces and swimming  
behavior of three benthic fish species

Paper I



# Flow field-induced drag forces and swimming behavior of three benthic fish species

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## ABSTRACT

Modern ethohydraulics is the study of the behavioral responses of swimming fish to flow fields. However, the exact drag forces experienced by fish remain poorly studied; this information is required to obtain a better understanding of the behavioral responses of fish and their current resistance strategies. We measured near-ground frontal drag forces on preserved individuals of three benthic fish species, round goby (*Neogobius melanostomus*), gudgeon (*Gobio gobio*) and bullhead (*Cottus gobio*), in a flow channel. The forces were compared to acoustic Doppler velocity (ADV) measurements and fish tracking data based on video observations of live fish in the flow channel. Overall, we observed drag coefficients ( $C_D$ ) of  $\sim 10^{-3}$  at Reynolds numbers  $\sim 10^5$ . The frontal drag forces acting on preserved fish with non-spread fins ranged from  $-1.96 \text{ mN}\cdot\text{g}^{-1}$  (force per fish wet weight, velocity  $0.55 \text{ m}\cdot\text{s}^{-1}$ ) to  $11.01 \text{ mN}\cdot\text{g}^{-1}$  (velocity  $0.85 \text{ m}\cdot\text{s}^{-1}$ ). Spreading the fins strongly increased the drag forces for bullhead and round goby. In contrast, the drag forces were similar for gudgeon with spread fins and all fish with non-spread fins. Video tracking revealed no clear relationship between the position of the fish in the flow field and the forces experienced by the preserved fish at these positions. Collectively, these results suggest that i) the differences in frontal drag forces between species are small in homogenous flow, ii) individuals chose their position in the flow field based on factors other than the drag forces experienced, and iii) whether fins are spread or non-spread is an essential quality that modulates species-specific differences. The methodology and results of this study will enable integration of flow measurements, fish behavior and force measurements and inform ethohydraulics research. More advanced force measurements will lead to a detailed understanding of the current resistance strategies of benthic fish and improve the design of fish passes.

## 1. Introduction

The successful passage of river barriers via fish passes is a global conservation goal and research topic (Katopodis and Williams, 2012; Williams et al., 2012). Successful passage depends on the physical and sensory capabilities, body morphology, behavior and movement phenology of the fish species (Rahel and McLaughlin, 2018). Flow measurements, fish behavior observations and modelling techniques are the main methods used to evaluate fish pass configurations (Wang et al., 2010; Puertas et al., 2012; Tsikata et al., 2014; Baki et al., 2016, 2017a, 2017b; Lima and Janzen, 2018). However, knowledge on the hydraulic preferences and swimming abilities of specific target species and life stages may enable the construction of fish passes with improved effectiveness, even for little-known benthic species (Williams et al., 2012). Laborde et al. (2020) pronounced the importance of further research on the characteristics of relevant species to enhance the

development of sustainable hydropower.

The literature indicates that specific, underappreciated hydrodynamic processes underlie benthic fish swimming. Most studies have focused on the performance of economically relevant fish in fish passes (Jansen et al., 1999; Aarestrup et al., 2003; Hirsch et al., 2016b). The swimming modes of benthic fish are less continuous than those of pelagic fish and rely more on intermediate or permanent contact with the ground. Body shape and pectoral fin usage are suggested to be highly relevant to the current resistance of benthic fish. Carlson and Lauder (2010) described the strategies used by benthic fish to resist currents with specialized body postures leading to negative lift forces. Flow field observations based on digital particle imaging close to the pectoral fins of Mottled sculpin (*Cottus bairdi*) revealed that the pectoral fins significantly altered the downstream flow field. These effects of the pectoral fins were suggested to increase negative lift forces and thereby increase station holding capability (Coombs et al., 2007).

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Even from a basic hydrophysical perspective, the drag forces acting on different benthic fish bodies are widely underappreciated. The kinematics of station holding by darter fish were estimated based on behavioral and flow observations; subtle body shape differences between the tested species were assumed to lead to important differences in station holding ability (Drucker, 2003; Carlson and Lauder, 2010, 2011).

Hydrodynamic forces are increasingly being measured by engineers, with a focus on the construction of artificial devices that imitate swimming fish (Newman, 1973; Barrett et al., 1999; McLetchie, 2003). This progress in the field of hydraulics has not been matched by the biological perspective of ethohydraulics, as existing measurements do not account for the species-specific and individual morphological characteristics of the fish. Here, we aimed to advance the field of ethohydraulics by studying benthic fish swimming from both a biological perspective (body shape, fin position and movement behavior) and hydraulic perspective (flow field and drag forces).

The invasive round goby (*Neogobius melanostomus* Pallas, 1814) is amongst Europe's 100 worst invasive species (Hirsch et al., 2016a) and has also invaded numerous North American habitats (Brown and Stepien, 2009). This small benthic fish species is currently spreading upstream into ecologically valuable tributaries in several river systems across the globe (Kornis et al., 2012). The round goby is confronted by several fish passes during its invasive passages, which raises the question of how the round goby—a benthic fish species—is hydraulically challenged during its passage of fish passes compared to native benthic fish.

In this context, invasion of the round goby serves as an ideal model to determine the importance of the species-specific morphological characteristics used to overcome drag forces in fish passes. To approach this topic, we performed experiments with round goby and two native bottom-dwelling fish species that inhabit similar riverine habitats: the gudgeon (*Gobio gobio* L.) and bullhead (*Cottus gobio* L.). The rationale behind this three-species approach was to detect differences in the drag forces acting on various morphologies in the overall understudied category of benthic fish. The mechanisms behind these individual responses to flow depending on body shape and swimming behavior remain unclear. We aimed to fill this knowledge gap with a three-pronged experimental approach in a swim canal by: 1. quantifying flow velocity in the flow field; 2. measuring the frontal drag forces acting on preserved fish bodies in a flow field; and 3. tracking the positions of live individuals in the flow field. Based on our video observations of living fish in currents, the preserved fish mimicked the body postures of live fish while swimming against flow. We expected homogenous flow conditions in the measuring chamber of the swim channel due to the flow straighteners in the flow channel (experiment 1). Furthermore, we expected body shape and fin variation to lead to differences in the frontal drag forces and their relationship with flow velocity. Thus, we measured the frontal drag forces for similarly sized preserved fish of all three species with spread and non-spread fins at one position in the swim channel while ramping up the flow velocity (experiment 2). Under the assumption that the swim channel creates a homogenous flow field but that the fish respond individually to local flow conditions based on their morphological characteristics, we expected to observe differences in the frontal drag forces depending on the specific location of different body shapes within the flow field. Therefore, we created maps of the drag forces experienced by the fish models at different locations in the flow field (experiment 3). Finally, under the assumption that fish behaviorally modulate the frontal drag forces they experience by changing their position within the swim canal, we expected that live individuals would spend more time at locations with lower frontal drag forces in the measuring chamber. Therefore, we video tracked the positions of live individuals across the chamber at different flow velocities (experiment 4).

## 2. Materials and methods

### 2.1. Fish sampling

Round goby ( $n = 26$ ) were sampled between May and October 2018 in the River Rhine in Basel, Switzerland, using minnow traps baited with dog food. Native species were sampled in June 2018 in tributaries of the River Rhine: bullhead ( $n = 13$ ) in the Maispracherbach and Wintersingerbach creeks in Magden and gudgeon ( $n = 23$ ) in the Spittelmattbach creek in Basel. All gudgeon, bullhead and 15 round goby were anaesthetized, marked with passive integrated transponders (PIT-Tags) and carefully transferred to aquaria in the University of Basel for swimming tests. All remaining round goby ( $n = 11$ ) were euthanized immediately after catching by an overdose of MS-222 and transported to the lab for preservation. Total length ( $T_L$ ) in cm and wet weight ( $W_W$ ) in g (Mettler Toledo PL1502-S) were determined in the lab. The round goby were sexed based on sexual dimorphism (Kornis et al., 2012). We could not unambiguously identify the sex of gudgeon or bullhead.

### 2.2. Ethics statement

All experiments were conducted according to local and federal law under permission Number 2934 of the Veterinary Office Basel Stadt.

### 2.3. Fish preservation

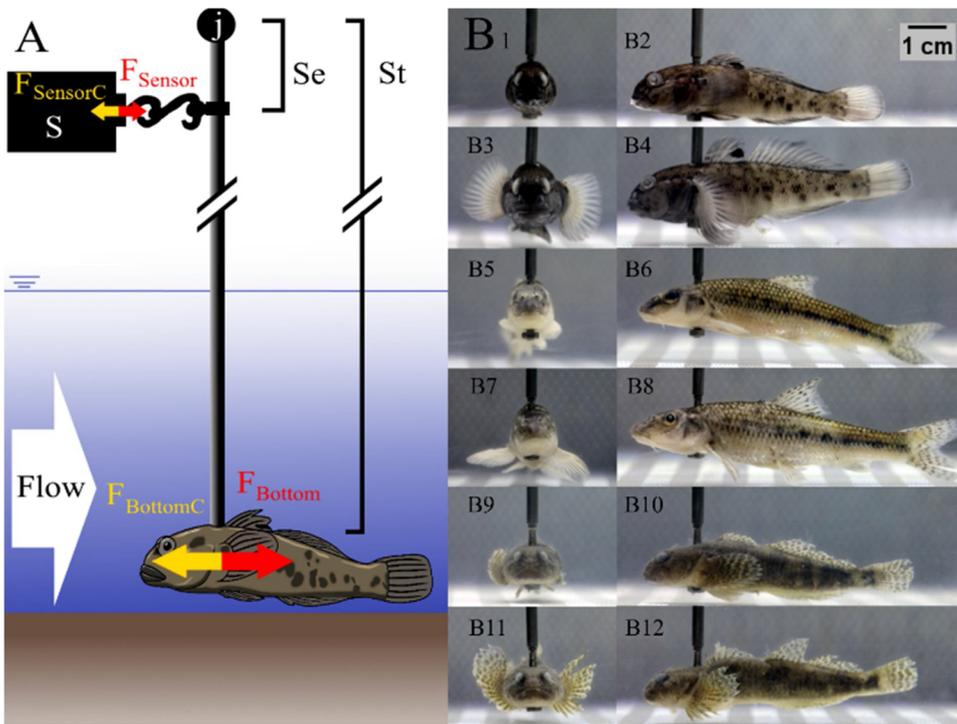
Nine round goby ( $T_L = 9.63 \text{ cm} \pm 1.91$  [standard deviation],  $W_W = 12.95 \text{ g} \pm 10.15$ ), 11 gudgeon ( $T_L = 11.04 \text{ cm} \pm 1.41$ ,  $W_W = 11.83 \text{ g} \pm 5.82$ ) and six bullhead ( $T_L = 11.00 \text{ cm} \pm 0.61$ ,  $W_W = 13.46 \text{ g} \pm 4.82$ ) were preserved with their fins laid onto their body, to achieve the non-spread fin treatment (nf). For all fish, fixation commenced with a bath of 4% formalin that completely covered the whole fish. This was done to avoid the effect of rigor mortis on fish flexibility and to maintain as comparable conditions between the fish as possible. To enable a comparison of only the effect of body shape on the forces experienced in the flow between the fish species, the bodies of the nf-treatment were adjusted to be as straight and symmetric as possible using needles before formalin fixation (S1). We assumed this body posture would provide the best representation of a fish overcoming increased current: when the fins are close to the body to decrease the body surface area exposed to the flow, as observed in the swimming videos of living fish.

The second group of fish were used to explore the effect of the fins on the frontal drag forces. We created a naturally spread fin configuration (sf treatment) for 17 round goby ( $T_L = 11.11 \text{ cm} \pm 1.81$ ,  $W_W = 18.20 \text{ g} \pm 9.79$ ), 12 gudgeon ( $T_L = 10.73 \text{ cm} \pm 1.16$ ,  $W_W = 10.59 \text{ g} \pm 4.53$ ) and seven bullhead ( $T_L = 11.36 \text{ cm} \pm 1.30$ ,  $W_W = 15.29 \text{ g} \pm 5.68$ ; S1). Needles were used to puncture the muscle tissues associated with the fins to spread the fins in a natural manner with as little impact on the body shape as possible.

After three days in the formalin solution, the fish were transferred through a graded series of ethanol solutions with increasing concentrations (24 h in 40 % ethanol, 24 h in 60 % ethanol and further storage in 75 % ethanol) to reduce shape changes of the fish induced in case of rapid concentration increases.

### 2.4. Force measuring device

A Vernier Go Direct Force and Acceleration Sensor (GDX-100609) and Vernier Graphical Analysis v4.4.0-945 software were used to measure the near-ground frontal drag forces acting on the fish in a swim tunnel (Loligo Systems, Swim Tunnel Respirometer #SW10250; 185 L volume, 88 \* 25 \* 25 cm measuring chamber). The sensor was fixed over the water surface (Fig. 1) and connected to a 50 cm long (3 mm-diameter) brass stick connected to a scaffold. A swivel connection



**Fig. 1.** Experimental setup (A) and the tested preserved individuals prior to the measurements in experiment 2 (B). The fish were fixed on the stick close to ground and the force ( $F_{Bottom}$ ) induced by the flow was transduced to the sensor (S) via a joint (j) and a flexible clamp connection between the sensor and the stick. The distance between the fish and joint (St) and the distance between the sensor connection and joint (Se) were used to calculate the force acting on the fish ( $F_{Bottom}$ ). The sensor was fixed on a scaffold, resulting in an opposing force ( $F_{SensorC}$  and  $F_{BottomC}$ ), keeping the fish in position. In experiment 2, the forces were measured for a single nf-round goby (B1, B2), sf-round goby (B3, B4), nf-gudgeon (B5, B6), sf-gudgeon (B7, B8), nf-bullhead (B9, B10) and sf-bullhead (B11, B12). The fish are displayed in frontal (odd numbers) and lateral (even numbers) views.

between the stick and scaffold ensured free oscillation of the stick on one axis. The sensor was connected to the stick 5 cm below the swivel via a flexible clamp connection. The drag force acting on the lower end of the stick with fish attached ( $F_{Bottom}$ ) was calculated using the lever principle:

$$F_{Bottom} = F_{Sensor} * A$$

with  $F_{Sensor}$  representing the force detected by the sensor and A being the quotient between the entire fixation stick length (St = 50 cm) and the distance from the swivel to the sensor connection (Se = 5 cm; Fig. 1).

$$A = \frac{St}{Se} = \frac{50}{5} = 10$$

Reference measurements without fish were performed to account for the drag force of the flow field on the fixation stick. To determine the force acting only on the fish ( $F_{Fish}$ ), the force acting on the stick ( $F_{Stick}$ ) was subtracted from the forces measured when the fish were placed at the end of the stick ( $F_{Bottom}$ ).

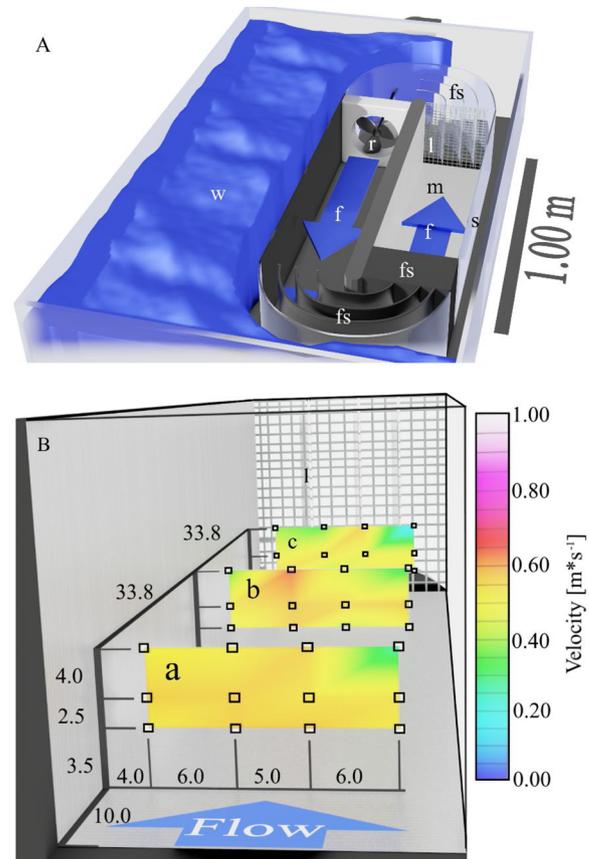
$$F_{Fish} = F_{Bottom} - F_{Stick}$$

Forty-five equidistant measurement points were chosen in the measuring chamber (Fig. 2, 4). The last row of measurement points in the downstream direction was located 10 cm upstream of the water outlet to ensure that the caudal fins of the preserved fish had no physical contact with the grid at the downstream end of the measuring chamber.

We exclusively measured frontal drag forces in the flow direction. The measuring device was adjusted to be exactly parallel to the flow channel plane, using spirit levels integrated into the scaffold. We maintained the distance to the ground (5–10 mm) and contact between the fish or stick and bottom was prevented to avoid the impact of uncontrolled friction on our measurements.

### 2.5. Force measurement procedure

The needles were removed from the preserved fish. After fixation on the measurement device (Fig. 1), the fish were photographed (Canon EOS 70D) in frontal and lateral view through the window in the



**Fig. 2.** Flow channel (A) with rotor (r), flow straighteners (fs), flow direction (f), window (s) and lattice (l). Fish were prevented from leaving the measurement chamber (m) by flow straighteners (upstream) and the lattice (downstream). The water (w) had a depth of 29 cm and covered the whole flow channel. The flow velocity is provided for the  $0.55 \text{ m} \cdot \text{s}^{-1}$  velocity step (B) with the locations of the acoustic Doppler (black squares) shown in three profiles (a, b, c) and distances in cm.

measuring chamber to determine the frontal projected surface area (FPSA) using ImageJ 1.52p. Then, the fish were adjusted over one measuring point and the sensor was reset to commence recording (zero velocity). The flow velocity was increased in a stepwise manner following a ramping design (see below) and frontal drag forces were measured for 60 s at each flow velocity step. A compilation of published data on benthic fish swimming performance found a positive relationship between size and swimming performance (Hirsch et al., 2016b). Therefore, we divided the drag force by the wet weight of the fish ( $\text{mN}\cdot\text{g}^{-1}$ ) to account for the size of individual fish.

The pectoral fins of nf-bullhead tended to spread during the preservation process (Fig. 1B9); thus, we artificially attached the pectoral fins by sewing three needle stitches using cotton sewing thread in this experiment. Preservation was satisfactory for round goby and gudgeon, thus artificial attachment of the fins was not necessary for these species.

## 2.6. Experiment 1: velocity

Flow measurements were conducted in the swimming chamber using a Nortek Vectrino Acoustic Doppler Velocimeter with the probe directed downwards in three transverse profiles within the measuring chamber; each transverse profile contained 12 measurement points (Fig. 2B, a, b, c). Each measurement was performed for 4 min at a data collection rate of 25 Hz. The data were processed using WinADV software and the mean flow velocities were illustrated using Tecplot 360 (Tecplot Inc.) for each point as linear interpolated values. Due to temporal restrictions, the measurements were performed for three ramping design velocities that were considered relevant to benthic fish swimming: 0.25, 0.55 and  $0.85 \text{ m}\cdot\text{s}^{-1}$  (Tudorache et al., 2008; Tierney et al., 2011).

## 2.7. Experiment 2: change in frontal drag force with velocity

This experiment was performed to determine the change in drag forces for the three species as velocity increased and the effect of fin position on the drag forces experienced. The measuring device was located over the center measuring point. Three individual nf- and sf-round goby, -gudgeon and -bullhead were adjusted one fish at a time on the fixation device and the drag forces were measured for 60 s at a rate of 100 Hz (to account for short-term fluctuations in the forces due to vortices) at velocities of 0.30, 0.35, 0.45, 0.55, 0.65, 0.75, 0.8, 0.85, 0.95, 1.05, 1.15 and  $1.25 \text{ m}\cdot\text{s}^{-1}$  (Nakayama, 1999):

$$C_D = \frac{2 \cdot F_{\text{fish}}}{\rho \cdot u^2 \cdot \text{FPSA}}$$

with  $\rho$  being the density of water at  $20^\circ\text{C}$  ( $998.2 \text{ Kg}\cdot\text{m}^{-3}$ ; Nakayama, 1999) and  $u$  being the velocity [ $\text{m}\cdot\text{s}^{-1}$ ]. Additionally, we computed the Reynolds number (Re; Reynolds, 1883):

$$Re = \frac{\rho \cdot u \cdot T_L}{\eta}$$

with  $\eta$  being the dynamic viscosity of water at  $20^\circ\text{C}$  ( $10^{-3} \text{ Pa}\cdot\text{s}$ ; Nakayama, 1999; Table 1).

Personal observations and fast Fourier transformation (FFT) of the reference drag forces indicated a sudden and steep increase in vibration of the stick at velocities greater than  $1.0 \text{ m}\cdot\text{s}^{-1}$  (S2). Therefore, we only included data recorded at velocities lower than  $1.0 \text{ m}\cdot\text{s}^{-1}$  in our analysis.

## 2.8. Experiment 3: force maps

Single preserved nf-round goby, nf-gudgeon and nf-bullhead specimens were tested at different locations in the measuring chamber (Fig. 2) to compare the local forces experienced with the positions of live fish at the same velocities (experiment 4). The frontal drag forces

**Table 1**

Mean velocities and standard deviation (SD) determined by acoustic Doppler in the measurement chamber for the different profiles (Fig. 2).

Channel Velocity [ $\text{m}\cdot\text{s}^{-1}$ ]	Profile	Mean Velocity [ $\text{m}\cdot\text{s}^{-1}$ ]	SD
0.25	a	0.239	0.062
	b	0.257	0.059
	c	0.208	0.065
0.55	a	0.523	0.086
	b	0.496	0.097
	c	0.435	0.124
0.85	a	0.801	0.031
	b	0.796	0.081
	c	0.763	0.039

were measured twice per second (2 Hz) over 60 s, resulting in 121 values per measurement point, treatment and velocity. To focus on the forces acting at different locations and at different velocities in the flow chamber, the measurements were performed for 45 measurement points at velocities of 0.25, 0.55 and  $0.85 \text{ m}\cdot\text{s}^{-1}$  for every treatment. Using the *filled.contour()* function of the *ggplot2* package in R i386 3.5.1, we created maps of the forces measured at different locations (Fig. 4). Furthermore, we compared the forcemaps of the different treatments by correlation analysis (Spearman) using the *ggpubr* package and *cor()* function of R.

## 2.9. Experiment 4: tracking

The locations of live fish in the measuring chamber were extracted from videos generated for another study on the comparative swimming behaviour and performance of benthic fish species (Egger et al., in preparation). A transparent cover was placed over the measuring chamber to prevent fish jumping out of the water. After the fish were acclimatised for 20 min at zero velocity, the flow velocity was successively ramped up to 0.15, 0.25, 0.35, 0.45 and  $0.55 \text{ m}\cdot\text{s}^{-1}$ . Each velocity step was maintained for 10 min and the fish were filmed from directly above the swim tunnel using a GoPro Hero 4<sup>®</sup> camera. All footage was analysed using Solomon Coder software (vers. beta 17.03.22). The position of individual fish in the measurement chamber for each completed velocity step was tracked using idTracker vers. 2.1 (Perez-Escudero and de Polavieja, 2011). If a fish became fatigued, the experiment was stopped for that individual and all completed velocity steps were included in the tracking analysis. This resulted in footage ranging between 45 and 172 min per individual (S3).

The R package *vec2dtransf* version 1.1 (Carrillo, 2012) was used to correct for the slightly different camera positions between trials. Round goby and bullhead swam close to or a few centimeters above the ground. However, a few individual gudgeon also moved higher up in the chamber water column; some swam up to 10 cm above the ground. Since the swimming occurred above the ground across all trials overall, we focused on the x- and y-coordinates in the plane field of the chamber for our analyses. Scatter plots were created based on the x- and y-coordinates of the fish position in every video frame and projected on the force maps (experiment 2) to enable a visual comparison (Fig. 4).

## 3. Results

### 3.1. Experiment 1: velocity

The velocity measurements showed the flow field was relatively uniform overall, but also indicated some differences in the transverse and longitudinal profiles of the flow field in the measurement chamber (Fig. 2, Table 1). There was a skewness in the velocity distribution of the different profiles. The maximum measured flow velocities of profile b shifted slightly to the left (downstream view) compared to the

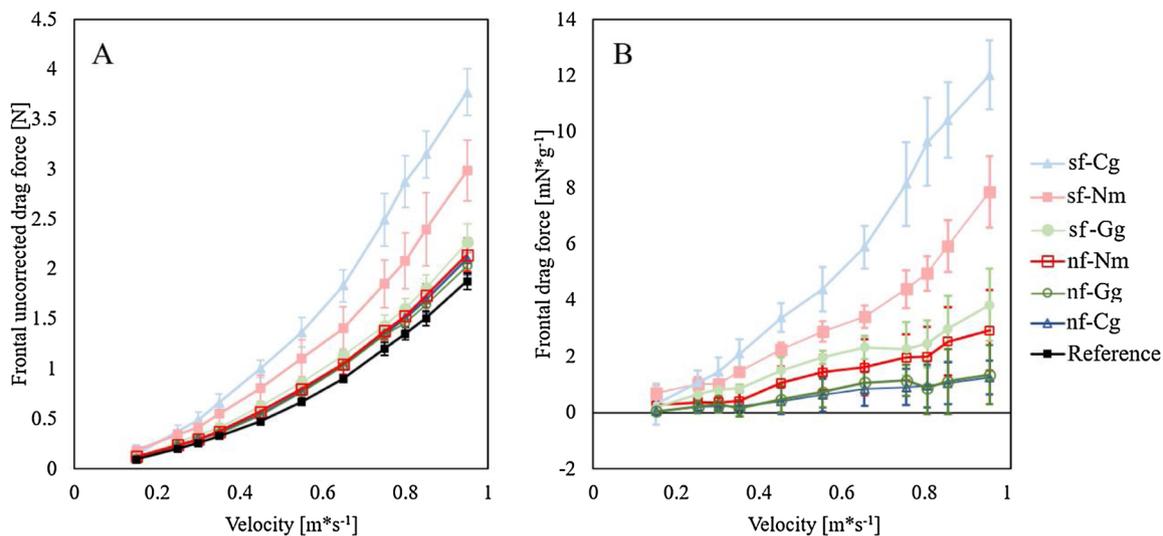


Fig. 3. Uncorrected forces acting on round goby (Nm), gudgeon (Gg) and bullhead (Cg) with spread fins (sf) and non-spread fins (nf) and the reference (fixation stick without fish) measured in the central location of the flow channel. Three individuals were tested for each group (A). The corrected forces (subtracted reference and division by the wet weight) also increased with velocity (B).

upstream profile (Fig. 2a). This skewness together with the flow differences at the different profiles is assumed to result from the 180° arc of the flow induced by the shape of the flow channel (Fig. 2), which may have led to longitudinal velocity distribution variations.

### 3.2. Experiment 2: change in frontal drag force with velocity

The forces experienced by the preserved fish in the flow field increased with the velocity (Fig. 3). Larger frontal drag forces per fish weight were detected for sf-bullhead and sf-round goby, while the frontal drag forces acting on all nf-fish were rather small (maximum  $2.93 \text{ mN}\cdot\text{g}^{-1} \pm 1.45 \text{ SD}$  for nf-round goby at  $0.95 \text{ m}\cdot\text{s}^{-1}$ ). As flow velocity increased, the forces acting on sf-gudgeon were similar to all nf-fish. This, together with the percentage of FPSA induced by the pectoral fins being reduced for sf-gudgeon compared to sf-bullhead and sf-round goby (Table 2), suggests that the pectoral fins of gudgeon have the smallest impact on the frontal drag forces experienced of all tested species. The mean percentage of FPSA induced by the pectoral fins for sf-gudgeon was  $23.63 \% \pm 2.39 \text{ SD}$ , for sf-round goby  $51.51 \% \pm 4.02 \text{ SD}$  and for sf-bullhead  $48.96 \% \pm 3.8 \text{ SD}$ . The proportion of FPSA induced by the fins for the nf-fish was generally smaller:  $3.09 \% \pm 5.36 \text{ SD}$  for round goby,  $2.90 \pm 5.02 \text{ SD}$  for gudgeon and  $1.05 \pm 1.43 \text{ SD}$  for bullhead. In addition, the point of fin insertion is more ventrally located and extends over a smaller area than in the other species, which likely contributes to reduced forces in sf-gudgeon (Fig. 1B).

Considering the FPSA of the preserved fish (Table 2), the frontal drag forces of the different treatments were in accordance with the FPSA exposed to the current. At high FPSA, a large frontal drag force was observed; sf-bullhead had the largest recorded FPSA (Table 2) and largest frontal drag forces of all tested treatments (Fig. 3). In contrast, smaller frontal drag forces were detected at lower FPSA (e.g. nf-gudgeon).

The largest influence of fin position on FPSA was observed for bullhead, with a difference of  $2.33 \text{ cm}^2$  of the mean FPSA between sf and nf, while the smallest impact was observed between sf- and nf-gudgeon ( $0.48 \text{ cm}^2$ ). The difference of the mean FPSA between sf- and nf-round goby was  $1.97 \text{ cm}^2$ . This suggests that the spread fin-treatment increased the FPSA for bullhead and round goby and thus—unlike gudgeon—live bullhead and round goby can markedly affect the drag force they experience.

The  $C_D$ -values of sf-fish were highest for sf-bullhead ( $8.19 \cdot 10^{-3}$ ) and lowest for sf-gudgeon ( $4.10 \cdot 10^{-3}$ ), while the  $C_D$ -values of nf-fish

were highest for nf-round goby ( $3.39 \cdot 10^{-3}$ ) and lowest for nf-bullhead ( $1.81 \cdot 10^{-3}$ ) at a velocity of  $0.95 \text{ m}\cdot\text{s}^{-1}$  and  $Re \sim 1 \cdot 10^5$ . In general, the sf-gudgeon displayed similar hydrodynamic characteristics to the nf-gudgeon. Up to 92.64 % of the drag force experienced by nf-gudgeon at  $0.35 \text{ m}\cdot\text{s}^{-1}$  was induced by the fixation stick (reference). In contrast, the lowest proportion of drag force due to the reference was measured for sf-bullhead (47.00 % at  $0.45 \text{ m}\cdot\text{s}^{-1}$ ). The forces measured on all nf-treatments were only slightly larger than the reference (Fig. 3), indicating the forces acting on nf-fish are generally small.

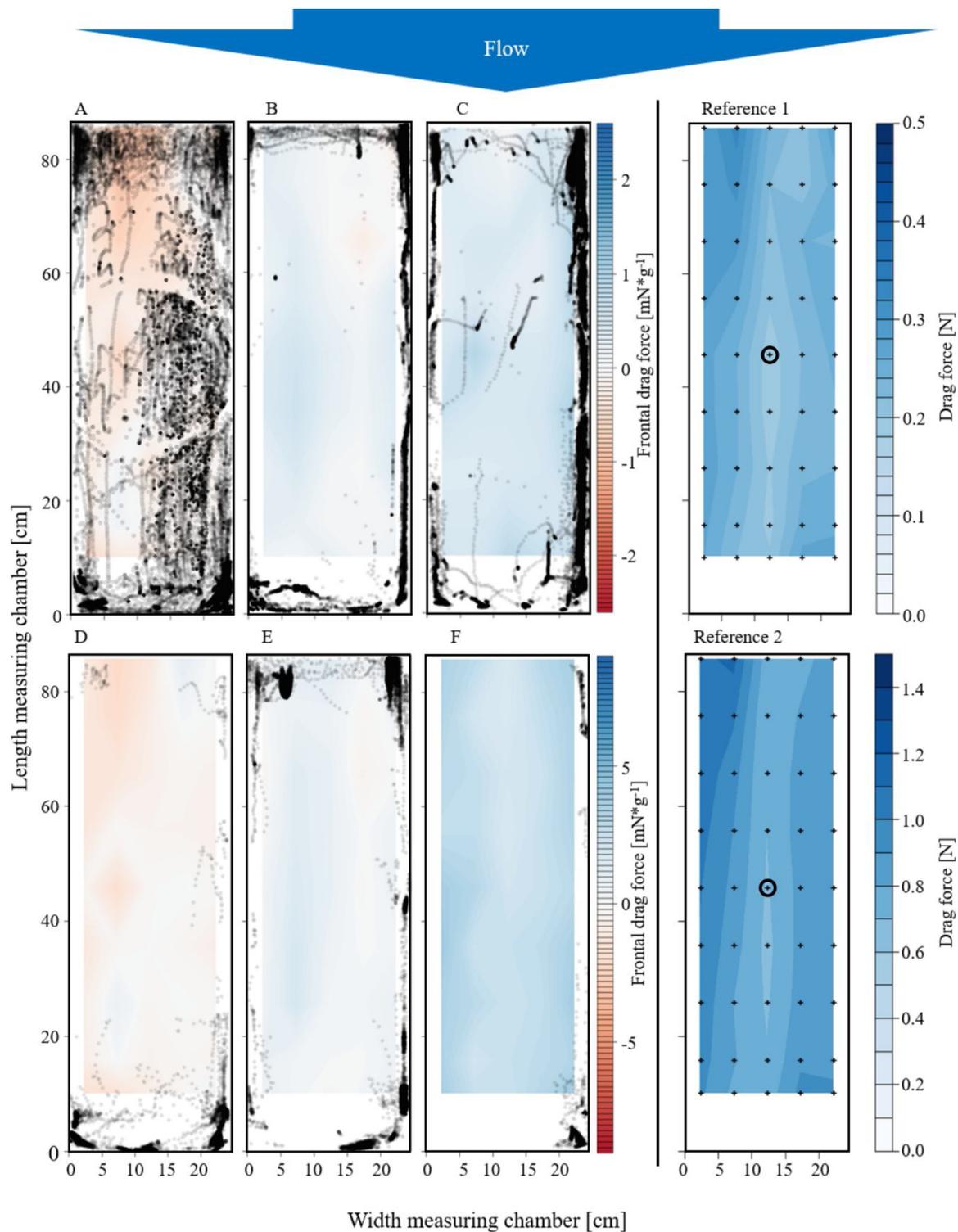
### 3.3. Experiment 3: force maps

Similarly to experiment 2, the drag forces experienced by the fish at the 45 different measurement points varied between the fin position treatments, fish species, and flow velocity. We recorded larger forces for sf-fish than nf-fish. The SDs of the frontal drag forces measured at different locations increased with velocity for every treatment (Table 3). Increasingly negative frontal drag forces were observed as velocity increased for nf-round goby. Positive frontal drag forces, which increased with velocity, were recorded for all sf-fish (Table 3).

The smallest mean frontal drag force, as well as the lowest FPSA, were observed for the nf-round goby compared to all other tested fish (Table 3). On the contrary, the sf-round goby displayed the largest FPSA of all treatments and experienced the largest frontal drag force. The smallest difference in FPSA between the two fin position treatments was observed for gudgeon (FPSA difference between sf- and nf-gudgeon was 21.03 % of the sf-gudgeon FPSA, for round goby 75.00 % and for bullhead 43.82 %). This was in agreement with small drag force differences between both fin position treatments (the difference became smaller as the velocity increased, up to the maximum difference of  $4.75 \text{ mN}\cdot\text{g}^{-1}$  observed at a velocity of  $1.15 \text{ m}\cdot\text{s}^{-1}$ ). This suggests fin position has minimal impact on the drag force experienced by gudgeon. Furthermore, the maximal frontal drag force observed for the nf-bullhead ( $8.87 \text{ mN}\cdot\text{g}^{-1}$ ) was explicitly larger compared to the drag forces for nf-round goby ( $-2.30 \text{ mN}\cdot\text{g}^{-1}$ ) and nf-gudgeon ( $-0.87 \text{ mN}\cdot\text{g}^{-1}$ ); this may be related to the slightly spread pectoral fin of the preserved nf-bullhead (Fig. 1B9), suggesting that small variations in fin adjustment (such as slightly spread fins) can also have a large impact on the frontal drag forces experienced.

#### 3.3.1. Force correlations

The spatial distribution of frontal drag forces was compared



**Fig. 4.** Bird's-eye view of the measuring chamber at a velocity of  $0.25 \text{ m} \cdot \text{s}^{-1}$  for nf-round goby (A), nf-gudgeon (B) and nf-bullhead (C) and at velocity of  $0.55 \text{ m} \cdot \text{s}^{-1}$  for nf-round goby (D), nf-gudgeon (E) and nf-bullhead (F) showing the frontal drag forces at the related locations. Grey dots represent the presence of one fish in one video frame in the measuring chamber. The drag force acting on the fixation stick is displayed for velocities of  $0.25 \text{ m} \cdot \text{s}^{-1}$  (Reference 1) and  $0.55 \text{ m} \cdot \text{s}^{-1}$  (Reference 2). The measurement points ( $n = 45$ ) are represented by black crosses at the references and the central point applied in experiment 1 is marked by black circles.

between round goby and the two other species by correlation analysis (Fig. 6). The 95 % confidence ellipses of sf-fish, separated from the ellipses of the nf-fish, were in agreement with the findings of experiment 2: the sf-fish experienced larger frontal drag forces than the nf-fish.

Furthermore, the nf- and sf-bullhead experienced stronger frontal drag forces than gudgeon at  $0.55$  and  $0.85 \text{ m} \cdot \text{s}^{-1}$  (Fig. 6B, C). As

inferred from the point clouds around the dashed line, the frontal drag forces acting on sf-bullhead were similar to those experienced by sf-round goby at  $0.25$ ,  $0.55$  and  $0.85 \text{ m} \cdot \text{s}^{-1}$  (Fig. 6A, B, C). In contrast, the frontal forces acting on nf-bullhead were always larger than the forces on nf-round goby.

The frontal forces acting on sf-gudgeon were always smaller than the forces acting on sf-round goby. However, at velocities of  $0.25$ ,  $0.55$

**Table 2**

Total length ( $T_L$ ), wet weight ( $W_W$ ), frontal projected surface area (FPSA), the proportion of the pectoral fins of the total FPSA (Fin FPSA), drag coefficients ( $C_D$ ) and Reynolds numbers (Re) measured for round goby (Nm), gudgeon (Gg) and bullhead (Cg) with spread fins (sf) and non-spread fins (nf) in experiment 2 at a velocity of  $0.95 \text{ m}\cdot\text{s}^{-1}$ .

Fish ID	$T_L$ [cm]	$W_W$ [g]	sex	FPSA [cm <sup>2</sup> ]	Fin FPSA [%]	Mean FPSA [cm <sup>2</sup> ]	$\pm$ SD FPSA [cm <sup>2</sup> ]	$C_D$ ( $\cdot 10^{-3}$ )	Mean $C_D$ ( $\cdot 10^{-3}$ )	SD $C_D$ ( $\cdot 10^{-3}$ )	Re ( $\cdot 10^5$ )	Mean Re ( $\cdot 10^5$ )	SD Re ( $\cdot 10^5$ )
sf-Nm-1	8.8	8.38	female	2.01	46.97	3.61	1.77	7.41	6.71	1.34	0.76	0.95	0.18
sf-Nm-2	10.1	14.21	male	3.29	52.98			7.57			0.96		
sf-Nm-3	11.8	21.73	male	5.52	54.58			5.17			1.12		
sf-Gg-1	11.1	10.49	undetermined	1.55	22.13	2.12	0.65	6.14	4.10	2.34	1.05	1.05	0.03
sf-Gg-2	11.3	10.49	undetermined	2.22	22.39			4.59			1.07		
sf-Gg-3	10.7	9.12	undetermined	2.85	26.39			1.55			1.01		
sf-Cg-1	10.8	15.68	undetermined	4.82	53.32	4.74	0.24	8.94	8.19	0.77	1.02	1.01	0.03
sf-Cg-2	10.8	17.85	undetermined	4.93	47.26			8.22			1.02		
sf-Cg-3	10.3	13.87	undetermined	4.47	46.31			7.40			0.98		
nf-Nm-1	8.3	6.65	female	1.30	0.00	1.64	0.32	3.07	3.39	1.73	0.83	0.87	0.04
nf-Nm-2	9.2	9.70	female	1.66	0.00			5.25			0.87		
nf-Nm-3	9.6	11.70	female	1.95	9.28			1.84			0.91		
nf-Gg-1	10.5	9.68	undetermined	1.53	8.69	1.69	0.40	3.31	1.90	1.31	1.00	1.06	0.14
nf-Gg-2	12.9	18.49	undetermined	2.15	0.00			1.67			1.22		
nf-Gg-3	10.2	8.84	undetermined	1.40	0.00			0.73			0.97		
nf-Cg-1	10.8	15.49	undetermined	2.17	0.00	2.42	0.49	2.08	1.81	0.70	1.02	1.08	0.05
nf-Cg-2	11.8	19.53	undetermined	2.98	2.68			2.35			1.12		
nf-Cg-3	11.5	17.93	undetermined	2.10	0.48			1.02			1.09		

and  $0.85 \text{ m}\cdot\text{s}^{-1}$  the frontal forces acting on nf-gudgeon were larger than those experienced by nf-round goby at the majority of measurement points, although the ellipses overlapped with the dashed line.

The formation of point clouds inside the ellipses shows a degree of similarity in the forces experienced by bullhead and gudgeon compared to round goby. The majority of correlations were not significant, indicating a large discrepancy between how drag forces act on different species at increasing velocities (nf-gudgeon and nf-round goby at  $0.25 \text{ m}\cdot\text{s}^{-1}$  [Fig. 5A,  $r = 0.114$ ,  $p = 0.45$ ], nf-gudgeon and nf-round goby at  $0.55 \text{ m}\cdot\text{s}^{-1}$  [Fig. 6B,  $r = -0.08$ ,  $p = 0.59$ ], both fin position treatments for bullhead and round goby at  $0.55 \text{ m}\cdot\text{s}^{-1}$  [Fig. 6B, sf:  $r = 0.09$ ,  $p = 0.55$ ; nf:  $r = -0.01$ ,  $p = 0.94$ ], nf-gudgeon and nf-round goby [ $r = 0.13$ ,  $p = 0.38$ ], as well as sf-bullhead and sf-round goby at  $0.85 \text{ m}\cdot\text{s}^{-1}$  [ $r = 0.18$ ,  $p = 0.24$ ]; Fig. 6C). In contrast, we detected significant correlations for the other eight comparisons, which suggests local differences in the frontal drag forces experienced between species. For example, there was a significant positive correlation, indicating increased similarity, between both bullhead fin position treatments and round goby at  $0.25 \text{ m}\cdot\text{s}^{-1}$  velocity (nf:  $r = 0.43$ ,  $p = 0.004$ ; sf:  $r = 0.49$ ,  $p = 0.001$ ). A similar positive correlation was observed between sf-gudgeon and sf-round goby ( $r = 0.64$ ,  $p < 0.01$ ). At a velocity of  $0.55 \text{ m}\cdot\text{s}^{-1}$ , a significant correlation was only detected between sf-gudgeon and sf-round goby ( $r = 0.62$ ,  $p < 0.01$ ). At  $0.85 \text{ m}\cdot\text{s}^{-1}$ , a significant correlation occurred between sf-gudgeon and sf-round goby ( $r = 0.48$ ,  $p < 0.01$ ), with a significant negative correlation between nf-bullhead and nf-round goby ( $r = -0.46$ ,  $p < 0.01$ ); this correlation

indicates that frontal drag forces were larger for round goby at locations where the frontal drag forces acting on bullhead were smaller, and vice versa. These data based on preserved fish support the notion that fish can reduce the drag forces they experience by changing their position within a small flow field.

Overall, the points representing the frontal drag forces measured at the central position in experiment 2 (Fig. 4, black circles) tended to cluster toward the center of the point clouds. Additionally, the points for sf-fish were close together and the points for nf-fish were close together. This indicates that the forces experienced by the tested fish were more similar in the center of the measurement chamber than at other locations.

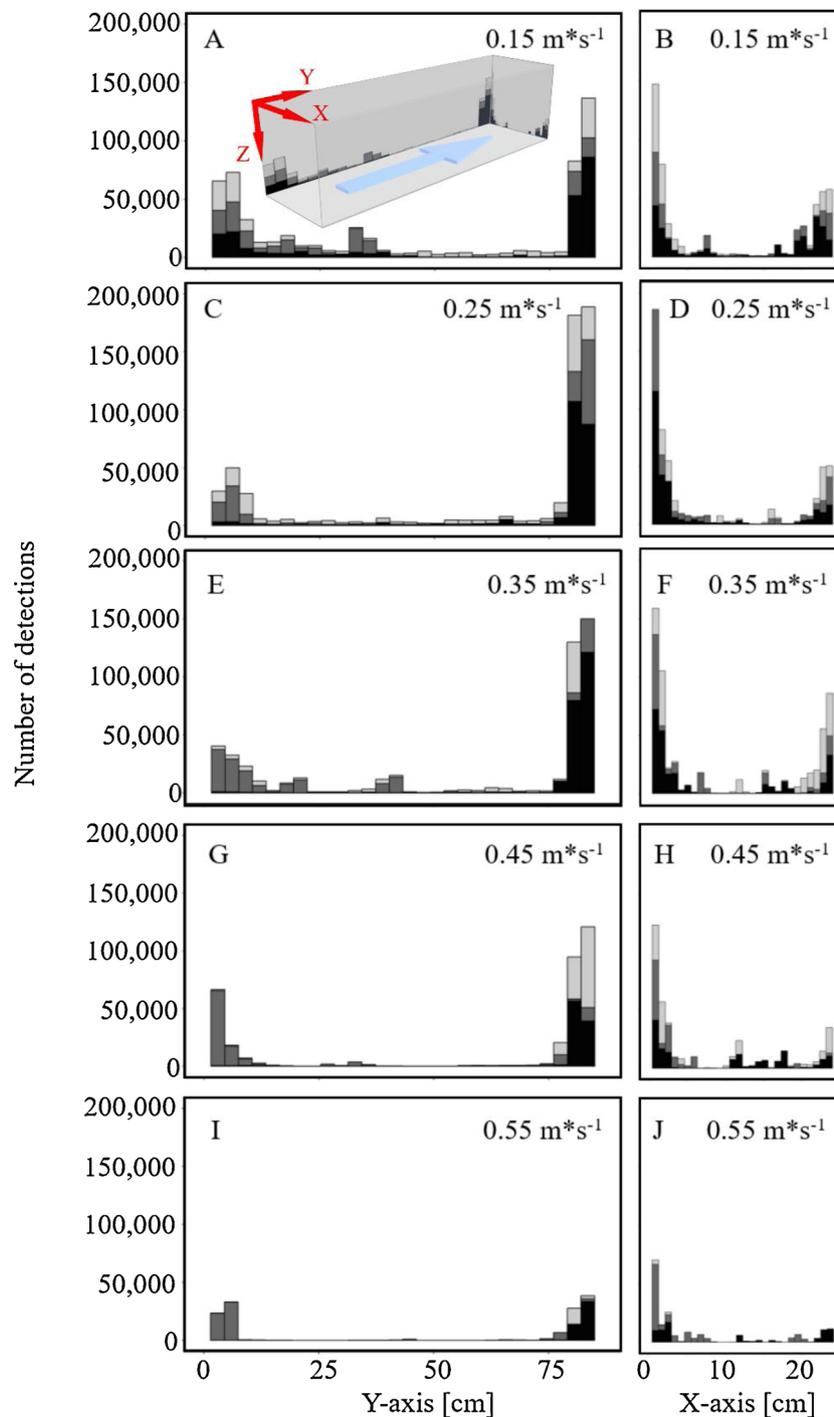
### 3.4. Experiment 4: tracking

Tracking of the positions of live fish within the chamber revealed a high density of records near the sidewalls and corners of the measuring chamber (Fig. 4, 5). As these locations were outside the area covered by the force and flow measurements, further quantification of the relationship between the positions of the fish and forces was unreasonable. However, some important insight can be extracted from the graphical combinations of the fish positions and forces (Fig. 4). Generally, we observed position records reduced as velocity increased, resulting from increased fish fatigue at stronger velocities (Fig. 4). The highest number of fish movements (as inferred from the scatter of recorded positions across the measuring chamber) was detected for round goby

**Table 3**

Frontal projected surface area (FPSA), the proportion of the pectoral fins of the total FPSA (Fin FPSA), total length ( $T_L$ ) and wet weight ( $W_W$ ) and mean and standard deviation (SD) of frontal drag forces in  $\text{mN}\cdot\text{g}^{-1}$  (mean) determined in experiment 3 for round goby (Nm), gudgeon (Gg) and bullhead (Cg) with spread (sf) and non-spread fins (nf) at different velocities ( $\text{m}\cdot\text{s}^{-1}$ ).

Fish ID	FPSA [cm <sup>2</sup> ]	Fin FPSA [%]	$T_L$ [cm]	$W_W$ [g]	$0.25 \text{ m}\cdot\text{s}^{-1}$		$0.55 \text{ m}\cdot\text{s}^{-1}$		$0.85 \text{ m}\cdot\text{s}^{-1}$		$1.15 \text{ m}\cdot\text{s}^{-1}$	
					Mean	SD	Mean	SD	Mean	SD	Mean	SD
sf-Nm-4	5.36	55.39	8.00	7.81	1.83	0.49	5.88	1.48	11.50	4.25	10.48	5.33
nf-Nm-4	1.34	0.00	9.00	9.43	-0.26	0.31	-0.51	0.81	-1.68	1.79	-2.30	3.54
sf-Gg-4	2.71	33.39	11.80	15.01	1.05	0.33	2.55	0.86	4.72	1.99	3.88	2.61
nf-Gg-4	2.14	11.87	11.40	11.26	0.21	0.23	0.53	0.61	0.48	2.08	-0.87	2.98
sf-Cg-4	3.39	62.15	9.90	11.42	1.69	0.31	6.22	0.99	14.40	2.19	18.42	4.29
nf-Cg-4	1.90	17.63	9.30	9.18	0.54	0.25	2.89	0.77	7.20	2.45	8.87	3.18



**Fig. 5.** Planar distribution of fish detections from the tracking analysis in the measurement chamber at different velocities ( $m*s^{-1}$ ) for round goby (black), gudgeon (grey) and bullhead (bright grey). View orientation is provided in a drawing of the measuring chamber (A) with the flow direction indicated (blue arrow). Each single recording across all the video frames for each individual and for each velocity step was recorded and stacked as a summed histogram, thus illustrating the individuals' whereabouts during the experiment.

at  $0.25 m*s^{-1}$ , which was also the treatment with the lowest measured forces at this velocity (Fig. 4A). In contrast, the lowest fish activity (i.e. the fewest fish position records) was detected for bullhead at  $0.55 m*s^{-1}$ , when the strongest forces were measured. Reduced scattering of the position of round goby was observed at  $0.55 m*s^{-1}$ , when our measuring device detected the strongest negative frontal drag forces.

#### 4. Discussion

The aim of this study was to increase our knowledge of how benthic

fish experience currents by comparing experimental drag force and flow measurements with fish tracking data. The frontal drag forces acting on fish depend on their fin position and location in the measurement chamber. In comparison to the strong effect of fin position on the frontal drag forces experienced by round goby and bullhead, the kind of species had a rather small effect on the forces experienced at both fin position treatments. The fins induced the most important interspecies differences in drag forces, indicating that live fish have divergent abilities to interact and manipulate the flow field surrounding their body (Carlson and Lauder, 2011). However, for gudgeon, their fins may

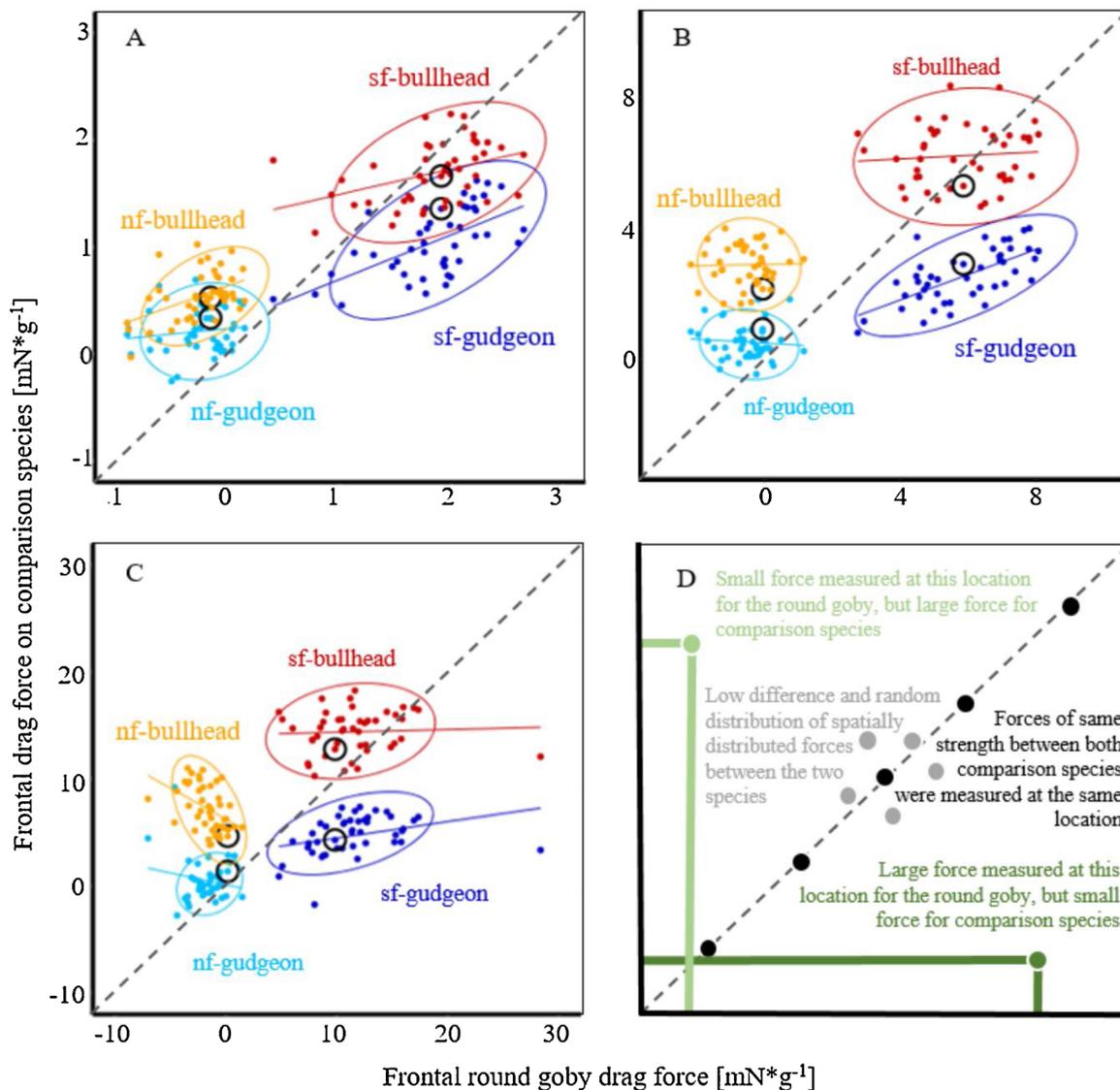


Fig. 6. Frontal drag force comparison by correlation between round goby and the two comparison species (bullhead and gudgeon) at velocities of 0.25 (A), 0.55 (B), and 0.85 m\*s<sup>-1</sup> (C) for fish with spread fins (sf) and non-spread fins (nf) and reading instruction for this figure (D). Every point represents one measurement point in the flow chamber (n = 45). The measurement point of experiment 1 is marked by a black circle for every treatment.

have minimal impact on the frontal drag forces experienced. Due to the small impact of the pectoral fins on the frontal drag forces experienced by gudgeon and their strong swimming capabilities, it is possible that the pectoral fins of gudgeon mainly exert a piloting function. This swimming mode is in accordance with the BCF mode (body and/or caudal fin locomotion), characterized by propulsion through a wave moving backwards through the body and caudal fins (Sfakiotakis et al., 1999). This swimming mode and fin function may enable gudgeon to swim in the water column at higher velocities (as observed in experiment 3) and is in accordance with Tudorache et al. (2008), who reported unexpectedly high critical swimming speeds, even though gudgeon are assumed to be bottom-dwellers. When comparing the morphology, relative size, and insertion of the pectoral fins between gudgeon and round goby and bullhead, it appears that the gudgeon's pectoral fins might have a less important function in modulating negative lift forces (Coombs et al., 2007). In contrast, round goby and bullhead may use their pectoral fins and higher FPSA (compared to gudgeon) to produce negative lift forces to resist the current (personal observation; Koehl, 1984; Coombs et al., 2007; Tudorache et al., 2008; Carlson and Lauder, 2010). Although we did not measure lift forces, it is likely that both species are able to adjust their fins to vertically deflect

the frontal drag force to the ground and increase friction.

Round goby diverged from gudgeon and bullhead, especially in their ability to change FPSA. Furthermore, round goby experience much stronger negative frontal drag forces than gudgeon and bullhead. Together with previous work demonstrating the ability of round goby to switch between the BCF and MPF (median and/or paired fins) swimming modes (Pennuto and Rupprecht, 2016), we assume round goby may be able to adapt their swimming mode to local flow conditions. This behavior could enable round goby to overcome fish passes and aid their spread into upstream tributaries. This flexibility may be a compensation for the poor morphological specialization of round goby (Jakubčinová et al., 2017) and could be another factor that explains the invasive success of this species.

Initially, the negative frontal drag forces—especially for the nf-round goby in experiment 2—seemed counterintuitive. However, Beal et al. (2006) reported that the bodies of dead fish produce enough propulsion at specific vortex conditions to overcome their own drag and move against the direction of flow. As the flow was altered by the 180° arc of the flow channel (Fig. 2) and we detected the strongest negative drag forces in the upstream area of the flow channel, it is likely that such propulsion occurred in our experiment. This could create

beneficial hydrodynamic conditions for round goby, potentially reducing the muscle activity required while swimming, as described for trout (*Oncorhynchus mykiss*; Liao et al., 2003). This phenomenon was especially observed for nf-round goby, and can be formulated as the hypothesis that round goby have an advantage in currents over bullhead and gudgeon. However, the tracking data did not reveal more points at areas with negative forces, thus further tests are necessary to support this conclusion.

Apart from behavioral adaptation, morphological adaptations to currents have been described in fish (Imre et al., 2002; Franssen et al., 2013; Pennuto and Rupprecht, 2016). Body shape was observed to diverge between individuals from stream and reservoir habitats in a cyprinid species (Franssen et al., 2013) and Imre et al. (2002) found juvenile brook charr (*Salvelinus fontinalis*) that inhabited habitats with high flow velocities had larger caudal fins and more slender bodies compared to those from low velocity habitats. Due to our small sample size, we have to be careful when deriving conclusions related to body shape-induced differences. However, the variation in the locations of the point clouds and directions of the correlations varying with velocity for some fish in experiment 3 suggest that the frontal drag forces differ between species due to morphological differences. Together with our findings of the high impact of fin position and behavioral differences between species, it is likely that our approach of measuring the drag forces using preserved fish is promising to advance our knowledge of the interactions between hydrodynamics and benthic fish swimming. Most importantly, using preserved fish excludes the confounding factors affecting fish behavior (such as adaptation, condition and temperature).

Although the flow velocity varied within the measurement chamber, the live fish did not follow the patterns of reduced drag force and reduced velocities. Instead, the fish preferred locations close to the side walls. This is assumed to be a behavioral response of the fish to the flow, aiming at reducing energetic costs, as described by Cook and Coughlin (2010) for rainbow trout. Acoustic Doppler could not reliably quantify the flow directly above the surface and in the corners of the chamber, where the fish were frequently located. So, although we could not achieve a quantitative comparison of locations and forces, we can still relate the patterns observed to current scientific knowledge. Haro et al. (2004) reported the lowest velocities near the walls and floor of an open-channel flume. Based on general hydrodynamic observations, the flow characteristics in the corners of a rectangular channel strongly differ from the flow in the center of the channel. Mean velocity is reduced in the corners due to the shear effect and secondary flows developed (Chow, 1959). We assume that, in our study, boundary effects and the secondary flow field in the corners of the channel at locations close at the ground and close to the wall were more favorable to fish than the open area of the measurement chamber. The importance of behavioral effects is evident from the large number of locations recorded at the downstream water outlet grid, which indicates the majority of fish were not motivated to swim and rested near the grid, where the physical structure of the grid and vortices may have supported their body against the flow. However, these problems of individual motivation are avoided in force measurements of preserved fish, and allowed species-specific flow characterization of the flow fields acting on fish bodies without the need to test living individuals. Measurements of preserved fish provide a more accurate representation of the forces fish have to overcome when ascending a fish pass, as the results are independent of fish motivation and behavior. Measurement of frontal drag forces helps to understand the effort fish have to invest when overcoming currents, without using live experimental animals, which is beneficial in terms of the uncertainties of planning and conducting experiments with living animals. Although we can only measure one factor at a time, either force or behavior, the combinatory approach holds promise for quantification of forces, which we assume are relevant to behavior. In the context of invasive species such as the round goby, additional knowledge on forces and the behavioral

response of the fish on these forces may inform the design of fish passes in which currents are adapted to impede or facilitate the migration of specific target species (Williams et al., 2012).

As a result of our decision to use preserved fish, we focused on the physical response of the fish bodies based on the sum of morphological and body posture characteristics. This is a methodological novelty compared to previous studies that measured the forces acting on artificial fish models with over-simplified shapes (Newman, 1973; Barrett et al., 1999; McLetchie, 2003). The use of multidirectional force sensors in future experiments will greatly advance our ability to fully describe the forces experienced by the bodies of fish.

Hydraulic modelling and measurements of swim canals or large fishways have enabled substantial advancements in ethohydraulics in recent years (Plew et al., 2007; Lindberg et al., 2013). These measurements were interpreted in the context of direct visual (Plew et al., 2007) or indirect automated tracking information on fish behavior (Lindberg et al., 2013). To the best of our knowledge, fast-swimming ‘flagship’ species—which have rather large body sizes—have been the focus of ethology, rather than benthic fish (Plew et al., 2007; Lindberg et al., 2013). For example, Lindberg et al. (2013) elaborately modelled the flow below a hydropower tailrace in a Swedish river. These hydraulic data were combined with ethological data on the movements and positions of Atlantic Salmon (*Salmo salar* L.) below the tailrace. Combination of these datasets enabled identification of the optimal position for a planned fishway entrance. Using a similar approach, but under more controlled conditions, Plew et al. (2007) mapped a flow chamber using acoustic Doppler and then compared the variation in the swimming acceleration and maximum speed of a galaxiid (*Galaxius maculatus*) with the flow variations. Due to the typically low Reynolds number of fish bodies, major energy expenditure should be required to overcome the drag acting against the body, at least for carangiform or subcarangiform swimmers, the most common swimming types among temperate freshwater fish. Since the drag force is proportional to velocity squared, the fish should both minimize overall drag and also vary their swimming velocity to conserve energy (Anderson et al., 2001). Therefore, fish should follow the path with minimal drag forces that requires minimal acceleration. Our study is the first to quantify the drag forces acting on the bodies of fish. This data can now be used to advance existing procedures to study fish passage. However, we did not observe that benthic fish follow force patterns in homogenous flow, suggesting that other factors influence the swimming behavior of benthic fish beyond frontal drag forces alone. Our data has the potential to advance traditional approaches, such as hydraulic modelling of flow velocities in a fish-way. Gisen et al. (2017) used fish-size-speed relations based on an ethohydraulic scale to make conclusions related to fish migration corridors. Our data, in combination with living fish behavior tracked as movement corridors and vicinity to structures as two novel parameters, could advance these approaches. These novel parameters have the potential to generate more realistic fish swimming models.

#### CRedit authorship contribution statement

**Joschka Wiegleb:** Conceptualization, Investigation, Methodology, Software, Formal analysis, Writing - original draft, Visualization, Project administration, Validation. **Philipp E. Hirsch:** Conceptualization, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Bernd Egger:** Conceptualization, Investigation, Methodology, Software, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Frank Seidel:** Conceptualization, Investigation, Methodology, Software, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Patricia Burkhardt-Holm:** Conceptualization, Investigation, Methodology, Writing - original draft, Writing - review & editing, Resources, Project administration.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.limno.2020.125812>.

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## 1. Supplemental material

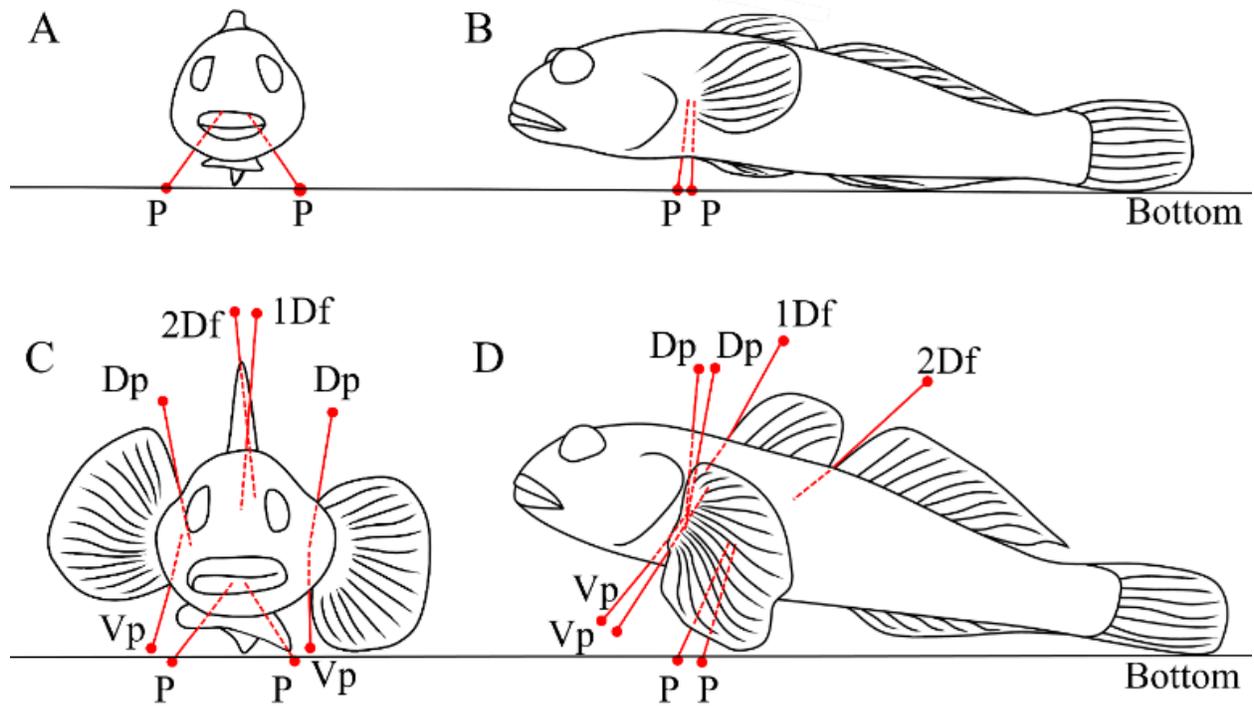


Figure S1: Positioning of needles during preservation of nf-fish (A, B) and sf-fish (C, D). Two needles per fish were used to ensure solid positioning in the preservation solution (P). Pectoral fins were fixed by dorsal (Dp) and ventral (Vp) punctuation. The dorsal fins were fixed using one needle per fin (1Df, 2Df).

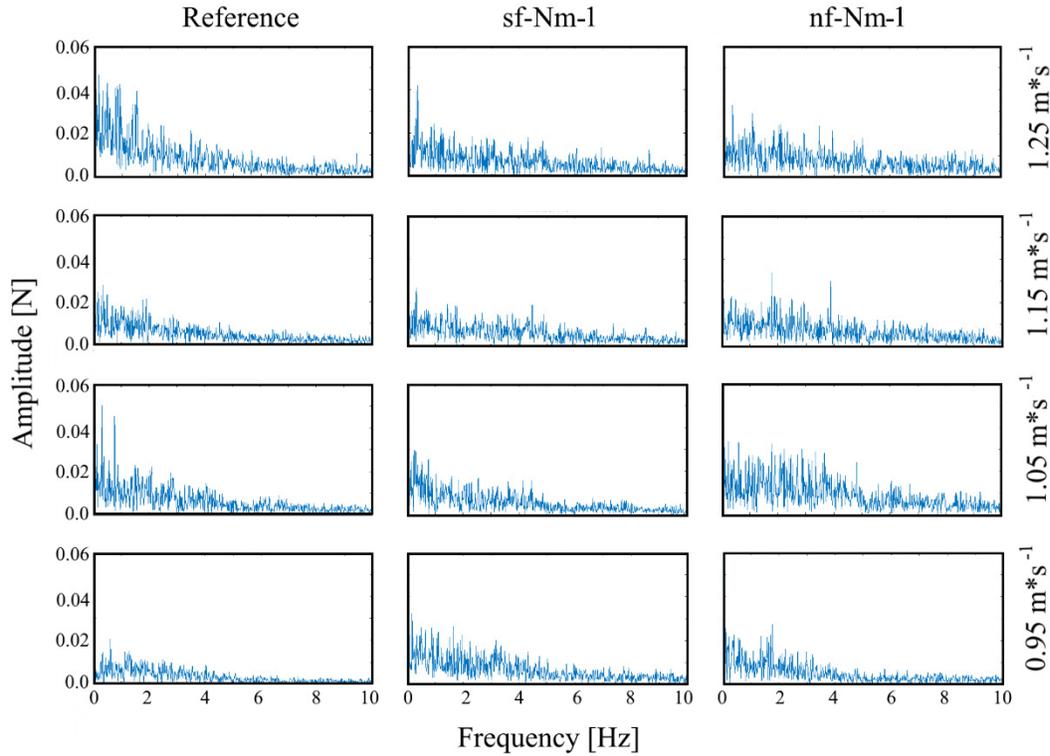


Figure S2: Fast Fourier transformation spectra for one individual sf- and nf-round goby in experiment 2 at different velocities.

Table S3: Number of individuals in the swimming performance tests and amount of footage analyzed during video tracking analysis (experiment 3). Proportion of unsuccessful tracking refers to the amount of footage analyzed.

Velocity [ $\text{m}\cdot\text{s}^{-1}$ ]		Round goby	Gudgeon	Bullhead
0.15	Tested fish [ $n$ ]	18	13	14
	Analyzed footage [minutes]	149.09	105.28	102.67
	Proportion unsuccessful tracking [%]	17.17	19.02	26.66
0.25	Tested fish [ $n$ ]	18	13	14
	Analyzed footage [minutes]	172.78	113.55	114.00
	Proportion unsuccessful tracking [%]	4.01	12.65	18.57
0.35	Tested fish [ $n$ ]	16	13	14
	Analyzed footage [minutes]	150.75	113.23	119.77
	Proportion unsuccessful tracking [%]	5.78	12.9	14.45
0.45	Tested fish [ $n$ ]	10	11	9
	Analyzed footage [minutes]	94.14	86.70	76.38
	Proportion unsuccessful tracking [%]	5.86	21.18	15.13
0.55	Tested fish [ $n$ ]	6	10	1
	Analyzed footage [minutes]	45.07	89.13	9.56
	Proportion unsuccessful tracking [%]	24.88	10.87	4.40

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*)

Paper II



# 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 Spittelmatzbach 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 Spittelmatzbach, 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

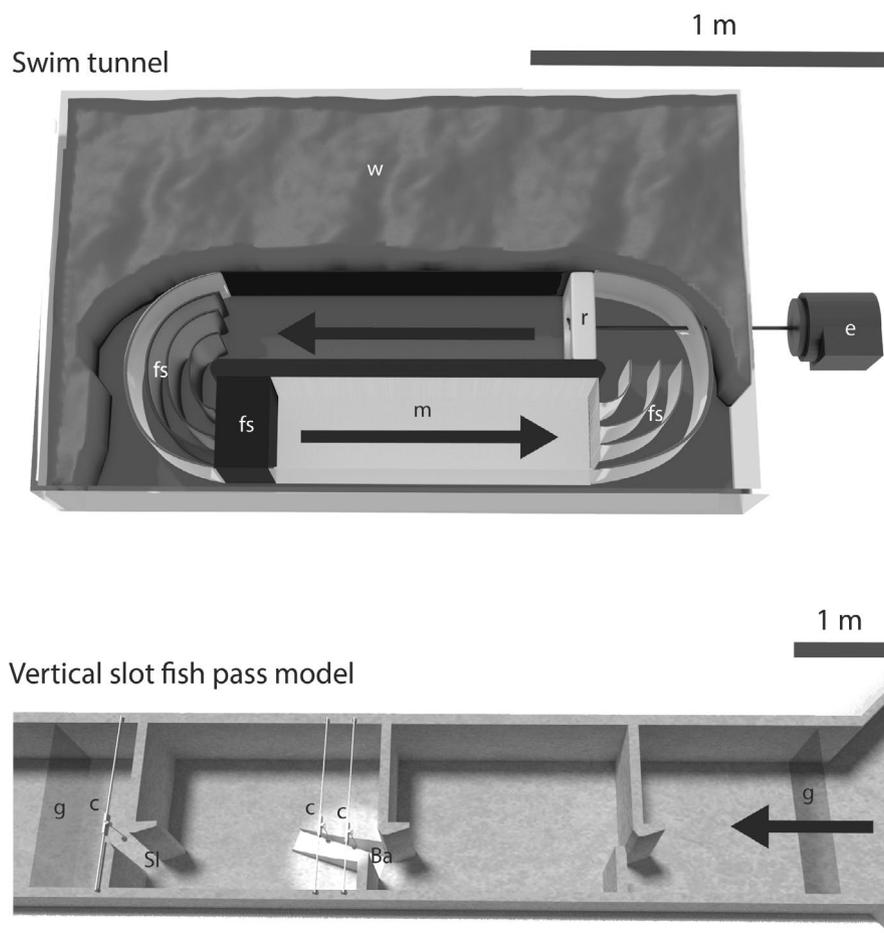
### 2.3.1 | Experiment 1: U<sub>crit</sub>

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<sub>sprint</sub>

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: $U_{\text{crit}}$

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 ( $U_{\text{crit}}$ ) 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: $U_{\text{sprint}}$

As with  $U_{\text{crit}}$  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.

$U_{\text{sprint}}$  was calculated analogous to  $U_{\text{crit}}$ :

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

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  $U_{\text{crit}}$  and  $U_{\text{sprint}}$ , we used an ANCOVA with species as the categorical predictor variable and the recorded  $U_{\text{crit}}$  and  $U_{\text{sprint}}$  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  $U_{\text{crit}}$  and  $U_{\text{sprint}}$ , 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  $U_{\text{crit}}$ , 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).

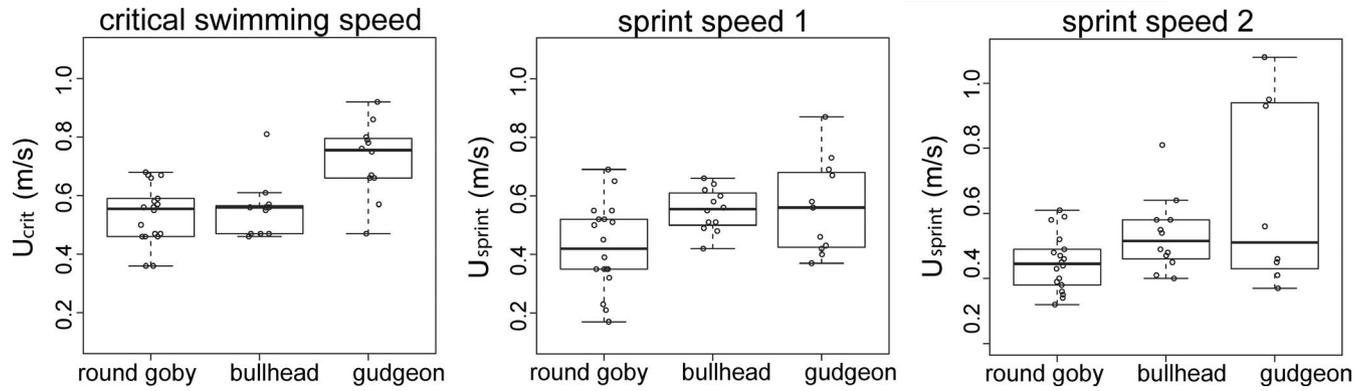
To statistically compare the capability of the three species to ascend across the barrier and through the unaltered slot, we performed Chi-squared tests for the passage rate, which was the most important categorical outcome. This allowed us to test the observed passage rates in all three species against 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

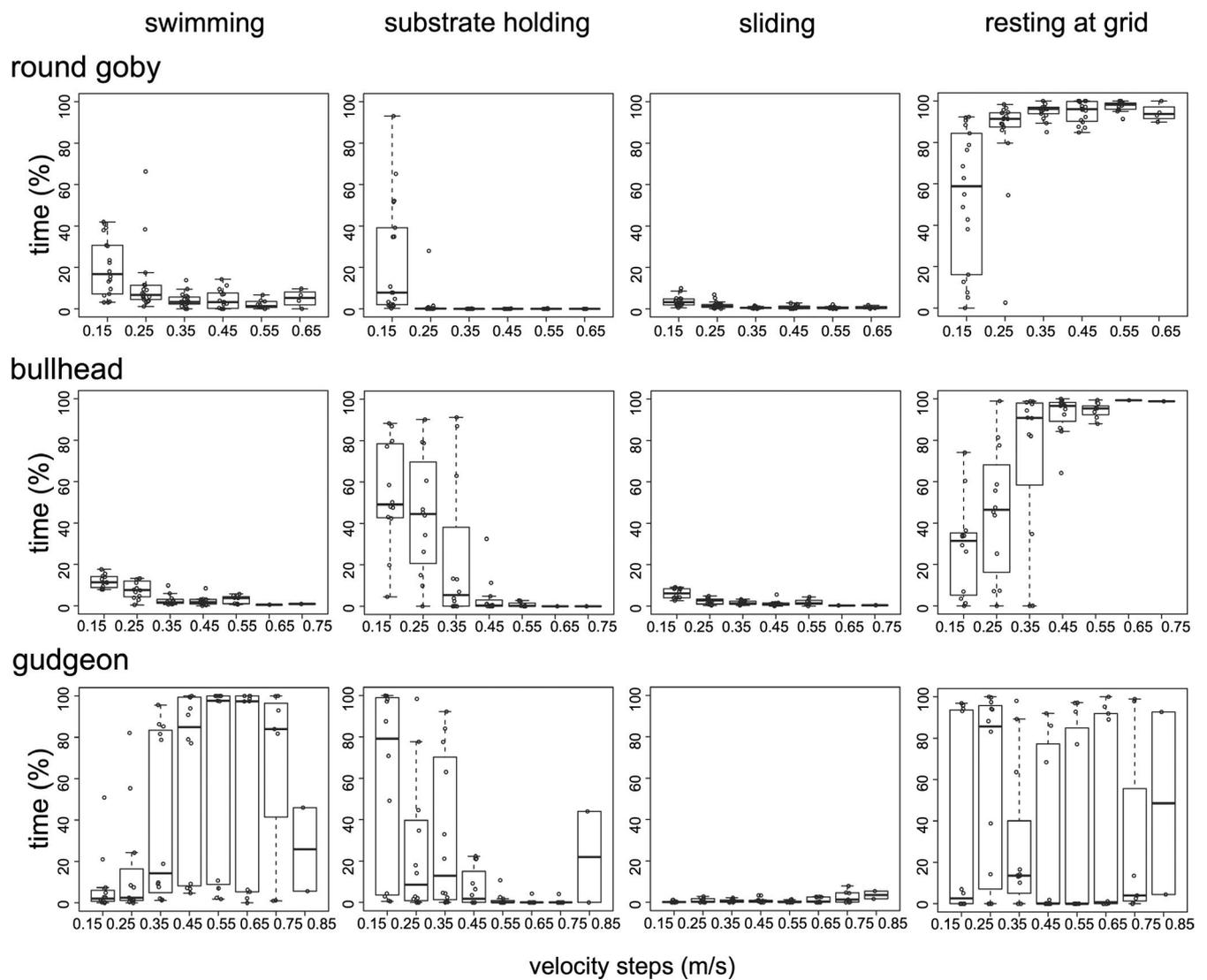
### 3.1 | Benthic fish swimming performance and behaviour

#### 3.1.1 | Experiment 1: $U_{\text{crit}}$

Gudgeon reached the highest  $U_{\text{crit}}$  values with  $0.72 \pm 0.13$  m/s ( $N = 12$ ), followed by bullhead ( $0.55 \pm 0.10$  m/s;  $N = 12$ ), and round goby ( $0.54 \pm 0.10$  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).

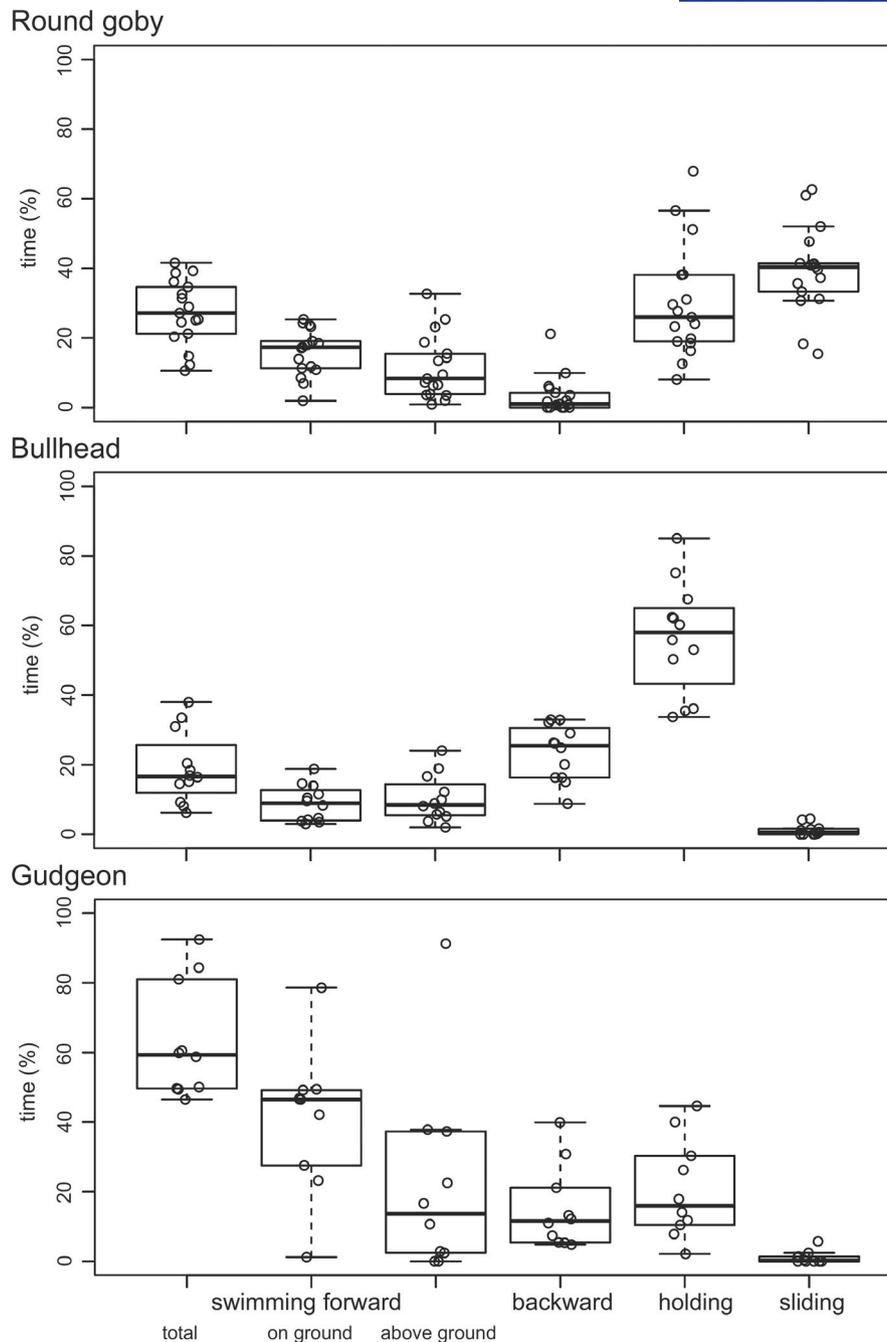
During  $U_{crit}$  trials, all three species spent on average less than 20 % of the time swimming in the first and second velocity increment (0.15 m/s and 0.25 m/s, respectively, see Figure 3). While bullhead and round goby spent even less time swimming with increasing water velocities ( $\geq 0.25$  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  $0.56 \pm 0.16$  m/s ( $N = 11$ ) and  $0.55 \pm 0.07$  m/s ( $N = 12$ ), respectively, and a lower sprint swimming performance for round goby with  $0.43 \pm 0.14$  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 ( $0.53 \pm 0.11$  and  $0.45 \pm 0.09$  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  $U_{\text{sprint}}$  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.

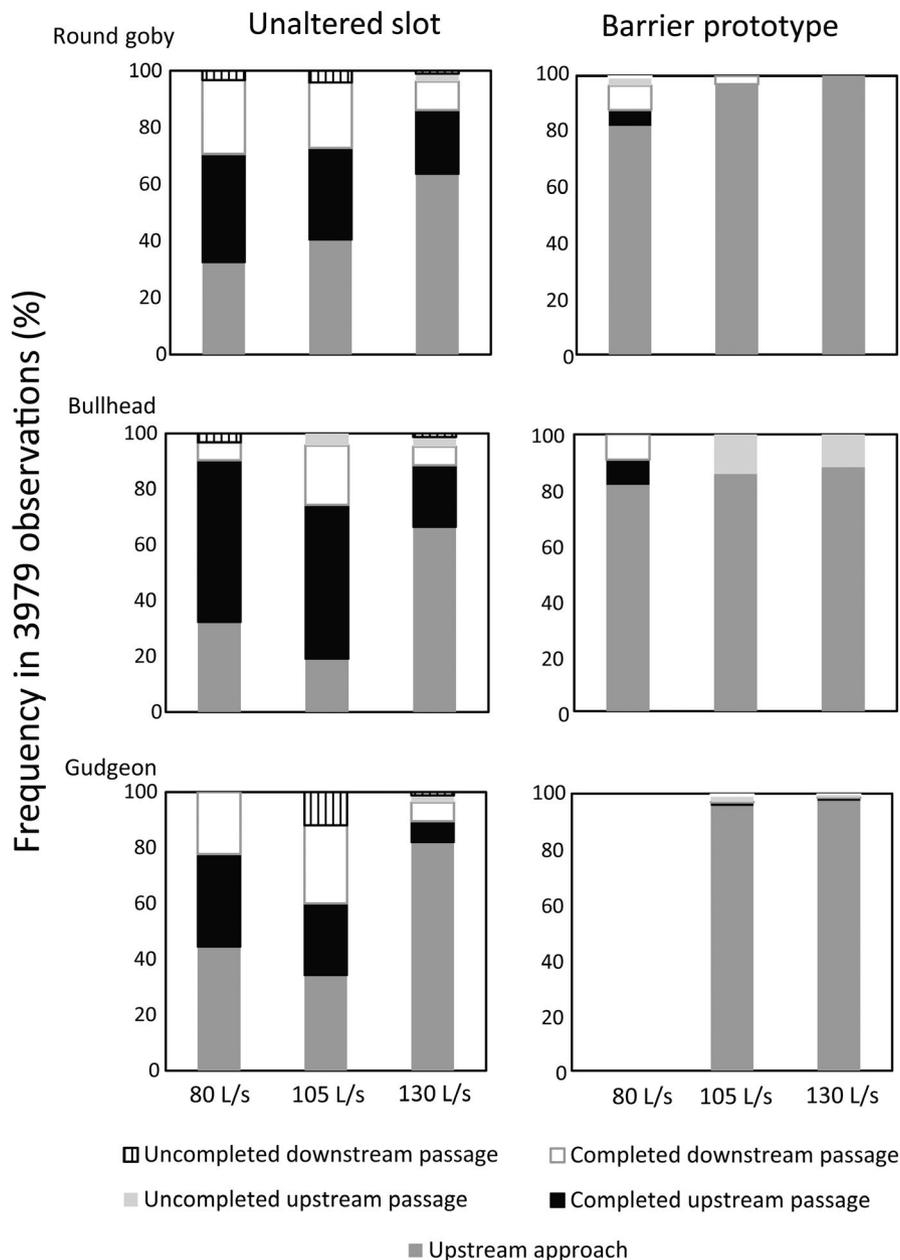
The majority (64 %) of events was recorded for gudgeon, while 28 % of the detected events were recorded for round goby and only 7 % of events were recorded for bullhead. The most frequent events were approaches of fish towards the unaltered slot or the barrier slot (Figure 5). For all three species tested, 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.

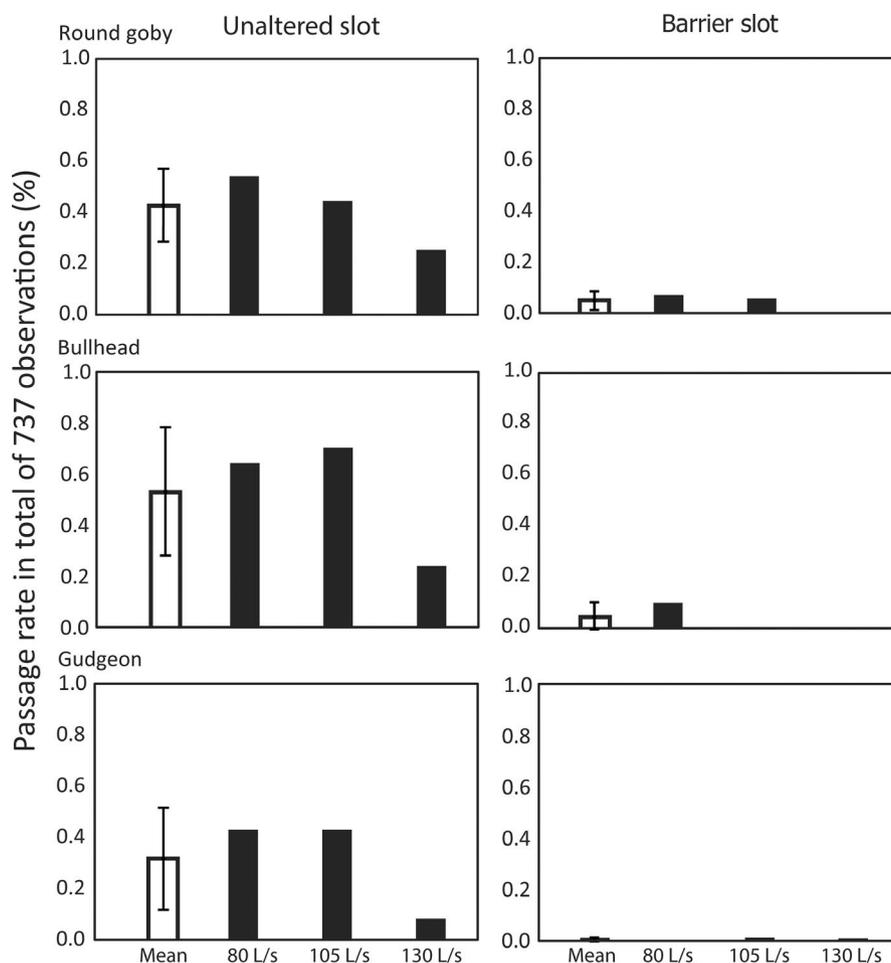
## 4 | DISCUSSION

### 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>	$\chi^2$	<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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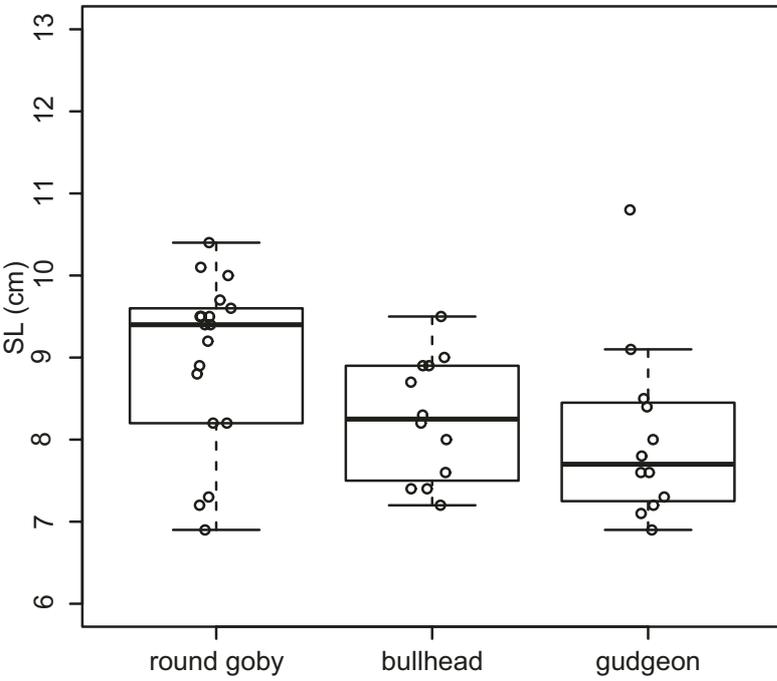
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## SUPPORTING INFORMATION

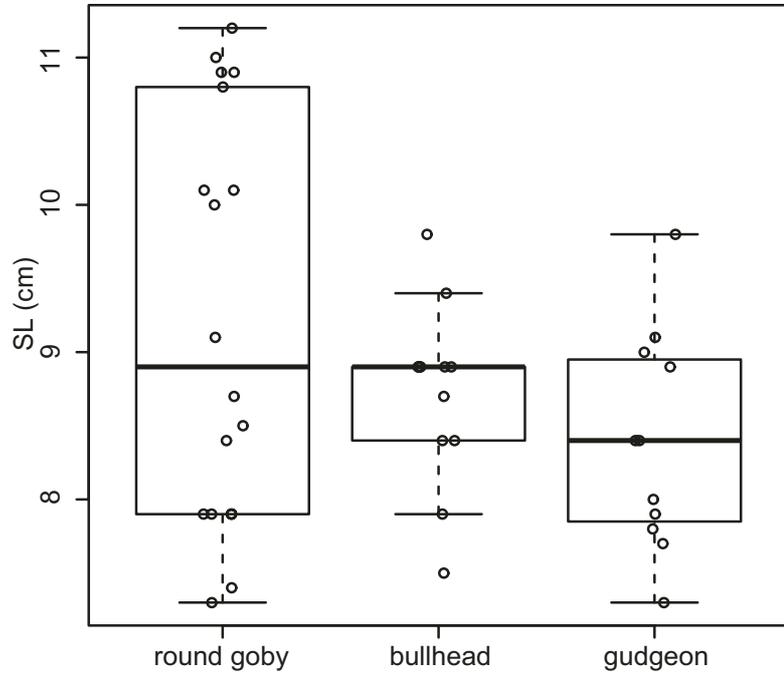
Additional supporting information may be found online in the Supporting Information section.

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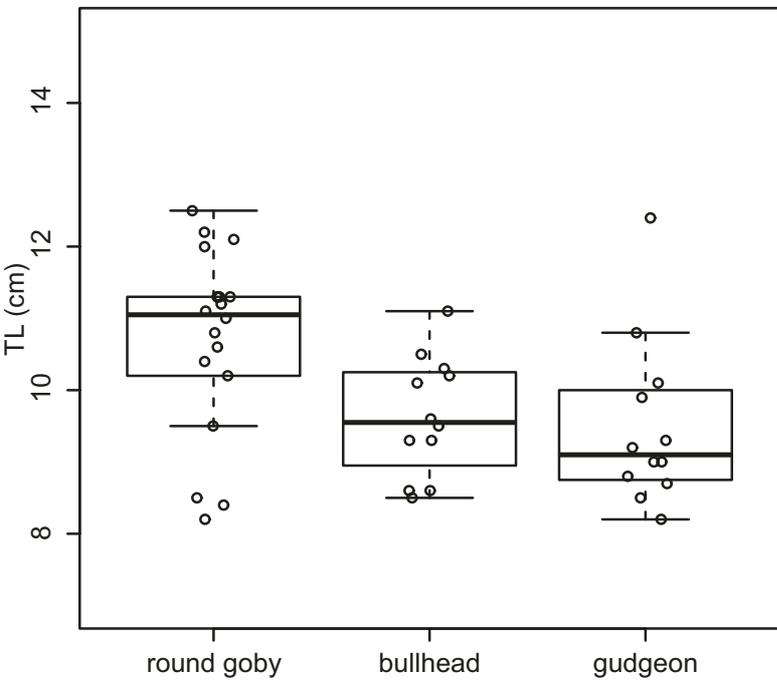
Ucrit standard length



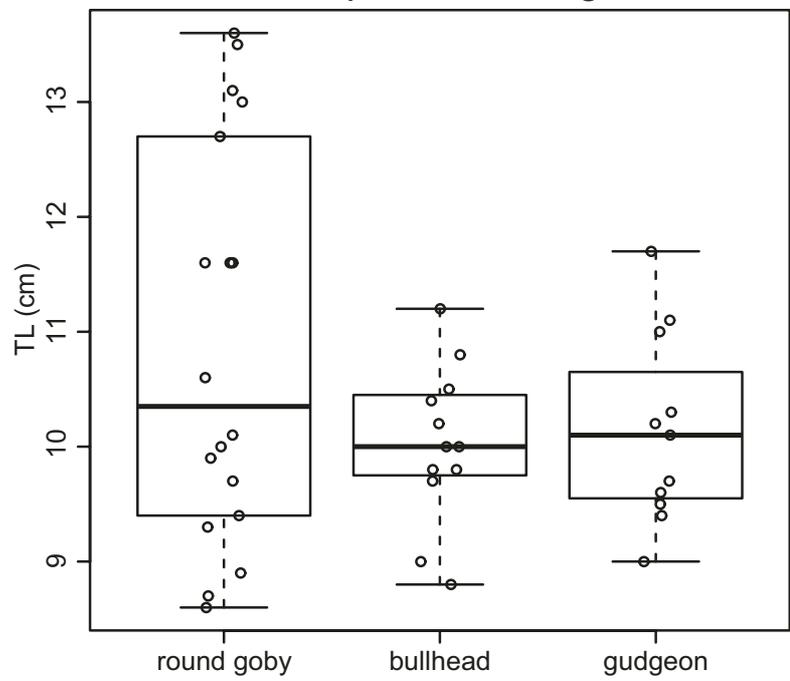
Usprint standard length



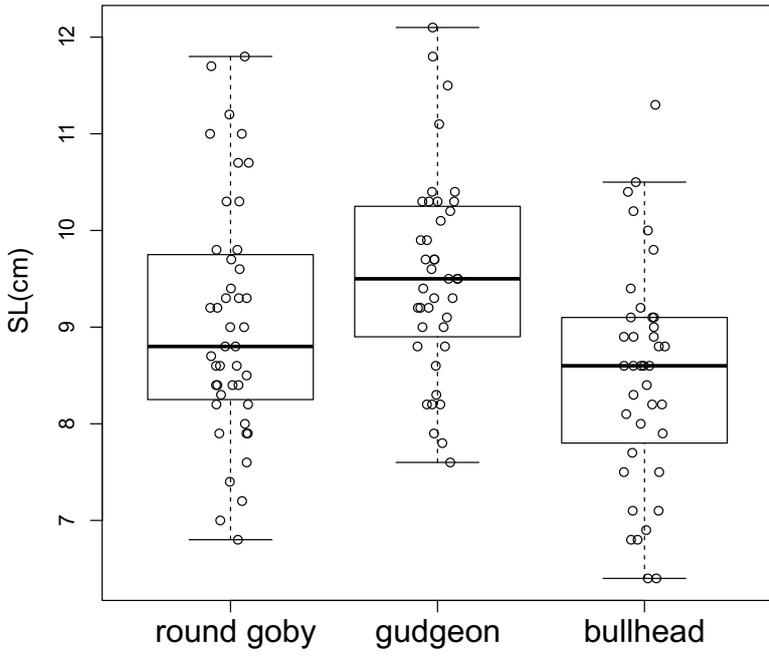
Ucrit total length



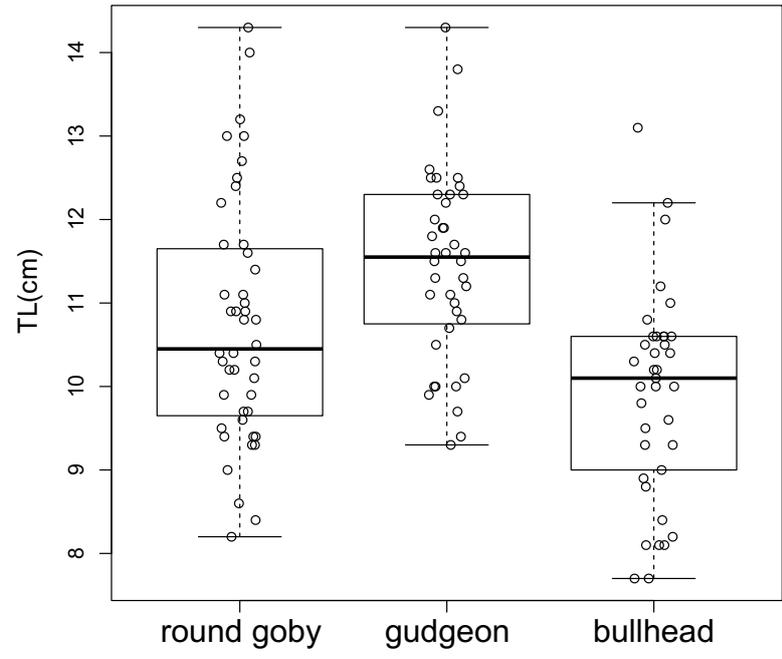
Usprint total length



vertical slot pass - standard length



vertical slot pass - total length



## Supplementary Table 1

Pearson correlations between swimming speed (either Ucrit or Usprint) and standard length (SL), total length (TL) and weight (W), analyzed for the whole dataset and species-specific subsets.

correlation	dataset	t	df	p-value	lower 95% CI	upper 95% CI	corr
Ucrit / SL	whole	-0.93056	40	0.35770	-0.4304546	0.165694	-0.14557
Ucrit / TL	whole	-0.68314	40	0.49850	-0.398319	0.203174	-0.10739
Ucrit / SL	bullhead	-0.6500	10	0.53040	-0.6949322	0.421250	-0.20132
Ucrit / TL	bullhead	0.11099	10	0.91380	-0.5498943	0.596961	0.03508
Ucrit / SL	gudgeon	-0.48549	10	0.63780	-0.667517	0.462426	-0.15175
Ucrit / TL	gudgeon	-0.49699	10	0.62990	-0.669504	0.459596	-0.15526
Ucrit / SL	round goby	1.75500	16	0.09838	-0.080111	0.731450	0.40179
Ucrit / TL	round goby	1.65950	16	0.11650	-0.101898	0.721069	0.38320
Usprint1 / W	whole	-3.40730	39	0.00154	-0.685581	-0.200903	-0.47895
Usprint1 / SL	whole	-2.70470	39	0.01008	-0.628259	-0.102280	-0.39743
Usprint1 / TL	whole	-2.89220	39	0.00623	-0.644559	-0.129309	-0.42024
Usprint1 / W	bullhead	0.43858	10	0.67030	-0.473888	0.659298	0.13737
Usprint1 / SL	bullhead	0.04974	10	0.96130	-0.563258	0.584355	0.01573
Usprint1 / TL	bullhead	0.30881	10	0.76380	-0.504872	0.635638	0.09719
Usprint1 / W	gudgeon	-0.28658	9	0.78090	-0.657463	0.535319	-0.09509
Usprint1 / SL	gudgeon	-0.29476	9	0.77490	-0.659003	0.533378	-0.09778
Usprint1 / TL	gudgeon	-0.57533	9	0.57920	-0.708205	0.463948	-0.18835
Usprint1 / W	round goby	-2.30600	16	0.03483	-0.783604	-0.042494	-0.49946
Usprint1 / SL	round goby	-1.97680	16	0.06557	-0.753960	0.030043	-0.44304
Usprint1 / TL	round goby	-2.07880	16	0.05408	-0.763612	0.007298	-0.46114
Usprint2 / W	whole	-1.61280	36	0.11550	-0.534877	0.065543	-0.25958
Usprint2 / SL	whole	-1.04590	36	0.30260	-0.465838	0.156549	-0.17173
Usprint2 / TL	whole	-0.85234	36	0.39970	-0.440521	0.187468	-0.14064
Usprint2 / W	bullhead	0.97629	10	0.35190	-0.335753	0.743090	0.29499
Usprint2 / SL	bullhead	0.23310	10	0.82040	-0.522428	0.621207	0.07351
Usprint2 / TL	bullhead	0.54366	10	0.59860	-0.448032	0.677462	0.16944
Usprint2 / W	gudgeon	0.67193	6	0.52660	-0.540978	0.816927	0.26454
Usprint2 / SL	gudgeon	0.68744	6	0.51750	-0.536648	0.818946	0.27021
Usprint2 / TL	gudgeon	0.70634	6	0.50650	-0.531342	0.821376	0.27707
Usprint2 / W	round goby	-1.13350	16	0.27370	-0.656015	0.222548	-0.27265
Usprint2 / SL	round goby	-1.20640	16	0.24520	-0.665857	0.205873	-0.28875
Usprint2 / TL	round goby	-1.29990	16	0.21200	-0.678094	0.184409	-0.30907

### Supplementary Material Table 2

Summary table of statistical descriptors of the nested ANCOVA for the  $U_{crit}$  data. The model was designed to test for statistical differences across the species in the different behaviour categories (swimming, station holding, falling backwards, resting at rear end of grid) nested in the velocity steps, nested within the species. The individuals' standard length was used as a co-variable.

	<b>swimming</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length (cm) <i>(co-variable)</i>	Fixed	1	13212.47	190	520.97	25.36	<0.0001
Species <i>(categorical predictor)</i>	Fixed	2	21056.80	190	520.97	40.42	<0.0001
Velocity steps <i>(nested within Species)</i>	Fixed	15	2790.74	190	520.97	5.36	<0.0001

	<b>station holding</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length (cm) <i>(co-variable)</i>	Fixed	1	1252.01	190	497.88	2.52	0.114452
Species <i>(categorical predictor)</i>	Fixed	2	8879.11	190	497.88	17.83	<0.0001
Velocity steps <i>(nested within Species)</i>	Fixed	15	4095.51	190	497.88	8.23	<0.0001

	<b>sliding</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length (cm) <i>(co-variable)</i>	Fixed	1	1.95	190	1.88	1.04	0.3094
Species <i>(categorical predictor)</i>	Fixed	2	64.95	190	1.88	34.55	<0.0001
Velocity steps <i>(nested within Species)</i>	Fixed	15	21.07	190	1.88	11.21	<0.0001

	<b>resting at grid</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length (cm) <i>(co-variable)</i>	Fixed	1	9700.91	190	2461.62	3.94	0.0486
Species <i>(categorical predictor)</i>	Fixed	2	26197.96	190	2461.62	10.64	<0.0001
Velocity steps <i>(nested within Species)</i>	Fixed	15	5194.61	190	2461.62	2.11	0.0110

## Supplementary Material Table 2

Summary table of statistical descriptors of the ANCOVA for the  $U_{\text{sprint}}$  data. The model was designed to test for statistical differences across the species in the different behaviour categories (swimming forward on the ground, swimming forward above ground, backward active swimming, backward slide, station holding). The individuals' standard length was used as a co-variable.

	<b>swimming forward on the ground</b>						
	Effect	df Effect	MS Effect	d Error	MS Error	F	p
Standard length (co-variable)	Fixed	1	238.17	35	134.92	1.76527	0.1926
Species (categorical predictor)	Fixed	2	3001.81	35	134.92	22.24894	0.000001

	<b>swimming forward above ground</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length (co-variable)	Fixed	1	49.38	35	256.45	0.192546	0.6635
Species (categorical predictor)	Fixed	2	451.85	35	256.45	1.761962	0.1866

	<b>backward active swimming</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length (co-variable)	Fixed	1	83.43	35	13.24	6.30	0.0168
Species (categorical predictor)	Fixed	2	9.70	35	13.24	0.73	0.4879

	<b>backward_slide</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length ( <i>co-variable</i> )	Fixed	1	398.13	35	127.13	3.13	0.0855
Species ( <i>categorical predictor</i> )	Fixed	2	1864.72	35	127.13	14.67	0.00002

	<b>station holding</b>						
	Effect	df Effect	MS Effect	df Error	MS Error	F	p
Standard length ( <i>co-variable</i> )	Fixed	1	44.02	35	248.16	0.18	0.6762
Species ( <i>categorical predictor</i> )	Fixed	2	4030.58	35	248.16	16.24	0.00001

#### Supplementary Material Table 4

The number of behavioural events for round goby, bullhead and gudgeon at the unaltered slot and the barrier slot at different water discharge rates in the vertical slot model.

**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, 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, but did not leave it downstream. Instead, the fish left the field of view in the upstream direction.

**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.

location	species	replicate	discharge rate (l/s)	completed upstream passage	completed downstream passage	uncompleted upstream passage	uncompleted downstream passage	approach	sum
slot	round goby		80	72	49	0	6	61	188
slot	gudgeon		80	3	2	0	0	4	9
slot	bullhead		80	18	2	0	1	10	31
slot	round goby		105	56	40	0	7	70	173
slot	gudgeon		105	75	82	0	35	100	292
slot	bullhead		105	26	10	2	0	9	47
slot	round goby	1	130	26	14	2	2	101	145
slot	gudgeon	1	130	36	34	9	6	315	400
slot	bullhead	1	130	12	6	0	2	29	49
slot	round goby	2	130	21	9	5	0	54	89
slot	gudgeon	2	130	25	17	10	2	277	331
slot	bullhead	2	130	4	1	3	0	32	40
slot	round goby	3	130	20	7	1	1	34	63
slot	gudgeon	3	130	24	25	9	6	326	390
slot	bullhead	3	130	17	3	2	0	38	60
slot	round goby	mean	130	22	10	3	1	63	99
slot	gudgeon	mean	130	28	25	9	5	306	374
slot	bullhead	mean	130	11	3	2	1	33	50
barrier	round goby		80	11	15	5	1	140	172
barrier	gudgeon		80						
barrier	bullhead		80	2	2			18	22
barrier	round goby		105	4	2			65	71
barrier	gudgeon		105	7	1	12	4	508	532
barrier	bullhead		105			1		6	7
barrier	round goby	1	130					34	34
barrier	gudgeon	1	130	4	1	5		222	232
barrier	bullhead	1	130			2		6	8
barrier	round goby	2	130					15	15
barrier	gudgeon	2	130	2		1	1	260	264
barrier	bullhead	2	130			1		14	15
barrier	round goby	3	130					42	42
barrier	gudgeon	3	130			1		91	92
barrier	bullhead	3	130			1		10	11
barrier	round goby	mean	130	0	0	0	0	30	30
barrier	gudgeon	mean	130	2	0	2	0	191	196
barrier	bullhead	mean	130	0	0	1	0	10	11

Flow, force, behaviour: Assessment of a  
prototype hydraulic barrier for invasive fish

Paper III

# Flow, force, behaviour: Assessment of a prototype hydraulic barrier for invasive fish

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Key words: tracking, hydraulic forces, swimming performance, fish pass, invasive species, random forest

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# Abstract

Migration barriers being selective for invasive species could protect pristine upstream areas. We designed and tested a prototype protective barrier in a vertical slot fish pass. Based on the individuals' swimming responses to the barrier flow field, we assumed this barrier would block the ascension of the invasive round goby, but allow comparable native species (gudgeon and bullhead) to ascend. The barrier was tested in three steps: flow description, quantification of forces experienced by preserved fish in the flow field, and tracking the swimming trajectories of ca. 43 live fish per trial and species. The flow and the forces were homogenous over the barrier, though gudgeon experienced significantly smaller forces than round goby or bullhead. The swimming trajectories were distinct enough to predict the fish species with a random forest machine learning approach (92.16% accuracy for gudgeon and 85.24% for round goby). The trajectories revealed round goby and gudgeon exhibited increased, but varied, swimming speeds and straighter paths at higher water discharge. These results suggest that passage of round goby was prevented at 130 L/s water discharge, whereas gudgeon and bullhead could pass the barrier. Our findings open a new avenue of research on hydraulic constructions for species conservation.

# Introduction

The majority of the world's rivers are fragmented by anthropogenic barriers (Belletti et al., 2020). The passage of fish across such barriers is crucial to ecological river connectivity and the functionality of aquatic ecosystems (Silva et al., 2018). Traditionally, various types of fish passes have been designed to support the passage of economically relevant fish species (Katopodis and Williams, 2012). However, fish pass design increasingly needs to respond to the demands for protection of specific species (United Nations, 1992). This often means meeting the individual requirements of native species for conservation purposes and, at the same time, hindering the upstream migration of invasive species. Therefore, a

combination of research approaches from fluid dynamics, engineering and behavioural ecology is necessary to account for the individual differences in swimming performance between species (Kemp, 2012). This idea has been implemented in studies applying robotics to describe basic fish swimming kinematics (Thandiackal et al., 2021) or studies linking flow measurements with the swimming behaviour of fish (Drucker and Lauder, 1999; Sagnes and Statzner, 2009; Porreca et al., 2017). Subsequent studies have focused on fish pass hydraulics (Larinier, 2008; Tsikata et al., 2014; Baki et al., 2017) or species compositions and fish swimming behaviour in fish passes (Jansen et al., 1999; Aarestrup et al., 2003; Knaepkens et al., 2005).

Substantial advances in our understanding of hydrodynamics in fish passes have been achieved in recent years (David et al., 2010; Puertaa et al., 2004; Wang, Bombač et al., 2014; Fuentes-Pérez et al., 2018), including estimates of passage rates based on computational modelling and flow velocity measurements (Plesiński et al., 2018; Sanchez et al., 2020). While some studies have numerically derived the hydrodynamics of fish from flow observations (Drucker and Lauder, 1999; Lauder and Madden, 2007; Carlson and Lauder, 2011), direct empirical measures of the forces experienced by fish in flowing water remain scarce (though see Van Wassenbergh et al., (2015) and Quicazan-Rubio et al., (2019) for recent advances).

To fill this knowledge gap on direct quantifications of the physical impact of flow on the swimming behaviour of fish, we combined hydrodynamics and fish behaviour observations into a unified three-step approach (Fig. 1) by characterising the flow field created by a specific fish pass design (Step 1), determining the physical effects of the flow on preserved individuals of specific target species (Step 2), and describing the behavioural responses of live fish in the same flow field (Step 3). We proposed this combinatory flow-force-behaviour approach would facilitate characterization of the functionality of fish pass designs and enable more precise evaluations of the suitability of prototype barriers for specific target species.

We applied this approach in the context of the upstream migration of the invasive round goby (*Neogobius melanostomus* Pallas, 1814). The round goby is a very successful aquatic invasive species that has populated numerous North American and European aquatic habitats (Kornis et al., 2012; Adrian-Kalchhauser et al., 2020). The upstream range expansion of this species into ecologically valuable headwaters is a severe environmental threat that can lead to important and irreversible ecosystem impacts (Phillips et al., 2003; Myles-Gonzalez et al., 2015; Ramler and Keckeis, 2020; Šlapanský et al., 2020). Ensuring the passage of native species and impeding the passage of invasive species over river obstacles is a major challenge for decision makers and requires advances in integrated interdisciplinary research (Rahel and McLaughlin, 2018). Hoover et al. (2003) tested the upstream swimming capabilities of round goby and questioned whether a hydraulic barrier could stop the upstream range expansion of this species. The same authors reported a hydraulic barrier for round goby—a bottom-dwelling species—would require an increased flow velocity, as well as an extended length of smooth substrate (Hoover et al., 2003b). The design of a hydraulic barrier, similar to Kerr et al. (2021), that can prevent the upstream movement of round goby, would be simple to realize, but ground-breaking achievement in conservation science. This idea of a selective hydraulic barrier was implemented in our prototype.

The present study follows our previous fish ecological experiments, in which we compared the upstream swimming performance of the round goby and two native species that inhabit the same or similar habitats and are described as benthic (bullhead, *Cottus gobio* L.) or semi-pelagic (gudgeon, *Gobio gobio* L.) swimmers (Egger et al., 2020). Based on these initial observations of swimming performance and upstream dispersal success, we now aimed to achieve a deeper mechanistic insight into the parameters that determine the species-specificity of a hydraulic barrier by comparing the impact of a prototype barrier vertical slot fish pass model on round goby, gudgeon and bullhead.

This evaluation fills an important research gap by providing data on a key component required to understand the behavioural responses of fish swimming in flow: The force the flow exerts on the fish body. For example, Li et al. (2021) investigated the swimming behaviour of *Schizothorax prenanti* when

swimming upstream a vertical slot and found behavioural adaptation to local flow patterns. We assumed that this behavioural response to flow might depend on individual body shape characteristics of the species. Therefore, we measured the forces experienced by real, preserved fish bodies to compare the hydrodynamic burden the different species experience based on the sum of their morphological characteristics (Wiegleb et al., 2020). Such variations in the forces experienced and swimming behaviour between species could provide the basis of a barrier prototype that provides species-specific passage.

The scientific logic behind our approach was to assess the functionality of the barrier with application of the three steps mentioned above: We described the flow to check whether we created a homogenous flow field over the barrier. The force measurements were expected to show differences in the hydrodynamics induced by the flow field between the species. We then compared the forces experienced by the fish with the swimming behaviour of live fish over the barrier to check whether the forces experienced by the fish over the barrier had an effect on the swimming behaviour. If yes, we assumed the barrier design created hydraulic conditions affecting the swimming behaviour of the tested fish species differently, impairing the passage of round goby whilst allowing native species to ascend in the best case. Overall, the research question was: Can the hydrodynamics within a barrier prevent the upstream passage of round goby while allowing passage to native, comparable species?

## Materials and Methods

### *Fish catch, maintenance and ethical approval*

We analysed video recordings of the swimming behaviour of live fish from a previous study (Egger et al., 2020) (experiments at Karlsruhe Institute of Technology). Bullhead and gudgeon were sampled in the River Alb in Karlsruhe by means of electrofishing for this study. The fish were immediately transported to the Karlsruher Institute for Technology, Germany (KIT). Round gobies were sampled between 22 and 29 March 2019 in the High Rhine in Basel, Switzerland, using minnow traps baited with dog food (Frolic)

and transported to the KIT. Details about the fish catchments and maintenance are provided in Egger et al. (2020).

### *Barrier design and flow channel setup*

All experiments were performed using a vertical slot fish pass model (scale 1:1.6) at the Theodor-Rehbock Hydraulic Engineering Laboratory at the KIT (Fig. 2). To record fish movements, we installed cameras in one vertical slot of the fish pass, above the prototype hydraulic barrier. The hydraulic barrier consisted of a three-dimensional stainless-steel structure (length: 1 m, width: 24 cm, roughness [ $k$ ] = 0.015 mm) made of 3 mm sheets. The hydraulic barrier was aligned to the direction of flow in the vertical slot fish pass and placed at an angle of 70 degrees to the partition walls to extend the field with the highest flow velocity created by the partition walls. To force the fish to travel the full length of the smooth barrier surface and maintain the withholding effect of the barrier, the barrier had two sidewalls that prevented fish from entering the barrier from the side. The height of the lateral walls of the barrier decreased with the direction of flow (0.75 m at the slot, 0.20 m in the centre [located 0.55 m from the end of the structure]) to increase stability of the barrier in the flow and to avoid flapping of the side walls (Fig. 2). The barrier was designed to geometrically separate the outflowing jet from the water body in the basin and the corresponding shear layer and prevent the fish from station holding due to its smooth surface. The experiments followed the protocol described by (Egger et al., 2020). After adjustment to the desired water discharge rate, the fish were released at the downstream end of the fish pass and able to move within the setup for two hours unaffected by human presence. Video footage was recorded for subsequent analysis. Because water discharges can vary in real vertical slot fish passes, we included three different water discharges (80, 105 and 130 L/s) in our experiments. The two lower discharge rates were chosen to increase the probability of recording migration behaviour of the live fish, because, based on previous research, they did not pose a challenge to the swimming capacities of the tested species (Egger et al., 2020). The 130 L/s water discharge was included in the experiment because we found this discharge led

to the most representative flow velocities compared to actual best-practice vertical slot fish passes (Bombač et al., 2017); thus, we focused our analyses on the data collected at 130 L/s water discharge. Flow and behavioural data were collected for all water discharges tested, while force data were only collected at 130 and 80 L/s.

*Step 1: Measurement of flow in the prototype hydraulic barrier*

The velocity in the prototype barrier was measured at 14 points (Fig. 3) as close as possible to the ground (2–3 cm) using an acoustic Doppler ADV probe (Vectrino, Nortek) for five minutes at every point at a nominal velocity range of 1.0 and 2.5 m/s, measurement volume of 7 mm<sup>3</sup> and sampling rate of 25 Hz. Flow data were processed using WinADV32 (V.2.031) and MATLAB 2019 to compute mean velocities, standard deviations and turbulent kinetic energy (TKE) for comparison with the force data (Supplementary Material 1).

*Step 2: Measurement of forces experienced by preserved fish in the prototype barrier*

Fish from previous behaviour experiments were euthanized with an overdose of MS 222 after the live fish swimming experiment, transferred to the lab at the University of Basel on ice and preserved in formalin and ethanol as described previously (Wiegler et al. 2020) (non-spread fins treatment). These preserved fish were employed in our experiments, rather than 3D-printed models of scanned fish in other studies (Van Wassenbergh et al., 2015), to provide a closer approximation of real fish bodies.

For the force measurements, we selected similarly sized samples of the three fish species. To account for variation within species, we replicated the force measurements using 5-7 individuals ( $n = 7$  at 130 L/s and  $n = 5$  at 80 L/s water discharge) of similar size-classes (see below) for every species. The fixation stick for the force measurements was inserted in the assumed centre of gravity of the fish body (Quicazan-

Rubio et al., 2019). The mean wet weight ( $W_w$ ) of round goby was 18.14 g ( $\pm$  9.01 standard deviation [SD]) and the mean total length ( $T_L$ ) was 11.0 cm ( $\pm$  1.7 SD). The mean  $W_w$  of gudgeon was 9.78 g ( $\pm$  2.89 SD) and the mean  $T_L$  was 11.6 ( $\pm$  1.0 SD), while the mean  $W_w$  of bullhead was 10.31 g ( $\pm$  3.19 SD) and the mean  $T_L$  was 9.8 cm ( $\pm$  1.0 SD).

The forces acting on the preserved round goby, bullhead and gudgeon in the flow field were measured using a water-resistant (IP 68) Nano17 Multi-Axis-F/T-Sensor (Schunk®) to determine the forces in three dimensions at a sampling rate of 1000 Hz. The multi-axis-force-torque-sensor was integrated in a stable PVC (polyvinyl-chloride) probe (Fig. 2), which sheltered the sensor against flow. The probe was installed at the same electronic carriage used for the flow measurements and approached the same measurement positions to ensure maximal comparability between force- and flow measurements. When submerging the sensor over the first measurement point, a ventile at the top of the probe was opened manually, allowing the water to enter the probe. When the water level inside the probe achieved the outside water level, we closed the ventile for the duration of the experimental run until the probe was lifted out of the water. This avoided water level, and thereby pressure, fluctuation in the probe which would have had an impact on the force measurement.

There was a connection from the sensor to the tested fish via a 10 cm long and 3 mm thick brass fixation stick (Fig. 2). This stick acted as a lever which transduced the force acting at the fish to the sensor, similar to earlier research (Wiegleb et al. 2020). For the measurement, the fish was positioned over the measurement point with a distance of 1 to 2 cm to the ground. This distance was chosen to avoid physical contact between fish and bottom every time because this would affect the force measurement through friction forces. The fish were always oriented with the head against the flow in the same angle as the hydraulic barrier ( $70^\circ$  to the partition walls).

The detected forces in three directions ( $F_x$ : cranial-caudal axis of the fish,  $F_y$ : left lateral and right lateral side of the fish,  $F_z$ : vertical axis) were used to compute the force acting at one time in three dimensional space applying the Pythagorean Theorem, resulting in the 3D-force ( $F_{3D}$ ).

$$F_{XY} = \sqrt{F_X^2 + F_Y^2}$$

$$F_{3D} = \sqrt{F_{XY}^2 + F_Z^2}$$

With  $F_{XY}$  being the force experienced by the fish on the  $F_X$  and  $F_Y$  plane (Supplementary Material 2, 3).

After transformation of the measured forces (force [N]<sup>-1.55</sup>) to approximate normal distributions, repeated measures one-way ANOVA was performed for the forces measured at different positions and pairwise comparisons were used to test for differences between species. Spearman's rank correlations were applied to test the relationships between the forces acting on the fish and flow measured at the corresponding measurement position.

### *Step 3: Observation of the behaviour of live fish over the prototype barrier*

To obtain a deeper understanding of the dependency of swimming behaviour on the flow conditions and the forces experienced by the preserved fish bodies in flow, we recorded the swimming behaviour of 39 - 45 live fish per species (round goby  $T_L = 10.43 \text{ cm} \pm 1.28 \text{ SD}$ , gudgeon  $T_L = 11.46 \text{ cm} \pm 1.13 \text{ SD}$  and bullhead  $T_L = 9.91 \text{ cm} \pm 1.22 \text{ SD}$ ) on the hydraulic barrier prototype. The behaviour of the fish was recorded using two IP 68 cameras (Security-Center IR CCTV-Camera, 380 TV-lines; Abus, Wetter, Germany) positioned vertically over the barrier (40 and 42 cm above). The cameras were placed the maximum vertical distance away from the barrier to achieve a large field of view while keeping the lenses of the cameras under water to obtain clear footage with minimal air bubble impact. The videos were recorded using Debut v 5.46 © NCH software and video processing was performed in Blender 2.79 (Community, 2017). With this program, the fish trajectories were manually recorded and event types were classified by one investigator as 'passage', 'uncompleted passage', 'return', 'uncompleted return' and 'approach' according to the criteria described in Supplementary Material 4.

In a previous study, we showed that the numbers of each type of event differed significantly between species at a water discharge rate of 130 L/s; no passages of round goby or bullhead through the barrier prototype were observed, while gudgeon were able to pass the barrier (Egger et al., 2020), while we focused on the inter-species variation in the swimming trajectories in the present study. Therefore, we recorded the trajectories of the fish on and near the barrier (Supplementary Materials 5) and extracted the following features reported by McLean and Volponi (2018) from every trajectory to characterize the swimming behaviour: mean swimming speed [m/s], variation in speed represented by the SD of the swimming speed [m/s], maximum acceleration [m/s<sup>2</sup>], distance covered [cm], sinuosity and straightness (McLean and Skowron Volponi, 2018) (Supplementary Material 6, 7, 8). Previous research showed that these features provide in-depth insight into the movements of animals (McLean and Volponi, 2018). Subsequently, we performed principal component analysis, similarly to (McLean and Volponi, 2018), to reduce the number of dimensions and identify the features that explain most of the variation in the data; 95% confidence ellipses were computed to visually compare the behaviour events observed for each species.

We then used a random forest model to mathematically assess whether the swimming trajectories are distinct enough between species to allow for a discrimination between species. The model ('randomForest' package in R) was designed, created, trained and validated to predict the fish species (response variable) exclusively with information about the trajectory features, event type and water discharge (predictor variables):

$$\text{species} \sim \text{flow} + \text{event type} + \text{mean swimming speed} + \text{variation in swimming speed} + \text{maximum acceleration} + \text{distance covered} + \text{sinuosity} + \text{straightness}$$

The model consisted of 50,000 trees with 6 (out of 8) variables randomly sampled at every node. To assess the model including all trajectories available, we performed cross validation and split the dataset

(131 trajectories) in three subsets of similar size (two subsets with 44 and one subset with 43 trajectories) with randomly selected tracks and equal proportion of trajectories recorded for round goby (47.33%), gudgeon (38.93%) and bullhead (13.74%) in every subset. This variation in trajectory frequency resulted from the varying number in the total data set of trajectories recorded for the different species. In the following, we combined two subsets to one training set which was used for training the model. This model was then validated by the third subset, which represented the test set. In sum, we trained the model three times with every subset serving as test set once it was trained with different combinations of the other subsets (Fig. 6).

Because we knew the species for all trajectories due to our study design, we were able to determine the mean accuracy over all trained models as the frequency of correctly predicted species from the total number of predictions. The importance of trajectory features were determined by the mean decrease in accuracy when excluding the variable while training [mda]. The ‘approach’ tracks reduced the model performance and were therefore excluded from the random forest approach. We included exclusively trajectories recorded over the barrier in this analysis.

# Results

## *Step 1: Flow over the prototype barrier*

The flow velocity varied over the barrier in terms of both speed (mean 0.91 m/s  $\pm$  0.08 SD) and TKE (mean 0.17 J/Kg  $\pm$  0.24 SD) (Supplementary Material 9). The flow speed was lower over the centre of the barrier than at both ends of the barrier, where we observed strong increases in velocity (1.11 m/s at position b1 and 0.99 m/s at position c5) and increases in TKE (0.66 J/Kg at c5, 0.58 J/Kg at b1, 0.51 J/Kg at c1 and 0.33 at a4; Fig. 3, Fig. 4B). The flow measurements revealed a moderate correlation between flow velocity and TKE ( $r = 0.78$ ,  $p < 0.01$ ; Fig. 4B) at 130 L/s water discharge (which is assumed representative for a prototype fish pass), indicating that the small-scale hydraulic properties (described by TKE) are not well represented in the mean velocities measured at the chosen points.

At 105 L/s water discharge, we observed a mean velocity of 0.70 m/s  $\pm$  0.05 SD with a mean TKE of 0.02 J/Kg  $\pm$  0.01 SD over the entire barrier (Supplementary Material 10). At 80 L/s, these values decreased to a mean velocity of 0.69 m/s  $\pm$  0.02 SD and mean TKE of 0.01 J/Kg  $\pm$  0.00 SD. There was a large increase in mean TKE (860%) between 105 and 130 L/s, while the mean velocity only increased by 29.47% between these discharges. In comparison, much smaller increases in velocity (1.45 %) and TKE (37.14 %) were observed between 80 and 105 L/s.

## *Step 2: Forces experienced by preserved fish over the prototype barrier*

We found gudgeon experienced significantly lower 3D-forces (mean 0.230 N  $\pm$  0.116) than the other species (round goby: 0.298 N  $\pm$  0.134, bullhead: 0.264 N  $\pm$  0.084) at 130 L/s water discharge (Fig. 4 A), with no significant differences observed between round gobies and bullhead (Supplementary Material 11). The corrected mean 3D-forces (reference force subtracted from the force measured for the fish) were 0.103 N  $\pm$  0.134 for round goby, 0.035 N  $\pm$  0.116 for gudgeon and 0.069 N  $\pm$  0.084 for bullhead at 130

L/s. At 80 L/s, we detected corrected mean 3D-forces of  $0.049 \text{ N} \pm 0.032$  for round goby,  $0.067 \text{ N} \pm 0.060$  for gudgeon and  $0.060 \text{ N} \pm 0.048$  for bullhead. When water discharge was increased from 80 to 130 L/s, the corrected mean 3D-forces for preserved round goby increased by 109% and 15% for bullhead, while they declined by 48% for gudgeon.

#### *Correlations between force and flow at 130 L/s water discharge*

In general, small but significant correlation coefficients were observed between the forces experienced by the preserved fish and the flow velocities at the corresponding measurement points in the barrier (Fig. 4A). This suggests a weak linear relationship between force and flow velocity in the barrier: although the flow velocity varied by a range of 0.30 m/s over the barrier, from a minimum of 0.81 m/s (position a1) to a maximum of 1.11 m/s (position b1), the forces measured for the preserved fish were similar between locations with strong and weak velocity. This suggests that the mean forces experienced by fish in the barrier did not correspond with the mean local flow velocity and the fish did not necessarily experience strong forces at locations with high velocity.

#### *Step 3: Swimming behaviour of live fish over the prototype barrier*

In total, 930 fish trajectories over or near the barrier were recorded and analysed (Supplementary Material 12, 13). The ‘passage’ trajectories observed at 130 L/s water discharge exhibited a homogenous spatial distribution over the barrier prototype for round goby and gudgeon (Fig. 5). In contrast, bullhead passed straight along the sides of the barrier at 130 L/s water discharge. Contrary to the ‘uncompleted passage’ trajectories of bullhead and gudgeon, most of the ‘uncompleted passage’ trajectories for round goby started at the upper right corner of camera 2 and left the lower left corner of the screen. This pattern, together with some round goby ‘passage’ trajectories entering the screen at the middle of the barrier (at 80 L/s), suggests gobies swam over the side walls of the barrier (Fig. 5). This behaviour was commonly

observed for round goby and may have been performed to reduce the distance needed to swim along the barrier for successful passage. All fish returned with relatively straight paths (Fig. 5, Supplementary Material 12) and immediately left the barrier swimming to the left or the right.

### *Principal component analysis*

The first principal component of the PCA explained 37.94% of the variation of all recorded trajectories and was best represented by the indices describing swimming speed ('mean speed', 'SD speed', 'maximum acceleration'), while the second principal component explained 18.06% of the variation and was best represented by the 'straightness' and 'sinuosity' indices. In general, the overlaid confidence ellipses in the PCA revealed the similarities of the trajectories assessment indices between the three species (Supplementary Material 14). The PCA was performed to obtain a general visual overview of the entire dataset based on 95% confidence ellipses. In general, the PCA suggested that the indices describing swimming speed ('mean speed', 'SD speed', 'maximal acceleration') better explain the variations in the 'passage' trajectories events for all species than 'sinuosity' and 'straightness'.

### *Random forest machine learning approach*

The random forest model predicted the species based on the trajectory features, the event type and the water discharge with an overall mean accuracy of 64.68%. For the different species, we achieved an accuracy of 85.24% for round goby, for gudgeon 92.16% and for bullhead 16.67% (Fig. 6). This shows that we were able to identify especially gudgeon and round goby only with information on swimming patterns (as represented by the trajectory features), the event type and the water discharge on a reliable level. The low prediction accuracy in bullhead is assumed to result from the decreased proportion of training trajectories for bullhead (13.74%) of the entire data set compared to round goby (47.33%) and gudgeon (38.93%).

With regard to the variable importance (represented by the mean decrease in accuracy when excluding the variable while training [mda]), we found the water discharge (mean 605.57 mda), distance (mean 112.80 mda) and event type (mean 55.32 mda) to be the most important variables for the accuracy of the model. The least important variables were variation in speed (mean 3.28 mda), mean speed (mean 23.28 mda) and sinuosity (mean 30.36 mda). The mean importance of the remaining predictor variables was 35.90 mda for straightness and 32.67 mda for maximum acceleration.

### *Comparison of 'passage' trajectories between species and water discharges*

The feature boxplots for only the 'passage' trajectories revealed similar overall behaviour between species, with adaptations in swimming behaviour to increased water discharge (Fig. 7). For example, both round goby and gudgeon increased their mean swimming speed at the highest water discharge: the 'mean swimming speed' for round goby was 1.00 m/s at 80 L/s and increased by 48% to 1.48 m/s at 105 L/s; a 116% increase in 'mean swimming speed' was observed for gudgeon from 0.91 m/s (105 L/s) to 1.97 m/s (130 L/s; Fig. 7). Similar trends were observed for the 'SD swimming speed', with a 28% increase from 0.88 to 1.13 m/s (between 80 and 105 L/s) for round goby and 125% increase from 0.77 to 1.77 m/s

(between 105 and 130 L/s) for gudgeon. In addition, round goby and gudgeon displayed straighter trajectories at higher water discharge. The straightness increased by 21% from 0.71 (80 L/s) to 0.86 (105 L/s) for round goby and by 35% from 0.66 (105 L/s) to 0.89 (130 L/s) for gudgeon. Although both species exhibited similar adaptations to swimming performance in response to increased flow, these behavioural changes appeared at different flow rates: between 80 and 105 L/s for round goby and 105 and 130 L/s for gudgeon. The absence of round goby ‘passage’ at the highest water discharge tested (130 L/s) and absence of gudgeon ‘passage’ at the lowest water discharge tested (80 L/s), together with their similar responses to increased flow, suggest both species use similar strategies to respond to the challenge of increased flow, but prefer different flow rates for passage. Round goby passed the barrier at weaker flow, while gudgeon passed at stronger flow. We excluded the bullhead from this comparison because only two trajectories crossing the camera screen (passage) were recorded at 80 L/s.

## Discussion

### *The flow-force-behaviour approach: filling the research gap*

In this study, we tested a prototype hydraulic barrier by (i) describing the flow field created, (ii) assessing the physical impact of the flow field on the bodies of preserved fish of three target species, and (iii) analysing the swimming behaviour of live fish over the barrier in the same flow field. Overall, we aimed to evaluate whether the hydrodynamic conditions within the barrier can selectively prevent the upstream migration of an invasive fish species. Our combined approach revealed: The hydrodynamic burdens experienced by the fish differed significantly between species. The fishes’ swimming behaviour in the flow field over the barrier was distinct enough to identify the fish species alone with information about the trajectories and the water discharge on a reliable level. In addition, the live fish responded with faster swimming speeds and straighter trajectories to the increased hydraulic forces experienced at higher water discharges. Gudgeon passed the barrier most frequently at 130 L/s water discharge. This behavioural

observation can be well connected to a significantly smaller hydraulic burdens experienced by gudgeon at 130 L/s water discharge compared to the other species.

These findings show that the species differed in their swimming behaviour when swimming across the barrier but had a similar behavioural response to the increased hydraulic burden at higher water discharge: Especially round goby and gudgeon swam faster and straighter across the barrier at increased water discharges.

Round goby did not pass the barrier at 130 L/s water discharge, contrary to gudgeon and bullhead, while round goby experienced stronger forces than gudgeon over the barrier. This suggests that the prototype hydraulic barrier created species-selective hydraulic conditions in the vertical slot fish pass. These conditions might have prevented the passage of round goby but enabled passage of gudgeon and bullhead in our experiments.

#### *Step 1: The flow field over the prototype selective barrier*

Our flow measurements indicated homogenous flow over the centre of the barrier and higher velocities and TKE values at both ends of the barrier. The flow field within a vertical slot without the barrier is described in the literature as being similar to that of a turbulent jet plane with a rapid longitudinal decay (Liu et al., 2006). Our barrier prototype was designed to separate this jet and the corresponding shear layer from the flow field in the basin over an extended distance to create a selective barrier effect. The acoustic Doppler measurements indicated the prototype successfully extended the turbulent jet plane. However, similarly to (Wiegleb et al., 2020), we were not able to measure the flow in the vicinity of the side walls or very close to the bottom of the barrier, as the smooth surface of the barrier reflected the acoustic signals and reduced the quality of the measurements close to the walls. Haro et al. (2004) described the flow field in a smooth surface rectangular flume with reduced flow and secondary vortex systems along the edges, which may also occur within our barrier. Indeed, the corners in our prototype

barrier provide suitable flow conditions for bullhead, as this was the only species that exhibited a clear tendency to swim along the edges when swimming across the barrier.

*Step 2: Force measurements — A key ingredient of understanding the interactions between flow and fish*

Force measurements represent a key link between the flow measurements and observations of live fish behaviour, and provide important insight into the species-specific hydraulic burdens experienced by the fish during their passage. While the flow speed varied in the vicinity of the barrier surface compared to the forces, the forces experienced by the preserved fish remained similar between measurement positions. This suggests that the forces experienced by the fish are not solely determined by the mean flow velocity, although a strong relationship between flow velocity and experienced drag force was previously reported under standardized conditions in a flow channel (Wiegler et al., 2020). However, this relationship was based on force measurements performed at one position in the flow field (Wiegler et al., 2020), while the force data in the present study were obtained from several measurement points with different hydraulic and geometric boundaries. That we accounted for several measurement points is one possible explanation for the weak correlation between the force and flow data: the present study reveals the flow field varies in the vicinity of the barrier surface, as reported in previous flow studies in open flume channels (Haro et al., 2004; Wiegler et al., 2020). Another reason for the weak correlation may be the complex shape of the fish. For example, flow from the side encountered a larger surface of body and tail than in case of flow from the front, when only the head surface of the fish was exposed to the flow. Therefore, the 3D-forces detected strongly depend on the direction of the flow encountered by the fish. This is an important aspect of this study that differs from measurements of one-dimensional drag force alone (one axis sensor (Wiegler et al., 2020)).

In general, we observed gudgeon experienced significantly smaller forces compared to round goby and bullhead at 130 L/s water discharge. One reason may be that gudgeon have a more streamlined body

shape. Variations in body shape can alter the drag forces experienced by fish: pregnant female guppies (*Poecilia reticulata*) experience much higher drag forces than similarly sized non-pregnant females (Quicazan-Rubio et al., 2019a). Furthermore, it is possible that the flow conditions support passive propulsion of gudgeon (Liao et al., 2003; Beal et al., 2006). However, it should be noted that the forces could not be measured directly on the ground, as placing the preserved fish in contact with the ground would have induced uncontrolled friction forces (Wiegleb et al., 2020).

The force measurements described the general physical impact of flow on the fish body over the barrier under standardized conditions. Research assumes that live fish have swimming modes corresponding to their body shape and locomotor mode (Blake, 2004). The locomotor modes of the fish we applied here were similar, especially between round goby and bullhead (Egger et al., 2020). Of course, by testing preserved fish, we were not able to account for kinematic modulations induced by movements of the fish. Therefore, it is possible that the live fish actually experienced lower forces because they adapted their swimming behaviour to the local flow conditions. Another point is that all objects have eigenfrequency and these are more or less excited during different water velocities and resulting disturbances at our force measurements. Knowing that muscle tone of the fish will also lead to a change in eigenfrequency of the fish oscillations, preserved fish will nevertheless provide a valid indication how resistance changes with increasing water velocity also based on induced oscillations and resulting water resistance. In addition, turbulence has been reported to potentially have strong impact on the fish swimming performance. On the one hand, because of destabilizing effects at specific relationships between vortex and fish size (Lupandin, 2005) and on the other hand, because of potential energetic support due to passive propulsion at specific vorticity (Beal et al., 2006). Due to the relatively small measurement volume of the acoustic Doppler point measurements ( $7 \text{ mm}^3$ ) however, such vortices with increased effect on the fish swimming performance of our tested fish were not detectable by our flow measurements, while their effect on the fish body was detected by the force measurements. Therefore, we assume that the fish body acts as a transducer that displays flow characteristics with more relevance to fish swimming than the acoustic

Doppler measurements. We propose force measurements with preserved fish or artificial models should be considered for future flow assessments to enable more precise characterization of the suitability of flow fields for specific species than numerical modelling of forces alone.

*Step 3: Behaviour of live fish over the barrier: general adaptations in speed, speed variation and straightness at increased flow*

Modern swimming performance tests are commonly based on enforced swimming and strict protocols of tested velocities (Tierney et al., 2011; Egger et al., 2020), while the observation of the free movement and voluntary ascending behaviour of the tested fish was an important quality of our experiments. Therefore, we were able to perform reliable predictions for the fish species only with information about the video recorded voluntary fish trajectories in combination with the water discharge. Indeed, to increase the precision of the random forest model we excluded the ‘approach’ trajectories from the random forest analysis. Together with the PCA, which included all trajectories and suggested rather low variation in the fish trajectories, we conclude that the species behaved similar when approaching the barrier but that differences in the swimming behaviour were increased when the fish were observed over barrier (while passage, return or uncompleted passage). These differences were strong enough that the trained random forest model was able to distinguish reliably between the trajectories of round goby and gudgeon. The low model accuracy for bullhead might result from the low proportion of bullhead trajectories from the entire training set. It might be possible to increase the bullhead prediction accuracy by increasing the number of bullhead trajectories in the model training set, but this requires the record of more bullhead trajectories.

Having a closer look at the trajectories of fish that completely passed the barrier (passage trajectories), we observed on the one hand a clear difference in the preferred water discharge for passage between the species, especially between round goby (preferred 80 L/s) and gudgeon (preferred 130 L/s). This

corresponds to the results of the random forest model, when ‘water discharge’ was the most important variable for discriminating between the species. On the other hand, we observed a very similar behaviour in all tested species: A general adaptation of the swimming trajectories was observed by increased speed, speed variation and straighter paths at increased flow. This observation corresponded to the random forest result, when ‘speed variation’, ‘sinuosity and ‘speed’ had the smallest or medium importance for discrimination between species. Considering this similarity in behaviour between species, we conclude that all species behaved similar when challenging increased flow, but that the fish species differed in their preferred water discharge for passing the barrier and their swimming styles concerning the ‘straightness’ and the length of trajectories (‘distance’) over the barrier.

Considering the variation in swimming behaviour between species, the significant differences between species in the forces experienced, and the observation that no round gobies passed the barrier at the highest water discharge tested, we assume that the hydrodynamics created by the prototype barrier prevented the passage of round goby. Successful passage of gudgeon and bullhead at 130 L/s water discharge supports the idea that such a barrier could provide a species-specific effect.

#### *Random forest model: Using the fish trajectories for species identification*

To our knowledge, we were the first who published the identification of video recorded fish in a vertical slot fish pass based on their swimming patterns using a modern machine learning approach. Indications for differences in swimming behaviour between species, especially in swimming speed and acceleration, have been reported previously by (Rodríguez et al., 2015). That these differences can be used to identify different species reliably with information extracted from their swimming paths and the present water discharge was shown in our study.

This technique might improve fish species identification with poor image quality or increased water turbidity because detailed records of fish body contours are not necessary for this approach, contrary to

fish identification methods based on fish body shape recognition (Shafait et al., 2016). Indeed, we visually screened the videos and performed the tracking manually which was very time consuming. There are modern computer vision techniques available which enable automated object detection and classification in videos (Han et al., 2018). A combination of computer vision techniques with automated fish identification based on swimming patterns would represent a promising tool for visual non-invasive fish pass monitoring. Because vertical slots in fish passes have to be passed by every fish passing the fish pass, vertical slots act as bottlenecks that can be monitored by camera systems, as described in our study and Belo et al. (2021). This might enable the reduction of more invasive techniques such as electro fishing (Knaepkens et al., 2005; Knaepkens, Maerten, and Eens, 2007) or implanted PIT-tags (Aarestrup et al., 2003) which implement a direct contact with the fish.

#### *Evaluation of the random forest machine learning approach*

With an accuracy of 92.16 % for gudgeon and 85.48% for round goby the model performed promisingly for these species. Indeed, the lower prediction accuracy in bullhead induced by the smaller amount of trajectories recorded for this species in our experiments represents one very important challenge when applying biological data to modern machine learning approaches. That our study aimed at observing exclusively voluntary swimming behaviour meant that we did not record a data set perfectly suitable for training machine learning models because of varying numbers of trajectories for the different species. Indeed, we showed that it is possible to identify fish based on swimming patterns extracted from underwater videos. With more data and further effort in the design and improvement of machine learning models, it might be possible to increase the identification accuracy in future.

#### *Limitations of the video observations*

Two cameras were used to observe the entire prototype barrier. However, we were not able to connect the paths of the fish crossing both screens (e.g., ‘passage’) as we were not able to identify individual fish leaving the screen and entering the other—especially as, at the lowest water discharge tested, round gobies swam over the side walls and into the barrier in the vicinity of the slot and were thereby only recorded by the upstream camera. This could be avoided by wide angle cameras in future experiments. Because of the possibility of recording the same fish multiple times, it is likely that the number of recorded events does not represent the actual number of recorded fish. Indeed, accepting this limitation actually creates an important strength of this study. As the fish were able to move freely through the fish pass model for an extended time of two hours and we avoided a “shooing effect” as well as a human presence during the experiments, we could observe voluntary swimming behaviour in a realistic fish pass setup. Furthermore, the three tested fish species are reported to predominantly swim near the ground at high velocities (Egger et al., 2020). However, vertical swimming was possible, but was not accounted for in our analysis due to the vertical views of both cameras that provided a planar projection of the fish paths over the ground. This issue could be avoided in future investigations by implementing additional cameras and performing tracking in 3D-space.

#### *Evaluation of the prototype hydraulic barrier and relevant future research*

The design of our prototype barrier to prevent the upstream passage of round goby follows the concept of a hydraulic barrier for round goby initially proposed by Hoover et al. (2003). The barrier evaluated in the present study has a simple construction and consists of a cut and shaped stainless-steel plate. Our experiments indicated that the prototype met the requirements (mentioned in the introduction) of sufficient length (1.00 m), flow velocity (0.91 m/s) and smoothness (stainless steel, roughness 0.015 mm) at a water discharge of 130 L/s; under these conditions, round goby were not able to pass the barrier while gudgeon and bullhead crossed the complete length of the barrier. This suggests the prototype barrier has a species-selective effect at a water discharge of 130 L/s. Indeed, Egger et al. (2020) reported a strong

reduction of the passage rate for all species tested at the barrier compared to the previous untreated slot, suggesting a general passage-reducing effect of the barrier in all tested species.

Due to the diverse palette of methods applied in our approach, we recommend models of fish pass facilities should be tested in the laboratory prior to implementation at dams and subsequent field assessments. We tested the prototype under laboratory conditions and assume that, in the field, vegetative growth or debris may alter the hydraulics and thereby impact the effectiveness of a barrier in a real fish pass over time. It should also be tested to what extent the video recordings are ready to be employed in the field. Further machine learning tests will show to what extent field conditions such as turbidity and air bubbles pose obstacles to identification of fish trajectories.

The prototype hydraulic barrier performed promisingly, though the mechanisms that such hydraulic barriers employ also have ecological ramifications. Studies have revealed that personality traits and motivation are relevant to the passage of round goby (Myles-Gonzalez et al., 2015; Hirschet al., 2017) and benthic fish swimming behaviour can vary in different seasons (Van Liefferinge et al., 2005). Therefore, evaluations of the actual impact of the barrier on benthic fish swimming behaviour require comparisons with an unaffected vertical slot and long-term field studies are necessary to test the performance of the barrier in a real fish pass. In addition, our data are representative for our scaled vertical slot fish pass model, but the barrier performance in fish passes of different type or dimensions will have to be assessed in further studies. However, this new evidence on benthic fish swimming and functionality, combined with the flow-force-behaviour approach applied in this study, are expected to inform the design and engineering of fish passes adapted to the requirements of specific ecosystems (Katopodis, 2005; Kemp, 2012).

# Declarations

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## *Conflicts of interests*

We declare we have no conflicts of interests.

## *Availability of data*

Data are available in the Supplementary Material.

## *Code availability*

Code used to analyse the data is available in the Supplementary Material.

## *Authors' contributions*

P.B.H. conceived the study. G. R. provided the force measurement system and gave instructions in particular for the force measurements and the analysis of the random forest model. All authors conceptualized the research. J. W. and P.E.H. performed the 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.

### *Ethics approval*

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).

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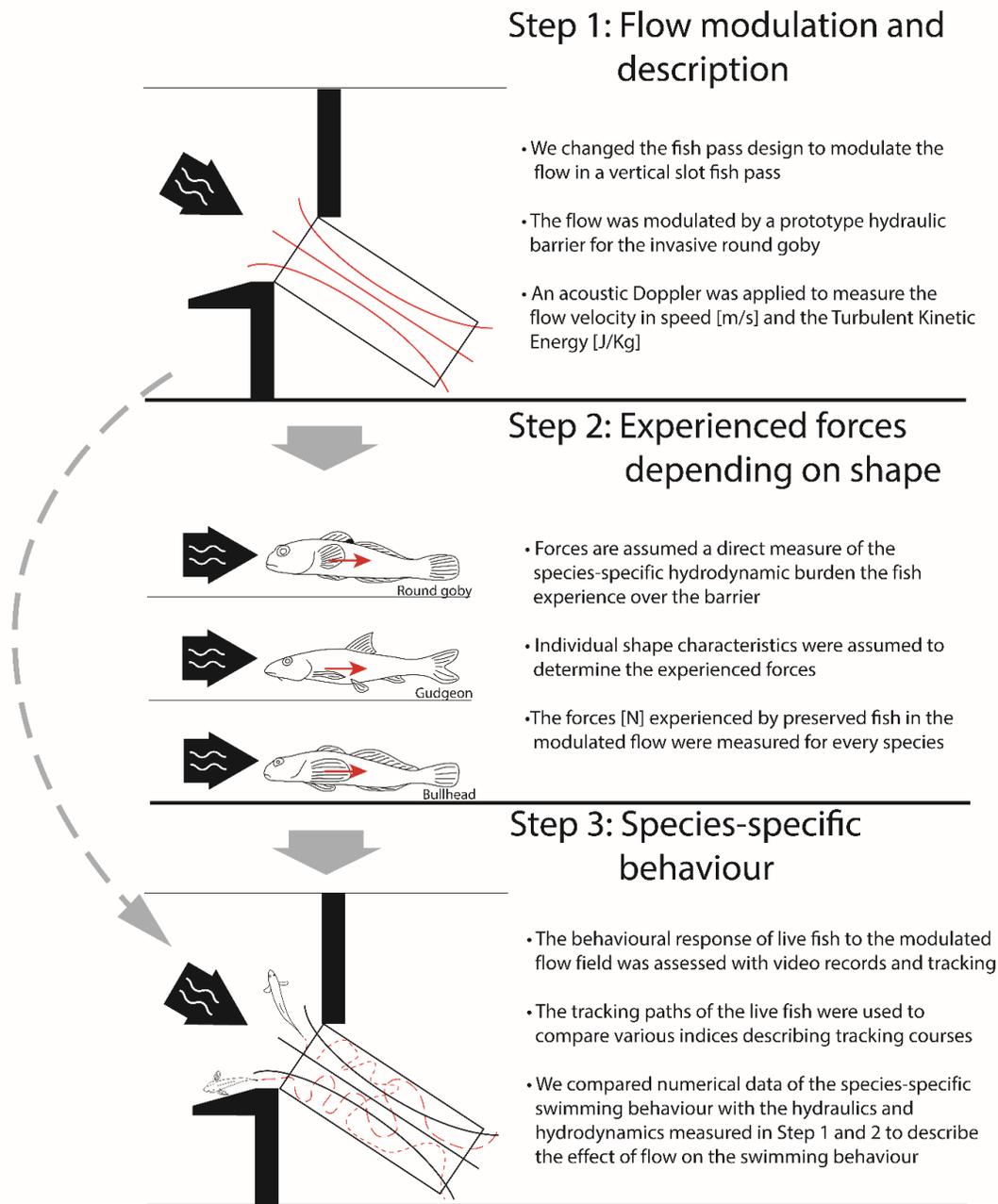
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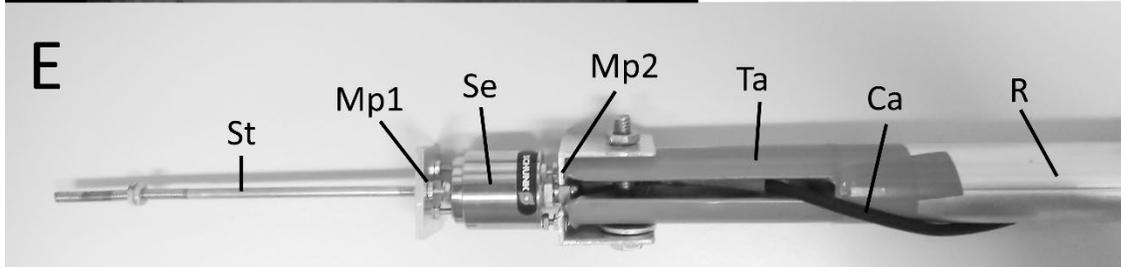
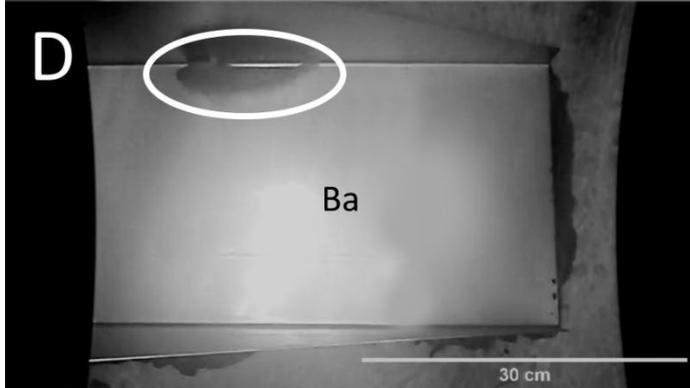
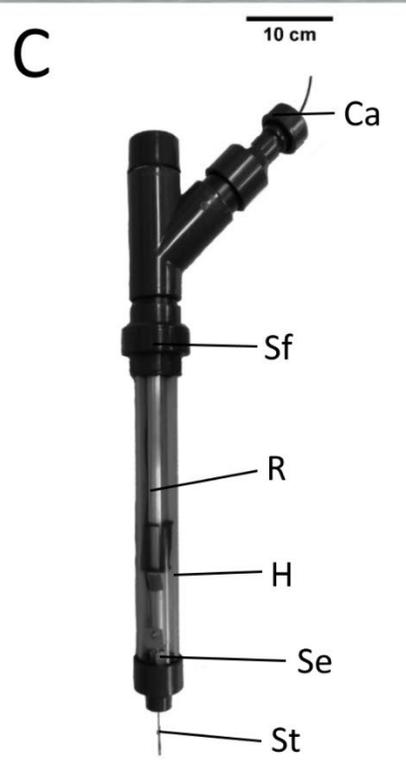
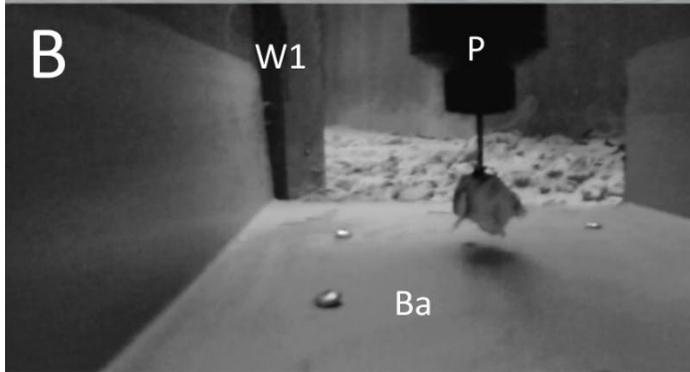
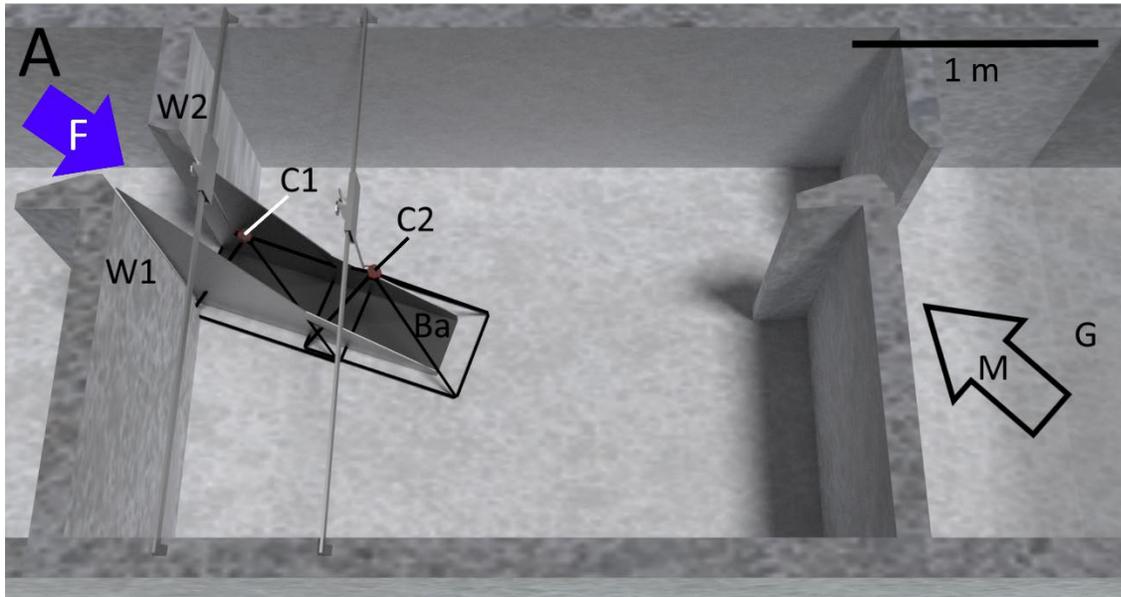
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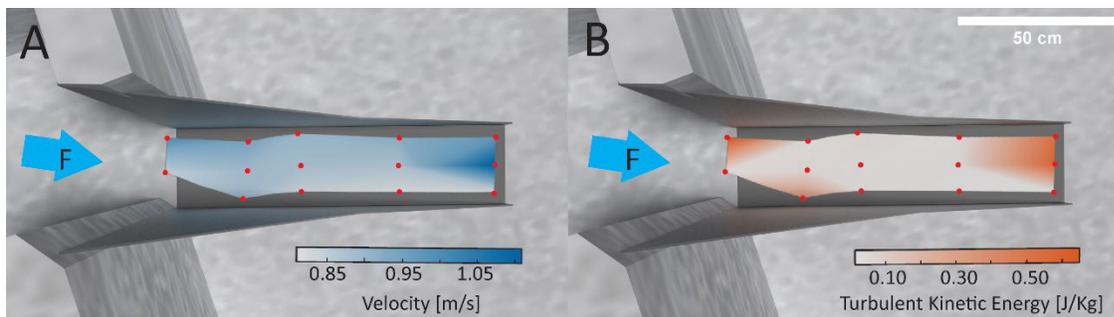
# Figures



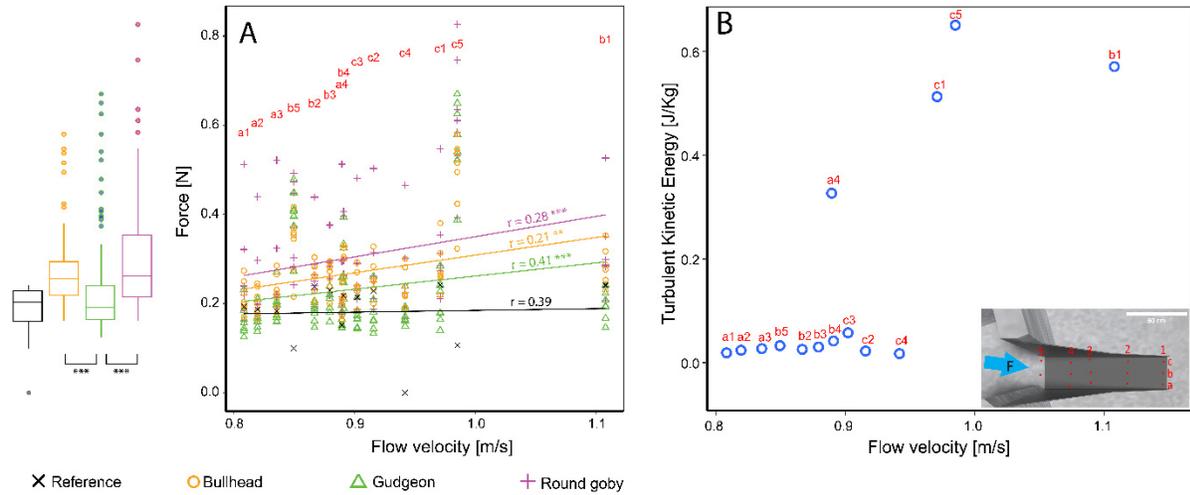
**Fig. 1** Schematic illustration of the experimental steps performed in this study to assess a hydraulic barrier for round goby (grey arrows). We included a hydrodynamic assessment (Step 2) in the common methodological approach (dashed grey arrows): adaptation of the flow within the fish pass design following flow description (Step 1) and design evaluation based on the behaviour of live fish (Step 3). The components assessed in each step of this study are highlighted in red and the direction of flow is represented by the black arrow



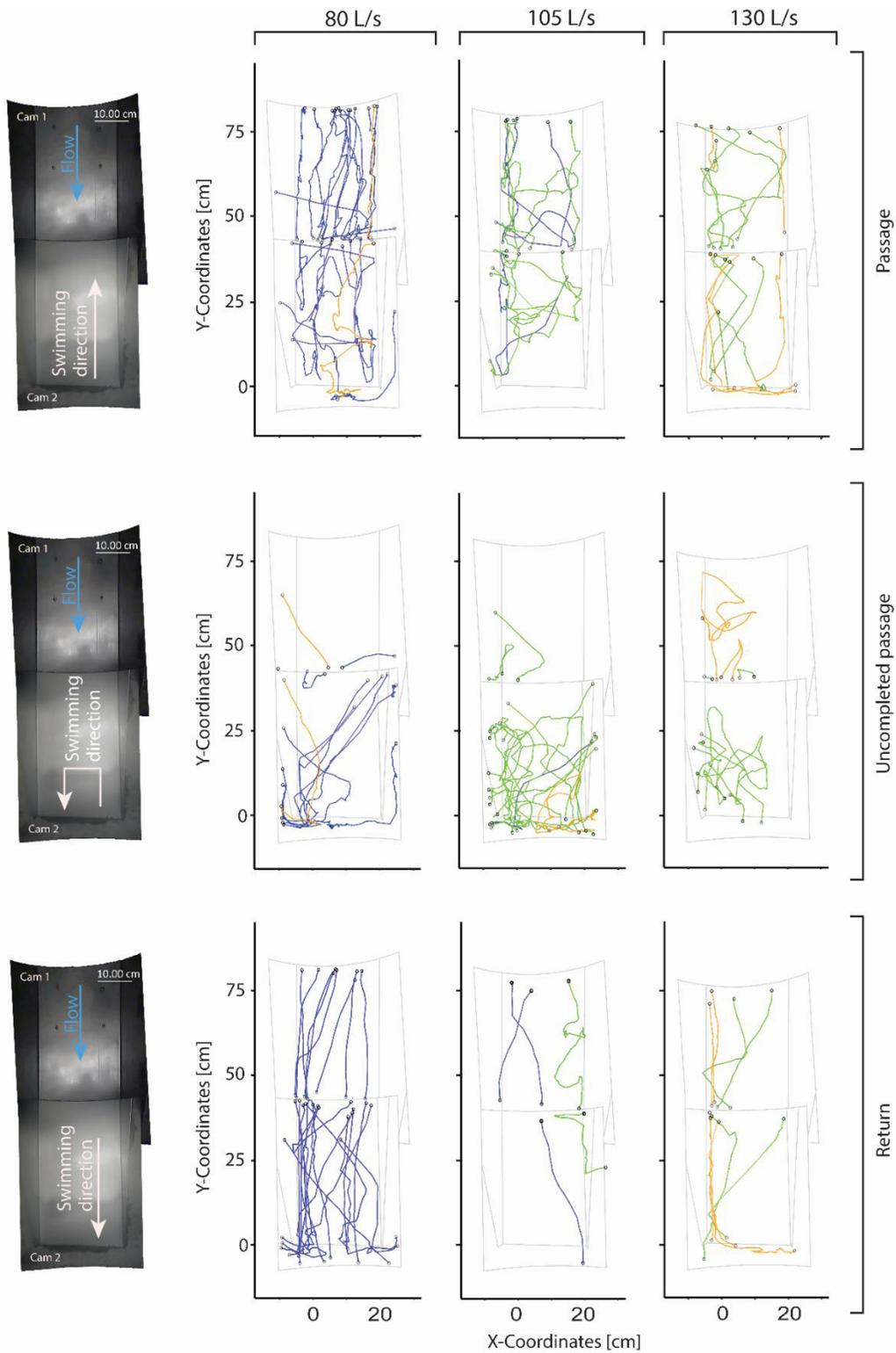
**Fig. 2** (A) Vertical slot fish pass model with the prototype selective barrier (Ba) positioned between partition walls (W1, W2). The fish were released at the downstream end of the model near the grid (G) and free to swim in the upstream direction (M) against the flow (F). Two cameras (C1, C2, view is represented by the black contours) recorded fish behaviour at the barrier. One camera frame (from camera C1) is provided in D showing one round goby passing the barrier (white ellipse). The left and right edges of the screen are curved as the footage was undistorted to enable tracking. The forces acting on preserved fish (a round goby connected to the sensor labelled P in B) were measured using a probe (C). The probe consisted of a force sensor (Se), which was connected to the 10 cm long fixation stick (St) via a mounting plate (Mp1) (E). The sensor was mounted on a mounting plate (Mp2) which was connected on a stable aluminium rod (R). We used a polyvinyl-chloride tape (Ta) to protect the sensor cable against damage from the aluminium rod holding the sensor. This rod was surrounded by a polyvinyl-chloride hull (H), which shielded the sensor from surrounding flow. The hull could be opened for maintenance by a screw connection (Sf) and the sensor cable (Ca) left the probe at the top of the probe. For the measurements, the preserved fish were connected with screws to the fixation stick.



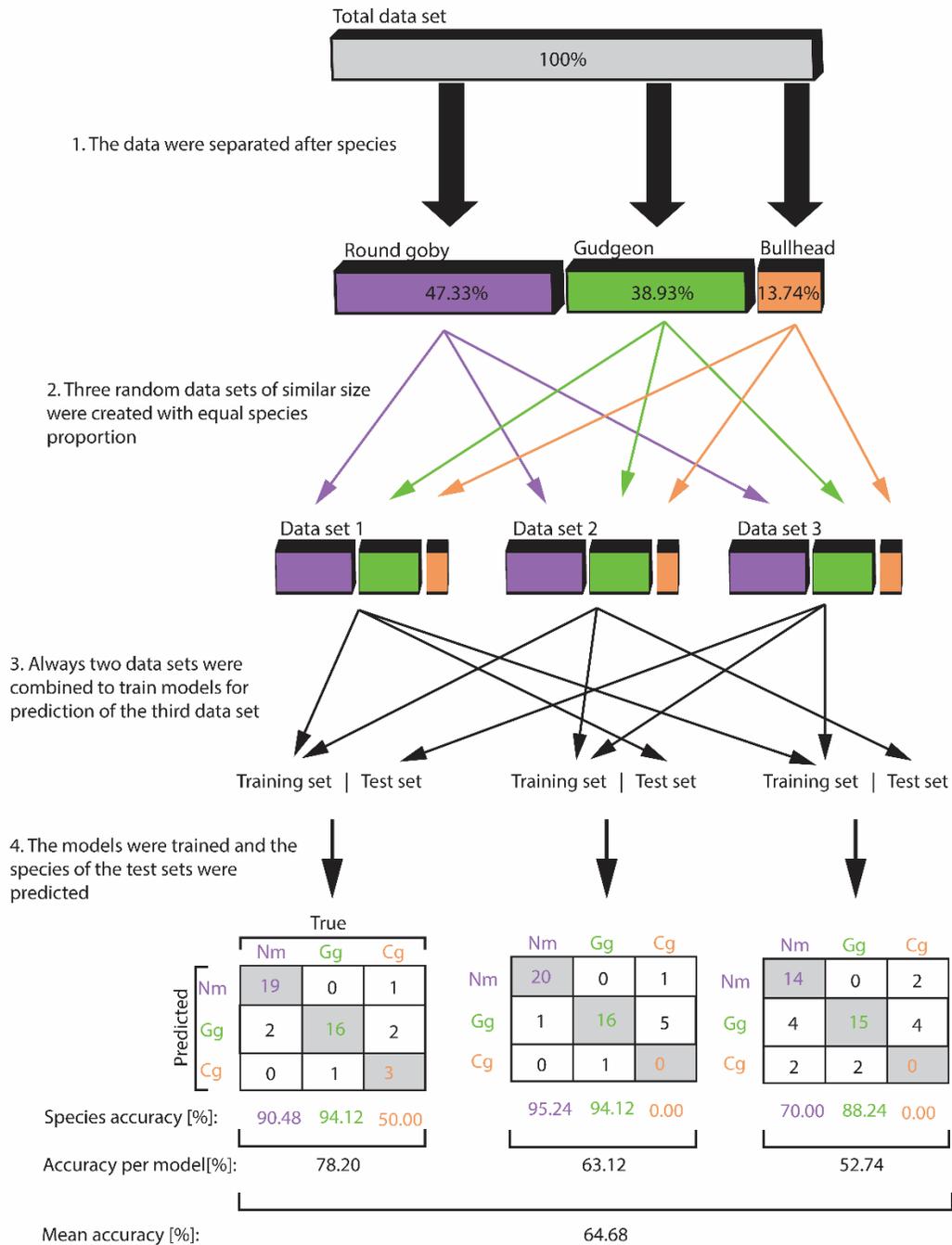
**Fig. 3** Flow velocity (A) and turbulent kinetic energy (B) over the prototype barrier at a water discharge of 130 L/s. Measurement points are indicated by the red spots and the flow direction is shown by the blue arrow labelled F. See Supplementary Material 3 for the flow data at 105 and 80 L/s water discharge.



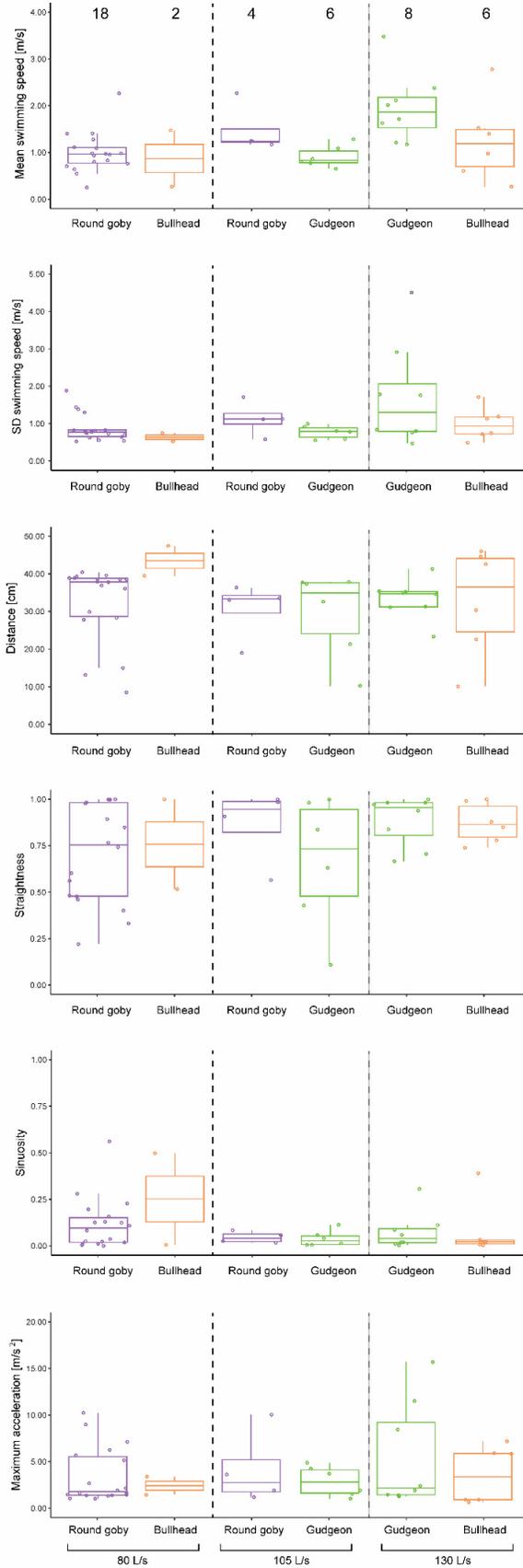
**Fig. 4** Correlation between flow velocity and the forces experienced by preserved fish (seven fish per species) **(A)** and correlation between flow velocity and turbulent kinetic energy ( $r = 0.78, p < 0.01$ ) **(B)** at a water discharge of 130 L/s. The boxplots on the left side of **A** represent the force distributions detected for the three fish species and the reference (one experimental run without fish). Statistically significant differences between the boxplots and regression lines are marked by asterisks (\*  $p < 0.1$ ; \*\*  $p < 0.05$ ; \*\*\*  $p < 0.01$ ). The location and designation of the measurement points are provided in the lower right inset of **B**, with the arrow labelled F representing the direction of flow.



**Fig. 5** Maps of fish trajectories during passage, uncompleted passage and return events for round goby (violet), gudgeon (green) and bullhead (orange) over the barrier. The views of both cameras (Cam 1 and Cam 2) are provided on the left.



**Fig. 6** Cross validation was applied to assess the accuracy of the random forest models trained with all trajectories recorded for round goby (Nm), gudgeon (Gg) and bullhead (Cg) over the barrier. The confusion matrices (4.) illustrate the number of correctly (grey boxes) and mispredicted (white boxes) trajectories.



**Fig. 7** Trajectory features of ‘passage’ events for the three fish species. The number of completed passage events recorded for each species is provided at the top of the figure. The boxplot centres represent the median and the values for the individual trajectories are represented by the individual points.

# Supplementary Material

## *Supplementary Material 05:*

### *Processing the tracking data*

To observe exclusively voluntary swimming behavior, we did not apply any shooring approaches to make the fish swim over the barrier, strictly avoided human presence next to the fish pass during the experiments and extended the experiment duration to 120 min. With this duration, the fish were able to adapt to the new environmental conditions after release in the fish pass model and we aimed at increasing the probability to observe informative numbers of fish behaviour events.

A part of the timeline data has been published previously (Egger et al.,2020), but in the present study we tracked the position of the fish during the timeline marker events as X, Y-screen coordinates. With reference markers with known distances (scales) we were able to compute swimming distances of the fish. Together with the known video frame rate of 25 frames per second (fps) we were able to compute swimming speeds. To account for the camera distortion of the videos, we corrected the footage using the video undistortion tool integrated in Blender before the tracking. Afterwards, the X and Y-coordinates of the fish were exported by a modified script from scummos (2012) (original script:

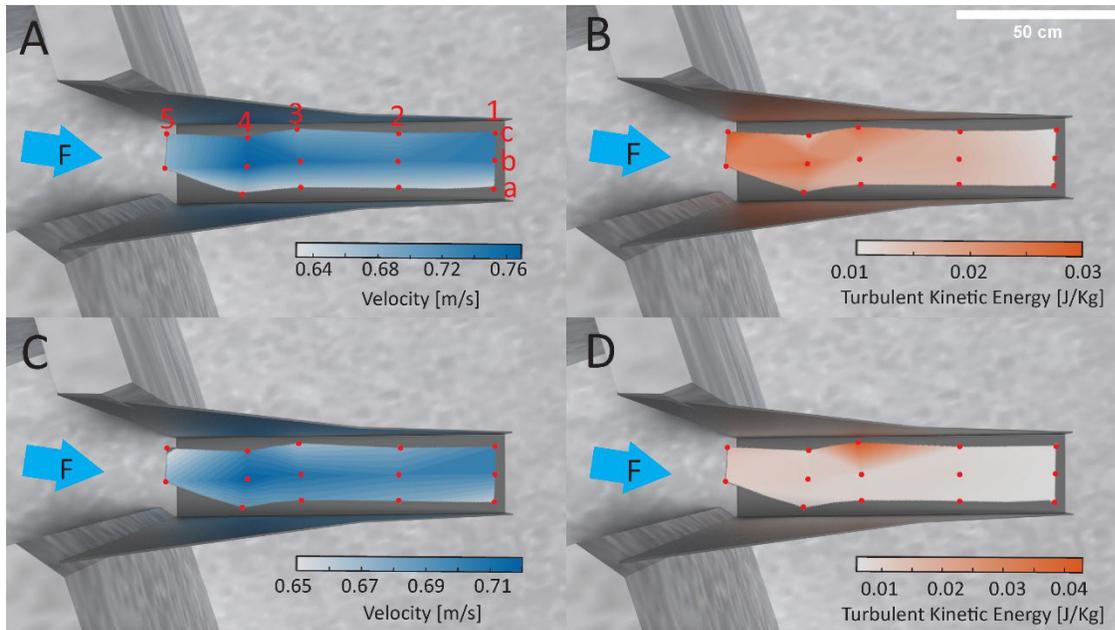
<http://scummos.blogspot.com/2012/11/blender-exporting-camera-tracking.html>), which has been modified by Renato Sousa already. In the following, we processed the exported tracks with Matlab 2019 and plotted the spatial courses of the tracks for visual comparisons. Furthermore, we applied the ‘trajr’ package (McLean et al., 2018) in R for processing and multivariate statistical comparison of the recorded tracks between species, events and water discharge.

*Literature*

Egger, B., Wiegand, J., Seidel, F., Burkhardt-Holm, P., & Hirsch, P. E. (2020). 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*). *Ecology of Freshwater Fish*, 30 (3), 391-405. <https://doi.org/10.1111/eff.12592>

McLean, D. J., & Skowron Volponi, M. A. (2018). trajr: An R package for characterisation of animal trajectories. *Ethology*, 124(6), 440–448. <https://doi.org/10.1111/eth.12739>

*Supplementary Material 10:*



**Supplementary Material 10:** Flow velocity at 105 L/s (A) and 80 L/s (C) water discharge and turbulent kinetic energy at 105 L/s (B) and 80 L/s (D) water discharge over the prototype barrier. Measurement points are indicated by the red spots and the flow direction is shown by the blue arrow labelled F.

Supplementary Material 12:

Table S 12: Track features computed for ‘approach’ (Ap), ‘passage’ (Pas), ‘return’ (Re), ‘uncompleted passage’ (UnCoPa) and ‘uncompleted return’ (UnCoRe) of round goby (Nm), gudgeon (Gg) and bullhead (Cg).

**Water discharge 80 L/s**

Event:	Ap		Pas		Re	UnCoPas		UnCoRe
	Cg	Nm	Cg	Nm	Nm	Cg	Nm	Nm
Tracks count	21	155	2	18	23	2	8	4
Mean speed [m/s]	0.11	0.44	0.87	1.00	1.87	1.04	0.98	0.56
SD of mean speed [m/s]	0.17	0.71	0.85	0.43	0.82	1.29	1.54	0.03
Mean speed variation [m/s]	0.17	0.52	0.63	0.88	1.13	0.55	1.16	0.72
SD of speed variation [m/s]	0.22	0.54	0.16	0.37	0.83	0.12	0.96	0.19
Mean max. acceleration [m/s <sup>2</sup> ]	1.46	2.86	2.42	3.48	4.07	4.06	6.68	3.83
SD max acceleration [m/s <sup>2</sup> ]	0.83	2.17	1.37	2.97	3.19	3.38	4.73	2.40
Mean distance [cm]	14.38	19.47	43.44	32.42	41.75	31.00	34.95	6.52
SD distance [cm]	12.75	14.20	5.62	10.12	4.95	8.25	16.61	5.15
Mean sinuosity	0.40	0.42	0.25	0.12	0.09	0.21	0.19	0.24
SD sinuosity	0.77	0.83	0.35	0.14	0.21	0.27	0.18	0.24
Mean straightness	0.71	0.77	0.76	0.71	0.92	0.75	0.63	0.34
SD straightness	0.30	0.24	0.34	0.27	0.14	0.35	0.28	0.13

**Water discharge 105 L/s**

Event:	Ap			Pas		Re		UnCoPas			UnCoRe	
	Cg	Gg	Nm	Gg	Nm	Gg	Nm	Cg	Gg	Nm	Gg	Nm
Tracks count	14	354	48	6	4	2	3	1	15	1	5	1
Mean speed [m/s]	0.07	0.50	0.66	0.91	1.48	0.80	3.14	0.08	1.01	1.04	0.85	0.79
SD of mean speed [m/s]	0.04	0.37	0.53	0.23	0.53	0.07	1.28	-	0.55	-	0.55	-
Mean speed variation [m/s]	0.14	0.51	0.59	0.77	1.13	0.74	0.85	0.29	0.92	1.66	0.99	0.74
SD of speed variation [m/s]	0.09	0.42	0.68	0.17	0.46	0.37	0.40	-	0.41	-	0.57	-
Mean max. acceleration [m/s <sup>2</sup> ]	1.68	1.76	1.97	2.89	4.19	2.65	2.23	5.12	3.85	7.96	3.71	1.51
SD max acceleration [m/s <sup>2</sup> ]	0.74	1.51	1.71	1.60	4.03	1.40	1.70	-	2.54	-	2.70	-
Mean distance [cm]	9.00	7.19	11.55	29.49	30.48	27.17	37.67	2.86	22.97	38.07	8.01	6.86
SD distance [cm]	11.01	7.05	9.39	11.37	7.80	14.33	5.10	-	14.62	-	6.12	-
Mean sinuosity	0.62	0.39	0.42	0.04	0.05	0.07	0.01	0.02	0.15	0.15	0.14	0.14
SD sinuosity	1.14	0.66	0.80	0.04	0.03	0.09	0.01	-	0.18	-	0.09	-
Mean straightness	0.70	0.76	0.82	0.66	0.86	0.87	1.00	0.80	0.72	0.80	0.65	0.60
SD straightness	0.30	0.29	0.23	0.35	0.20	0.19	0.00	-	0.27	-	0.24	-

**Water discharge 130 L/s**

Event:	Ap			Pas		Re		UnCoPas		UnCoRe
	Cg	Gg	Nm	Cg	Gg	Cg	Gg	Cg	Gg	Gg
Tracks count	27	147	33	6	8	5	4	2	7	4
Mean speed [m/s]	0.29	0.49	0.63	1.26	1.97	1.60	1.92	1.32	1.59	1.08
SD of mean speed [m/s]	0.18	0.33	0.33	0.88	0.74	0.70	0.20	0.19	0.37	0.19
Mean speed variation [m/s]	0.46	0.52	0.66	1.00	1.73	1.14	1.39	0.76	1.47	1.18
SD of speed variation [m/s]	0.29	0.37	0.55	0.44	1.38	0.53	0.85	0.19	0.58	0.52
Mean max. acceleration [m/s <sup>2</sup> ]	1.87	1.47	1.83	3.57	5.51	4.54	4.99	1.12	5.37	4.29
SD max acceleration [m/s <sup>2</sup> ]	1.25	1.14	1.52	3.04	5.64	3.02	3.93	0.27	3.14	3.30
Mean distance [cm]	12.45	4.56	6.44	32.70	33.38	36.55	38.21	10.99	13.62	4.48
SD distance [cm]	9.22	3.85	4.93	14.38	5.12	6.66	6.62	10.62	5.00	1.23
Mean sinuosity	0.49	0.58	0.42	0.08	0.08	0.01	0.04	0.23	0.11	0.38
SD sinuosity	0.62	0.80	0.69	0.15	0.10	0.02	0.05	0.14	0.11	0.27
Mean straightness	0.73	0.78	0.81	0.87	0.89	0.92	0.98	0.14	0.66	0.35
SD straightness	0.31	0.26	0.25	0.11	0.13	0.15	0.02	0.03	0.20	0.13

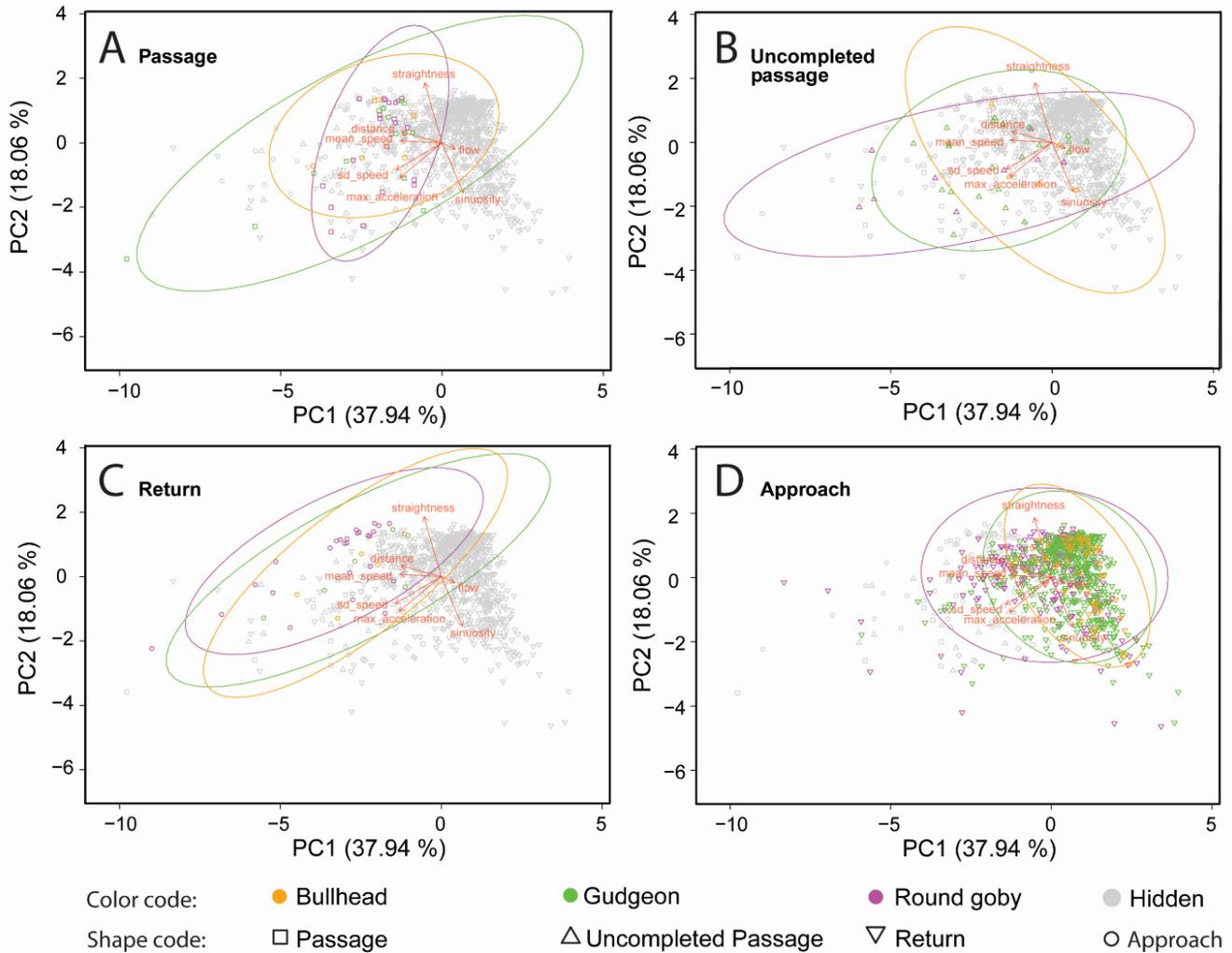
**Please note:** In a previous study (Egger et al., 2020) we reported no passage of bullheads at water discharge of 130 L/s while we recorded passage tracks for bullhead at 130 L/s in this study. This appeared

because we observed bullheads passing the camera view entirely but returning immediately after passage at 130 L/s water discharge. We therefore assumed bullhead did not pass the barrier and recorded ‘uncompleted passage’ in (Egger et al., 2020) but the tracks of these paths completed all requirements for ‘passage’ and ‘uncompleted passage’ for this tracking analysis. Therefore, we recorded ‘passage’ and ‘uncompleted passage’ for bullhead at 130 L/s water discharge corresponding the event criteria. Immediate returns after passage were only recorded for bullhead at 130 L/s water discharge.

### *Literature*

Egger, B., Wiegand, J., Seidel, F., Burkhardt-Holm, P., & Hirsch, P. E. (2020). 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*). *Ecology of Freshwater Fish*, 30 (3), 391–405. <https://doi.org/10.1111/eff.12592>

Supplementary Material 14:



**Supplementary Material 14:** Principal component analysis of trajectory features of the three fish species

across all discharges overall. The graphs illustrate the correlations between the first (PC1) and second (PC2) principal components. The amount of variance explained by the corresponding component is indicated in brackets. **A-D** show the same dataset, with only the indicated tracks highlighted. Ellipses represent the 95% confidence interval.

Against the stream: Hydraulic forces and passage behaviour of benthic fish in a vertical slot fish pass

Paper IV

# Against the stream: Hydraulic forces and passage behaviour of benthic fish in a vertical slot fish pass

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Key words: force, hydrodynamics, fish pass, round goby, gudgeon, bullhead

## Abstract

The flow field in the slot area of vertical slot fish passes must be passed by upstream migrating fish and can affect the passage success of fish species. To describe how this flow field affects benthic fish species (round goby *Neogobius melanostomus* Pallas, 1814; gudgeon *Gobio gobio* L.; bullhead *Cottus gobio* L.) and their passage behaviour differently, we applied a three step-approach in a vertical slot fish pass: we measured the flow velocity (i), the 3D-hydraulic forces experienced by preserved fish (ii), and assessed passage of live fish using video records (iii). Our data showed that 3D-forces are a more direct measure for the flow field suitability for specific species than flow measurements. The species experienced significantly different 3D-forces in the flow field. Gudgeon experienced the smallest forces together with increased passage behaviour at the highest water discharge tested (130 L/s) compared to the lower discharges. Bullhead showed similar passage behaviour across all water discharges tested (80, 105, 130 L/s) together with vertical forces pressing bullhead to the bottom at 130 L/s. Compared to the other species, round goby experienced moderate forces with increased passage behaviour at lower water discharge (80 L/s). Considering that fish passage behaviour in fish depends on numerous factors, the hydraulic forces represent one parameter that is controllable by the design of the fish pass by adapting the flow field: the physical burden the flow field creates for the individual species. This insight informs fish pass engineers and supports the design of fish passes adapted to fish communities of the corresponding ecosystems.

# 1. Introduction

The passage of fish across anthropogenic barriers is important to maintain the ecological river connectivity and the functionality of aquatic ecosystems (Silva et al., 2018). The majority of the world's rivers is fragmented today (Belletti et al., 2020) and the need to reduce barriers for all species of the aquatic ecosystems has been anchored in the Convention on Biological Diversity of the United Nations (United Nations, 1992). Fish passes are an established management option to enable fish passage across these fragmenting obstacles (Katopodis & Williams, 2012). To enable passage, numerous types of fish passes have been developed in the past with a focus to support predominantly species with economic relevance (Katopodis & Williams, 2012). In the last years, there has been increasing appreciation of the need to support not only economically relevant but also other native species that represent important ecosystem components (Silva et al., 2018).

Such species, that are less economically relevant but represent important ecosystem components are benthic fish, such as gudgeon (*Gobio gobio* L) and bullhead (*Cottus gobio* L.) Some benthic fish have specialized swimming styles to resist flow and hold station in microhabitats (Carlson and Lauder 2011; Gilbert et al. 2016). How benthic fish can hold their position against the flow is partly understood. One mechanism which enabled station holding at increased water flow was reported to be the creation of negative lift forces by the adjustment of the pectoral fins (Carlson & Lauder, 2011). Indeed, knowledge about the performance of small-bodied, bottom-dwelling species in fish passes and how they move upstream against the flow is rare (Knaepkens et al., 2007). When swimming upstream in a fish pass, benthic fish have to leave the flow-sheltering structures on the river bed and swim actively in the free water column, where they are exposed to the flow field.

Beside native species, also invasive species can use fish passes to disperse upstream. Important impacts on invaded ecosystems have been reported even for non-migratory benthic fish species such as invasive

Ponto-Caspian gobies (Hirsch et al., 2016). Especially further upstream migration of the invasive round goby (*Neogobius melanostomus* Pallas, 1814) can have negative impact on ecosystems (Kornis et al., 2012; Tierney et al., 2011).

By impeding passage of invasive species, fish passes could support aquatic biodiversity (Vélez-Espino, McLaughlin, Jones, & Pratt, 2011). Puertas et al. (2012) proposed to design fish passes that create flow fields adapted to the requirements of the target fish species to support their passage through a species-oriented fish pass design. Indeed, integrated interdisciplinary research is needed to develop species selective fragmentation as a management option for aquatic environments (Rahel & McLaughlin, 2018).

(Castro-Santos, Cotel, and Webb 2009) revealed that variation in fish body shape between species can determine passage success in fish passes. A reason for that might be that swimming performance of fish species depends on the body shape of fish (Ohlberger et al., 2006; Rubio-Gracia, García-Berthou, Guasch, Zamora, & Vila-Gispert, 2020; Pierre Sagnes & Statzner, 2009). Nevertheless, to design fish passes that create flow fields adapted to the species requirements, it is necessary to understand how the flow affects the body of the species differently and thereby the passage behaviour because of its individual shape.

Several studies describe the flow fields in fish passes (Baki et al., 2017; Larinier, 2008; Liu et al., 2006). However, the direct effect of the flow field on the fish body in a fish pass is, to our knowledge, unknown. Some researchers measured the direct hydraulic forces acting on fish bodies from flowing water under standardized conditions (Barrett et al. 1999; Quicazan-Rubio et al. 2019; Wiegleb et al. 2020; McLetchie 2003) but there is no evidence about the hydraulic forces the fish encounter while passage of a real fish pass. Evidence about how the flow individually affects the swimming behaviour of invasive and native migrating fish might enable the evaluation of existing fish passes and the adaptation of future fish pass constructions to the requirements of the corresponding ecosystem.

The flow field induces forces on the fish that affect the passage behaviour of the fish species differently (Wiegleb et al. (2021)). We therefore applied a three-step approach that described the effect of different

flow fields induced by varied water discharge on fish passage in a vertical slot fish pass by: i) assessing the flow field, ii) measuring the forces acting on fixed fish bodies within this flow field iii), and comparing these forces with actual upstream passage behaviour of live fish moving freely upstream and downstream through the vertical slot. Based on the assumption that fish migration is hydraulically mediated (Goodwin et al., 2014), we expected that higher water discharge lead to higher forces to be overcome by upstream moving fish. Because these hydraulic forces assumed vary between species, we expected that lower hydraulic burden in a species are observed together with increased live fish passage behaviour. Following our three-step approach, we hypothesized: The forces experienced by preserved fish differ between species in the flow field of a vertical slot at different water discharges(I) and correspond to passage behaviour of live fish (II).

## 2. Material and Methods

### *2.1. Flow channel setup*

The experiments were performed in a vertical slot fish pass test rig at the Theodor-Rehbock Hydraulic Laboratory at Karlsruhe Institute of Technology (KIT), Germany (Fig. 1), that has been applied in a previous publication (Wiegleb et al. 2021). Vertical slot fish passes are one of the main types installed at transvers structures (weirs) to enable upstream fish passage (Wu et al., 1999). Vertical slot fish passes consist of a rectangular channel with partition walls containing vertical openings which separated the channel into pools. The flow through these slots creates a jet with accelerated flow velocities-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 shaped the vertical slots (width: 28 cm) with a pool length between partition walls of 2.40 m. To assess the effect of various water discharges on the performance of the different species in the vertical slot fish pass, we performed our experiments at three water discharges (80, 105 and 130 L/s), while 130 L/s was assumed most representative for the conditions in real fish passes (Bombač et al., 2017). The fish pass test rig from our experiments had a slope of zero degrees and the water discharge was adjusted via a recirculation pump. According to the adjusted water discharge, we measured the water depth of the different basins to maintain equal flow conditions between the trials. The water depth downstream from the assessed vertical slot was 38 cm at 130 L/s, 46 cm at 105 L/s and 66 cm at 80 L/s water discharge. Upstream the vertical slot, the water level was 50 cm at 130 L/s, 51 cm at 105 L/s and 56 cm at 130 L/s water discharge.

### *2.2. Flow measurements*

The flow was measured similar to Wiegleb et al. (2021). An acoustic Doppler ADV probe (Vectrino, Nortek) to measure the flow in three dimensions was mounted at an electric carriage (Isel) (Fig. 1) which

was programmed to drive a pattern of 19 measurement points one by one in the vertical slot (Fig. 2). The flow was measured as close as possible to the ground (ca. 2 cm above ground) for five minutes at every measurement point. A nominal velocity range of 1.0 and 2.5 m/s, measurement volume of 7 mm<sup>3</sup> and a sampling rate of 25 Hz were specifications for the Acoustic Doppler measurement probe. The raw flow data were processed using WinADV32 (V.2.031) and MATLAB 2019 and we computed mean velocities [m/s], standard deviations and Turbulent Kinetic Energy (TKE) [J/Kg] as a measure of turbulence in the vertical slot (Quaranta, Katopodis, Revelli, & Comoglio, 2017).

### *2.3. Fish catch, maintenance and ethical approval*

In the present study, we tested the same fish used for swimming performance experiments in the same vertical slot fish pass model applied by Egger et al. (2020) and performed preservation in Formalin according to (Wiegleb et al. 2020). Electrofishing was applied to catch bullhead and gudgeon in the River Alb in Karlsruhe (Germany). The fish were immediately transported to the KIT. Between 22<sup>nd</sup> and 29<sup>th</sup> March 2019, we caught round gobies in the High Rhine in Basel, Switzerland, using minnow traps. Afterwards, round gobies were transported to the KIT. At the KIT, all fish were held in six polyethylene tanks (Craemer, Germany, dimensions 91 x 59 x 48 cm) with flow through water supply. See Egger et al. (2020) for details about the fish catchment and maintenance. After the swimming experiments (Egger et al. 2020, Wiegleb et al. 2021), the fish were euthanized with an overdose of MS-222 and transported to our lab in Basel, Switzerland, on ice for preservation in Formalin. 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).

The forces experienced by the fish were measured after preservation within the vertical slot at water discharge of 130 L/s (n = 7) and 80 L/s (n = 5) for comparison of the forces experienced at different water discharges (Table 2).

Table 2: Mean total length ( $T_L$ ) and mean wet weight ( $W_w$ ) with corresponding standard deviation (SD) and sample size ( $n$ ) of fish tested at the force measurements for 130 and 80 L/s water discharge.

	Mean $T_L$ [cm]	SD $T_L$ [cm]	Mean $W_w$ [g]	SD $W_w$ [g]	$n$
<b>130 L/s water discharge</b>					
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
<b>80 L/s water discharge</b>					
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

#### 2.4. The force measurement probe

We applied the same measurement system in the same vertical fish pass model from Wiegleb et al. (2021). The 3D-force measuring probe was mounted at an electric carriage (Isel) (Fig. 1) which was programmed to drive a pattern of 15 measurement points one by one in the vertical slot (Fig. 2; red points). Four measurement points from the flow assessment could not be approached by the force measurement probe because of its size. As soon as the probe was positioned over a measurement point, we started the measurement manually and a 3D-Force/Torque-sensor (Nano17, ®ATI) recorded forces and torque in X-, Y- and Z-axis simultaneously at a frequency of 1000 Hz over a period of 60 seconds. After this time, we stopped the measurement manually and proceeded to the next measurement point. The preserved fish connected to the sensor mimicked body postures of fish swimming upstream (straight body postures and pectoral fins attached to the body) and were positioned as close as possible to the ground but with a distance ensuring that there has never been physical contact between fish and ground (ca. 2 cm). Physical contact to the ground would have induced uncontrolled friction and thereby impact on the force measurements. Egger et al. (2020) assessed the swimming performance in round goby, gudgeon, and bullhead and observed that the fish predominantly swam slightly above ground, which was assumed in

accordance with the measurement height in the present study. In addition, to maintain comparability between the force and the flow measurements, the forces were measured at the same positions as the flow measurements in the present study.

The probe consisted of an outer PVC-U-hull that protected the sensor against lateral flow. The sensor represented the core of the probe and was installed at the lower end of the probe (Fig. 1 C). This design was chosen to keep the brass stick (the force transducer and the connection between fish and sensor) as short as possible. This reduced the impact of the fixation stick on the forces observed and increased the precision of the measurements. The sensor was water resistant (IP 68) which enabled wet application of the sensor.

#### *2.5. Measuring the forces experienced by the fish: Procedure of an experimental run*

The preserved fish were perforated in dorso-ventral direction in the assumed center of gravity, similar to Wiegand et al. (2020) and (P. Sagnes et al., 2000), before the fish was fixed between two nuts (one dorsal and one ventral) on the fixation stick. In the following, we adjusted the fish in an angle of  $110^\circ$  to the partition walls (Fig. 5; D). We chose this angle of  $110^\circ$  as an approximation of the fish orientation to the predominant flow direction of the vertical slot flow field. To ensure comparability of the forces experienced at the different measurement points, we maintained this angle for every measurement point. A wire clamp (ca. 1 cm long) pierced the fish at both sides of the spine and was fixed at the fixation stick to prevent lateral rotation of the fish around the Z-axis. At the beginning of every experimental run, we reset the sensor at zero flow velocity in a plastic barrel. As a quality control and to determine the force induced by the fixation stick, we performed a reference run and measured the forces at the 15 measurement positions without fish.

#### *2.6. Processing of the raw force data*

Because the fish was 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 the vectoral size of the forces experienced by the fish, we computed strength [N] and the direction [°] of the force vectors experienced per time step (n = 60,000 per fish and measurement point) from the three force components detected by the sensor (X-, Y-, Z-axis) using the Pythagorean Theorem (see Wiegleb et al. 2021). These 3D-force vectors represent the force the fish experience at a corresponding time point and their means across the measurement period of 60 seconds were then used to compare the forces experienced by preserved fish with flow velocity measurements at the same measurement points. In addition, the means of the 3D-forces were used to detect significant differences in the forces experienced between species. For comparisons of the planar forces (plane parallel to the ground surface) between species, we computed the mean 2D-force vectors and their directions from the X-and Y-axis force component. In addition, we used only the Z-force component to compare the mean vertical forces experienced between species.

### *2.7. Software and statistics*

All statistics were computed in R v.4.0.2 using the ‘stats’ package. The flow velocities and TKE were compared between water discharges using pairwise t-tests. If the data were not normally distributed (Shapiro-Wilk test), the samples were compared with pairwise Wilcoxon-tests.

To detect differences in the 3D-forces experienced in the vertical slot, we first tested the force data for normal distribution (Shapiro-Wilk test) and tested for significant differences between species using a One-way repeated measures ANOVA. A repeated measures ANOVA was chosen to account for the

repeated measures of the fish at the different measurement points. In the following, we performed pairwise t-tests to identify the species with significantly differing forces experienced within the vertical slot.

To test whether there was a linear relationship between flow and force data, we performed Spearman linear regression. The same appeared for comparisons between the flow velocity and TKE.

The lift force experienced by the fish in the vertical slot fish pass were compared by repeated measures ANOVA applied to the vertical force component (Z-axis) and pairwise t-test for pairwise comparisons. The-force vectors were computed in MATLAB (R2019b).

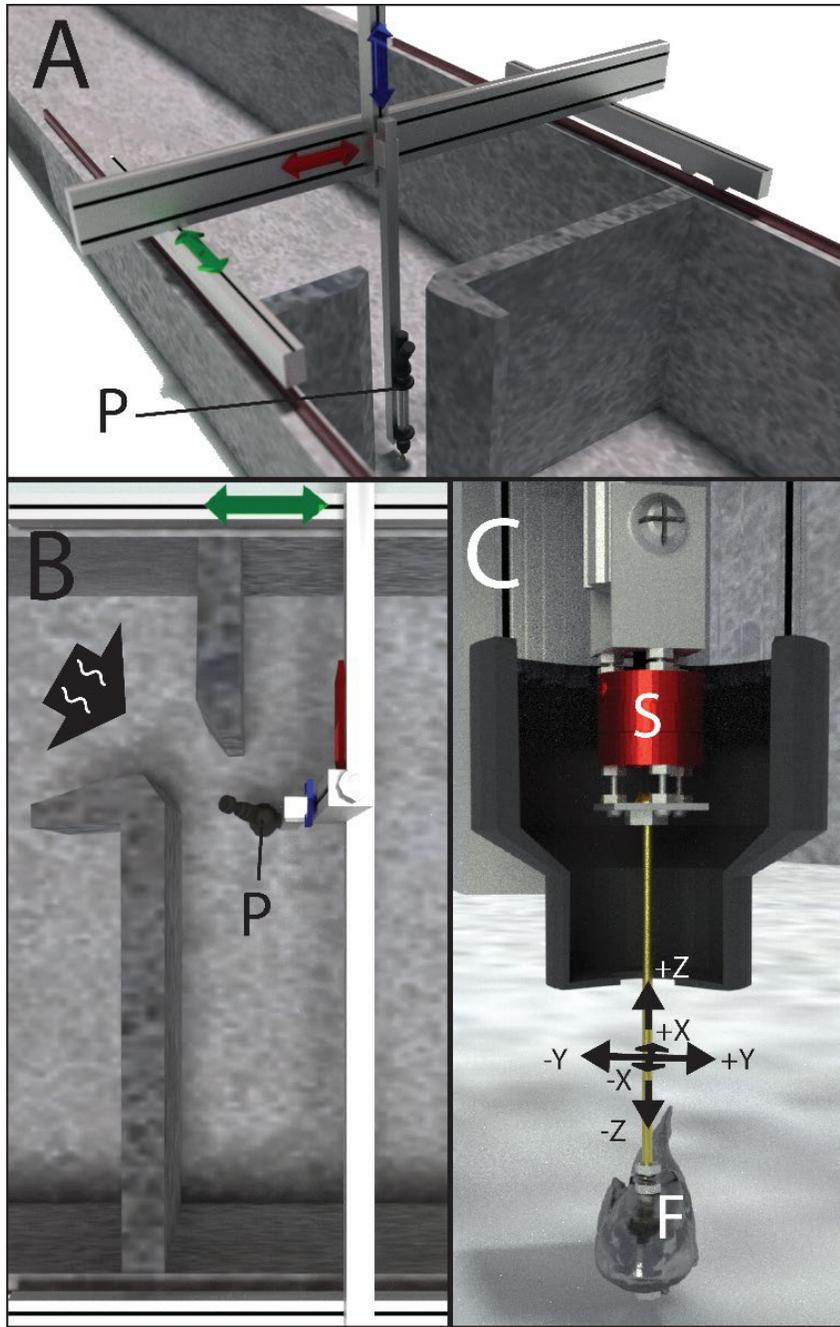


Figure 1: A: The probe (P) for measuring the 3D-forces experienced by preserved fish near the ground was mounted on a carriage, which was programmed to adjust the probe position on the X- (green), Y- (red) and Z-axis (blue) near a vertical slot in a vertical slot fish pass model (B); B: The flow direction is provided by the black arrow; C: The force sensor (S) was mounted at the lower end of the probe and was

connected to the fish (F) via a 3 mm diameter brass stick of length 10 cm. The force sensor measured forces in X-, Y- and Z-direction (C) with the X-axis angle of  $110^\circ$  to the partition wall and following the longitudinal body axis of the fish (F).

### *2.8. Live fish passage behaviour*

To detect possible relationship between the experienced forces and the actual passage behaviour, we recorded the fish moving across the vertical slot over time by a video camera. The fish were initially released downstream the vertical slot at the beginning of the experiments and were free to move through the vertical slot for two hours, unaffected by human presence. We tested every species for three times at 130 L/s, because this discharge was assumed representative for real fish passes, and once at 105 and 80 L/s water discharge. The species were tested separately, and we tested 39 – 45 live fish per experiment with mean total fish length ( $T_L$ ) in round goby of 10.43 cm  $\pm$  1.28 Standard deviation (SD), in gudgeon of 11.46 cm  $\pm$  1.13 SD and in bullhead of 9.91 cm  $\pm$  1.22 SD. A camera (Security-Center IR CCTV-Camera, 380 TV-lines, IP 68, Abus, Wetter, Germany) above the vertical slot was used to film the fish passage behaviour during the experiments duration of 2 hours.

Because the decision to migrate upstream an obstacle in fish also depends on the frequency of approaches to such obstacles (Silva et al., 2018), we differentiated between the following event types during the video analysis: ‘passage’, ‘uncompleted passage’, ‘return’, ‘uncompleted return’ and ‘approach’. While passage frequencies extracted from the videos were reported in Egger et al. (2020), we concentrated on the distribution of ‘passage’ and ‘return’ events between species in the present study. Details about the live fish swimming experiments are provided by Egger et al. (2020).

### 3. Results

#### *3.1. The flow in the vertical slot*

All fish migrating upstream the vertical slot must pass the area between the two side walls. In this area were two measurement points, one in the centre (position g9) and one close to a side wall (position h9) (Fig. 2). Our experiments revealed that the flow velocity was higher in the slot centre compared to the measurement point at the side wall across all investigated water discharges. In contrast, the TKE was generally higher at the side wall than in the slot centre: At 130 L/s water discharge, we measured flow velocities from 1.04 m/s (g9) to 0.97 m/s (h9). The velocity in the slot centre (g9) was 7.22 % faster than the velocity in the vicinity of the side wall. At 105 L/s, we measured with 0.83 m/s in the centre (g9) a flow velocity being 5.06 % higher than the velocity at the side wall (0.79 m/s, h9). Similarly, the velocity was 5.55 % higher in the centre (0.76 m/s, g9) compared to the side wall (0.72 m/s, h9) at 80 L/s water discharge. Contrary to that tendency of increased flow velocity in the slot centre, we recorded with 0.073 J/Kg (h9) a TKE being 40.38 % higher than 0.052 J/Kg (g9) at 130 L/s water discharge. At 105 L/s water discharge, the TKE at point h9 was 0.043 J/Kg and at point g9 0.030 J/Kg (increase of 43.33 %), and at 80 L/s water discharge the TKE at point h9 was 0.017 J/Kg and at point g9 0.013 J/Kg (increase of 30.77 %).

The overall assessed flow field 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 flow velocity between water discharges (Fig. 3). The mean flow velocity at 130 L/s across all measurement points was 0.744 m/s  $\pm$ 0.214, the mean velocity at 105 L/s was 0.700 m/s  $\pm$ 0.204 SD and the mean velocity at 80 L/s was 0.714 m/s  $\pm$ 0.048 SD. Indeed, the SD was remarkably smaller at 80 L/s compared to the other water discharges (Fig. 3). This suggests that although the mean velocity was similar between water discharges, the velocity was more homogenous between measurement points at the smaller water discharge (80 L/s), while the flow gradient increased between measurement positions at 105 (Supplementary Material 01) and 130 L/s (Fig. 2). This led to increased flow velocity in the central area

of the vertical slot, whereas the velocity decreased at the outer measurement points (e.g. 3, 4, d6, d7) at 130 and 105 L/s.

The Turbulent Kinetic Energy (TKE) was largest near the side walls with a shift between 130 L/s and 80 L/s: At 130 L/s, the largest TKE was measured at point h8 (1.061 J/Kg), while the point of largest TKE was determined 4 (0.088 J/Kg) when measured at 80 L/s. The mean TKE at 130 L/s was 0.151 J/Kg  $\pm$ 0.248, at 105 L/s mean TKE was 0.163  $\pm$ 0.353 and at 80 L/s the mean TKE was 0.022 J/Kg  $\pm$ 0.019.

Comparing the flow velocity with TKE by means of linear correlation, we did not observe linear relationships between the flow velocity and TKE at 130 L/s ( $r = 0.37$ ,  $p = 0.099$ ) (Fig. 4 C) and 80 L/s ( $r = -0.36$ ,  $p = 0.104$ ) (Fig. 4 F). This suggests that the flow conditions varied locally across the measurement points in the vicinity of the vertical slot.

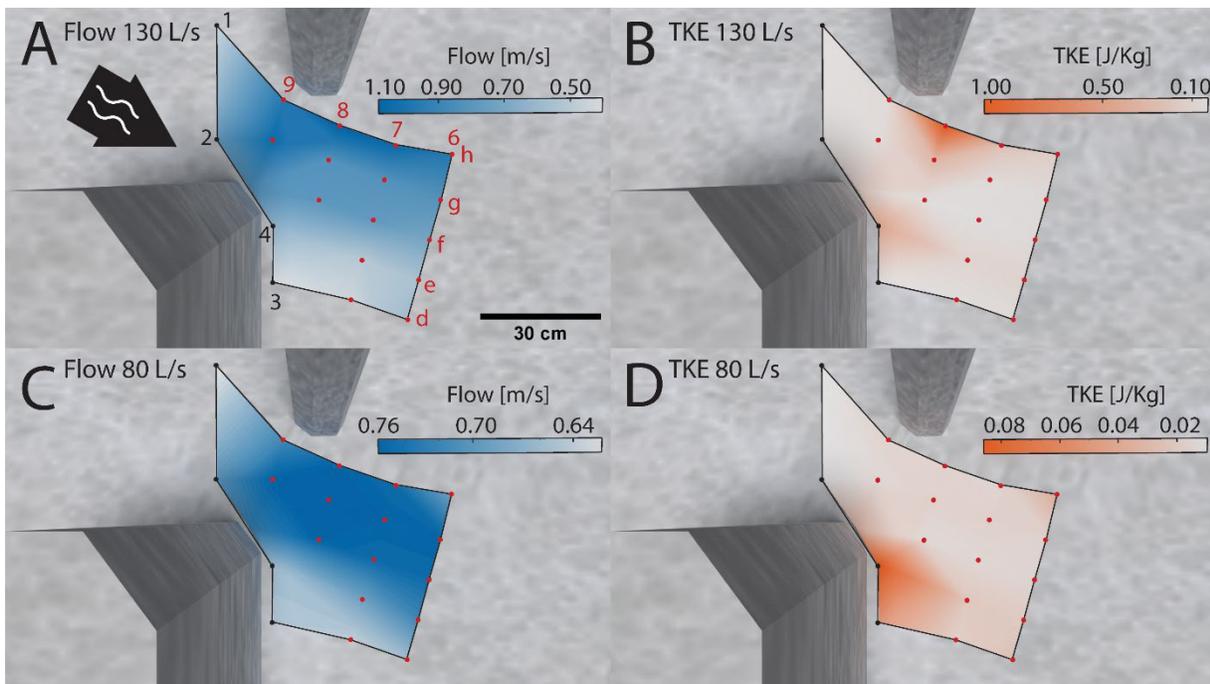


Figure 2: Mean flow velocity (A, C) and Turbulent Kinetic Energy (TKE) (B, D) measured at the different measuring points (red dots) near the vertical slot at different water discharges. The flow

measurements included four points, (points 1, 2, 3, 4 in black), which were not included in the force measurements.

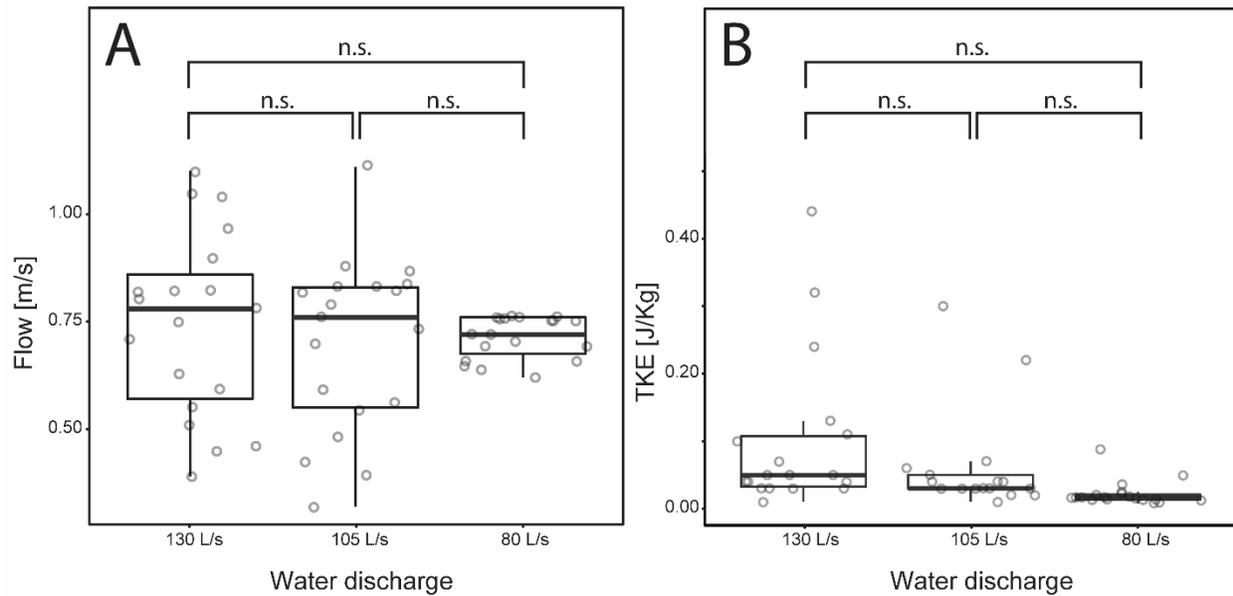


Figure 3: Flow velocity (A) and Turbulent Kinetic Energy (TKE) (B) measured by the acoustic Doppler at the different measurement points near the vertical slot in the fish pass model. We did not observe any significant differences ( $p$  has never been smaller than 0.05) (n.s.) between the water discharges. Three outliers (130L/s: 1.06 J/Kg; 105 L/s: 1.52 and 0.53 J/Kg) are lying outside the ordinate range in B.

### 3.2. The 3D-forces in the vertical slot experienced by preserved fish

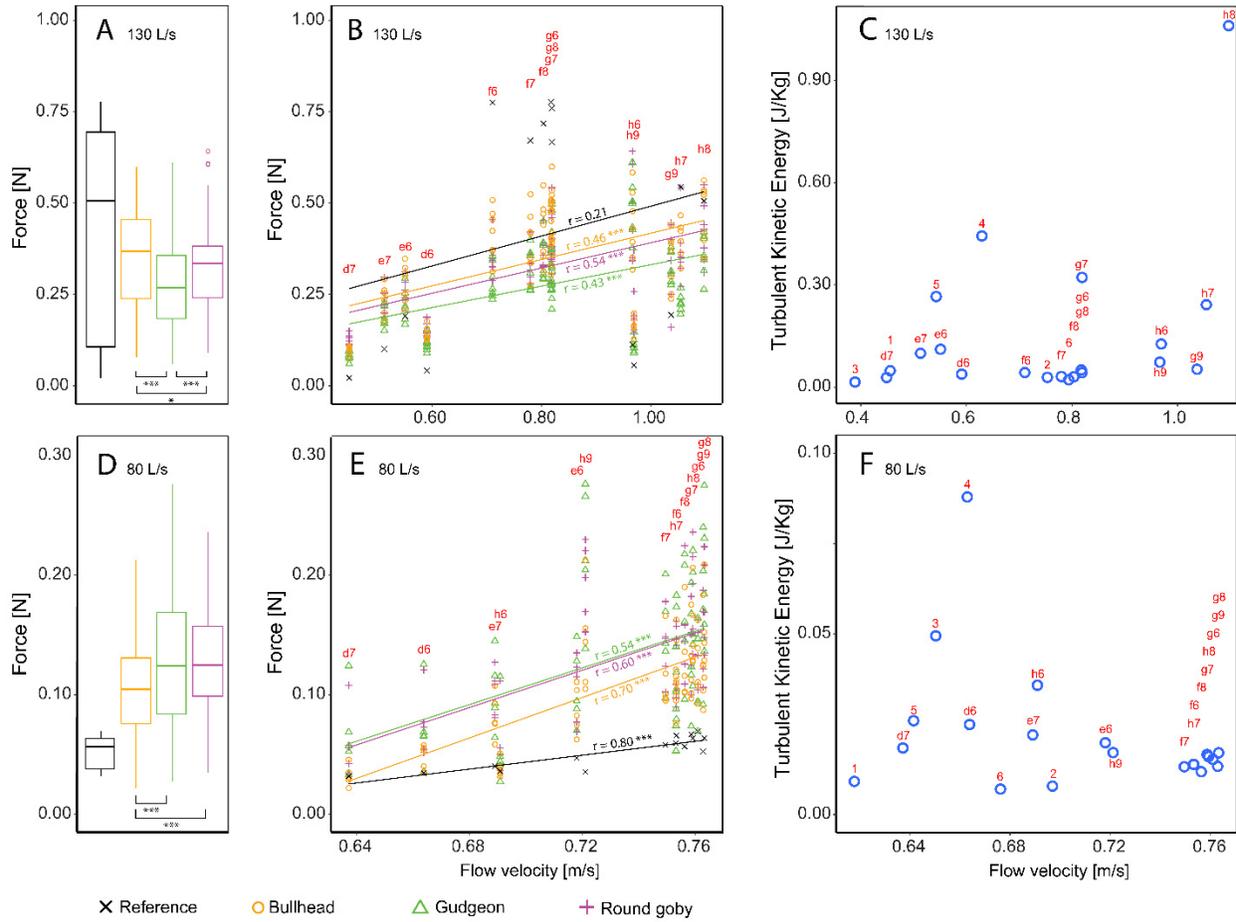


Figure 4: The 3D-forces experienced by the fish and measured at 130 L/s (A) and 80 L/s (D) water discharge with significant differences between species marked by asterisks (\*:  $p < 0.10$ ; \*\*:  $p < 0.05$ ; \*\*\*:  $p < 0.01$ ). The dependency of the 3D-forces from the water flow velocity over the different measurement points is provided for 130 L/s (B) and 80 L/s (E) water discharge. We tested seven fish per species at 130 L/s water discharge and five fish per species at 80 L/s water discharge. The black reference markers represent force measurements recorded by the fixation stick without an attached fish. Similar to A and D, the asterisks represent the significance level of the correlation in B and E. The dependency of the Turbulent Kinetic Energy from the velocity over the different measurement positions is provided in C (130 L/s) and F (80 L/s).

We found significantly different mean 3D-forces between species in the vertical slot: Gudgeon ( $0.272 \text{ N} \pm 0.120 \text{ SD}$ ) experienced significantly smaller mean 3D-forces than round goby ( $0.322 \text{ N} \pm 0.121 \text{ SD}$ ) and bullhead ( $0.345 \text{ N} \pm 0.137$ ) at 130 L/s water discharge (Fig. 4). The reference measurement (force experienced only by the stick, without fish) indicated the largest mean forces of all tested groups at 130 L/s ( $0.409 \text{ N} \pm 0.309 \text{ SD}$ ) with the largest forces detected at central locations near the slot (e.g. f6, f7, f8, g6, g7, g8).

While bullhead experienced the strongest mean forces compared to the other fish at 130 L/s water discharge, at 80 L/s bullhead experienced the significantly smallest forces ( $0.105 \text{ N} \pm 0.046 \text{ SD}$ ) compared to round goby ( $0.128 \text{ N} \pm 0.050 \text{ SD}$ ) and gudgeon ( $0.129 \text{ N} \pm 0.061 \text{ SD}$ ) (Fig. 4). There were no significant differences detected between the forces experienced by round goby and gudgeon, revealing the forces were of similar strength between both species at 80 L/s water discharge.

Comparing the forces to the flow velocity measured at the corresponding measurement points, we found considerable variation but also significant positive linear relationships for every species and at both tested water discharges (Fig. 4). This reveals that the fish experienced larger forces at positions with larger flow velocity, and the other way round, they experienced smaller forces at locations with smaller velocity.

### 3.3. Planar forces (X- and Y-direction) experienced by the preserved fish above ground

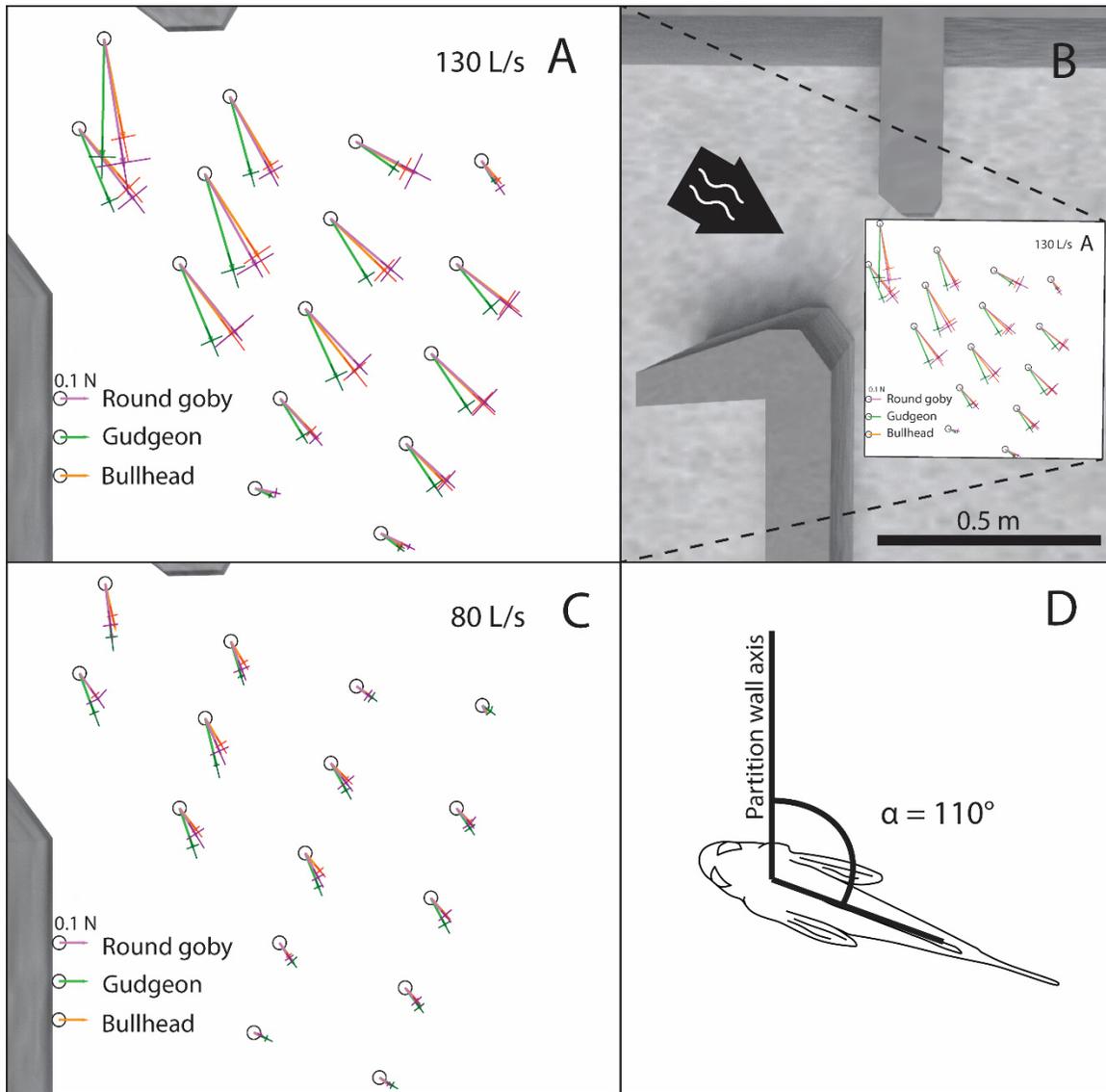


Figure 5: Direction and length of mean force vectors experienced by preserved fish at different measurement points near the vertical slot at 130 (A) and 80 L/s (C) water discharge. Error bars at the end of the vector arrows represent the standard deviation in vector length (in Newton [N]) and direction (in degrees [°]). The position of the measurement points (black circles) in the vertical slot fish pass model is provided in B with flow direction represented by the black arrow. The fish were oriented at the measurement probe with an angle of  $110^\circ$  ( $\alpha$ ) to the partition walls (D).

We observed the fish were predominantly pressed to the left side (from the fish's perspective) in the vicinity of the vertical slot. This left-side tendency was largest for gudgeon at both water discharges (mean angle 130 L/s:  $163.15^\circ \pm 18.05$  SD, mean angle 80 L/s:  $164.78^\circ \pm 21.00$  SD), while the angles seemed similar for round goby (mean angle 130 L/s:  $179.09^\circ \pm 19.49$  SD, mean angle 80 L/s:  $168.34^\circ \pm 21.65$  SD) and bullhead (mean angle 130 L/s:  $174.16^\circ \pm 16.18$  SD, mean angle 80 L/s:  $172.02^\circ \pm 16.20$  SD) (Fig. 5). The fish encountered the flow predominantly from the right side and were thereby pressed to the left.

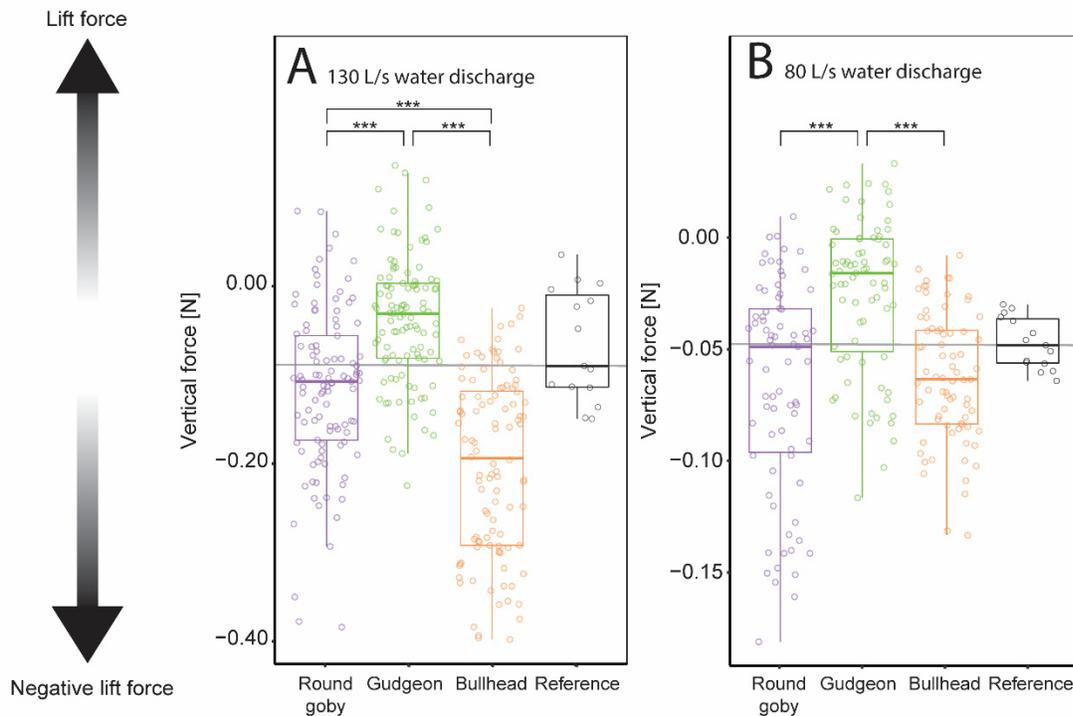


Figure 6: Vertical forces (lift force) experienced by preserved fish ( $n = 7$  fish per species at 130 L/s and  $n = 5$  fish at 80 L/s water discharge) at 15 measurement points near the vertical slot. Significant differences between species are marked with asterisks (\*\*\*:  $p < 0.01$ ). The Reference median was slightly smaller than point zero of the force sensor scale (ordinate) which presumably resulted from pressure variation

over the measurement points. Therefore, the forces experienced by the fish should be compared to the Reference (measurement without fish) when discriminating between lift- and negative lift forces.

#### *3.4. Lift forces*

The lift forces (vertical force component) differed significantly between all species at 130 L/s water discharge. Compared to the Reference (mean lift force:  $-0.087 \text{ N} \pm 0.063 \text{ SD}$ ), gudgeon experienced positive lift forces ( $-0.037 \text{ N} \pm 0.072 \text{ SD}$ ) while bullhead experienced negative lift forces ( $-0.202 \text{ N} \pm 0.100 \text{ SD}$ ) at 130 L/s (Fig. 6). Round goby lift forces ( $-0.116 \text{ N} \pm 0.091 \text{ SD}$ ) were rather similar to the reference. At 80 L/s water discharge, we observed the same tendency of significantly increased lift force in gudgeon ( $-0.025 \text{ N} \pm 0.034 \text{ SD}$ ) compared to round goby ( $-0.066 \text{ N} \pm 0.048 \text{ SD}$ ) and bullhead ( $-0.062 \pm 0.030 \text{ SD}$ ). The reference lift force at 80 L/s water discharge was  $-0.047 \text{ N} \pm 0.011 \text{ SD}$ .

#### *3.5. Live fish passage behaviour across the vertical slot*

There was an important change in the live fish passage behaviour between the lower water discharge (80 L/s) and the higher water discharges (105 and 130 L/s). While most of the passages (77.42%) and returns (92.45%) were observed for round goby at 80 L/s, gudgeon displayed an increased proportion of passages (47.77%) and returns (62.60%) at 105 L/s and 130 L/s (passages: 45.95%, returns: 65.52%) compared to 80 L/s water discharge (Fig. 7). Bullhead displayed similar passage and return proportions over all tested water discharges. Corresponding to the increased movement activity in gudgeon at the higher water discharges, we observed an increased number of fish approaches to the vertical slot without subsequent passage (Fig. 8).

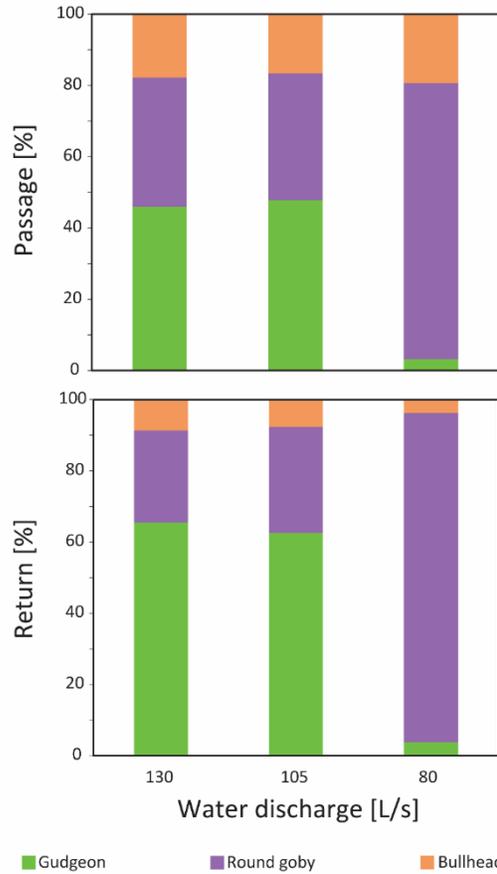
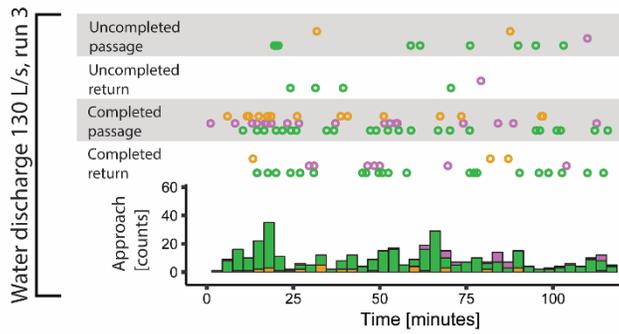
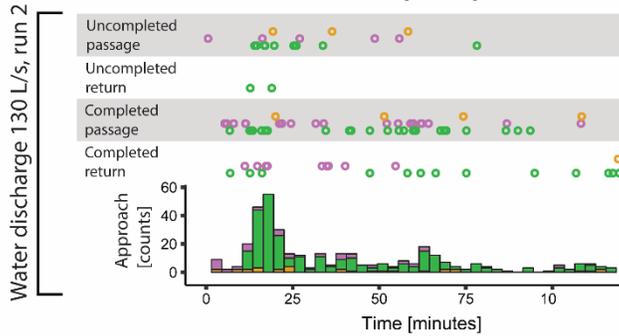
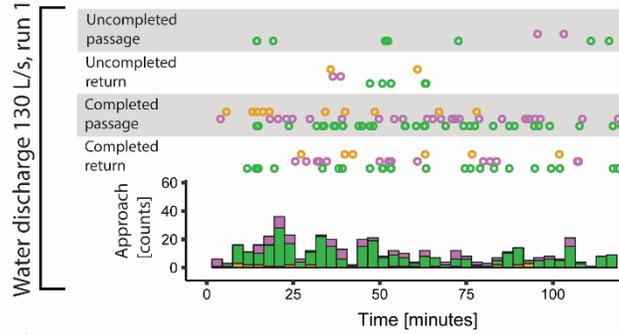
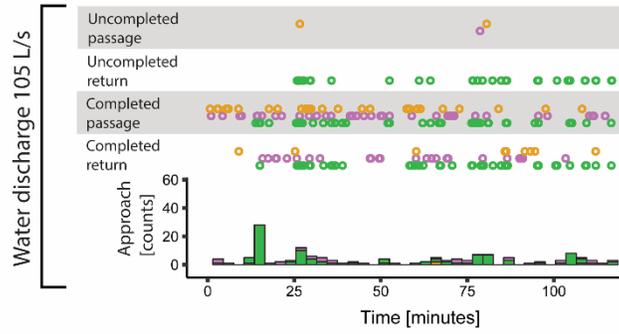
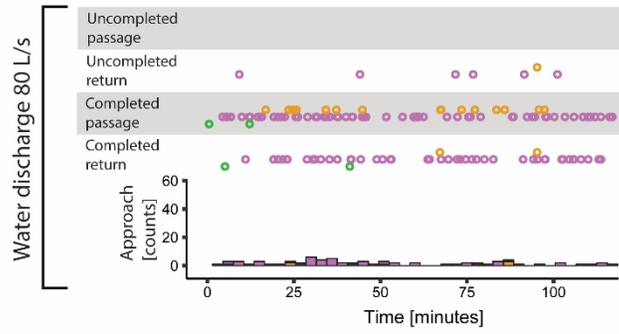


Figure 7: Proportion of live fish that passed the vertical slot in upstream direction (passage) and downstream direction (return) per species and water discharge. 100 % is the total amount of passages or returns observed at the corresponding water discharges. Three runs were performed at 130 L/s water discharge, while one experimental run was performed for both, the 80 and 105 L/s water discharge.



Round goby
  Gudgeon
  Bullhead

Figure 8: Distribution of behaviour events observed for the different species in the vertical slot over time at different water discharges. Each event is represented by one circle. Due to the high frequency of ‘approaches’, we represented this event type in histograms. Three runs were performed at 130 L/s water discharge, while one experimental run was performed for both, the 80 and 105 L/s water discharge.

## 4. Discussion

### *4.1. The hydraulic burdens of the three species: Filling the research gap*

With application of the three-step approach, we provide a detailed and species-oriented description of the flow field benthic fish encounter when swimming upstream a vertical slot fish pass. We found the forces experienced by the fish differed significantly between the three tested fish species and varied between water discharges. Together with smallest forces experienced compared to the other species, we observed increased passage activity in gudgeon at 130 L/s compared to 80 L/s. This observation supports that the experienced hydraulic forces may have affected the slot passage behaviour in gudgeon. Considering that higher flow velocities lead to stronger hydraulic forces (Wiegleb et al. 2020), we assume the hydraulic burdens affected the swimming behaviour especially at the higher water discharge. This corresponds to our finding that bullhead did not show increased passage behaviour at 80 L/s, although the smallest 3D-forces compared to the other species were observed for bullhead at this water discharge.

Based on these findings, our observations suggest that flow fields can have selective effect on the passage behaviour of individual fish species. Therefore, adapting the designs of fish passes in a way that the created flow fields can support or impede passage of specific species (Rahel & McLaughlin, 2018) should be considered for future ecosystem management measures.

### *4.2. How do the fish experience the flow? Hydraulic forces as a species oriented measure of the flow field*

To understand how the fish actually perceive the flow, there is a need to directly measure the effect of the flow field on the fish body. This has been implemented by several studies that aimed at perceiving the flow field from a fish perspective –via artificial lateral line systems (Chambers et al., 2014; Juan Francisco Fuentes-Pérez et al., 2015; Venturelli et al., 2012). Such probes are commonly designed with simplified shapes of fish and do not account for individual morphological characteristics of

specific species. Morphology in fish has been shown to be directly related to swimming costs (Ohlberger et al., 2006) and several studies showed morphological adaptation in fish from riverine habitats (Dashinov et al., 2020; Franssen et al., 2013; Imre, 2002; Meyers & Belk, 2014). To account for the effect of the individual body shapes of the species on the hydraulic burden, we assessed the forces experienced using real and preserved fish.

Our live fish observation was a result of a mixture of all parameters affecting the swimming behaviour of the fish. Beside boldness, exploration or activity (Lothian & Lucas, 2021) such factors as fish condition, temperature or seasonality could have affected the migration behaviour between the species. These factors were reduced as much as possible in our experiments due to the study design, but cannot be entirely avoided when working with live fish. Live fish swimming observations provide insight about how fish respond under the present conditions to a specific flow field of a fish pass design, but conclusions about the general effect of the flow field on the fish behaviour is limited.

#### *4.3. Hydraulic forces and their relevance for fish swimming behaviour*

To our knowledge, we provide and publish the first measurements of hydraulic forces experienced by real, preserved fish in a realistic environment that the fish encounter in fish passes. Indeed, measuring hydraulic forces does not account for the general swimming behaviour of live fish that depend on the individual species biology (Blake, 2004; Coombs et al., 2007; Sfakiotakis et al., 1999). Round goby and bullhead are described to perform predominantly burst-and-hold swimming styles (Egger et al. 2020) and Tierney et al. (2011) reported that round goby can be a powerful swimmer. In addition, a general rheophilic tendency has been reported for the round goby (Tierney et al., 2011), which is supported by the present study as there was increased passage behaviour at 80 L/s water discharge. Indeed, rheophily in round goby was not continuous across the tested water discharges as round goby activity was reduced at higher water discharges in the present study. Furthermore, gudgeon showed well swimming performance as revealed by high  $U_{crit}$  values (Tudorache et al., 2008), similar to subcarangiform swimming (Egger et al., 2020). Despite these species-specific swimming styles, the

hydraulic burdens represented the overall fish passage behaviour observed for live fish at 130 L/s water discharge. It is possible that the increase of turbulence between 80 and 130 L/s water discharge made the fish adapt their passage behaviour to the hydraulic burden. Turbulence is reported to have important impact on the swimming performance in fish (Lupandin, 2005) and can have positive as well as negative impact on fish swimming performance. Fish can make use of areas of reduced vorticity to save energy (Facey & Grossman, 1992) and also experience passive propulsion under specific flow conditions (Beal et al., 2006). Although the reference detected larger forces than experienced by the fish especially at 130 L/s water discharge, we do not assume that the fish experienced passive propulsion in our experiment because we never observed forces directed against the flow direction. Indeed, the force stabilizing effect of the fish compared to reference measurements described in the present study agrees with the finding from (Facey & Grossman, 1992) that morphological adaptation in benthic fish reduces the energetic advantage in using microhabitats in turbulent flow.

An increased capability for station holding in bullhead and round goby contrary to gudgeon has been reported by (Egger et al., 2020). When station holding, the fish can escape the flow using sheltering regions in the bottom substratum. In addition, the fish can support station holding by pressing their body onto the ground using specific pectoral fin postures (Carlson & Lauder, 2011). In our experiments, bullhead experienced the strongest 3D-forces and negative lift forces compared to the other species at the highest water discharge. It is possible that these negative lift forces supported the passage in bullhead at higher water discharge thus bullhead was the only species with unchanged passage behaviour across all water discharges. In contrast, the round goby passage behaviour changed importantly between the higher discharges (130 and 105 L/s) compared to 80 L/s but the round goby experienced inconspicuous forces being similar to the reference in the vertical direction. Considering that the round goby swimming style is similar to that of bullhead, this might indicate that other factors besides hydraulic forces may have affected the round goby swimming behaviour in our experiments.

Our findings correspond to studies describing a general rheotactic tendency at lower water discharge (Tierney et al., 2011) and flow avoidance by using shelter at increased velocities (Pennuto &

Rupprecht, 2016), but it is still an open question why the round goby showed reduced passage behaviour at higher water discharge compared to bullhead. Considering that round goby was described a surprisingly powerful swimmer (Tierney et al., 2011), it is possible that the round goby swimming behaviour is less specialized than bullhead and round goby respond to the forces of increased flow by reduced activity. Nevertheless, while bullhead might have profit from negative lift forces, the opposite could have been the case for gudgeon: Increased lift forces at higher water discharge might have supported the continuous, subcarangiform swimming mode above the ground (Egger et al., 2020).

#### *4.4. Evaluation of the force measurement approach*

Our results reveal that measuring the forces acting on preserved fish bodies can support the hydraulic description of fish passes to assess their suitability for specific target species. While acoustic Doppler measurements indicated similar flow velocities at different water discharges, the differences in the forces across different species highlight the discrepancy between unified flow conditions and actual hydraulic burden on the species level. Beside the forces acting on the fish on the three direction axes (X, Y, Z), we were able to compute the strength of the 3D-forces and their direction over the experimental time and thereby provided a detailed description of the physical burden the fish encounter during passage. In addition, the force measurements used preserved fish and are thus independent of various biological factors influencing swimming, such as adaptation to the test facility, daily form, feeding, parasite load, fatigue, personality, and motivation. Another advantage of force measurements is the possibility to assess the forces acting on bodies that are specifically tailored to the a specific research question (e.g. it is possible to adapt shapes using 3D-print-technology (Quicazan-Rubio et al. 2019)). Indeed, by using force measurements, it is possible to assess a flow field independently from live fish swimming behaviour and to assess the suitability, as well as the unsuitability, of the flow field for passage of specific species.

Nevertheless, we have considerations for future studies performing force measurements with fish. The most important aspect might be that it is not possible to measure the direct forces experienced by live and swimming fish, which has also been reported by Drucker and Lauder (2003). Fixation of a live fish to a force sensor would imply a significant amount of pain to the fish and the fish would probably not show any natural behaviour under these conditions. We therefore decided to approximate as much as possible to the live fish swimming conditions by using real, preserved fish and mimicking swimming fish in its preserved body posture (Wiegleb et al. 2020). With maintaining equal conditions between species (e.g. similar fish size, same measurement positions, same water discharges), we created a promising approach to describe the general burdens the fish encounter when challenging the flow. This is a necessary reduction of complexity and deviation from nature to be able to detect differences across species. Further discussion of the methodological and technical specifics of the applied force measurements approach is provided in Supplementary Material 02.

#### *4.5. Implementation for future fish pass assessment and future research*

Force measurements have the potential to represent a refinement of the common approach, which is to describe the functionality of fish passes by flow field description and live fish behaviour observations. Thereby, the force measurements provide a new and direct way to assess the flow field created in the fish pass for the physical requirements of target fish species in a standardized way. Because the force measurements do not require live fish, they avoid animal experiments which improves fish welfare and makes the results more replicable. In addition, the force measurements provided important insights about the hydraulic burden benthic fish experience during passage and how these burdens differ between species. This allows quantifications of parameters (forces) which traditionally could only be gleaned from mathematical models with many untested assumptions (e.g. Drucker and Lauder 1999; Sällström and Ukeiley 2014). Further research is needed to understand the specialized swimming behaviour in benthic fish and the factors determining passage behaviour.

We can now describe this piece of the total puzzle of parameters determining whether a fish migrates upstream a vertical slot or not. This puzzle is very close to the condition that can be changed by adaptation of the fish pass design: the water flow conditions. Thereby, we described a valuable measure enabling the assessment of fish pass designs for the suitability of specific target species which can be applied in the laboratory or in the field at existing systems. Future research should focus on the refinement of this measurement technique and the relationship of the forces experienced in flow and the behavioural response of the live fish to these forces.

## Competing interests

We declare we have no competing interests.

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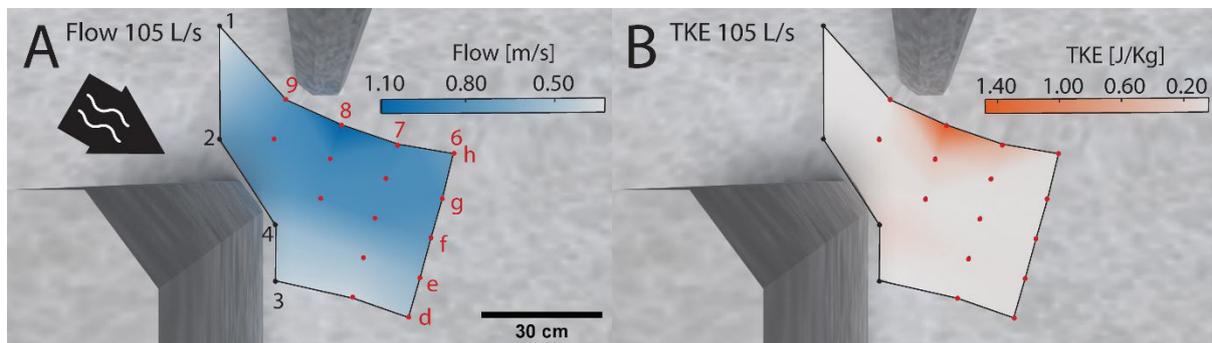
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## Supplementary Material



Supplementary Material 01: Mean flow velocity (A) and Turbulent Kinetic Energy (TKE) (B) measured at the different measuring points (red dots) near the vertical slot at water discharge of 105 L/s. The flow measurements included four points, (points 1, 2, 3, 4 in black), which were not included in the force measurements.

### *Supplementary Material 02: Detailed evaluation of the force measurement approach*

The force measurements performed promising by providing a more direct measure of the flow impact on the fish than conventional flow assessments. Indeed, beside the fish, also the fixation stick was exposed to the flow and the sensor thereby detected the sum of both, the force experienced by the fish and the stick. We initially intended to correct the force measured for the fish with the force detected for only the stick in the reference run to describe the exact forces experienced by only the fish, but we decided against this when we observed the increased vibration of the fixation stick in the reference at 130 L/s. Indeed, the temporal proceedings of the forces (Fig. S1) suggest that the forces measured with fish was not influenced by increased vibration and even the fish connected to the sensor stabilized the fixation stick (indicated by the absence of vibration at the measurement with fish at 130 L/s compared to the reference at 130 L/s). Therefore, we conclude that the force data were useful to compare the forces between species rather than determining exact forces experienced by preserved fish.

For precise description of the exact forces the fish experience in the flow it is necessary to perform the measurement without fixation stick. This could be possible if integrating the sensor directly in the fish body at the assumed center of gravity. Thereby, we would have avoided the application of the fixation stick and would have been able to measure the torque experienced by the fish over the x-, y- and z-axis in addition to the forces. This would have provided a more detailed picture of how the fish experiences the flow field, but integration of the sensor in the fish body was not applicable in our study due to the small size of the fish tested. However, due to the sensor size, this approach seems to be applicable for larger fish or upscaled 3D-models of smaller fish in future studies.

The angle between the fish and the partition walls was chosen to be  $110^\circ$  to the partition walls of the vertical slot at every measurement point. This angle was the same from our previous study (Wiegleb et al. 2021) and was chosen to maintain maximal comparability between studies. Indeed, that the fish were commonly pressed to the left side in the present study highlights that the fish angle should be adapted in future fish pass assessments. The drag force fish experience in flowing water depends on the surface exposed to the flow (Wiegleb et al. 2020) and it is likely that fish adapt their body alignment against the flow direction to decrease drag forces and measuring the forces from the front seems to be more appropriate. Nevertheless, our results revealed that the flow direction is very variable over time and it might not be possible to adapt the fish direction in flow direction every time during the measurements. An appropriate solution for future experiments seems to be a loose connection between fish and fixation stick, in a way that the fish body can rotate freely around the stick and adapt its position after the direction resulting in the lowest drag. Indeed, it has to be considered that this approach neglects forces experienced from the side because the force data alone will not provide information about the alignment direction of the fish –only about the forces experienced. A more suitable option seems to perform flow measurement to determine the mean flow direction for each measurement point and then to adapt the fish alignment to the relating flow direction at every measurement point. This ensures that the fish angles are adapted to the requirements of the test flow, accounts lateral forces and provides a standardized procedure enabling comparisons of the forces between species.



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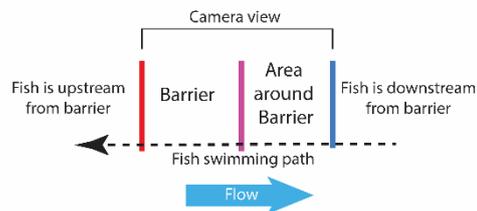
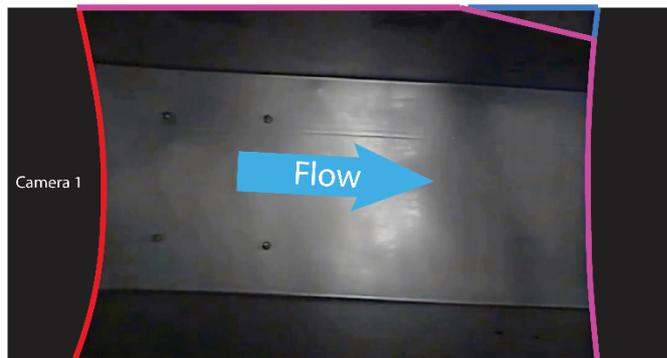
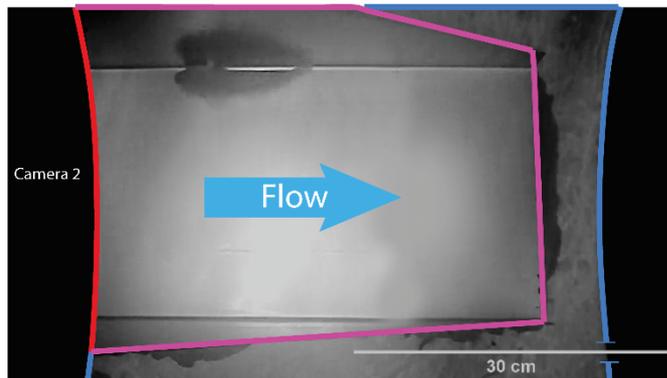
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# Appendix



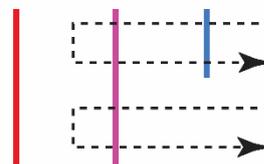
## Passage

The fish entered the camera view at the downstream screen edge or entered the barrier directly, crossed the barrier and left the camera view in upstream direction.



## Uncompleted passage

The fish entered the camera view at the downstream screen edge or entered the barrier directly, were observed over the barrier with the complete body and left the camera view again in downstream direction.



## Return

The fish entered the camera view from upstream and left in downstream direction.



## Approach

The fish approached the barrier from downstream direction, did not enter the barrier with the complete body and left the camera view in downstream direction.



**Appendix 1:** Criteria for categorization of fish behaviour events at the prototype hydraulic barrier.

**Appendix 2:** Personal contributions to the present study are highlighted with black boxes

	Joschka Wiegleb	Patricia Holm	Philipp Hirsch	Bernd Egger	Georg Rauter	Frank Seidel	Johannes Hilpert	Peter Reimann	Hirwis
<b>Paper I</b>									
Conceptualization	■	■	■	■		■			
Flow measurements							■		
Construction force measurement system								■	
Force measurements	■								
Live fish swimming experiments				■					
Analysis flow data						■	■		
Analysis force data	■								
Analysis swimming data				■					
Figure design	■								
Writing first draft	■								
Writing manuscript	■	■	■	■		■			
Editing manuscript	■	■	■	■		■			
<b>Paper II</b>									
Conceptualization	■	■	■	■		■			
Swimming experiments Basel				■					
Swimming experiments KIT	■		■	■					
Implementation of Video records at KIT	■								
Screening of videos from the KIT	■								■
Analysis of video screening data from KIT	■								
Figure design	■			■					
Writing first draft				■					
Writing manuscript	■	■	■	■		■			
Editing manuscript	■	■	■	■		■			
<b>Paper III</b>									
Conceptualization	■	■	■	■	■	■			
Barrier design	■	■	■	■		■			
Construction force measurement system					■				
Construction force measurement probe	■								
Flow measurements	■								
Force measurements	■								
Live fish swimming experiments	■		■	■					■
Analysis flow data	■								
Analysis force data	■								
Screening videos of live fish and tracking	■								■
Analysis tracking data	■								
Figure design	■								
Writing first draft	■								

	Joschka Wiegleb	Patricia Holm	Philipp Hirsch	Bernd Egger	Georg Rauter	Frank Seidel	Johannes Hilpert	Peter Reimann	Hiwis
Writing manuscript	■	■	■	■	■	■			
Editing manuscript	■	■	■	■	■	■			
<hr/>									
<b>Paper IV</b>									
Conceptualization	■	■	■	■	■	■			
Flow measurements	■								
Force measurements	■								
Live fish swimming experiments	■		■	■					
Analysis flow data	■								
Analysis force data	■								
Screening videos of live fish	■								■
Analysis of live fish passage data	■								
Figure design	■								
Writing first draft	■								
Writing manuscript	■	■	■	■	■	■			
Editing manuscript	■	■	■	■	■	■			
<hr/>									
<b>Accompanying text</b>									
Conceptualization	■								
Figure design	■								
Writing	■								
Editing	■								