Fish body geometry reduces the upstream velocity profile in subcritical flowing waters

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Abstract
Fish body geometry is highly variable across species, affecting the fluid-body interactions fish rely on for habitat choice, feeding, predator avoidance and spawning. We hypothesize that fish body geometry may substantially influence the velocity experienced by fish swimming. To test this hypothesis, we built nine full-scale physical prototypes of common freshwater fish species. The prototypes were placed in a large laboratory flume and upstream time-averaged velocity profiles were measured with increasing distance from the anterior-most location of each body. The measurements revealed that the body geometry can have a significant influence on the velocity profile, reducing the flow field at a distance of one body length upstream of the fish. Furthermore, it was found that the upstream velocity profiles from the nine fish species investigated in this study can be normalized to a single fit curve based on the freestream velocity and fish body length under subcritical flow conditions. These findings are significant, because they show that conventional point velocity measurements overlook the reducing effect of the fish body on the upstream flow field, creating a systematically biased representation of the velocity experienced by fish in subcritical flowing waters. This bias is illustrated by velocity field maps created with and without the presence of the physical models for three different fish species. Finally, we provide an example of how point velocity measurements can be recalculated to provide upstream velocity field maps closer to “the fish’s perspective”.

Keywords Ethohydraulics · Fish habitat · Fish body morphology · Flow velocity · Spatial scales

Introduction
Successful ecosystem management requires effective analytical approaches based on physical descriptors to estimate the spatial–temporal distributions of fish and their habitats (Brownscombe et al. 2021). A key physical descriptor in lotic habitats is the flow velocity (García-Vega et al. 2021), which facilitates drift feeding (O’Brien and Showalter 1993) and gravel spawning (Kondolf et al. 2008) and is also the main parameter used to study and classify fish swimming performance (Katopodis and Gervais 2016).

Historically, fish habitats are surveyed by in situ sampling of the fish’s location and surrounding physical environment (Nestler et al. 2019). The parameters most frequently used to describe the physical environment are the average water depth, time-averaged velocity, substrate composition, vegetation and cover (Wheaton et al. 2010). These data are often recorded as point values, where it has been pointed out that the scale dependency of physical habitat parameters remain largely unexplored (Crook et al. 2001). Additionally important to the study of fish habitats is improving the understanding of their variability across space, identifying the physical conditions causing this variation, and determining the extent to which these conditions are scale dependent or may be considered as independent (Gido et al. 2006).

Locally, fish microhabitat conditions are dynamically driven by the river flow regime, and can be used to explain and predict fish community attributes in unregulated and regulated rivers (Senay et al. 2017). These community attributes are needed to better reflect the size-dependent needs of the distribution of fish species life stages across multiple spatial scales (Santos et al. 2011). In addition to the fish size, recent studies have begun to explore more complex relationships between fish body geometry (morphometrics) on attempt rate
and passage success through culverts (Goerig et al. 2020), including the development and application of automated image analysis software (Navarro et al. 2016). These studies are some of the first to explore how fish body geometry relates to conventional assessments of the critical swimming speed of fish outside of laboratory settings, and are important, because the swimming speed is a widely used metric to classify fish swimming performance (Cano-Barbacil et al. 2020). To classify swimming performance, tests are carried out in swim tunnel respirometers based on the highest velocity at which fish can maintain speed for predetermined time intervals over which the velocity is incrementally increased until fatigue is observed (Webb 1971). In contrast to habitat models, which use the velocity’s physical units (m/s), the swimming speeds are often considered scaled to the fish’s body length ($L_{\text{fish}}$/s). This is an important distinction, as it directly includes the size of the organism as the characteristic length scale. The use of the body length thus provides a normalized velocity to investigate fish swimming capabilities as a function of their body geometry.

Advancing our ability to understand the relevance of measured physical flow parameters in lotic ecosystems and their relations to fish body geometry has valuable implications for environmental research and management. By improving our knowledge of the underlying physics of fish and flow interactions, we expect advances across multiple domains, including improving the cross-study transferability of fish habitat, swimming, behavioural and energetics research findings, all of which play significant roles in improving fish species distribution predictions.

Freshwater fish species exhibit a broad range of morphological traits (Brosse et al. 2021) and experience a wide range of velocities in ambient flows. Previous works have shown that fish use their lateral line system to sense near-body changes in the velocity field (Bleckmann 1994) and correspondingly, the major findings of the presented work highlight the need to consider that fish body geometry may impact the velocity upstream of a fish. The magnitude of the distortion a fish’s body causes on the flow field is not commonly included in either laboratory or field assessments, and is also highly likely to influence the fish’s flow sensing ability. To address this, we recommend the use of a body length-dependent velocity correction. Once applied, the corrected measurements can provide a standardized reference velocity for the further investigation and cross-comparison of the upstream flow conditions experienced by fish swimming freely in lotic systems.

### Materials and methods

#### Laboratory flume and hydraulic setups

All measurements in this study were conducted in a large glass-walled laboratory flume at the Technical University of Darmstadt, Germany. The flume has a constant width of 2 m, a wall height of 1.2 m and a total length of 40 m, as shown in Fig. 1. The flume bottom has zero slope, where both the upstream and downstream ends are at the same vertical elevation, and is supplied with water by two elevated tanks and one additional pump, with a maximum flow rate of 1 m$^3$/s. The flume water supply was equipped with electromagnetic flow meters (PROMAG 33F, Endress + Hauser Group Services AG, Switzerland; 10 D 1425 A; Fischer & Porter, Germany) which continuously displayed the discharge during experimentation. The water level in the flume was adjusted and maintained throughout the experiments by manually operating a sluice gate at the end of the flume. Three different hydraulic setups (H1, H2, H3—Table 1) were chosen for the experiments. The velocities were set by adjusting the discharge while maintaining a fixed water depth ranging from 0.7 to 0.75 m. The highest velocity in the flume was 0.63 m/s, measured at the centroid of the cross-section 14.5 m downstream of the inlet. We chose velocities at which fish show clear rheotactic alignment with the flow, and therefore the minimum velocity was set to be above 0.3 m/s and the middle velocity was set to 0.48 m/s.

#### Fish-shaped bodies

To evaluate the impact of fish body geometry on the upstream velocity profile, nine different fish body shapes (FS), of eight common freshwater fish species were manufactured (Table 2, Fig. 1). Each fish body was designed using the computer aided drafting software SolidWorks 2019 (Dassault Systems, France) and the model of each fish was based on the 3D models of fish donated by Dosch Design Kommunikationsagentur GmbH (Marktheidenfeld, Germany) from imagery collected of live fish, and modified to fit the morphometric ratios presented in Schwevers and Adam (2019). For all physical prototypes, the anterior 1/3 of the bodies were kept rigid for mounting purposes, while the remaining posterior 2/3 was made from cast flexible silicon with a Shore hardness of 8. The rigid parts were
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Fig. 1 Laboratory flume and measurement setup used in this study: a location of the flume sampling area (red); b position and orientation of the fish-shaped physical model (FS) in the flume cross-section; c measuring principle of the ADV in front of the fish’s nose: ultrasonic waves are transmitted, reflected at in the flow transported particles in a small sampling volume and received again by the ADV. Due to the Doppler phase shift between two signals, the water velocity can be estimated; d measurement setup using a chub-shaped body in the hydraulic flume.

Table 1 Overview of the hydraulic conditions during the laboratory flume experiments

| Hydraulic setup no. | Water supply       | Flow rate [m³/s] Mean (min–max) | Water depth [m] Mean (min–max) | Mean freestream velocity at investigated location [m/s] Mean (± stdev, min–max) | Reynolds/Froude number of freestream [-] |
|---------------------|--------------------|---------------------------------|--------------------------------|--------------------------------------------------------------------------------|------------------------------------------|
| H1                  | Gallery tank       | 0.490 (0.485–0.495)             | 0.7 (0.68–0.72)                | 0.35 (± 0.041, 0.19–0.49)                                                      | 575,538/0.13                            |
| H2                  | Gallery tank       | 0.700 (0.693–0.707)             | 0.75 (0.73–0.77)               | 0.48 (± 0.060, 0.26–0.69)                                                      | 814,096/0.17                            |
|                     | Roof tank          | 0.070 (0.069–0.071)             |                                 |                                                                                |                                          |
| H3                  | Gallery tank       | 0.700 (0.693–0.707)             | 0.72 (0.69–0.75)               | 0.63 (± 0.065, 0.41–0.87)                                                      | 1,055,072/0.24                          |
|                     | Roof tank          | 0.087 (0.086–0.088)             |                                 |                                                                                |                                          |
|                     | Additional pump    | 0.173 (0.172–0.174)             |                                 |                                                                                |                                          |

Where applicable, values are reported as the time-average ± standard deviation as well as the range of values (minimum–maximum). Similar to a natural flow environment, the hydraulic conditions in the large laboratory flume varied over time and space due to local turbulence and discharge fluctuations in the water supply pipes caused by the pumps. The investigated location of the mean freestream velocity was in the centroid of a cross-section 14.5 m downstream of the inlet.
3D printed, using the Form 3 commercial stereolithography printer (Formlabs Inc. USA) using the Formlabs Durable resin. The posterior (tail) portions of the bodies, molds were 3D printed using the same technique and material. The bodies, including fins were cast using a non-toxic duplication silicone Elite Double 8 (Zhermack SpA, Italy).

**Acoustic Doppler velocimetry**

All velocity measurements in this study were performed using a commercial Acoustic Doppler Velocimeter (ADV, Vectrino Standard, Nortek AS, Norway) which was mounted in the flume directly upstream of the fish-shaped body and was configured to record with a sampling rate of 25 Hz (Fig. 1c, d). The transmitter at the ADV centre emits two ultrasonic pulses with a known time offset. The pulses are reflected from particles in a small, cylindrical sampling volume at a distance of 5 cm below the transmitter, and are received at four small bar-shaped receivers. The configuration of the device is depending on the quantity of transported particles, the flow velocity and the positioning of the probe in relation to solid boundaries and had been adjusted individually depending on the quality parameters correlation and SNR (signal to noise ratio). The final ADV velocity data consisted of the three Cartesian velocity vector components \(u, v, w\).

**Laboratory open channel flume tests**

The full study consists of three tests that build on one another, in which the ADV probe head was placed at a distance, \(d\) upstream of each FS. This allowed for the point-wise comparison between the undistorted freestream velocity, \(u_\infty\), and the distorted velocity, \(u_d\) at different distances, \(d\) upstream of the fish-shaped body.
Test (1): pre-analyses

A pilot study using all three hydraulic setups H1, H2, H3 (Table 1) was first undertaken to determine the measurement protocol for the detailed experiments carried out in Test 2. It, therefore, did not require the use of all probes, but rather a subset of them (FS1, FS4 and FS9) which were representative of the range of physical scales (small, medium, large) and fish swimming types included in this study. The results of Test 1 were used to determine the time duration required for stationary statistical analysis and the distances at which the ADV should be mounted upstream of the fish shapes anterior-most point for all measurement. This was done by recording velocities upstream of each of the three fish-shaped bodies, and determining the sampling duration required to provide a stable mean value and standard deviation. The protocol established for ADV measurements upstream of fish-shaped bodies is as follows: at each measurement point of the upstream velocity profile, five minutes of ADV measurements at 25 Hz were recorded. It was determined that a minimum duration of 1.5 min was required, as this resulted in a constant time-averaged mean and constant standard deviation. These durations were checked against the literature, and were found to be similar to previous investigations of ADV sampling rates and durations in laboratory flumes (Springer et al. 1999; Díaz Lozada et al. 2021). Furthermore, it was found that a value of 1 cm was the minimum distance between the fish shape and the ADV without creating signal reflections from the body surface. The upper distance limit of 50 cm was defined as it was the maximum distance at which clearly no distortion in the upstream flow profile was detected using the largest fish-shaped body (FS9). The distance increments from 1 to 10 cm from the body were made in 1 cm steps to capture the rapid decrease of the upstream flow velocity approaching the anterior-most point.

Test (2): velocity profiles upstream of fish-shaped bodies

Based on Test 1, a cross-section 14.5 m downstream of the inlet was chosen for Test 2 as the sampling location as it corresponded to the most stable region of steady, uniform flow (Fig. 1a, b). The ADV and fish-shaped bodies were mounted on a robotic gantry, controlled by an electric motor to user-defined coordinates. The position was chosen as the middle of the cross-section to minimize the influence of the walls, ensuring a symmetric flow around the bodies (Fig. 1b–d). The distance between the nose (anterior-most point) of the fish-shaped body and the measurement volume of the ADV ranged between one and fifty centimetres as established in Test 1 (Fig. 1).

This second series of measurements were conducted for all nine fish-shaped bodies, using hydraulic setup H2 (Table 1) and following the protocol established in Test 1 using 5-min ADV measurement durations at 25 Hz and recording distorted velocity in several distances upstream of the fish. Here, we opted to maintain the 5-min duration measurements for future research use to compare turbulence levels upstream of the fish body. To assess the potential effects of alternative freestream velocities on the flow distortion, the results of Test 1 using FS1, FS4 and FS9 in other hydraulic conditions with higher and lower velocities (H1 and H3) were added for the full experiment. These data of Test 1 and 2 were evaluated as upstream velocity profiles and used to generate a fit curve which can be used to correct the distortion of the upstream velocity caused by the presence of the body (“Data post-processing”, Fig. 4, Eq. 1).

Test (3): planar velocity field measurements

Test 3 was intended as a proof-of-concept application of the flow distortion function, which was established in Test 2. We tested the efficacy of the correction using three common European fish species (FS1, FS3 and FS9), again choosing
them to span the range of length scales, and obtained ADV measurements of 1.5-min duration at 25 Hz using hydraulic setup H2. To choose a more complex flow environment, a series of four planar velocity measurements (ADV-only, and ADV with the bodies FS1, FS3 and FS9) was conducted upstream of a 1:1 scale horizontal fish protection rack, where the velocities due to the structure of the rack and for selecting hydraulic setup H2 varied in a similar range to that covered by the tested velocities in Test 2. Subsequently, this allowed a limited application of the established correction equation to these field measurements. The rack was angled at 55° to the main streamwise flow direction, and included a vertical bypass slot extending from the flume bottom to the water surface, as illustrated in Fig. 2. This hydraulic model setup was chosen as it represents a controlled environment physically similar to those wild fish encounter during downstream passage around hydropower plants. Goulet et al. (2008) highlight that “only the near flow field can communicate outside information to the lateral line”. We were interested in investigating how the presence of the three different fish-shaped bodies changes the corresponding flow velocity maps. During the experiments with the three fish-shaped bodies FS1, FS3 and FS9, the ADV point measurements were made at a fixed upstream distance of 1 cm from the anterior-most point of each body, which was determined in Test 1 to be the closest point. The number of point measurements obtained for each of the planar velocity field measurements differed for each body due to their minimal possible distance to the rack: FS1 (n = 85), FS3 (n = 79) and for FS9 (n = 55). The measurement locations for FS3 are shown in Fig. 2b–c, and for FS1 and FS9 in the appendix (Figs. 9a, 10a). A second set of 85 ADV-only point measurements was taken under the same flow setup, but without the presence of a fish-shaped body, which were used as the control data set (undistorted velocity field). It was observed in previous experiments in the same flume with fish at an angled rack that fish often move close to the bottom. Therefore, we chose our measurement volume at 6 cm above the bottom of the flume (Fig. 2a). As in Test 2, the velocity measurements were time-averaged for every point to create maps of (a) the spatial distribution of the undistorted velocity field without the presence of the fish-shaped body, and (b) the potentially distorted velocity field 1.0 cm upstream of the fish-shaped body (Figs. 5, 9, 10). These maps are commonly used in laboratory and field studies to evaluate habitat and bioenergetics models of freshwater fish in lotic ecosystems. Here, again, it is important to clarify that Test 3 was carried out to verify the practical application of the flow distortion function established from Test 2.

Data post-processing

All ADV velocity data were post-processed to remove spikes using the software WinADV (Wahl 2004) applying the phase-space threshold despiking method of Gorring and Nikora (2002), modified by Wahl (2003), and the time-series were edited using Python (Version 3.7.11) to provide the time-averaged, streamwise velocity as well as the standard deviation at each single measurement point. Subsequently, curve fitting was applied for the data of Test 1 and 2 to obtain functions that describe the course of the point data the best as (a) a function of distorted velocity, \( u_d \) over distance, \( d \) (Figs. 3b, 6, 7, and 8), and (b) a normalised function of distorted velocity, \( u_d \) to freestream velocity, \( u_{\infty} \) over distance, \( d \) to fish body length, \( L_{\text{fish}} \) (Fig. 4).

Fit curve performance was evaluated using non-linear least squares, and a hyperbolic function was found as the best fit using the SciPy library (scipy.optimize.curve_fit). To examine further relations between fish geometry and the distortion of the upstream velocity field, the body geometries were classified as either belonging to fish which typically inhabit the “freestream” or are “bottom oriented”, and according to the swim types of “weak”, “intermediate” or “strong”. The cross sections for each body were estimated as the product of the width and height and plotted over the fish length, as shown in Fig. 3a.

The mean velocity data of Test 3 were compiled with the corresponding Cartesian coordinates of the flume system to map the field data two-dimensionally for all four measurement series (ADV-only, ADV-FS1, ADV-FS3, ADV-FS9) using the ParaView (Version 5.7.0) software. Additionally, the general distortion function presented in the result “Effect of fish body type on the upstream velocity profile” was applied to the ADV-only measurements to model the effect of different fish shape on the flow field. The results were subsequently used to contrast modelled and measured ADV-FS maps and therefore validate the gained function (“Application of flow distortion function”).

Results

Effect of fish body type on the upstream velocity profile

The results of both the upstream velocity profiles and planar velocity measurements upstream of the fish protection rack support the main hypothesis of this work, that a fish-shaped body can distort the upstream velocity field. This finding is illustrated by a visual comparison of the different upstream velocity profiles in Fig. 3b and the planar velocity field maps with and without a fish-shaped body in Fig. 5a, b. The upstream velocity profiles, including the measurement
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Fig. 3 Distortion of the upstream velocity profile by fish-shaped bodies: a comparison of the area to total body length relationship, the scaled ellipses correspond to the maximal body dimension (width and height), colored for each fish-shaped body by hydraulic preference and swim type. The dashed grey line indicates the allometric relation between the different fish species; b measured flow velocity profiles upstream of the fish-shaped bodies, shown with a logarithmic scaling of the horizontal axis. The velocity $u_d$ is the streamwise velocity at each measurement point along the profile, and $d$ is the streamwise distance from the most anterior point of the fish body.

uncertainty expressed as the standard deviation for each fish-shaped body are provided in the appendix (Figs. 6, 7, 8).

The cross-section areas of the different fish species reflect interspecific similarities, or allometric relations, which are dependent on the fish total body length (Fig. 3a). This characterization follows a trend, where increasing body length corresponds to larger cross-section areas. Due to this relation, we chose the total length of the fish-shaped body as a geometric scaling factor for further investigations. The graph indicates that bottom-oriented fish species tend to lie under the indicated allometric curve, while freestream swimmers tend to lie above it. Considering the individual velocity profiles for each fish shape and its geometry, it was found that the highest flow distortion occurs for the longest body and the lowest distortion by the shortest body (Fig. 3b).

To compare the systematic reduction of the upstream velocity caused by the fish-shaped body, normalized functions of the streamwise velocity were fit for each hydraulic setup (Table 1). This resulted in a total of three fit curves (Fig. 4a–c) where it was observed that the individual curves were not found to differ substantially. Due to this similarity, the data from all three hydraulic setups were fit to a single hyperbolic curve. This resulted in a fit equation of the measured velocity, $u_d$, based on the freestream velocity, $u_\infty$, the distance from the anterior-most point to the ADV measurement location, $d$, and the total body length of the fish-shaped body, $L_{fish}$ (Fig. 4d):

$$\frac{u_d}{u_\infty} = 1 - \frac{L_{fish}}{158 \cdot d}$$

We stress here that the fit curve established in this work has been verified only for the tested ranges of velocities, from 0.35 to 0.63 m/s, for fish with total body lengths of 15–40 cm and the subcritical flow conditions present in the large open channel laboratory flume. It is worth noting that for small $d/L_{fish}$ ratios, the uncertainty of the equation increases due to a smaller number of measurements. The above function is suitable for use at low Froude numbers (Fr) corresponding to subcritical flows where Fr < 1. This is because for critical or supercritical flows where Fr > 1, large flow distortions are not propagated upstream of a submerged body (Bureau of Reclamation 2001).

The reduction of the upstream velocity profile was observed for all fish-shaped bodies, reaching a value of around only 0.6% of the freestream velocity at one body length ($dL_{fish} = 1$). This is considered as the distance of negligible effect, and is highlighted as the grey region in Fig. 4.

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Based on the results shown in “Effect of fish body type on the upstream velocity profile”, a clear workflow for velocity correction using Eq. (1) was established and applied in Test 3 using the planar ADV-only velocity measurements:

1. Evaluate the undistorted freestream velocity, $u_\infty$, without the presence of a fish-shaped body by measurement or CFD;
2. Verify if the velocities are within the limits of applicability of the flow distortion function ($0.35 \text{ m/s} < u_\infty < 0.63 \text{ m/s}$);
3. Choosing the distance, $d$, and the length of the fish, $L_{\text{fish}}$, which are of interest for a certain investigation but within the here given limits ($15 \text{ cm} < L_{\text{fish}} < 40 \text{ cm}$) and determining the distortion (reduction) of the freestream velocity in Eq. (1):

4. Apply the flow distortion function (Eq. 1) to the undistorted flow field to create velocity maps for the distorted flow field, $u_d$, as experienced by the fish-shaped body.

This method was carried out in Test 3 for three different fish-shaped bodies (FS1: $L_{\text{fish}} = 15 \text{ cm}$, FS3: $L_{\text{fish}} = 20 \text{ cm}$, FS9: $L_{\text{fish}} = 40 \text{ cm}$) at a distance of 1 cm upstream of the fish, whereby based on step 3 the following fit equations were derived from Eq. (1):

FS1 ($L_{\text{fish}} = 0.15 \text{ m}$) : $u_d = \left(1 - \frac{0.15[\text{m}]}{158 \cdot 0.01[\text{m}]_d} \right) u_\infty = 0.905 \cdot u_\infty$

$u_{d} = \left(1 - \frac{0.20[\text{m}]}{158 \cdot 0.01[\text{m}]_d} \right) u_\infty = 0.873 \cdot u_\infty$

Fig. 4 Upstream velocity profile plots and fit curves for all setups and fish-shaped bodies. The normalized streamwise velocity $u_d/u_\infty$ is plotted against the dimensionless length scale $d/L$ using a logarithmic scaling of the horizontal axis. a The upstream profile for a freestream velocity, $u_\infty$ of 0.35 m/s (FS 1, 4 and 9); b upstream profile for 0.48 m/s (all FS); c upstream profile for 0.63 m/s (FS 1, 4 and 9); d measurements from all experiments summarized as a single plot, the insert figure compares the results of this study with a replotting of the results found in Stewart et al. (2014). In the tests of Stewart et al. (2014), the fish was propelled (0.2 m/s shown) through still water. The right axis of d indicates the percentage reduction of the freestream flow velocity.
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Fig. 5 Planar velocity fields of ADV-only, ADV-FSS and after correction: a measured planar velocity field for ADV-only; b measured planar velocity field in 1 cm distance to FS3; c velocity field map based on the flow distortion function. The orientation of the vectors in the ADV-only flow field in a do not deviate strongly from those observed upstream of the fish-shaped bodies in b, indicating that the orientation of the flow field was not highly altered by the presence of the body.

\[
F_{9}(L_{\text{fish}} = 0.40 \text{ m}) : u_d = \left( 1 - \frac{0.40 \text{[m]}}{158 - 0.01 \text{[m]}} \right) u_\infty = 0.747 \cdot u_\infty
\]  

(4)

In the above equations, the ADV-only point measurements correspond to the values for \( u_\infty \). After applying the flow distortion function, the distorted velocities, \( u_d \) (Fig. 5c) were verified by comparing the values with direct measurements taken 1 cm upstream of the fish-shaped body (Fig. 5b). The results are shown for FS3 in Fig. 5, and additional figures are provided for FS1 and FS9 in the appendix (Figs. 9, 10). It should be noted that some of the freestream velocities are slightly above and below the tested range of \( 0.35 \text{ m/s} < u_\infty < 0.63 \text{ m/s} \) in this work.

A comparison between the different fish sizes also in generally shows that larger fish experience a more pronounced reduction of the freestream velocity, and that the spatial extent of this reduction is also greater for larger bodies than for smaller bodies (Fig. 4, Eq. 1).

Discussion

The results of the measurements clearly showed that for all eight species investigated, a systematic reduction of the upstream velocity profile was observed. Although our work used distinct fish-shaped bodies, the general findings are in substantial agreement with those performed on hydrofoils, submerged cylinders or similar streamlined shapes (Deng et al. 2021; Lake 1971). The major advantage of the flow distortion function is that the undistorted flow field can be measured or even simulated using computational fluid dynamics (CFD) and the corresponding distorted velocity field may be easily estimated using the fish’s body length.

Our work differs from previous fish related studies because they focus largely on the velocity, pressure and vorticity fields and their development downstream of the submerged bodies, few works have specifically investigated the upstream flow. We compared our findings with the results of Stewart et al. (2014), who analyzed the upstream flow field via PIV (Particle Image Velocimetry) and CFD (Computational Fluid Dynamics) and were found to be a good agreement with our work, as presented in Fig. 4d. Stewart et al. (2014) observed a reduction of the upstream velocity profile for a moving fish-shaped object towed through still water. The cause of the reduction in their study was attributed to the presence of a bow wake, similar to that found upstream of large vessels traveling at low speed. Thus, if a swimming fish is considered in a moving fluid, the relative velocity between the fish and the flow should be taken for further analysis. As discussed in Montgomery et al. (1997), fish may use the flow around their body to detect stationary objects which distort the self-produced field. Other previous works have proposed the detection length scale of fish’s lateral line-sensing system (Coombs 1999) by using the total body length as the scaling factor. Our study supports these results by providing physical evidence that the extent of the active sensory space is strongly correlated with the fish total body length and the relative velocity between the fish and the flow. It should be noted that previous works have also found that the total body length can be a key factor for evaluating the swimming speed (Adam and Lehmann 2011; Nikora et al. 2003; Katopodis and Gervais 2016).

Despite the conclusive evidence provided in this investigation using replicated experiments under a range of flow conditions, we wish to point out that several limitations remain.
First, due to varying flow conditions for each measurement and slight positioning differences (sub-centimeter) of the measurement device in front of the fish shapes, the time-averaged upstream velocity profiles should be considered including standard measurement uncertainty, expressed as the standard deviation of the velocity of each point. Second, although this work covered both lotic and benthic freshwater species as physical models, the measurements were made only using static fish-shaped bodies, and thus do not cover the entire spectrum of freshwater fish body morphologies, and do not consider swimming kinematics. For example, we did not consider the yawing motion of the fish's head during swimming, and therefore, the major findings of our work should be considered as physically analogous to the gliding phase of fish swimming. Third, we wish to point out that our experimental investigation was focused solely on determining the effect of the time-averaged upstream velocity profile with increasing distance from the anterior-most point. This choice was purposeful, as the time-averaged velocity is the most common flow measurement for studies of fish habitats, behaviour and swimming speed. Finally, it should be noted that the effects of the fish body shape on the upstream turbulence profile were not considered in this work. This particular topic has been investigated in the course of our investigation, and will be presented as a technical publication based on rapid distortion theory as a follow-up to this work.

The results of this study provide key insights needed to refine both lab and field flow velocity measurements investigating fish habitat usage, swimming speed and in situ observations of feeding and spawning activities.

Considering fish swimming, the observed reduction of the upstream velocity profile is significant because current field methods typically assume that the measured undisturbed velocity remains the same for all fish species and life stages. The experimental evidence gathered in this work shows that this assumption is largely unwarranted when considering the subcritical flows fish experience in nature. Future works will use the same body shapes and computational fluid mechanics simulations of turbulent flows to explore the three-dimensional velocity fields around the different body geometries, covering a wider range of flow velocities, body orientations and the presence of obstacles. We have also begun conducting field investigations with ADV and fish-shaped bodies in rivers and nature-like fishways to compare the findings of the laboratory study with the types of highly turbulent flows fish encounter in nature.

The major finding of this work, that fish body geometry reduces the upstream velocity profile, may have wide-ranging implications for monitoring and improving fish passage designs. We hope that our work encourages the aquatic sciences community to critically consider flowing waters from “the fish’s perspective” in future laboratory and field investigations, and in the evaluation of previous works based on point measurements of the time-averaged velocity.

Appendix

See Figs. 6, 7, 8, 9 and 10.

![Fig. 6](image-url) Individual plots of the upstream velocity profile for each of the fish-shaped bodies with increasing distance from the anterior-most point, for hydraulic setup H1. The lower rightmost panel includes the results of the fit curves for each body.
Fish body geometry reduces the upstream velocity profile in subcritical flowing waters.

Fig. 7 Individual plots of the upstream velocity profile for each of the fish-shaped bodies with increasing distance from the anterior-most point, for hydraulic setup H2. The lower rightmost panel includes the results of the fit curves for each body.

Fitted curves – $u_x \approx 0.48 \text{ m/s}$

- **FS1 - Gudgeon**: $u_d = 0.4766 - 0.00033/d$; $R^2 = 0.75$
- **FS2 - Perch**: $u_d = 0.4718 - 0.000099/d$; $R^2 = 0.92$
- **FS3 - Roach**: $u_d = 0.4746 - 0.0000112/d$; $R^2 = 0.90$
- **FS4 - Nase**: $u_d = 0.4737 - 0.000057/d$; $R^2 = 0.95$
- **FS5 - Burbot**: $u_d = 0.4717 - 0.000063/d$; $R^2 = 0.94$
- **FS6 - Chub (small)**: $u_d = 0.4698 - 0.000092/d$; $R^2 = 0.93$
- **FS7 - Barbel**: $u_d = 0.4696 - 0.000045/d$; $R^2 = 0.90$
- **FS8 - Bream**: $u_d = 0.4668 - 0.000080/d$; $R^2 = 0.95$
- **FS9 - Chub (large)**: $u_d = 0.4848 - 0.000194/d$; $R^2 = 0.99$
Fig. 8 Individual plots of the upstream velocity profile for each of the fish-shaped bodies with increasing distance from the anterior-most point, for hydraulic setup H3. The lower rightmost panel includes the results of the fit curves for each body.

Fig. 9 Planar velocity field measurements for FS1: a measurement grid of 85 points in front of a fish protection rack angled at 55°; b measured planar velocity fields in 1 cm distance to FS1; c velocity field map based on point velocity measurements without the presence of a fish-shaped body after applying the flow distortion function. The freestream velocity has been distorted using Eq. (2)
Fish body geometry reduces the upstream velocity profile in subcritical flowing waters

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Data availability  The datasets generated during and/or analysed during the study are available from the corresponding author on reasonable request.

Code availability  Code availability is not applicable to this study, as no software application or custom code was created or used in this project.

Declarations

Conflict of interest  The authors declare that no conflicts or competing interests exist.

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Fig. 10  Planar velocity field measurements for FS9: a measurement grid of 55 points in front of a fish protection rack angled at 55°; b measured planar velocity fields in 1 cm distance to FS9; c velocity field map based on point velocity measurements without the presence of a fish-shaped body after applying the flow distortion function. The freestream velocity has been distorted using Eq. (4)
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