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Bo-yu Chen

Sichuan University

Sheng-liang Wu

China Three Gorges Corporation

Jia Li

Sichuan University

Dan-lin Peng

China Three Gorges Corporation

Gu-peng Zhang

China Three Gorges Corporation

Xi-liang Tang

China Three Gorges Corporation

Jiang Yu

China Three Gorges Corporation

Ruidong An

anruidong@scu.edu.cn

Sichuan University <https://orcid.org/0000-0002-9895-2418>

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Experimental Study on Hydrodynamic Preferences and Collective Behavior of Fish Groups During Upstream Migration in Non-Uniform Flow

Bo-yu Chen¹, Sheng-liang Wu^{2*}, Jia Li¹, Dan-lin Peng², Gu-peng Zhang², Xi-liang Tang², Jiang Yu², Rui-dong An^{1*}

1. State Key Laboratory of Hydraulics and Mountain River Engineering, Sichuan University, Chengdu 610065, China

2. China Three Gorges Corporation, Wuhan 430010, China

Biography: Bo-yu Chen (1996-), Male, PhD candidate, E-mail: cby96@foxmail.com

Corresponding authors: Rui-dong An, E-mail: anruidong@scu.edu.cn; Sheng-liang Wu, E-mail: wu_shengliang@ctg.com.cn

Abstract: Fish passage facilities are critical for restoring longitudinal river connectivity and sustaining fish migration in dammed rivers. However, their effectiveness is compromised because fish struggle to locate entrances amid complex hydrodynamic conditions, and existing behavioral assessments rely on solitary fish in simplified, homogeneous flows. To address this gap, we constructed a large-scale non-uniform open-channel flow field with pronounced velocity gradients and turbulence, and quantified the collective responses of *Schizothorax prenanti* groups to flow heterogeneity during upstream migration. This study aimed to (a) map migration route selection and hydrodynamic preferences, (b) quantify collective movement patterns and group cohesion, and (c) evaluate how collective movement affects swimming performance under non-uniform flows. The results showed that fish groups preferred regions with lower hydrodynamic loads. Order parameter analysis revealed that despite transient phase transitions induced by turbulence, highly ordered schooling remained the dominant migration mode. By compressing inter-individual distances to within 0.4 m, the groups migrated upstream under more complex hydrodynamic conditions. As fish entered regions of higher flow velocity, their mean swimming speed increased from $0.458 \text{ m}\cdot\text{s}^{-1}$ to $1.042 \text{ m}\cdot\text{s}^{-1}$. A maximum swimming speed of $2.06 \text{ m}\cdot\text{s}^{-1}$ was recorded in the highest-velocity region, although fish spent less than 1% of observation time there. Therefore, the design of fish passage facilities and the restoration of river connectivity should consider the continuity of low-velocity approach corridors, the spatial organization of flow transition zones, and the continuous length of high-hydrodynamic-load regions, so that hydrodynamic design better matches the upstream movement requirements of fish groups.

Keywords: Fish groups; Upstream movement; Non-uniform flow; Collective behavior; Fish passage facilities.

0. Introduction

To meet growing global demands for water supply, hydropower, flood control, and navigation, more than 58,000 large dams have been built worldwide. These dams have fragmented over half of the world's rivers into separate reaches ^[1]. Although these projects have played an important role in socioeconomic development, their construction has also substantially altered natural flow regimes and blocked fish migration routes. These changes have led to sharp declines in the populations of many fish species ^[2,3]. Fish passage facilities (FPFs) are an important measure for restoring longitudinal river connectivity and supporting fish migration ^[4,5]. However, the overall performance of existing FPFs remains unsatisfactory. Their effectiveness depends not only on whether fish can locate the entrance but also on how they respond to changing hydrodynamic conditions along the passage route ^[6]. Therefore, understanding how fish use the hydrodynamic environment is key to linking the hydraulic design of FPFs with their actual upstream movement behavior.

Fish sensory systems, particularly the lateral line system, are highly sensitive to hydrodynamic stimuli and can guide behavioral adjustments in response to flow heterogeneity ^[7,8]. Previous studies have shown that flow velocity (U) is one of the key factors that trigger rheotaxis in fish ^[9,10]. When encountering regions with different flow velocities, fish often show clear preferences for specific velocity ranges. For example, *Schizothorax wangchiachii* primarily occupies regions with flow velocities of 0.20 to 0.35 m·s⁻¹ ^[11]. In addition, fish generally avoid regions of high turbulence intensity to maintain swimming stability ^[12]. Thus, their ability to sense and use local hydrodynamic conditions may influence their swimming behavior. This provides a theoretical basis for designing efficient fish passage routes based on hydrodynamic conditions ^[13].

For schooling fish, upstream movement also involves dynamic adjustments in relative positions and movement patterns among group members. For example, Eurasian minnows (*Phoxinus phoxinus*) spend more time schooling and are more likely to adopt side-by-side positions at higher flow velocities ^[14]. Experiments with pairs of zebrafish (*Danio rerio*) further show that directional coordination and spacing between individuals may respond differently to changes in flow conditions ^[15]. These studies suggest that collective behavior in fish involves at least two related aspects that do not always change together. One is the extent to which group members move in the same direction, and the other is how closely they remain together in space. Both aspects are particularly important when fish groups cross interfaces between different flow regions, as individual members experience flow changes at different positions and times. They must therefore adjust their own movements while maintaining contact with neighboring fish.

In recent years, research has expanded to more complex hydrodynamic environments. Grass

carp (*Ctenopharyngodon idella*) groups change their spatial organization and upstream movement patterns in flumes containing pebble obstacles ^[16]. Experiments combining respiratory metabolic measurements with kinematic analysis have also shown that, under turbulent conditions, giant danio (*Devario aequipinnatus*) swimming in groups use less energy than those swimming alone. The volume occupied by the group also changes under these conditions ^[17]. Filella et al. ^[18] combined behavioral rules with flow effects in numerical simulations and identified a collective turning pattern in fish groups. They also found that the flow environment increased both the average swimming speed of fish groups and the randomness of their behavior. These studies suggest that hydrodynamic conditions may influence group cohesion, structural order, and movement states in fish ^[19].

Despite growing understanding of interactions between fish and hydrodynamic conditions, most experiments are still conducted in confined environments with relatively uniform flow, such as circular or small rectangular flumes ^[20,21,15]. These simplified settings limit the full expression of voluntary swimming behavior and may not accurately reflect behavioral strategies in natural, non-uniform flow fields. This is particularly relevant to environments with strong velocity gradients, which are common in tailwater areas downstream of dams ^[22,23]. Creating representative non-uniform flow fields under controlled experimental conditions and systematically quantifying collective behavior in fish groups are therefore key steps toward addressing these research gaps. To this end, we used a large flume with adjustable flow to establish a system for simultaneous observation of complex flow fields and fish behavior. We also developed a set of metrics to quantify collective movement in fish groups. We combined these metrics with local hydrodynamic preferences and upstream trajectories to analyze how fish groups use the hydrodynamic environment and adjust their collective movement. The findings provide experimental evidence to support the design and evaluation of low-velocity corridor continuity and flow transition zones in fish passage facilities.

1. Materials and methods

1.1 Experimental setup

Hydraulic and fish behavior experiments were conducted in a recirculating open-channel flume at the State Key Laboratory of Hydraulics and Mountain River Engineering, Sichuan University. The flume measured 20.50 m × 4.00 m × 1.00 m and consisted of an upstream tank, a swimming test section, a downstream pool, and a return channel (Figure 1). The swimming test section was 14.00 m long, 3.00 m wide, and 0.50 m high, with a horizontal bed and smooth sidewalls. A Cartesian coordinate system was defined with the X, Y, and Z axes aligned with the

streamwise, transverse, and vertical directions, respectively. A motor-driven propeller conveyed water from the return channel to the upstream tank. Water then entered the swimming test section through flow-straightening tubes spanning its full width. During the experiments, the discharge was maintained at $0.60 \text{ m}^3 \cdot \text{s}^{-1}$ and the mean water depth at 0.30 m. To create clear transverse differences in flow velocity, grids measuring $0.10 \text{ m} \times 0.05 \text{ m} \times 0.80 \text{ m}$ were arranged differently across the test section entrance. The corresponding zones were designated Zone I, Zone II, and Zone III, with different downstream flow velocities. An acclimation area measuring $1.00 \text{ m} \times 3.00 \text{ m} \times 0.50 \text{ m}$ was located at the downstream end of the swimming test section. It was separated from the main test area by a removable mesh panel. Subsequent behavioral analyses focused mainly on the region extending from 1.00 to 11.00 m downstream of the test section entrance. Two overhead cameras (WIM SkyStar) recorded fish movements at 30 frames per second, providing trajectories in plan view for subsequent analyses of spatial occupancy and collective behavior.

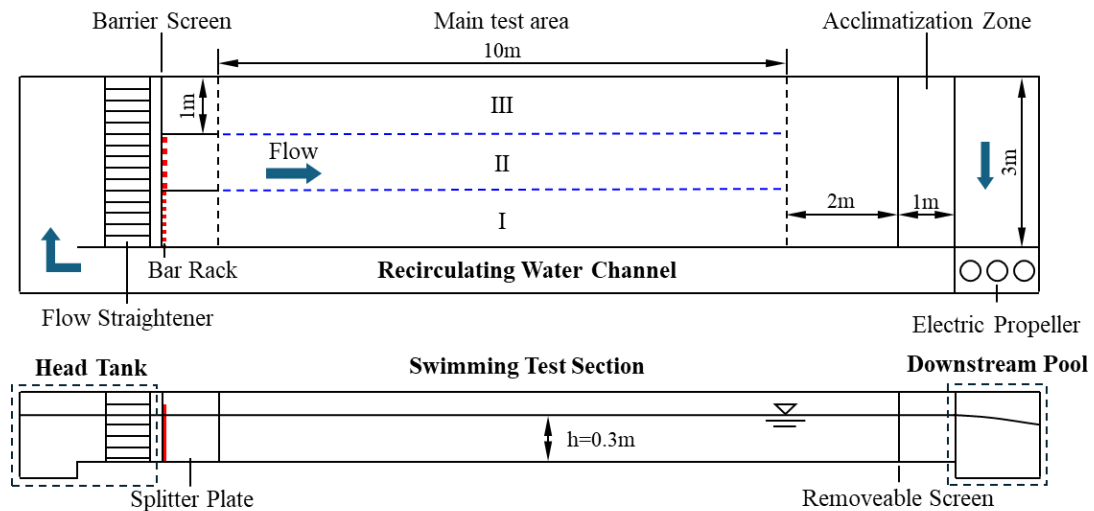


Figure 1 Overall layout and dimensions of the recirculating open-channel flume. The experimental system consisted of an upstream tank ($3.00 \text{ m} \times 3.00 \text{ m} \times 1.00 \text{ m}$), a swimming test section ($14.00 \text{ m} \times 3.00 \text{ m} \times 0.50 \text{ m}$), a downstream pool containing a motor-driven propeller ($3.50 \text{ m} \times 4.00 \text{ m} \times 1.00 \text{ m}$), and a return channel ($18.50 \text{ m} \times 1.00 \text{ m} \times 1.00 \text{ m}$). Blue arrows indicate the flow direction, red symbols indicate the inlet grids, and dashed blue lines mark the boundaries between the three transverse flow zones.

1.2 Hydraulic characteristics

The background flow field was measured using an acoustic Doppler velocimeter (ADV, Nortek Vectrino). Instantaneous velocity components in the streamwise, transverse, and vertical directions were recorded as u , v , and w , respectively. Measurement points were spaced 0.25 m apart in the streamwise direction and 0.10 m apart in the transverse direction. In regions near the sidewalls

where direct ADV measurements were not possible, velocities were estimated by fitting a logarithmic function to data from adjacent measurement points. All measurements were taken 0.15 m below the water surface, while the mean water depth was maintained at 0.30 m throughout the experiments. At each point, data were recorded continuously for 60 s at a sampling frequency of 50 Hz, with correlation values maintained above 80%.

Six hydrodynamic metrics were calculated, including flow velocity (U), transverse velocity gradient (grad_y), horizontal Reynolds shear stress (τ_{uv}), turbulence intensity (TI), turbulent kinetic energy (TKE), and swimming drag (D ; Table 1). Following Kerr et al. [24], D was calculated using the mean flow velocity together with transverse and vertical velocity fluctuations to represent spatial variation in background hydrodynamic loading. In the hydrodynamic distribution maps, grad_y and τ_{uv} retained their signs to describe flow structure and directional characteristics. In subsequent behavioral analyses, their absolute values were used to represent the magnitudes of the transverse velocity gradient and shear stress, respectively.

Table 1 Hydrodynamic metrics used to characterize the background flow field. Here, $\bar{u}$, $\bar{v}$, and $\bar{w}$ denote the mean velocity components; u' , v' , and w' denote velocity fluctuations; σ_u , σ_v , and σ_w denote the standard deviations of the corresponding velocity components; and ρ denotes water density.

Metric	Notation	Units	Equation
Flow velocity	U	$\text{m}\cdot\text{s}^{-1}$	$(\bar{u}^2 + \bar{v}^2 + \bar{w}^2)^{0.5}$
Transverse velocity gradient	grad_y	s^{-1}	$\partial u / \partial y$
Horizontal Reynolds shear stress	τ_{uv}	Pa	$-\rho \overline{u'v'}$
Turbulence intensity	TI	$\text{m}\cdot\text{s}^{-1}$	$(\sigma_u^2 + \sigma_v^2 + \sigma_w^2)^{0.5}$
Turbulent kinetic energy	TKE	$\text{m}^2\cdot\text{s}^{-2}$	$0.5 (\overline{u'^2} + \overline{v'^2} + \overline{w'^2})$
Swimming drag	D	Dimensionless	$D \propto U \sqrt{U^2 + \sigma_v^2 + \sigma_w^2}$

1.3 Fish holding and experimental procedures

Schizothorax prenanti, a species that migrates to reproduce, was selected for this study. Experimental fish were supplied by the Fisheries Research Institute of the Sichuan Academy of Agricultural Sciences. A total of 100 healthy individuals were transported in three successive batches to the State Key Laboratory of Hydraulics and Mountain River Engineering for holding. All fish were sexually mature, with a mean age of 3 years and a body length of 31.0 ± 4.0 cm. During holding, fish were fed commercial feed once daily until 24 h before testing to reduce the effects of digestion on the experiments. The holding tanks were supplied with pre-aerated tap water. More than 50% of the water was replaced daily, and continuous aeration was provided to maintain dissolved oxygen above 6.5 mg/L and pH between 7 and 8. Medical-grade ice packs

were used to maintain the water temperature at 18.83 ± 0.24 °C. Fish health was checked daily, and individuals showing signs of disease or visible wounds were promptly isolated.

Previous studies have shown that three or more fish can form a group ^[25]. Group formation is significantly more frequent when 8 to 10 fish are present ^[26]. Therefore, 10 fish were used in each trial to ensure that the observed movements were representative of group behavior. Ten independent trials were conducted, with each fish used only once. All trials took place between 09:00 and 15:00 using the fixed entrance arrangement described in Section 2.1. Before each trial, fish were transferred from the holding tanks to the downstream acclimation area and allowed to acclimate for 60 min. The removable mesh barrier was then raised to begin a 30 min observation period. During this period, fish could swim freely, and their movements were continuously recorded by the overhead cameras. After each trial, the fish were returned to the holding tanks. Upstream passage timing began when at least three fish had entered the main test area. Timing ended when fish had reached its upstream boundary. Passage time was defined as the interval between these two events. All experimental procedures were approved by the Ethics Review Committee of Sichuan University.

1.4 Behavioral quantification and statistical analysis

1.4.1 Route classification and hydrodynamic preference

Individual fish trajectories were extracted from video recordings using TrackMate ^[27], and behavioral metrics were calculated at 30 Hz. Local hydrodynamic preferences were quantified by comparing conditions at the positions occupied by fish with those available within the group's instantaneous mechanosensory field of detection (MFoD) ^[24]. Each fish's MFoD was represented by a circular area centered on its position, with a radius of 0.465 m ($R = 1.5$ BL, where BL denotes body length) ^[28]. The group's instantaneous MFoD was defined as the union of all individual MFoD circles. Hydrodynamic parameters within this area represented the environmental conditions available to the group at that moment.

For each trial, normalized frequency distributions were calculated at each time point for the hydrodynamic conditions used by fish and those available locally. These distributions, denoted by S_u and S_s , respectively, were then averaged over time. For hydrodynamic bin b in trial k , the preference ratio was calculated as

$$P_{h,k}(b) = \frac{S_{u,k}(b)}{S_{s,k}(b)} \quad (1)$$

A preference ratio of 1 indicates that the proportion of use matches the proportion of local availability for that hydrodynamic condition. A ratio greater than 1 indicates use above local

availability, reflecting a relative preference. A ratio below 1 indicates use below local availability. For each hydrodynamic bin, group-level hydrodynamic preference was calculated as the mean of the trial-specific preference ratios weighted by passage time:

$$P_{gh}(b) = \frac{\sum_{k=1}^{10} P_{h,k}(b) \Delta t_k}{\sum_{k=1}^{10} \Delta t_k} \quad (2)$$

Here, Δt_k denotes the passage time in trial k .

1.4.2 Metrics for evaluating collective behavior in fish

Under complex flow conditions, fish follow behavioral rules to coordinate their movements in different ways in response to environmental changes. To quantify these collective behaviors, we used polarization (P) and milling (M) as two key order parameters from statistical physics^[18]. These parameters describe collective behavior as objectively defined states rather than subjective descriptions, allowing us to examine relationships between flow structure and group movement. Let $\mathbf{v}_i(t)$ denote the velocity vector relative to the ground obtained from the trajectory of fish i . Its unit movement vector, $\mathbf{e}_i(t)$, and the group polarization were calculated as

$$\mathbf{e}_i(t) = \frac{\mathbf{v}_i(t)}{\|\mathbf{v}_i(t)\|}, \quad (3)$$

$$P(t) = \frac{1}{N(t)} \left\| \sum_{i=1}^{N(t)} \mathbf{e}_i(t) \right\| \quad (4)$$

Polarization ranges from 0 to 1, with higher values indicating greater alignment of movement directions among group members.

The radial unit vector pointing from the group centroid to fish i was defined as $\mathbf{e}_i^r(t) = [\mathbf{r}_i(t) - \mathbf{r}_c(t)] / \|\mathbf{r}_i(t) - \mathbf{r}_c(t)\|$. The milling parameter was calculated as

$$M(t) = \frac{1}{N(t)} \left| \sum_{i=1}^{N(t)} \mathbf{e}_i^r(t) \times \mathbf{e}_i(t) \right| \quad (5)$$

Here, the cross product refers to its signed component perpendicular to the observation plane. Higher M values indicate a greater degree of coordinated rotation around the group centroid.

Using the classification thresholds adopted by Filella et al.^[18], collective movement at each time point was assigned to one of four patterns. These were Schooling ($0.5 < P \leq 1$, $0 < M \leq 0.4$), Turning ($0.5 < P \leq 1$, $0.4 < M \leq 1$), Milling ($0 < P \leq 0.5$, $0.4 < M \leq 1$), Swarming ($0 < P \leq 0.5$, $0 < M \leq 0.4$). For each trial and flow zone, we calculated the proportion of time the fish group spent in each movement pattern.

The internal structure of the fish group, representing its cohesion during upstream movement, was quantified using nearest-neighbor distance (NND) and the area of collective structure (A_c).

These metrics describe local spacing between individuals and the overall spatial extent of the group, respectively (Figure 2).

At each observation time, the individual closest to the group centroid was defined as the focal fish, f . NND was defined as the minimum distance between the focal fish and any other individual in the group:

$$\text{NND}(t) = \min_{j \neq f} \|\mathbf{r}_f(t) - \mathbf{r}_j(t)\| \quad (6)$$

The area of collective structure, A_c , was defined as the area of the convex hull enclosing the positions of all group members. For a convex hull with m vertices arranged in cyclic order, its area was calculated using the shoelace formula:

$$A_c(t) = \frac{1}{2} \left| \sum_{j=1}^m (x_j y_{j+1} - x_{j+1} y_j) \right| \quad (7)$$

Here, $(x_{m+1}, y_{m+1}) = (x_1, y_1)$. NND and A_c were expressed in m and m^2 , respectively.

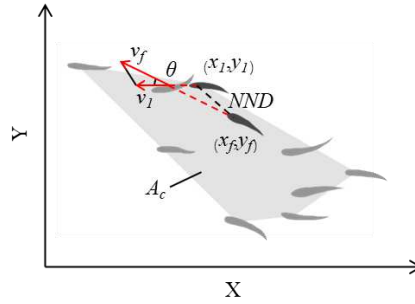


Figure 2 Schematic of the spatial distribution of fish within a group. The vectors v_f and v_i ($i=1,2,\dots,n$) represent the velocities of the focal fish and the other tracked fish, respectively ($\text{m}\cdot\text{s}^{-1}$). The angle between v_f and v_i is denoted by θ ($^\circ$). The dashed black line indicates the nearest-neighbor distance (NND, m) between the focal fish and its nearest neighbor. The shaded polygon represents the convex hull enclosing the fish group, whose area is the area of collective structure (A_c , m^2).

1.4.3 Hydrodynamic exposure and swimming speed

Hydrodynamic exposure experienced by the fish group was described using the mean background flow velocity within the group's instantaneous MFoD (U_{MFoD}) and the background flow velocity at each fish's position ($U_{\text{encounter}}$) as two metrics. U_{MFoD} was calculated by averaging the flow velocities across all grid cells within the group's MFoD. $U_{\text{encounter}}$ was obtained at each fish's position using bilinear interpolation. Swimming speed relative to the water was defined as the magnitude of the difference between the fish's ground-relative velocity vector and the local background flow velocity vector:

$$U_{\text{fish},i}(t) = \|\mathbf{U}_{\text{ground},i}(t) - \mathbf{U}_{\text{encounter},i}(t)\| \quad (8)$$

Here, $\mathbf{U}_{\text{ground},i}$ is the ground-relative velocity vector calculated from the individual trajectory, and $\mathbf{U}_{\text{encounter},i}$ is the background flow velocity vector at the same position. Maximum swimming speed (U_{max}) was defined as the highest valid U_{fish} value recorded within each flow zone during the analyzed upstream movement.

1.4.4 Statistical analysis

Each trial was treated as an independent replicate. Passage time was reported as the mean $\pm$ standard deviation (SD) and the observed range. Differences between TR1 and TR2 were assessed using the Mann–Whitney U test. For collective movement patterns, the trial-level proportions of time spent in each pattern were compared between TR1 and TR2 within the same flow zone. These comparisons used a two-sided exact permutation Mann–Whitney U test. Paired comparisons between Zone I and Zone II within the same route used a two-sided exact permutation Wilcoxon signed-rank test. Statistical significance was set at $p < 0.05$.

Frequency distributions of NND and A_c were calculated with equal weight assigned to each trial. For each NND or A_c bin, the corresponding hydrodynamic conditions were first averaged within each trial and then summarized across the trials represented in that bin. The corresponding central 80% empirical range was defined by the 10th and 90th percentiles of the distribution with equal weighting across trials.

2. Results

2.1 Experimental hydrodynamic characteristics

The inlet configuration produced a large-scale non-uniform flow field with three distinct velocity zones (Figure 3a). Mean flow velocity increased from $0.28 \text{ m}\cdot\text{s}^{-1}$ in Zone I to $0.51 \text{ m}\cdot\text{s}^{-1}$ in Zone II and $0.99 \text{ m}\cdot\text{s}^{-1}$ in Zone III (Table 2). Zone I formed a relatively continuous low-velocity corridor, whereas Zone III maintained the highest velocities throughout the study area, reaching a maximum of $1.33 \text{ m}\cdot\text{s}^{-1}$ near the upstream end and generally decreasing downstream.

Higher transverse velocity gradients were mainly concentrated near the interfaces between adjacent flow zones. A distinct transverse velocity-gradient band approximately 0.4 m wide formed at the Zone I–Zone II interface, with a peak gradient of 5.77 s^{-1} , while a second band extended downstream along the Zone II–Zone III interface. Horizontal Reynolds shear stress also showed pronounced local peaks near the zone interfaces, while turbulence intensity and turbulent kinetic energy were elevated within the transition bands, reaching maxima of 30.10 Pa, $0.40 \text{ m}\cdot\text{s}^{-1}$, and $0.08 \text{ m}^2\cdot\text{s}^{-2}$, respectively (Figure 3b–e). Swimming drag followed a spatial pattern similar to that of flow velocity, with the highest values concentrated in Zone III (Figure 3f). The ranges and

mean values of all six hydrodynamic metrics for the three zones are summarized in Table 2.

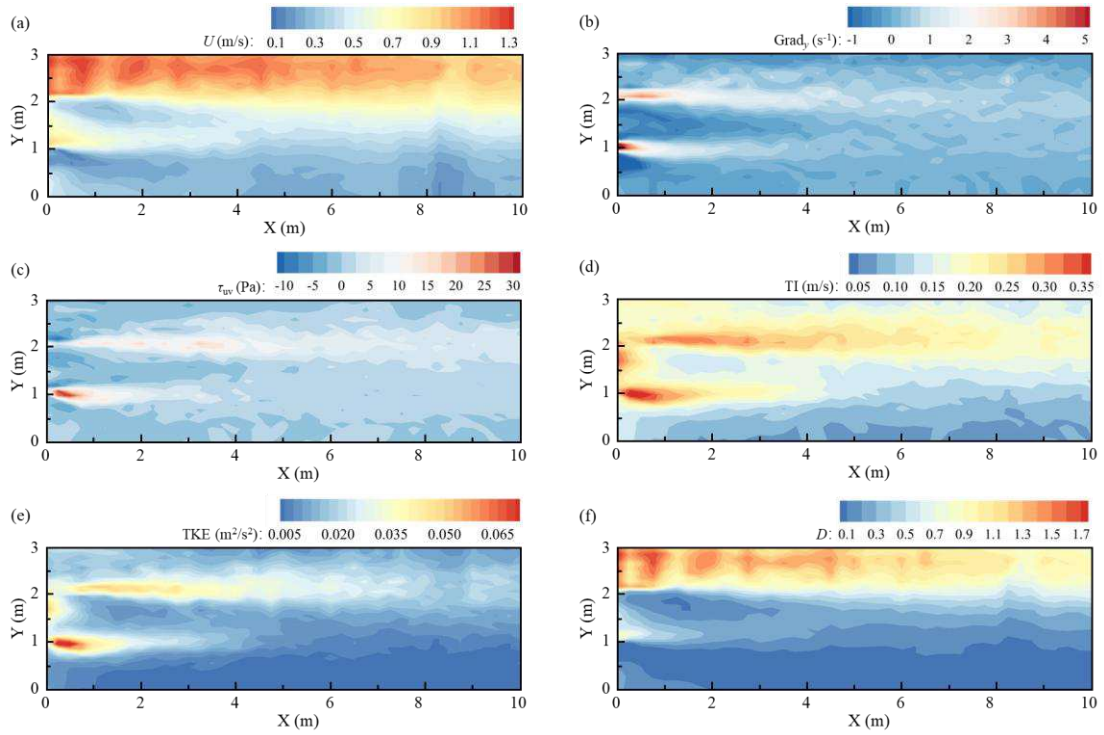


Figure 3 Spatial distributions of hydrodynamic parameters within the study area: (a) flow velocity (U , $\text{m}\cdot\text{s}^{-1}$); (b) transverse velocity gradient (grad_y , s^{-1}); (c) horizontal Reynolds shear stress (τ_{uv} , Pa); (d) turbulence intensity (TI, $\text{m}\cdot\text{s}^{-1}$); (e) turbulent kinetic energy (TKE, $\text{m}^2\cdot\text{s}^{-2}$); and (f) swimming drag (D).

Table 2 Ranges and mean values of hydrodynamic parameters in Zone I, Zone II, and Zone III.

Zone	$U(\text{m}\cdot\text{s}^{-1})$		$\text{grad}_y(\text{s}^{-1})$		$\tau_{uv}(\text{Pa})$		$\text{TI}(\text{m}\cdot\text{s}^{-1})$		$\text{TKE}(\text{m}^2\cdot\text{s}^{-2})$		D	
	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average
I	0.09~0.51	0.28	-	-	5.17~30.10	0.8	0.05~0.40	0.11	0.00~0.08	0.01	0.02~0.28	0.08
II	0.28~0.94	0.51	-	-	7.73~28.00	1.88	0.09~0.35	0.17	0.00~0.06	0.02	0.08~0.90	0.29
III	0.46~1.33	0.99	-	-	10.9~83.5	1.64	0.12~0.32	0.2	0.01~0.05	0.02	0.23~1.79	1.01

2.2 Upstream route selection and hydrodynamic preferences

Trajectory tracking revealed two recurring upstream route patterns, designated Typical Route 1 (TR1, $n = 6$) and Typical Route 2 (TR2, $n = 4$; Figure 4a,b). Along both routes, fish groups began upstream movement in the low-velocity Zone I and entered Zone III only near the upstream boundary of the study area. In TR1, groups remained close to the wall within Zone I through most

of the study area and entered Zone II only in the upstream section, at approximately $x = 1-3$ m. In TR2, groups left Zone I farther downstream, repeatedly crossed the Zone I-Zone II interface near $x = 5-7$ m, and then continued upstream mainly through Zone II.

Mean spatial occupancy distributions further confirmed the differences in space use between the two routes (Figure 4c,d). In TR1, groups spent 75.7% of occupancy time in Zone I and 23.6% in Zone II, with a local occupancy peak at the upstream transition into Zone II. In TR2, occupancy was concentrated in Zone II (62.1%), with a secondary peak spanning the Zone I-Zone II interface near $x = 5-7$ m, consistent with the repeated crossings. The occupancy proportion in Zone III was below 1% for both routes, at 0.6% for TR1 and 0.5% for TR2. These results indicated that fish groups spent very little time in the highest-velocity zone, mainly during the final stage of upstream movement.

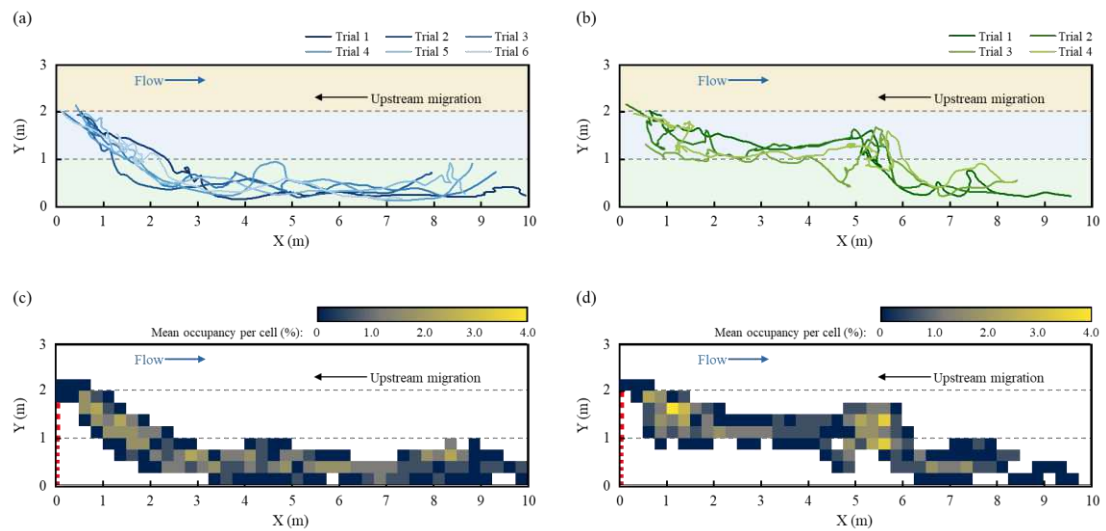


Figure 4 Upstream routes and spatial occupancy of fish groups. Panels (a) and (b) show group centroid trajectories for TR1 ($n = 6$) and TR2 ($n = 4$), respectively. Panels (c) and (d) show the corresponding spatial occupancy maps, with a grid size of $0.25 \text{ m} \times 0.25 \text{ m}$.

Passage time was significantly shorter for TR1 than for TR2 ($50.2 \pm 5.5 \text{ s}$ vs. $75.8 \pm 17.2 \text{ s}$; $p = 0.010$; Figure 5). TR2 also showed greater variation among trials, with a wider range of passage times. Thus, repeated crossings between flow zones in TR2 were associated with longer and more variable passage times.

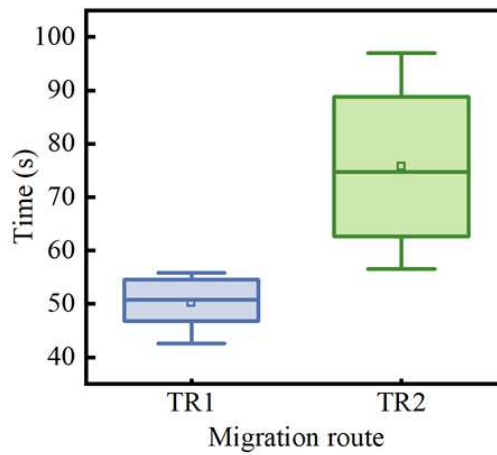


Figure 5 Upstream passage times for the two typical routes. Boxes represent the interquartile range, horizontal lines indicate medians, square markers indicate means, and whiskers show the observed ranges for TR1 ($n = 6$) and TR2 ($n = 4$).

Figure 6 shows the preferences of fish groups for different hydrodynamic conditions within the MFoD. Fish groups did not use local hydrodynamic conditions in proportion to their availability. Preference was strongest at low flow velocities, with the highest mean preference ratio at $0.15\text{--}0.20 \text{ m}\cdot\text{s}^{-1}$ ($Ph = 1.306$); use also exceeded availability at $0.25\text{--}0.30 \text{ m}\cdot\text{s}^{-1}$ ($Ph = 1.108$). Most bins between 0.50 and $1.20 \text{ m}\cdot\text{s}^{-1}$ were used less than expected, with 95% confidence intervals entirely below $Ph = 1$. The same tendency held for the remaining metrics, whose highest preference ratios all occurred in the lowest available bins, $|grad_y|$ (1.106 at $0\text{--}0.25 \text{ s}^{-1}$), $|\tau_{uv}|$ (1.178 at $0\text{--}0.50 \text{ Pa}$), TI (1.151 at $0.125\text{--}0.150 \text{ m}\cdot\text{s}^{-1}$), TKE (1.085 at $0\text{--}0.005 \text{ m}^2\cdot\text{s}^{-2}$), and D (1.175 at $0\text{--}0.05$), while use fell below availability at higher values ($|grad_y| > 1.25 \text{ s}^{-1}$; $|\tau_{uv}| > 3.50 \text{ Pa}$; $TI > 0.175 \text{ m}\cdot\text{s}^{-1}$; $TKE > 0.015 \text{ m}^2\cdot\text{s}^{-2}$; $D > 0.10$). Overall, fish groups preferentially occupied conditions characterized by lower flow velocity, weaker transverse gradients, lower shear, and lower turbulence.

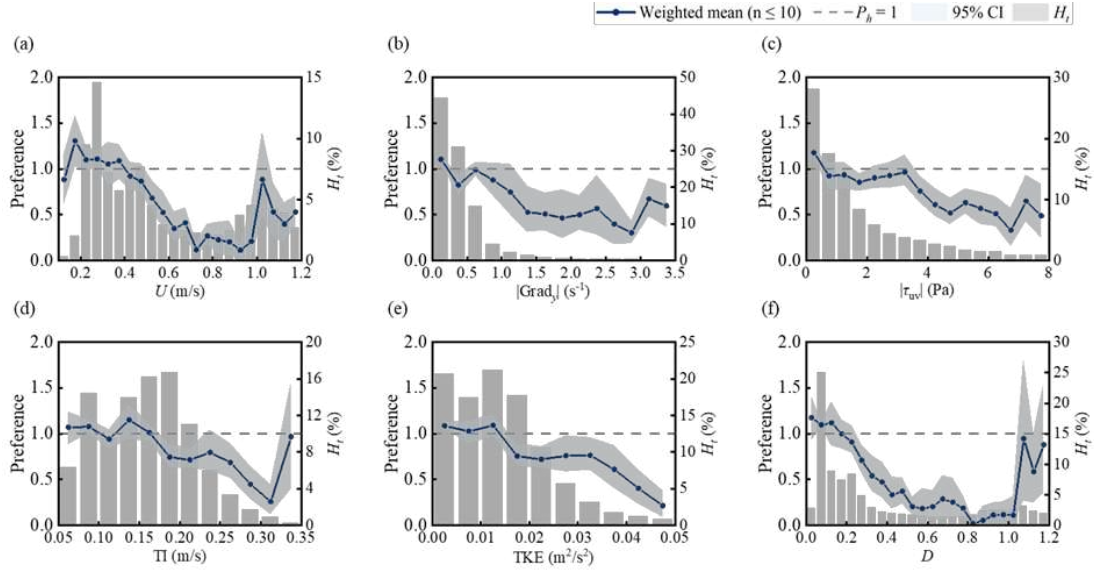


Figure 6 Hydrodynamic preferences during upstream passage. Preference ratios (Ph) are shown for (a) flow velocity (U); (b) absolute transverse velocity gradient ($|\text{grad}_y|$); (c) absolute Reynolds shear stress ($|\tau_{uv}|$); (d) turbulence intensity (TI); (e) turbulent kinetic energy (TKE); and (f) the swimming drag (D). Dark blue curves represent weighted means across 10 independent trials, and light blue shading indicates 95% confidence intervals. Gray distributions show the relative availability of each hydrodynamic condition within the instantaneous MFoD (H_t). Dashed lines indicate $\text{Ph} = 1$. Values of $\text{Ph} > 1$ indicate a relative preference for the corresponding hydrodynamic conditions.

2.3 Collective movement patterns during upstream passage

Based on polarization (P) and milling (M), fish group movements during upstream passage were classified as Schooling, Turning, or Swarming. No Milling was detected. Schooling dominated along both routes and in both flow zones analyzed, whereas Turning and Swarming occurred more often at transitions between flow zones (Figure 7a,b). Along TR1, fish groups mainly maintained Schooling within Zone I, with mixed movement patterns occurring more frequently during upstream transitions into Zone II and Zone III. Along TR2, Turning and Swarming alternated with Schooling as fish groups moved from Zone I into Zone II. After entering Zone II, they showed more sustained Schooling. Figure 7c-e shows the spatial distributions of individuals under representative group movement patterns.

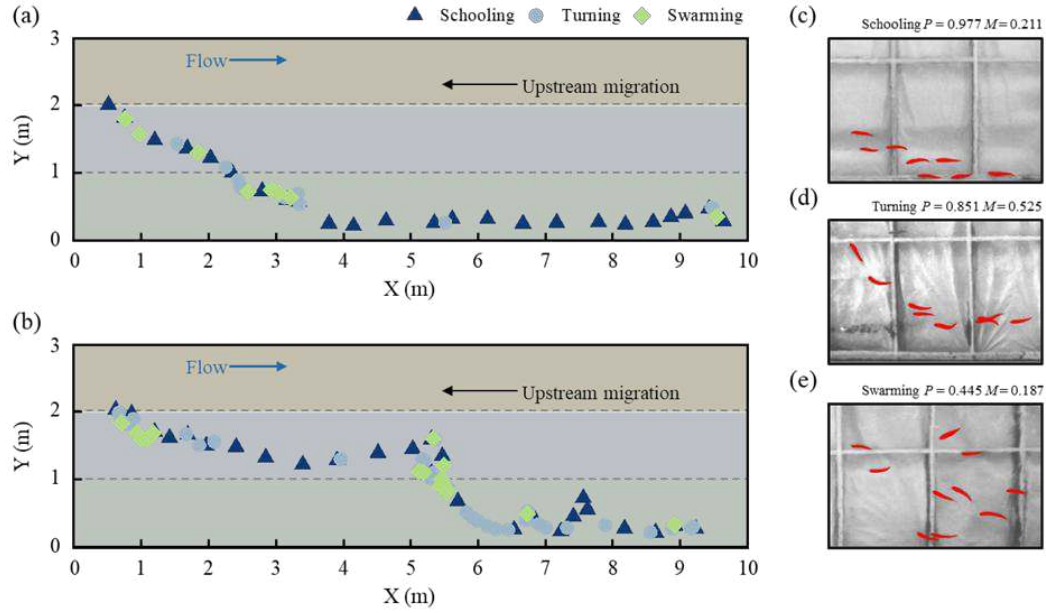


Figure 7 Spatial distributions of collective movement patterns and representative group structures during upstream passage. Panels (a) and (b) show representative group centroid trajectories for TR1 and TR2, respectively. Different symbols indicate the collective movement pattern at each observation time. Background bands indicate Zone I, Zone II, and Zone III, and arrows indicate the flow and upstream movement directions. Panels (c), (d), and (e) show individual positions during representative Schooling ($P = 0.977$, $M = 0.211$), Turning ($P = 0.851$, $M = 0.525$), and Swarming ($P = 0.445$, $M = 0.187$) patterns, respectively. Red markers indicate fish positions.

The proportions of time spent in each movement pattern further showed that the median proportion of Schooling was higher in TR1 than in TR2 in both zones. The values were 78.2% versus 64.4% in Zone I ($p = 0.019$) and 64.7% versus 51.1% in Zone II ($p = 0.038$). In Zone I, the proportion of Turning was also lower in TR1 than in TR2, at 9.9% and 19.2%, respectively ($p = 0.038$). No other comparisons between routes were statistically significant, including Swarming in Zone I and Turning and Swarming in Zone II ($p > 0.05$; Figure 8). Within TR1, the median proportion of Schooling was significantly lower in Zone II than in Zone I ($p = 0.031$). The proportion of Swarming increased from 9.9% to 16.6% ($p = 0.031$), whereas Turning did not differ significantly between the two zones ($p > 0.05$). For TR2, none of the three collective movement patterns showed significant differences between Zone I and Zone II ($p > 0.05$).

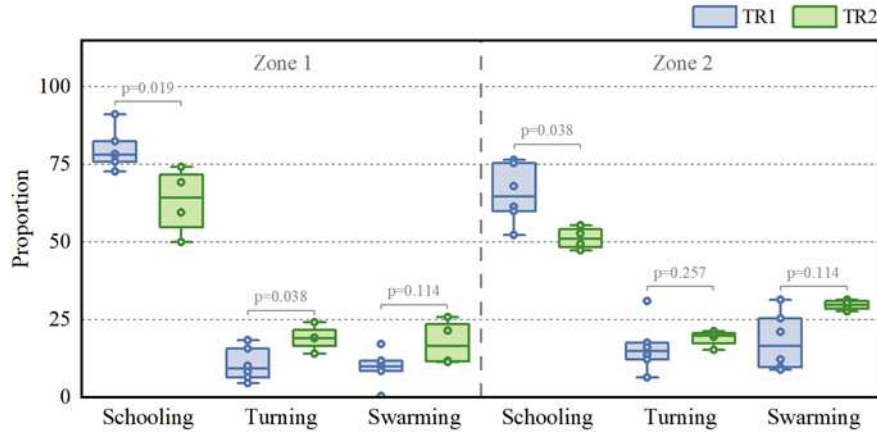


Figure 8 Proportions of time spent in collective movement patterns in Zone I and Zone II. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers extend to 1.5 times the interquartile range. Only Zone I and Zone II are shown because brief occupancy of Zone III provided limited observations for comparisons of collective movement patterns.

2.4 Group cohesion during upstream passage

Nearest-neighbor distance (NND) was below 0.4 m in 91.2% of observations during upstream passage (Figure 9). The most frequent range was 0.2 – 0.3 m (28.5%), followed by 0.1–0.2 m (26.7%) and 0 – 0.1 m (20.4%); the remaining 8.8% of observations had $\text{NND} \geq 0.4$ m. Thus, small inter-individual distances characterized most of the upstream passage, but observations were spread across several NND bins rather than concentrated at the smallest spacing.

Hydrodynamic conditions associated with NND showed a clear non-monotonic, trough-shaped pattern (Figure 9a–f). At intermediate NND (0.2–0.3 m), the medians across trials for all six metrics reached or approached their lowest levels, with values of $0.294 \text{ m}\cdot\text{s}^{-1}$ for flow velocity (U), 0.143 s^{-1} for absolute transverse velocity gradient ($|\text{grad}_y|$), 0.724 Pa for absolute Reynolds shear stress ($|\tau_{uv}|$), $0.103 \text{ m}\cdot\text{s}^{-1}$ for turbulence intensity (TI), $0.0061 \text{ m}^2\cdot\text{s}^{-2}$ for turbulent kinetic energy (TKE), and 0.097 for swimming drag (D). When NND increased to 0.4–0.5 m, these medians rose to $0.369 \text{ m}\cdot\text{s}^{-1}$, 0.299 s^{-1} , 1.751 Pa , $0.162 \text{ m}\cdot\text{s}^{-1}$, $0.0133 \text{ m}^2\cdot\text{s}^{-2}$, and 0.155 , respectively, and remained high at 0.5–0.6 m. All six metrics were also higher in the tightest spacing class ($\text{NND} < 0.1 \text{ m}$) than at 0.2–0.3 m. Overall, hydrodynamic loading was lowest at intermediate NND and increased toward both smaller and larger spacing.

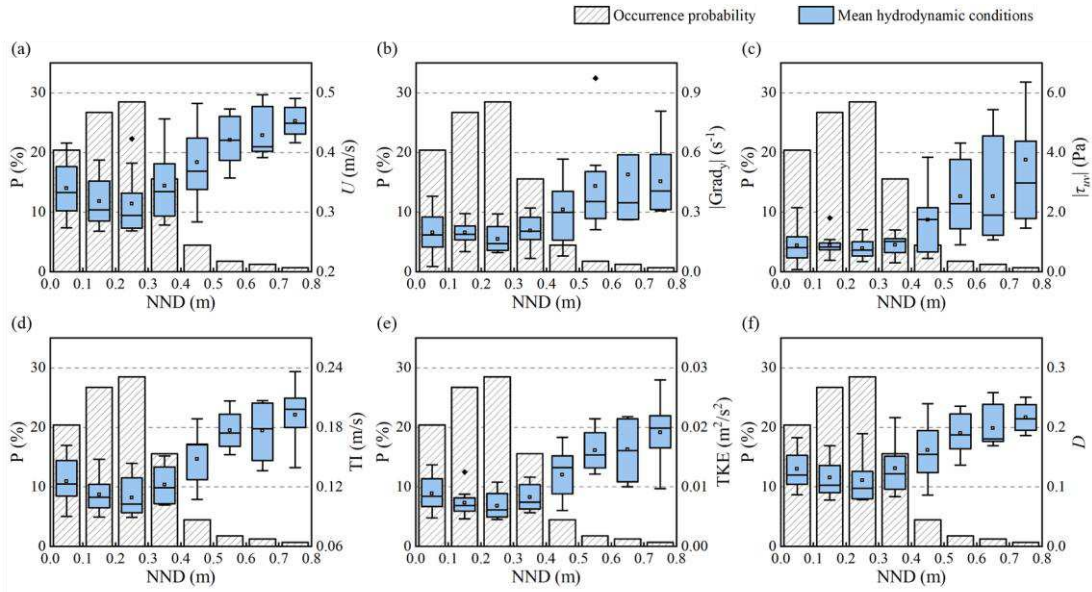


Figure 9 Occurrence probabilities of nearest-neighbor distance (NND) and associated hydrodynamic conditions: (a) flow velocity (U); (b) absolute transverse velocity gradient ($|\text{grad}_y|$); (c) absolute Reynolds shear stress ($|\tau_{uv}|$); (d) turbulence intensity (TI); (e) turbulent kinetic energy (TKE); and (f) the swimming drag (D). Diagonally hatched bars show occurrence probabilities in bins of 0.1 m. Box plots summarize the trial-level mean values for trials represented in each bin. Observations with $\text{NND} \geq 0.8$ m accounted for 0.6% of the total and are not shown.

The area of collective structure (A_c) showed a similar concentrated distribution (Figure 10). Observations with A_c between 0.2 and 0.8 m² accounted for 61.2% of the total, with the largest proportion at 0.2–0.4 m² (28.6%), followed by 0.4–0.6 m² (22.3%) and 0.6–0.8 m² (10.3%); 15.2% of observations had $A_c < 0.2$ m², and 84.6% had $A_c < 1.0$ m².

A_c exhibited the same trough-shaped relationship with hydrodynamic loading (Figure 10a–f). Medians were lowest in the intermediate A_c bins of 0.2–0.6 m², ranging from 0.312 to 0.362 m·s⁻¹ for U , 0.149 to 0.155 s⁻¹ for $|\text{grad}_y|$, 0.644 to 0.662 Pa for $|\tau_{uv}|$, 0.104 to 0.110 m·s⁻¹ for TI, 0.0066 to 0.0069 m²·s⁻² for TKE, and 0.099 to 0.111 for D . At A_c of 0.8–1.0 m², these medians increased to 0.411 m·s⁻¹, 0.231 s⁻¹, 1.218 Pa, 0.148 m·s⁻¹, 0.0113 m²·s⁻², and 0.185, respectively, and all six metrics were higher at $A_c < 0.2$ m² than in the 0.2–0.4 m² range. Thus, both NND and A_c indicated minimum hydrodynamic loading at intermediate levels of group compactness.

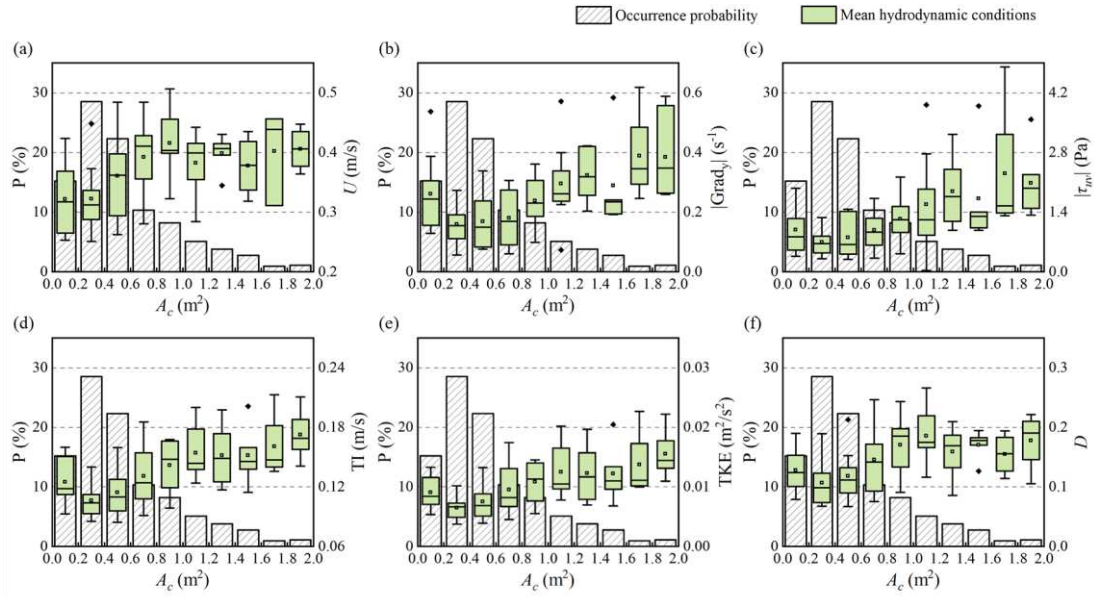


Figure 10 Occurrence probabilities of the area of collective structure (A_c) and associated hydrodynamic conditions: (a) flow velocity (U); (b) absolute transverse velocity gradient ($|\text{grad}_y|$); (c) absolute Reynolds shear stress ($|\tau_w|$); (d) turbulence intensity (TI); (e) turbulent kinetic energy (TKE); and (f) the swimming drag (D). Diagonally hatched bars show occurrence probabilities in bins of 0.2 m². Box plots summarize the trial-level mean values for trials represented in each bin. Observations with $A_c \geq 2.0$ m² accounted for 1.1% of the total and are not shown.

The most frequently observed ranges of NND and A_c , with cumulative proportions above 80%, are summarized in Table 3. NND mainly ranged from 0.05 to 0.39 m, and A_c from 0.16 to 1.11 m². The hydrodynamic ranges associated with these main NND and A_c ranges overlapped closely.

Table 3 Main ranges of hydrodynamic conditions associated with the group cohesion metrics NND and A_c .

Parameter	Range	U (m·s ⁻¹)	$ \text{grad}_y $ (s ⁻¹)	$ \tau_w $ (Pa)	TI (m·s ⁻¹)	TKE (m ² ·s ⁻²)	D
NND (m)	0.05–0.39	0.24–0.48	0.01–0.41	0.05–1.87	0.07–0.17	0.003–0.015	0.06–0.24
A_c (m ²)	0.16–1.11	0.24–0.49	0.01–0.40	0.05–1.93	0.07–0.18	0.003–0.016	0.06–0.25

2.5 Swimming performance of fish groups in non-uniform flow

Hydrodynamic exposure increased steadily as fish groups moved from Zone I to Zone III (Figure 11). The mean flow velocity available within the group's MFD (U_{MFD}) increased from 0.292 ± 0.018 m·s⁻¹ in Zone I to 0.459 ± 0.018 m·s⁻¹ in Zone II. It increased further to 0.704 ± 0.074 m·s⁻¹ in Zone III. The mean background flow velocity at individual fish positions ($U_{\text{encounter}}$) showed the same spatial trend. It rose from 0.263 ± 0.008 m·s⁻¹ in Zone I to 0.417 ± 0.020 m·s⁻¹ in Zone II and 0.753 ± 0.078 m·s⁻¹ in Zone III. Compared with U_{MFD} , $U_{\text{encounter}}$ was 10.0% lower in Zone I and 9.2% lower in Zone II, but 7.0% higher in Zone III.

Swimming speed increased alongside hydrodynamic exposure (Figure 11). Mean swimming speed (U_{fish}) rose from $0.458 \pm 0.147 \text{ m}\cdot\text{s}^{-1}$ in Zone I to $0.574 \pm 0.182 \text{ m}\cdot\text{s}^{-1}$ in Zone II. It increased further to $1.042 \pm 0.332 \text{ m}\cdot\text{s}^{-1}$ in Zone III. Relative to Zone I, these values represented increases of 25.3% in Zone II and 127.5% in Zone III. Maximum swimming speed (U_{max}) also increased across the three zones, from $1.19 \text{ m}\cdot\text{s}^{-1}$ in Zone I to $1.45 \text{ m}\cdot\text{s}^{-1}$ in Zone II and $2.06 \text{ m}\cdot\text{s}^{-1}$ in Zone III. Mean U_{fish} exceeded mean $U_{encounter}$ in all zones, with absolute differences of 0.195, 0.157, and $0.289 \text{ m}\cdot\text{s}^{-1}$ in Zone I, Zone II, and Zone III, respectively.

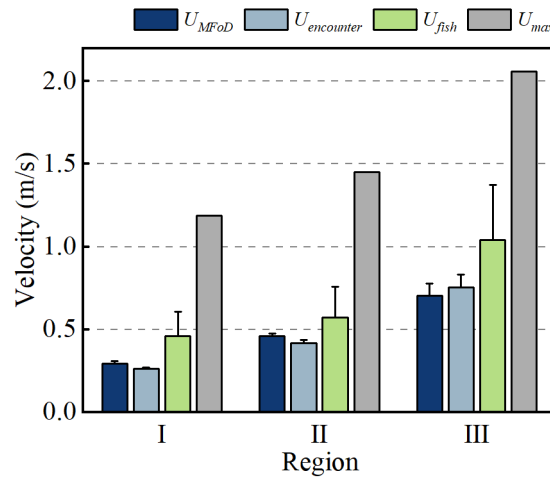


Figure 11 Hydrodynamic exposure and swimming performance of fish groups in the three experimental zones. U_{MFoD} denotes the mean flow velocity within the group's sensory range, $U_{encounter}$ denotes the mean background flow velocity at individual fish positions, U_{fish} denotes mean fish swimming speed, and U_{max} denotes maximum valid swimming speed. Bars for U_{MFoD} , $U_{encounter}$, and U_{fish} represent zone means, and error bars indicate standard deviations (SD).

3. Discussion

3.1 Hydrodynamic preferences and upstream routes of fish groups

By comparing the actual positions occupied by *S. prenanti* groups with the hydrodynamic conditions that were instantaneously available within their mechanosensory field of detection (MFoD), this study revealed local hydrodynamic selection by fish groups in a heterogeneous flow field. Overall, the fish groups preferred hydrodynamic conditions with lower flow velocity, weaker lateral velocity gradients, lower shear stress, and lower turbulence intensity (Figure 6). Compared with defining preference based only on overall spatial occupancy, this comparison with locally available conditions further indicates that fish groups can make directional spatial choices according to the hydrodynamic conditions available to them. Lower flow velocities may help reduce the hydrodynamic load that fish need to overcome while maintaining upstream movement and may also reduce movement disturbances caused by velocity gradients, shear, and turbulent

fluctuations. This finding is consistent with observations that brown trout tend to use areas with lower resistance in complex flow fields ^[24], and it also agrees with previous findings that individual *S. prenanti* prefer relatively low flow velocities and low turbulence in heterogeneous flow fields ^[23].

However, local hydrodynamic preferences alone cannot fully account for the actual upstream routes taken by the school. Although fish generally prefer conditions associated with a lower hydrodynamic load, TR1 and TR2 differed markedly in both their upstream paths and their transit times. The upstream performance of the school therefore appears to depend not only on the hydrodynamic conditions it selects, but also on interactions among individuals within the group. Mozzi et al. ^[29] found that flow velocity influenced not only the spatial positions selected by the Italian riffle dace, but also that, as the flow velocity increased, a larger group size could further enhance exploratory behavior and swimming activity. This result indicates that, even under similar hydrodynamic conditions, different groups may differ in their degree of exploration and in the spatial extent of their space use, owing to interactions among individuals within the group ^[30]. Taken together with the findings of the present study, local hydrodynamic conditions primarily delimit the space available to the school and its relative suitability, whereas interactions within the group may further decide when the school leaves the low-velocity corridor and how it traverses different flow regions.

3.2 *Collective movement behavior in non-uniform flow*

Analysis of the order parameter showed that the collective movement patterns of the fish groups changed continuously with the flow conditions experienced during upstream movement. Schooling was the dominant behavior throughout the upstream passage, whereas Turning and Swarming occurred more often in transition zones between different flow regions. No clear Milling behavior was detected during the experiments, which may be related to the continuous directional upstream movement of the fish groups. Under conditions with a clear direction of incoming flow, the fish need to maintain overall movement toward the upstream direction. Therefore, a movement pattern involving continuous rotation around a relatively stable group centroid may be restricted. Previous studies have shown that the spatial organization and movement synchrony of fish groups can affect swimming stability and energy use. Therefore, highly organized collective movement may be more suitable for sustained migration ^[31].

In contrast, when fish groups cross the boundaries between different flow regions, individuals at different spatial positions experience different hydrodynamic conditions. This may make it more difficult for the group to maintain directional alignment and stable relative positions among

individuals. Therefore, the frequent occurrence of Turning and Swarming in transition zones may reflect changes in group structure in response to local changes in the flow field. These changes may include adjustments in the relative positions of individuals, group splitting and regrouping, and possible changes in leadership relationships ^[32]. From this perspective, Schooling is more likely to represent a relatively stable state of directional upstream movement, whereas Turning and Swarming may represent transitional movement states when fish groups cross hydrodynamic boundaries.

Fish group cohesion further showed a non-monotonic relationship with the background hydrodynamic conditions. At moderate levels of cohesion, with $NND = 0.2\text{--}0.3\text{ m}$ and $Ac = 0.2\text{--}0.6\text{ m}^2$, the overall hydrodynamic conditions experienced by the fish groups were at their lowest levels. In contrast, higher hydrodynamic levels were observed when the group structure became either more compact or more dispersed. The compact group structures observed under higher hydrodynamic conditions may reflect a behavioral response in which fish reduce the distance between individuals to maintain contact and overall coordination. Previous studies have shown that grass carp exhibit stronger group cohesion under higher flow conditions ^[16]. Schools of giant danio also become more compact with increasing swimming speed under turbulent conditions and show lower movement energy costs than individuals swimming alone ^[17]. At the same time, higher hydrodynamic conditions also be associated with larger NND and Ac . Unlike compact aggregation, this expansion of the group may be related to differences in individual movement caused by non-uniform flow. When individuals experience large differences in local flow velocity and flow direction, it becomes more difficult for them to maintain stable relative positions, which may lead to an expansion of the school structure ^[14].

3.3 *Swimming performance during upstream passage*

According to the results, we found that the swimming performance of fish groups was influenced not only by local flow conditions, but also by the movement demands they faced in different regions. In Zone I and Zone II, the mean flow velocity at the actual positions of the fish was approximately 9% to 10% lower than the mean velocity available within the MFoD of the fish group. In contrast, after the fish entered Zone III, the flow velocity they actually experienced was higher than the mean available velocity in this region, while the mean swimming speed increased from $0.458\text{ m}\cdot\text{s}^{-1}$ in Zone I to $1.042\text{ m}\cdot\text{s}^{-1}$ in Zone III. This spatially coordinated change indicates that as the fish moved from a low velocity corridor into a region with higher flow velocity, the swimming ability required to maintain upstream movement also increased. A similar relationship between local flow conditions and swimming behavior has also been observed in individually

swimming *S. prenanti* [23].

However, swimming speed alone cannot fully represent the movement load experienced during swimming, because this load also depends on how long fish are exposed to high velocity conditions. In this study, the residence time in Zone III accounted for less than 1% of the total observation time, indicating that the highest swimming speeds mainly occurred within a high velocity region of very short duration near the end of the upstream passage. Previous studies have shown that the distance fish can pass depends on swimming speed, endurance, and the strength of opposing flow. Castro-Santos et al. [33] explained changes in passage distance for brook trout and brown trout under different hydrodynamic conditions by combining voluntary swimming speed distributions with endurance relationships. Similarly, although Iberian barbel and northern straight-mouth nase can reach high swimming speeds, the distance they can sustain decreases as flow velocity increases [34]. Therefore, high flow velocity does not necessarily create an impassable hydrodynamic barrier. When the spatial extent of a high velocity region and the duration of exposure are sufficiently limited, fish may still cross it by briefly increasing burst swimming speed.

In addition, the maximum burst swimming speed observed in this study ($2.06 \text{ m}\cdot\text{s}^{-1}$) was 34.6% higher than the corresponding value measured for this species in enclosed flume ($1.53 \text{ m}\cdot\text{s}^{-1}$) [35]. Kern et al. (2018) noted that conventional small annular flumes often constrain the natural swimming behavior of fish (e.g., the burst-and-coast mode) because of spatial restriction and flow homogenization, thereby leading to an underestimation of swimming capacity. In contrast, the large-scale non-uniform flow field established in our open-channel flume provided a degree of freedom much closer to that of a natural river channel, enabling the fish to fully execute anaerobic sprints

3.4 Implications for fish passage facility design

The continuous use of low velocity corridors by fish groups suggests that the design of fish passage facilities should not only provide locally suitable hydrodynamic conditions, but also consider the spatial continuity of these favorable areas along the migration direction. Previous experiments in vertical slot fishways showed that *S. prenanti* usually moved through areas with low flow velocity and low turbulence near the pool walls before passing through the slot [36]. At the larger scale of dam tailwater areas, model identified swimming corridors and telemetry observations have also highlighted the relationship between available upstream routes and whether fish can reach potential entrances [6].

Transition zones between different flow regions also deserve attention. In this study, more

frequent movement across different regions occurred together with longer passage times, while Turning and Swarming were also mainly concentrated near the boundaries between different flow regions. Therefore, if the main direction of the upstream passage route can be well aligned with the entrance direction, this may help reduce the need for repeated lateral movement and directional adjustment near the entrance. Fishway experiments with Iberian barbel have shown that changes in opening arrangement can affect both passage success and movement paths within pools, indicating that structural layout can alter the behavioral effects of the local turbulent environment ^[12].

In addition, the continuous length of high velocity regions is another parameter with direct engineering relevance. Compared with a single value of maximum allowable flow velocity, limiting the continuous length of high-hydrodynamic-load regions along the upstream migration direction, and providing low-velocity regions that fish can readily enter between successive high-load segments, may help reduce the endurance demands imposed by long-distance upstream migration.

3.5 Limitations

The available measurement techniques limited our ability to characterize flow-field changes within moving fish groups. Resolving these within-group flow dynamics is important for understanding interactions among individuals and the effects of group size on collective behavior ^[17]. Advances in computational methods now allow fish group movements to be simulated together with their interactions with complex flow fields ^[37,38]. Future studies could integrate such computational approaches with empirical observations of collective movement in non-uniform flow. Such integration could provide further insight into the mechanisms underlying collective behavior, including those related to biomechanics ^[39,40].

A further limitation is that only one inlet-velocity arrangement, increasing from low to high, was tested. In natural rivers, habitat heterogeneity, such as hydraulic refuges behind boulders, creates flow fields with varying degrees of complexity ^[41]. Whether fish groups can adopt collective movement strategies that improve swimming efficiency relative to solitary individuals under such conditions remains unclear. Future experiments incorporating a wider range of hydrodynamic configurations are therefore needed to address this question.

4. Conclusion

This study revealed the spatial use, collective movement behavior, and swimming responses of *Schizothorax prenanti* groups in a nonuniform flow field, providing further insight into how

fish groups adapt to complex hydrodynamic environments. The results showed that, among the locally available conditions, fish groups preferentially selected areas with lower flow velocity, weaker lateral velocity gradients, lower shear, and lower turbulence intensity. At the same time, the fish groups formed two different upstream routes within the same nonuniform flow field. TR1 mainly moved along a continuous low velocity corridor, whereas TR2 left this corridor earlier and crossed laterally between different flow regions several times. These findings indicate that upstream movement by fish groups is influenced not only by local hydrodynamic conditions, but also by the spatial continuity of favorable flow regions and adjustments in group movement paths.

The adaptation of fish groups to flow heterogeneity was also reflected in dynamic changes in collective organization. Schooling was the main movement pattern during upstream passage, whereas Turning and Swarming occurred mainly in transition zones between different flow regions. At the same time, fish group cohesion showed a clear non-monotonic relationship with the background hydrodynamic conditions. Moderate NND and Ac were generally associated with lower hydrodynamic levels, whereas higher hydrodynamic conditions could be associated with either more compact group configurations or spatial expansion of the school. Therefore, fish groups do not respond to increasing hydrodynamic effects in a single way, but may dynamically adjust directional alignment, inter-individual spacing, and group spatial structure according to local differences in flow conditions.

The swimming performance of the fish groups further reflected this process of spatial adaptation. As the fish entered regions with higher flow velocity, both their mean and maximum swimming speeds increased markedly, with a maximum effective swimming speed of $2.06 \text{ m}\cdot\text{s}^{-1}$ recorded in Zone III. However, the fish spent less than 1% of the total observation time in this region, and this exposure occurred mainly near the end of the upstream passage. Overall, upstream movement by fish groups in a nonuniform flow field is a dynamic process shaped by local hydrodynamic selection, adjustments in collective organization, and swimming ability. Based on these findings, the design and evaluation of fish passage facilities should not focus only on local peak flow velocity, but should also consider the continuity of migration routes, the spatial structure of nonuniform flow, and the length of regions with high hydrodynamic loads. Passage time and the overall upstream movement process of fish groups should also be considered when evaluating whether a facility truly meets their behavioral requirements.

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Peng: Investigation, Data curation, Supervision. **Gupeng Zhang:** Investigation, Data curation.
Xiliang Tang: Visualization, Data curation. **Jiang Yu:** Data curation. **Ruidong An:** Writing –
review & editing, Conceptualization, Methodology, Resources, Supervision, Funding acquisition.

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