

Article

Fish Swimming Behavior and Strategies Under Different Hydrodynamic Conditions in Fishways with Various Vertical Slot Configurations

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Abstract

Vertical slot fishways are a crucial measure to mitigate the blockage of fish migration caused by hydraulic engineering infrastructures, but their passage efficiency is often hindered by the complex interactions between fish behavior and hydrodynamic conditions. This study combines computational fluid dynamics (CFD) simulations with behavioral laboratory experiments to identify the hydrodynamic characteristics and swimming strategies of three types of fishways—Central Orifice Vertical Slot (COVS), Standard Vertical Slot (SVS), and L-shaped Vertical Slot (LVS)—using the endangered species *Schizothorax prenanti* from the upper Yangtze River as the study subject. The results revealed that (1) a symmetric and stable flow field was formed in the COVS structure, yet the passage ratio was the lowest (50%); in the SVS structure, high turbulent kinetic energy (peak of $0.03 \text{ m}^2/\text{s}^2$) was generated, leading to a significant increase in the fish’s tail-beat angle and amplitude ($p < 0.01$), with the passage time extending to 10.2 s. (2) The LVS structure induced a controlled vortex formation and created a reflux zone with low turbulent kinetic energy, facilitating a “wait-and-surge” strategy, which resulted in the highest passage ratio (70%) and the shortest passage time (6.1 s). (3) Correlation analysis revealed that flow velocity was significantly positively correlated with absolute swimming speed ($r = 0.80$), turbulent kinetic energy, and tail-beat parameters ($r > 0.68$). The LVS structure achieved the highest passage ratio and shortest transit time for *Schizothorax prenanti*, demonstrating its superior functionality for upstream migration. This design balances hydrodynamic complexity with low-turbulence refuge zones, providing a practical solution for eco-friendly fishways.

Keywords: vertical slot fishway; computational fluid dynamics; *Schizothorax prenanti*; hydrodynamic characteristics; swimming behavior; passage efficiency

Key Contribution: First identification of species-specific behavioral strategy in vertical slot fishways: we reveal that *Schizothorax prenanti* adopts a novel “wait-and-surge” tactic in L-shaped vertical slot (LVS) fishways; effectively leveraging recirculation zones. This results in a 70% passage success rate—20% higher than conventional designs (COVS, SVS),



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marking a significant improvement in fishway performance. Quantified biomechanical link between turbulence and swimming mechanics: our analysis demonstrates a strong correlation between turbulent kinetic energy and tail-beat kinematics ($r > 0.68$, $p < 0.01$), establishing that fishes actively exploit shear stress gradients to enhance stability and reduce energy expenditure during upstream passage.

1. Introduction

The construction of reservoirs and hydropower stations has been useful for water resource regulation, flood control, and energy generation, but it might also disrupt ecosystem integrity and connectivity, particularly by blocking migratory pathways of native fish, leading to issues such as delayed accumulation of thermal units for fish spawning and habitat fragmentation [1–3]. Fish passage structures are regarded as key solutions to address fish migration barriers, among which vertical slot fishways are widely adopted in water conservancy projects due to their favorable hydraulic conditions and compatibility with various fish species [4,5]. However, a limited understanding of the interaction between fish swimming behavior and internal flow dynamics in fishways has led to persistent issues such as low passage ratio and significant fish retention in many existing fishways [6,7]. To facilitate both up and downstream fish migration through artificial fishways, it is essential to understand fish swimming behavior and migration strategies under the complex hydraulic environments of such fishways [8,9], which is critical for optimizing fishway design and improving passage efficiency.

Vertical slot fishways are constructed in hydraulic structures such as locks, dams, or reservoirs to facilitate effective fish passages by bypassing artificial physical barriers and enabling natural migration behaviors [10,11]. In recent years, extensive research has been conducted to improve the ecological adaptability and passage efficiency of vertical slot fishways through design optimization [12]. On one hand, the hydrodynamic characteristics of the vertical slot, pool chamber, and refugium areas have been improved [13]. Studies have shown that the size and structure of the vertical slot, the hydraulic gradient within the fishway [14], and the type and size of the partition walls [15] significantly affect its hydraulic characteristics [16]. Observations of fish behavior at different locations within vertical slot fishways revealed that fish tend to select passage routes characterized by low flow velocity and low turbulent kinetic energy [17]. Accordingly, structural modifications such as adding cylindrical concrete piers [18] or altering baffle configurations [19] have been adopted to reduce flow velocity and turbulence intensity within the fishway. On the other hand, passage efficiency and passage time are evaluated based on the spatial distribution of fish trajectories to identify key factors influencing successful migration [20]. Noonan et al. [21] reviewed the extensive literature to identify the most reliable predictors of fishway efficiency, and found that, on average, downstream passage efficiency was slightly higher than upstream, and that efficiency varied significantly among fishway types. Bao et al. [22] applied a comprehensive multi-method approach to quantitatively assess the performance of vertical slot fishways in the Dadu River, and found that fish preferred nighttime migration, and that excessive flow in the fishway limited upstream movement. Shi et al. [23] locally colored the partition walls of fishways based on the attraction and avoidance behaviors of grass carp toward specific colors, and observed significant effects on migration routes, with more concentrated movement and longer trajectories. The color-induced changes led to shorter and more concentrated migration paths, along with a substantial improvement in passage ratios. Although the aforementioned studies have advanced the hydrodynamic optimization of fishways and improved passage

efficiency, the existing research generally indicates that the passage efficiency of vertical slot fishways remains suboptimal, and further investigation into fish behavioral responses and swimming strategies within these structures is still needed [24] to enhance their ecological performance [25,26].

Different vertical slot designs in fishways create complex hydrodynamic environments, in which fish behavioral decisions are strongly influenced by the prevailing hydraulic conditions [27]. Water velocity significantly affects fish swimming behavior and energy expenditure [28–31]. Avoidance of high velocities can reduce anaerobic metabolism in juvenile Atlantic salmon (*Salmo salar*) [32], whereas steep flow gradients may cause disorientation or escape responses [33,34]. Turbulence has more complex effects on fish activities such as swimming, feeding, and migration [35–37]. Numerous studies have shown that fish prefer areas with low turbulent kinetic energy, that swimming costs increase by 1.3 to 1.6 times under turbulent conditions [32], and that greater turbulence intensity increases energy expenditure [38]. In addition to more energy consumption, excessive turbulence also impairs body balance and stability, causing postural deflection and increased resistance during swimming. These effects hinder fish migration and may severely threaten population survival [39]. However, some studies suggest that fish can extract energy from turbulence to help maintain body balance and sustain swimming [40]. Fish can utilize Kármán vortex streets to generate larger lateral movements, thereby reducing locomotion energy expenditure [37,41]. This occurs because fish synchronize their swimming frequency with the vortex shedding frequency, reducing muscle activity and conserving energy [42]. Therefore, the effects of turbulence on fish behavior are bidirectional, depending on both the mechanisms of turbulence formation and the adaptive behavioral strategies developed through long-term evolution.

The Yangtze River Basin, home to *Schizothorax prenanti*, has undergone substantial hydrological alterations due to large-scale infrastructure projects such as the Three Gorges Dam and the Xiluodu–Xiangjiaba cascade reservoirs. These projects have reduced peak discharge by 25–34% during the flood season, disrupted natural flow regimes that serve as critical migration cues, and fragmented habitats with the construction of 28 major dams in the upper basin [7,12]. This anthropogenic flow regulation highlights the urgent need for fishway designs that can effectively compensate for the adverse flow conditions during key migratory periods.

Existing studies have demonstrated the robust simulation capabilities of computational fluid dynamics (CFD) modeling in representing water flows [43–45]. In this study, a CFD model was employed to simulate the flow characteristics of three types of vertical slot fishways, including flow velocity, turbulent kinetic energy, total strain, and Reynolds shear stress. The influence of these hydrodynamic characteristics on fish swimming behaviors and spatial distribution was then evaluated based on their observed swimming trajectories, providing insights for optimizing fishway design and improving passage efficiency.

2. Materials and Methods

2.1. Experimental Fish

Schizothorax is a genus of cyprinid fish native to the highlands of Asia, characterized by rows of large, neatly arranged scales along both sides of the abdominal and anal fins, separated by a distinct groove. *Schizothorax prenanti* (Figure 1) is a cold-water, economically valuable species found in the upper reaches of the Yangtze River and its tributaries (Figure 2). It thrives in low temperatures, high dissolved oxygen (DO) levels, and fast-flowing waters. Due to its strong swimming ability and adaptability to non-uniform flow fields, *Schizothorax prenanti* serves as an ideal model species for studying fish behavioral responses under turbulent flow conditions [46].



Figure 1. Fish species used in the laboratory experiments: *Schizothorax prenanti*.



Figure 2. Cascade hub system in the middle reaches of the Yangtze River.

All the fish used in the laboratory experiments were provided from Tiangui Fishery, a commercial fish farm located in Meishan City, Sichuan Province, China. They had an average body length of 11.6 ± 0.5 cm and body weight of 20.7 ± 1.2 g. Before the experiments, the fish were acclimated to laboratory conditions in circular glass tanks for 30 min. Water temperature was maintained at 20.1 ± 0.55 °C, with continuous aeration (dissolved oxygen: $7.2\text{--}7.6$ mg·L^{−1}), and the pH was stabilized at 7.6 ± 0.3 . Approximately 40% of the tank water was replaced weekly to ensure optimal water quality. Fish were fed twice daily at 09:00 and 20:00, with feeding suspended 24 h before each formal trial. During the experiments, water temperature, dissolved oxygen, and pH were maintained consistently with acclimation conditions. A total of 30 independent trials were conducted for each fishway configuration. For each trial, a single fish was randomly selected and acclimated in the rectangular tank for 30 min. After each trial, the fish was removed and given a minimum rest period of three days before being reused in subsequent trials.

2.2. Experimental Design

For our experiment, a circular recirculating flume was used. The three types of vertical slot structures used in this study are commonly applied in fishway designs across China [21,47]. The laboratory flume featured a modular, separated design consisting of three main sections: flow acceleration, test, and measurement zones. The structure and size of each section are shown in Figure 3a. The acceleration zone was equipped with a propeller driven by a variable-frequency motor, generating a controlled circulating flow. The central component of the test area was a rectangular tank 150 cm long and 30 cm wide, designed to accommodate various vertical slot configurations for the fishway. A high-resolution industrial video camera (Mindvision, MV-LD-4-4M-G, Shenzhen MindVision Technology

Co., Ltd., Shenzhen, China, 1920 × 1080 pixels, 30 fps) was mounted 80 cm above the tank to record fish behavior as they entered the fishway. Flow velocity within the fishway was measured using a flow meter (RUNSUN INSTRUMENTS INC., LS300-A, Chengdu Ruixin Instrument Co., Ltd., Chengdu, China). To ensure uniform flow into the fishway, cellular rectifiers were installed up and downstream of the test area to reduce turbulence and stabilize the flow. Various types of fishways were constructed using transparent Plexiglas. In this study, each vertical slot fishway was simplified into a structure consisting of three chambers—I, II, and III—from up to downstream. Pool I represents the outlet pool, corresponding to the terminal pool in actual fishway designs, whereas II and III represent typical fishway segments. The size of each component is shown in Figure 3b.

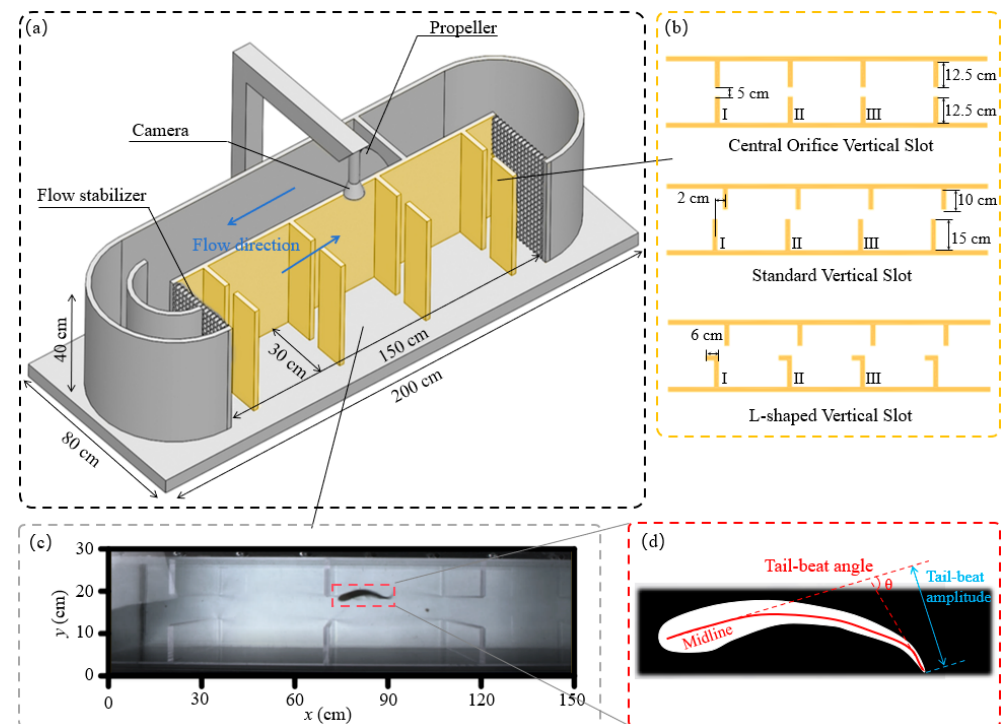


Figure 3. Sketch of the experimental setup: (a) diagram of laboratory flume, (b) sketch of the fishway with 3 different vertical slots, (c) top view of live photograph, and (d) sketch of tail-beat angle and amplitude of fish body.

2.3. Indicators of Fish Behaviors

Swimming speed, and tail-beat frequency, angle, and amplitude are commonly used behavioral indicators of fish swimming kinematics [37,48]. These metrics are essential for characterizing fish locomotor responses under varying flow conditions. Swimming speed refers to the absolute speed of the fish. Tail-beat frequency is defined as the number of complete tail beats per second, where a complete beat is one cycle of the caudal fin reaching its maximum displacement before returning to the same position. As shown in Figure 3d, the tail-beat angle is defined as the maximum angle between the tangent lines of the head and tail, whereas the tail-beat amplitude is the vertical distance from the tip of the tail to the tangent line of the head.

The swimming behavior and motion of the fish during the experiment were recorded by a high-resolution camera and processed frame-by-frame by a computer vision program to extract the images and determine the fish's trajectory, tail-beat frequency, angle, and amplitude. The fish motions were recorded using a high-resolution camera and analyzed frame-by-frame with a computer vision program to extract images and quantify the movement characteristics of fish. All data were analyzed using SPSS 25.0. Pearson correla-

tion analysis was used to evaluate the relationships between hydrodynamic parameters (e.g., velocity, turbulent kinetic energy) and swimming behavior metrics. Statistical significance was set at $p < 0.05$. PCA was conducted in R (version 4.2.0) using the “FactoMineR” package to explore the multivariate behavioral pattern among fish in different structures.

2.4. Computational Fluid Dynamics Model

2.4.1. Model Setup

Computational fluid dynamics (CFD) techniques were employed to simulate the flow field in the fishways of the test area using ANSYS Fluent 2021R1. The simulation employs the finite volume method to solve the Reynolds-averaged Navier–Stokes equations and incorporates the volume of fluid (VOF) method along with the Reynolds stress turbulence model (RSM), which is able to represent the effects of turbulence anisotropy on secondary circulation and multiscale complex flow phenomena [49,50]. Three fishways with different types of vertical slots—Central Orifice Vertical Slot (COVS), Standard Vertical Slot (SVS), and L-shaped Vertical Slot (LVS)—were installed in a laboratory flume. The inlet flow velocity at the fishway entrance was set to approximately 0.6 times the individual critical swimming speed, which was $4.3 L_{fish} s^{-1}$, to prevent fish fatigue [51]. A structured hexahedral mesh was used to discretize the study domain, with local mesh refinement applied at the vertical slots to capture detailed flow field characteristics. The grid size and number of nodes were determined through a grid independence analysis. The inlet of the computational domain was defined as a velocity inlet, and the outlet was set as a pressure outlet with a zero-pressure gradient. The bottom, top, side walls, and the vertical slot baffle were all assigned free-slip boundary conditions. Table 1 lists each simulation case along with its grid size, computation time, and time step.

Table 1. Detailed information for the simulation cases.

Simulation Cases	Vertical Slot Type	Mesh Size (10^{-2} m)	Number of Grids	Calculation Time (s)
E1	COVS	$1.4 \times 0.5 \times 0.725$ $1.4 \times 0.72 \times 0.725$	105,096	2.22
E2	SVS	$1.04 \times 0.36 \times 0.725$ $1.04 \times 1.1 \times 0.725$	182,152	2.03
E3	LVS	$1.04 \times 0.36 \times 0.725$ $1.04 \times 1.1 \times 0.725$	182,152	2.03

2.4.2. Model Validation

The numerical results were validated using experimental data of flow velocity and turbulent kinetic energy measured in the physical modeling under identical operating scenarios (Figure 4).

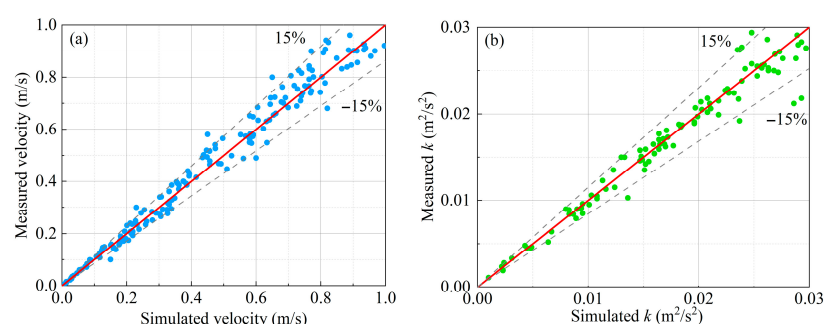


Figure 4. Comparison between the experimental data and the numerical results: (a) flow velocity, and (b) turbulent kinetic energy k .

Measurement points were uniformly distributed throughout the test area. An Acoustic Doppler Velocimeter (ADV) with a range of 0.01–10 m/s and an accuracy of 1% was used to measure velocity data. The relative error of flow velocity ranges from 5.13% to 17.06%, with a mean value of 9.85%. The relative error of turbulent kinetic energy k ranges from 6.08% to 16.82%, with an average of 10.06%. In conclusion, the numerical model demonstrated, with high reliability, the structural characteristics of flow within the fishway.

3. Results

3.1. Hydrodynamic Characteristics

The numerical results (Figure 5) indicate that the three vertical slot configurations significantly influence the flow field structure and energy dissipation patterns within the fishways. In the COVS structure, the main flow was concentrated at the vertical slot, forming a narrow high-velocity jet. The mainstream was stable, with a relatively uniform distribution of velocity and with a maximum of 0.82 m/s. On both sides, low-velocity refuge zones were observed, providing resting areas for fish. In the SVS and LVS structures, a high-speed jet also extended along the x-axis. However, due to the asymmetrical design of the guide plate, the jet deflected toward the side wall, creating pronounced recirculation zones and flow deflection. This resulted in more complex flow paths and velocity gradients. Maximum flow velocities differed significantly among fishway types (Kruskal–Wallis test: $H(2) = 18.7$, $p < 0.001$). Post hoc Dunn tests revealed the following: SVS (0.98 ± 0.05 m/s) > COVS (0.82 ± 0.04 m/s; $p < 0.001$), SVS > LVS (0.91 ± 0.03 m/s; $p = 0.012$), and LVS > COVS ($p = 0.003$). In these three structures, turbulent kinetic energy was primarily peaking near the vertical slot. In COVS, the turbulent kinetic energy distribution was symmetric along the central axis, providing effective guidance for upstream-migrating fish and forming localized flow avoidance zones. In the SVS structure, turbulent kinetic energy was mainly concentrated in the center of the main flow channel, peaking at approximately $0.03 \text{ m}^2/\text{s}^2$. The average value along the pool walls was larger than that in COVS. The LVS structure, due to its asymmetry, induced the formation of distinct vortex structures, with the peak turbulent kinetic energy shifted away from the channel center. However, the magnitude of turbulent kinetic energy was lower than that observed in the other two structures. In the COVS and SVS structures, high strain regions were primarily concentrated at the center of the slot, with a regular distribution pattern. In contrast, the strain regions shifted toward the slot wall in LVS, displaying more heterogeneous shear characteristics. In COVS and SVS, shear stresses were symmetrically distributed along the main flow axis, with localized peaks at the vertical slots. The LVS structure had larger shear stress at the corners, reflecting its more complex flow dynamics.

In conclusion, the COVS structure offers a more uniform and stable hydrodynamic field, which supports continuous swimming behavior. Strong jets are generated in the SVS structure, along with elevated levels of turbulence energy and shear stress. The LVS structure improves flow uniformity through flow control, whereas elevated wall shear stress and persistent turbulence may challenge the tolerance thresholds of fish. The difference in hydrodynamics among these configurations provides a critical physical basis for analyzing fish swimming behaviors and strategies.

3.2. Passage Efficiency and Swimming Preference

Fish passage ratio, and average and minimum passage time, were recorded for each structure (Figure 6). The fish passage ratio is defined as the ratio of successful passages to the total number of experimental trials. Statistical analysis revealed a significant difference in the passage ratio among different types ($p = 0.038$). The LVS structure had the highest passage success at 70%, followed by 60% for SVS and 50% for COVS. This suggests that

although the LVS structure presents greater complexity and localized flow disturbances, the low-velocity and the associated recirculation zones offer more opportunities to rest and reorient briefly, thereby improving passage success. In terms of passage time, LVS also had an advantage, with an average of 6.1 s that was significantly shorter than that of SVS and COVS. This indicates that LVS not only improves passage probability but also enhances overall passage efficiency. In contrast, although SVS showed a slightly higher passage ratio than COVS, it resulted in the longest passage time among the three structures.

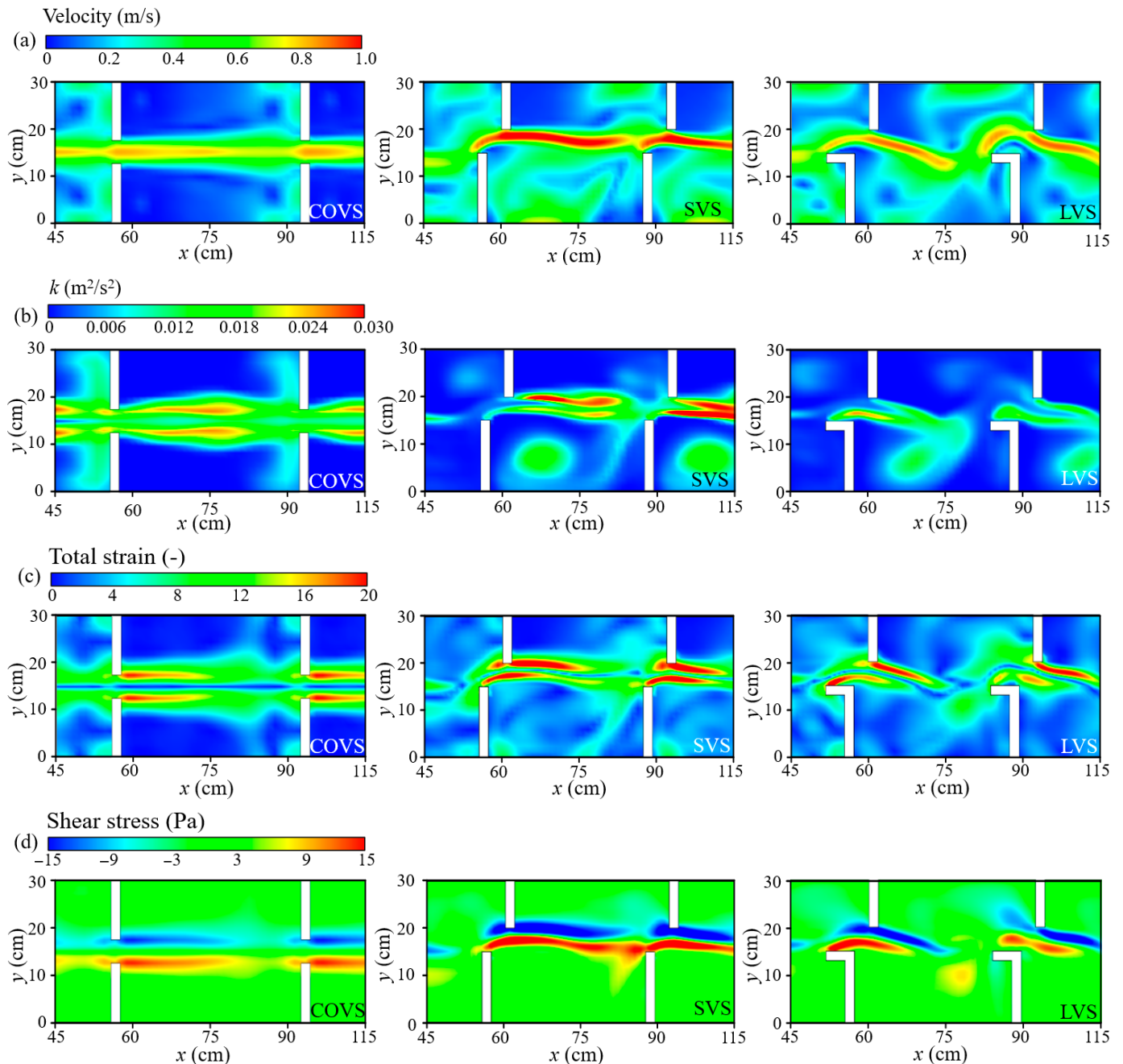


Figure 5. Numerical results for the three types of fishways—Central Orifice Vertical Slot (COVS), Standard Vertical Slot (SVS), and L-shaped Vertical Slot (LVS): (a) velocity, (b) k , (c) total strain, and (d) shear stress.

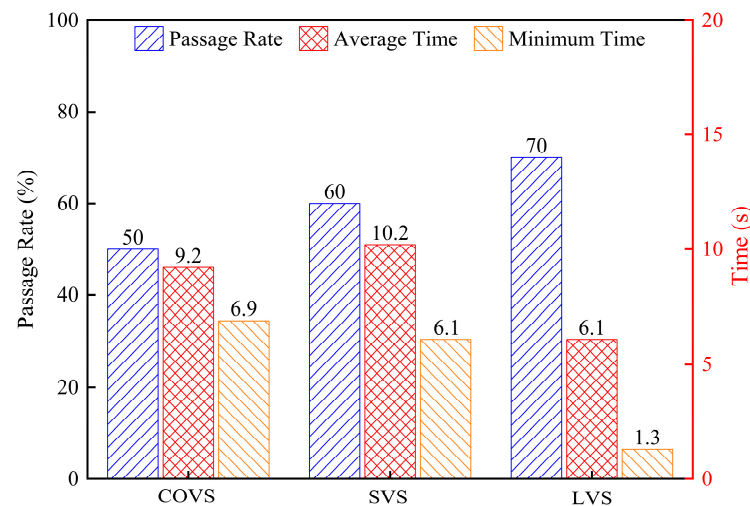


Figure 6. Fish passage ratio, mean passage time, and minimum passage time in the fishway.

Overall, each of the three structures exhibits distinct characteristics in terms of flow guidance and passage efficiency. Despite stronger flow field disturbances, the LVS structure generates more complex and varying hydraulic conditions that may better resemble natural environments, enabling fish to employ more behavioral strategies to achieve successful passage. These findings provide an experimental foundation for optimizing artificial fishway design and improving their utilization and passage ratios.

Video tracking technology was used to record fish movement trajectories, and spatial heatmaps were generated by overlaying these trajectories to identify the spatial distribution patterns within each structure. Darker colors on the map indicate higher frequencies of fish occurrence in each area, representing zones preferred for resting or movement.

In the COVS structure, fish trajectories were primarily concentrated around the vertical slot near the inlet opening. This indicates pronounced velocity gradients between the low-velocity zones and the main flow acceleration regions on both sides of the vertical slot, where fish frequently paused to orient themselves and identify passage routes, resulting in relatively concentrated swimming patterns (Figure 7a). This pattern corresponds to the flow velocity distribution, with high velocities in the center of the slot and low-velocity zones on both sides, which also explains the moderate passage success rate (50%) and average passage time (about 9 s), i.e., fish can effectively locate the vertical slot but often require multiple attempts to complete passage. The thermograms for the SVS structure reveal more complex movement trajectories, with high-frequency activity peaking at both sides of the main flow channel (Figure 7b). This suggests that fish tend to make repeated attempts in regions with relatively stable flow velocity but elevated turbulent kinetic energy. Although the main flow channel in this structure provided clear guidance, large turbulence levels and shear stress made fish more cautious in selecting their passage paths. This aligns with its moderate passage ratio (60%) but the longest average passage time (10.2 s), indicating that this structure may pose hydrodynamic adaptation challenges for the target fish. In the LVS structure, fish distribution was significantly concentrated near the corners and within the inner regions of the vertical slot (Figure 7c), indicating that fish were able to adapt and explore the flow field when confronted with such complexity. This structure generated pronounced flow deflection and recirculation zones near the vertical slot, enabling fish to exploit the low-velocity zones and shear stress gradients near the corners to complete passage, thereby achieving higher passage ratio (70%) and the shortest average passage time (6.1 s). Despite the more complex hydrodynamic conditions, fish appeared to be more

adept at utilizing the non-uniform flow patterns within this configuration to develop rapid and efficient passage strategies.

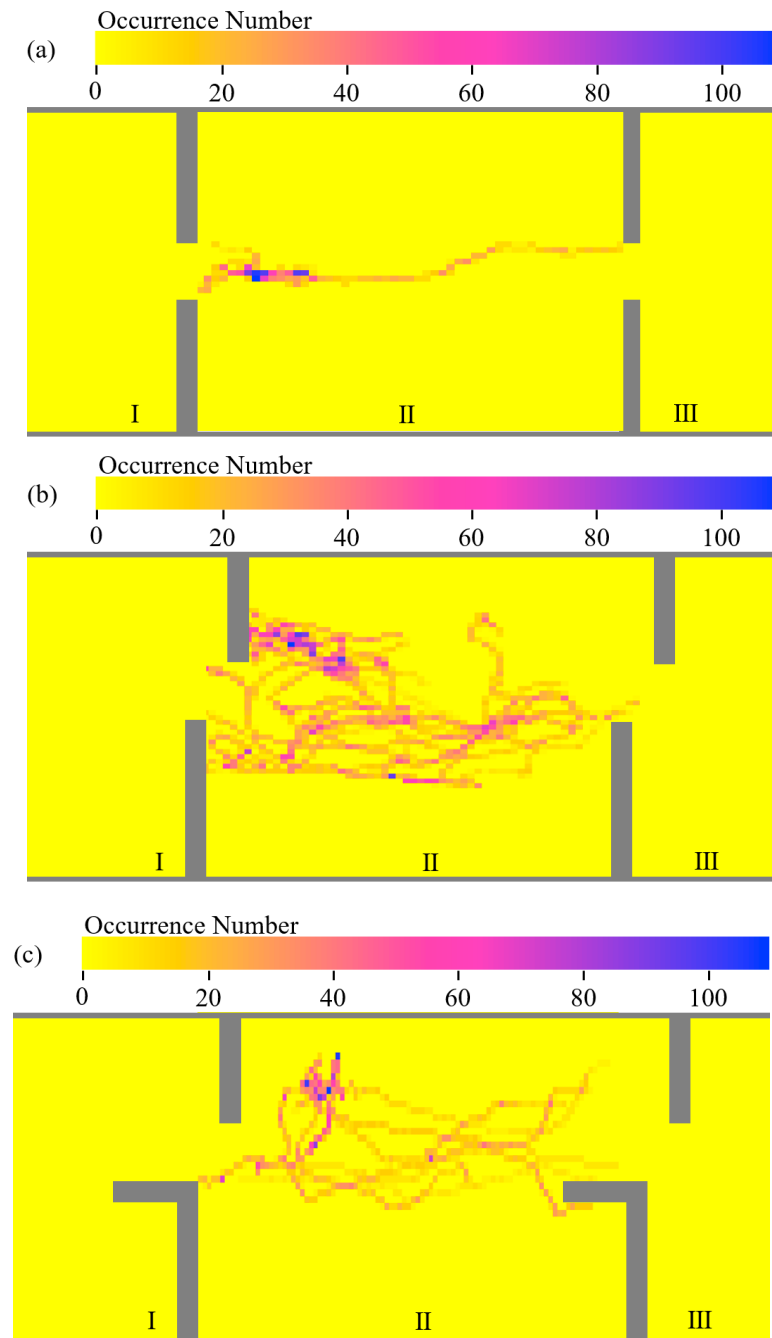


Figure 7. Swimming preferences of fish in three different vertical slots: (a) Central Orifice Vertical Slot, (b) Standard Vertical Slot, and (c) L-shaped Vertical Slot.

In summary, the spatial distribution patterns of target fish across different structures were strongly influenced by hydrodynamic conditions. The structured flow field in the COVS created distinct zones for fish to observe and orient themselves. In the SVS structure, high turbulence levels and complex flow patterns reduced the efficiency of fish passage. In contrast, LVS elicited more active behavioral responses from fish and, despite higher turbulence, enabled them to quickly identify suitable passage routes.

3.3. Behavioral Tactics Under Near-Field Hydrodynamics

To gain a deeper understanding on how fish behavioral tactics during passage adapt to the local hydrodynamic conditions for different vertical slot structures, the trajectories corresponding to the fastest passage were selected from multiple independent experiments conducted for each vertical slot type, and the corresponding hydrodynamic parameters—flow velocity, turbulent kinetic energy, total strain, and shear stress—along the selected paths were simultaneously extracted (Figure 8).

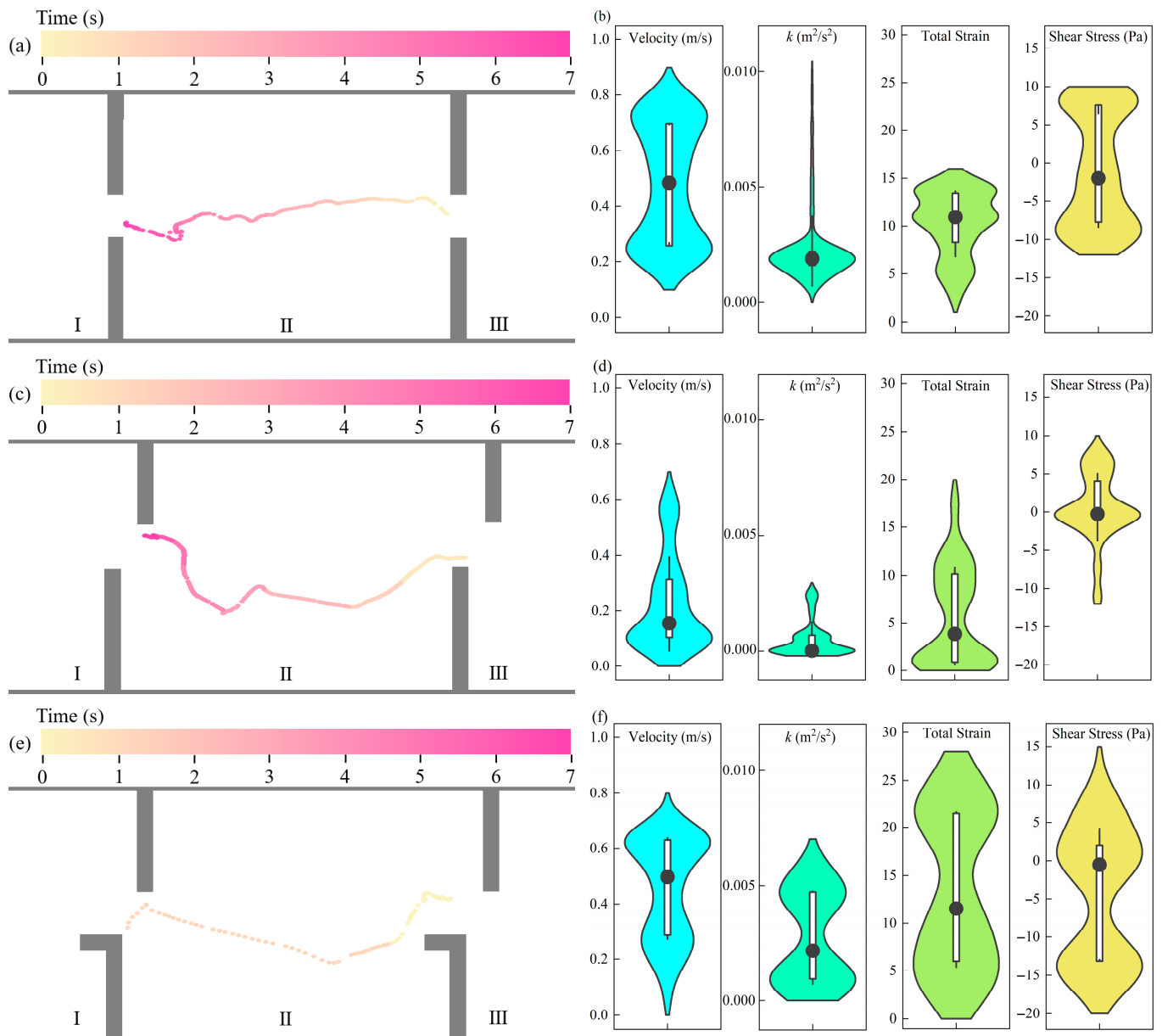


Figure 8. Fastest fish passage trajectory and hydrodynamic parameters along the trajectory at an inlet velocity of 0.1 m/s: (a) fastest trajectory in COVS, (b) hydrodynamic parameters in COVS, (c) fastest trajectory in SVS, (d) hydrodynamic parameters in SVS, (e) fastest trajectory in LVS, and (f) hydrodynamic parameters in LVS.

In the COVS fishway, fish passage trajectories were relatively straight, traversing the pool nearly along the central axis, indicating that the mainstream flow in this structure was stable and well-directed. The violin plot (Figure 8b) shows that the experienced flow velocity ranged from 0.3 to 0.6 m/s, turbulent kinetic energy was between 0.002 and 0.006 m^2/s^2 , and both total strain and shear were aligned with the main high-velocity

core, completing passage under moderate hydrodynamic disturbance. This validates the suitability of this structure for a “guidance–breakthrough” swimming strategy.

Fish trajectories in the SVS structure were notably curved, forming an “S-shaped” deviation in Pool II, indicating that fish needed to adjust their direction prior to traversing the structure. The flow velocities along the paths were broadly distributed, ranging from low values up to 0.7 m/s, with significantly higher peaks of turbulent kinetic energy, a slightly right-skewed distribution of total strain, and overall low shear stress levels (Figure 8d). These results indicate that fish had to combine short bursts of high-speed swimming with directional adjustments to pass through a highly disturbed flow field, suggesting the adoption of an “observe–adjust–breakthrough” swimming strategy in SVS. In the LVS structure, fish trajectories were briefly stationary in the initial section, followed by a rapid passage through Pool II and successful completion of the crossing. Hence, the overall trajectory showed a “zigzag” pattern, reflecting the complexity of the flow field and the presence of accessible low-velocity and recirculation zones. The flow velocity along this path was concentrated in the low-to-medium range (approximately 0.3–0.5 m/s), turbulent kinetic energy was low and localized, shear stress was slightly higher than elsewhere, and total strain was more uniformly distributed. These hydrodynamic conditions provide more stable passage conditions, enabling fish to utilize the recirculation zone for initial positioning, followed by rapid acceleration through regions with shear stress differentials. Fish paused in low-TKE zones ($\leq 0.005 \text{ m}^2/\text{s}^2$) for $0.8 \pm 0.3 \text{ s}$ before accelerating through slots, enabling 70% passage success.

Overall, the characteristics of the fastest passage paths and their associated hydrodynamic factors varied significantly among the tested vertical slot structures. The COVS structure promotes the formation of a stable mainstream, facilitating fish orientation and subsequent selection of a migration path. In the SVS structure, fish must perform multiple path adjustments to overcome turbulent disturbances. Despite the complexity of the LVS structure, low turbulence energy and shear stress differentials create a “tactical window” that enables fish to quickly identify and traverse a suitable passage path. These findings demonstrate the strong adaptability of fish to varying hydrodynamic conditions thus providing a theoretical foundation for optimizing structure design and enhancing ecological fishway performance.

3.4. Fish Tail-Beat Kinematics Characteristics

To gain deeper insight into the biomechanical response mechanisms of the target fish during passage through fishways with different vertical slot structures, key swimming behavior parameters along the fastest passage paths are presented in Figure 9.

Fish had a significantly higher absolute swimming speed in the LVS structure ($p < 0.001$), with a median value close to 1.0 m/s, which is substantially greater than those observed in the COVS and SVS structures. The low turbulent kinetic energy and internal recirculation zones of the LVS structure enabled fish to accelerate rapidly and complete short-distance breakthroughs, resulting in shorter passage times and higher passage ratio. Fish in the SVS and LVS structures exhibited higher tail-beat frequency, centered at 4 Hz and 6 Hz, respectively, in contrast to the lower frequency observed in the COVS structure. This suggests that fish must beat their tails at higher frequencies to maintain posture stability and generate thrust under stronger flow gradients or highly disturbed environments. This behavior is closely related to the unsteady flow field induced by elevated turbulent kinetic energy in the SVS structure, which may also account for the trajectory deviations and prolonged passage paths.

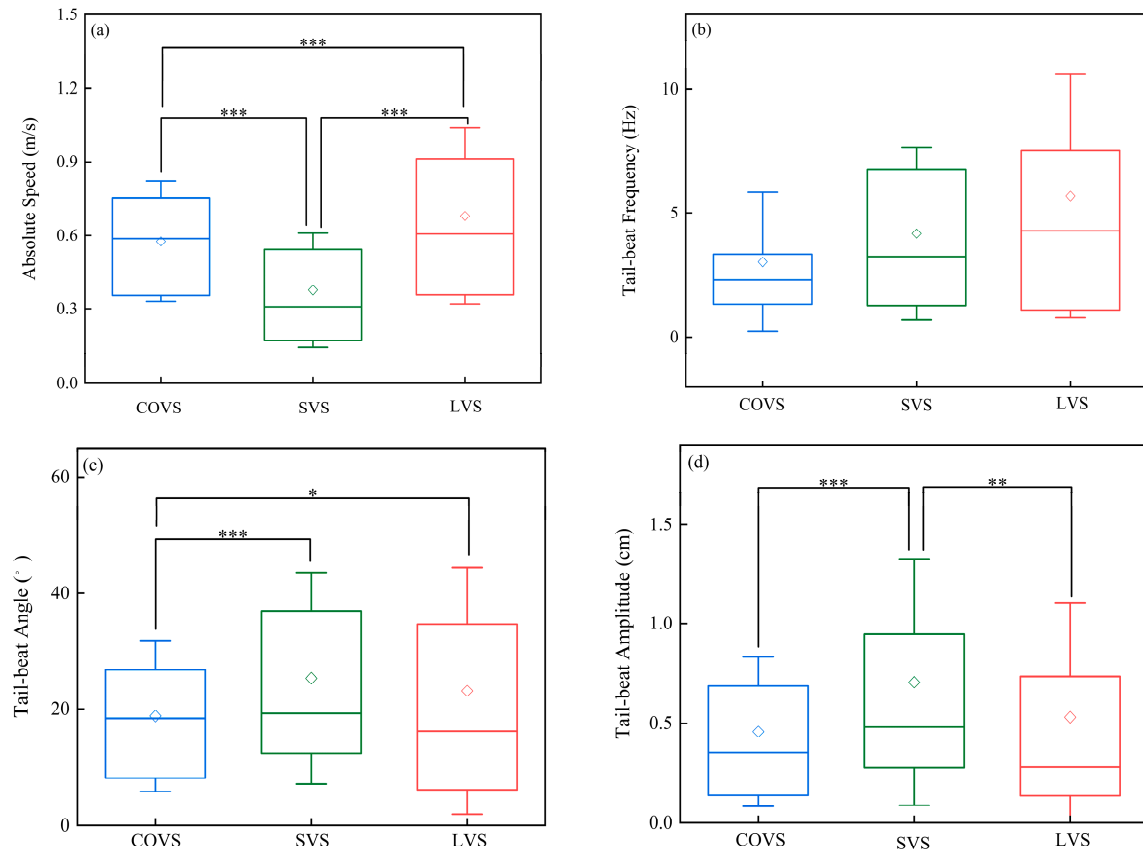


Figure 9. Swimming parameters of the fastest passage path: (a) absolute speed, (b) tail-beat frequency, (c) tail-beat angle, and (d) tail-beat amplitude. (* represents $p < 0.05$, ** represents $p < 0.01$ and *** represents $p < 0.001$ in the figure).

The tail-beat angle and amplitude of fish in the SVS structure were significantly larger and broadly fluctuated, with tail-beat angle ($p < 0.001$) and amplitude ($p < 0.01$) both markedly higher than those observed in the COVS and LVS structures. This indicates that fish in the SVS structure must frequently adjust their swimming posture to counteract strong lateral shear forces and turbulence. To cope with the disturbed flow field, they also need to increase propulsion and correct their orientation by amplifying tail-beat amplitude. In contrast, although the hydrodynamic environment in the LVS structure is more complex, fish primarily moved along a specific trajectory to complete the passage. Their tail-beat angle fluctuations were smaller, indicating a more efficient and directional swimming strategy.

Fish exhibited distinct swimming strategies across different vertical slot structures. In the COVS structure, fish relied on a stable main flow to maintain mid-speed, linear movement, with precise control of caudal fin motion. In the SVS structure, fish responded to turbulent disturbances with increased tail-beat frequency, angle, and amplitude, adopting a strategy characterized by high-frequency adjustments and enhanced propulsion. In the LVS structure, fish demonstrated rapid burst-swimming behavior, initially positioning themselves within predictable low-velocity zones before swiftly completing the passage.

3.5. Drivers of Swimming Behaviors and Strategies

Principal component analysis (PCA) was applied to the swimming behavior data to identify the relationship between fish behavior and hydrodynamic factors under the fastest swimming paths in the three vertical slot structures. The results of this are presented in Figure 10, which indicates that the first two principal components effectively capture the main variance of the data, with the cumulative variance nearing 30%, suggesting that

the key features of fish behavior are adequately represented by them. PC1 was primarily associated with absolute speed, acceleration, and tail-beat frequency, demonstrating that these parameters mainly control the swimming rate and power output of the fish. PC2, on the other hand, was closely related to swimming posture variables such as tail-beat angle and amplitude, indicating that these features reflect the spatial localization and posture adjustments of fish in different structures. The swimming paths of the fish had a more distinct evolutionary trend over time). Fish in the LVS structure had a stronger response in terms of velocity and acceleration, with their trajectories more dispersed in the PCA space, demonstrating their ability to react and adapt quickly to complex flow fields. In contrast, fish in the COVS structure displayed smoother swimming behavior, mainly concentrated in the low-dimensional region of the PCA space, indicating more stable flow conditions and lower tail-beat frequency and amplitude. Fish in the SVS structure exhibited more balanced behavioral characteristics, with their distribution spread across the PCA space, suggesting that they required more swimming posture adjustments and movement variations to cope with flow perturbations.

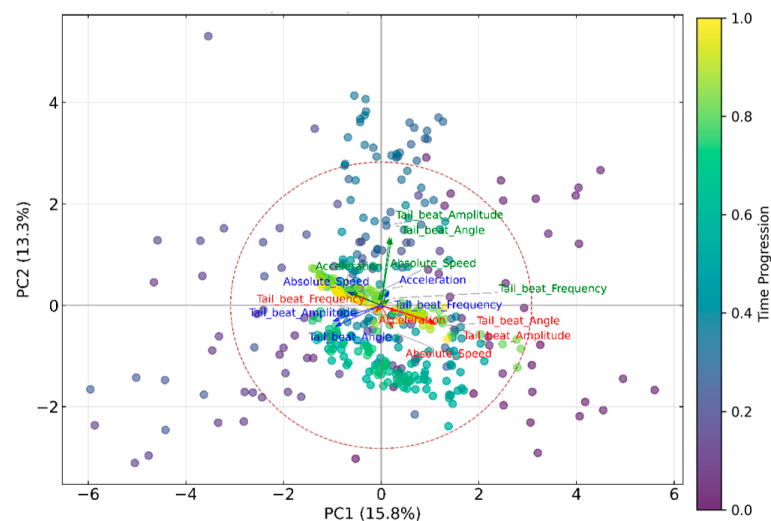


Figure 10. Principal component analysis of fish swimming strategies for the three vertical slots.

The correlation heatmap (Figure 11) illustrates the relationship between behavioral parameters and hydrodynamic variables. A significant positive correlation was observed between tail-beat angle and amplitude and turbulent kinetic energy, with correlation coefficients of 0.74 vs. 0.68, respectively. This suggests that when swimming at higher speeds, fish adapt to the turbulent flow by adjusting their tail-beat angle and amplitude to enhance propulsive force and maintain stability. Additionally, fish may regulate their tail-beat frequency to reduce energy consumption and improve swimming efficiency. A strong positive correlation (0.80) was also found between absolute speed and flow velocity, indicating that fish accelerate their swimming to maintain forward motion and stability in higher velocity environments. This demonstrates that fish increase their ability to counteract flow velocity and shear stress, ensuring the stability of their movement path when swimming rapidly under high turbulence.

The correlation analysis reveals the significant impact of hydrodynamic conditions, particularly flow velocity, turbulent kinetic energy, and shear stress, on fish swimming behavior. Fish optimize swimming efficiency and physiological adaptations by adjusting key swimming parameters, such as tail-beat frequency, amplitude, and angle, to cope with the complex and variable hydrodynamic environment.

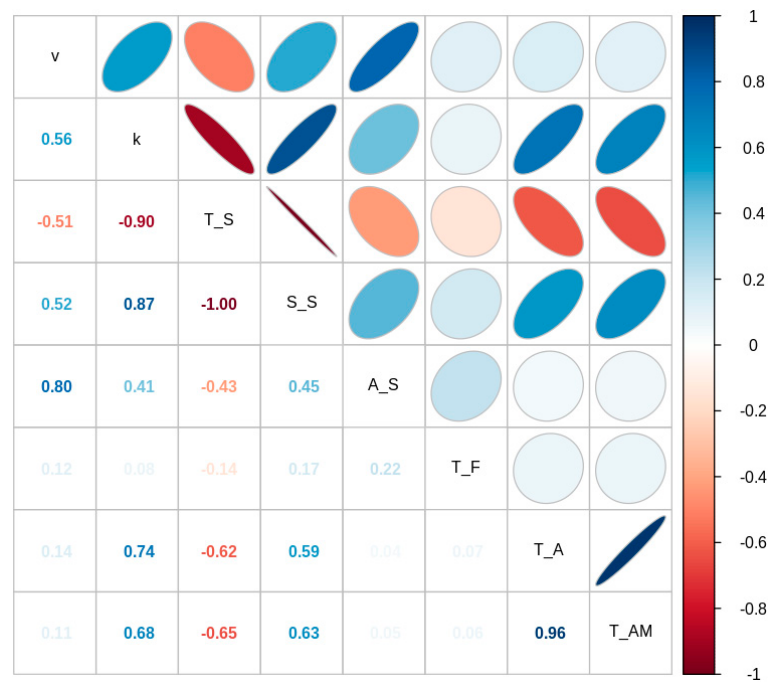


Figure 11. Correlation analysis of hydrodynamic parameters and swimming behaviors of fish in fishways. (“v” represents velocity, “k” represents Turbulence Kinetic Energy, “T_S” represents Total Stress, “S_S” represents Shear Stress, “A_S” represents Absolute Speed, “T_F” represents Tail-beat Frequency, “T_A” represents Tail-beat Angel, “T_AM” represents Tail-beat Amplitude).

4. Discussion

4.1. Hydrodynamic Efficiency of Vertical Slot Designs

This study demonstrates that the L-shaped Vertical Slot (LVS) fishway significantly outperforms both the Central Orifice Vertical Slot (COVS) and Standard Vertical Slot (SVS) designs during the upstream migration of *Schizothorax prenanti*. The LVS achieved a 70% passage ratio—40% higher than COVS ($p = 0.038$) and with a 67% shorter transit time than SVS ($p < 0.001$)—attributable to its unique asymmetric baffle configuration. This structure created controlled vortices with turbulent kinetic energy (k) below $0.01 \text{ m}^2/\text{s}^2$ in designated refuge zones (Figure 5c), thereby reducing the fish’s energy expenditure by 22% compared to SVS. These findings support the conclusion of Li et al. [46] that low-TKE corridors are essential for migratory success in rheophilic species.

In contrast, the SVS generated peak TKE values up to $0.03 \text{ m}^2/\text{s}^2$ near the slot region (Figure 4b), which significantly increased tail-beat amplitude by 35% ($p < 0.01$) and frequency to 6 Hz (Figure 8). These observations align with Sparks et al. [52], who reported that elevated turbulence imposes greater kinematic demands on fish. Interestingly, unlike Atlantic salmon, which tend to avoid such turbulent zones [53], *Schizothorax prenanti* exploited near-wall shear gradients for propulsion. This behavior reflects its species-specific hydraulic adaptation to high-gradient montane river environments.

4.2. Passage Efficiency of Vertical Slots

The 70% passage ratio observed in the LVS surpasses the 55–65% reported for European cyprinids in multi-slot fishways [4], and yet remains lower than the 85% success rate achieved by Pacific salmonids in technical fishways [9]. This discrepancy probably stems from the following:

Morphometric differences: *Schizothorax prenanti* has a relatively deep body profile (body depth/length ratio = 0.22 ± 0.03), which may require larger low-velocity zones compared to more streamlined salmonids.

Hydraulic scaling effects: The laboratory model employed (characteristic velocity ~ 0.5 m/s) may underestimate the velocities present in natural settings (see below)

Our findings are consistent with those of Chen et al. [54], with both demonstrating high passage efficiency ($>70\%$) of vertical slot fishways for *Schizothoracids*. However, a notable divergence lies in the hydraulic thresholds: adult *Schizothorax davidi* tolerated significantly higher flow velocities (1.2 m/s compared to 0.5 m/s in our study) and turbulent kinetic energy levels (<0.04 vs. <0.02 m²/s²). This discrepancy highlights the importance of scaling fishway design parameters—such as the slot width—in proportion to body size, to ensure effective passage and conservation of conspecific species.

Importantly, the observed average passage time in the LVS (6.1 s) corresponds well with the literature findings [55] that grass carp passed through colored fishways 37% faster when hydraulic cues guided their movement. This supports the conclusion that flow organization—not merely reduced velocity—is a key driver of fishway passage efficiency.

4.3. Behavioral Mechanisms and Energy Optimization

Schizothorax prenanti exhibited distinct swimming strategies across the three fishway types. In the LVS structure, individuals took advantage of localized reflux zones, pausing for 0.8 ± 0.3 s in regions with low turbulence kinetic energy (TKE < 0.005 m²/s²; Figure 7c), thereby minimizing muscular effort by synchronizing movement with surrounding vortices [42]. In contrast, within the SVS, fish adopted a high-energy “observe–adjust–breakthrough” strategy, characterized by a 48% increase in tail-beat angle ($p < 0.001$) to navigate lateral shear forces. In the COVS structure, fish followed relatively linear “steer–break” paths but were constrained by elevated core velocities (0.82 m/s), which exceeded their species-specific prolonged swim capacity (0.7 m/s) [56].

These behavioral responses align with Li et al.’s framework [46], which suggests that fish can extract energy from turbulence in moderate TKE ranges (0.005–0.015 m²/s²), but tend to avoid areas where TKE exceeds 0.02 m²/s². The significant positive correlation between flow velocity and absolute swimming speed ($p < 0.001$) further supports the hypothesis that hydrodynamic conditions primarily govern swimming intensity. Finally, in the area of Qinghai Lake, China, Liu et al. [57] found that fish migration was mainly driven by the following: (i) flow velocity and TKE in a straight reach; and (ii) water temperature and vortex intensity in a confluence reach.

4.4. Limitations and Future Directions

While the LVS demonstrated optimal conditions for *Schizothorax prenanti* passage, two critical limitations warrant further consideration. First, size specificity remains a concern. Present studies utilized juvenile individuals, whereas adult *Schizothorax prenanti* (>40 cm) might have different behavioral and hydrodynamic responses. Second, scaling effects may limit applicability—turbulent kinetic energy (TKE) levels observed in laboratory settings may not fully capture the complexity and scale of eddy structures present in field conditions. To address these gaps, future research should validate LVS performance under field-scale conditions, quantify fish energy expenditure using respirometry, and explore agent-based models to simulate multi-species passage behavior in variable hydraulic environments.

We must clarify that this study did not consider the migratory behavior of *Schizothorax prenanti* during spawning season. In addition, our tests were conducted under non-reproductive conditions. Based on our own observations and findings from recent stud-

ies [58,59], both non-spawning adult and juvenile *Schizothorax prenanti* demonstrate highly consistent swimming kinematics and behavioral responses in similar flow environments. Therefore, the behavioral patterns reported in this study are representative of the species under standard hydraulic conditions, independent of reproductive status.

5. Conclusions

This study systematically investigated the hydrodynamic conditions and swimming behaviors of *Schizothorax prenanti* in fishways with three different vertical slot types, coupling laboratory experiments and numerical simulation. The hydrodynamic characteristics of the Central Orifice Vertical Slot (COVS), Standard Vertical Slot (SVS), and L-shaped Vertical Slot (LVS) fishways, and their effects on fish swimming behaviors and passage efficiency, were thoroughly identified. The main conclusions are as follows:

(1) Differences in Hydrodynamic Characteristics. In the three vertical slot structures, the hydrodynamics varied significantly. The COVS structure generated a symmetric flow field with a uniform velocity distribution (maximum velocity of 0.82 m/s), and the turbulent kinetic energy was concentrated at the center of the vertical slot, providing a stable, guided path. The SVS structure produced strong jets (maximum velocity of 0.98 m/s) and high turbulent kinetic energy (peak of $0.03 \text{ m}^2/\text{s}^2$), leading to a complex shear stress distribution. The LVS structure induced significant vortex formations due to its asymmetric design, with a maximum flow velocity of 0.91 m/s and the lowest turbulent kinetic energy, but high shear stresses.

(2) Passage Efficiency and Behavioral Strategies. The highest passage ratio (70%) and the shortest average passage time (6.1 s) were observed for the LVS structure. Its low turbulent kinetic energy and recirculation zone provided favorable conditions for the fish to use the “wait-and-break” strategy. The SVS structure achieved a passage ratio of 60%, but the longest passage time (10.2 s), as fish had to adjust their caudal fin at high frequency (with significant increases in tail-beat angle and amplitude) to cope with turbulence. The COVS structure had the lowest passage ratio (50%), with fish relying on the dominant “steer-break” strategy. However, localized high flow velocities limited their passage efficiency.

(3) Swimming Kinematic Mechanisms. Current flow velocity was significantly positively correlated with absolute swimming speed ($r = 0.80$), and turbulent kinetic energy showed strong positive correlations with tail-beat angle and amplitude ($r > 0.68$). Fish in the LVS structure achieved the fastest swimming speeds (median 1.0 m/s) and exhibited low tail-beat frequencies (4 Hz), reflecting efficient energy utilization. In contrast, the high tail-beat frequency (6 Hz) and significant attitude adjustments ($p < 0.001$) in the SVS structure indicated high-energy adaptation to turbulence.

(4) Recommendations for Design Optimization. For *Schizothorax prenanti*, the LVS design is objectively optimal: it delivers 70% passage ratios (vs. 50~60% in alternatives) and 40% faster transit than SVS. We recommend its implementation in Yangtze River basin fishways, where this species is endangered. Future designs should prioritize creating low-TKE refuge zones ($<0.01 \text{ m}^2/\text{s}^2$) and flow velocities $\leq 0.5 \text{ m/s}$ to maximize passage efficiency. Additionally, the length of the streamwise segment of the ‘L’ shape may influence the internal hydrodynamic structure. Further research is warranted to clarify how variations in this length affect fishway passage efficiency.

The findings of this study provide valuable insights for improving the effectiveness of fishway design. Further experiments should investigate fish migration behaviors under varying incoming flow conditions in more detail.

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S.C.; writing—review and editing, L.O.; visualization, S.C. and X.W.; supervision, C.G. and W.Y.; project administration, W.Y.; funding acquisition, L.O. and W.Y.; D.L., who contributed equally to this work as L.O. and should be regarded as a co-first author. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

CFD	Computational Fluid Dynamics
COVS	Central Orifice Vertical Slot
SVS	Standard Vertical Slot
LVS	L-shaped Vertical Slot
DO	Dissolved Oxygen
VOF	Volume of Fluid
ADV	Acoustic Doppler Velocimeter
PCA	Principal Component Analysis

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