

Article

Behavioral Responses of Migratory Fish to Environmental Cues: Evidence from the Heishui River

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Abstract

Hydropower infrastructure has profoundly altered riverine connectivity, posing challenges to the migratory behavior of aquatic species. This study examined the post-passage migration efficiency of *Schizothorax wangchiachii* in a regulated river system, focusing on upstream and downstream reaches of the Songxin Hydropower Station on the Heishui River, a tributary of the Jinsha River. We used radio-frequency identification (RFID) tagging to track individuals after fishway passage and coupled this with environmental monitoring data. A Cox proportional hazards model was applied to identify key abiotic drivers of migration success and to develop a predictive framework. The upstream success rate was notably low (15.6%), with a mean passage time of 438 h, while downstream success reached 81.1%, with an average of 142 h. Fish exhibited distinct diel migration patterns; upstream movements were largely nocturnal, whereas downstream migration mainly occurred during daylight. Water temperature (HR = 0.535, $p = 0.028$), discharge (HR = 0.801, $p = 0.050$), water level (HR = 0.922, $p = 0.040$), and diel timing (HR = 0.445, $p = 0.088$) emerged as significant factors shaping the upstream movement. Our findings highlight that fishways alone may not ensure functional connectivity restoration. Instead, coordinated habitat interventions in upstream tributaries, alongside improved passage infrastructure, are crucial. A combined telemetry and modeling approach offers valuable insights for river management in fragmented systems.

Keywords: fish migration; monitoring and assessment; passage effectiveness; post-passage behavior; abiotic environmental factors

Key Contribution: This study is the first to systematically elucidate the behavioral response mechanisms of fish during upstream and downstream migration in natural river sections after passing through a fishway. It identifies the key environmental factors influencing migration and clarifies the positive and negative feedback mechanisms of abiotic factors such as water temperature, discharge, and water level on migration efficiency. These findings provide scientific evidence and decision-making support for ecological hydraulic regulation and operation.



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1. Introduction

The Jinsha River Basin in southwestern China is a vital region for water resource provisioning and ecological services. It plays an essential role in sustaining the region's environmental stability and underpinning socio-economic development. Over recent decades, however, the rapid expansion of hydraulic infrastructure to support economic growth has caused notable disruption to the ecological integrity of this system. In particular, dam and reservoir construction, alongside artificial regulation of flow regimes, has led to a pronounced breakdown in rivers' longitudinal connectivity and ecological continuity [1]. The Songxin Dam on the Heishui River forms a complete physical barrier, directly severing the natural flow and entirely disrupting the river's longitudinal ecological connectivity. These transformations have had far-reaching implications for riverine biodiversity, fish migration patterns, and the recovery of aquatic habitats. In some areas, fish populations have become critically threatened due to habitat fragmentation and barriers to movement [2,3].

To address these concerns, various mitigation strategies have been developed by researchers and conservation managers. Approaches such as fish restocking, installing fishways, and restoring tributary habitats have all been applied to support ecological resilience [4–6]. Among these options, habitat restoration in tributaries has been recognized as particularly valuable. This method rehabilitates secondary channels to offer suitable spawning and refuge zones for fish affected by habitat degradation in the mainstem. It supports the maintenance and recovery of fish populations through natural reproduction and recolonization from healthier sub-habitats [7]. Simultaneously, fish passage structures have gained prominence due to their dual function: enabling hydropower operation while facilitating migratory routes for aquatic species [8]. While not without limitations, these strategies have helped to mitigate some of the fragmentation impacts and enhance fish conservation efforts at the watershed scale.

Despite ongoing advances in fish passage research, much remains unknown about how fish behave and migrate after they have navigated a dam structure, particularly in the context of their movements between mainstem rivers and tributary habitats. Once fish pass through a barrier, they often face abrupt ecological shifts, and their capacity to adapt to these new conditions is poorly understood [9]. Key questions persist: Are fish able to reach upstream spawning areas with sufficient efficiency? Do they successfully return to downstream habitats after spawning? And to what extent do habitat restoration efforts in tributaries complement the structural functionality of fish passage facilities [10]? These uncertainties constrain our ability to accurately assess the ecological outcomes of passage interventions and limit the development of management strategies based on fish behavior. Restoration efforts risk falling short of their intended goals without a clearer understanding of post-passage movement dynamics. To address these gaps, there is a pressing need for studies that track behavioral responses and migration patterns following dam passage, with a focus on how fish navigate the interconnected landscapes of mainstems and tributaries. Exploring these dynamics enriches our understanding of aquatic behavioral ecology and supports the development of more ecologically integrated design and management practices. In the long run, such insights will be critical for improving river connectivity, optimizing hydraulic infrastructure, and achieving sustainable watershed governance.

Understanding the drivers of fish migration is essential for interpreting their behavioral patterns. Both biotic factors (e.g., species-specific traits, physiological conditions) and abiotic environmental factors (e.g., discharge, flow velocity, water level, temperature, and diel cycle) play crucial roles in shaping migratory behavior [11]. Recent studies have explored fish responses to individual environmental variables. For instance, brook trout (*Salvelinus fontinalis*) exhibit significantly stronger upstream movement under high discharge conditions [12]. *Parazacco spilurus* tend to avoid high-velocity and turbulent

zones during swimming [13]. Mullet (*Chelon ramada*) is most active between sunrise and sunset, with 60% of individuals initiating upstream migration between 12:00 and 19:00 [14]. American shad (*Alosa sapidissima*) shows greater upstream motivation and success under elevated temperatures [15]. However, most existing research focuses on single-factor influences, lacking systematic investigation of interactive effects among multiple environmental drivers. This limitation hinders the identification of key determinants of migration success and thus restricts the formulation of targeted restoration and regulation strategies.

In this context, the present study focused on the upstream and downstream reaches of the Songxin Hydropower Station on the Heishui River, a tributary of the Jinsha River. Using radio-frequency identification (RFID) technology, we tracked fish movements post-dam passage to characterize behavioral patterns during upstream and downstream migration within the natural river channel. We quantitatively assessed migratory success and efficiency and developed a Cox proportional hazards regression framework to identify critical environmental factors influencing fish movement. In addition to examining fish swimming behavior post-passage, this study established a comprehensive indicator system and predictive model for assessing the effects of various environmental variables on migration efficiency.

The findings provide scientific guidance for restoring river connectivity and optimizing reservoir operation strategies. Through in-depth analysis of key influencing factors, we propose adaptive measures to mitigate the ecological impacts of hydraulic structures. This research contributes to ongoing efforts in ecological restoration and fish conservation in the Jinsha River Basin while offering a theoretical and practical reference for similar river systems globally.

2. Materials and Methods

2.1. Study Area

The Heishui River is a primary left-bank tributary of the Jinsha River, located in Sichuan Province, southwestern China. It has been designated as a priority habitat conservation river for fish within the reservoir area of the Baihetan Hydropower Station. At present, three hydropower stations have been constructed along the mainstem of the Heishui River, among which only the Songxin Hydropower Station is equipped with a fish passage facility. In this study, we selected the river sections immediately upstream and downstream of the Songxin Station (Figure 1) as the study area to investigate the efficiency and influencing factors of post-dam upstream and downstream fish migration.

2.2. Upstream and Downstream Migration Tracking Experiment

2.2.1. Experimental Subjects

The shortlip schizothoracin (*Schizothorax wangchiachii*), a cyprinid fish belonging to the subfamily Schizothoracinae (family Cyprinidae, order Cypriniformes), represents both a key economic species and a conservation target in the Jinsha River basin. This cold-water migratory fish serves as a representative species of the mountainous river ecosystems in southwestern China. The fish community in the Heishui River is primarily composed of species from the families Cyprinidae, Cobitidae, and Nemacheilidae, with the occasional presence of piscivorous birds as potential predators. This study conducted upstream–downstream movement tracking experiments specifically targeting *S. wangchiachii*. The fish used in the upstream and downstream tracking experiments were healthy individuals collected from the Heishui River Basin in Ningnan County, Liangshan Yi Autonomous Prefecture, Xichang City, Sichuan Province.

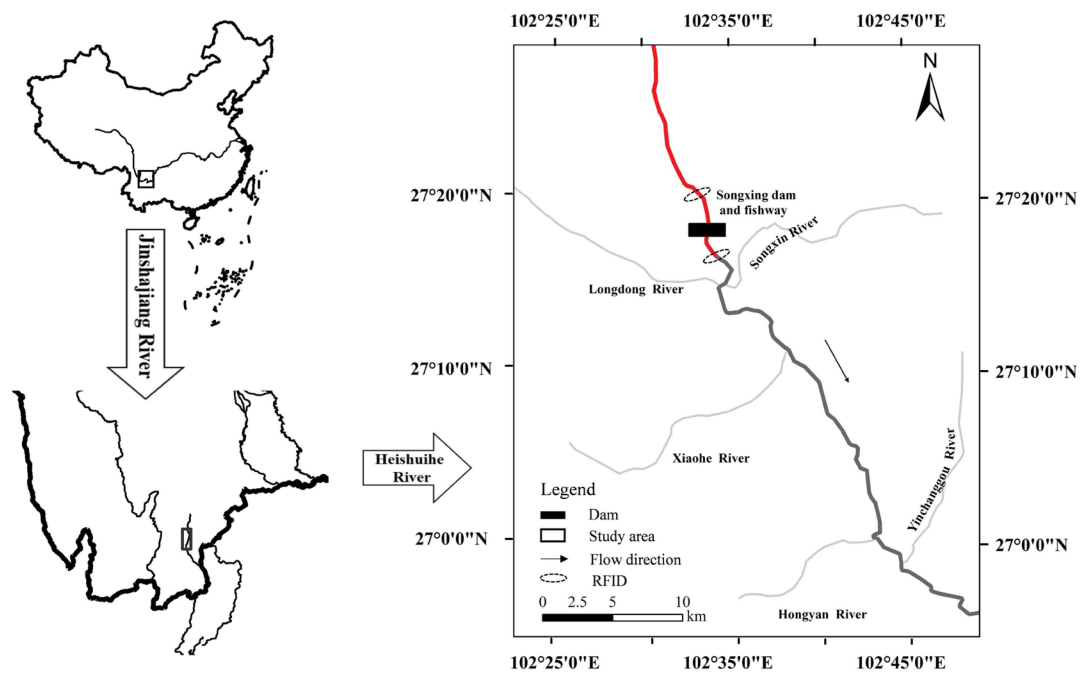


Figure 1. Geographical location of research area.

For the upstream tracking experiment, individuals of the target species *Schizothorax wangchiachii* that had passed through the fishway from the downstream reach of the Songxin Hydropower Station and successfully migrated toward the upstream area of the dam were studied. A set net was deployed at the fishway outlet to capture these fish after they exited the fishway. To ensure biological consistency and data reliability, only individuals deemed “healthy” based on standard field criteria were included in the experiment. Specifically, selected fish exhibited normal swimming posture and responsiveness, intact fins and scales, no external injuries or deformities, and quick recovery after handling. These fish were then released near the fishway outlet for the upstream tracking experiment.

For the downstream experiment, fish that migrated downstream through the ecological replenishment (supplementary water) channel from the upstream section were captured using a set net installed near the fishway inlet. Healthy individuals were selected and released near the fishway inlet for downstream movement observation.

Before PIT tag implantation, all selected fish were anesthetized using MS-222 (tricaine methanesulfonate) at a 0.10 mg/L concentration. Morphological measurements were recorded for each fish. The average body length of the tagged fish was 249.71 ± 96.70 mm, and the average body weight was 247.93 ± 34.55 g.

All equipment and PIT tags were disinfected with medical alcohol prior to use. PIT tags were surgically implanted into the abdominal cavity of each fish. Before the formal experiment, preliminary release tests were conducted using healthy individuals to ensure suitability. In total, 90 healthy fish were released for the upstream and downstream tracking experiments, respectively.

2.2.2. Experimental Equipment

The experimental setup utilized a Radio Frequency Identification (RFID) riverine monitoring system (Model RF-D, dual-channel detection system), which included antenna arrays, mounting bases, and solar panels. The antenna arrays were installed in a cross-sectional configuration across the full width of the river at both the upstream and downstream sites, ensuring complete channel coverage for fish detection. This dual-channel system could detect both the timing and position of fish passage. Its detection range is limited to fixed

antenna sites, and it cannot continuously track fish movement in open river stretches. A schematic diagram of the RFID device deployment is provided in Figure 2. The system was capable of real-time, continuous fish monitoring under all weather conditions, powered solely by solar energy. All detection data were stored locally in the RFID reader and could be periodically retrieved for analysis.

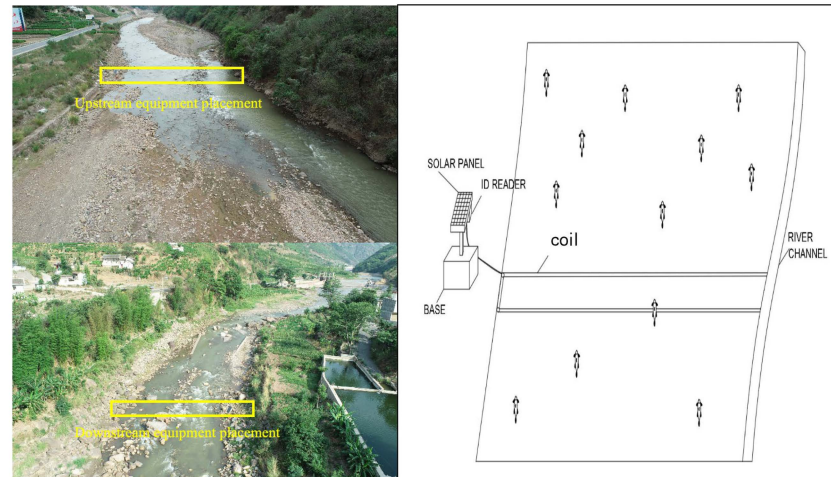


Figure 2. Schematic diagram of river layout of RFID device.

2.2.3. Experimental Procedure

This study was conducted during the fish migration season (March to May) in the Heishui River. The upstream and downstream channels at the study site measured 40 m and 30 m in width, with average water depths of 1.0 m and 0.8 m, respectively. Prior to release, passive integrated transponder (PIT) tags were surgically implanted into the body cavity of each study fish. RFID monitoring systems were deployed using frame-supported structures at locations 1.5 km upstream and downstream of the Songxin Dam. These systems continuously recorded each detected fish's tag ID and precise passage time. We identified key abiotic factors influencing post-passage fish movement by integrating RFID detection data with environmental variables (river discharge, water temperature, diel cycle) collected from the 40 m wide upstream channel and 30 m wide downstream channel.

2.3. Data Analysis

To evaluate the effectiveness of upstream and downstream fish passage, we quantified several performance indicators, including upstream travel time, upstream passage rate, the number of individuals recorded in both directions, downstream passage rate, and passage velocity. The metrics were calculated as follows:

$$P_{ij} = \frac{N_i}{N_j} \times 100\% \quad (1)$$

where P_{ij} is the passage success rate between RFID antenna i and j ; N_i , N_j represent the number of individuals detected at antenna i and j , respectively.

$$T_{ij} = T_i - T_j \quad (2)$$

where T_{ij} is the travel time between antenna i and j ; T_i , T_j are the detection timestamps at each respective antenna.

$$V_{ij} = \frac{L_i - L_j}{T_{ij}} \quad (3)$$

where V_{ij} is the migration velocity and L_i, L_j are the distances of antenna i and j , respectively, from the fishway entrance.

$$P_{Qc} = \frac{Q_{i+1} - Q_i}{Q_i} \times 100\% \quad (4)$$

where P_{Qc} is the flow variation index; Q_i and Q_{i+1} are the discharges at time steps i and $i+1$, respectively. A positive value indicates rising flow, a negative value indicates falling flow, and the absolute magnitude represents the degree of fluctuation.

$$P_{Tc} = \frac{T_{i+1} - T_i}{T_i} \times 100\% \quad (5)$$

where P_{Tc} is the temperature variation index; T_i and T_{i+1} are the water temperatures at time steps i and $i+1$, respectively. A positive value indicates warming, a negative value indicates cooling, and a larger absolute value reflects greater fluctuation.

To identify the key factors affecting the upstream and downstream migration of fish in the river, this study selected biotic and abiotic factors related to fish attraction to the fishway entrance. These factors included river discharge (UQ), river water level (WL), flow fluctuation rate (QC), temperature variation rate (TC), temperature (T), fish body length (BL), and diel rhythms (DR), all of which are related to passage efficiency.

To identify the key factors influencing the efficiency of upstream and downstream migration after dam passage and to quantify their relative effects, we focused on *Schizothorax wangchiachii* and constructed a Cox proportional hazards regression model using a time-to-event analytical approach. This method models the hazard function—i.e., the probability of successful passage—as a function of multiple environmental covariates affecting attraction to and movement through the fishway.

Model selection was based on the Akaike Information Criterion (AIC) to avoid potential multicollinearity among explanatory variables, which evaluates model performance by balancing fit and complexity. The optimal model was selected by minimizing ΔAIC . The Cox regression model, AIC formulation, and model weight calculations are expressed as follows:

$$h(t, x) = h_0(t) \exp(\beta x^T + b_i) \quad (6)$$

$$AIC = 2k - 2\ln(L) \quad (7)$$

$$w_i = \exp(-0.5 \Delta iAIC) / \sum_{i=1}^n \exp(-0.5 \Delta iAIC) \quad (8)$$

In the Cox proportional hazards model, $h_0(t)$ represents the baseline hazard function when the covariate vector x equals zero; this function is estimated from the sample data and reflects the underlying risk independent of covariates. The β coefficients represent the effect sizes of the influencing factors, and ε denotes the random effect term. L is the likelihood function, k is the number of model parameters, and w_i indicates the Akaike weight for the optimal model.

Data processing was performed using Microsoft Office, and visualizations were generated with Origin 2021 to present the research findings effectively. Data analysis was performed using SPSS Statistics (Version 19.0, IBM Corp., Armonk, NY, USA) and RStudio (Version 4.1.3, RStudio, PBC, Boston, MA, USA). Differences between groups were tested using one-way analysis of variance (ANOVA, e.g., passage duration and fish body length) and non-parametric tests (e.g., diel passage timing, success rate classifications), with a significance threshold set at $p < 0.05$. Survival analysis via the Cox proportional hazards regression model was conducted in R to evaluate the influence of environmental variables on upstream migration performance. The optimal model was identified based on the Akaike Information Criterion (AIC), and the key influencing factors were visualized through forest

plots and nomograms to illustrate trends and facilitate probability-based prediction. All quantitative results are presented as means $\pm$ standard deviations (Means $\pm$ SDs).

3. Results and Analysis

3.1. Upstream and Downstream Passage Success Rates in River Sections

In this study, RFID antennas were deployed across both upstream and downstream river sections. *Schizothorax wangchiachii* that successfully passed through the fishway were designated as the upstream experimental group, while those that exited the downstream passage facility were designated as the downstream group. The upstream and downstream migration experiments were each divided into three replicates. The passage success rates for each group are presented in Table 1.

Table 1. The upstream and downstream passage rates on the Heishui River.

	Release Location	Number Released	Number Arrived	Passage Success Rate (%)
Upstream Section	1 m from the fishway exit	30	4	13.33%
	20 m from the fishway exit	30	5	16.67%
	30 m from the fishway exit	30	5	16.67%
Downstream Section	1 m from the fishway entrance	30	18	60.00%
	20 m from the fishway entrance	30	26	86.67%
	30 m from the fishway entrance	30	29	96.67%

The passage success rates for the upstream migration trials were 13.33%, 16.67%, and 16.67%, with an average upstream success rate of 15.6%. No statistically significant differences were observed among the three groups. In contrast, the downstream passage success rates were notably higher, at 60.0%, 86.67%, and 96.67%, with an average of 81.1%. Notably, the downstream success rate for fish released 1 m below the dam was relatively lower. This may be attributed to the proximity of the release point to the fishway entrance, allowing some individuals to counter-swim into the fishway rather than proceeding downstream.

Overall, fish released in the downstream section demonstrated a significantly higher passage success rate compared to those released in the upstream section. The majority of fish exhibited a preference for downstream migration.

3.2. Evaluation of Passage Efficiency in Upstream and Downstream River Sections

Passage time is a primary indicator for assessing the efficiency of fish movement through river reaches. Generally, shorter durations reflect more favorable hydraulic conditions for migration, while longer times may signal either physical impediments or behavioral responses such as exploratory movements or temporary holding in suitable habitat zones.

As shown in Figure 3, there was a clear contrast in passage times between upstream and downstream migrants. Fish moving upstream through the upper river section exhibited substantially prolonged durations, with an average passage time of 438 h, which included extended periods of holding or resting in the natural channel after exiting the fishway. Most individuals completed this migration within a 0–600 h window, although some outliers extended beyond this range. In contrast, downstream-moving fish required significantly less time, averaging 142 h, with the majority passing through within 0–300 h, approximately half the time required for upstream migration. This temporal difference highlights the greater energetic and navigational demands associated with upstream passage compared to downstream drift.

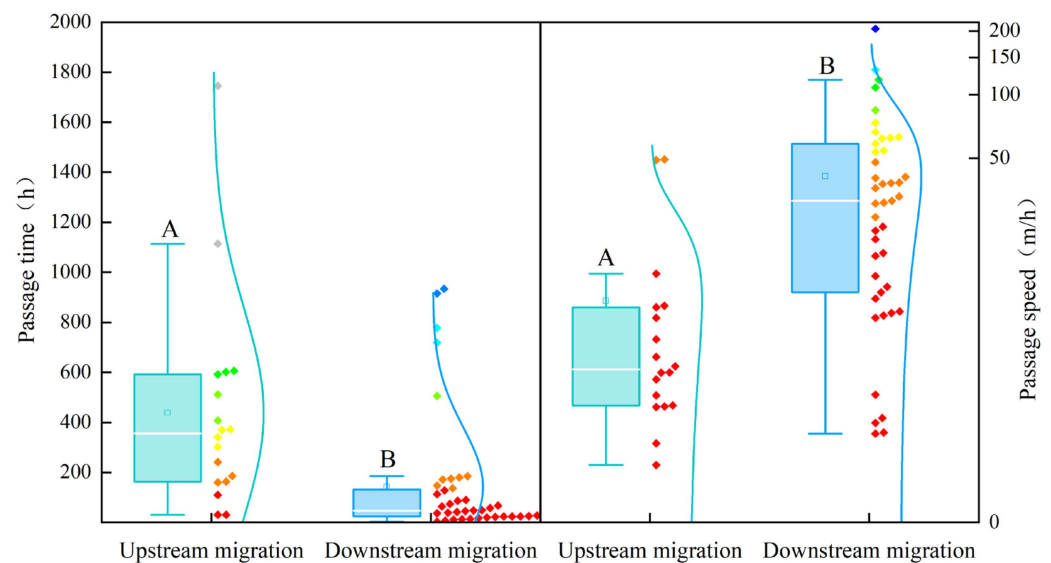


Figure 3. Upstream and downstream passage time and speed of fishes in upstream and downstream channels. The color of points represents the intensity of their indicator values, while the curves depict the clustering density of different indicators. while distinct letters indicate statistically significant differences ($p < 0.05$).

The passage velocity is another important indicator for evaluating the efficiency of fish movement through river sections. Faster passage velocities suggest that the flow conditions are favorable for fish migration or that the river section lacks suitable habitat for fish. Conversely, slower passage velocities may indicate complex flow conditions unsuitable for upstream migration or the presence of favorable habitat that causes fish to stop and rest during their migration. In this study, the upstream and downstream passage velocities in the river sections are shown in Figure 3. It was found that fish migrating upstream in the upper river section exhibited relatively slower velocities, with a mean of 9.91 m/h, concentrated between 0 and 10 m/h. On the other hand, downstream passage occurred at much faster velocities, with a mean of 50.79 m/h and a range of 0 to 200 m/h.

These results indicate that fish do not migrate continuously upstream after passing through the dam. Instead, there appears to be an alternating upstream movement and resting process. When the flow rate in the upstream river section is too high, making it difficult for fish to overcome the current, or when fish encounter preferred suitable habitats, they will stop migrating upstream. On the other hand, when flow rates are lower, allowing easier upstream migration, and changes in hydrological conditions alter the fish habitat, the fish will resume their upstream movement. This results in longer passage times and slower velocities. In contrast, downstream migration occurs because the flow at the fishway entrance is too strong for *Schizothorax wangchiachii* to swim upstream. After a prolonged struggle against the current, fish become fatigued and passively drift downstream. During downstream migration, fish recover and search for suitable habitats, leading to shorter passage times and faster velocities.

3.3. Diel Rhythms of Upstream and Downstream Migration in River Sections

Diel variation in passage time for upstream and downstream migrations at the Songxin Dam site is illustrated in Figure 4. For upstream migrants, the mean passage time varied across diel periods, with the most extended durations recorded in the morning (587.4 h), night (553.1 h), and afternoon (421.9 h). In contrast, the early morning hours showed the shortest mean passage time of 216.4 h. Notably, the number of fish passing during night

exceeded those moving during daylight hours, with 10 individuals migrating at night compared to 8 during the day.

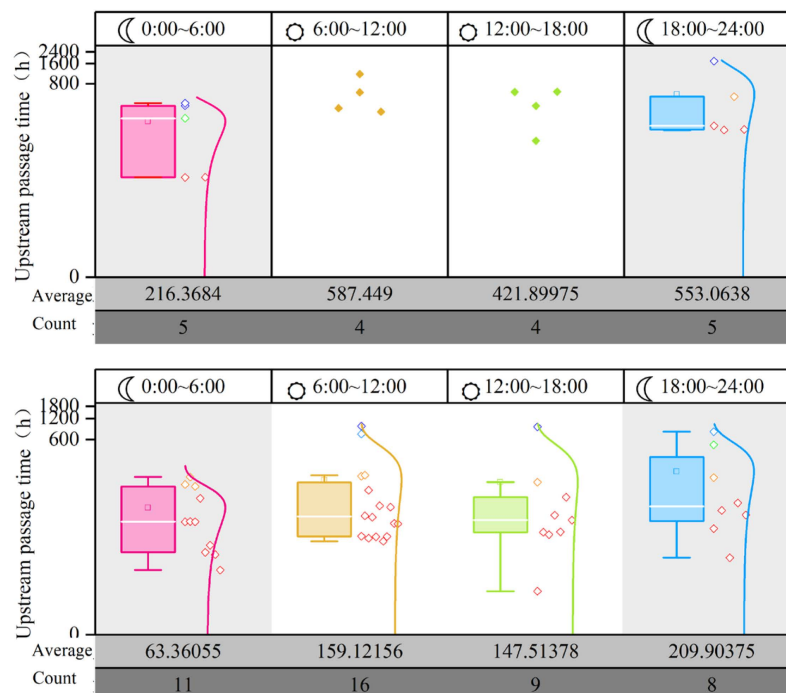


Figure 4. Circadian rhythm of upstream and downstream passage time in river channel. “Average” represents the mean indicator values during different time periods, while “Count” indicates the number of successful passages within each period. The same convention applies to subsequent figures.

In the downstream reach, a different diel pattern emerged. Although passage durations remained longer in the daytime periods of 159.1 h in the morning, 147.5 h in the afternoon, and 209.9 h at night, the shortest passage time occurred in the early morning (63.36 h). However, the distribution of passage events revealed the opposite behavioral tendency: 16, 9, and 8 fish passed during the morning, afternoon, and night, respectively, while only 11 individuals migrated in the early morning.

Together, these findings suggest a clear diel rhythm in fish migratory behavior. The upstream passage was more efficient and frequent during nighttime, while downstream movement appeared more concentrated during daylight, particularly in the early morning and morning periods. These diel differences likely reflect adaptive strategies to optimize energy use, reduce predation risk, and align with favorable flow and light conditions.

The diel rhythms of upstream passage velocity at the Songxin Dam site, both upstream and downstream, are shown in Figure 5. These results indicate that the upstream passage velocities during the morning, afternoon, and night were lower than during the early morning hours. The passage velocities in the four time periods were 3.31 m/h, 5.66 m/h, 6.08 m/h, and 22.43 m/h, respectively.

Similarly, in the downstream river section, the passage velocities during the morning, afternoon, and night were lower than those during the early morning hours. The passage velocities for the four time periods were 34.43 m/h, 37.67 m/h, 33.62 m/h, and 61.57 m/h, respectively. These findings suggest that fish are most active during the early morning hours in both upstream and downstream river sections.

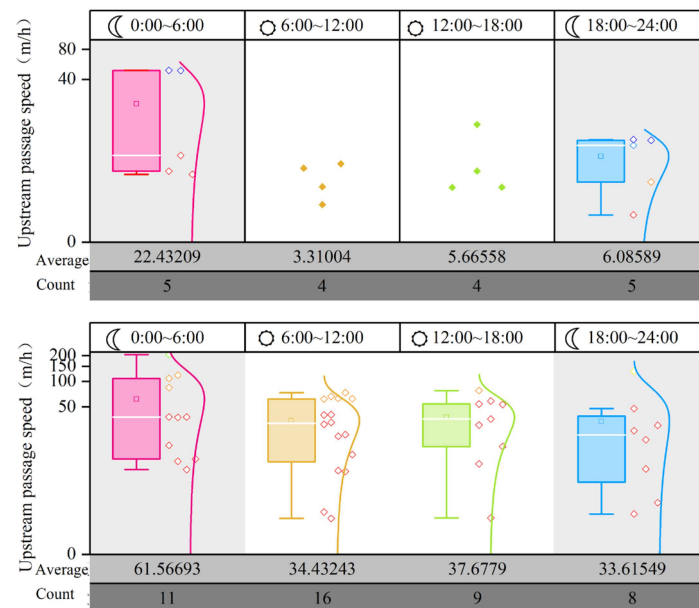


Figure 5. Circadian rhythm of upstream and downstream passage velocity in river channel.

The diel rhythms of upstream passage time at the Songxin Dam site, both upstream and downstream, are shown in Figure 6. These results indicate no significant differences in the body length of fish during upstream and downstream migrations. In the upstream section, the body lengths during the morning, afternoon, night, and early morning were 246.5 mm, 244.5 mm, 233.8 mm, and 252.8 mm, respectively. In the downstream section, the body lengths during the morning, afternoon, night, and early morning were 263.8 mm, 259.1 mm, 247.1 mm, and 248.6 mm, respectively.

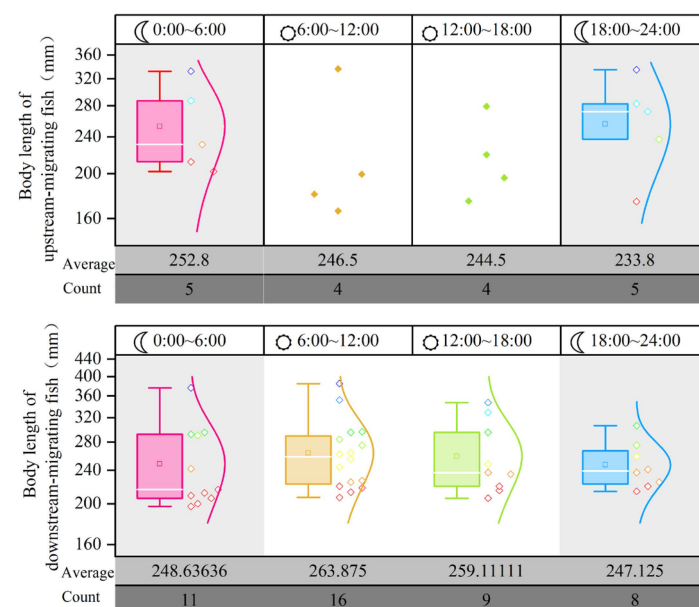


Figure 6. Circadian rhythm of fish average body length in the upstream and downstream channels.

Notably, individuals undertaking upstream migration tended to be larger in body size, particularly during early morning hours, whereas those migrating downstream were generally smaller. This suggests a possible tendency for larger individuals to engage more actively in upstream movement.

3.4. Influence of Environmental Factor Variations on Upstream and Downstream Passage Efficiency in River Sections

This study assessed the effects of flow conditions on downstream passage efficiency in upstream and downstream river reaches (Figure 7), aiming to identify flow thresholds that optimize migratory success. In the upstream section, the observed flow range was divided into three intervals: 0–6 m³/s, 6–12 m³/s, and 12–18 m³/s. Fish passage only occurred at the lower and upper flow ranges, with 11 and 7 individuals successfully migrating, respectively, while no fish passed in the intermediate range (6–12 m³/s). This mid-range flow showed significantly reduced passage success compared to the other intervals ($p < 0.05$), indicating a non-linear response where moderate flows may create unfavorable turbulence or reduce directional cues.

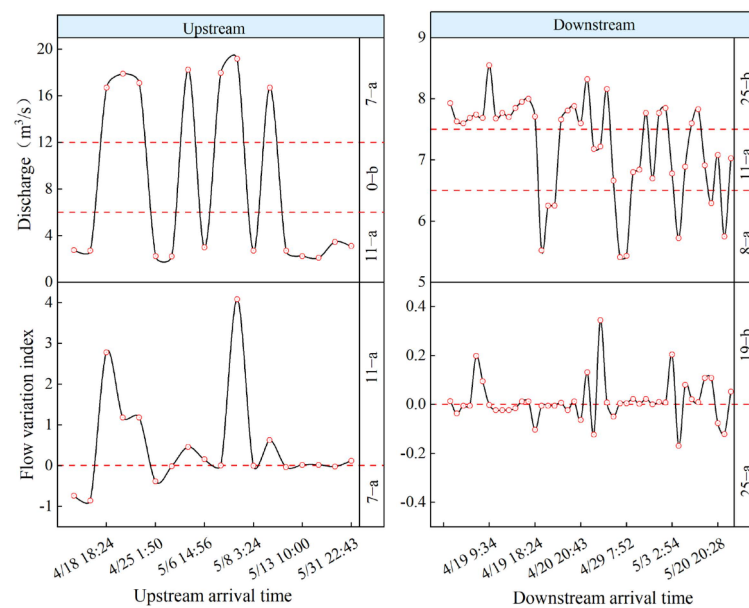


Figure 7. The up-down rule of fish in response to the flow change process. The dashed lines in the figure partition the indicator values into distinct ranges. The numbers in the right box indicate the counts of fish passages within each value range. Shared letters denote non-significant differences ($p > 0.05$), while distinct letters indicate statistically significant differences ($p < 0.05$). This convention applies consistently throughout.

The flow was categorized into three intervals in the downstream reach: 5.0–6.5 m³/s, 6.5–7.5 m³/s, and 7.5–9.0 m³/s. A clear trend emerged, with downstream passage success increasing with flow magnitude: 8, 11, and 25 fish passed within these respective intervals. The highest success occurred in the 7.5–9.0 m³/s range, significantly exceeding the lower flow groups ($p < 0.05$). These findings suggest contrasting flow preferences for different migration directions: fish tend to favor lower flow conditions for upstream migration, where reduced velocity eases movement, and higher flows for downstream migration, which provide hydraulic support and reduce energy expenditure.

Analysis of the flow variation index further revealed hydrodynamic differences between river sections. The upstream reach experienced wider fluctuations (−1 to 4), while the downstream reach remained relatively stable (−0.2 to 0.4). In the upstream section, 11 fish migrated successfully during rising flow and 7 during falling flow, with no statistically significant difference, although success rates were slightly higher under rising conditions. Notably, the variation index approached zero during falling flow, indicating limited fluctuation, whereas rising flow corresponded with larger index values, suggesting that moderate increases in discharge may facilitate upstream movement by enhancing flow cues.

In contrast, downstream migration showed a reverse pattern. Passage success was higher during falling flow, with 25 fish compared to 19 during rising flow ($p < 0.05$). However, flow variability remained low across both phases, suggesting that even small shifts in discharge direction can influence behavioral decisions, likely by modifying microhabitat turbulence or flow guidance efficiency. These results highlight the importance of fine-scale hydrological variability in shaping fish migration behavior and suggest that passage efficiency depends not only on absolute flow rates but also on the stability and direction of flow changes.

The observed migration patterns under varying flow conditions may be explained by upstream-migrating fish's habitat preferences and movement strategies. These individuals typically favor low-velocity microhabitats, such as near riverbanks or within submerged vegetation beds. During rising flow conditions, the river width expands, increasing the surface area and distributing discharge over a broader cross-section. As water passes over gravel bars or vegetated banks, localized velocity decreases, creating more favorable pathways for upstream movement. This may explain the increased upstream migration success and the concurrent decline in downstream movements observed under rising water conditions.

Conversely, during falling flow events, the reduction in discharge and turbulence initially supports upstream migration by lowering energetic barriers. However, if the water level drops excessively, exposed sandbars and a reduced wetted perimeter compress the active channel, concentrating flow in the midstream zone. Under such conditions, bank-oriented fish may lose access to shallow passage routes or even become stranded, resulting in failed upstream attempts. Consequently, some individuals may revert to downstream movement, a response reflected in the higher downstream passage counts observed during falling flows. This behavioral asymmetry also accounts for the smaller flow variation index during falling stages compared to rising ones.

Temperature-mediated migration responses are presented in Figure 8. During the March to May monitoring period, water temperatures ranged from 14 °C to 24 °C and were divided into three categories: 14–18 °C, 18–21 °C, and 21–24 °C. In the upstream reach, successful passage counts were 1, 13, and 4, respectively. Migration success peaked in the 18–21 °C range, which was significantly higher than in the other two intervals ($p < 0.05$). A similar trend was observed downstream, where 36 fish migrated at 18–21 °C, compared to 0 and 8 at the lower and upper ranges, respectively ($p < 0.05$).

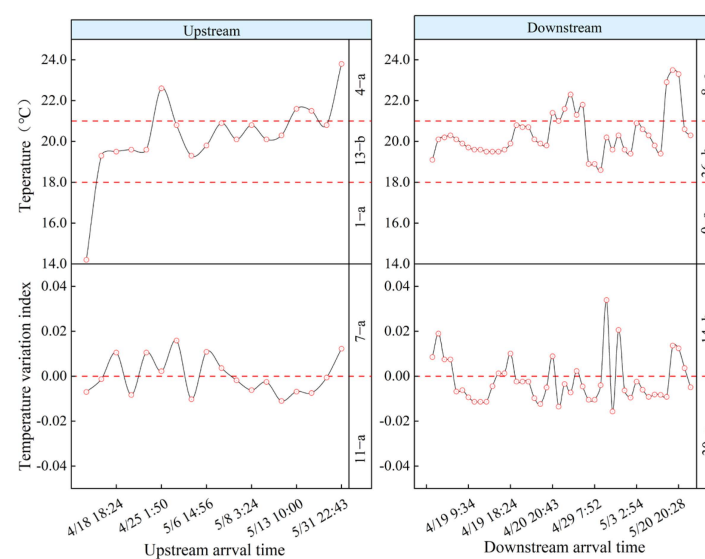


Figure 8. The up-down pattern of fish in response to water temperature changes.

These results suggest that fish exhibited optimal migratory activity within a moderate temperature band (18–21 °C), likely reflecting a thermally favorable zone for metabolic performance, neuromuscular coordination, and sensory perception. Elevated or suppressed temperatures outside this range may induce physiological stress or reduce behavioral responsiveness, thereby limiting migration success. This thermally sensitive behavior underscores the importance of maintaining thermal regimes within species-specific tolerances in regulated river systems.

The results from the river temperature variation index (Figure 8) indicate that temperature fluctuations in both the upstream and downstream river sections were relatively small. In the upstream section, during cooling periods, 11 fish migrated upstream, while 7 fish migrated upstream during warming periods. In the downstream section, 30 fish migrated downstream during cooling, and 14 fish migrated downstream during warming. Furthermore, the downstream passage success was significantly higher during the cooling period than during the warming period ($p < 0.05$). The warming process predominantly occurred during the daytime, while the cooling process occurred mainly at night, further confirming that fish are more active at night.

Temperature is one of the most critical environmental factors affecting the survival and growth of aquatic organisms. Temperature, within certain limits, supports fish migration. However, when temperatures exceed the optimal range, extreme temperatures can cause metabolic stress, triggering an escape response in fish. In this study, fish were most active within the 18–21 °C range, during which upstream and downstream migration were most efficient. This does not necessarily mean that fish prefer this temperature range, but it could indicate that fish experience less metabolic stress, thus resulting in better migration performance. When migration efficiency is poor, it could be because fish have paused their migration and remained in their habitat. Therefore, further analysis is required to fully understand how temperature affects fish migration behavior.

3.5. Identification and Prediction of Key Factors Influencing Upstream and Downstream Migration Behavior of Fish

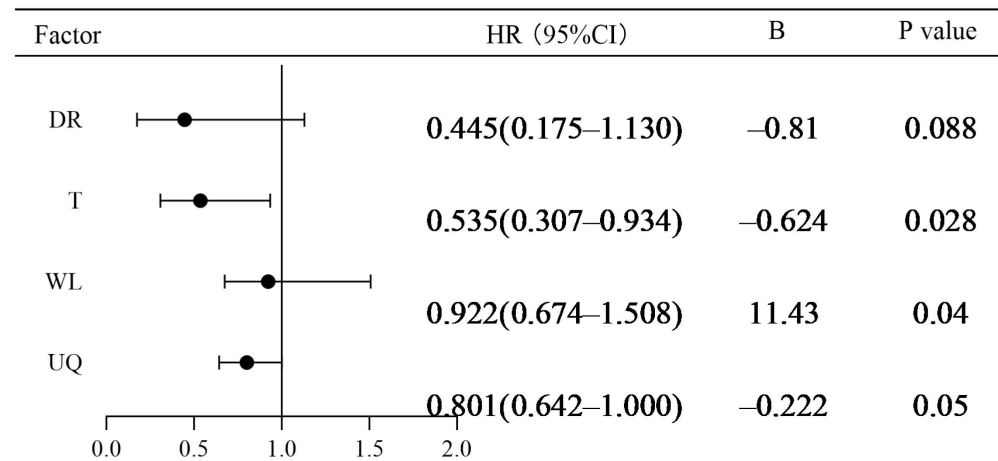
To identify the key factors affecting the upstream and downstream migration of fish in the river, this study selected biotic and abiotic factors related to fish attraction to the fishway entrance. These factors included river discharge (UQ), river water level (WL), flow fluctuation rate (QC), temperature variation rate (TC), temperature (T), fish body length (BL), and diel rhythms (DR), all of which are related to passage efficiency. A survival analysis using the Cox proportional hazards regression model was constructed, and the Akaike Information Criterion (AIC) was used to select the optimal model, thereby identifying the key factors influencing the efficiency of fish migration in upstream and downstream directions. The conclusions derived from the Cox proportional hazards model are specific to the migratory period.

The optimal model for upstream passage efficiency is shown in Table 2. After four iterations, the optimal model included UQ, WL, T, and DR factors. The lowest AIC value was 66.2, with a weight (w_i) of 0.43. The results of the Cox proportional hazards regression model for upstream migration efficiency are shown in Figure 9. The results indicate that diel rhythm, temperature, flow fluctuation rate, and fishway water depth were hindering factors and were negatively correlated with the probability of upstream migration success. The passage success rate was higher at night than during the day ($HR = 0.445$, $p = 0.088$). Within a certain range, lower temperatures were associated with better upstream migration efficiency ($HR = 0.535$, $p = 0.028$). Similarly, lower flow fluctuation rates were associated with better upstream migration efficiency ($HR = 0.801$, $p = 0.05$). Within a certain range, higher water levels also correlated with better upstream migration efficiency ($HR = 0.922$, $p = 0.04$).

Table 2. Optimal model selection of river uplink effect based on Akaike Information Criterion (AIC) criterion.

Number	Model	AIC	Δ AIC	w _i	w _i /w _j
1	UQ + WL + T + BL + DR + QC + TC	71.16	2	0.156563017	2.718281828
2	UQ + WL + T + BL + DR + QC	69.16	1.96	0.1597258	2.664456242
3	UQ + WL + T + DR + QC	67.2	1	0.258128777	1.648721271
4	UQ + WL + T + DR	66.2	0	0.425582405	

Note: Upstream river discharge (UQ), upstream river water level (WL), upstream river flow fluctuation rate (QC), upstream temperature variation rate (TC), temperature (T), fish body length (BL), and diel rhythms (DR).

**Figure 9.** Forest map of fishway channel ascending effect. Note: In the figure, HR represents the hazard ratio, CI denotes the confidence interval, and B represents the regression coefficient, with the same notation applied throughout.

The optimal model for the fishway entrance attraction effect is shown in Table 3. After three iterations, the optimal model included the factors FQ, BQ, BL, and DR. The lowest AIC value was 317.39, with a weight (w_i) of 0.549. The results of the Cox proportional hazards regression model for downstream passage efficiency are shown in Figure 10. The findings indicate that diel rhythm and body length were hindering factors and were negatively correlated with upstream success. The downstream passage success rate was higher at night than during the day (HR = 0.511, $p < 0.001$), and smaller body length was associated with better downstream migration efficiency (HR = 0.994, $p = 0.11$). Fishway discharge and inflow discharge were facilitating factors. The larger the fishway discharge, the better the downstream passage efficiency (HR = 1.118, $p = 0.001$), and the larger the inflow discharge, the better the downstream passage efficiency (HR = 1.902, $p = 0.011$).

Table 3. Optimal model selection of river descending effect based on Akaike Information Criterion (AIC) criterion.

Number	Model	AIC	Δ AIC	w _i	w _i /w _j
1	FQ + BQ + T + BL + DR + Place	320.96	1.95	0.207015322	2.651167
2	FQ + BQ + BL + DR + Place	319.01	1.62	0.244152446	2.247908
3	FQ + BQ + BL + DR	317.39	0	0.548832233	

Note: Fishway discharge (FQ); Inflow discharge (BQ); Temperature (T); Fish body length (BL); Release location below the dam (Place); Diel rhythm (DR).

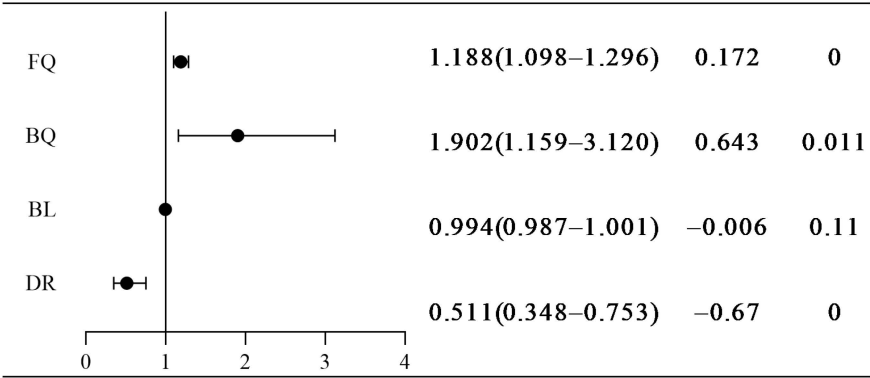


Figure 10. Forest map of downstream effect of river.

We constructed a nomogram to predict the success probability of upstream and downstream migration of fish within the river based on the AIC criterion and Cox proportional hazards regression model (Figure 11). The nomogram predicts the probability of success based on the impact of each factor in the form of a scoring system. The first column (Points) represents the score assigned to each environmental factor. After summing the scores of all aspects, the corresponding total score (Total Points) is identified. Finally, the success probability is calculated by estimating the probability based on the total score.

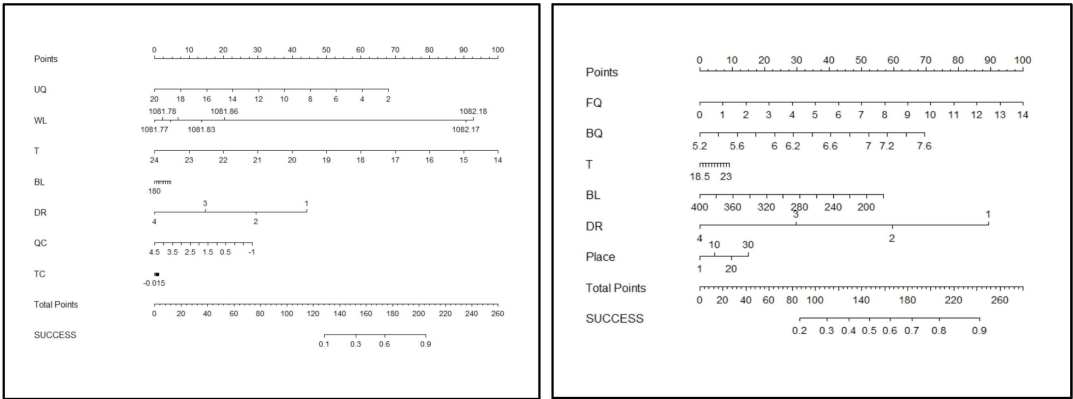


Figure 11. Column line graph for predicting fish upstream success probability. (Left) Fishway entrance attraction success rate. (Right) Fishway upstream passage success rate.

To evaluate the model’s predictive accuracy, we used downstream migration as an example. Under this scenario, the total score of influencing variables reached 200, corresponding to a predicted success probability of 80%. The observed average downstream success rate was 81.1%, closely aligning with the model prediction. This consistency supports the model’s effectiveness in estimating migration success probabilities.

4. Discussion

4.1. Differences in Upstream and Downstream Migration Behavior and Ecological Behavioral Explanations

Fish exhibit marked differences in their upstream and downstream migratory behaviors following dam passage, reflecting more than just a response to the flow direction. These variations are shaped by a combination of ecological, physiological, and behavioral mechanisms, including navigation strategies, sensory integration, energy management, and risk avoidance [16].

Upstream migrants, in particular, face the challenge of swimming against the current while locating suitable spawning or feeding habitats. The process requires active decision-making and behavioral flexibility. In our observations, fish frequently paused, changed direction, or explored alternate routes shortly after exiting the fishway. Such behaviors likely stem from disorientation in altered flow environments and the absence of continuous environmental cues [17]. Migratory fish use a suite of sensory information ranging from current gradients and minor temperature shifts to geomorphic features and chemical signals [18]. When these cues are disrupted, individuals may hesitate, backtrack, or engage in repetitive searching.

Diel rhythm further modulates migratory performance. Fish in this study moved more efficiently at night, a pattern consistent with prior findings across multiple species [19,20]. Reduced light and predation risk and calmer hydraulic conditions may promote safer and less energetically costly passage. Hormonal factors such as melatonin, which increases in concentration after dark, are thought to influence migration drive and spatial orientation [21]. From an adaptive standpoint, nighttime migration could represent an evolved strategy that balances movement efficiency with survival during high-energy reproductive phases [22].

Energetically, upstream migration demands sustained activity and navigation, requiring fish to regulate their effort while maintaining directionality [23]. The intermittent movement patterns we recorded showed brief pauses followed by resumed progress, which are consistent with a “burst-and-rest” strategy. This behavior, common in long-distance migrants like salmon and sturgeon, allows individuals to exploit low-flow refugia to recover energy reserves before continuing [24].

Downstream migration, in contrast, is often flow-assisted and less reliant on active navigation. Fish recorded during downstream passage showed higher consistency in path choice and significantly shorter transit durations, suggesting a more passive and energetically efficient mode of movement [12]. At certain times, particularly during shifts in temperature or discharge, fish also exhibited group-synchronized movement, a pattern observed in other systems [25]. These events have direct implications for fish protection strategies during dam discharge regulation.

Significantly, the ecological functions of upstream and downstream migration differ. While upstream journeys are typically reproductive in nature, downstream movements are more often related to feeding, growth, or seasonal relocation. These distinct goals shape the timing and duration of migration and the behavioral risk thresholds and energy budgets involved [24]. Understanding these differences is essential for designing restoration efforts that account for the full migratory cycle.

Overall, upstream migration presents greater behavioral complexity and physiological demands. It is characterized by frequent decision points, higher environmental uncertainty, and greater energy costs. These attributes make the upstream phase particularly sensitive to fragmentation and habitat disruption, reinforcing the need for targeted restoration efforts and improved fishway functionality.

4.2. Mechanisms of Non-Biotic Environmental Factors Influencing Migration Efficiency

Abiotic environmental conditions play a foundational role in shaping the migratory performance of fish. Rather than acting in isolation, these factors affect fish indirectly by altering their physiological readiness, sensory processing, and behavioral strategies in response to riverine conditions [26,27]. In our study, three variables—water temperature, discharge, and diel rhythm—emerged as dominant influences on upstream and downstream migration after dam passage, showing distinct response patterns and threshold effects.

Among these, temperature proved to be especially critical. It governs various biological functions, including metabolic rate, muscular efficiency, endocrine responses, and sensory acuity [28]. Our findings suggest that fish movement peaked in efficiency when water temperatures ranged between 18 and 21 °C—likely close to the species' thermal optimum [15]. When temperatures deviated beyond this window, either higher or lower, migration became less frequent and more erratic, probably reflecting metabolic suppression, impaired orientation, or increased stress [29,30].

Upstream migrants performed better under both low ($<6 \text{ m}^3/\text{s}$) and high ($>12 \text{ m}^3/\text{s}$) discharges, while success rates dropped significantly in moderate flow conditions ($6\text{--}12 \text{ m}^3/\text{s}$). This pattern may be attributed to the turbulence regime: intermediate flows can generate disorganized hydraulic conditions that reduce directional cues and increase navigational uncertainty, especially in morphologically complex river sections [12,31]. In addition to hydraulic disorientation, moderate flows may trigger sublethal physiological stress or elevate perceived predation risk, which can further discourage active upstream movement. For downstream migrants, high flow appeared to enhance passage by functioning as a transport mechanism, allowing passive movement with reduced energy demands [12,27]. Even so, excessively strong currents, particularly near confluences or sharp bends, can misdirect fish or pose mechanical risks.

Diel rhythms also played a crucial role. Our monitoring revealed that fish were more likely to pass successfully during nighttime hours, a result consistent with many studies showing that fish adjust their migration timing to minimize predation risk and exploit periods of lower environmental disturbance [20,32]. Lower light levels reduce visual threats and may coincide with slight cooling and hydrodynamic stability, enhancing cue detection and orientation. Neuroendocrine factors such as melatonin secretion may also be involved in this behavioral modulation [21].

In addition to static conditions, we also observed that variability, especially sudden fluctuations in temperature and discharge, adversely affected migration. Under unstable conditions, fish were more likely to pause, turn back, or fail to locate passage routes. Higher passage rates were observed when flow and temperature remained steady, reinforcing the importance of environmental predictability for sensory-based navigation [33].

These findings suggest that a complex interaction of thermal physiology, hydrological structure, and behavioral timing shapes fish migration. For river managers, this underscores the need to account for average environmental conditions and their variability and timing. Creating targeted “ecological windows” defined by temperature, flow, and diel cycles may help to improve passage efficiency, especially in post-dam environments where conditions are often highly altered.

4.3. New Findings and Differences

In the international literature, research on fish migration has predominantly centered on evaluating the effectiveness of fish passage structures—especially about attraction flow designs and hydraulic performance for iconic migratory species such as salmonids and eels [27,31,33]. Much of this work is rooted in North American and European river systems, where standardized fishway types and long-term monitoring platforms have allowed for detailed assessments. The prevailing question in these studies tends to be: “Can fish get through?”

In contrast, the present study pivots the focus to what happens after fish pass through engineered structures. We explore how fish behave as they continue their migration into natural river sections, particularly in upstream and downstream reaches of dammed systems, and how they respond to a dynamic set of environmental cues. This behavioral continuation phase remains under-explored in current research, especially in high-altitude,

mountainous tributary systems like the Heishui River, where field-based tracking data are sparse.

In many established systems, studies on passage performance often revolve around metrics like passage probability, velocity, and delay within artificial structures such as vertical slot or spiral fishways designed for Pacific salmon (*Oncorhynchus* spp.) or European eel (*Anguilla anguilla*) [33,34]. However, relatively little attention is paid to whether these individuals successfully reconnect with upstream habitats after passage, and even fewer studies extend to their behavioral integration into natural ecosystems post-passage [35].

Our work differs in both geographical scope and ecological focus. It centers on *Schizothorax wangchiachii*, a native fish species in a plateau tributary in southwestern China. We documented migration patterns across dam boundaries and into surrounding river sections using RFID tracking. Unlike typical salmonids, *Schizothorax* displayed unique behavioral adaptations when navigating under the joint influence of temperature thresholds, hydraulic complexity, and diel rhythms, offering new perspectives for understanding migratory decision-making in non-model species and understudied ecological contexts.

Interestingly, while previous studies have shown that high flow conditions generally facilitate upstream movement in species like brook trout [12], our findings revealed that *Schizothorax* had the lowest passage success under moderate flow. This discrepancy underscores the need to move beyond hydrodynamic explanations alone and consider species-specific cognition and habitat preference in interpreting migration behavior [36].

The same applies to diel rhythm. While American shad (*Alosa sapidissima*) is known to migrate more actively during daylight [15], our data show that *Schizothorax* increased migration activity significantly at night. This divergence reflects distinct adaptations to light cycles and highlights that species may follow fundamentally different behavioral rules in response to the same environmental driver [21].

Our findings expand the international body of work by introducing new species, ecological conditions, and research dimensions. In particular, we offer a behavioral lens on post-passage ecological connectivity, providing practical insights for designing species-appropriate restoration strategies in mountainous river systems where conventional fish-way approaches may fall short.

4.4. Relationship Between Fish Passage Facility Attraction Effect and Tributary Habitat

While fish passage facilities have seen substantial improvements in recent years with advances in flow field optimization, structural accessibility, and hydraulic performance, ensuring true “ecological connectivity” remains a broader challenge. Structural success does not necessarily translate to ecological effectiveness [27,37]. Our field observations revealed that even after successfully passing through the fishway, some individuals displayed behaviors such as prolonged holding, exploratory circling, or even re-entry into downstream sections. These behaviors suggest that the fishway itself is only part of the solution: what lies upstream may be equally important.

From a behavioral ecological standpoint, fish migration involves not just passing through a barrier but also responding to the quality and configuration of habitats on either side [38]. If the upstream environment lacks functional habitat elements—such as cover, flow refuges, or suitable substrates—fish may abandon migration efforts altogether despite having navigated the structural obstacle. In our case, *Schizothorax wangchiachii* often paused or reversed course shortly after passing the dam, likely reflecting their perception of habitat discontinuity or suboptimal conditions in the upstream reach.

This problem is compounded in river systems that have undergone significant morphological alteration. Sudden changes in depth, bank structure modifications, and sediment homogenization can diminish microhabitat heterogeneity and reduce the availability of

behavioral cues that typically guide fish toward suitable habitats [35]. This challenge is particularly evident in regulated rivers with deep reservoirs and steep longitudinal gradients, where upstream reaches often lack the spawning and feeding features required by migratory species.

International studies increasingly highlight that the long-term success of passage systems is tied to habitat continuity and post-passage conditions. Migratory species such as salmonids, sturgeon, and cyprinids rely on specific environmental cues including flow velocity, substrate type, and water temperature for reproductive site selection [39]. Passage alone does not ensure successful recruitment unless these upstream habitats are accessible, functional, and attractive.

Current tributary habitat interventions, particularly in semi-urbanized river systems, often focus on aesthetic or structural improvements such as riparian planting or channel re-contouring without adequately considering species-specific behavioral needs. Our findings argue for a shift in design logic: fishways should not be treated as isolated “passage devices” but as functional connectors within a broader ecological system. This implies integrating fishway exits with ecologically informed habitat patch areas offering shelter, rest, directional cues, and spawning functionality.

In practice, this could include configuring low-velocity zones, shallow riffle-glide transitions, gravel beds, or vegetated margins near fishway exits to encourage continued upstream movement. During this behavioral transition zone, directional flow signals should also be preserved to maintain fish orientation. Ultimately, meaningful restoration of full-process connectivity in regulated river systems can only be achieved when ecologically functional habitats complement physical passage. This aligns with broader evidence suggesting that effective fish passage depends on structural connectivity and habitat quality beyond the barrier [39].

5. Conclusions

Based on RFID tagging and environmental monitoring data, this study systematically evaluated the post-passage migratory behavior and efficiency of *Schizothorax wangchiachii* in the upstream and downstream sections of the Songxin Hydropower Station on the Heishui River. The results show that downstream migration success was significantly higher than upstream, with much shorter travel times. Migration patterns demonstrated clear diel rhythms: upstream migration mainly occurred at night, while downstream movements were concentrated during daylight hours. Cox proportional hazards modeling identified water temperature (optimal at 18–21 °C), discharge, water level, and diel timing as key abiotic factors influencing migration efficiency. Upstream migration was favored under nocturnal, low-fluctuation, and moderate water level conditions, whereas downstream migration was more efficient under higher flow and stable cooling conditions. The study also observed potential pausing and reversal behaviors during upstream movement, suggesting fish may encounter challenges due to complex hydraulics or insufficient habitat connectivity. In conclusion, while fishways can provide structural connectivity, achieving full ecological connectivity requires coordinated habitat restoration and ecological flow management to support sustained fish migration.

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Institutional Review Board Statement: This study adheres to the guidelines of the China Three Gorges University for the use of wild animals. Animals were fostered following the Guide to the Care and Use of Experimental Animals. No fish casualty occurred in this study. All procedures were approved by the animal protection committee of China Three Gorges University.

Data Availability Statement: Some or all data, models, or code that support the findings of this study are available from the corresponding author upon reasonable request. Informed consent was obtained from all subjects involved in the study.

Conflicts of Interest: All authors declare that the research was conducted in the absence of any commercial or financial relationships.

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