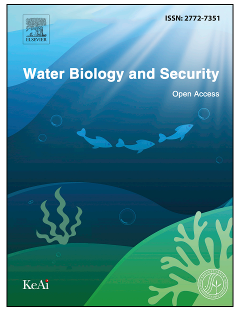

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Passage efficiency and behavioral performance of *Schizothorax davidi* through different sections of a long vertical slot fishway

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Abstract

Fish passage facilities are constructed worldwide to enable fish to pass anthropogenic obstacles (i.e., dams) and re-establish river connectivity. The construction of these facilities involves sophisticated engineering designed to attract fish and enable passage. The behavior of fish encountering these structures, particularly in long vertical slot fishways, has been poorly studied. This study was conducted on the Daduhe River in Southwest China to quantify the upstream passage efficiency and performance of tagged *Schizothorax davidi* in different sections of a long vertical slot fishway spanning 1228.3 m. The overall passage efficiency was 13% although the passage efficiency in seven sections (A0-A1, A1-A2, A2-A3, A3-A4, A4-A5, A5-A6, A6-A7) ranged from 43% to 100% reflecting differences in slope among sections. The highest passage efficiency was documented in rest pool sections with a slope of 0 (A3-A4, 100% and A6-A7, 100%) and during passage through the dam itself (A5-A6, 90.0%). The lowest passage efficiency was section A2-A3, where a garbage interception facility affected passage efficiency. Average transit time from A0 to A7 was 85.2 hours and ranged from 8.8 to 237.6 hours. Transit speed varied over various sections. The first section (i.e., A0-A1) had slow transit speeds which presumably was influenced by acclimation and recovery from tag implantation. After this, the transit speed had a slight increase but decreased again. Additionally, more than half (5 out of 9 fish) of the fish fell back after reaching the most upstream section and reascended the fishway which tripled the total passage time for those individuals. No significant diel activity rhythms were observed, but a strong bimodal distribution was noted in fish transit time when passing the first monitoring site. Cox-proportional hazards model showed that transit time was negatively correlated with body size but positively correlated with water level and water temperature. Our study provides valuable insights into activity when passing through a long fishway, which can inform design of fishway structures and operational patterns to improve upstream passage efficiency. Specifically, we

recommend increasing the number of resting pools and maintaining appropriate water levels to reduce transit time and fallback frequency in long fishways.

Keywords Behavior, Cox's proportional hazards regression, Migratory fish, Passage structures, Passive Integrated Transponder

1. Introduction

Dams are widely used for power generation, irrigation, and flood control (Wang et al., 2017). More than 45,000 dams above 15 m high have been constructed worldwide, and thousands more are currently planned or under construction (Zarfl et al., 2014). The proliferation of these structures has interrupted river connectivity and caused habitat fragmentation (Park et al., 2008; Hall et al., 2011). Globally, 63% of rivers longer than 1000 kilometers are no longer free-flowing (Grill et al., 2014). Furthermore, these impediments on rivers have blocked the routes that migratory fish may use to reach spawning, feeding or overwintering habitats to complete their life cycles (Baras and Lucas, 2001; Zhuang et al., 2016). As a result, dams have had adverse consequences on fish communities including reduction of fish abundance, genetic isolation, and loss of diversity (Letcher et al., 2007; Lundqvist et al., 2008; Hall et al., 2011; Nislow et al., 2011). As a consequence of increased dam construction, dam-induced river connectivity issues have received increasing attention in recent decades.

Measures to re-establish habitat connectivity include dam removal and fishway installation (Thieme et al. in press). Although dam removal has become increasingly common in many countries (Mckay et al., 2013), the more common method is the implementation of human-made fish passage structures such as nature-like bypasses, pool and weir passes, and many other types of fishways (Clay, 1995). Vertical Slot Fishways (VSFs) are the most favored fishway design in China, because VSF provide passage at an extensive range of water depths and provide fishes with gliding places (Cao et al., 2013). Moreover, this type of fishway is effective in small streams as well as large rivers and, given its design, can be placed in narrow valleys (FAO, 2002; Zhang et al., 2014). The number of VSFs construction has increased rapidly in recent decades, but effective passage studies are infrequently undertaken (Tummers et al., 2016; Silva et al., 2018). VSFs rely on the ability of fish to find, enter, and pass through a structure, though conditions enabling these movements are not always provided. Fishway use varies greatly depending on structural (i.e., length, pools and so on), environmental (i.e., water velocity, water flow and so on) and biological factors (species, body size and so on) (Roscoe and Hinch, 2010). Parts of VSFs often perform poorly, particularly for fish with poor swimming abilities (Bunt et al., 2012; Noonan et al., 2012). Hence, the assessment of fishway efficiency is crucial to determine if they are functioning effectively and to identify areas for improvement.

The approach and evaluation criteria used in assessing fishways have been inconsistent (Hershey, 2021). Over the last few decades, most evaluations have focused on the overall efficiency which includes both attraction and passage efficiency (Noonan et al., 2012). Recently, there has been growing awareness that passage performance should be assessed not only for overall fishway efficiency but also for different sections within a fishway (Ovidio et al., 2017). Studies on passage efficiency can help understand whether fish are failing to pass a given fishway, while quantifying passage behavior helps interpret the mechanisms behind passage failure and the fitness of fish (Ovidio et al., 2017). For example, there are some indications that transit times reflect delay, which is related to maturation and spawning (Castro-Santos and Haro, 2003). Measuring migration speeds and time during passage will help researchers understand how fish use energy in the fishway and how long they stay in resting pools for alleviating exhaustion (Castro-Santos et al., 2017). Fishway efficiency and fallback can help us to identify which sections of a fishway are resulting in low fish passage efficiency or high fallback, and where remediation efforts should be provided to improve fishway efficiency (Matthew et al., 2014). Furthermore, behavioral studies within fish passage (e.g. transit time) can help predict post-passage survival and the ability of fish to accomplish various life-history events (i.e., spawning) (Nyqvist et al., 2017). Passive Integrated Transponder (PIT) technology is widely used to assess fishway efficiency (Noonan et al., 2012; Ovidio et al., 2017; Hershey, 2021) and can provide detailed metrics on fish behavior during passage (Matthew et al., 2014), such as transition time, transition speeds, and transition routes, to evaluate fishway performance.

In China, fish passage has been required by a federal law since 2002 to support fish migration and, as a result, many new VSFs have been built or are planned (Shi et al., 2015). VSFs are currently the most popular type of fishway in China, accounting for 68% of fishways (Cao et al., 2016). In general, VSFs in China tend to be long, often exceeding 1km in length (i.e., Zhentouba fishway, Duobu fishway, Zangmu fishway, Shaping fishway) (Bao et al., 2019; Xia et al., 2022; Xue et al., 2022; Yao et al., 2023). Given their length, VSFs often have sophisticated structural characteristics such that conditions experienced by fish vary depending on where they are in the fishway. Despite VSFs being common, there is limited data available to understand the effectiveness of long VSFs, especially with respect to the mechanisms of passage failure. The Daduhe River in Southwest China exhibits high levels of fragmentation due to the construction of anthropogenic barriers since 1980. This river has the greatest level of fragmentation among all the 13 hydroelectricity bases, with 15 existing and 14 additional dams planned, and three fish passage facilities with 10 more being planned. The ZTB fishway is the first VSF on the Daduhe River in Southwest China, which was designed for six economically-valuable (assessed by Sichuan province) and imperiled species (RLCV, Red List of China's Vertebrates, 2016) including *Schizothorax davidi* (*S. davidi*), *Schizothorax pregnanti* (*S.pregnanti*), *Euchiloglanis davidi* (*E. davidi*), *Onychostoma sima* (*O. sima*), *Gobiobotia nudicorpa* (*G. nudicorpa*) and *Beaufortia szechuanensis* (*B. szechuanensis*) (Bao et al., 2019).

Schizthorax davidi is an economically-valuable but imperiled species (RLCV, Red List of China's Vertebrates, 2016) that migrates upstream for spawning during August to September every year (Yang et al., 2010; Luan et al., 2016). Nevertheless, the population abundance of *S.davidi* has experienced a sharp decline in recent decades due to overfishing and dam-induced fragmentation (He et al., 2021; Zhang et al., 2024). While fishways are regarded as one of the most obvious ways to restore populations of the species, the long ZTB fishway has low passage efficiency (28.6%; Bao et al., 2019). Recognizing the need to better understand and improve passage success at the ZTB fishway, an extensive telemetry array was designed to suit the complicated structure of this long fishway and to assess (1) overall and section-level passage efficiency, (2) behavior of *S. davidi* in different sections, and (3) factors affecting transit time. This research will provide important information on section-specific passage which is necessary to determine if there is need for refinement of this fishway and to inform the design of other fishways.

2. Materials and Methods

2.1 Study site

The Daduhe River (Figure 1), located in Sichuan province, Southwest China, is the largest tributary of the Minjiang River, and a secondary tributary of the upper Yangtze River. The total length of the Daduhe River is about 1,062 km, with a basin area of 77,400 km^2. The ZTB fishway is 1228.3 m long, overall height of 30 m, and is located on the left bank of the river. There are 20 resting pools and the average gradient of sloped sections is 3%, (Figure 2A and 3). The fishway comprises three entrances, an attraction system (φ50 mm Polyvinyl chloride), two observation rooms (4 m × 5 m, width × length), 249 baffles, 248 pools (2 m × 2.5 m, width

× length), 20 resting pools with a slope of 0 (2 m × 5 m, width × length), and three exits (Figure 2A and 3). However, during our study only one entrance (Entrance 3) and one exit (Exit 3) were in operation. A constriction device in the observation chamber both ensured that fish swam near the window for video identification, and intercepted garbage flowing down the fishway (Figure 2C). The altitude at the bottom of the fishway exit is 620 m, the water depth of the fishway was designed to range from 1 m to 2.5 m.

2.2 Collecting and tagging fish, and deploying telemetry

The study was approved by the ethics committee of the Institute of Hydrobiology, Chinese Academy of Sciences, and was conducted on the ZTB fishway during the peak migratory season for *S. davidi* i.e., from August 25 to September 20 in 2018. All fish samples collected from the entrance (A0 in Figure 2) inside the ZTB fishway with a cage between August 25 to 30 in 2018. Large-sized individuals that tended to be sexually mature were selected and kept temporarily in a container with aerated water and others were released. During the collecting period, the container was continuously supplied with water from the Daduhe river when the mean water temperature was 9.47 ± 0.06 ℃, dissolved oxygen concentration was 8.33 ± 0.02 mg/L, and pH was 8.05 ± 0.05. The fish were fed once daily with commercial pellets (F28, Floating compound feed for freshwater fish; Sichuan CITICO Feed Co., Ltd, Chengdu, China) at approximately 5% of their body mass. After collecting the fish, they were anaesthetized with eugenol (0.02 g/L), weighed (BW, g), measured for total and standard length (TL, SL, cm), and tagged with PIT tags (Biomark 8.3 mm × 1.4 mm; 0.02 g in the air; 134.2 kHz; full duplex) on August 31, 2018. Methods followed the procedures outlined in Castro-Santos et al. (2003). After the surgery, all 70 tagged fish were transferred into a well-aerated tank with fresh river water until recovery, for an average of 24 hours (Griffioen et al., 2022) and then released at the point of capture within the ZTB fishway (A0) on September 1, 2018. Seven fixed locations, cross-channel, swim-through full-duplex PIT antennae (0.5 m × 2 m, width × height) were deployed along the fishway during the study (Figure 2B). The first antennae (A1) was located near the entrance and was approximately 5 m upstream of the fish release site. Other antennae (A2 to A7) were located approximately 385 m, 685 m, 705 m, 825 m, 845 m and 1225 m upstream of the fish release site respectively (Figure. 2A). A3 and A4 were placed at either end of the resting pool (slope 0) to quantify resting time; A5 and A6 were placed at either end of the culvert through the dam (slope 0) to detect the effect of the culvert on fish movement.

Before releasing fish, we tested the sensitivity of antennae with a tag to make sure that tagged fish could be recorded when passing through antennae, and then ran the logging equipment continuously from September 1 to 20, 2018. The system was decommissioned after there was a period of one week with no valid tag detections. When a tagged fish was detected, the date, time, detection period, and unique tag ID number were recorded and stored on an SD card in the data logger.

The PIT data from the antennae were downloaded (once a week) and standardized to ensure accurate calculation of transit time, transit speed, fallback frequency, rest time and fallback ratio (Table 1). Water temperature and water level in the fishway were logged using an automated temperature and water level logger (HOBO, Onset Computer Corporation, Bourne, MA, USA) with a 15 min interval throughout the study. During the study period (September 1 to 20, 2018), the mean water temperature was 18.6 ℃ (SD = 0.2 ℃) and ranged from 18.1 to 19.0 ℃. The mean water level within the fishway was 1.1 m (SD = 0.4 m) and varied (0.2 to 2.1m) frequently unlike many other systems where VSFs have been studied. The flow velocities within the fish passage varied from 0–2.0 m/s. Maximum velocity occurred on the slot ranged from 1.1–2.0 m/s (1.5 ± 0.2 m/s, mean ± SD); minimum velocity in the resting pools ranged from 0–0.2 m/s (0.1 ± 0.1 m/s, mean ± SD); velocities near the constriction device ranged from 1.2–1.6 m/s (1.3 ± 0.3 m/s, mean ± SD). Passage efficiency was calculated as the percentage of fish that were detected in A1, A2, A3, A4, A5, A6 and A7, respectively, among 70 fish released in A0. Among them, A0 to A7 represents the overall passage efficiency, while others represent the partial passage efficiency (Table 1).

2.3 Statistical analyses

Kaplan–Meier survival curves (Cox and Oakes, 1984) were plotted using the first detection time of observed individuals at antennae and the end time of censored individuals to estimate transit time between two antennae. Data were examined for normality and homogeneity of variance prior to determining suitability of parametric or non-parametric statistical approaches. Kruskal-Wallis tests were used to compare the fish condition and transit speed between sections of the fishway. Mann-Whitney tests were used to test whether the passage counts were different between day (8:00 am–8:00 pm) and night (8:00 pm–8:00 am) based on the PIT tag data. Relationships between biological (body length and fish condition), environmental (water levels and temperature) variables and transit time (Table 1) were estimated using Cox's proportional hazards regression with time-varying covariates (Castro-Santos et al., 2013; Allison, 2010). The analyses were carried out using the "coxme" package version 2.2-16 in R (R Core Team, 2020; Therneau, 2020), by including fixed effects and nested random effects. The independent explanatory variables of water level, water temperature, body length, and fish condition factor (Fulton's KFL = $10^5 \times$ weight/length^3) were predicted to have an effect on transit time, representing fixed effects in the model (Goerig and Castro-Santos, 2016). Body length and fish condition factor were not used together in a model due to their correlation (r = –0.7, $p < 0.01$). Fish tag ID was included as a random effect in the model to estimate the variance among individual fish in the baseline hazard function (Goerig and Castro-Santos, 2016). Hazard ratios (HRs) were obtained by exponentiating the coefficients estimated for each covariate. We used the Akaike information criterion (AIC) to select the best model(s), using ΔAIC < 2 as a good model.

All data analyses and graphics were performed using R version 4.0.2 (ggplot2 package version 3.3.2) (Goerig and Castro-Santos, 2016; Wickham, 2016) and ArcGIS 10.5 (ESRI, 2011). The significance level was set at $p < 0.05$.

3. Results

3.1 Passage efficiency

A total of 70 individuals (body length: 334 ± 36 mm; range from 242 to 438 mm) were PIT-tagged in the experiment, 68 of which were detected at the first antennae A1, representing a tag return rate of 97% (Table 2). The remaining two fish may have fallen back from the entrance of the fishway and were never recorded during the 20-day monitoring period. The passage efficiencies varied among different sections of the fishway (Table 2); A0-A1 (97%, n = 68), A1-A2 (43%, n = 29), A2-A3 (48%, n = 14), A3-A4 (100%, n = 14), A4-A5 (71%, n = 10), A5-A6 (90%, n = 9), and A6-A7 (100%, n = 9). Overall passage success was 12.9% (9/70). When the slope between two adjacent monitored sites was 0, the passage performance was uniformly high (e.g., A3 = A4, A6 = A7, A5 close to A6). Fish condition factor was not associated with patterns of section-specific passage (Kruskal-Wallis test, all $p > 0.05$), but average values of condition factor tended to increase for fish as that successfully ascended the fishway suggesting that fish with lower condition factor were those that were failing.

3.2 Behavioral metrics and variations

Transit time and speed from A0 to A7 varied substantially within and among individuals (Table 2). *Schizothorax davidi* moved through the fishway with an average time 85.2 h (from 9.0 to 237.6 h). The average transit time from A0-A1 was 20.4 h and two passage patterns were observed in this section: 75% of the detected individuals passed relatively quickly within 2 h but the remainder required over 30 h to pass (Figure 4). In addition, the transit speed at the first antennae was relatively slow (mean: 9.3 m/h; range: 0.02–166.7 m/h) (Table 2). The transit speed in the following sections was slightly higher than the former section. The highest speeds occurred in the sections where slope is 0, such as A3-A4 (mean: 225.7 m/h; range: 1.5–1000.0 m/h) and A6-A7 (mean: 339.3 m/h; range: 8.9–900.0 m/h), except for the section of A5-A6 (mean: 16.8 m/h; range: 0.3–76.9 m/h). The transit speed at A5-A6 was significantly different from A3-A4 and A6-A7, respectively (Kruskal-Wallis test, both $p < 0.05$), while there was no significant difference between the others (Kruskal-Wallis test, all $p > 0.05$). The migration routes of nine fish that successfully arrived at A7 revealed that they more frequently fell back at A1 and A7 and took much more time passing those stations compared to the other PIT stations. Moreover, some fish showed the phenomenon of repeated round trips, such as IDs 4463 and 4659, whose routes were A1-A7-A1 (Figure 5). No evidence for diel activity patterns was identified based on patterns of detection (Mann-Whitney test, $p > 0.05$).

3.3 Effect factors on behavioral performance

The best model for assessing transit time included water temperature, water level, and body length as explanatory variables. (ΔAIC from closest competing model = 2.0, Table 3). The body length of fish had a significant relationship with transit time: longer fish had a shorter transit time such that each additional mm decreased the transit time by 2% (HR = 1; $p < 0.05$, Table 4). Water level was positively correlated with transit time, such that an increase of 1.0 m led to a 10% increase in the hazard of transit time (HR = 1.1; $p < 0.05$, Table 4). Aside from the fixed effects in the model, some unexplained variability remained, and 40% of the variability in transit times was from variability between fish (Table 4).

4. Discussion

To alleviate river fragmentation caused by hydropower dams, upstream passage facilities have been designed and implemented with the assumption that it would be possible to achieve passage efficiencies that exceed 90% (Lucas and Baras, 2001; Ferguson et al., 2002). Yet, a review by Bunt et al. (2012) found that the average VSF passage efficiency was 45% (range =

0–100%, median = 43%) for 26 species of anadromous and potamodromous fishes in six countries including Canada, Denmark, Russia, Scotland, Sweden and the United States of America. The passage efficiency estimated in our study was 12.9% for *S. davidi,* which by all accounts is low compared to another study on the same species (28.6%; Bao et al., 2019). However, inconsistency in fish passage assessment methods is universal based on the review by Hershey (2021), which influences efficiency estimates. Therefore, when conducting fishway evaluation studies, researchers have been encouraged to embrace tagging techniques and other approaches that make their results more comparable.

Passage efficiency can differ across fishway structure, fish species, and hydraulic conditions, e.g., species, fishway length, and water level (Noonan et al., 2022). The swimming ability of fish is a critical factor in determining passage efficiency for some species. *Schizothorax davidi* is regarded as having low critical swimming speed (0.8 m/s) and burst speed (1.2 m/s) (Hou et al., 2018). Presumably those swimming abilities contribute to the low passage efficiency observed here relative to other species. All else being equal, if fishway length or slope tend to be negatively correlated with passage efficiency, a longer or steeper fishway would increase the energy expenditure of the migrating fish and thus potentially decrease passage efficiency (Hershey, 2021). The fishway in our study is 1228.3 m, which is longer than most others that have been studied, so it is not unsurprising that such a long fishway may have somewhat low efficiency. Water levels and their fluctuation frequency within fishways can have a significant effect on passage efficiency (Bravo-Córdoba et al., 2021). In our study, the water level in this system varied from 0.2 to 2.1 m and fluctuated hourly which was inconsistent with the target operational conditions (i.e., 1 to 2.5 m). We expect that if water levels were higher and less variable (i.e., within the design range), passage efficiency would be higher.

Although the literature is being populated with a growing number of fishway passage efficiency estimates, relatively few studies assess passage within different sections of a fishway to determine if and where there are areas that are particularly challenging. The ZTB VSF fishway passage efficiency had a sharp decline in the second section (A1-A2, 42.64%), which indicated that this section is a key bottleneck and should be targeted for improvement. Notably, this section has a constriction device used to collect garbage which presumably changed the hydraulic conditions or otherwise deterred fish from passing. Additionally, the passage efficiency was low in the 3rd section (A2-A3, 48.27%) which we believe is due to the use of non-standard baffles and the lack of bottom substrate (which had been displaced after construction), resulting in a high turbulence. These bottlenecks may also block *S. prenanti* (which has a similar swimming ability to *S. davidi*) and some other weaker swimming species or smaller individuals. Unfortunately, no swimming performance data exist for the other four species of interest in this system (i.e., *E. davidi, O. sima, G. nudicorpa and B. szechuanensis*). Restoring the substrate within the sections where it has been eroded/lost would be desirable. Although the sixth section is located across the dam and rather devoid of light, the passage efficiency (A5-A6, 90%) was not affected by the lack of light, and it was as high as that for the resting pool.

Fish that spend significant time in the fishway may experience a loss of motivation and a deterioration of physiological condition (e.g., energy loss, stress) before arriving to spawning grounds, or a reduction of the probability of finding optimal environmental conditions (Nyqvist et al., 2017). Given that the ultimate goal of evaluating passage efficiency is to improve it and promote the spawning success of passing fish, it will be increasingly important to ascertain detailed information on movement behaviors during passage. This will help researchers identify the factors limiting passage and predict post-passage survival and spawning success. Given this perspective, our results highlight the need for more research on movement behaviors and to develop an integrated method to assess passage efficiency, especially for quantifying transition time and identifying when and where fallback occurs. The total transit time from A0-A7 (average: 85.2 h; ranged: 9.0–237.6 h) was longer than a previous study (average: 29.7 h; ranged: 6.4–88.8 h) for this species at this facility (Bao et al., 2019). A few individuals required a longer time (>50 hours) to move through the fishway, though most fishes passed through within 20 h. This phenomenon of two patterns of passage has been found in other studies, suggesting the fishway was also being used for purposes other than passage (e.g., Kim et al., 2016; Yoon et al., 2015).

Environmental variables such as water level and water temperature are important factors influencing individual transit time (Harbicht et al., 2020). In this study, these variables were positively correlated with transit time. This can be explained by the optimum range of temperatures for this species (Souchon et al., 2012). *Schizothorax davidi* is a cold-water fish species that prefers lotic and cold habitat for spawning (16–18 ℃) (Yuan et al., 2013), and thus, water temperatures beyond this range may reduce activity (Bravo-Córdoba et al., 2014). Water level in the fishway is a proxy for discharge. Appropriate discharge triggers fish migration and has the potential to attract more fish to the fishway (Weaver, 1963). However, if the velocities exceed the swimming capabilities of fish, they may be unable to continue upstream migration, or may fallback multiple times, increasing the risk of injury, fatigue, and failure (Figure 5) (Reischel et al., 2003; Nyqvist et al., 2017; Kemp et al., 2011). It is important to note that the water levels during our study fluctuated greatly (0.2 to 2.1 m) and frequently (hourly) unlike many other systems where VSFs have been constructed. When the water level was between 0.5 and 2.0 m, more signals and individual fish were detected, especially between 1.0 and 1.5 m (Figure 6). However, the ratio value (detections/fish number: the number of signals detected divided by the number of tagged fish detected) was highest when the water level was between 2.0 and 2.5 m, indicating that the frequency of fallbacks occurring at this time was relatively high (Figure 6), which may increase transit time (Kemp et al., 2011; Castro-Santos et al., 2017).

Fish body length was negatively correlated with transit time. Some possible interpretations are that that larger individuals had a stronger swimming ability or they tended to have greater migratory motivation (Goerig and Castro-Santos, 2016).

How various sections influence individual variation in movement behavior in fishways is poorly understood. In our study, the results revealed that transit speed varied in different sections of the fishway. However, transit speed did not gradually decrease with distance as we expected. Variable water levels, fish acclimation, slope, or exhaustion may have influenced our findings. For instance, transit speed was markedly lower in the first segment (A0-A1), having a gradual increase from A1 to A4, decreasing from A4-A6, and increasing again in the final segment (A6-A7) which may reflect the time for acclimation at A0-A1, resulting in a slower speed. Having an increase in A1-A2 after acclimation, the transit speed decreased at A2-A3 presumably due to physiological exertion. The section A3-A4 is the resting pool (slope = 0) where fish can recover (if needed). The transit speed was higher at that section, and then decreased again at A4-A5. We observed that the transit speed was lowest for A5-A6, although the slope is 0. The possible reason is that this section passes through the dam with almost no light and slow water flow, forming a suitable environment for fish to hold. Transit speed increased at A6-A7 which is a section with a slope of 0 that enables the fish to pass with relative ease.

In addition, successful migrating fish at the first (A1) and last antennae (A7) were detected more frequently than at other monitoring stations (Figure 5). This may be due to acclimation at A1 and water velocity at A7 resulting in a high proportion of fish stranding/holding near the exit (Castro-Santos et al., 2013; Goerig and Castro-Santos, 2016; Bao et al., 2019). However, we did not find diel activity patterns in fishway use in this study, while previous fishway studies have indicated that some species use fishways with noticeable peaks in the afternoon, evening or night depending on their underlying ecology (i.e., walleye (*Sander vitreus*) is a crepuscular species, channel catfish is a nocturnal species; Atlantic salmon is a diurnal species, and so on) (Ali et al., 1997; Gowans et al., 1999; Thiem et al., 2013). Interestingly, we previously found most fish tended to enter this fishway at night (Bao et al., 2019). This highlights that diel use of the fishway may vary among species. Moreover, migration behavior is essentially a circadian activity but once fish have entered the artificial and novel environment, migration may be independent of rhythm and become a continuous process.

5. Conclusion

Our results underline the importance of the assessment of various sections efficiency and quantification of behavior performance when conducting passage evaluations, especially at long-distance fishways. On the one hand, this can help to identify bottlenecks within the fishway, and where to modify fishway structure and adjust operational patterns to improve passage efficiency. On the other hand, this can help to promote the development of an integrated method to assess passage efficiency. The results indicated that the overall passage efficiency was low, there was a bimodal distribution in their transit time when passing the initial section (A0-A1), and a sharp decline in the second (A1-A2) and third (A2-A3) sections. We suggest modifications should be conducted in these two sections. The garbage should be cleaned in a timely manner, and the removal of the constriction device should also be considered. The baffles need calibration and sediment needs be removed. The transit time was longer in the ZTB fishway than most other VSF structures, with the length of passage and fallback as the critical drivers. Fallback was found to be caused by frequent and severe water level fluctuations, a prediction that could increase efficiency through reduced fallback and events and transit times in general. More efficient passage may result in reduced energy consumption and, consequently, fish arriving to spawning sites in a healthier state and timely manner for spawning.

Ethical statement

The study was approved by the ethics committee of the Institute of Hydrobiology, Chinese Academy of Sciences.

Declaration of competing interest

The authors declare no conflict of interest. Steven J. Cooke is an editorial board member for *Water Biology and Security* and was not involved in the editorial review or the decision to publish this article.

Authors' contributions

JHB wrote the main manuscript text and all authors edited the manuscript; XW, WWL, CSZ performed research and analyzed data; XYM, DXZ, WMT, HYL prepared the tables; YQ and MD prepared the figures. All authors read and approved the final manuscript.

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Availability of data and materials

Please contact authors for data requests.

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Table 1 Definitions of the behavioral metrics used in this study

Passage efficiency and behavioral metrics	**Definitions**
Ratio (detections/ID)	The number of detected signals divided by the number of detected tagged individuals
Passage efficiency, E_p	The percentage of fish that were detected in A1, A2, A3, A4, A5, A6 and A7 among 70 fish released in A0, respectively. Among them, A0 to A7 represents the overall passage efficiency, while others represent the partial passage efficiency
Transit time	Time between the release time in A0 and first detection time in A1, A2, A3, A4, A5, A6, and A7, respectively
Transit speed	Transit distance (A0-A1, A0-A2, A0-A3, A0-A4, A0-A5, A0-A6, A0-A7) divided by corresponding transit time, respectively, (expressed as fish speed/meter of fishway)
Rest time	Time spent in the resting pool
Fallback	Detection of a fish at a downstream antennae after detection at an upstream antennae due to water velocities exceeding swimming capacity
Fallback ratio	The number of fallback individuals divided by the number of tagged individuals
Fallback frequency	The frequency of fallback events

Table 2 Percentage of passing number, transit time and speed of the tagged fish when passing seven fishway sections on the Daduhe River in Southwest China

Monitoring sites (distance between sites. m)	**Slope (%)**	**K_{mean} (Fish Condition Factor)**		**N detected (released=70)**	**Percentage passage**	**Transit speed (m/h)**	
		Mean	**Range**			**Mean**	**Range**
A0-A1 (5)	3.3%	0.9	0.7-1.2	68	97%	9.3	0.02–166.7
A1-A2 (380)	3.3%	0.9	0.7-1.2	29	43%	58.0	4.1–264.0
A2-A3 (300)	3.3%	0.9	07-1.2	14	48%	26.1	6.7–55.7
A3-A4 (20)	0	0.9	0.7-1.2	14	100%	225.7	1.5–1000.0
A4-A5 (120)	3.3%	0.9	0.7-1.1	10	71%	77.7	10.5–146.3
A5-A6 (20)	0	1.0	0.8-1.1	9	90%	16.8	0.3–76.9
A6-A7 (380)	0	1.0	0.8-1.1	9	100%	339.3	8.9–900.0

Table 3 List of good models for transit time based on the Akaike information criterion (AIC), ∆ AIC is the difference between AIC of the model and AIC of the best model

Model	RE	AIC	∆ AIC	AIC Wt	Cum.Wt	LL
BL+WL+Temp	(1|ID)	74.03	1.99	0.13	0.86	-33.02
BL+WL	(1|ID)	74.63	2.60	0.09	0.95	-34.32
WL	(1|ID)	77.30	5.26	0.02	0.98	-36.65
FCF	(1|ID)	77.35	5.31	0.02	1.00	-36.67

Note: Random effect (RE); Body length (BL); Water level (WL); Temperature (Temp); Fish condition factor (FCF); ∆ AIC is the difference between AIC of $model_i$ and AIC of the best model; Akaike weight of $model_i$ (wi) is interpreted as the probability that model i is the best model given the data; Log-likelihood (LL).

Table 4 Effect of environmental variables on transit time and hazard ratios (HR) based on the best selected transit time model

Fixed effects	*B* (Coef.)	HR (exp(coef))	*p*-value
BL (cm)	-0.02	0.98	0.05
WL (m)	0.10	1.11	0.03
Temp (℃)	4.97	143.68	0.18
Random effect (fish ID)			
N (fish ID)			
Std. Dev.		0.64	
Variance		0.40	

Note: Body length (BL); Water level (WL); Temperature (Temp); Estimates (*B*) and hazard ratios (HR) of parameters for the best-fitting model. HR are computed for each parameter by exponentiating the estimates; Significance level (*p*).

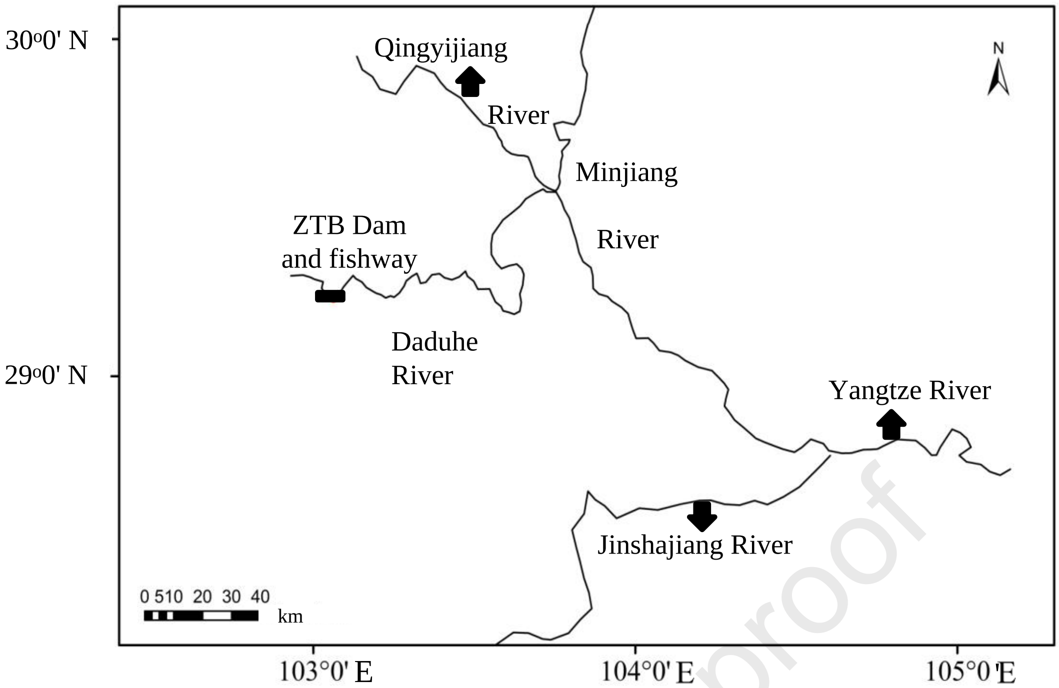


Figure 1. Study site location: the location of the studied fishway at the ZTB Dam, Daduhe River, Southern China.

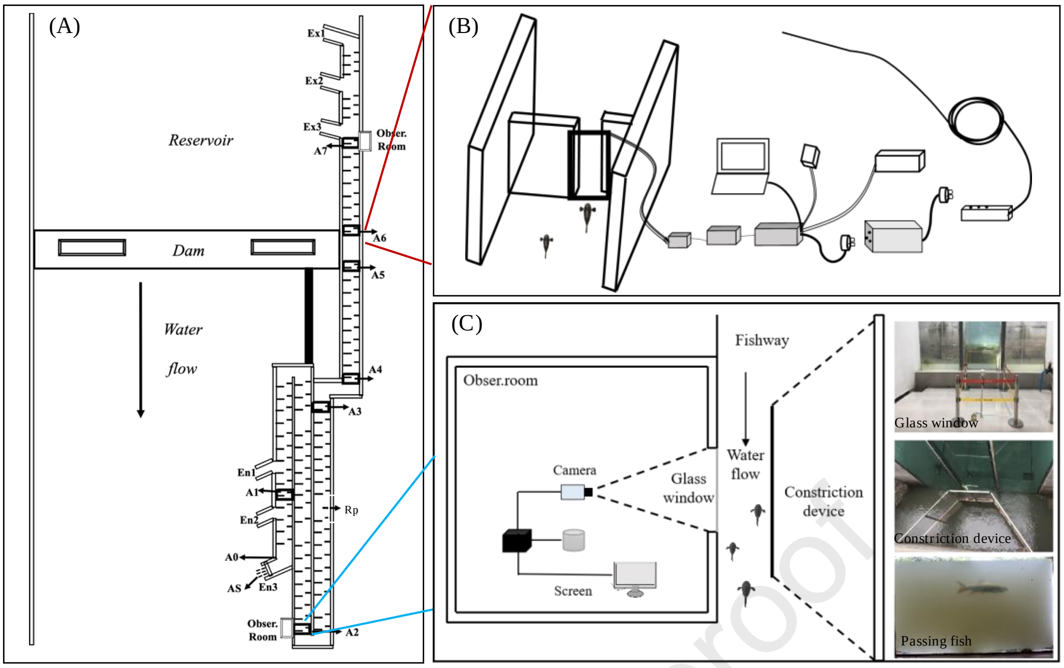


Figure 2. Main features of the fishway: (**A**) Plan view of the fishway, location of observation room. A1, A2, A3, A4, A5, A6, A7 indicate locations of PIT antennae; Rp (Resting pool); (**B**) PIT system; (**C**) Structure of vertical slot and PIT antennae. Ⅰ: antennae; Ⅱ: tagged fish.

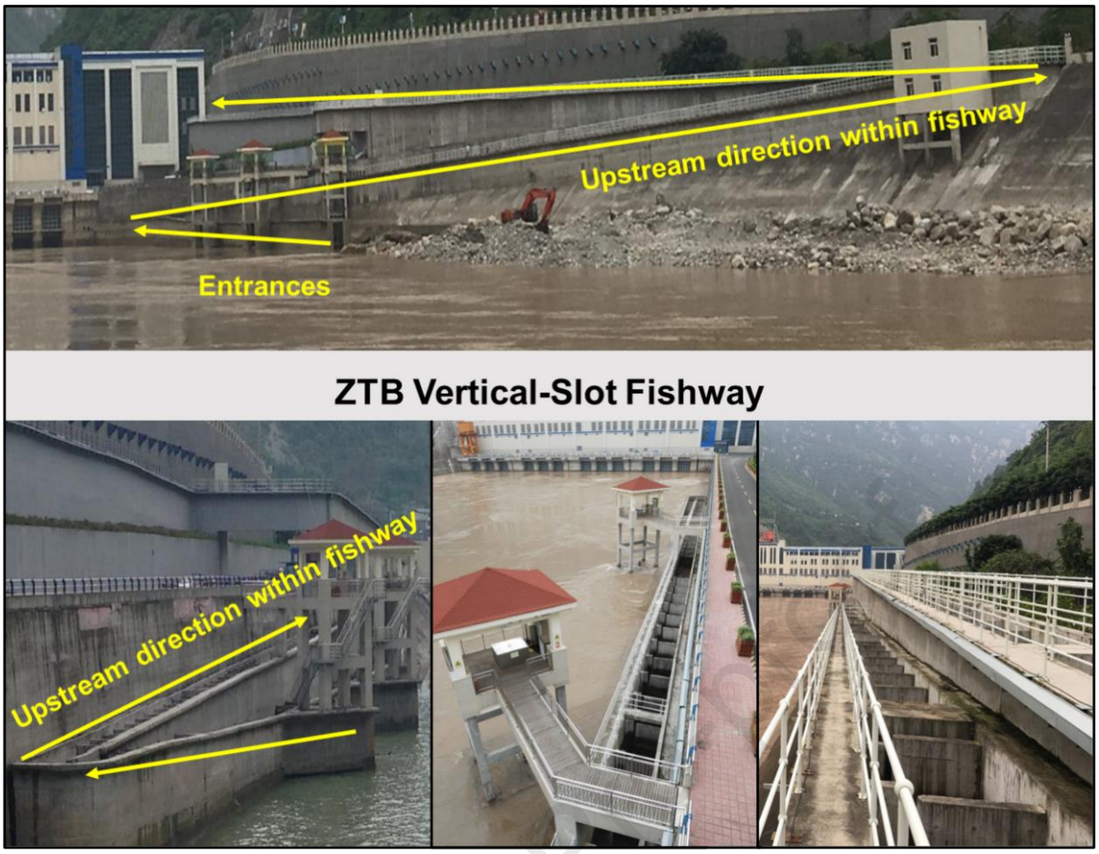


Figure 3. Photographs of ZTB fishway.

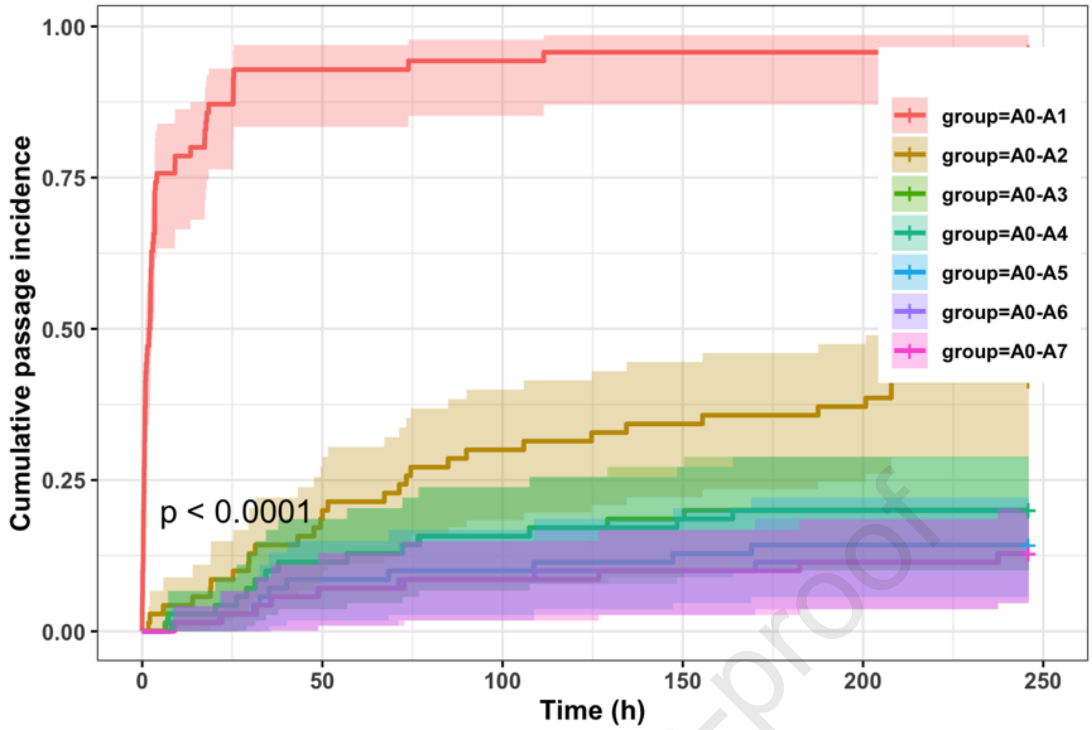
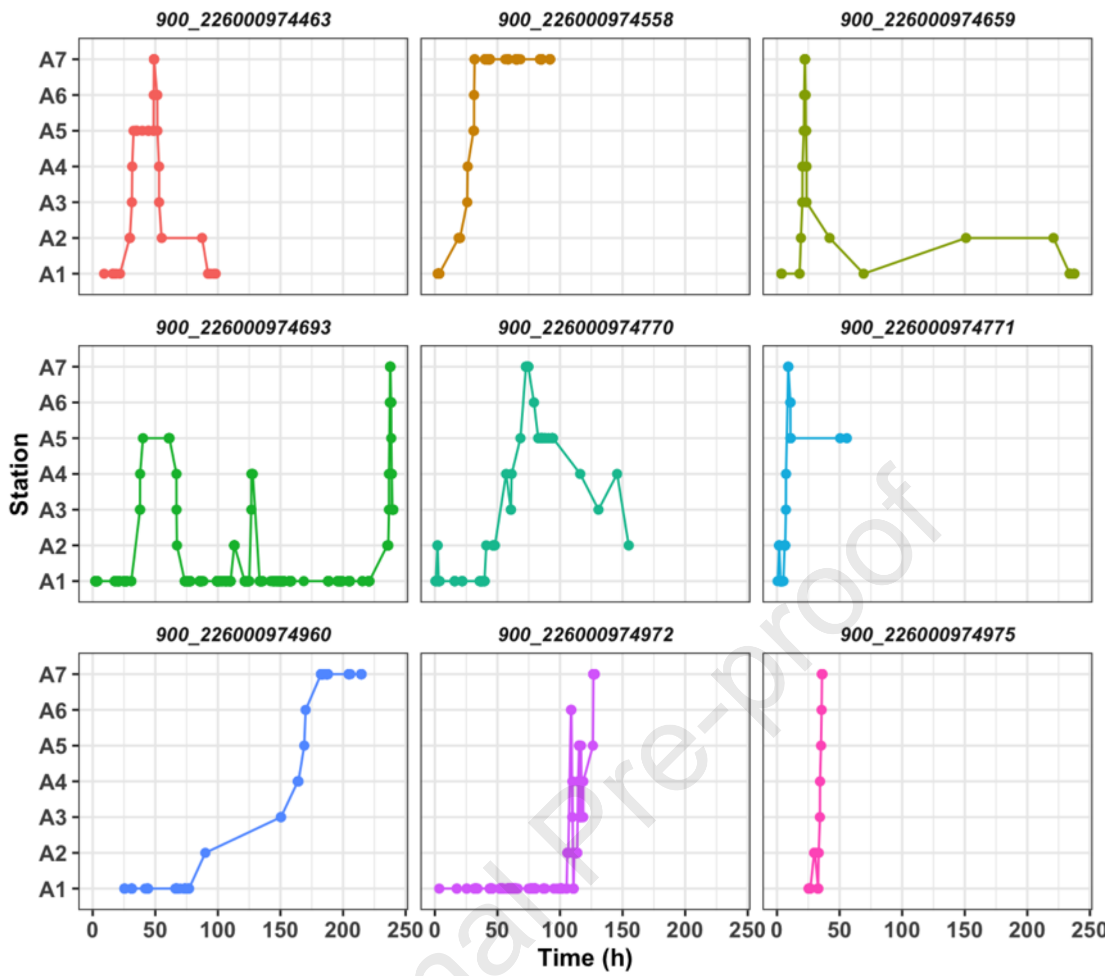


Figure 4. Cumulative incidence curves (i.e., Kaplan-Meier curves) representing the proportion of fish that passed the fishway on their first time as a function of time. Shading indicates upper and lower 95% confidence interval.



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17 **Figure 5.** The migration routes of the nine fish that successfully reached A7 in the fish passage.

18

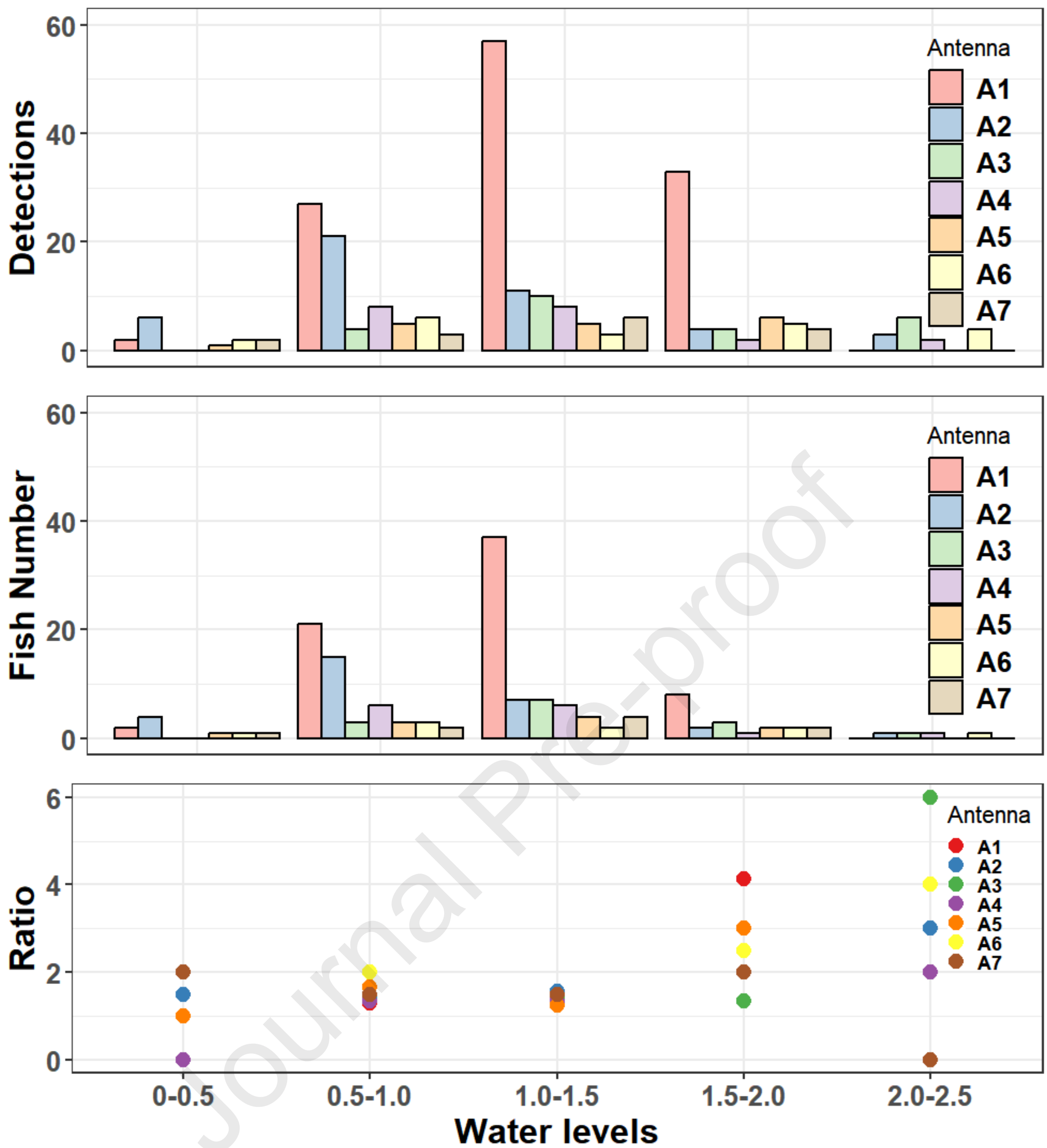

Figure 6. The detected signals, fish ID number and their ratio (detections/fish number: The number of detected signals divided by the number of detected tagged fish) at different water levels.

Highlights

- Assessing overall and different sections passage efficiency.
- Quantifying the behavioral metrics and variations of migratory fish in different sections.
- Analyzing the factors affecting behavioral metrics.
- Providing valuable information to inform design and operational changes.