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Enhancing Fish Passage Efficiency: Lessons from UHE Porto Primavera's Fish Ladder

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Abstract: Dams severely affect aquatic environments and block the longitudinal migration of fish. In order to mitigate the negative effects generated by these developments, fish passes, or fishways, are implemented in dams with the purpose of restoring river connectivity and allowing the movement of migrants. Nevertheless, fishways in neotropical areas often face design and construction issues that can reduce their efficiency and selectively disadvantage species with limited swimming capabilities. This study analyzes how a fish ladder on the Paraná River influences the black armored catfish (*Rhinelepis aspera*), a benthic, long-distance migratory species important to commercial fisheries. A total of 200 individuals were PIT-tagged and monitored for four months. The results showed that although many fish successfully located the fishway, only a small portion (3.5%) managed to complete the ascent. The interaction between the hydraulic characteristics of the fishway and the fish condition factor played a significant role in ascent performance. Our findings underscore the importance of assessing fishway suitability for benthic neotropical species to support conservation efforts in the Upper Paraná River Basin. To improve passage rates for *R. aspera*, we recommend optimizing flow conditions by adjusting orifice and notch configurations, incorporating roughness elements, and modifying resting pool designs. These adaptations would reduce energy expenditure for ascending fish, enhancing fishway performance and contributing to the sustainability of migratory species in this region.

Keywords: armored catfish; migration; fishways; neotropics; fisheries conservation

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1. Introduction

South America is renowned for its extraordinary mega fish diversity [1], particularly in its major river basins, such as the Amazon, Orinoco, and Paraná-Paraguay [2]. The Amazon Basin, for instance, is home to around 2411 fish species [2], and the Orinoco River Basin also boasts impressive fish diversity (1002 species). Similarly, the Paraná River system holds more than 508 fish species, and the Paraguay system has approximately 277 fish species [3]. Legally designated protected areas exist throughout the river basin [4], and they are crucial for fisheries and biodiversity sustainability and conservation.

A significant portion of these species are currently threatened due to habitat loss or degradation. Major causes of habitat disruption include widespread land-use changes, the construction of hydroelectric dams, and water diversion for irrigation, along with urbanization in certain areas [2]. Additionally, invasive species [5] and climate change pose a potential risk to global biodiversity [6] and inland fishery resources [4].

The construction of large hydropower dams, especially in the Paraná River Basin, poses a significant threat to migratory species [7]. Dams create physical barriers that impede fish migration, disrupting essential routes for reproduction and feeding [8]. The fragmentation of rivers and habitat loss associated with dams can also lead to significant reductions in aquatic biodiversity, with some fish species facing population declines [9] or extinction due to their inability to adapt or find new migration routes. The construction of hydropower infrastructure continues to expand worldwide [10–12], with much of this growth occurring in developing nations [13]. The future of the free-flowing stretches of the Upper Paraná River Basin is at risk due to a projected 505% increase in the number of medium-sized dams [14]. This increase is likely due to the depletion of large hydraulic potentials from the construction of large hydropower plants over the past 50 years.

Building fish passes or fishways around the globe is essential for effective environmental management, especially in areas where water infrastructure can disrupt fish migration routes [15–18]. Failing to address and protect the migratory needs of fish populations during the planning and construction of such infrastructure can lead to substantial environmental, social, and financial repercussions. Thus, targeted engineering solutions, supported by comprehensive guidelines, robust legislation, and effective policies, are crucial to safeguarding fish populations [19].

According to [18], there is no single fishway design that can adequately accommodate all fish species. Fish passes, at best, can only minimize the impact on the aquatic ecosystem, and the degree of benefit provided by a fishway largely depends on its operational design characteristics [19]. For example, some fish pass designs may be more suitable for commercially important species, such as short and steep passages designed for salmon in the Northern Hemisphere [20], which may not adequately meet the needs of tropical species.

The effectiveness of fish passes is frequently questioned due to their complex design and the diverse range of species they need to accommodate. Design flaws and operational problems can block fish migration, while inadequate maintenance and misuse by anglers can further reduce the functionality of these structures [21]. Fish passes must be designed for local conditions and maintained over time, which requires ongoing funding [16,21]. Addressing the complex behavior of fish in response to hydraulic conditions in diverse aquatic environments, especially in large rivers and tropical systems, is critical for improving fishway designs. Research has shown that understanding the flow fields that influence fish attraction and guidance is essential for creating effective fish passage structures. Advances in fish tracking technology have revealed the significance of hydraulic characteristics such as velocity, turbulence, and flow patterns, demonstrating that simple adjustments to flow dissipation could be insufficient [22].

To address this, both current and future hydropower plants must ensure connectivity between critical habitats for migratory species by incorporating fishways [14]. These fishways must be designed to accommodate the biological needs and swimming capabilities of Neotropical migratory fish species [23]. Properly designed and implemented fishways in hydropower dams within the Upper Paraná River Basin are essential for maintaining connectivity and, consequently, the conservation of neotropical long-distance migratory species [14,24].

Among the migratory species is *Rhinelepis aspera* (Spix & Agassiz, 1829) (Siluriformes, Loricariidae), commonly known as the black armored catfish, which is distributed in the Amazon and Orinoco River Basins and in the Paraná-Paraguay system [25]. Like other loricariids, it has a depressed body shape covered by bony plates and the modification of the mouth to an oral sucker disk, which is used, besides for feeding, for the attachment to various substrates [26]. It is notable for its morphological and behavioral adaptations that ensure its survival and reproductive success in specific habitats. *R. aspera* can reach a maximum total length of 49.5 cm [27] and a body weight of up to 4 kg [28]. This fish undertakes long-distance migrations for spawning, which occurs between December and February, with gonadal maturation beginning in October [7,29,30]. This species inhabits environments with strong currents with the stone substrate [31], and its morphological adaptations, typical in benthic species, such as the dorsoventrally flattened body, well-developed pectoral fins, and long caudal peduncle, are crucial for stabilization, movement in strong current environments [32], and bottom swimming. These features allow the black suckermouth to anchor itself to rocky substrates and efficiently explore the benthic environment despite turbulent conditions [31,33]. However, dam construction and other anthropogenic actions have led to siltation and habitat degradation, resulting in a significant decline in its populations and highlighting the urgent need for conservation measures [34].

The existence of free-flowing river stretches in the main channel of the Upper Paraná River and tributaries, as well as protected areas, has contributed to the maintenance of *R. aspera*. Due to its ecological and economic importance for regional fishing, the species is the target of research in the fish ladder of the Porto Primavera Hydroelectric Power Plant in the Upper Paraná River. Previous studies indicated that *R. aspera* faces difficulties ascending this fish ladder [23]. This device was initially designed for a length of 520 m [35], $\Delta h = 0.40$ m, and resting pools with zero slope [36]; however, after construction, it is finally 472.5 m long and $\Delta h = 0.45$ m [24]. Considering that changes in dimensions in relation to the original design could result in hydraulic conditions that compromise fish passage performance, that is, reduce the efficiency of the fish ladder, and the limited information available on its specific hydraulic features, this study evaluated (i) the structural and hydraulic characteristics of the fish ladder; (ii) the attractiveness and efficiency of the system by recording the entry time and transition time of fish in the ladder; (iii) whether biological variables such as length, weight, and the fish condition factor, as well as hydraulic variables such as flow velocity and turbulence, affect the ascension of *R. aspera*.

2. Materials and Methods

2.1. Study Area: Fish Ladder

The Upper Paraná River Basin is the most regulated in South America, with 389 dams, but only 9% of them have fishways [14]. Large reservoirs are found in the main channel of the Paraná River such as Itaipu and Porto Primavera and pass through the Upper Paraná River Floodplain, a 230 km river unobstructed stretch between these reservoirs, a crucial area for fish diversity conservation. Large undammed tributaries are in this area and in the Porto Primavera Reservoir that include protected areas providing diverse environmental conditions, access to spawning habitat, a refuge for early life stages, and promoting ecological heterogeneity and maintenance of biodiversity [37,38].

The Engenheiro Sergio Motta Hydroelectric Power Plant, also known as Porto Primavera, generates 1540 MW using 14 four-blade Kaplan turbines, with a dam of 10.2 km long, 16 surface spillways with discharge capacity up to 53,600 $m^3\ s^{-1}$, and 1 navigation lock [24,39]. The Porto Primavera Reservoir is approximately 190 km long [24], displaying large free-flowing tributaries [14] that continue to provide a suitable spawning environment for potamodromous fish [38].

The actual fishway is a fish ladder type (pool and weir with bottom orifices) at Porto Primavera Dam (Figure 1). It was built on the left side of the dam to allow fish to migrate upstream to tributaries and maintain longitudinal connectivity [24]. According to [24], the fish ladder is 472.5 m long, and the pools are 5.0 m wide, 8.0 m long, and 2.0 m high. It has 50 weirs and pools with three bottom orifices and three notches each, and a 0.45 m water level difference between them [24]. Only one notch and one bottom orifice were open during the study period. Three pools along the ladder were designed as fish resting areas.

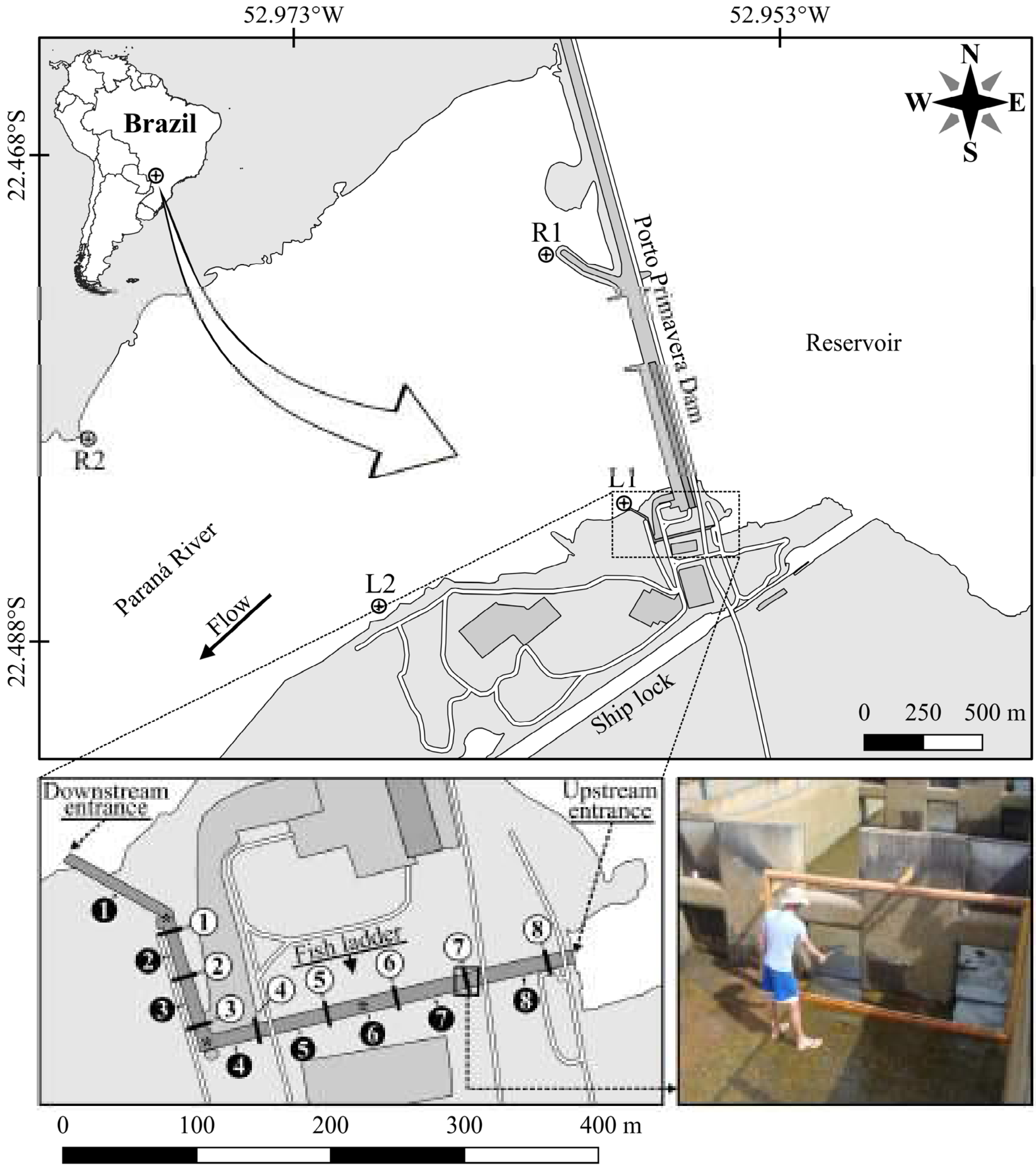

Figure 1. Map of the study area highlighting the fish release sites downstream of the Porto Primavera Dam, Upper Paraná River, and the fish ladder. Details on the fish ladder are shown as the location of the antennas (numbers 1–8), sections (numbers 1–8 in a black circle), resting pools (*), and the installation of the antenna. Release sites: R1 and R2—right riverbank; L1 and L2—left riverbank.

2.2. Altimetric and Topographic Measurements

Planialtimetric topographic measurements were conducted on the fish ladder to identify any critical changes in slope or structure, using a topographic level and a fiberglass tape measure to determine altimetric and planimetric data, respectively. Measurements were conducted at the bottom, central portion, upstream, and downstream of each pool. The slope is determined as the division of pool length (usually 8 m), including the plank thickness (0.3 m) between the height difference among consecutive notches (usually 0.45 m).

During the topographic survey, measurements of the water level of each pool (central region) were also taken using a graduated aluminum ruler.

The results were compiled to provide elevation profiles, slope, width, length and height, elevation quotas, and water depth in the pools. These data were used for analysis of the hydraulic characteristics of the fish ladder.

2.3. Hydraulic Measurements

Topographic data were transformed into hydraulic variables by using the formulae proposed in [40,41] in similar types of fishways.

The total discharge (Q) was calculated from the following equation:

$$Q = Q_s + Q_n \tag{1}$$

where Q_s is the discharge in the submerged orifice, and Q_n is the discharge over the top notches.

The equation below was used to calculate Q_s:

$$Q_s = \Psi A_s \sqrt{2g\Delta h} \tag{2}$$

where A_s = 0.8 × 0.8 m^2 (orifice area). The discharge coefficient can be estimated as Ψ = 0.876.

The equation below was used to calculate top notches Q_a:

$$Q_n = \frac{2}{3}\mu\sigma b_n\sqrt{2g}{h_n}^{1.5} \tag{3}$$

where h_n is the head of the notch; μ is the discharge coefficient (0.6); σ is the drowned-flow reduction factor; b_n is notch width.

The drowned flow reduction factor was calculated from

$$\sigma = \left(1 - \left(1 - \frac{\Delta h}{h_n}\right)^{1.5}\right)^{0.386} \tag{4}$$

which is valid for the range $0 \leq \frac{\Delta h}{h_n} \leq 1$; for $\Delta h > h_n$, $\sigma = 1$.

The volumetric power dissipation (W/m^3) (hereafter referred to as VPD), used as a measure of turbulence, was obtained from

$$VPD = \frac{\rho \cdot g \cdot \Delta h \cdot Q}{B \cdot h_m \cdot (l_b - d)} \tag{5}$$

where the following variables are defined:

Δh is the difference in water level (m);

Q is the total discharge in the fishway (Q = 1.87 m^3/s, which is in accordance with the mean flow discharge of the fishway);

B is the pool width (5 m);

h_m is the mean water depth (m);

ρ is water density (997 kg/m^3);

g is gravitational acceleration (9.81 m/s^2);

l_b is the pool length;

d is the plank thickness (0.3 m).

2.4. Capture, Tagging and Fish Release

A total of 200 fish were captured downstream of the dam near the fish ladder using a cast net (13 mm mesh between adjacent nodes) in December 2015. The fish were kept in cages (1.0 × 1.0 × 1.5 m) for 30 min near the riverbank for recovery after capture. They were anesthetized with benzocaine 75 mg L^{-1} diluted in ethyl alcohol (92.8°) before tagging. The fish were measured (total length), weighed, and tagged. PIT tags (Passive integrated transponder, model RI-TRPWR2B-30; HDX-Half duplex, Texas Instruments, Dallas, TX, USA), size 32 mm, were used. The tags were inserted into the abdominal cavity through an incision in the posteroventral region, and a 10% iodine solution was applied to the tag insertion site for asepsis purposes.

Four release sites were established, two on each riverbank (Figure 1), and the distance from the release sites to the ladder entrance was about L1 = 0 km; L2 = 1.2 km; R1 = 1 km; R2 = 2.3 km (Figure 1). After recovering of the tagging procedure, 50 tagged fish were released at each site.

The tagged fish were mature adults (25 cm [7]), with total body length ranging from 30.2 cm to 47.5 cm (mean of 38.7 cm) and body weight from 470 g to 1400 g (mean of 853 g). Table 1 shows the total body length (TL), total body weight (TW), and condition factor (K) (calculated as $100 \times TW/TL^3$ in order to compare the relative robustness) of the fish tagged and released in the different sites downstream Porto Primavera Dam.

Table 1. Mean values and standard deviations (±SD) of total body length (TL), total body weight (TW), and condition factor (K) of fish tagged and released in the different sites downstream of Porto Primavera Dam. * There were no significant differences between release sites ($p > 0.15$ in all cases).

Release Sites	TL (cm) *		TW (g) *		K *	
	Mean	±SD	Mean	±SD	Mean	±SD
R1	38.7	2.45	841	165.95	2.81	0.30
R2	38.3	2.81	836	164.14	2.89	0.26
L1	38.7	2.81	861	175.84	2.90	0.32
L2	39.1	3.23	875	216.68	2.95	0.84

The fish procedures in this study were in accordance with the Ethics Committee on the Use of Animals of the State University of Western Paraná (Protocol number 63/09). A voucher specimen of *R. aspera* was deposited in the Zoology Museum of the State University of Londrina (catalog number MZUEL 18392).

2.5. Monitoring of Fish Passage

The fish movements in the ladder were monitored from December 2015 to April 2016 using a Multireader Radio Frequency Identification (RFID) system (model S2000, Texas Instruments, Dallas, TX, USA). This system consisted of eight readers, arranged in a linear mode, and with a frequency of 134.2 kHz installed in the ladder [42]. Eight (A1–A8) rectangular antennas (3.0 m × 1.5 m) were made (one for each reader), fixed to wooden frames, and distributed along the ladder. The electromagnetic field of the antennas was adjusted to a range of around 1.5 m for PIT readings, significantly covering both openings (notch and bottom orifice) (Figure 1). Considering that the species studied is benthic with exclusively bottom-swimming behavior, this ensures that the antenna covers the entire orifice, enabling fish detection and recording.

The first antenna (A1) was located 96.56 m from the downstream entrance of the fish ladder, in the first resting pool (pool 11 located in Section 1—S1), and the last antenna (A8) was located 42.4 m from the water intake (Figure 1, Table 2). The distance between A1 and A8 was 331.62 m, and the other antennas (A2 to A7) were distributed equidistantly when possible, totaling 8 Sections (S1–S8) (Figure 1, Table 2). The second resting pool is between the interval of A3 and A4 (pool 22 located in Section 4—S4), and the third resting pool is between antennas 5 and 6 (pool 36 located in Section 6—S6) (Figure 1, Table 2).

The system was functional for 99.8% of the study period.

Table 2. Characteristics of the fish ladder at the Porto Primavera Dam: accumulated distance, accumulated quota, mean slope, water level height (hm), Δh, and pool length in the sections. * Values without considering resting pools; ** where resting pools are located.

Sections	Pools	Accumulated Distance (m)	Accumulated Quota (m)	Slope (%)	h_m (m)	Δh (m)	Length (m)
S1 **	1–11	96.56	4.30	4.64 *	1.20	0.39	8.05 *
S2	12–17	144.71	6.68	4.67	1.20	0.40	8.03
S3	18–21	176.8	8.31	4.90	1.00	0.42	8.02
S4 **	22–27	241.4	10.63	4.32 *	1.15	0.40	8.00 *
S5	28–33	289.61	13.02	4.41	1.20	0.40	8.04
S6 **	34–37	331.84	14.56	4.33 *	0.90	0.40	8.03 *
S7	38–43	379.99	17.02	4.40	1.33	0.40	8.03
S8	44–49	428.18	19.15	4.05	1.33	0.38	8.03

2.6. Data Analysis

The proportion of tagged fish that arrived at the fish ladder and the time taken from the release to the first detection in antenna 1 was used to assess the attraction and entrance (entry rate and entry time). Comparisons between the four release sites were conducted via time-to-event or Survival Analysis [43]. Specifically, Kaplan–Meier curves were applied to represent them [44], and a Log-rank test was used to assess the possible significant differences ($p < 0.05$). All fish without attempts were included as right-censored observations, assigning them the total time duration of the trial. The Kaplan–Meier method [44] was applied to graphically represent the survival curves related to the time. The variables of total body length, total body weight, and fish condition factor were analyzed through Survival Analysis to verify if they have a significant effect on the time to locate the fish ladder.

The efficiency of the fish ladder was evaluated using Survival Analysis. Kaplan–Meier method was applied to graphically represent the maximum quota (elevation) reached by the fish in the fish ladder.

To compare the ascent time between the different sections in the fish ladder, we standardized this response variable, transforming it into ascent time per meter of ascended height. For this analysis, Section 1 was excluded (it is not possible to differentiate the time spent by fish in the river and between the first pool and the first antenna). Cox regression was performed to analyze the effects of the total body length (cm), total body weight (g), fish condition factor (K), flow velocities (m/s), and the VPD (W/m^3) on the ascent time in the fish ladder.

The entry rates and ascent time were analyzed with the log-rank tests, using the PROC LIFETEST package and Cox regression with PROC PHREG package, both from SAS software (SAS OnDemand: SAS Studio 3.81, SAS Institute Inc., Cary, NC, USA). $p < 0.05$ were considered as a reference value for statistically significant differences. In cases where the data do not follow a non-normal distribution, the reference statistic is the median and not the mean.

3. Results

3.1. Structural and Hydraulic Characteristics

The mean slope of the fish ladder corresponded to 4.5% (minimum of 3.5% and maximum of 5.4%), with the greatest slope recorded in the S3 (4.9%), and the pools had a mean length of 8.00 m (Table 2).

Variations in the height of the water level (h_m) were observed in the sections, from 0.90 m (S6) to 1.33 m (S7 and S8), as well as Δh varied from 0.38 m (S8) to 0.42 m (S3) (Table 2).

The resting pools, theoretically designed with zero slopes, actually have 2.28% (pool 11–S1), 1.52% (pool 22–S4), and 2.19% (pool 36–S6), and their lengths also varied, with 16.04 m, 24.59 m, and 18.14 m, respectively.

The estimated value of fishway discharge during the study period was in the range of 1.8–2 m^3/s.

Among the fish ladder sections analyzed (Table 3), the highest median of flow velocities was observed in the S2 (median of 2.53 m/s) and S4 (median of 2.51 m/s), while the lowest was recorded in the S6, with 0.66 m/s. Maximum flow velocities above 3.00 m/s were recorded in the S1 (3.17 m/s) and S4 (3.29 m/s) (Table 3). The highest median of VPD was observed in the S2, with 118.32 W/m^3, and the lowest in S6, with 8.45 W/m^3 (Table 3). The maximum VPD was observed in a pool of S4, with 198.65 W/m^3 (Table 3).

Table 3. Main hydraulic characteristics of the fish ladder by sections (S1–S8) at the Porto Primavera Dam. VPD: Volumetric power dissipation.

Sections	Flow Velocity (m/s)			VPD (W/m^3)		
	Median	Minimum	Maximum	Median	Minimum	Maximum
S1	1.94	0.82	3.17	72.28	10.42	174.11
S2	2.53	2.20	2.74	118.32	101.16	163.42
S3	2.19	0.78	2.60	100.81	12.62	143.00
S4	2.51	1.45	3.29	102.44	44.31	198.65
S5	2.32	1.81	2.64	113.55	64.28	150.58
S6	2.52	0.66	2.89	99.83	8.45	155.59
S7	2.34	1.94	2.45	115.33	74.54	126.05
S8	2.19	1.51	2.51	110.11	47.59	132.53

3.2. Entry Rate and Entry Time

Considering the 200 tagged fish, 142 fish (71.0%) found the ladder and were detected at antenna 1. The entry rates ranged from 62% (R2) to 80% (L1), and the median spent time by the fish to be detected in the first antenna varied from 22.00 to 53.50 days (Table 4). Fish length, weight, and condition factor for the different release sites are shown in Table 4.

Table 4. Number of fish and entry rate (%), time spent by the fish to find the ladder, total body length (TL), total body weight (TW), and condition factor (K) of *Rhinelepis aspera* tagged in the different release sites and detected in the first antenna of Porto Primavera fish ladder.

Release Sites	N	%	Time (Days)		TL (cm)		TW (g)		K	
			Median	±SD	Median	±SD	Median	±SD	Median	±SD
R1	33	66	22.00	25.05	38.50	2.64	850.00	184.26	2.71	0.29
R2	31	62	24.00	23.16	38.30	2.73	830.00	164.07	2.99	0.27
L1	40	80	53.50	26.03	38.15	2.67	830.00	167.22	2.82	0.34
L2	38	76	46.00	23.12	39.50	3.32	885.00	215.59	2.87	0.93

The survival curves were not significantly different between release sites (Log-Rank: $\chi^2 = 2.05$, $p > 0.05$) (Figure 2). Pair-wise comparisons (Tukey–Kramer) between strata performed for the Log-Rank test also showed no significant differences ($p > 0.05$) between sites on the right bank with those on the left bank, indicating that the fish entrance probabilities were not significantly different between the release sites. In general, the survival rates drop progressively as time passes, particularly after around 50 to 70 days post-release.

The Cox regression showed that total body length, total body weight and fish condition factor did not influence the fish entry rate in relation to the different release sites.

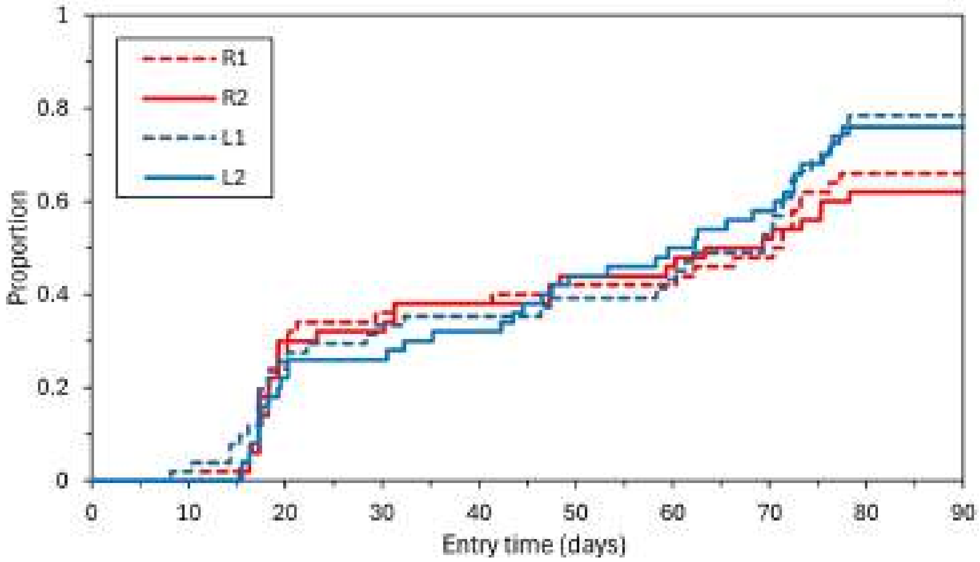

Figure 2. Kaplan–Meier curves representing the proportion of *Rhinelepis aspera* detected at antenna 1 (first entry) since the release date for the four released sites (R1, R2, L1, and L2) in the Porto Primavera fish ladder.

3.3. Passage Performance

Related to the passage success, of the 142 fish that were detected at the first antenna, most fish (80.3%) reached up to 6.7 m elevation (A2) (Figure 3). Afterward, several fish (40.3%) failed to reach beyond the 8.3 m elevation, reaching A3. Most fish failed during ascent in the downstream sections; thus, S4 (A4) was just reached by 28% of individuals. Only 3.5% of fish successfully ascended the fish ladder (Figure 3) during the study period. None of the studied covariates, neither hydraulic nor biological, was significantly related to passage success results.

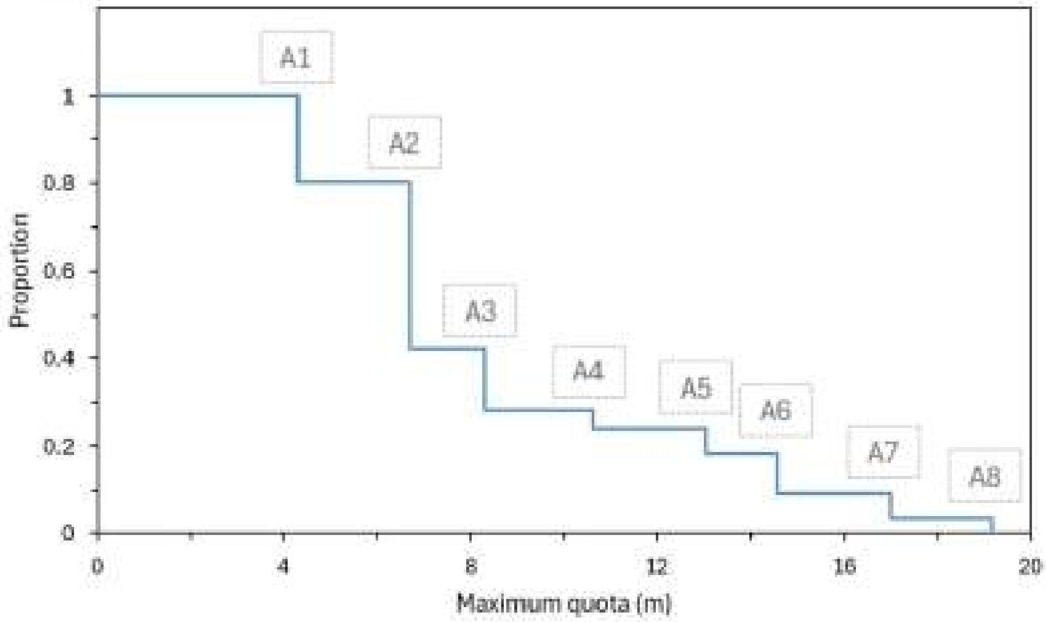

Figure 3. Kaplan–Meier curve representing the proportion of maximum quota (m) reached by *Rhinelepis aspera* in the Porto Primavera fish ladder (the quota of the different antennas is represented by A1–A8).

Regarding the ascent time, globally, the median time per meter of height ascended was 4.1 min/m (Interquartile range = 1.3–12.1 min/m). Making the comparison between fishway sections, there were significant differences (p-value = 0.001) (Figure 4), mainly due to the slower passage (more ascent time) in S2 and S3.

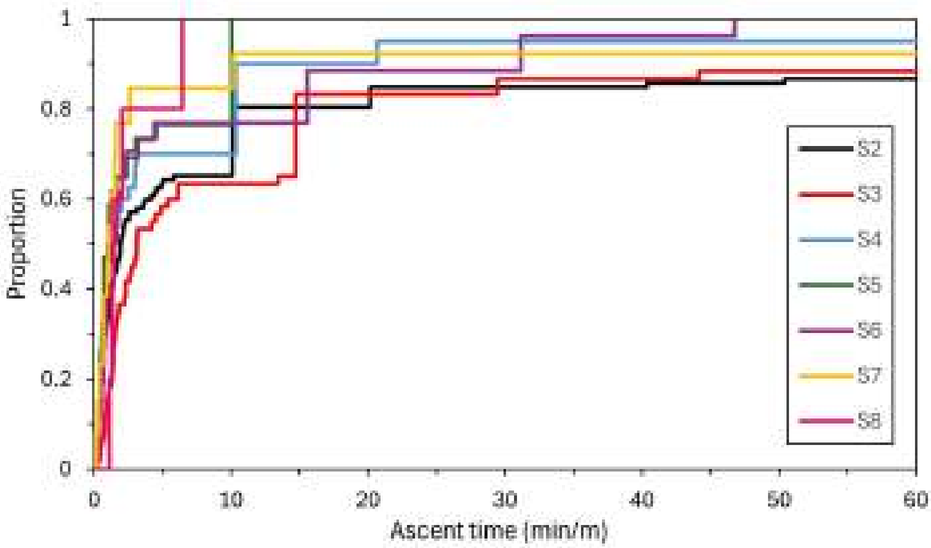

Figure 4. Kaplan–Meier curves for the proportion of fish and respective ascent time (standardized to minutes per meter of height ascended, min/m) in the different Sections (S2–S8) of the Porto Primavera fish ladder. S1 is not comparable with the rest of the sections (S1 corresponds to the time between the release site and the first detection at antenna 1).

The Cox regression analysis verified how hydraulics (median values of flow velocity and VPD) and biological covariates (body length, body weight, and fish condition factor) interact in the ascent time with the different sections of the fish ladder. Regarding the total body length and total body weight of the fish, there were no significant effects related to them (p-values > 0.500). However, the condition factor had a significant effect on ascent time (p-value = 0.009) (Table 5). Since the estimated value for K is negative, this indicates that an increase in K is associated with a reduction in the hazard ratio of ascent, i.e., fish with higher values of K tend to take longer to ascend the ladder. Comparing between sections, the more affected by this effect were S2, S3, and S4 (p-value < 0.05) (Figure 5).

Table 5. Parameter estimates and standard errors (SE) of the Cox regression analysis on the covariates: fish condition factor (K), median flow velocity (m/s), and median volumetric power dissipation (VPD) (W/m^3). * Covariate in the respective Section. † Note that the reference level is Section 8.

Parameter	Parameter Estimate	SE	p-Value
K	−1.44087	0.55506	0.0094
K * Section 2	2.09742	0.71417	0.0033
K * Section 3	1.25620	0.56007	0.0249
K * Section 4	6.25415	1.15722	<0.0001
K * Section 5	1.23071	0.69863	0.0781
K * Section 6	1.33860	1.21249	0.2696
K * Section 7	0.66263	1.86039	0.7217
K * Section 8 †	Ref. level		
VPD	−0.39711	0.97057	0.6824
VPD * Section 2	−0.02793	0.06636	0.6738
VPD * Section 3	−0.07844	0.09554	0.4117
VPD * Section 4	−0.19481	0.08226	0.0179
VPD * Section 5	−0.02127	0.03108	0.4938
VPD Section 6	−0.08122	0.11003	0.4604
VPD * Section 7	.	.	.
VPD * Section 8 †	Ref. level		

Table 5. *Cont.*

Parameter	Parameter Estimate	SE	*p*-Value
Flow velocity	−13.71208	33.51355	0.6824
Flow velocity * Section 2	−0.76746	4.38501	0.8611
Flow velocity * Section 3	−1.97048	0.81032	0.0150
Flow velocity * Section 4	−4.98133	4.32886	0.2498
Flow velocity * Section 5	−0.85594	1.90351	0.6530
Flow velocity * Section 6	0.16605	4.36909	0.9697
Flow velocity * Section 7	.	.	.
Flow velocity * Section 8 †	Ref. level		

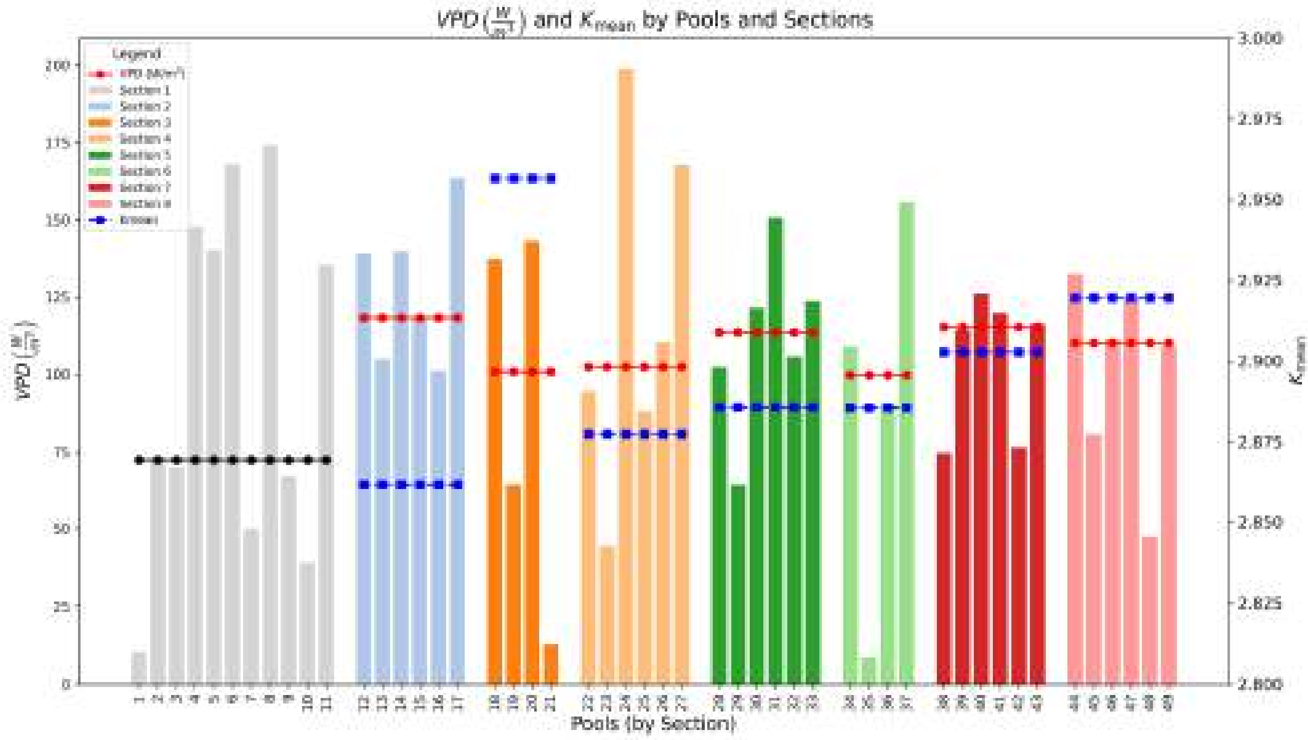

Figure 5. Volumetric power dissipation (VPD) (W/m^3) along the pools and mean fish condition factor (K) of *Rhinelepis aspera* in the different sections in the Porto Primavera fish ladder. -·- is VPD median (W/m^3) in the Section 1, and -·- is VPD median (W/m^3) in Sections 2–8.

The median flow velocity and VPD by itself did not have a significant effect on the ascent time, but they did have it at the interaction with certain sections (Table 5). For VPD (Figure 5), there was a correlation with S4 (more VPD means more ascent time), and for flow velocity, the significant effect occurred in S3 (more flow velocity means more ascent time).

4. Discussion

Our study provides a comprehensive overview of the effectiveness of the fish ladder at Porto Primavera Dam in the Upper Paraná River, highlighting the complexity of the challenges faced by migratory fish, specifically the black armored catfish, *R. aspera*. Although a significant percentage of fish located the ladder, a very small fraction managed to complete the ascent of the fishway. The interaction between the hydraulic characteristics of the ladder, such as variations in flow velocity and VPD, as well as the fish condition factor played a crucial role in the ascent performance of this device. These findings highlight the need for adjustments in the design of the ladder and the management of hydraulic factors to improve the passage efficiency for migratory species.

4.1. Structural and Hydraulic Characteristics

The fish ladder's structural and hydraulic features analyzed indicated possible impacts on fish passage efficiency. The presence of steep drops between pools and their related high values of flow velocity and VPD in some Sections might increase the energy expenditure for fish attempting to ascend in lower Sections (S1 to S4), highlighting the need for careful design to accommodate diverse species. Specifically, the high water level difference between pools (0.4 m) created flow velocity fields close to 3 m/s and even higher in some orifices of S1, S2, S4, and S6, while design recommendations avoid surpassing 2 m/s to reduce intra and interspecific selection of individuals [40,45,46]. A steeper slope decreases the fish-friendly area within the pool, and the VPD becomes less optimal at higher slopes [47].

Resting pools play a crucial role in fish ladders, providing areas where fish can recover energy before continuing their ascent [22]. Long resting pools, while providing space for recovery, can present unexpected challenges for migratory fish. After direct observations during several migration campaigns, the accumulation of fish and their long-term permanence in these pools seem to be evidence of possible problems. Furthermore, long pools can alter fish behavior, causing them to stop for longer periods than necessary, which can even result in disorientation or demotivation, compromising the continuation of the migration. Reference [40] recommends that resting pools should not exceed 6 to 8 m in length, but the resting pools in the Porto Primavera fishway range from 16 to 24 m. The design guidelines [41] also mention maximum cumulative differences in level between resting pools of approximately 2 m, which is not the case here (more than 4 m). Nevertheless, design data and recommendations for neotropical and benthic fish are necessary.

The ladder's mean slope of 4.5% was consistent with recommended generic guidelines for fish ladders (7–12% in [40,46]). However, the initial Sections, 1 to 3, had slightly steeper slopes (4.7–4.9%), which could influence ascent for benthic species such as the black armored catfish and could suggest an upper limit for this *R. aspera*. The slope is a critical parameter in fish passage design and directly influences the flow characteristics within the pool [48].

4.2. Entry Rate and Entry Time

The entry rate on these trials may be considered quite high (between 62 and 80%), being in the upper range of the meta-analyses carried out on this subject [49–51]. If we analyze the difference between release locations, the entry rates and entry time were similar in all cases. This was unexpected because we previously assumed that fish released on the same bank as the fishway (left bank) would locate it more quickly. Moreover, other experiences in the same area showed a faster location by fish released in the left bank [24]. This difference could be attributed both to fish origin and the main river flow. All fish were captured in the same area, and they had knowledge about this river section (experienced vs. naive fish [52]). Therefore, they could easily find the main migration route (the main river flow runs along the left bank), where the fishway is placed.

Considering that the spawning migration of *R. aspera* occurs between December and February [7,29,30], the entry rate is in accordance with it, showing a progressive decline, especially 50–70 days after release (mid-December was the date of fish release). This period is crucial in the spawning migration (*piracema* in indigenous language), as fish need to move upstream in a timely manner to reach the spawning sites. Sometimes, fish may have missed their peak reproductive period or arrived at the spawning grounds in a fatigued state, reducing their chances of successful reproduction.

4.3. Passage Performance

The performance of the fish ladder, as evidenced by the proportion of fish reaching different elevations, indicates a significant challenge for most fish. The finding that only 3.5% of fish successfully ascended the entire fish ladder underscores the difficulties posed by this device. The fact that most fish did not surpass 8.3 m suggests that either the ladder's hydraulic conditions or structural elements, such as weirs and resting pools, are not fully conducive to fish passage for this species. Nevertheless, it was not possible to clearly conclude why some fish managed the entire fishways and most failed in the downstream sections. Fish size and condition factors did not explain the strong selection caused by the whole fishway. Ref. [45], working with cyprinids, observed that at lower flow velocities (<2 m/s), size is the main factor explaining the swimming performance; thus, larger individuals swim up more efficiently. In contrast, at high flow velocities, the shape becomes the essential explanatory variable; thereby, streamlined body shapes with a higher relative position of the tail and a narrower caudal peduncle are more efficient and thus more skilled at overcoming a velocity barrier. In our case, condition factor as a morphological indicator was not able to explain the difference in passage success, although, as discussed in the next paragraphs, this does have an influence on the ascent time.

In addition, there are other causes related to motivation that also influence passage success but are hardly measurable [53]. Probably, like many potamodromous fish species, *R. aspera* shows a partial migration behavior, with the existence of some individuals that only develop short movements (resident fish) and others that complete long-distance movements (mobile fish) [54–56] and more motivated to ascend the fishway.

On the other hand, the fish condition factor significantly influences ascent time, with higher K values associated with longer ascent times. This implies that fish in higher conditions may encounter greater challenges during ascent, possibly due to greater flow resistance (lower hydrodynamics), increased energy demands, or suboptimal conditions in specific ladder sections. The interaction between K and ladder sections further suggests that the effect of fish condition on ascent time varies by section, with some more demanding Sections (S2, S3, and S4). Anyway, sometimes condition factors per se cannot explain the influence of body morphology in swimming performance, and more complex indicators are necessary [45]. *Rhinelepis aspera*, with its morphological and ecological characteristics, presents some limitations that may affect its performance in ascending the Porto Primavera fish ladder. The flattened body and the suction cup-shaped ventral mouth are adaptations for life in rocky bottoms and environments with strong flow [31], where the species can attach itself to the substrate and withstand strong currents [32]. Therefore, another possible problem is the lack of roughness or naturalized substrate at the bottom of the pools.

Failure during the ascent of the fishway, especially in S2 and S3, could also likely be attributed to fish fatigue. Fatigue becomes more probable as the fish ascend, particularly if there are insufficient opportunities to rest or recover between sections. This can result in a gradual reduction in ascent success as fish become increasingly exhausted. Addressing this issue would require improving resting opportunities and managing flow conditions to reduce energy expenditure, allowing the fish to regain strength as they progress. Flow velocity's impact on ascent time was complex. In general, the median flow velocity was more or less homogeneous in the whole fishway, and it did not significantly affect the ascent time, but in the specific case of Section 3, there was a significant effect (higher flow velocity means longer ascent times).

Turbulence is one of the main factors that may affect the fish swimming performance [57,58], and VPD (volumetric power dissipation) is considered the main fishway design parameter related to turbulence due to its simplicity and wide application [40,41]. Detailed analysis in this study showed that VPD varied between different sections of the fish ladder, which may have a direct impact on the fishway passage. The results emphasize that Section 4 requires special attention due to the significant effect of the VPD (higher values of VPD are related to a slower ascent). Although median values of VPD are in accordance with the main design recommendations, *R. aspera* may have characteristics that make it more sensitive to high levels of VPD compared to other species. In any case, it is worth discussing the relevance of the use of this parameter for fishway assessment, at least as the only indicator of turbulence, as it oversimplifies turbulence characteristics [59].

Results shown here indicate that the first sections of the fishway may be key in case of considering improvements with the aim of improving the *R. aspera* fishway upstream passage. Also, future research should explore how specific modifications to the structure can improve it, e.g., testing different combinations of open orifices/notches in the weirs of the pools to improve the hydraulic conditions for fish passage. Some other possible improvements may be related to increasing bed roughness/naturalization and increasing pool depths.

These findings underscore the necessity of evaluating and, if needed, modifying fish ladders to accommodate a diverse range of species, particularly those that are more vulnerable or exhibit poor swimming performance. Environmental factors such as water temperature, dissolved oxygen, precipitation, and fish stress during passage, along with variable operational conditions of the power plant, can significantly influence fish behavior and passage performance. Acknowledging these factors is vital for a comprehensive understanding of fishway efficiency, as they may affect ascent success and ecological outcomes beyond the current study's scope.

Moreover, a four-month observation period may not fully capture the complexities of *R. aspera* movement patterns, especially given the seasonal variations in river flow and temperature. This limitation highlights the need for future research to prioritize longer-term monitoring, which would provide deeper insights into fish behavior and passage success across different environmental conditions and seasons.

In addition, the sample size (n = 200) poses a challenge in analyzing the whole passage success in such a large fishway, particularly considering the low ascent rate of 3.5%. However, 80.3% of fish offered data for the analyses, and 59.7% reached almost the middle of the fish ladder, supporting the robustness of the analyses. The logistical difficulties of capturing and tagging a bottom fish in the expansive Paraná River, coupled with high ambient temperatures, restricted our sample size to 50 fish per release site. While our study offers valuable insights into the factors affecting fish passage, it also emphasizes the importance of larger sample sizes in future research. Targeted tagging of individuals exhibiting migratory behavior could further enhance statistical power, enabling more robust detection of significant effects and ultimately contributing to more effective management strategies for fish ladders.

5. Conclusions: Implications for Fish Ladder Design and Management

The study highlights the significant challenges *R. aspera* faces in ascending the Porto Primavera fish ladder, particularly due to the present design and hydraulic conditions. The findings show that although many fish successfully locate the fish ladder, only a small fraction manage to complete the ascent, probably due to issues related to turbulence and high drops between pools (which mean high flow velocities). The interaction between hydraulic characteristics and fish condition factors seems to play a relevant role in migration performance.

To improve the fish ladder's effectiveness, the design should be adjusted to optimize flow conditions by changing the combinations of opened orifices/notches, adding roughness elements, and experimenting with other shapes for the resting pools. These changes would create more suitable conditions for *R. aspera* to ascend the ladder with less energy expenditure. Furthermore, monitoring and adaptive management are critical for ensuring the ladder continues to meet the needs of migratory species, particularly those with specific morphological and behavioral traits like *R. aspera*. By implementing these recommendations, the Porto Primavera fish ladder can enhance fish migration success and contribute to the sustainability and conservation of migratory species in the Upper Paraná River Basin.

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