environments

Article

Assessment of the Attractiveness and Passage Efficiency of Different Fish Passage Solutions at a Hydropower Plant by Combining Fine Scale 2D-Telemetry and Hydraulic Numerical Modelling

Séverine Renardy [1,*], Utashi D. Ciraane [2], Jean-Philippe Benitez [1], Arnaud Dierckx [1], Justine Gelder [1], Ana T. Silva [3], Pierre Archambeau [2], Benjamin Dewals [2], Michel Pirotton [2], Sébastien Erpicum [2] and Michaël Ovidio [1]

[1] Freshwater and Oceanic Sciences Unit of Research (UR-FOCUS), Management of Aquatic Resources and Aquaculture Unit (UGERAA), Laboratory of Fish Demography and Hydroecology (LDPH), University of Liège, 4020 Liège, Belgium
[2] Urban and Environmental Engineering Unit of Research (UR-UEE), Laboratory of Hydraulics in Environmental and Civil Engineering (HECE), University of Liège, 4000 Liège, Belgium
[3] Norwegian Institute for Nature Research (NINA), 7485 Trondheim, Norway
* Correspondence: severine.renardy@uliege.be

Abstract: Mitigation measures for downstream-migrating Atlantic salmon smolts (*Salmo salar* L.) are commonly insufficiently attractive to enable safe entrance and passage with no delay. Combining 2D telemetry with hydrodynamic modelling has been shown to be a good tool to better understand the influence of hydrodynamic factors on the migration route choice of fishes. In this study, we investigated the smolt downstream migration at a hydropower plant in Belgium that offers five migration routes, including two Archimedes screws and one nature-like fishway. At the hydropower plant, the Archimedes screws were the most used migration routes, due to higher discharges and more important water depths at their entrance. The weir and the canal intake were less used by the smolts. The nature-like fishway turned out to be less used, with 23% of the smolts. Its associated crossing time was significantly longer, probably due to shallow water depths and high flow velocities. The nature-like fishway had the potential to become a good migration route for salmon smolts after improvements to increase attractiveness and passage efficiency. Moreover, the Archimedes screws were not detrimental to the smolts and did not cause any significant delays to the crossing time.

Keywords: nature-like fishway; Archimedes screw; etho-hydraulics; hydrodynamic modelling; behaviour

check for updates

Citation: Renardy, S.; Ciraane, U.D.; Benitez, J.-P.; Dierckx, A.; Gelder, J.; Silva, A.T.; Archambeau, P.; Dewals, B.; Pirotton, M.; Erpicum, S.; et al. Assessment of the Attractiveness and Passage Efficiency of Different Fish Passage Solutions at a Hydropower Plant by Combining Fine Scale 2D-Telemetry and Hydraulic Numerical Modelling. *Environments* **2023**, *10*, 107. https://doi.org/10.3390/environments10070107

Academic Editor: Chin H. Wu

Received: 19 May 2023
Revised: 14 June 2023
Accepted: 20 June 2023
Published: 22 June 2023

1. Introduction

Migratory species have been highly impacted by river fragmentations due to human activities, such as navigation and hydropower production [1]. These disruptions gradually delay both upstream and downstream migrations [2,3]. River fragmentation has caused drastic reductions, and the extinction of entire populations of several migratory species, such as the Atlantic salmon (*Salmo salar* L.), by impeding free movements and limiting access to functional habitats between marine and freshwater ecosystems [4,5].

Several mitigation measures have been proposed to re-establish free up- and downstream movements of fish at navigation dams and hydropower plants [5]. Significant progress has been made in mitigation measures to restore the upstream migration of different fish species, including Atlantic salmon adults, with some that have demonstrated good performance [6], but downstream migration still remains a challenge [7,8]. This situation is highly problematic for downstream-migrating salmon smolts due to their narrow time window to reach the ocean [9,10]. Currently, most of the solutions for downstream migration include adapted hydropower plant management [11], the use of behavioural and physical barriers [12,13] and downstream bypasses [14,15]. "Fish-friendly" turbines (e.g., the Archimedes screw), with low rotational speed, large blade spacing and the absence of extreme pressure change [16] have also been developed to facilitate downstream passage of fish [16,17] and may, in some cases, be considered as a migration route for the downstream-migrating smolts [3]. Although initially designed for upstream migration, nature-like fishways, have been shown to be used by fishes for downstream passage [18,19] and can therefore be considered as a mitigation measure to ease smolt downstream passage, but this situation is currently poorly studied [20,21].

However, the performance of different kinds of mitigations measures for downstream migration, such as behavioural and physical barriers or downstream bypasses, usually turns out to still be insufficient to allow a safe and rapid passage of smolts [7,8] and to increase seaward escape rate [3,22]. Depending on the site configuration, the efficiency of migration routes varies highly. The use of a downstream bypass may vary between 0% and 97% [23], whereas the use of an Archimedes screw usually varies between 8% and 48% [3,24,25]. Based on the behavioural response of the smolts, in some cases, the Archimedes screws turn out to be an unattractive migration route for the downstream-migrating smolts, depending on the configuration of the hydroelectric site [26,27]. The efficiency of nature-like fishways is usually low with 3% to 12% of the smolts [20], despite the fact that it can reach 41% [21].

To date, little attention has been dedicated to understanding the behavioural response of fish approaching hydropower plants and associated migration routes. However, facing hydropower plants during the downstream migration will induce the expression of a wide inter-individual diversity of smolt research behaviour to find an attractive and safe migration route [22,26,27]. Behavioural responses can range from simple and direct behaviour to complex behaviour with multiple back-and-forth movements [22]. The majority of the smolts generally performed one or two passage attempts before crossing the hydropower plant [26,28]. Sometimes, the smolts may reject on multiple occasions an available migration route to move to another route [22,27]. Poor knowledge of the smolt research behaviour upstream of the migration routes leads to poor understanding of their attractiveness, and that may explain the great variability in the use of the migration route. Identifying the fine-scale behaviour of smolts upstream of hydropower plants would enable to assess the attractiveness of the available migration routes present at a migration barrier and then to better identify the solutions to be implemented to increase the chances of a rapid passage at hydropower plants with multiple migrations routes.

The factors that influence a smolt's choice of a migration route are not well understood. Hydraulic conditions such as flow velocity and water depth will influence the smolt behaviour upstream of a migration barrier [29,30]. However, the relation between the fine-scale behaviour of the smolts and hydraulic conditions associated with mitigation measures is rarely identified [27,31]. Combining hydraulic modelling and smolts tracking provides a better understanding of how hydrodynamic conditions influence smolts' behaviour upstream of migration barriers.

In this study, we investigated the downstream migratory behaviour of Atlantic salmon smolts at a hydropower plant in the Ourthe River using manual 2D radio telemetry, where the hydrodynamic conditions have been modelled numerically. The hydropower site offers five available migration routes, including two fish-friendly Archimedes screws and a nature-like fishway. The first aim of the study was to identify the smolt behavioural tactics upstream of the hydropower plant and to assess the attractiveness and use of the different migration routes. The second aim was to evaluate the environmental factors that influence smolt behavioural tactics.

2. Materials and Methods

2.1. Study Area

The Chanxhe hydropower plant is located in the lower part of the Ourthe River, which is a tributary of the Meuse River in Belgium (Figure 1a). The Meuse River is a large international river that is 950 km long, with a catchment area of 36,000 km^2. With its source in France, the Meuse River flows across Belgium until reaching the North Sea in the Netherlands. The Ourthe River is a medium-sized river that is 235 km long, with two sources located in the Belgian Ardennes, and with a total catchment area that extends over 3672 km^2. The lower Ourthe River is characterised as a barbel zone [32] with the potential for the presence of 29 fish species, dominated in biomass by rheophilic and ubiquitous cyprinids. In the whole river, the prevailing macro-invertebrate communities are currently indicative of the good (16/20) water quality status (Public Service of Wallonia—AQUABIO). In the low part of the Ourthe River, the mean discharge is 43.6 $m^3\ s^{-1}$ and during the smolts downstream migration from April to May, the average discharge is 26 $m^3\ s^{-1}$ and the mean temperature is 12.8 °C, according to data since 2014.

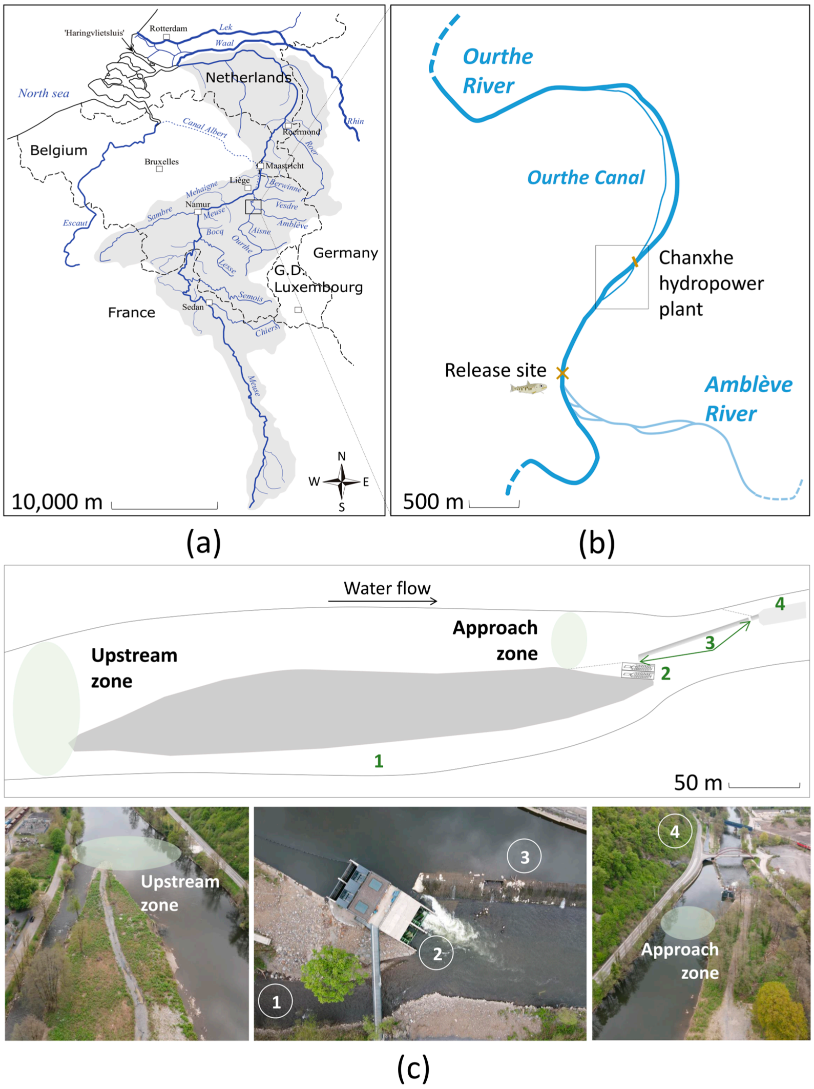


Figure 1. Schematic and photographic representations of the studied site. (**a**) Overview of the Meuse River basin including the Ourthe River. (**b**) Overview of the lower part of the Ourthe River with the studied river stretch. (**c**) Schematic and photographic representations of the Chanxhe hydropower plant and associated migration routes: (1) the nature-like fishway, (2) the Archimedes screws, (3) over the weir and associated opened incision gates and (4) the canal intake.

The Chanxhe run-of-river hydropower plant is located 28.4 km upstream from the confluence of the Ourthe River with the Meuse River (Figure 1b). The Chanxhe hydropower plant offers five different migration routes for downstream-migrating Atlantic salmon smolts (Figure 1c): the nature-like fishway, the two Archimedes screws, the weir and associated incision gates and the canal intake. The site is equipped with a 103 m long and 2.4 m high old weir, built during the 19th century to enable navigation on the river. On the left bank, the weir extends into the former navigation canal, now unused. The canal intake, which still exists, derives a very low discharge from the main river. On the right bank of the weir, there are two Archimedes screws (Figure 1c), each with a nominal electric power of 210 kW, a length of 13 m, a diameter of 4.25 m, a rotational speed from 4 to 25 revolutions per minute and a nominal functioning discharge of 11 $m^3 s^{-1}$. Three incision gates are present on the weir. The first incision is located on the right part of the weir close to the Archimedes screws, the second at the middle of the weir and the last one on the left part of the weir near the canal intake. The incision gates are, respectively, 2.12, 5.05 and 1.8 m long and 0.77, 1.01 and 0.67 m deep. The second incision gate was constantly closed during the whole smolt tracking. A small stretch 410 m upstream of the hydroelectric site creates an island on the right bank of the river. This river branch with a continuous steep slope and limited discharge and water depth forms a nature-like fishway exiting downstream of the Archimedes screws.

The located zone 410 m upstream of the Chanxhe hydropower plant is defined as the upstream zone, which includes the main river course and the entrance of a nature-like fishway (Figure 1c), whereas in the main river, the approach zone has been defined 50 m upstream of the hydropower plant.

2.2. Smolts Tagging and Tracking

The studied Atlantic salmon smolts were 1-year-old hatchery-reared individuals from the Erezee hatchery in Belgium. Hatchery-reared smolts usually started their downstream migration the day of tagging as observed during previous studies [26,27]. Tracking wild smolts was impossible due to their small size and low weight, making them unable to support the transmitter. There was a total of 25 smolts used, with a mean fork length of 162.9 mm $\pm$ 8.9 mm and a mean body mass of 49.2 g $\pm$ 8.9 g. The smolts were transported in an equipped van from the hatchery to the release site in a 600 L oxygenated tank. The tagging process was performed in the field near the release site. The smolts were anaesthetised with 0.2 mL L^{-1} of phenoxyethanol and surgically tagged with a transmitter in their body cavity. The radio transmitter (Advance Telemetry Systems – ATS, Isanti, USA) used was a Model F1410 with a frequency of 40 MHz, dimensions of 7 mm $\times$ 15 mm, a mass in air of 1.0 g, and an expected life span of 14 days. An additional small incision was made independently of the main incision by using a thin steel cannula to enable the passage of the external antenna. The 8 mm incision was closed with absorbable suture material (VICRYL® Suture JV398, Edinburgh, Scotland) and disinfected with eosin (see [3,26]). The average time of surgery was around 10 min per individual. The releases in the river were performed after a full recovery around two hours after the surgery. The smolts were divided into four groups of six (G1 to G3) or seven (G4) individuals each. Each release group consisted of a limited number of individuals to be able to track each smolt manually and accurately upstream of the hydropower plant. The groups were released 1330 m upstream from the hydropower plant at around 4–5 pm on different dates to experience different environmental conditions.

The radio-tagged smolts were manually and intensively tracked by a team of 4 to 5 operators just after their release until the hydropower plant crossing. The smolts that did not pass the plant on the evening/night of the release day were tracked less intensively during the following days until the site crossing. The tracking was performed using portable receivers (ATS Model Fieldmaster) and either directional (low-frequency loop) or non-directional antennas (magnetic roof-mount dipole) (see [26,27]). Directional antennas were used to locate smolts with a precision of 5 m^2 (see [26,27]), which helped to identify the precise research behaviour upstream of the hydropower plant.

During the experimental period, water temperature (°C) was recorded every hour using data loggers (Tidbit Onset, Bourne, USA) installed at the Chanxhe hydropower plant. Discharge data ($m^3 s^{-1}$) were obtained by the hydrological office of the Public Service of Wallonia (SPW-SETHY, Namur, Belgium) at the Comblain-au-Pont hydrological station, with measurements taken every 5 min. The water temperature during the smolt tracking period ranged from 11.5 °C to 16.8 °C, while discharge ranged between 12.8 $m^3 s^{-1}$ and 20.9 $m^3 s^{-1}$.

2.3. Smolt Behavioural Metrics

Several quantitative behavioural metrics useful to describe the smolt migratory behaviour were highlighted based on the smolt tracking:

(1). Adaptation time: median time (hours) required for the smolts to initiate the downstream migration after the release event, which corresponds to the time between the release time and the initiation of migration.

(2). Arrival time: median time (hours) to reach the upstream zone, where there is the emergence of the nature-like fishway, which corresponds to the time between the migration initiation and the first detection in the upstream zone (see [27]).

(3). Migration route use: the percentage of smolts using each available migration route compared to all the tagged smolts that initiated the downstream migration (see [27]).

(4). Research time: median time (hours) required by the smolts to pass through the hydropower plant. It corresponds to the time between the first detection in the approach zone and the last detection upstream of the plant (see [27]).

(5). Crossing time: median time (hours) required by the smolts to pass through the entire study site. It corresponds to the time between the first detection in the upstream zone and the last detection upstream of the plant or the first detection downstream of the nature-like fishway.

The individual **behavioural tactic** expressed by the smolts to cross the hydropower plant was identified. A behavioural tactic refers to the specific expressed research behaviour when crossing a hydropower plant, including the number of approached migration routes and the research time (see [27]). The four different behavioural tactics are: "proactive explorer", "reactive explorer", "proactive non-explorer" and "reactive non-explorer".

2.4. Hydrodynamic Numerical Modelling

To combine the planar characteristics of fish trajectories obtained by telemetry with detailed hydrodynamic conditions encountered by smolts approaching the hydropower plant, the flow conditions were numerically modelled with a 2D hydrodynamic approach, i.e., solving depth-integrated flow equations with the flow solver WOLF2D. WOLF2D solves the shallow water equations on a Cartesian grid using a finite volume technique. In simple terms, on each grid cell, the software computes the temporal evolution of the water depth and both flow velocity components in the main flow plane. In continuous development for more than 20 years by the HECE research group of the University of Liège, WOLF2D has been massively validated by various hydraulic and environmental studies and projects [22,33,34].

The main data required by the numerical model are the topography/bathymetry of the study area and the discharges. The topography/bathymetry of the Chanxhe hydropower site was first extracted from LIDAR (light detection and ranging) data collected by an airborne survey provided by the Public Service of Wallonia (1 point per m^2—0.15 m elevation accuracy) and then completed by interpolation of 1D cross sections of the main river bed for the area below water. In total, 365 points were surveyed manually in the nature-like fishway with a GPS (SinoGNSS N3) to refine the bathymetry data in this complex shallow water area. The resulting digital elevation model covered 1400 m of the river length upstream of the hydropower plant with a horizontal resolution of 0.5 × 0.5 m (596,937 grid cells) and vertical accuracy of 0.15 m.

The discharge extracted from the Comblain-au-Pont hydrological station (SPW, 2023) located 135 m upstream of the first grid cell was used as upstream boundary conditions for the simulation. The weir and the opened incision gates were modelled as a broad-crested weir (discharge coefficient equal to 0.385) while the incision gates closed either by a piece of metal or wood were modelled as a sharp-crested weir (discharge coefficient equal to 0.42). This means that the discharge passing over the weir or the incision gates was calculated at each time step by the numerical model depending on the upstream head value (i.e., the water level upstream of the weir). Similarly, the discharge in the canal intake was calculated from the upstream head depending on critical flow conditions at the two circular pipes located downstream in the canal. The discharge through the two Archimedes screws was deduced from the site operations (one observation every 20 min) after cleaning, filtering and conversion of the data collected from the site operator. In the nature-like fishway, no boundary condition was imposed since flow conditions were supercritical at the downstream extremity of the river stretch.

The numerical model has been validated compared to on-site measurements (river gauging—10% accuracy) carried out by SPW on 6 May and 23 September 2022. The maximum difference between the simulated and measured discharges in the nature-like fishway was 18% while the maximum difference between the water depths was 3% in the canal intake.

As a result of the small variation in discharge during each of the four smolt release events, four scenarios simulating the mean discharge observed in the river and through the Archimedes screws during each smolt release event have been considered (Figure 2).

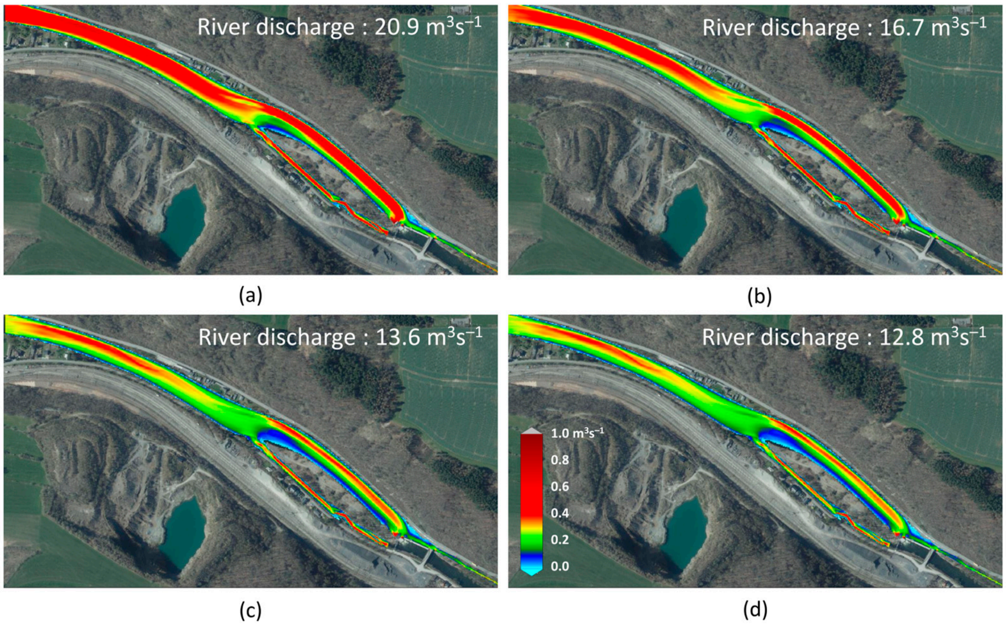


Figure 2. Specific discharges (coloured scale) of the simulated hydraulic scenarios at the Chanxhe hydropower plant used as boundary condition at the site entrance for each release event, (**a**) 1st release group, (**b**) 2nd release group, (**c**) 3rd release group and (**d**) 4th release group.

Bathymetry measurements highlighted the topographic profile of the river, especially the differences between the main river (Figure 3a) and the nature-like fishway (Figure 3b). The main river profile has a relatively continuous slope counter-balanced at the end, near the intake canal, by a rapid elevation in topography to create a small reservoir for the Archimedes screws (Figure 3a). The reservoir is characterised by low velocity values (range 0.14–0.37 m s^{-1}) with important water depths (range 0.37–2.25 m), whereas the nature-like fishway possesses an irregular steep profile characterised by high velocities, which reached 2.19 m s^{-1}, and shallow waters (range 0.03–0.72 m) as observed during the topographic survey (Figure 3b). The Froude number is a ratio of the forces of inertia and gravitation and allows us to characterise the flow in rivers. The Froude number varied between 0.03 and 0.18 in the main river. On the other hand, the Froude number was usually more significant in the nature-like fishway. At the entrance of the nature-like fishway, the Froude number was around 0.60, and the mean Froude number throughout the route was 0.66, but varied between 0.17 and 2.40.

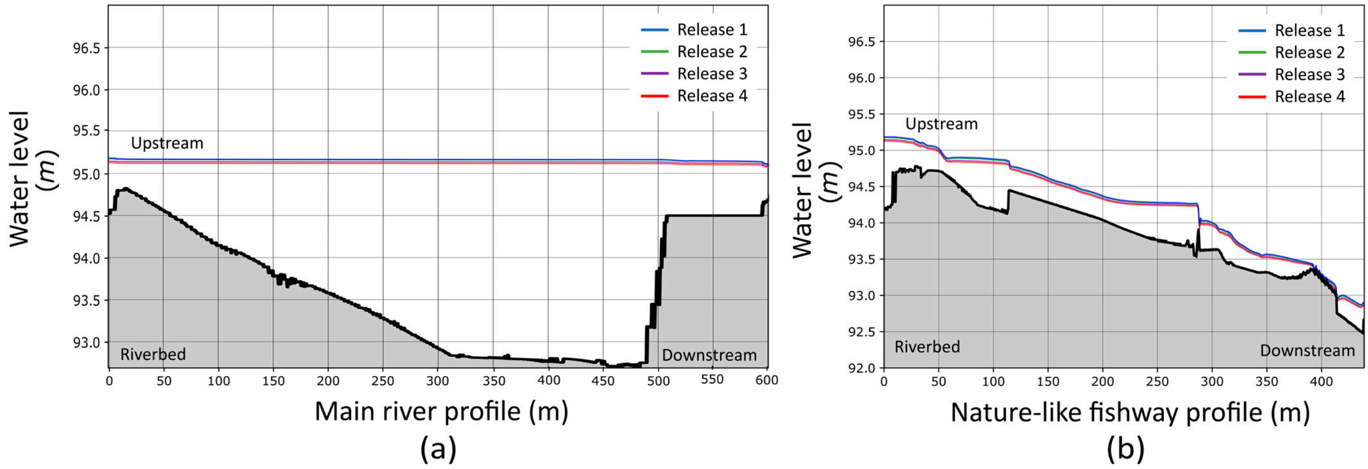


Figure 3. The topographic profile of (**a**) the main river and (**b**) the nature-like fishway from the upstream zone to downstream of the Chanxhe hydropower plant.

Depending on the release date, the discharge through the nature-like fishway ranged from 3.4 $m^3 s^{-1}$ to 4.6 $m^3 s^{-1}$ (Table 1). At the hydropower plant, one or two Archimedes screws were operating depending on the release date. The turbine discharge varied between 5.6 $m^3 s^{-1}$ and 11.7 $m^3 s^{-1}$. The discharge over the weir and through the incision gates varied between 2.9 $m^3 s^{-1}$ and 3.4 $m^3 s^{-1}$ and discharge toward the intake canal was relatively constant with around 1 $m^3 s^{-1}$.

Table 1. Hydraulic conditions encountered by tagged smolts.

		Measured				Computed from Numerical Models				
			Archimedes Screw			Nature-like Fishway		Weir		Intake Canal
Group	Release Event	Mean Total Discharge (m^3/s)	N Turbines	Mean Discharge ($m^3 s^{-1}$)	% of Total Discharge	Mean Discharge ($m^3 s^{-1}$)	% of Total Discharge	Mean Discharge ($m^3 s^{-1}$)	% of Total Discharge	Mean Discharge ($m^3 s^{-1}$)
1	20-04	20.9	2	11.7	56.0	4.6	22.0	3.4	16.3	1.2
2	26-04	16.7	1	7.9	47.3	4.3	25.7	3.4	20.4	1.1
3	03-05	13.6	1	6.0	44.1	3.8	27.9	2.9	21.3	1.0
4	10-05	12.8	1	5.6	43.8	3.4	26.6	2.9	22.7	0.9

2.5. Statistical Analyses

The obtained data violated the assumptions of normality (Kolmogorov–Smirnov, $p < 0.05$), and therefore non-parametric tests were used. All statistical analyses were carried out by using the software R (version 3.4.2).

We first conducted analyses in relation to the first objective of identifying the smolt behavioural tactics upstream of the hydropower plant and assessing the attractiveness and the use of the different migration routes, specifically in relation to the nature-like fishway. At the release site, the adaptation time was compared between the release events by using a Kruskal–Wallis (KW) test. In the upstream zone, the smolts' choice between the main river and the nature-like fishway was compared with a random distribution using Pearson's χ^2 test. In the approach zone, the number of smolts per migration route was compared with a random distribution using Fisher's exact test. Crossing time and research time were compared between the migration routes and the release events by using Kruskal–Wallis (KW) and Dunn tests.

In a second step, analyses were performed to respond to the second objective of trying to understand the potential influence of environmental and hydrodynamic factors on smolt behavioural tactics during downstream migration. We compared the environmental and hydrodynamic characteristics of the main river and the nature-like fishway (e.g., flow velocity, discharge, and water depth) using Dunn tests. These analyses allowed us to investigate how variations in these factors might have influenced the behavioural tactics expressed by the smolts.

Discharge: in the upstream zone, the use of the nature-like fishway by the smolts was tested according to the proportion of associated discharge passing towards this route by using a Dunn test. Once in the approach zone, the influence of the discharge on the number of approached migration routes by the smolts was tested by using a Spearman correlation. The use of the Archimedes screws by the smolts to cross the hydropower plant was tested according to the proportion of associated discharge diverted towards the screws by using Fisher's exact test. The correlation between the river discharge and the crossing time of the smolts was tested by using a Spearman correlation.

Flow velocity: in the approach zone, the use of a migration route depending on the associated flow velocity was compared with a random distribution by using Fisher's exact test, below and over 0.5 m s^{-1}, based on observations of Renardy et al. [22]. The relationship between the crossing time and the mean encountered flow velocities throughout the nature-like fishway or the main river was tested by using a Spearman correlation.

Water depth: The relationship between the crossing time and the mean encountered water depths throughout the nature-like fishway or the main river was tested by using a Spearman correlation.

3. Results

Among the n = 25 tested smolts, 96% (n = 24) left the release site, after a median adaptation time of 0h42 and initiated the downstream migration before dusk. The adaptation time did not differ between the release groups (KW test, n = 24 smolts, χ^2 = 5.8, df = 3, $p > 0.1$). 88% of the smolts (n = 22) were detected in the upstream zone with a median arrival time of 2h36. Of these individuals, 23% (n = 5) approached and used the nature-like fishway, whereas the other 77% of smolts (n = 17) moved toward the hydropower plant (Table 2 and Figure 4). The choice between one of these two migration routes did not differ significantly from a random distribution (Pearson's χ^2 test, p = 0.08). The conditions of flow velocities, water depths and the Froude number at the entrance varied significantly between the main river and the nature-like fishway (Dunn test, all $p < 0.001$). The main river was characterised by lower flow velocities (Figure 4) and higher water depths. The majority of smolts used the main river, which was associated with 72–78% of the total river discharge. The smolts used the nature-like fishway to downstream migrate when the proportion of discharge increased from 22 to 28% of the total river discharge (Dunn test, n = 22 smolts, $p < 0.01$).

Table 2. The migration routes used by the smolts for each release group.

Group	Release Event	Nature-like Fishway	Archimedes Screw	Weir		Intake Canal	Unknown Route	Total
				1st Incision Gate	2nd Incision Gate			
1	20-04	0	2	0	1	1	2	6
2	26-04	0	3	0	1	1	1	6
3	03-05	3	1	1	0	0	1	6
4	10-05	2	2	0	1	2	0	7

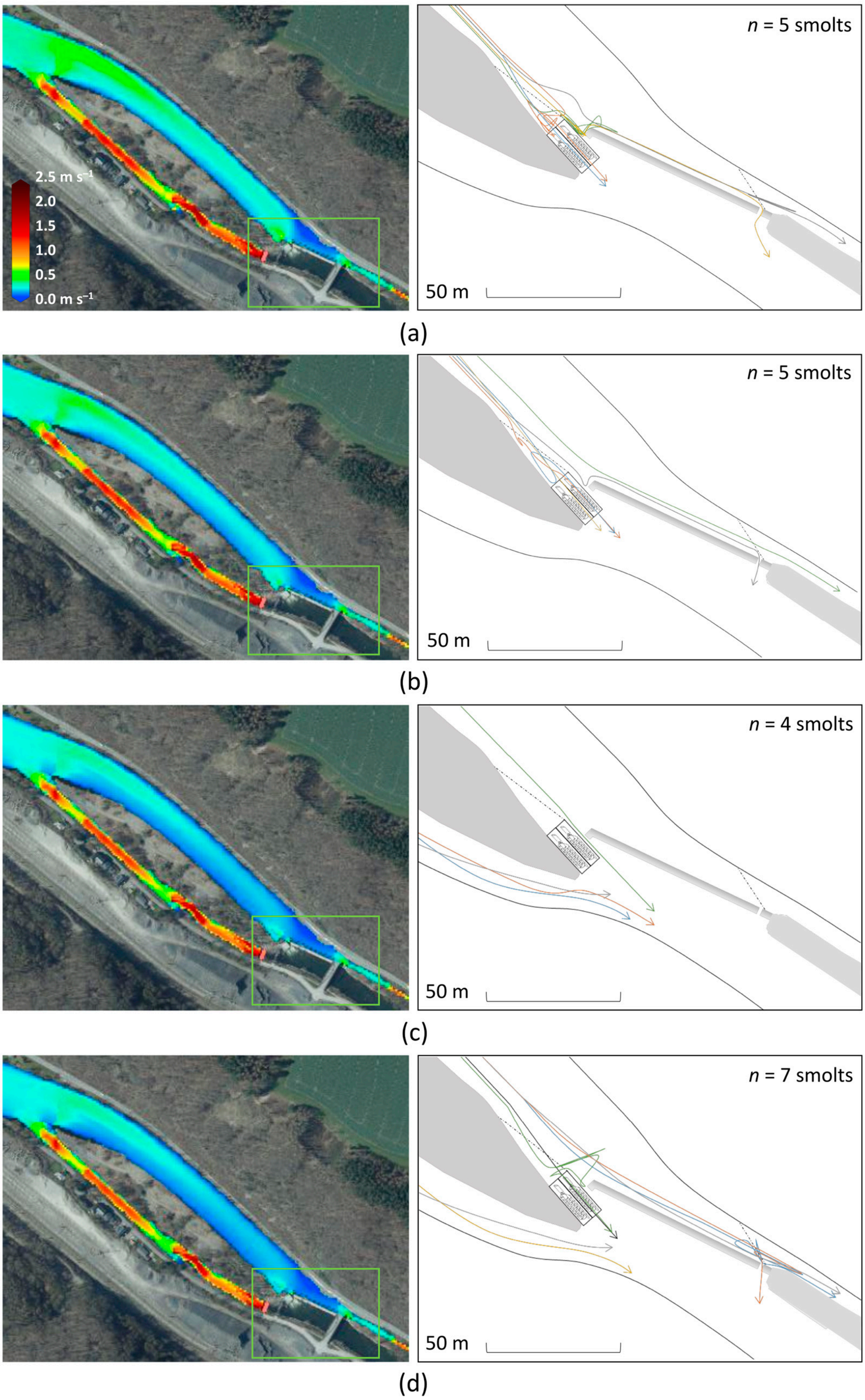
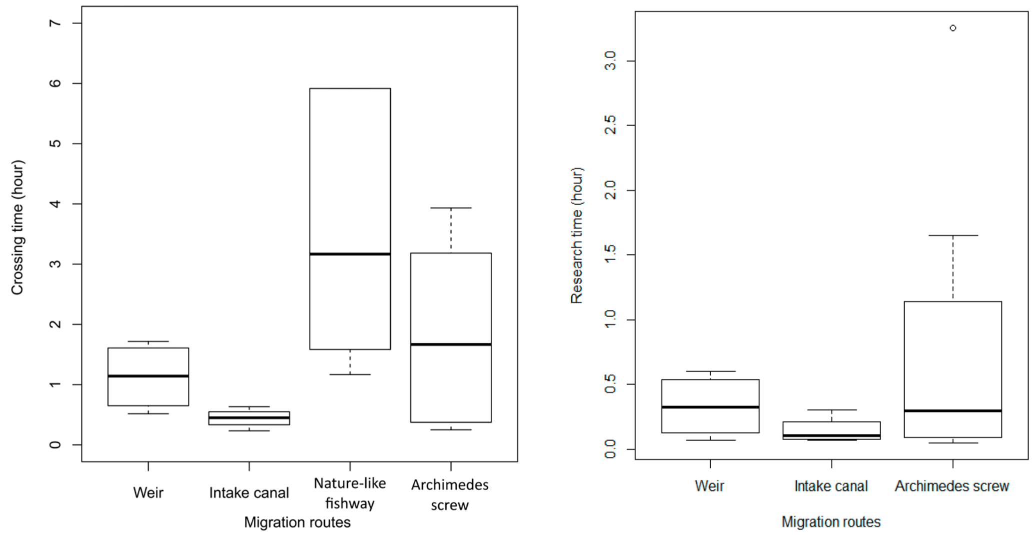


Figure 4. Combination of the twenty-one smolt trajectories (indicated by a coloured arrows) and specific water velocities (indicated by a coloured scale) of the simulated hydrological scenario at the Chanxhe hydropower plant for each release event, (**a**) 1st release group, (**b**) 2nd release group, (**c**) 3rd release group and (**d**) 4th release group. One of the twenty-two smolts is not represented due to an incomplete migration trajectory.

Once in the approach zone, $n = 8$ smolts approached first the Archimedes screw and the $n = 8$ other smolts approached first the weir (Figure 4). The first-approached migration route is unknown for one smolt. On average, the smolts rejected the first-approached migration route once and approached another route. The number of approached migration routes by the smolts before the plant crossing was not influenced by the discharge (Spearman's correlation, $n = 16$ smolts, rho = -0.39, $p > 0.1$). All the smolts that reached the approach zone crossed the hydropower plant. The passage mainly took place (75% of the smolts) during dusk or the night. The migration route used is known for 94% of them ($n = 16$). More than half of the smolts ($n = 9$) passed on the first approach. The Archimedes screw was the most used migration route with 50% of the smolts ($n = 8$) (Table 2). The Archimedes screw directed 72–78% of the incoming discharge at the hydropower plant (44–56% of total river discharge), but the proportion of associated discharge did not influence its use by the smolts to cross the hydropower plant (Fisher's exact test, $n = 16$ smolts, $p > 0.1$). The other 50% of smolts used an alternative migration route with lower associated discharges and passed through the incision gates (25%, $n = 4$) or the intake canal (25%, $n = 4$) (Table 2). The use of a migration route did not differ significantly from a random distribution (Fisher's exact test, $n = 16$ smolts, $p > 0.1$). The majority of the smolts (75%) used a migration route (the Archimedes screw or the canal intake) characterised by flow velocities below 0.5 m s^{-1} at their entrance (Figure 4). This distribution did not differ significantly from a random distribution (Fisher's exact test, $n = 16$ smolts, $p > 0.1$).

The behavioural tactic to find a migration route was defined for $n = 16$ smolts that passing through the Chanxhe hydropower plant. The different tactics were expressed by the smolts in equal proportions. Eight smolts approached only one migration route, with two expressing the "proactive non-explorer" tactic and six expressing the "reactive non-explorer" tactic. The remaining eight smolts approached multiple migration routes before crossing the site, with three expressing the "proactive explorer" tactic and five expressing the "reactive explorer" tactic.

The median crossing time required to cross the entire site was 01h10 (Figure 5a). There was no correlation between the smolt crossing time and the river discharge (Spearman's correlation, $n = 21$ smolts, rho = -0.30, $p > 0.1$). The crossing time differed significantly between the main river and the nature-like fishway (Dunn test, $n = 21$ smolts, $p = 0.02$), with a longer crossing time through the nature-like fishway. Although a correlation was found between the encountered flow velocities and water depths with the crossing time of the smolts, those were low (Spearman's correlation, $n = 21$ smolts, rho = 0.38, $p = 0.09$ and rho = -0.39, $p = 0.08$, respectively). Elevated flow velocities, shallow water depths and a significant slope could slow down smolts in their migration progression (Figure 4). Upstream of the hydropower plant, the median research time was 00h11 (Figure 5b), but did not differ between the migration routes used (KW test, $n = 16$ smolts, $\chi^2 = 1.2$, df = 2, $p > 0.1$) and the release events (KW test, $n = 16$ smolts, $\chi^2 = 3.5$, df = 3, $p > 0.1$).



(**a**) (**b**)

Figure 5. Behavioural metrics expressed by the smolts depending on the migration route used to cross the study site: (**a**) the crossing time and (**b**) the research time.

4. Discussion

In this study, we investigated the downstream migratory behaviour of Atlantic salmon smolts using manual 2D radio telemetry at a hydropower plant that offers five potential migration routes, including a nature-like fishway, two fish-friendly Archimedes screws, the weir with two incision gates and a canal intake. Manual tracking has the advantage of identifying the fine-scale behaviour of the smolts upstream of the Chanxhe hydropower plant by recording of numerous precise positions for each individual. Due to technical limitations of this tool on simultaneous tracking of a large number of individuals, in this study, only a small number of smolts could have been tracked simultaneously. Using additional automatic listening receivers would have been useful to track more smolts. However, it is more difficult to obtain 2D trajectories of the smolts with automatic tracking devices, especially if the number of antennas is insufficient. Another alternative would be to combine manual radio telemetry with automatic RFID telemetry to easily increase the number of fish and more accurately assess the attractiveness and efficiency of migration routes, such as the nature-like fishway. Hydrodynamic modelling was useful in identifying the environmental and hydrodynamic conditions upstream of the hydropower plant, even if the variability of the conditions was low. The small number of tracked individuals and the low variability of discharge conditions during the study do not allow a complete vision of what would have happened during the entire smolt migration season, especially under extreme environmental conditions. Therefore, strong and significant statements on the influence of environmental and hydrodynamic conditions on the migratory behaviour and on the choice of a migration route could not be demonstrated, but clear tendencies have been highlighted. An additional tracking with a larger number of individuals would be necessary to statistically confirm the results obtained in this study.

All of the smolts except one individual left the release site and initiated downstream migration after a median adaptation time of 0h42. A negative impact of the tagging on smolt mortality is unlikely as the ratio between weights of the transmitter and of the smolts was less than 2.5%. No smolt was affected by the surgery during the recovery phase before release events. Tagging methodology was the same as previous studies that used mobile tracking on Atlantic salmon (*Salmo salar* L.) smolts or Brown trout (*Salmo trutta* L.) [26,27,35]. Therefore, we assume that predation by cormorants might have been the most plausible explanation for the missing individual, as there were several cormorant colonies in the vicinity of the release site. Predation is the main natural cause of mortality during smolt downstream migration [10,36]. Cormorants, avian predators, are known to be a significant threat to smolts [3,37,38]. The hatchery-reared smolts remained highly sensitive to environmental cues triggering downstream migration [39] and usually expressed rapid initiation of downstream migration once released in rivers [14,26,27].

Once in the upstream zone, 23% of the smolts approached and used the nature-like fishway and the 77% other smolts moved toward the hydropower plant. The nature-like fishway appeared to be less attractive to the smolts. The environmental and hydrodynamic conditions at its entrance were sub-optimal to the smolts, with a low mean water discharge of 4.0 m^3 s^{-1}, an elevated mean water velocity of 0.9 m s^{-1} and a low mean water depth of 0.35 m. Migrating smolts are able to perceive a danger of an inadequate migration route with unsuitable associated hydrodynamic conditions, and therefore try to find a safer way [7,22,29,40,41]. The choice of the smolts between these two migration routes might have depended on the discharge repartition. As suggested in the literature, the downstream-migrating smolts usually tend to follow the main flow [7,11,22,27,30,42], and therefore migrate through the main river. The nature-like fishway was associated with 22–28% of the total river discharge, which corresponds to a mean discharge of approximately 4.0 m^3 s^{-1}. In previous studies, the associated discharge of nature-like fishways varied between 0.3 m^3 s^{-1} [20,43], 0.6 m^3 s^{-1} [44] and 11.0 m^3 s^{-1} [21]. Depending on the percentage of the total discharge diverted toward the nature-like fishway, its use by the smolts ranged from 3% to 12% (equivalent to 2.3% and 6% of the total discharge) [20] and 41% (29.7% of the total discharge) [21]. In our study, the nature-like fishway was used by 23% of the smolts, which is consistent with the literature. Fjeldstad et al. [45] highlighted an increasing bypass migration by the smolts with an increasing proportional diversion of the total flow toward the bypass. The discharge proportion toward the nature-like fishway seems to be insufficient to enable elevated use by the smolts. Increasing the proportion of the total flow diverted to the nature-like fishway, would enable an increase of its utilisation by the smolts. On the other hand, Kärgenberg et al. [44] observed an use of a nature-like fishway by 80% of the smolts, which was provided by about 10% of the flow. In our study, the low use of the nature-like fishway, despite having a more elevated proportion of discharge, may indicate the influence of other environmental conditions. Flow velocity and water depth are considered also as hydraulic clues in the selection of a migration route [27]. Elevated water velocities and shallow water depths at the entrance of the nature-like fishway may have repulsed the smolts from using this migration route. Typically, smolts are attracted to flow velocities between 0.2 m s^{-1} and 0.5 m s^{-1} [22,27,46] and prefer water depths greater than 1.5 m [27], contrary to the conditions present in the nature-like fishway. Therefore, the use of a nature-like fishway will depend on the associated discharge, the river discharge, as well as flow velocities and water depths.

The remaining 77% of the smolts were detected in the approach zone, and the weir and the Archimedes screws were equally approached at 50%. Prior to crossing the hydropower plant, the smolts rejected the approached migration route once on average, with 53% of the smolts not rejecting the first-approached migration route and crossing the hydropower plant through this route. Renardy et al. [27] highlighted a mean number of rejections of a migration route of 6.5, probably due to the presence of inadequate migration routes. In this study, the low number of rejections could suggest that the first migration route approached appeared to be sufficiently attractive for the smolts. All the smolts successfully passed through the hydropower plant, and the Archimedes screws were the most used migration routes, with 50% of the smolts using them. In the literature, the Archimedes screw use varied between 5% ([27]—4 migration routes), 8.1% ([25]—3 migration routes), 43% ([24]—5 migration routes) and 48% ([3]—2 migration routes). The smolts usually approached and used the migration route with the highest associated proportion of discharge, as already observed by Fjelstad et al. [45] and Havn et al. [24]. In our study, the Archimedes screws diverted 72–78% of the incoming discharge at the plant. The fish-friendly design of the Archimedes screw does not guarantee that smolts will not be repulsed by characteristics at the turbine intake [27,47]. In this study, the characteristics of the turbines' intake did not appear to frighten and repulse the smolts. All the smolts who used the Archimedes screw to cross the plant passed through it in less than 6 min. Renardy et al. [3] observed a similar tendency with a median time to cross the Archimedes screw of 1 min. The other smolts that did not follow the main flow passed by the weir through the incision gates (25%) and by the intake canal (25%). The low use of the two alternative migration routes may be due to shallow depths at their entrance varying between 0.6 and 0.8 m. Water depths less than 1 m are usually less approached by the smolts if greater depths are available [27]. The intake canal appeared to be a sub-optimal and unsafe migration route, as half of the smolts that used this route never managed to cross it and to continue the downstream migration. Slack water and a low slope in the intake canal may have engendered smolt disorientation and may have stopped smolt downstream migration. Standing waters induce a weaker instinct to migrate and reduce migration success [48]. Low flow velocities (<0.15 m s^{-1}) usually cause smolt disorientation and a loss of stimulation of the smolts to move downstream [22,40]. At this particular migration barrier, the Archimedes screw turned out to be the most suitable and safe migration route compared to the intake canal due to its more elevated attractiveness and due to its low direct impact on smolt downstream migration.

The median crossing time required to cross the entire site, both via the main river or by the nature-like fishway, was 01h10. The crossing time differed significantly between the main river and the nature-like fishway, with a longer crossing time through the nature-like fishway. The median crossing speed in the nature-like fishway was 0.04 m s^{-1}. Nyqvist et al. [21] reported a similar trend with a very low median crossing speed of 0.01 m s^{-1} through a nature-like fishway. In one un-impounded river stretch, Aarestrup et al. [49] obtained a high variation of progression speeds ranging from 0.01 m s^{-1} to less than 0.23 m s^{-1}, but also observed speeds of 0.38 m s^{-1} [38], 0.61 m s^{-1} [50] and 0.94 m s^{-1} [51]. The correlations between encountered flow velocities or water depths and crossing time were low, but these variables may have still have influenced and delayed smolt downstream migration. Water velocities greater than 0.2 m s^{-1} usually promote downstream movements of the smolts [22,46], but can become repulsive beyond a certain threshold. In the nature-like fishway, the combination of a shallow average water depth of 0.35 m and water velocities that reached around 2 m s^{-1} in some areas may have induced hesitation in the smolts to migrate rapidly. Furthermore, the topographic profile of the nature-like fishway, of which the slope is 4.8‰, may also have contributed to the smolts' reluctance to migrate downstream rapidly. Persson et al. [52] observed a similar trend of slower smolt downstream migration in a river stretch associated with a steep slope (9.9‰) and high flow velocities (ranging from 0.85 to 1.14 m s^{-1}). The significant migration delays through the nature-like fishway suggest that the associated characteristics are suboptimal for facilitating smolt downstream migration. To improve downstream migration through the nature-like fishway, water depths should ideally be increased and the slope reduced in order to reduce flow velocities.

At the Chanxhe hydropower plant, the median research time was 11 min, which is similar to research times observed at overspill weirs [53], ranging from 2 to 32 min. The median required time to cross a medium-sized hydropower plant offering multiple migration routes varied between 0.5 h ([24], with five migration routes; [43], with eight migration routes), 0.2 and 0.9 h ([13], with three migration routes) but can reach up to 4.5 h ([27], with five migration routes). At first sight, the Chanxhe hydropower plant appears to be less impactful to the smolts during downstream migration compared to other hydropower plants studied in the literature. The associated isolated impact appeared to be therefore negligible, but the smolts still have multiple subsequent migration barriers to cross before reaching the sea. Cumulative delays caused by migration barriers will gradually increase during downstream migration [3] and may cause a mismatch between migration timing and the physiological window that prevents the smolts reaching the sea in time [54].

All four behavioural tactics were expressed in equal proportions by the smolts upstream of the Chanxhe hydropower plant. Among the smolts, 31% were proactive and crossed the hydropower plant rapidly, of which 60% used a safe migration route such as the Archimedes screws or the weir. The more hesitant smolts were considered as reactive, but their research time varied between 0h06 and 3h15, which remained relatively low for some of them. In total, 50% of the smolts did not explore and cross the hydropower plant by the first-approached migration route. Renardy et al. [26] and Marschall et al. [54] highlighted the same trend to cross a hydropower plant during the first or the second attempt for the majority of the smolts. At Chanxhe hydropower plant, among the smolts who explored the plant, 50% used the intake canal. After having approached multiple migration routes, the smolts used an unsafe migration route. Despite facing similar environmental conditions, the smolts expressed different behavioural tactics to find a migration route and cross the migration barrier, which might suggest the potential influence of an individual personality [26,55–57]. The fish, characterised by a more pronounced migratory behaviour and a greater tendency to explore new environments, are typically associated with a bolder behavioural trait [58,59]. Lothian and Lucas [57] demonstrated that bolder and more active Brown trout (*Salmo trutta*) individuals would be more willing to cross migration barriers efficiently during migration. The behavioural tactic "reactive explorer" appears to be a suboptimal tactic, inducing in most cases more significant migration delays and not preventing the smolts from entering an unsafe migration route [27]. Spending more time upstream of a migration barrier increases the chances of smolts being forced into an unsafe migration route [60,61]. To improve downstream migration through hydropower plants, it is important to consider all the different behavioural tactics used by the smolts. This can be achieved through the installation of guiding systems that direct non-explorer smolts towards safe migration routes and physical barriers that prevent explorers and non-explorers from entering unsafe migration routes. Additionally, migration routes need to be sufficiently attractive to minimise hesitation in smolts, promote proactivity, and reduce delays caused by hydropower plants.

Author Contributions: Conceptualization, S.R., J.-P.B. and M.O.; methodology, S.R., J.-P.B. and M.O.; software, P.A., M.P. and S.E.; formal analysis, S.R., U.D.C., J.-P.B. and M.O.; investigation, S.R., U.D.C., J.-P.B., A.D., J.G., P.A., B.D., S.E. and M.O.; data curation, S.R. and U.D.C.; writing—original draft, S.R.; writing—review and editing, S.R., U.D.C., J.-P.B., A.T.S., S.E. and M.O.; project administration, S.E. and M.O.; funding acquisition, S.R., S.E. and M.O. All authors have read and agreed to the published version of the manuscript.

Funding: Financial support for this study was provided by the Public Service of Wallonia, and more precisely the DNF (Département de la nature et des forêts—Service de la Pêche) (Meuse Salmon programme—N° 22/04464—Funding in 2022). Séverine Renardy received a Ph.D. research grant from FNRS-FRIA (Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture) for a project on the smolt downstream migration.

Data Availability Statement: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Acknowledgments: We thank Niels Duchesne for authorising access to the hydropower plant during the study and the SPW (Public Service of Wallonia) SETHY for the discharge data. We thank the team of the CoSMos hatchery of Erezée for the acquisition of Atlantic salmon smolts.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Nilsson, C. Fragmentation and Flow Regulation of the World's Large River Systems. *Science* **2005**, *308*, 405–408. [CrossRef] [PubMed]
2. Benitez, J.-P.; Dierckx, A.; Nzau Matondo, B.; Rollin, X.; Ovidio, M. Movement Behaviours of Potamodromous Fish within a Large Anthropised River after the Reestablishment of the Longitudinal Connectivity. *Fish. Res.* **2018**, *207*, 140–149. [CrossRef]
3. Renardy, S.; Colson, D.; Benitez, J.; Dierckx, A.; Goffaux, D.; Sabbe, J.; Rabouan, A.; Detrait, O.; Nzau Matondo, B.; Sonny, D.; et al. Migration Behaviour of Atlantic Salmon Smolts (*Salmo salar* L.) in a Short and Highly Fragmented Gravel-bed River Stretch. *Ecol. Freshw. Fish* **2022**, *31*, 499–514. [CrossRef]
4. Parrish, D.L.; Behnke, R.J.; Gephard, S.R.; McCormick, S.D.; Reeves, G.H. Why Aren't There More Atlantic Salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **1998**, *55*, 281–287. [CrossRef]

5. Katopodis, C.; Williams, J.G. The Development of Fish Passage Research in a Historical Context. *Ecol. Eng.* **2012**, *48*, 8–18. [CrossRef]
6. Benitez, J.-P.; Dierckx, A.; Rimbaud, G.; Nzau Matondo, B.; Renardy, S.; Rollin, X.; Gillet, A.; Dumonceau, F.; Poncin, P.; Philippart, J.-C.; et al. Assessment of Fish Abundance, Biodiversity and Movement Periodicity Changes in a Large River over a 20-Year Period. *Environments* **2022**, *9*, 22. [CrossRef]
7. Williams, J.G.; Armstrong, G.; Katopodis, C.; Larinier, M.; Travade, F. Thinking like a Fish: A Key Ingredient for Development of Effective Fish Passage Facilities at River Obstructions: Fish Behaviour Related Fish Passage at Dams. *River Res. Appl.* **2012**, *28*, 407–417. [CrossRef]
8. Fjeldstad, H.-P.; Pulg, U.; Forseth, T. Safe Two-Way Migration for Salmonids and Eel Past Hydropower Structures in Europe: A Review and Recommendations for Best-Practice Solutions. *Mar. Freshw. Res.* **2018**, *69*, 1834. [CrossRef]
9. McCormick, S.D.; Hansen, L.P.; Quinn, T.P.; Saunders, R.L. Movement, Migration, and Smolting of Atlantic Salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **1998**, *55*, 77–92. [CrossRef]
10. Thorstad, E.B.; Whoriskey, F.; Uglem, I.; Moore, A.; Rikardsen, A.H.; Finstad, B. A Critical Life Stage of the Atlantic Salmon *Salmo salar*: Behaviour and Survival during the Smolt and Initial Post-Smolt Migration. *J. Fish Biol.* **2012**, *81*, 500–542. [CrossRef]
11. Szabo-Meszaros, M.; Forseth, T.; Baktoft, H.; Fjeldstad, H.; Silva, A.T.; Gjelland, K.Ø.; Økland, F.; Uglem, I.; Alfredsen, K. Modelling Mitigation Measures for Smolt Migration at Dammed River Sections. *Ecohydrology* **2019**, *12*, e2131. [CrossRef]
12. Scruton, D.A.; McKinley, R.S.; Kouwen, N.; Eddy, W.; Booth, R.K. Improvement and Optimization of Fish Guidance Efficiency (FGE) at a Behavioural Fish Protection System for Downstream Migrating Atlantic Salmon (*Salmo salar*) Smolts. *River Res. Appl.* **2003**, *19*, 605–617. [CrossRef]
13. Tomanova, S.; Courret, D.; Alric, A.; De Oliveira, E.; Lagarrigue, T.; Tétard, S. Protecting Efficiently Sea-Migrating Salmon Smolts from Entering Hydropower Plant Turbines with Inclined or Oriented Low Bar Spacing Racks. *Ecol. Eng.* **2018**, *122*, 143–152. [CrossRef]
14. Ovidio, M.; Renardy, S.; Dierckx, A.; Nzau Matondo, B.; Benitez, J.-P. Improving Bypass Performance and Passage Success of Atlantic Salmon Smolts at an Old Fish-Hostile Hydroelectric Power Station: A Challenging Task. *Ecol. Eng.* **2021**, *160*, 106148. [CrossRef]
15. Tomanova, S.; Courret, D.; Richard, S.; Tedesco, P.A.; Mataix, V.; Frey, A.; Lagarrigue, T.; Chatellier, L.; Tétard, S. Protecting the Downstream Migration of Salmon Smolts from Hydroelectric Power Plants with Inclined Racks and Optimized Bypass Water Discharge. *J. Environ. Manag.* **2021**, *284*, 112012. [CrossRef]
16. Cefas, A. *Assessment of Damage to Smolts Caused by Archimedes Screw Hydropower Turbines*; TRI Potter, P. Davison & A. Moore: Lowestoft, UK, 2012.
17. Hogan, T.W.; Cada, G.F.; Amaral, S.V. The Status of Environmentally Enhanced Hydropower Turbines. *Fisheries* **2014**, *39*, 164–172. [CrossRef]
18. Celestino, L.F.; Sanz-Ronda, F.J.; Miranda, L.E.; Makrakis, M.C.; Dias, J.H.P.; Makrakis, S. Bidirectional Connectivity via Fish Ladders in a Large Neotropical River: Maintaining Connectivity via Fish Ladders. *River Res. Appl.* **2019**, *35*, 236–246. [CrossRef]
19. Sanz-Ronda, F.J.; Fuentes-Pérez, J.F.; García-Vega, A.; Bravo-Córdoba, F.J. Fishways as Downstream Routes in Small Hydropower Plants: Experiences with a Potamodromous Cyprinid. *Water* **2021**, *13*, 1041. [CrossRef]
20. Havn, T.B.; Thorstad, E.B.; Teichert, M.A.K.; Sæther, S.A.; Heermann, L.; Hedger, R.D.; Tambets, M.; Diserud, O.H.; Borcherding, J.; Økland, F. Hydropower-Related Mortality and Behaviour of Atlantic Salmon Smolts in the River Sieg, a German Tributary to the Rhine. *Hydrobiologia* **2018**, *805*, 273–290. [CrossRef]
21. Nyqvist, D.; Elghagen, J.; Heiss, M.; Calles, O. An Angled Rack with a Bypass and a Nature-like Fishway Pass Atlantic Salmon Smolts Downstream at a Hydropower Dam. *Mar. Freshw. Res.* **2018**, *69*, 1894. [CrossRef]
22. Renardy, S.; Takriet, A.; Benitez, J.-P.; Dierckx, A.; Baeyens, R.; Coeck, J.; Pauwels, I.S.; Mouton, A.; Archambeau, P.; Dewals, B.; et al. Trying to Choose the Less Bad Route: Individual Migratory Behaviour of Atlantic Salmon Smolts (*Salmo salar* L.) Approaching a Bifurcation between a Hydropower Station and a Navigation Canal. *Ecol. Eng.* **2021**, *169*, 106304. [CrossRef]
23. Klopries, E.-M.; Deng, Z.D.; Lachmann, T.U.; Schüttrumpf, H.; Trumbo, B.A. Surface Bypass as a Means of Protecting Downstream-Migrating Fish: Lack of Standardised Evaluation Criteria Complicates Evaluation of Efficacy. *Mar. Freshw. Res.* **2018**, *69*, 1882. [CrossRef]
24. Havn, T.B.; Sæther, S.A.; Thorstad, E.B.; Teichert, M.A.K.; Heermann, L.; Diserud, O.H.; Borcherding, J.; Tambets, M.; Økland, F. Downstream Migration of Atlantic Salmon Smolts Past a Low Head Hydropower Station Equippped with Archimedes Screw and Francis Turbines. *Ecol. Eng.* **2017**, *105*, 262–275. [CrossRef]
25. Moore, A.; Privitera, L.; Ives, M.J.; Uzyczak, J.; Beaumont, W.R.C. The Effects of a Small Hydropower Scheme on the Migratory Behaviour of Atlantic Salmon *Salmo salar* Smolts. *J. Fish Biol.* **2018**, *93*, 469–476. [CrossRef] [PubMed]
26. Renardy, S.; Benitez, J.-P.; Tauzin, A.; Dierckx, A.; Nzau Matondo, B.; Ovidio, M. How and Where to Pass? Atlantic Salmon Smolt's Behaviour at a Hydropower Station Offering Multiple Migration Routes. *Hydrobiologia* **2020**, *847*, 469–485. [CrossRef]
27. Renardy, S.; Ciraane, U.D.; Benitez, J.-P.; Dierckx, A.; Archambeau, P.; Pirotton, M.; Erpicum, S.; Ovidio, M. Combining Fine-Scale Telemetry and Hydraulic Numerical Modelling to Understand the Behavioural Tactics and the Migration Route Choice of Smolts at a Complex Hydropower Plant. *Hydrobiologia* **2023**, *850*, 3091–3111. [CrossRef]
28. Nyqvist, D.; Greenberg, L.A.; Goerig, E.; Calles, O.; Bergman, E.; Ardren, W.R.; Castro-Santos, T. Migratory Delay Leads to Reduced Passage Success of Atlantic Salmon Smolts at a Hydroelectric Dam. *Ecol. Freshw. Fish* **2017**, *26*, 707–718. [CrossRef]

29. Enders, E.C.; Gessel, M.H.; Williams, J.G. Development of Successful Fish Passage Structures for Downstream Migrants Requires Knowledge of Their Behavioural Response to Accelerating Flow. *Can. J. Fish. Aquat. Sci.* **2009**, *66*, 2109–2117. [CrossRef]
30. Silva, A.T.; Bærum, K.M.; Hedger, R.D.; Baktoft, H.; Fjeldstad, H.-P.; Gjelland, K.Ø.; Økland, F.; Forseth, T. The Effects of Hydrodynamics on the Three-Dimensional Downstream Migratory Movement of Atlantic Salmon. *Sci. Total Environ.* **2020**, *705*, 135773. [CrossRef]
31. Vergeynst, J. Fish Behaviour in the Vicinity of a Navigation Lock Complex: The Challenges. In Proceedings of the 7th International Symposium on Hydraulic Structures, Aachen, Germany, 15–18 May 2018. [CrossRef]
32. Huet, M. Biologie, profils en long et en travers des eaux courantes. *Bull. Fr. Piscic.* **1954**, *175*, 41–53. [CrossRef]
33. Erpicum, S.; Dewals, B.; Archambeau, P.; Detrembleur, S.; Pirotton, M. Detailed Inundation Modelling Using High Resolution DEMs. *Eng. Appl. Comput. Fluid Mech.* **2010**, *4*, 196–208. [CrossRef]
34. Dewals, B.; Kitsikoudis, V.; Angel Mejía-Morales, M.; Archambeau, P.; Mignot, E.; Proust, S.; Erpicum, S.; Pirotton, M.; Paquier, A. Can the 2D Shallow Water Equations Model Flow Intrusion into Buildings during Urban Floods? *J. Hydrol.* **2023**, *619*, 129231. [CrossRef]
35. Ovidio, M.; Dierckx, A.; Bunel, S.; Grandry, L.; Spronck, C.; Benitez, J.P. Poor Performance of a Retrofitted Downstream Bypass Revealed by the Analysis of Approaching Behaviour in Combination with a Trapping System. *River Res. Appl.* **2017**, *33*, 27–36. [CrossRef]
36. Furey, N.B.; Martins, E.G.; Hinch, S.G. Migratory Salmon Smolts Exhibit Consistent Interannual Depensatory Predator Swamping: Effects on Telemetry-based Survival Estimates. *Ecol. Freshw. Fish* **2021**, *30*, 18–30. [CrossRef]
37. Koed, A.; Baktoft, H.; Bak, B.D. Causes of Mortality of Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo Trutta*) Smolts in a Restored River and Its Estuary. *River Res. Appl.* **2006**, *22*, 69–78. [CrossRef]
38. Brevé, N.; Vis, H.; Spierts, I.; de Laak, G.; Moquette, F.; Breukelaar, A. Exorbitant Mortality of Hatchery-Reared Atlantic Salmon Smolts *Salmo salar* L., in the Meuse River System in the Netherlands. *J. Coast. Conserv.* **2014**, *18*, 97–109. [CrossRef]
39. Karppinen, P.; Jounela, P.; Huusko, R.; Erkinaro, J. Effects of Release Timing on Migration Behaviour and Survival of Hatchery-Reared Atlantic Salmon Smolts in a Regulated River. *Ecol. Freshw. Fish* **2014**, *23*, 438–452. [CrossRef]
40. Coutant, C.C.; Whitney, R.R. Fish Behavior in Relation to Passage through Hydropower Turbines: A Review. *Trans. Am. Fish. Soc.* **2000**, *129*, 351–380. [CrossRef]
41. Kerr, J.R.; Kemp, P.S. Masking a Fish's Detection of Environmental Stimuli: Application to Improving Downstream Migration at River Infrastructure. *J. Fish Biol.* **2019**, *95*, 228–237. [CrossRef]
42. Karppinen, P.; Hynninen, M.; Vehanen, T.; Vähä, J. Variations in Migration Behaviour and Mortality of Atlantic Salmon Smolts in Four Different Hydroelectric Facilities. *Fish. Manag. Ecol.* **2021**, *28*, 253–267. [CrossRef]
43. Havn, T.B.; Thorstad, E.B.; Borcherding, J.; Heermann, L.; Teichert, M.A.K.; Ingendahl, D.; Tambets, M.; Sæther, S.A.; Økland, F. Impacts of a Weir and Power Station on Downstream Migrating Atlantic Salmon Smolts in a German River. *River Res. Appl.* **2020**, *36*, 784–796. [CrossRef]
44. Kärgenberg, E.; Thorstad, E.B.; Järvekülg, R.; Sandlund, O.T.; Saadre, E.; Økland, F.; Thalfeldt, M.; Tambets, M. Behaviour and Mortality of Downstream Migrating Atlantic Salmon Smolts at a Small Power Station with Multiple Migration Routes. *Fish. Manag. Ecol.* **2020**, *27*, 32–40. [CrossRef]
45. Fjeldstad, H.P.; Uglem, I.; Diserud, O.H.; Fiske, P.; Forseth, T.; Kvingedal, E.; Hvidsten, N.A.; ØKland, F.; Järnegren, J. A Concept for Improving Atlantic Salmon *Salmo salar* Smolt Migration Past Hydro Power Intakes. *J. Fish Biol.* **2012**, *81*, 642–663. [CrossRef] [PubMed]
46. Ben Jebria, N.; Carmigniani, R.; Drouineau, H.; De Oliveira, E.; Tétard, S.; Capra, H. Coupling 3D Hydraulic Simulation and Fish Telemetry Data to Characterize the Behaviour of Migrating Smolts Approaching a Bypass. *J. Ecohydraulics* **2021**, *6*, 1–14. [CrossRef]
47. Haraldstad, T.; Höglund, E.; Kroglund, F.; Haugen, T.O.; Forseth, T. Common Mechanisms for Guidance Efficiency of Descending Atlantic Salmon Smolts in Small and Large Hydroelectric Power Plants: Guidance Efficiency of Descending Smolts at Hydroelectric Power Plants. *River Res. Appl.* **2018**, *34*, 1179–1185. [CrossRef]
48. Honkanen, H.M.; Orrell, D.L.; Newton, M.; McKelvey, S.; Stephen, A.; Duguid, R.A.; Adams, C.E. The Downstream Migration Success of Atlantic Salmon (*Salmo salar*) Smolts through Natural and Impounded Standing Waters. *Ecol. Eng.* **2021**, *161*, 106161. [CrossRef]
49. Aarestrup, K.; Nielsen, C.; Koed, A. Net Ground Speed of Downstream Migrating Radio-Tagged Atlantic Salmon (*Salmo salar* L.) and Brown Trout (*Salmo trutta* L.) Smolts in Relation to Environmental Factors. In *Aquatic Telemetry*; Thorstad, E.B., Fleming, I.A., Næsje, T.F., Eds.; Springer: Dordrecht, The Netherlands, 2002; pp. 95–102. [CrossRef]
50. Urke, H.A.; Kristensen, T.; Ulvund, J.B.; Alfredsen, J.A. Riverine and Fjord Migration of Wild and Hatchery-Reared Atlantic Salmon Smolts. *Fish. Manag. Ecol.* **2013**, *20*, 544–552. [CrossRef]
51. Harbicht, A.B.; Nilsson, P.A.; Österling, M.; Calles, O. Environmental and Anthropogenic Correlates of Migratory Speeds among Atlantic Salmon Smolts. *River Res. Appl.* **2021**, *37*, 358–372. [CrossRef]
52. Persson, L.; Kagervall, A.; Leonardsson, K.; Royan, M.; Alanärä, A. The Effect of Physiological and Environmental Conditions on Smolt Migration in Atlantic Salmon *Salmo salar*. *Ecol. Freshw. Fish* **2019**, *28*, 190–199. [CrossRef]

53. Newton, M.; Barry, J.; Dodd, J.A.; Lucas, M.C.; Boylan, P.; Adams, C.E. A Test of the Cumulative Effect of River Weirs on Downstream Migration Success, Speed and Mortality of Atlantic Salmon (*Salmo salar*) Smolts: An Empirical Study. *Ecol. Freshw. Fish* **2019**, *28*, 176–186. [CrossRef]
54. Marschall, E.A.; Mather, M.E.; Parrish, D.L.; Allison, G.W.; McMenemy, J.R. Migration Delays Caused by Anthropogenic Barriers: Modeling Dams, Temperature, and Success of Migrating Salmon Smolts. *Ecol. Appl.* **2011**, *21*, 3014–3031. [CrossRef]
55. Haraldstad, T.; Haugen, T.O.; Kroglund, F.; Olsen, E.M.; Höglund, E. Migratory Passage Structures at Hydropower Plants as Potential Physiological and Behavioural Selective Agents. *R. Soc. Open Sci.* **2019**, *6*, 190989. [CrossRef] [PubMed]
56. Haraldstad, T.; Haugen, T.O.; Olsen, E.M.; Forseth, T.; Höglund, E. Hydropower-Induced Selection of Behavioural Traits in Atlantic Salmon (*Salmo salar*). *Sci. Rep.* **2021**, *11*, 16444. [CrossRef]
57. Lothian, A.J.; Lucas, M.C. The Role of Individual Behavioral Traits on Fishway Passage Attempt Behavior. *Ecol. Evol.* **2021**, *11*, 11974–11990. [CrossRef]
58. Fraser, D.F.; Gilliam, J.F.; Daley, M.J.; Le, A.N.; Skalski, G.T. Explaining Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration. *Am. Nat.* **2001**, *158*, 124–135. [CrossRef] [PubMed]
59. Chapman, B.B.; Hulthén, K.; Blomqvist, D.R.; Hansson, L.-A.; Nilsson, J.-Å.; Brodersen, J.; Anders Nilsson, P.; Skov, C.; Brönmark, C. To Boldly Go: Individual Differences in Boldness Influence Migratory Tendency: Boldness Influences Migratory Tendency. *Ecol. Lett.* **2011**, *14*, 871–876. [CrossRef] [PubMed]
60. Scruton, D.A.; Pennell, C.J.; Bourgeois, C.E.; Goosney, R.F.; King, L.; Booth, R.K.; Eddy, W.; Porter, T.R.; Ollerhead, L.M.N.; Clarke, K.D. Hydroelectricity and Fish: A Synopsis of Comprehensive Studies of Upstream and Downstream Passage of Anadromous Wild Atlantic Salmon, *Salmo salar*, on the Exploits River, Canada. *Hydrobiologia* **2008**, *609*, 225–239. [CrossRef]
61. Svendsen, J.C.; Aarestrup, K.; Malte, H.; Thygesen, U.H.; Baktoft, H.; Koed, A.; Deacon, M.G.; Fiona Cubitt, K.; Scott McKinley, R. Linking Individual Behaviour and Migration Success in *Salmo salar* Smolts Approaching a Water Withdrawal Site: Implications for Management. *Aquat. Living Resour.* **2011**, *24*, 201–209. [CrossRef]