



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

Séverine Renardy · Utashi D. Ciraane · Jean-Philippe Benitez · Arnaud Dierckx · Pierre Archambeau · Michel Piroton · Sébastien Erpicum · Michaël Ovidio

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Abstract Mitigation measures for downstream migratory Atlantic salmon smolts (*Salmo salar* L.) at migration barriers usually turn out to be insufficient to enable safe and quick passage, probably due to a lack of knowledge about their behavioural responses. Combining manual 2D tracking with hydrodynamic modelling has been rarely performed but might be useful to highlight environmental factors influencing smolt behavioural tactics and the choice of a migration route. We investigated the smolt downstream migration at a hydropower plant that offers five migration routes, including a Kaplan turbine and a fish-friendly Archimedes screw. Four behavioural tactics were defined to describe the smolt expressed behaviour, which was mainly complex and hesitant. The majority of the smolts approached more than one migration route before crossing the site and the Kaplan turbine turned out to be the most approached route, contrary to the Archimedes screw.

Hydrodynamic modelling highlighted that flow velocity and water depth were used as hydraulic cues in the selection of a migration route, as the smolts preferred higher flow velocities and water depths. The comprehension of the factors influencing the research behaviour at hydropower plants may be useful to design attractive mitigation measures and to guide the smolts efficiently towards safe routes.

Keywords Hydroelectricity · Ethohydraulics · Archimedes screw · Kaplan turbine · 2D telemetry

Introduction

Rivers have been fragmented to enable human activities, such as hydropower production (Nilsson et al., 2005). These disruptions have caused drastic reductions and even the extinction of entire populations of several migratory species, such as the Atlantic salmon (*Salmo salar* L.) (Parrish et al., 1998), by impeding free movement (Katopodis & Williams, 2012) and by gradually delaying migration (Renardy et al., 2022). The Atlantic salmon is one of the most sensitive species to migration barriers due to its complex life cycle, including both marine and freshwater migrations (McCormick et al., 1998). This situation is highly problematic for downstream migrating smolts due to their narrow time window to reach the ocean (McCormick et al., 1998; Marschall et al., 2011; Thorstad et al., 2012). In addition to delaying smolt

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S. Renardy (✉) · J.-P. Benitez · A. Dierckx · M. Ovidio
UR-FOCUS, Management of Aquatic Resources
and Aquaculture Unit, Laboratory of Fish Demography
and Hydroecology (LDPH), University of Liège, Liège,
Belgium
e-mail: severine.renardy@uliege.be

U. D. Ciraane · P. Archambeau · M. Piroton · S. Erpicum
UR-UEE, Laboratory of Hydraulics in Environmental
and Civil Engineering (HECE), University of Liège, Liège,
Belgium

downstream migration, the confrontation with hydropower stations will induce injuries and direct and indirect mortality due to energy expenditure and the passage through an unsafe migration route as classical turbines (Coutant & Whitney, 2000; Fu et al., 2016; Nyqvist et al., 2017; Ovidio et al., 2017; Renardy et al., 2021, 2022).

Several mitigation measures have been proposed to re-establish free up- and downstream movements at hydropower plants (Katopodis & Williams, 2012). Upstream movements of spawning salmon have been greatly enhanced. On the contrary, downstream migration still remains strongly affected (Fjeldstad et al., 2018; Williams et al., 2012). Numerous measures are designed for downstream migration to enable rapid barrier crossing and to reduce as much as possible smolt mortalities, such as improved hydropower plant management (Szabo-Meszaros et al., 2019), behavioural and physical barriers (Scruton et al., 2003; Tomanova et al., 2018) and downstream bypasses (Ovidio et al., 2021; Tomanova et al., 2021). Fish-friendly turbines (e.g. the Archimedes screw) with low rotational speed, large blade spacing, and the absence of extreme pressure change (Cefas, 2012) have also been developed to ensure safe passage (Hogan et al., 2014). Brackley et al. (2018) highlighted very low mortality rate following direct injection into an Archimedes screw. With the use of sensors, Pauwels et al. (2020) highlighted, on the other hand, highly chaotic physical conditions in the Archimedes screw that may sometimes cause serious injuries. The performance of mitigation measures for downstream migration usually turns out to still be insufficient to facilitate a safe and quick passage of smolts (Williams et al., 2012; Fjeldstad et al., 2018) and to enable a sufficient seaward escape rate (Renardy et al., 2021, 2022). Bypass efficiency varies from 0 to 97% depending on the site configuration (Klopries et al., 2018), with a bypass use of 32% for Nyqvist et al. (2017; three available migration routes) or 88% for Tomanova et al. (2021, five available migration routes). Moreover, environmental conditions influence the use of the bypass as Havn et al. (2018; 2020) observed a variable use of the bypass according to the year of tracking from 2014 to 2016, with a bypass use of 83%, 95% and 60%, respectively.

Poor knowledge about the attractiveness of downstream passage structures may explain their low efficiency. To date, little attention has been dedicated to

the understanding of the behavioural response of fish approaching such systems. Confrontation of smolts to hydropower plants during the downstream migration will induce the expression of a more or less complex research behaviour to find a safe and attractive migration route (Renardy et al., 2020, 2021). The expressed research behaviour is specific to each individual notably depending on their intrinsic character (Haraldstad et al., 2019; Lothian et al., 2021). In the literature, smolts behaviour at hydropower plants is mainly characterised using automatic 1D telemetry (Thorstad et al., 2017; Newton et al., 2019; Havn et al., 2020; Ovidio et al., 2021; Renardy et al., 2022). On the other hand, fine-scale behaviour of the smolts has rarely been documented through qualitative tracking, such as 2D telemetry (Renardy et al., 2020). Qualitative tracking of a small number of individuals provides more accurate and detailed data on the smolt behaviour. Characterisation of the fine-scale behaviour of smolts upstream of hydropower plants will enable a better assessment of the attractiveness of the available migration routes present at a migration barrier.

Scientists know very little about what makes the mitigation measures attractive. It has already been shown that the hydrological conditions such as flow velocity will influence the behaviour of the smolts upstream of a migration barrier (Enders et al., 2009; Silva et al., 2020; Renardy et al., 2021). However, the relation between the fine-scale behaviour of the smolts and hydrological conditions associated with mitigation measures is rarely identified. Combining hydraulic modelling and behavioural tracking will enable a better understanding of the influence of hydrological conditions on smolts' behaviour upstream of migration barriers (Vergeynst 2018).

In this study, we investigated the downstream migratory behaviour of Atlantic salmon smolts using manual 2D radio telemetry, at a hydropower plant in the Ourthe River (Belgium), of which hydrodynamic conditions are known from numerical modelling. The hydropower plant offers five potential migration routes, including a Kaplan turbine and a fish-friendly Archimedes screw. In 2018, a first preliminary smolts tracking has been carried out in order to identify the diversity of research behaviour (Renardy et al., 2020). In this study, the smolt tracking is combined with hydrodynamic modelling to obtain more precise analyses on the behavioural response of the smolts

upstream of a hydropower plant. The first aim of the study was to identify the behavioural tactics expressed by the smolts to find a migration route to cross the hydropower plant, including the (a) approached, (b) used migration routes and (c) the research time. The second aim was to assess which biological and environmental factors influence smolt behavioural tactics. The effect of hydraulic conditions was notably highlighted by combining hydrodynamic modelling and fine-scale behaviour of the smolts.

Materials and methods

Study area

The study site is the Méry hydropower plant, located in the lower part of the Ourthe River, a main tributary of the Meuse River (Fig. 1A). The international Meuse River is 950 km long, with a catchment area of 36,000 km². Its source is in France, then the river flows across Belgium and reaches the North Sea in the Netherlands. The Ourthe River is a medium-sized river 235 km long, with two sources located in the Belgian Ardennes at an altitude of 506 m and 512 m and with a total catchment area that extends over 3,672 km². The lower Ourthe River corresponds to a barbel zone (Huet, 1949) with the potential presence of 29 fish species, dominated in biomass by rheophilic and ubiquitous cyprinids. In the whole river, prevailing macro-invertebrate communities are currently indicative of good (16/20) water quality (Public Service of Wallonia—AQUABIO). From 2014 to 2020, in the lower part of the Ourthe River, during the smolts downstream migration from April to May, the average water discharge was 34.4 m³s⁻¹ (range 6.7–172.4 m³s⁻¹) and the mean temperature was 13.2 °C (range 12.4–14.1 °C).

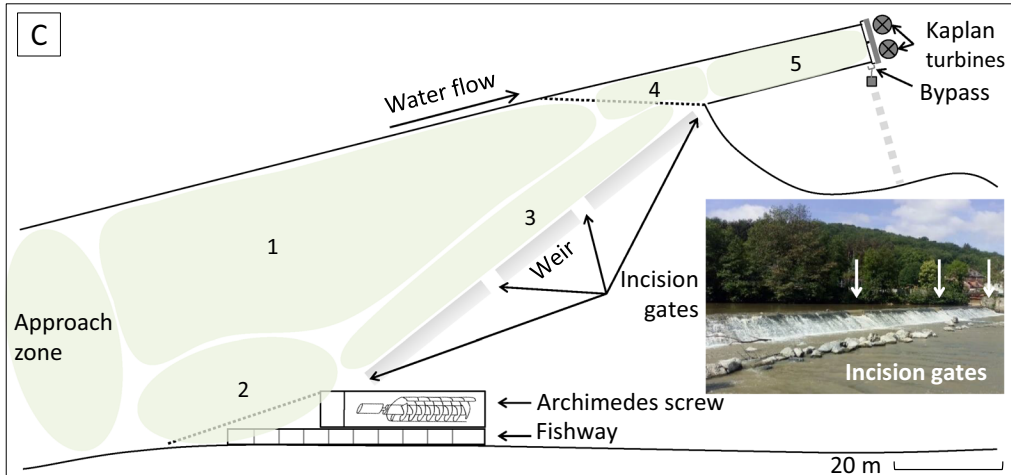
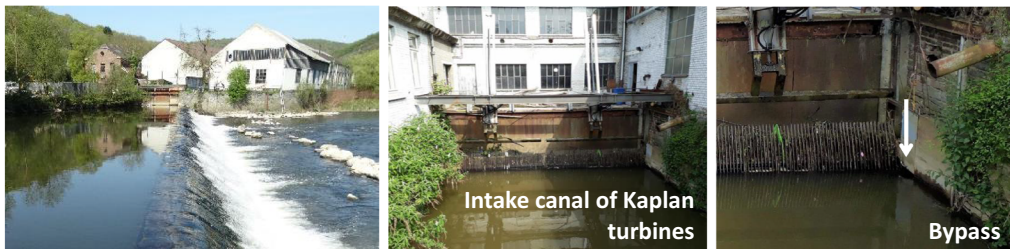
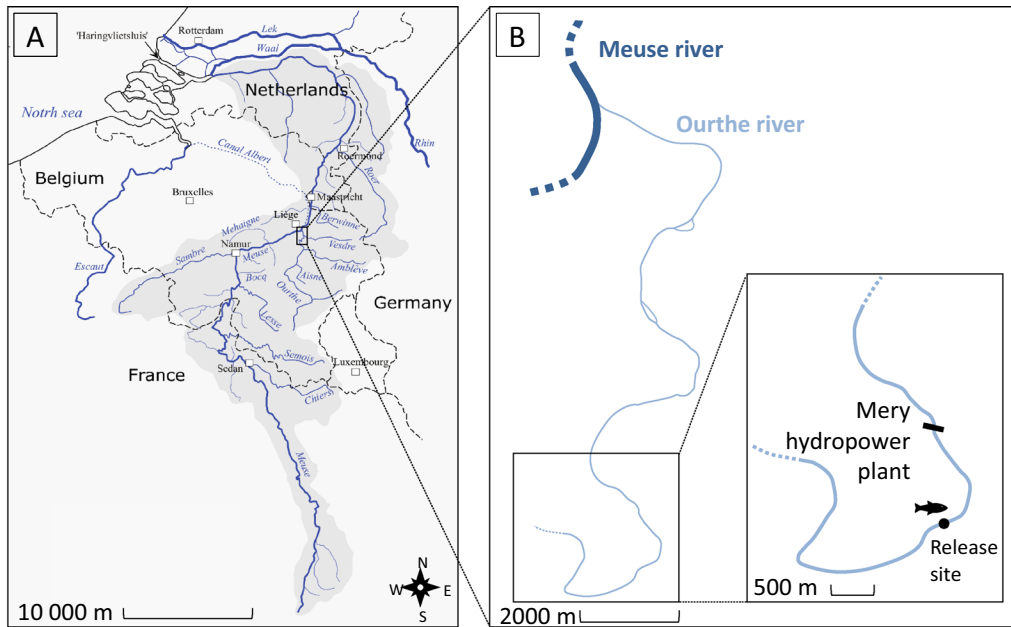
The Méry run-of-river hydropower plant is located 12.7 km upstream from the confluence of the Ourthe River with the Meuse River (Fig. 1B). The site is equipped with an 86 m long and 1.8 m high weir, placed at an angle across the width of the river, with two Kaplan turbines on the left bank and an Archimedes screw on the right bank (Fig. 1C). During the study, only one Kaplan turbine was in operation. The turbine in operation is characterised by an electric power of 120 kW, a nominal flow of 6 m³s⁻¹, a rotational speed of 250 revolutions per minute, a diameter

of 1.8 m, a head of 2.5 m and is associated with a 67° angle trash rack with a 50 mm bar spacing. A downstream migration bypass with a 480 × 300 mm rectangular inlet was installed in 2007 on the right side of the trash rack. According to Larinier & Couret (2008), the recommended functioning discharge would be 0.4 m³s⁻¹, but the actual bypass discharge varies between 0.1 and 0.2 m³s⁻¹. A mercury lamp was placed at the entrance to increase the bypass attraction. The fish using the bypass are guided through a pipe system into a submerged holding pool that serves as a capture trap (1 m long, 0.8 m wide and 0.8 m high) from which they are manually collected for monitoring (Teichert et al., 2020). Four incision gates are located on the weir. The 1st and the 4th incision gates are 0.5 m long and 0.2/0.4 m deep; whereas, the 2nd and 3rd are 3 m long and 0.4/0.3 m deep. On the right bank of the river, an Archimedes screw and a vertical slot basin fishway were installed in 2018. The Archimedes screw has an electric power of 100 kW, a length of 4.5 m with a diameter of 3.7 m, a rotational speed of 22.8 revolutions per minute and a nominal functioning discharge of 7.5 m³s⁻¹. The fishway is 42 m long, with 10 pools (2 m × 3 m) with 0.4 m wide slots. The nominal discharge is 0.7 m³s⁻¹ and is associated with an attraction discharge of 0.3 m³s⁻¹.

The Méry hydropower plant offers five potential different migration routes for downstream migrating Atlantic salmon smolts (Fig. 1C): from the right to left bank, the vertical slot fishway, the Archimedes screw, the weir and associated incision gates, the Kaplan turbines and the downstream bypass. Upstream of the hydropower plant, six different areas have been defined, including five zones (numbered from 1 to 5) and an approach zone, situated 50 m upstream of the site (Fig. 1C). Concerning the five zones: zone 2 corresponds to the area upstream of the Archimedes screw and the fishway; zone 3 is the weir area; zone 5 includes the area upstream of the Kaplan turbines and bypass; zone 4 covers an intermediate area between the intake canal entrance and the end of the weir area and zone 1 corresponds to the remaining area that is not associated with a migration route.

Smolts tagging and tracking

We used 1-year-old hatchery-reared smolts ($n=36$) from the Erezee hatchery (Belgium) with a mean fork length of 161.1 mm (range 149–185 mm) and a mean



◀**Fig. 1** Schematic representation of the river of interest. (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 Méry hydropower plant with the approach zone, the different studied zones (numbered from 1 to 5) and the five associated migration routes

body mass of 48.4 g (range 38–68 g). Tracking wild smolts was impossible due to the difficulty to capture them by electric fishing the day of tracking but also because their size and weight are often insufficient to support the weight of the transmitter. Previous studies (Ovidio et al., 2017; 2021; Renardy et al, 2020; 2022) demonstrated that hatchery smolts usually started their downstream migration the day of tagging which is an advantage for manual tracking studies. The smolts were transported with 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. Before the release events, the smolts were anaesthetised with 0.2 ml l⁻¹ of phenoxyethanol. After a 10 mm incision, the smolts were surgically equipped with a radio transmitter in their body cavity between the pelvic and the anal fins (Advanced Telemetry Systems; Model F1410; frequency 40 MHz; 7 mm × 15 mm × 7 mm; pulse rate 40 ppm; mass in air 1.0 g; expected life time 14 days). An additional small hole was made independently of the main incision using a thin-steel cannula to enable the passage of the external antenna. Once the radio transmitter correctly inserted, the incision was closed with two stitches using absorbable suture material (VICRYL® Suture JV398) and disinfected with eosin. The mean time of surgery was around 10 minutes per individual. The smolts were released at the release site after a full recovery around two hours after the surgery. The tagged smolts were divided into six groups (G1 to G6) with six individuals each (Table 1). The six groups were released 1200 m upstream from the hydropower plant at around 4–5 pm at different dates to experience contrasting environmental conditions. Fork length and body mass were not different between the six release groups [Kruskal–Wallis (KW) test, both $P > 0.1$].

Water temperature (°C) was recorded every hour during the survey using data loggers (Tidbit Onset) installed at the Méry hydropower plant. Water discharge data (m³s⁻¹) were recorded by the hydrological office of the Service Public de Wallonie

(SPW-SETHY, Belgium) at the Sauheid station, 9 km downstream of Méry site, with one measurement every hour. During each group tracking, water temperature and water discharge of the river and through each turbine were homogeneous. Average water temperature varied from 7 °C to 12.2 °C and water discharge was between 17.3 and 49.2 m³s⁻¹ depending on group (Table 1). Depending on the release date, the discharge of the Kaplan turbine varied between 3.3 and 7 m³s⁻¹ and between 6.4 and 7.5 m³s⁻¹ for the Archimedes screw (Table 1). Water discharge over the weir varied between 7.1 and 34.7 m³s⁻¹, and the water level over the weir varied between 0.08 and 0.25 m. The 4th incision gate was opened during the entire tracking. The 1st one was opened during the first three release groups and closed during the last three release groups. The 2nd and 3rd were closed for the first three release groups, and they were opened for the last three release groups. When the 2nd and 3rd incision gates were opened, the water level varied between 0.326 and 0.334 m in the 2nd incision gate and between 0.245 and 0.255 m in the 3rd incision gate.

The radio-tagged smolts were manually intensively tracked just after their release until the hydropower plant crossing. The smolts that did not pass the site on the evening/night of the release day and were tracked less intensively during the following days until the site crossing. For each release group, a mean of six tracking sessions were performed. Manual tracking was performed by 5 operators on foot or by car using portable receivers (ATS Model Fieldmaster) and directional (Low-Frequency loop) and non-directional antennas (Magnetic Roof-Mount Dipole). Directional antennas were used to locate smolts with high precision (see Ovidio et al., 1998; Renardy et al., 2020) and enabled us to identify the precise research behaviour of the smolts upstream of the hydropower plant. From the 8th of April to the 9th of May 2021, a total of 1,250 smolts' positions were recorded after a total of 83 h of manual radio tracking over a tracking distance of 2000 m.

Smolt behavioural metrics

Several quantitative behavioural metrics useful to describe the smolt migratory behaviour were defined.

Table 1 Smolt groups' characteristics and hydrological conditions during tagged smolts tracking

Group	Release event		River discharge		Water temperature		Kaplan turbine	Archimedes screw	Weir discharge	
	N°	N smolts	Day	Minimum (m ³ /s)	Maximum (m ³ /s)	Average (°C)	Daily (m ³ /s)	Daily (m ³ /s)	Minimum (m ³ /s)	Maximum (m ³ /s)
1	6	08 Apr	25.2	31.7	7.0	6.4	6.6	12.2	18.7	
2	6	14 Apr	47.2	49.2	7.0	7.0	7.5	32.7	34.7	
3	6	21 Apr	21.2	29.5	10.9	6.5	7.0	7.7	16.0	
4	6	28 Apr	19.6	20.3	12.2	6.1	6.4	7.1	7.8	
5	6	04 May	17.3	19.5	10.6	3.3	6.7	7.3	9.5	
6	6	06 May	17.3	19.9	10.4	3.3	6.4	7.6	10.2	

- *Arrival time*: median time (in hours) to reach the Méry hydropower plant that corresponds to the time between the migration initiation and the first detection in the approach zone at the hydropower plant (see Renardy et al., 2022).
- *Research time*: median time (in 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 last detection upstream of the plant (see Renardy et al., 2020; 2022).

We also identified the behavioural tactics individually performed to cross the hydropower plant.

- *Behavioural tactic*: expressed research behaviour by the smolts to cross a hydropower plant, which includes, notably, the approached migration routes and the research time (see Renardy et al., 2022). Based on the observed behaviour of the smolts, four different behavioural tactics were highlighted.

The first two behavioural tactics concern the smolts that approached more than one migration route.

- Tactic “*proactive explorer*”: crossing the hydropower plant with a lower research time than the time of the first quartile (Q25) of the associated distribution.
- Tactic “*reactive explorer*”: crossing the hydropower plant with a more elevated research time than the time of the first quartile (Q25) of the associated distribution.

The last two behavioural tactics include the smolts that approached only one migration route.

- Tactic “*proactive non-explorer*”: crossing the hydropower plant with a lower research time than the time of the first quartile (Q25) of the associated distribution.
- Tactic “*reactive non-explorer*”: crossing the hydropower plant with a more elevated research time than the time of the first quartile (Q25) of the associated distribution.

Hydrodynamic numerical modelling

The detailed hydrodynamic conditions observed at Méry hydropower plant during the smolts survey were modelled using the flow solver WOLF2D, developed by the HECE research group at Liège University for more than 20 years (Ercicum et al., 2009; Renardy et al., 2021). The software solves the shallow water equations on a Cartesian grid using a finite-volume technique. On each computational cell, it computes the time evolution of water depth and both components of flow velocity in the main flow plane. The solver has been extensively validated considering varied flow conditions (for instance, Ercicum et al., 2009; 2010a; Li et al., 2021) and has been used to compute flood inundation maps along more than 800 km of rivers in Wallonia (Ercicum et al., 2010b), including Meuse and Ourthe Rivers. The choice of 2D modelling was dictated by the recorded smolt trajectories which were also planar (2D radio telemetry).

The model has been applied to the survey site depicted on Fig. 1C. Main input data were the topography/bathymetry of the site. The topography/bathymetry of Méry site was gained by combining “Light Detection And Ranging” (LiDAR) data collected from an air-borne survey lead by the Public Service of Wallonia (1 m horizontal resolution and 0.15 m vertical accuracy) and a manual bathymetric survey in the river bed obtained with a GPS Trimble R10 and a Leica total station. The bathymetric survey consisted of 298 points with horizontal and vertical accuracy estimated to 0.10 and 0.05 m, respectively. The bathymetric survey points were linearly interpolated on a regular grid of 0.50×0.50 m cells and combined to the LiDAR data on the banks to get a complete high-resolution digital elevation model (DEM) of the whole study site. Weir geometry, including incisions, and turbines inlet were added manually considering drawings of the structures. The resulting DEM included 165,064 cells and covered a 230.9 m long reach of the Ourthe River upstream of the Méry weir, including the channel to the Kaplan turbines, with an overall 0.5 m horizontal resolution and a better than 0.15 m vertical accuracy.

Considering the small variations of discharges observed during the tracking of each smolts group, four steady-state hydrological and turbines operation scenarios have been defined for the simulations (Fig. 2; Table 2). The river discharge was prescribed

as inlet boundary condition at the upstream of the numerical model. Discharge value deduced from the daily production records were prescribed as outlet boundary condition at the Kaplan turbine and the Archimedes screw. Discharge value was also prescribed as inlet boundary condition at the fishway. A head–discharge relation was prescribed at the weir and the incisions to automatically control the water level in the modelled area depending on the excess discharge released over the weir and the incisions. Considering the weir and incisions geometry, the discharge coefficient value was equal to 0.385 (broad crested weir) and 0.42 (sharp crested weir), respectively.

For each of the four hydrological and hydropower plant operation scenarios detailed in Table 2, flow velocity and water depth have been computed in the whole modelled area and flow parameters value at each recorded smolt position were extracted from the flow computation results and investigated as hydrodynamic data in the sequel.

Statistical analyses

Because the data violated the assumptions of normality (Kolmogorov–Smirnov, $P < 0.05$), non-parametric tests were used. All statistical analyses were performed using the software R (version 3.4.2).

We first performed analyses to respond to the first objective and to describe the expressed research behaviour of the smolts upstream of the hydropower plant. Smolt research behaviour was compared between the different release groups, such as the first approached migration route using Fisher’s Exact test and the number of approached migration routes and the research time using Kruskal–Wallis (KW) and Dunn tests. Time spent by the smolts in the vicinity of the different migration routes was compared between the different release groups, using KW tests. The different migration routes were compared with each other in terms of the number of approaches per smolt and the time spent by the smolts in the vicinity using KW and Dunn tests. The used migration route was compared between the release groups, using Fisher’s Exact test. The effect of the incision opening was also tested on the use of the weir as a migration route, using a Pearson’s χ^2 test.

As the second step, analyses were completed to respond to our second objective on the influence of

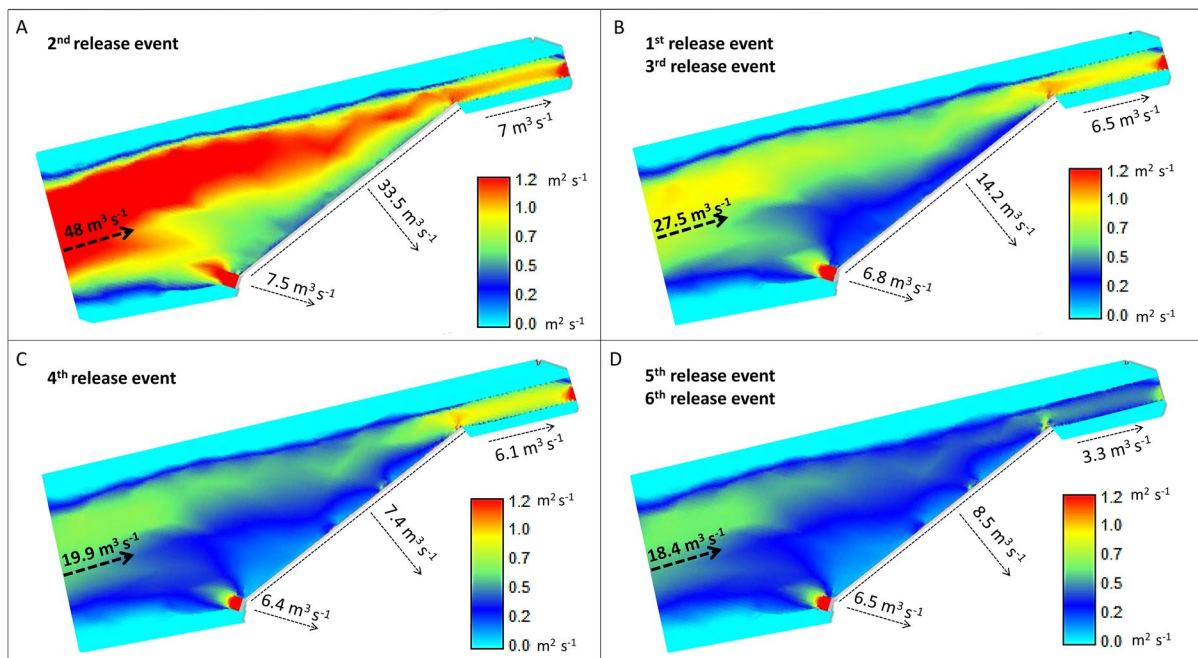


Fig. 2 Specific water discharges (coloured scale) of the simulated hydrological scenario at the Méry hydropower plant for each release event, **A** from highest to **D** lowest water discharge that is used as boundary condition at the site entrance (arrow)

Table 2 Hydrological and hydropower plant operation scenarios considered for hydraulic numerical modelling and associated release events

Config N°	Release event Day(s)	River discharge (m^3s^{-1})	Kaplan turbine (m^3s^{-1})	Archimedes screw (m^3s^{-1})	Weir discharge (m^3s^{-1})	Opened incisions
1	08 Apr & 21 Apr	27.5	6.5	6.8	14.2	1; 4
2	14 Apr	48.0	7.0	7.5	33.5	1; 4
3	28 Apr	19.9	6.1	6.4	7.4	2; 3; 4
4	04 May & 06 May	18.4	3.3	6.6	8.5	2; 3; 4

biological and environmental factors on smolt behavioural tactics. Water depth and flow velocity value (absolute value and orientation) were extracted from the numerical simulations for 1,179 smolts positions:

- Discharge: The research behaviour was compared to the water discharge of the river to assess its influence, using KW tests for the first approached migration route and the used migration route. Spearman correlations were used for the number of approached migration routes and the research time. The effect of the discharge ratio between the Kaplan turbine and the Archimedes screw

was also tested on the used migration route using a KW test. The number of migration route rejections was linked to river water discharge using a Spearman correlation.

- Flow velocity: Distribution of all available flow velocities and of flow velocities at smolts' locations were compared between the release groups, using KW tests. Used flow velocities were also compared between individuals of the same release group, using KW tests. The influence of the flow velocity on the smolt positions was investigated by means of the preference index. The preference index is the ratio between availability and utilisation.

tion for each release group. Availability represents all absolute velocity values available in the hydraulic model, and utilisation represents the velocity values at the positions where smolts were detected. The study uses a class subdivision of 0.1 m/s for this analysis. The Mann–Whitney (U) test was performed to compare the used and available flow velocities.

- Water depth: available water depths and used water depths were compared between the release groups, using KW tests. Used water depths were also compared between individuals of the same release group, using KW tests. The effect of the water depth variation on smolts was assessed using the preference index as for the absolute velocity, considering classes of 0.5 m.

Results

Smolt behavioural tactics

Amongst the $n=36$ released smolts, 89.9% ($n=32$) were detected in the approach zone with a mean arrival time of 01h51 (median=00h51). The smolts spent a mean time of 5 minutes (median=00h03) in the approach zone. 88% of the smolts followed the main flow towards the weir and the intake canal of the Kaplan turbines. The intake canal of the Kaplan turbines was entered by $n=18$ smolts, of which $n=11$ approached the turbine trash rack first and $n=7$ were detected just upstream of the bypass. The weir was first approached by $n=10$ smolts and the Archimedes screw by $n=4$ individuals. The first approached migration route differed between the release groups (Fisher's Exact test, $P=0.047$). Water discharge did not influence the first approached migration route (KW test, $\chi^2=0.12$, $df=3$, $P>0.1$). Of the $n=32$ smolts, 84% ($n=27$) approached more than one migration route, of which 28% ($n=9$) approached four migration routes. Only five smolts did not explore as they were detected close to only one migration route. The number of approached migration routes differed significantly between the release groups (KW test, $\chi^2=12.7$, $df=5$, $P=0.03$), which was significantly lower for the 2nd release group, with a higher discharge than for the other five release groups (RE) (Dunn test, RE1 to RE6, $P=0.01$, $P=0.02$, $P=0.006$, $P=0.0005$ & $P=0.004$) (Fig. 3).

The more the discharge increased, the more the number of approached migration routes decreased (Spearman's correlation, $\rho=-0.67$, $P<0.001$). For the second release event, water discharge was $48 \text{ m}^3\text{s}^{-1}$, of which $33.5 \text{ m}^3\text{s}^{-1}$ was redirected over the weir (Fig. 3) and the smolts tended to approach only up to two migration routes. The Kaplan turbine was the most approached migration route with 81% of the smolts ($n=26$), contrary to the Archimedes screw, which was approached by 41% of the smolts ($n=13$). The weir was also the most approached migration route with 81% of the smolts ($n=26$). The bypass was approached by 69% of the smolts ($n=22$).

Before crossing the site, in addition to approaching several available migration routes, 68.8% of smolts approached the same migration route several times (Fig. 4). The Archimedes screw was approached on fewer occasions than the weir (Dunn test, $P=0.003$), the bypass (Dunn test, $P=0.01$) and the Kaplan turbine (Dunn test, $P=0.002$). The smolts rejected the approached migration route on average 6.5 occasions before crossing the site. River discharge had an influence on the hesitating behaviour of the smolts (Spearman's correlation, $\rho=-0.59$, $P<0.001$), with a reduction of the migration route rejections when the discharge increased.

The smolts spent different periods of time in the different zones (Fig. 4). Only three smolts were detected in the approach zone a second or third time. Based on smolts' positions per zone, fish positions were mostly detected either in the intake canal area (zone 5) (42%) or in the weir area (zone 3) (27%); whereas, the remaining zones represented less than 10% of detections, respectively. The smolts spent a median time of 01h49 in the intake canal area (zone 5) and more particularly 00h13 in the bypass area. Time spent in the intake canal area (zone 5) varied significantly between the release groups (KW test, $\chi^2=16.4$, $df=5$, $P=0.006$), with the absence of smolt detections in this zone during the second release event. In contrast, the time spent in the Archimedes screw area and in the weir area did not differ significantly between the release groups (KW tests, $P=0.07$ and $P=0.08$, respectively). The smolts were detected for a median time close to zero in the Archimedes screw area (zone 2) and of 00h14 in the weir area (zone 3). The time spent varied significantly between the Archimedes screw, weir and intake canal areas (KW test, $\chi^2=28.3$, $df=2$, $P<0.001$) (Fig. 4).

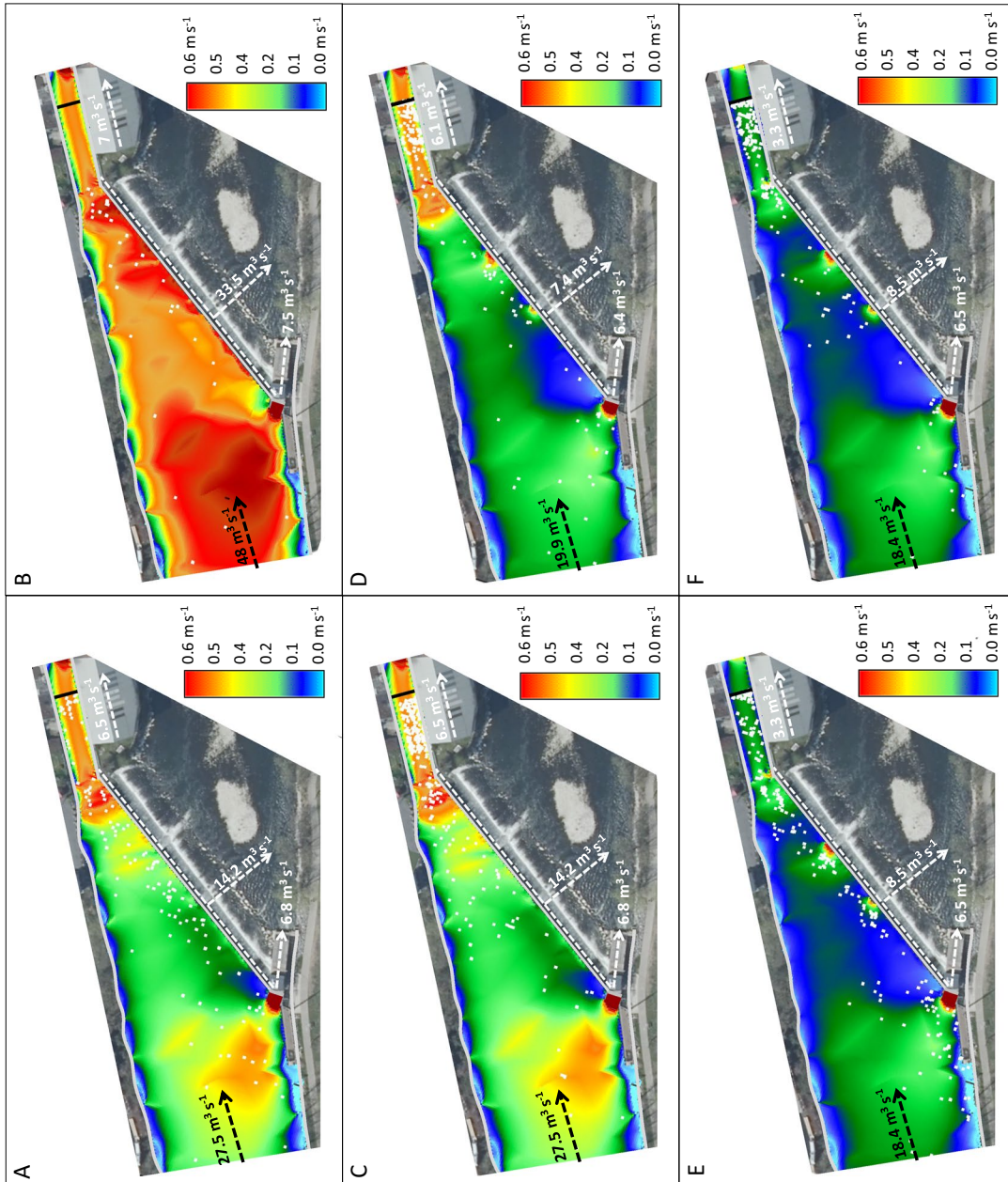


Fig. 3 Overlay of all recorded smolt positions (white dots) upstream of Méry hydropower plant with the simulated flow velocity conditions (absolute values) and the distribution of water discharges for the six release events. (A) First release event to (F) sixth release event

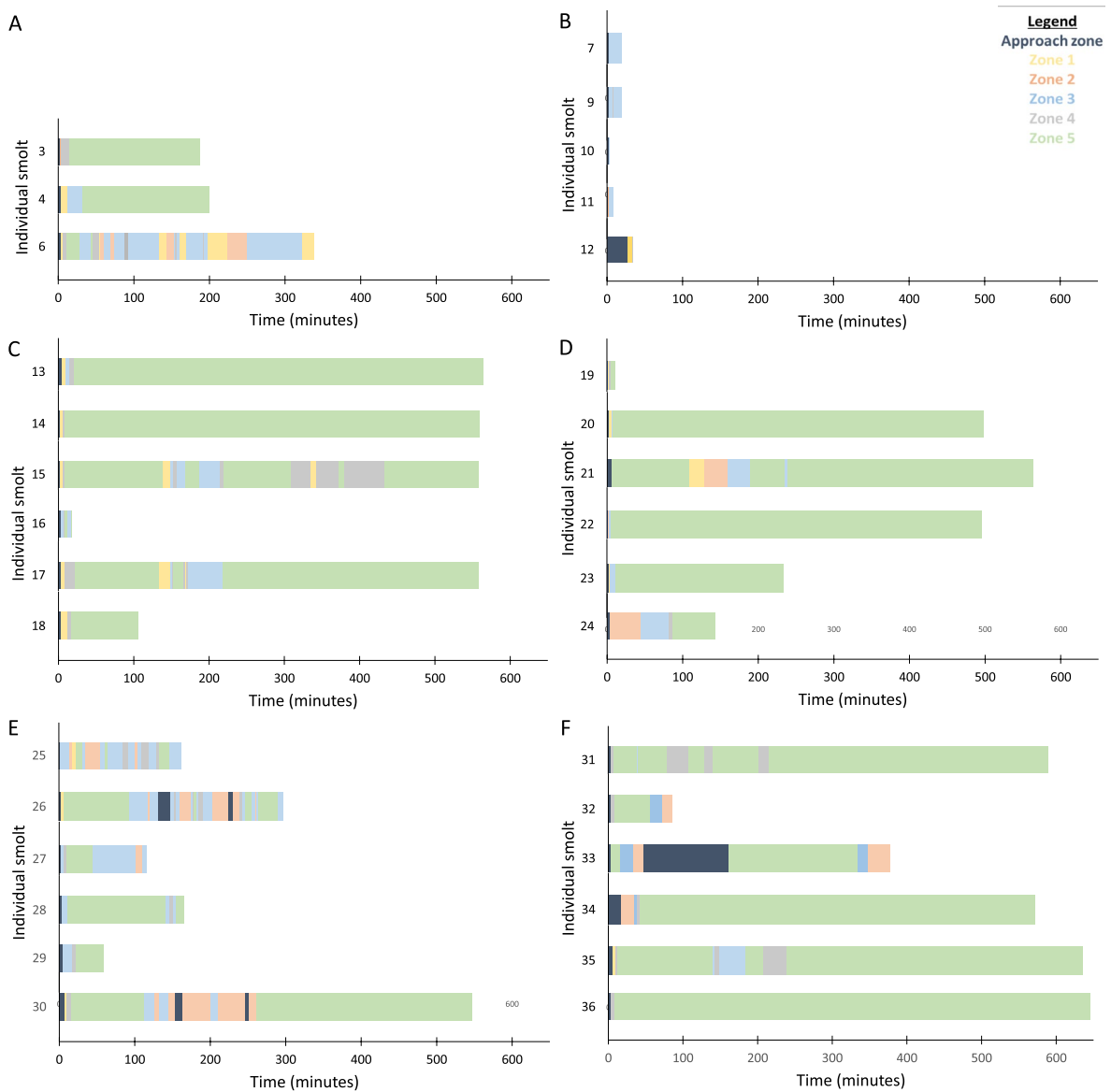


Fig. 4 Research behaviour of the smolts in each zone according to the time for each release event. (A) 1st release event. (B) 2nd release event. (C) 3rd release event. (D) 4th release event. (E) 5th release event. (F) 6th release event

The research time required to find a migration route varied between 00h03 and 11h16 and differed significantly between the release groups (KW test, $\chi^2=14.3$, $df=5$, $P=0.01$) (Fig. 4). Research time required to cross the hydropower plant was significantly lower for the 2nd release group than for the five other release groups (Dunn test, RG1 to RG6, $P=0.008$, $P<0.001$, $P=0.009$, $P=0.03$ & $P=0.002$). Water discharge did not significantly

influence the research time (Spearman’s correlation, $\rho=-0.32$, $P=0.066$) but tended to decrease when river discharge increased. Amongst the 32 smolts, 75% ($n=24$) were reactive given a required research time greater than 01h38. Only eight smolts turned out to be proactive by crossing the site in less than 01h38.

All the $n=32$ smolts detected in the approach zone crossed the hydropower plant, but for 31% of them, the migration route used was unknown. Nine

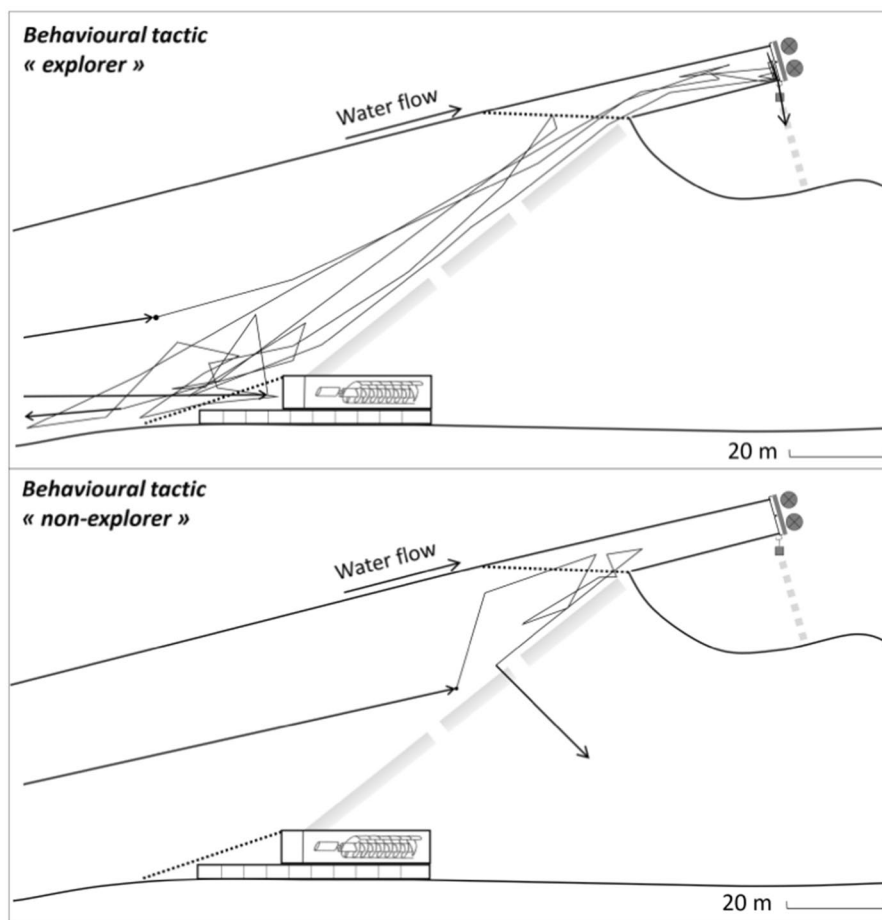


Fig. 5 Representation of the behavioural tactics expressed by smolt in relation with the exploration: explorer tactic (top figure) and non-explorer tactic (bottom figure)

smolts (28%) used the first approached migration route to pass. The most used migration route was the weir with 41% of the smolts ($n=9$). The incision gates' opening did not increase the use of the weir as a migration route (Pearson's χ^2 , $P>0.1$). For the other smolts, 36% ($n=8$) passed by the Kaplan turbine, 18% ($n=4$) by the bypass and 5% ($n=1$) by the Archimedes screw. No smolt used the vertical slot fishway from upstream to downstream to cross the hydropower plant. The migration route used to cross the hydropower plant slightly differed between the release groups (Fisher's Exact test, $P=0.06$). Water discharge and the ratio Kaplan turbine/Archimedes screw discharge did not influence the migration route used by the smolts (KW test, $\chi^2=1.9$, $df=3$, $P>0.1$ & $\chi^2=1.6$, $df=3$, $P>0.1$).

Four different behavioural tactics to find a migration route were highlighted, based on the number of approached migration routes and the research time. The first two behavioural tactics concerned 27 smolts who approached more than one migration route (Fig. 5), of which 2 expressed the behavioural tactic "proactive explorer" and 25 expressed the tactic "reactive explorer". The other 5 smolts expressed the tactic "proactive non-explorer" and approached only one migration route (Fig. 5). None of the smolts expressed the tactic "reactive non-explorer" (Fisher's Exact test, $P=0.04$).

Among the 22 smolts, whose migration route to cross the hydropower plant is known, 77% ($n=17$) were considered to be explorers, of which seven used an unsafe migration against ten smolts who

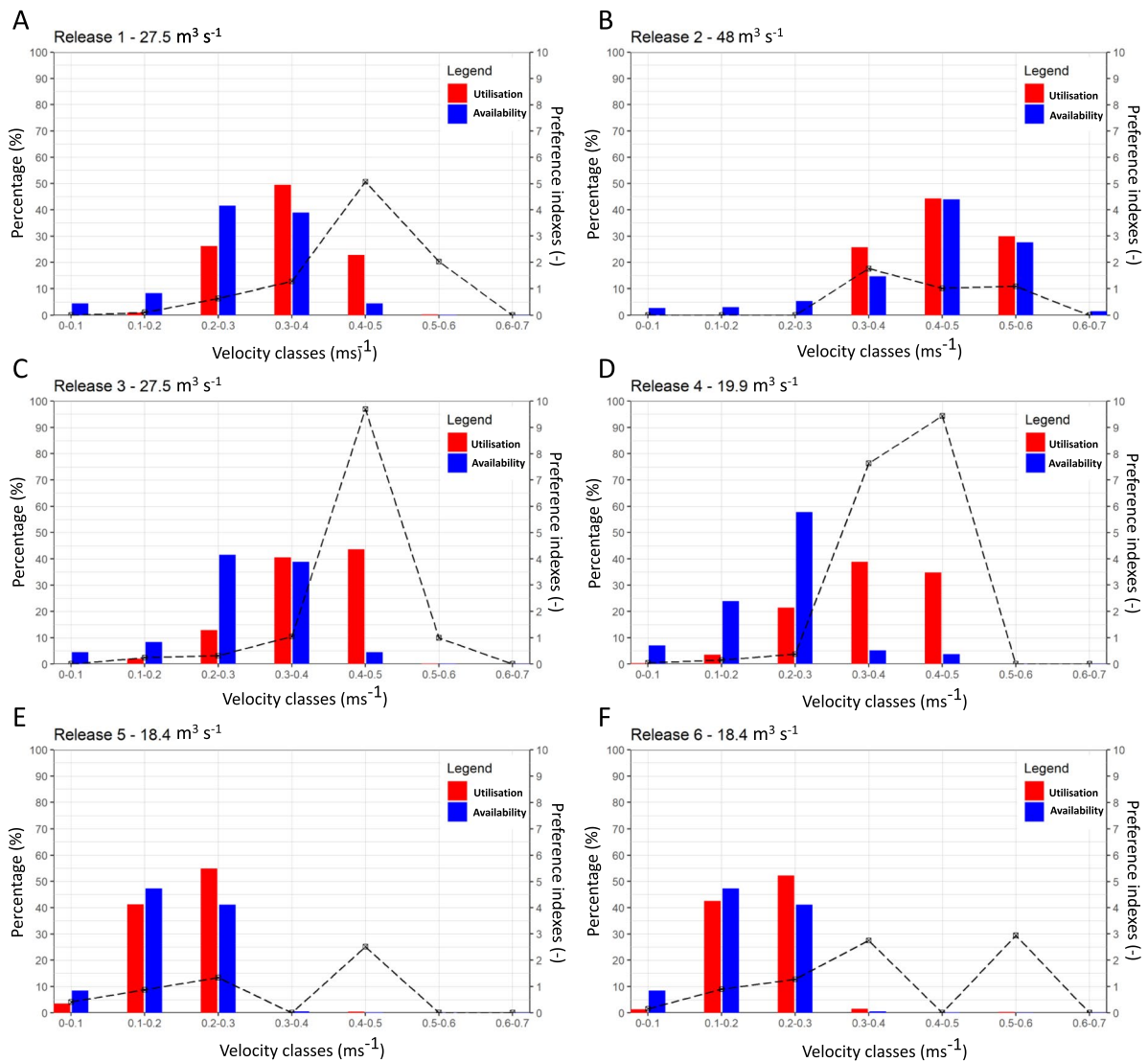


Fig. 6 Distributions of available and used flow velocities by the smolts upstream of the hydropower plant for each release event. Preference index is represented by dots. (A) First release event to (F) sixth release event

used a safe one. The non-exploring smolts were more likely to use a safe migration route with four smolts against one individual, who used an unsafe route.

Influence of hydrodynamic factors

Depending on the release group, the smolts encountered significantly different flow velocities (KW test, $\chi^2=558.2$, $df=5$, $P<0.001$). Absolute flow velocities at smolts locations (used velocities) varied

significantly between the release groups (KW test, $\chi^2=697.1$, $df=5$, $P<0.001$) (Fig. 6). Used water velocities did not differ significantly between individuals of the same release group (KW tests, RG2 $P=0.2$, RG3 $P=0.2$, RG4 $P=0.06$, RG5 $P=0.1$), except for the first and sixth release groups (KW test, $\chi^2=15.3$, $df=2$, $P<0.001$ & KW test, $\chi^2=16.1$, $df=5$, $P=0.001$). The smolts tended to use the highest available absolute velocities from 0.2 to 0.5 ms⁻¹ compared to all available absolute velocities (U test,

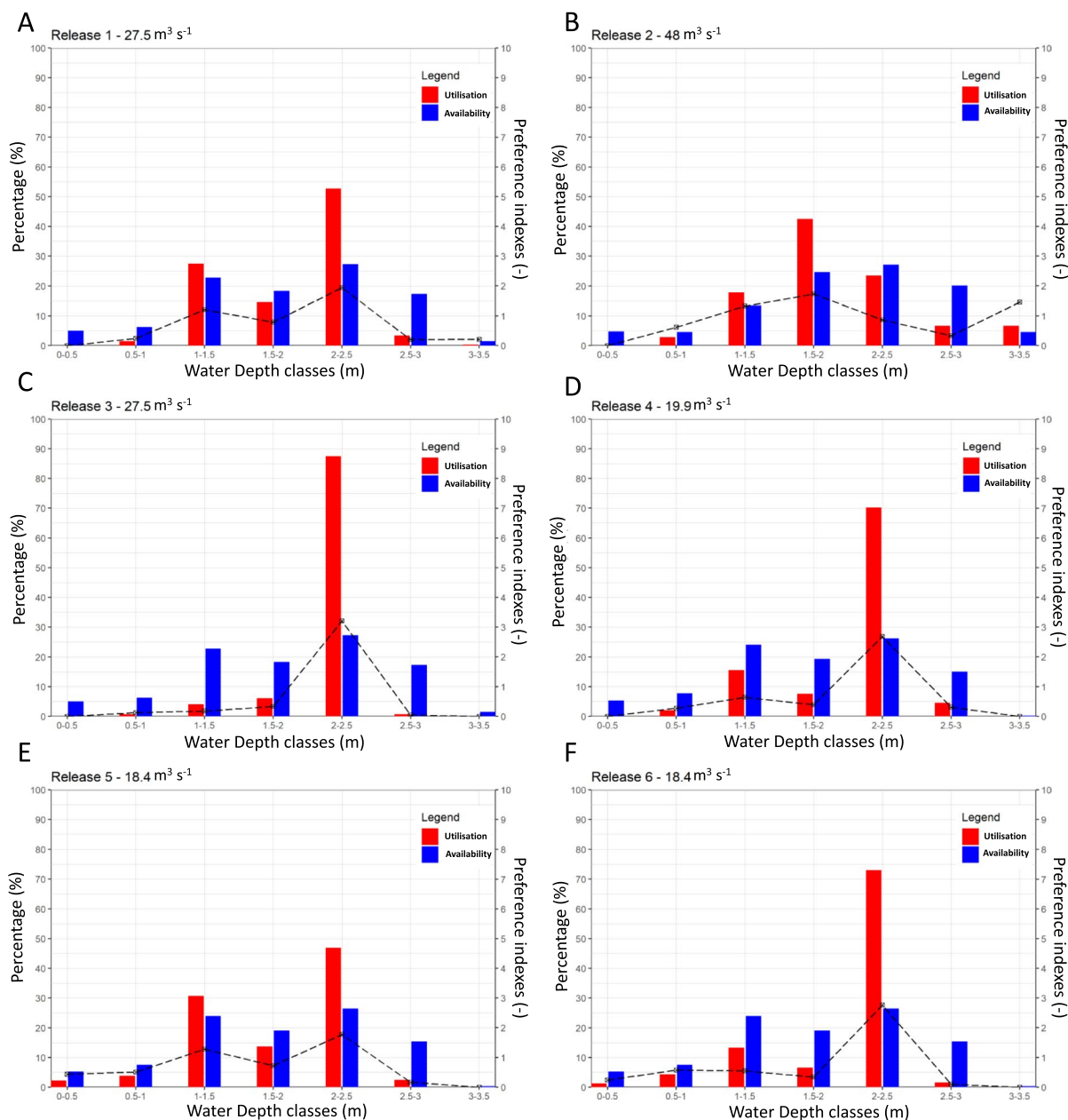


Fig. 7 Distributions of water depths available and used by the smolts upstream of the hydropower plant for each release event. Preference index is represented by dots. (A) First release event to (F) sixth release event

$P < 0.001$), with a more elevated preference index for the 0.4–0.5 m s⁻¹ range from 1.0 to 9.7 (Fig. 6).

Depending on the release group, water depths encountered and used by the smolts differed significantly (KW test, $\chi^2 = 1535.6$, $df = 3$, $P < 0.001$ & KW test, $\chi^2 = 1535.6$, $df = 3$, $P < 0.001$) (Fig. 7). Except the second and third release groups (KW test,

$\chi^2 = 9.1$, $df = 4$, $P = 0.06$ & KW test, $\chi^2 = 2.5$, $df = 5$, $P > 0.1$), the used water depths differed significantly between individuals within the same release group (KW tests, RG1 $P = 0.001$, RG4 $P = 0.002$, RG5 $P = 0.001$, RG6 $P = 0.007$). The most preferred water depth range for the smolts was the 2–2.5 m range with a preference index varying between 1.8

and 3.2, except for the second release group for which the 1.5 to 2 m class had the highest preference index (1.7) (Fig. 7). The 2–2.5 m range corresponds to the intake canal area (zone 5), and the 1–1.5 m range corresponds to the weir area (zone 3). The smolts rarely used extreme water depth values (shallow waters below 1 m and deep waters above 3 m) as shown by a preference index less than 1 for all release groups except the second one.

Discussion

In the present 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 Kaplan turbine and a fish-friendly Archimedes screw. Manual tracking has the advantage to identify the fine-scale behaviour of the smolts in the upstream zone of a hydroelectric site, with the recording of numerous precise positions for each individual, which is sometimes more difficult with automatic tracking devices if the number of antennas is insufficient. On the other hand, manual tracking did not enable simultaneous tracking of a large number of individuals, which explains the small number of smolts tracked simultaneously. Using additional automatic listening receivers would have been beneficial to acquire the exact time of the hydropower plant crossing in the absence of the manual tracking team. Coupled with the hydrodynamic modelling of the river upstream of the hydropower plant, this tracking method allowed a better understanding of the influence of environmental and hydrodynamic conditions on the research behaviour and the choice of a migration route.

Although the smolts released in the Ourthe River were hatchery-reared individuals, 97.2% of the smolts initiated their downstream migration and 88.9% reached the approach zone upstream of the hydropower plant. As observed in previous studies (Renardy et al., 2020, 2021; Ovidio et al., 2021), hatchery-reared smolts usually expressed rapid downstream migratory behaviour once released in the river. The smolts remained highly sensitive to the environmental cues triggering downstream migration (Karpinen et al., 2014). Only one smolt never initiated the downstream migration and moved to upstream parts of the river and three other smolts initiated rapidly

their downstream migration and suddenly stopped before reaching the hydropower plant. These smolts probably died due to predation, as observed by Thorstad et al. (2012) and Furey et al. (2021). A potential negative impact of the tagging procedure on the smolts is unlikely as the ratio between weights of transmitter and of the smolt was less than 2.5% for 94% of the smolts and none was affected by the surgery during the recovery phase. Tagging methodology was identical to those of previous studies carried out using mobile tracking on Atlantic salmon parrs/smolt (Ovidio et al., 2007; Renardy et al., 2020) with an absence of mortality after tagging.

Once upstream of the hydropower plant, 87% of the smolts followed the main river flow, of which 56% headed towards the intake canal of the Kaplan turbines. Only 13% of the smolts did not follow the main flow and first approached the Archimedes screw. The smolts spent significantly more time in the Kaplan intake canal area, with 42% of the smolt locations obtained during smolt tracking. The Kaplan turbine and the weir turned out to be one of the most approached migration routes with 81% of the smolts, contrary to the Archimedes screw, which was approached by 41% of the smolts. Renardy et al. (2020) highlighted a lower approach rate (38%) of the Kaplan turbines during a preliminary tracking study at this site. Hydrodynamic modelling indicated that the site configuration induced the orientation of the main discharge towards the weir and the Kaplan intake canal. Even if the turbinated flow is comparable between the Kaplan and the Archimedes screw, only 25% of the river discharge was towards the screw. The downstream migrating smolts usually follow the main flow, as observed previously (Williams et al., 2012; Szabo-Meszaros et al., 2019; Silva et al., 2020; Karppinen et al., 2021; Renardy et al., 2021). Migration routes with an elevated associated discharge are usually more approached by the smolts, as is often the case for the turbine intake canal (Thorstad et al., 2017; Havn et al., 2018), but sometimes the smolts approach and use pathways with lower associated discharge (Kärgerberg et al., 2020). The bypass was approached by 69% of the smolts and turned out to be approached by fewer smolts despite being well positioned in relation to the site configuration. Considering these observations, the intake canal of the Kaplan turbine is more attractive than the other available migration routes, due to the typology

of the hydropower plant that redirects the main discharge towards this route. However, the elevated time spent in the intake canal area suggests a disorientation and a hesitation behaviour of the smolts once in this zone, probably due to the decrease in current velocity. Despite a recommended bar spacing of 25 mm (Larinier & Couret, 2008), the trash rack with a 50-mm bar spacing might repulse the smolts from using the Kaplan turbine as a migration route for some time.

Amongst the smolts detected upstream of the hydropower plant, five smolts did not explore and approached only one migration route before crossing the study site. The other 84% approached more than one migration route. We observed a complexity in the expressed behaviour, as 68.8% of smolts approached the same migration route several times, demonstrating their hesitation to select a route. Compared to the other migration routes, the Archimedes screw was approached on fewer occasions. The average number of rejections of a migration route reached 6.5. Renardy et al. (2021) highlighted the same tendency with the approach of both available migration routes by migrating smolts, and on several occasions, before crossing the site. However, in some cases, the tendency to cross a hydropower plant during the first or the second attempt was observed for the majority of the smolts (Nyqvist et al., 2017; Renardy et al., 2020). Hydrodynamic modelling allows us to highlight that the complexity of the behaviour expressed by the smolts depend on river discharge and increase with the reduction of the discharge. Low discharge might induce a weaker instinct to migrate, as already observed by Hvidsten et al. (1995), Persson et al. (2019) and Honkanen et al. (2021). A comparable phenomenon was observed by Nyqvist et al. (2017) and Renardy et al. (2021), with a more direct research behaviour before crossing the hydropower plant when the discharge was high. The hesitating behaviour upstream of the Méry hydropower plant, especially at low discharge, may suggest a low attractiveness of all migration routes and, therefore, may induce the expression of a more complex research behaviour of the majority of the smolts. The hesitating smolts tended to approach all the migration routes, even those with lower associated discharge. Migrating smolts may avoid a migration route due to the perception of a danger or due to inadequate configuration and associated hydrodynamic conditions and

therefore, they may try to find a safer way (Coutant & Whitney, 2000; Enders et al., 2009; Williams et al., 2012; Kerr & Kemp, 2019; Renardy et al., 2021).

Upstream of the hydropower plant, the smolts had a preference for higher flow velocities, from 0.2 to 0.5 ms⁻¹, which is consistent with the observations of Piccolo et al. (2008). The flow velocity preference tended to be similar between individuals except for two release groups, which might suggest that flow velocities greater than 0.2 ms⁻¹ will usually attract the majority of the smolts. Renardy et al. (2021) and Ben Jebria et al. (2021) observed that downstream movements of smolts were favoured when the flow velocity was greater than 0.2 ms⁻¹. Concerning the water depth, the preference of the smolts was the 2–2.5 m range, except for the second release group, that was the 1.5–2 m range. The approached water depths tended to differ between individuals of the same release group, suggesting that despite a preference for the 2–2.5 m range, the smolts may use other available water depth ranges to find a migration route. Flow velocity and water depth seem to be used as hydraulic cues in the selection of a migration route.

All the smolts, who approached the hydropower plant, succeeded to pass. The most used migration route was the weir with 41% of the smolts, despite 81% of smolts having approached it. Opening the incision gates did not favour rapid passage over the weir. Except for the second release group, water level over the weir varied between 7.8 and 14.1 cm that could be insufficient to encourage the smolts to use this migration route to cross the hydropower plant. Concerning the other smolts, 36% used the Kaplan turbine, 18% the bypass and 5% the Archimedes screw, but 0% used the vertical slot fishway. The choice of a particular migration route by the smolts was volitional, without entrainment, given their ability to approach and reject the migration routes and to resist the highest flow velocities. Amongst the smolts, 64% used a safe migration route to cross the hydropower plant. Among the smolts who used the Kaplan turbine, seven smolts explored the hydropower plant before crossing the site. Moreover, passage through the Kaplan turbine may be underestimated; as out of the ten smolts with an unknown migration route, nine were last recorded in the intake canal area and were not found in the bypass. Renardy et al. (2020) observed a lower use of the Kaplan turbine with 17.6% and a higher use of the bypass for 41.2% of

the smolts. Despite the ideal position in the extension of the intake canal, the bypass turned out to be little used. The low use of the bypass by smolts may be explained by its very low functional flow and a suboptimal design, notably its orientation in relation to the direction of the water flow, limiting linear water flow without turbulence. The entry of a bypass is one of the most important parameters influencing its efficiency (Enders et al., 2009; Klopries et al., 2018). Upstream of the bypass, smolts were in positive rheotaxis (head upstream) and tended to resist entering into the structure, which might indicate the perception of danger. Depending on the configuration of the bypass, the use varies greatly and may reach 81% to 87% (Tomanova et al., 2018) and 95% (Havn et al., 2018) when properly designed. Concerning the Archimedes screw, the migration route was poorly used, despite its fish-friendly characteristics. Renardy et al. (2020) and Moore et al. (2018) highlighted the same tendency with a low Archimedes screw use of 11.8% and 8.1%, respectively. On the other hand, Havn et al. (2017) and Renardy et al. (2022) observed a more elevated use of an Archimedes screw of 43% (5 migration routes) and 48% (2 migration routes), respectively. The use of the Archimedes screw will depend on its position in relation to the configuration of the migration barrier, and in our study site, the main water discharge was not oriented to the Archimedes screw. Furthermore, the Archimedes screw may produce turbulent flow that might repulse and frighten the smolts, as already suggested by Renardy et al. (2020). Fish-friendly turbines could still have characteristics at the turbine intake that will prevent the smolts from using it to cross hydropower plants (Haraldstad et al., 2019), such as visible rotating blades. Although initially designed for upstream migration, fishways may be considered as a route for downstream migration, as is the case for nature-like fishways for downstream migrating smolts (e.g. Havn et al., 2018; Nyqvist et al., 2018; Molina-Moctezuma and Peterson, 2021). More classical fishways (e.g. Denil or vertical slot) in principle are less suitable for downstream migrating smolts as observed by Calles and Greenberg (2009), Renardy et al. (2020) and Ovidio et al. (2017; 2021), but sometimes the smolts may use these fishways as a migration route (Havn et al., 2017; 2018; 2020). Other species may also use fishways as a downstream migration route (Gutfreund et al., 2018; Celestino et al., 2019; Sanz-Ronda

et al., 2021). In this study, the ten smolts for which the migration route used is unknown may, therefore, have used the vertical slot fishway to cross the hydropower plant.

The median research time required to find a migration route was 4.5 h. The research time was four times higher than the research time observed previously at the same site of 1 h (Renardy et al., 2020). Amongst the 32 smolts, only 25% turned out to be proactive and crossed the site in less than 1.6 h. In the literature, the median required time to cross a medium-sized hydropower plant offering multiple migration routes was reported as 0.5 h by Havn et al. (2017, 5 migration routes) and Havn et al. (2020, 8 migration routes) and from 0.2 to 0.9 h by Tomanova et al. (2018, 3 migration routes). Ovidio et al. (2017, 4 migration routes) reported a research time of less than 1 h for the major proportion (70%) of the smolts. On the other hand, the research time was similar to the research time obtained at a large-sized hydropower plant, with a median time of 4.8 h (Renardy et al., 2021).

The behaviour expressed by the smolts turned out to be more complex and more hesitant than the smolt behaviour observed by Renardy et al. (2020) at the same hydropower plant, whilst under similar water discharge conditions. Water temperature during smolt tracking was different between the two tracking periods. In 2021, the mean water temperature was 9.6 °C compared to a mean water temperature of 14.2 °C in 2018. Water temperature below 10 °C (Teichert et al., 2020) has probably engendered a weaker instinct to migrate downstream and to cross the hydropower plant rapidly, inducing a more elevated delay upstream of the hydropower plant. The migration delay generated by this isolated hydropower plant was significant and may impede the smolts reaching the sea in time, especially as they still have several migrations barriers to cross. Cumulative delays generated by migration barriers will gradually increase during the downstream migration as observed by Renardy et al. (2022) and may cause a mismatch between migration timing and the physiological window that prevents the smolts reaching the sea in time (Marschall et al., 2011).

Four different behavioural tactics to find a migration route were defined and can be applied to smolt behaviour of any future studies. Amongst the smolts detected upstream of the hydropower plant, 78%

expressed the behavioural tactic “reactive explorer”. Concerning the others, 6% expressed the tactic “proactive explorer” and 16% expressed the tactic “proactive non-explorer”. The majority of smolts showed a tendency to explore their environment before crossing a hydropower plant that in most cases increased the research time spent upstream of the migration barrier. The behavioural tactic “reactive explorer” does not seem to be the best tactic to express, inducing in most cases a more elevated migration delay and the risk of using anyway an unsafe migration route. An elevated research time sometimes induced a passage of the smolts through the turbine (Scruton et al., 2008; Svendsen et al., 2011).

Conclusions

In conclusion, the present study highlighted the hesitating behaviour that may be expressed by the smolts facing a migration barrier, offering several unattractive and non-optimal migration routes and inducing significant delays for the downstream migration. Based on the expressed behaviour of the smolts, four behavioural tactics to find a migration route were highlighted. These behavioural tactics may be used in the future studies to categorise the fish behaviour more easily in the vicinity of migration barriers. Behavioural response of the smolts upstream of hydropower plants could be explained partially by hydrodynamic modelling, which shows the interest to have a transversal approach (biological and engineering sciences) considering the smolt fine-scale behaviour and also the biological and environmental factors that may influence smolt behaviour. This manual 2D tracking combined with the hydrodynamic modelling highlighted the influence of several factors on smolt behaviour, such as site configuration, water discharge, flow velocity and water depth. The smolts tended to follow the main flow, approached flow velocities greater than 0.2 ms^{-1} and preferred areas with a water depth of 2 to 2.5 m. The small number of tracked individuals and the low variability of the water discharge conditions during the study do not allow a complete vision of what would have happened during the entire smolt migration season, especially under more extreme environmental conditions. It would be interesting to replicate this study with more smolts, both wild- and hatchery-reared individuals and by diversifying the encountered environmental conditions.

The comprehension of the factors influencing the research behaviour at the hydropower plant may be useful to design attractive and optimal mitigation measures and to guide the smolts efficiently towards safe routes.

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Author contributions Writing of the paper: SR, UDC and MO. Conceived and designed the investigation: SR, JPB and MO. Performed field and/or laboratory work: SR, JPB, AD, PA, SE and MO. Analysed the data: SR, UDC, MO, SE and JPB. Contributed materials, reagents and/or analysis tools: MO, PA and SE. Paper proofreading: JPB, MO, SE and MP.

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

Declarations

Competing Interests The authors have no competing interests to declare.

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