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PRIMARY RESEARCH PAPER

How and where to pass? Atlantic salmon smolt's behaviour at a hydropower station offering multiple migration routes

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Abstract We studied downstream migration behaviour of Atlantic salmon smolt at a hydropower station that offers four safe (weir, new incision gate on weir, downstream bypass and Archimedes screw) and one potentially unsafe (Kaplan turbines) migration routes. We followed hatchery smolts using radio (n = 17) and RFID (n = 200) telemetry. They were released 1.2 km upstream of the hydropower station in spring 2018, in four groups, at different water discharge (18 to 37.2 m^3s^{-1}) and temperature (12.2–17.6°C) conditions. For radio-tagged smolts, the repartition of the migration routes was 41.2% for the bypass, 17.6% for both the Kaplan turbine and the weir, 11.8% for the Archimedes screw, 0% for the new incision and 11.8% of unknown route. For the RFID-tagged smolts, the repartition was 38.0% for the bypass, 56.5% for the weir or the Kaplan, 4.5% for the new incision and 1.0% for the Archimedes Screw. The median time to cross the hydropower station was 58 min, and 88.2% of the smolts succeed to continue their downstream migration. The results demonstrate a diversity of choices of migration routes and underline the importance to optimise the position of fish-friendly turbines and fish passes at hydropower stations to increase their attractiveness.

Keywords *Salmo salar* · Downstream migration · Fish trajectory · Fish telemetry · Fish passage · Archimedes screw

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Introduction

Dams, navigation weirs and hydropower stations have caused a drastic reduction in, and the extinction of, several migratory fish species, impeding free movement (Larinier & Travade, 2002; Katopodis & Williams, 2012; Haraldstad et al., 2018) and preventing or limiting access to functional habitats (Larinier & Travade, 1998; Fullerton et al., 2010; Monnerjahn 2011). The Atlantic salmon (*Salmo salar* Linnaeus, 1758) was one of the most affected species by river fragmentation, with consequent major reductions and even the extinction of some strains in different river basins of Europe and America (Philippart et al., 1994; Parrish et al., 1998; Larinier, 2001; Thorstad et al., 2012).

Important progress has been made in improving the free upstream movement of spawning adult salmon, with technical or nature-like fish passes (Katopodis & Williams, 2012; Silva et al., 2018). Although some upstream passes are still ineffective, progress is significant and performance is increasingly acceptable (Benitez et al., 2015, 2018; Silva et al., 2018). Downstream passage efficiency is much less studied than upstream passage (Wilkes et al., 2018a, b). For downstream migration at the smolt stage, cumulative obstacles must be crossed in fragmented rivers, from upstream to the estuary, in order to reach growing areas; this remains a major and complex problem in many anthropised rivers (Larinier & Travade, 2002; Fjeldstad et al., 2012; Newton et al., 2018). Confrontation with hydropower stations during smolt downstream migration causes delays, injuries and direct and indirect mortality due to energy expenditure (Marschall et al., 2011; Nyqvist et al., 2016; Ovidio et al., 2017a), predation close to the weir (Coutant & Whitney, 2000; Koed et al., 2002; Brevé et al., 2014) and passage through turbines (Coutant & Whitney, 2000; Serrano et al., 2009; Fu et al., 2016). The impact of the turbines depends on the type of model and associated diameter, rotational speed, water head and blade characteristics (Larinier & Travade, 1998; Larinier, 2008). The cumulative impact of the succession of multiple hydropower stations on downstream migration may be considerable and is a major problem for smolts that have to travel long distances in rivers (Thorstad et al., 2012, 2017). This is especially due to the narrow smolt migration window that prevents the escape of part of the population to the ocean in time (McCormick et al., 1998; Marschall et al., 2011; Thorstad et al., 2012) and, as a consequence, reduces the subsequent number of returning spawning adult salmons in subsequent years (Thorstad et al., 2017).

Interest in facilitating downstream migration at hydropower stations has generally increased in recent years (Katopodis & Williams, 2012; Silva et al., 2018). Fish-friendly trash-racks as well as downstream bypasses have been developed and tested to prevent smolts from entering the turbines and to mitigate the negative effects of hydropower stations on migration (Coutant & Whitney, 2000; Larinier & Travade, 2002; Albayrak et al., 2018; Klopries et al., 2018; Tétard et al., 2019). Despite these efforts, the performance of such measures is still challenging and often insufficient to facilitate the safe and quick passage of most downstream migrating smolts (Holbrook et al., 2011; Calles et al., 2012; Ovidio et al., 2017a; Silva et al., 2018; Haraldstad et al. 2018). Fish-friendly turbines (e.g. the Archimedes screw) may also be used as a potential migration route. Such measures would enable the safe passage of fish thanks to the morphology, blade spacing, slow rotational speed and the absence of extreme pressure, which reduce the risk of injury or death (Cefas, 2012; Ecogea, 2010; Brown et al., 2012; Wilkes et al., 2018b). Observations of very low mortality have mainly been reported following direct injection of fish into the turbine (Brackley et al., 2018). However, little attention has been given to the behavioural response of fish approaching these structures and the implications in terms of delay, attraction and efficiency. Piper et al. (2018) and Havn et al. (2017) reported an unexpectedly low use of the Archimedes screw in some hydropower stations configurations. Despite the increased research on measures to mitigate downstream migration in fragmented rivers, little is known about the factors that influence the choice of a migration route by individual smolt at a hydropower station, and especially when the typology of the site is complex and offers multiple migration routes. Some authors already mention the effect of flow (Fjeldstad et al., 2012; Cheng and Gallinat, 2014), temperature (Castro-Santos & Perry, 2012), smolt physiological state (Coutant & Whitney, 2000; Fjeldstad et al., 2012; Tétard et al., 2019) and the season progression (Nyqvist et al., 2016; Tétard et al., 2019) on the final choice of a migration route. A better comprehension of the choices also requires information of fish beyond the hydropower station, before their final choice of a migration route, but such an approach has been very little considered yet (see Svendsen et al., 2011; Pelicice et al., 2015; Nyqvist et al., 2016).

In this study, we investigate the downstream migration behaviour of individual smolts of Atlantic salmon *Salmo salar* at a hydropower station installed along the Ourthe river, a tributary to the Meuse river (Belgium), which is topologically complex and offers five potential migration routes, including potentially unsafe Kaplan turbines and four safe routes (a fish-friendly Archimedes screw, a downstream bypass, a weir and a new incision gate on the weir). Observations were performed using both radio and RFID (Radio Frequency Identification) telemetry. The overall aim of this study was to test the performance of the retrofitted bypass and the potential attractiveness of the new Archimedes screw compared to the conventional Kaplan turbines. More specifically, we determined (1) the variability of smolt individual behaviour when they arrived at hydropower station, (2) the quantification of the migration routes used by smolts, and the relationship with water discharge, water temperature, season progression and smolt body length, (3) the time required to cross the hydropower station and (4) the downstream migratory patterns and the speed of smolts once the hydropower station has been crossed.

Materials and methods

Study area

The study site, the Méry hydropower station, is situated in the lower part of the river Ourthe, a tributary of the river Meuse (Fig. 1, W1). The river Ourthe is a typical medium-sized highland river some 235 km long, with its source in the Belgian Ardennes at an altitude of more than 500 m, and whose total catchment area extends over 3672 km^2. The confluence with the Meuse is located in the city of Liège at an altitude of 63 m, which represents a global slope of 2.5‰. In the Ourthe, the average water discharge is 54.7 m^{3}s^{-1} and the mean annual temperature is 11.4°C. The lower Ourthe 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 the Méry hydropower station to the confluence with the Meuse, the river Ourthe is fragmented by six physical obstacles (Fig. 1; W1 to W6) which delimit six river stretches (Fig. 1A–F).

The Méry hydropower station is located 12.7 km upstream from the confluence with the Meuse, at a place where the mean annual discharge is 43.7 m^{3}s^{-1}. On the left side, the site is equipped with two Kaplan turbines of 2 × 6 m^{3}s^{-1} nominal flow, with a rotational speed of 250 revolutions per minute, a diameter of 1.8 m, over a head of 2.5 m, associated with a trash-rack of 67° angle composed of bars spaced 50 mm apart. A downstream migration bypass 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 m^{3}s^{-1} but the actual discharge varies between 0.1 and 0.2 m^{3}s^{-1}, from a 480 × 300 mm rectangular inlet. 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 (Fig. 2). On the right bank, an Archimedes screw and a vertical pool-type fishway were installed in 2018. The Archimedes screw has a length of 4.5 m with a diameter of 3.6 m, a rotational speed of 22.8 revolutions per minute and a nominal functioning discharge of 7 m^{3}s^{-1}. The new fishway is 32 m long with 10 pools, functioning at 0.7 m^{3}s^{-1} and it is associated with an attraction discharge of 0.3 m^{3}s^{-1}. A new incision gate was created on the weir next to the Archimedes screw (Fig. 2).

The hydropower station of Méry offers five different potential migration routes for the downstream migrating Atlantic salmon smolts (Fig. 2): (i) over the weir, (ii) through the intake channel and finally the Kaplan turbines after passage of the trash-rack, (iii) through the intake channel and finally the downstream bypass, (iv) through the Archimedes screw and (v) through the new incision gate (0.4 m high and 0.52 m long) next to the Archimedes screw. The vertical slot fishway of the study site was not considered as a downstream migration route, as it is only adapted for upstream movement. Among these migration routes, the use of the Kaplan turbines is the only one that may cause mortality. Based on the typology of the site and the turbine, the theoretical mortality rate is estimated at 17.6% (Larinier & Travade, 2002; Fu et al., 2016).

After the passage of the Méry hydropower station (W1), the smolts are confronted with five weirs (W2 to W6) that are not equipped with hydroelectric turbines (Fig. 1), with delta heights ranging from 1.6 to 4 m, before the confluence with the river Meuse. The study site was divided into six river stretches (from A to F) delimited by the presence of weirs (W1 to W6) in the migratory trajectory of the smolts (Fig. 1).

Tagging of smolts and environmental data

After the extinction of Atlantic salmon in the river Meuse basin in the 1930s, a restoration program started in the 1990s (Philippart et al., 1994). However, given that the population is still not self-sustainable (not enough returning salmon), a salmon hatchery is

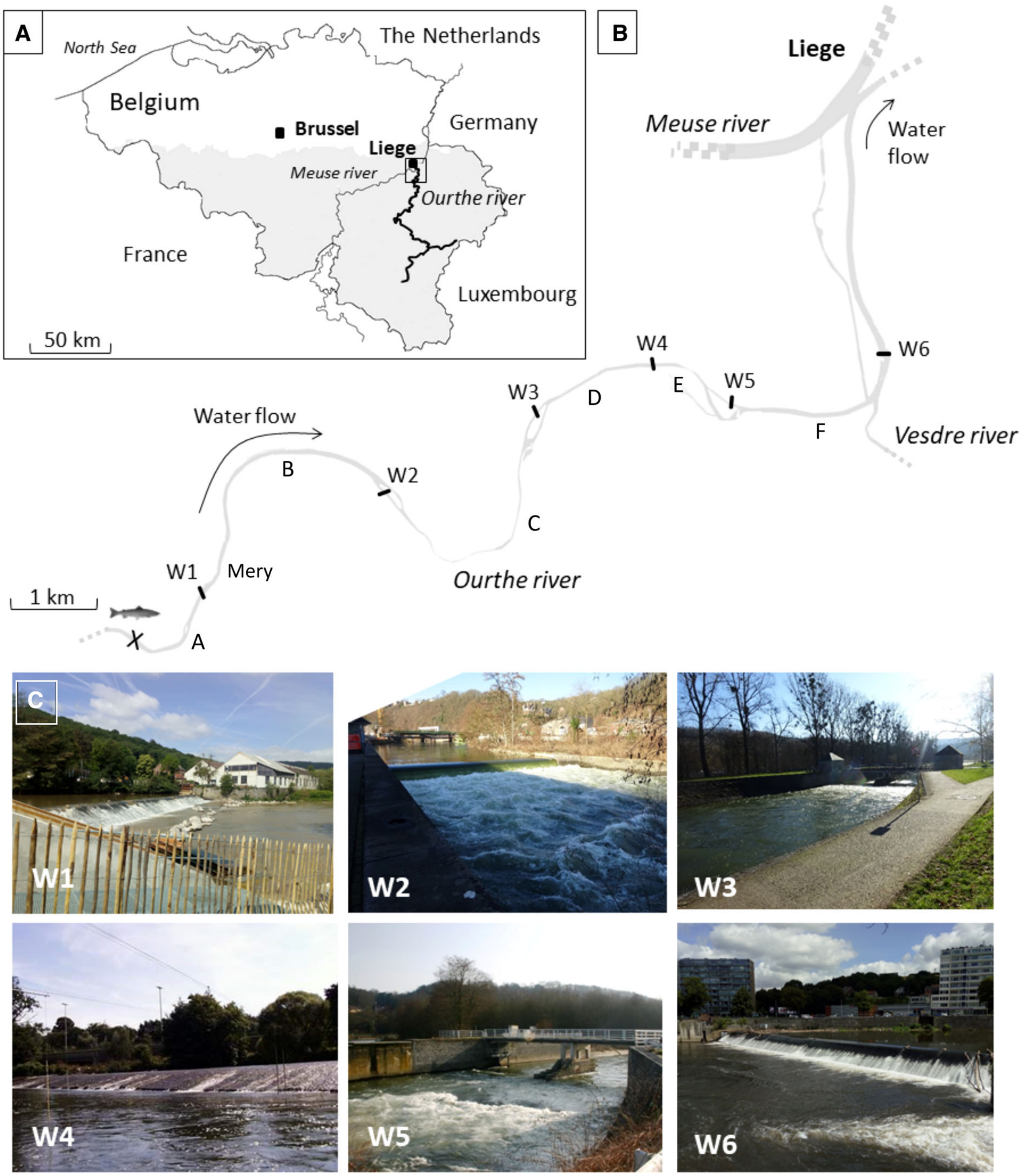

Fig. 1 The river Ourthe basin in Belgium (**A**). Localisation of the six studied weirs in the river Ourthe (**B**). Photographic representation of the six studied weirs in the river Ourthe (**C**)

required to produce juveniles for restocking the river. We used 217 1-year-old smolts (fork length between 143 and 196 mm and body mass between 31 and 84 g) from the Erezee Hatchery (Belgium). The smolts were first anaesthetised with 0.2 ml l^{-1} of phenoxyethanol. After a 10-mm incision, $n = 17$ smolts were surgically equipped with a radio transmitter in their body cavity (Advance Telemetry Systems; Model F1410;

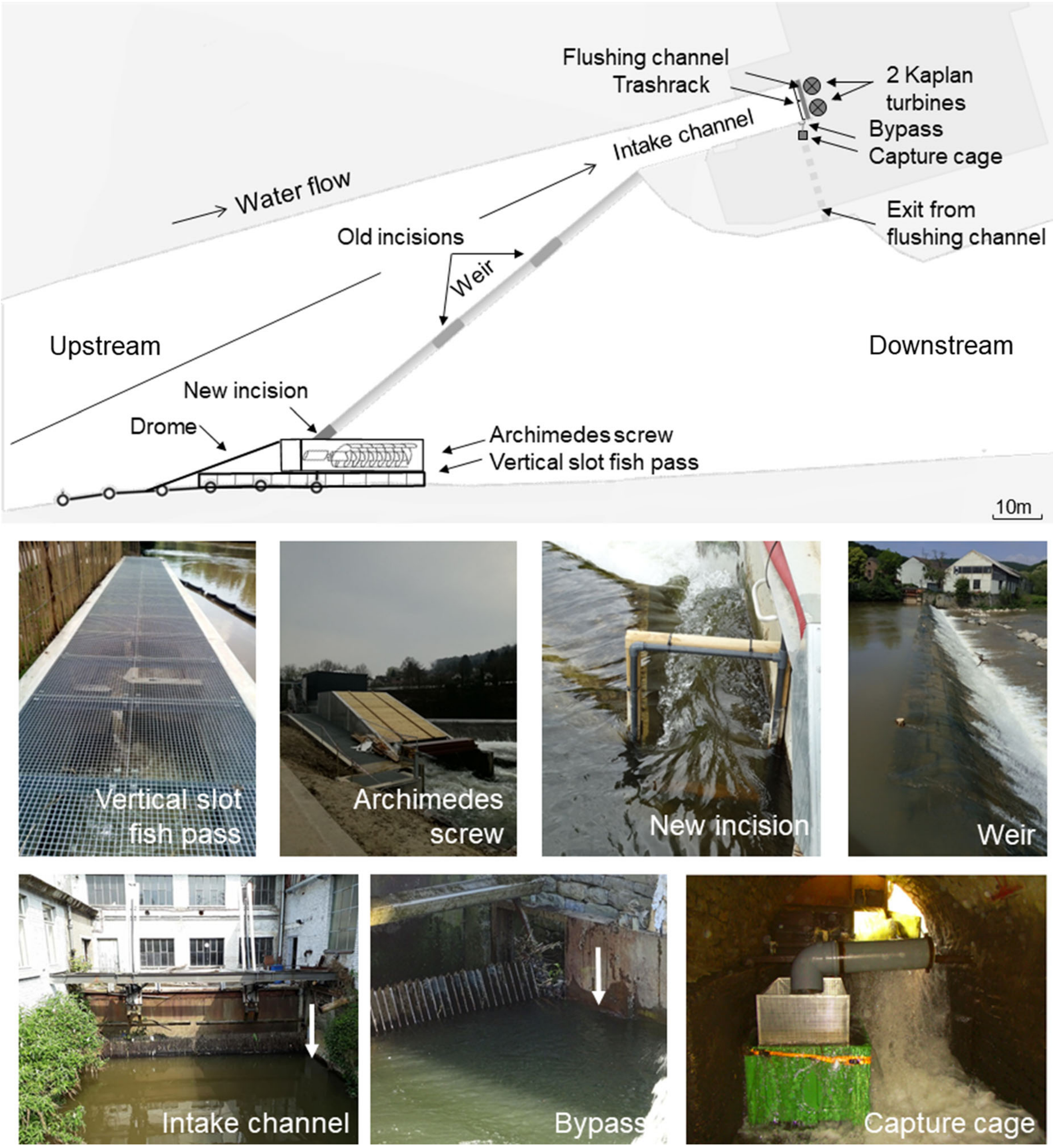

Fig. 2 Schematic and photographic representations of the hydroelectric production site of Méry (W1) in the Ourthe with the locations of the main structures

frequency 45 MHz; 7 mm × 15 mm; mass in air 1.0 g; expected life time 20 days). The incision was closed with two stitches using absorbable suture material (Ovidio & Philippart, 2002). In addition, $n = 200$ smolts were equipped with a half-duplex RFID-tag surgically implanted into the body cavity after an incision of 3 mm (Transponder TIRIS Texas Instrument; 2 mm × 23 mm; mass in air 0.8 g) without the need of suture (Ovidio et al., 2017a). All tagged smolts were placed for 1 h in basins with river water to recover before being released. Water temperature (°C) was recorded every hour during the study using data loggers (Tidbit Onset) installed at Méry. Discharge data (m^3s^{-1}) were provided by the Wallonia Public Service of Hydrological Studies (SETHY, Walloon Region, Belgium), with one measurement every hour.

Recording of tagged smolts after release

All tagged smolts were divided into four groups (G1 to G4) and released at different periods (Table 1). Release dates were mainly established according to the water discharge and its associated temperature in order to have variable environmental conditions and to determine their effect on the behaviour of smolts migrating downstream. Smolts were released 1200 m upstream from the Méry hydropower station on the day of tagging (Fig. 1B).

With the participation of five operators, the radio-tagged smolts were manually and continuously tracked from the release site to their most downstream position, representing a maximum of 14 km of river investigated (Fig. 1B, river stretch A to F). Active tracking was done on foot or by car using portable receivers (ATS Model Fieldmaster) and directional (Low Frequency loop) and non-directional antennas (Magnetic Roof-Mount Dipole) from the time of release until the last possibility of location. Non-directional antennas were used to detect the smolts at a greater distance in order to approach them more rapidly, especially after they passed the Méry hydropower station. Directional antennas were used for locating smolts with precision (see Ovidio et al., 1998) and enabled us to identify the precise research behaviour of smolts' upstream of the Méry hydropower station. From 9 April to 25 May 2018, a total of 485 smolts positions were recorded after a total of 70 h of manual radio tracking, and 87 smolts were detected with the automatic listening RFID telemetry system.

In order to track the smolts equipped with an RFID-tag, two automatic antennas were installed at the Méry hydropower station, one at the entrance to the Archimedes screw and the other at the new incision gate. Combined with an automatic RFID detection station (CIPAM®, France), the date and time of individual smolt codes were recorded when the fish entered the 0.6 m-diameter detection area of one of the antennas. The smolts that entered the capture trap of the bypass downstream device were also identified with a portable RFID reader during monitoring. RFID tracking was used as a complementary method to radio-telemetry in order to collect more data on the proportion of downstream migration routes used. However, the RFID-tagging did not allow us to distinguish passage between the weir and the Kaplan turbines.

The data from the radio and RFID tracking enabled a number of quantitative passage metrics and behavioural descriptors to be established when the smolts were confronted by the Méry hydropower station:

Travel time to reach Méry: hourly time needed for radio-tracked individual smolts to reach the Méry hydropower station. This travel time corresponds to the time between the release time and the first detection upstream of Méry.

Migration route use: the percentage of individual smolts using each migration route at the Méry hydropower station in comparison with all the tagged smolts released upstream (for radio-tagged and RFID-tagged smolts). The use of the bypass as a migration

Table 1 Characteristics of the experimental conditions encountered by the tagged smolts in each group

Group	Date of release	Time of release	*N* = Radio/RFID	Hydraulic conditions			Turbine activity	
				Discharge (m^3/s)	Temperature (°C)	[O_2] (mg/l)	Kaplan turbines	Archimedes screw
G1	9-04-18	21:00	4/50	37.2	12.2	13.9	1 (6 m^3s^{-1})	Yes (7 m^3s^{-1})
G2	19-04-18	18:30	4/50	24.1	16.2	13.2	1 (6 m^3s^{-1})	Yes (7 m^3s^{-1})
G3[a]	26-04-18	15:45	5/50	18	14	12.2	1 (6 m^3s^{-1})	Yes (7 m^3s^{-1})
G4	17-05-18	16:15	4/50	20.1	17.6	9.5	1 (6 m^3s^{-1})	Yes (7 m^3s^{-1})

Discharge and temperature correspond to the conditions during the time of release

[a]During the third release, five smolts were marked with a radio transmitter

route represents overall bypass efficiency (Ovidio et al., 2017a).

Adjusted bypass efficiency: the percentage of individual radio-tagged smolts captured in the downstream bypass trap in comparison with those that entered in the intake channel of the Kaplan turbines (for radio-tagged smolts) (Ovidio et al., 2017a).

Research time related to each migration route at the Méry hydropower station: the average hourly time required to cross the Méry hydropower station for each migration route. The research time corresponds to the time spent upstream of the hydropower station between the first and last locations of smolts with radio tags.

After their passage through the hydropower station of Méry, different behavioural metrics were used to describe the behaviours of the smolts:

Overall median migration speed: the calculated speed of the radio-tagged smolts (ms^{-1}) between the release site and the last location, as far downstream as possible.

Median migration speed: the calculated speed of the radio-tagged smolts (ms^{-1}) in each stretch, based on the greatest possible covered distance in a certain time.

Data analysis

Because data violated the assumptions of normality (Kolmogorov–Smirnov, $P < 0.05$), non-parametric tests were used. We analysed the approach behaviour of radio-tagged smolts by calculating the travel time and the speed to reach Méry and the proportion by migration route of individuals detected first. To investigate the proportion of smolts by migration route used to cross the hydropower station, the number of RFID or radio-tagged smolts that used each route was divided by the total number of smolts released. To check if the choice of a migration route at the hydropower station of Méry was randomly selected, we compared the repartition of migration routes used by radio-tagged and by RFID-tagged smolts to a uniform repartition (same percentage for each migration route) using a χ^2 test. To compare the distribution of the radio-tagged smolts through the migration routes used in relation to research time, water discharge (m^3s^{-1}), temperature (°C) and season progression (Julian days), we used a Kruskal–Wallis test followed by the Mann–Whitney test with Bonferroni–Holm correction for post hoc pairwise comparisons. These tests were also used to compare the distribution of both the body length and the research time to cross the hydropower station according to the migration routes used for the radio-tagged smolts as well as the distribution of the body length per migration route for the RFID-tagged smolts. A time to event graphical representation of migration routes used was constructed at the hourly scale for each group of radio-tagged individuals. A passage frequency was then calculated for each release group of radio-tagged smolts, by dividing the maximum time to pass by the number of individuals in the group. Once the Méry hydropower station was crossed, downstream migratory patterns were established for each radio-tagged smolt using all its recorded positions along the Ourthe river. In order to assess the speed of the smolts after the hydropower station, we analysed the median migration speed in each river stretch and the overall median migration speed. A Kruskal–Wallis test was performed to analyse the influence of the river stretches on the migration speed and the influence of the migration route used at the hydropower on the subsequent swimming speed. A Spearman rank correlation was made to assess the relationship between the body length of the smolts and their migration speeds. All statistical analyses were performed using the software R (version 3.4.2), and the significance level was set at $P < 0.05$.

Results

Research and passage behaviour of the smolts

After the release, the radio-tagged smolts took a median travel time of 1:01 h (range 0:40–4:19 h) with a median speed of 0.38 ms^{-1} (range 0.09–0.65 ms^{-1}, $n = 15$) to reach the Méry hydropower station. Research and passage behaviours were not identified for two radio-tagged smolts belonging to G1 group (11.8%). At their arrival of hydropower station, 35.3% of smolts (Table 2; Fig. 3, smolts 9, 11, 12, 14, 16 & 17) moved first towards the intake channel of the Kaplan turbines which leads to the bypass or the Kaplan turbines. Regarding the other passage routes, 29% of smolts were approached first the weir (smolts 1, 5, 8 & 10), 23.5% the Archimedes screw (smolts 4, 6, 13 & 15) and 0% the new incision gate.

Table 2 Characteristics of the research behaviour of each radio-tagged smolts upstream of the Mery dam

Smolts	Travel time to reach Mery	First approached passage route	Intermediate approached passage route	Final passage route used	Period of the day D/C/N	Research time (h)	Continued migration downstream of Mery
1	03:52	Weir	–	Weir	N	00:04	Yes
2	–		Bypass/Kaplan turbines	–			?
3	–						Yes
4	02:38	Archimedes screw	New incision	Weir	C	20:48	Yes
5	00:45	Weir	–	Kaplan turbines	N	04:47	Yes
6	04:19	Archimedes screw	New incision	Archimedes screw	C	22:46	Yes
7	00:53	Weir	–	Bypass	N	28:42	No
8	00:59	Weir	–	Weir	C	00:11	Yes
9	01:15	Bypass	Kaplan turbines	Bypass	C	04:30	Yes
10	00:59	Weir	–	Bypass	D	01:38	Yes
11	01:01	Bypass	–	Bypass	D	00:49	Yes
12	03:40	Bypass	Kaplan turbines	Bypass	C	00:50	Yes
13	00:40	Archimedes screw	New incision	Archimedes screw	D	00:58	Yes
14	01:01	Bypass	–	Bypass	D	00:20	Yes
15	01:23	Archimedes screw	Bypass	Kaplan turbines	D	02:30	Yes
16	00:50	Bypass	–	Kaplan turbines	D	00:20	Yes
17	01:07	Bypass	–	Bypass	D	00:46	Yes

D, C and N mean day, crepuscular and night

Regarding the passage behaviour, we observed that 41.2% of these smolts used the bypass very quickly (Table 2; Fig. 3 smolts 7, 9, 10, 11, 12, 14 & 17) and 17.6% used the Kaplan turbines (smolts 5, 15 & 16). Three smolts used the weir (17.6%) as their final migration route after a simple approach trajectory (smolts 1 & 8) or a more complex movement pattern with the approach of another migration route (smolt 4). The two smolts (11.8%) using the Archimedes screw as their last migration route approached first the new incision gate (smolts 6 & 13). The new incision gate was not used by radio-tagged smolts (0%). For the radio-tagged smolts, the adjusted bypass efficiency was 63.6% (7 of the 11 smolts that enter the intake channel of the Kaplan turbines). For the RFID-tagged smolts, the repartition of the migration route was 38.0% for the bypass, 56.5% for the weir and/or the Kaplan (not distinguishable), 4.5% for the new incision and 1.0% for the Archimedes Screw. The repartition of the migration routes used by radio- and RFID-tagged smolts (Fig. 5A and B, respectively) was significantly different from a uniform repartition (radio-tagged: χ^2 test, $\chi^2 = 29.1$, df = 4, $P < 0.001$; RFID-tagged: χ^2 test, $\chi^2 = 35.4$, df = 3, $P < 0.001$).

The median time taken by the radio-tagged smolts to cross the hydropower station was 00:58 h (mean = 5:59 h, range 00:04–28:42 h, 88.2%) (Table 2). Few smolts (17.6%) needed more than 20:00 h to cross the Méry hydropower station. No difference was observed in the research time required for smolts to cross the hydropower station when compared to the migratory routes used (Kruskal–Wallis test, $\chi^2 = 2.59$, df = 3, $P = 0.459$). Most of the radio-tagged smolts (47.1%) crossed the hydropower station before dusk between 17:23 and 20:08 h (Table 2). Other smolts (23.6%) passed during dusk between 20:25 and 20:56 h while two smolts (11.8%) passed during the night at 23:24 h and 00:56 h.

From the G1 to G4 releases, the environmental conditions varied (temperature range = 12.1–17.6°C and water-flow range 18–37.2 m^3s^{-1}) and the migration routes used by the radio-tagged smolts changed over time. The use of the weir as migration route occurred only for smolts of G1 and G2 during high

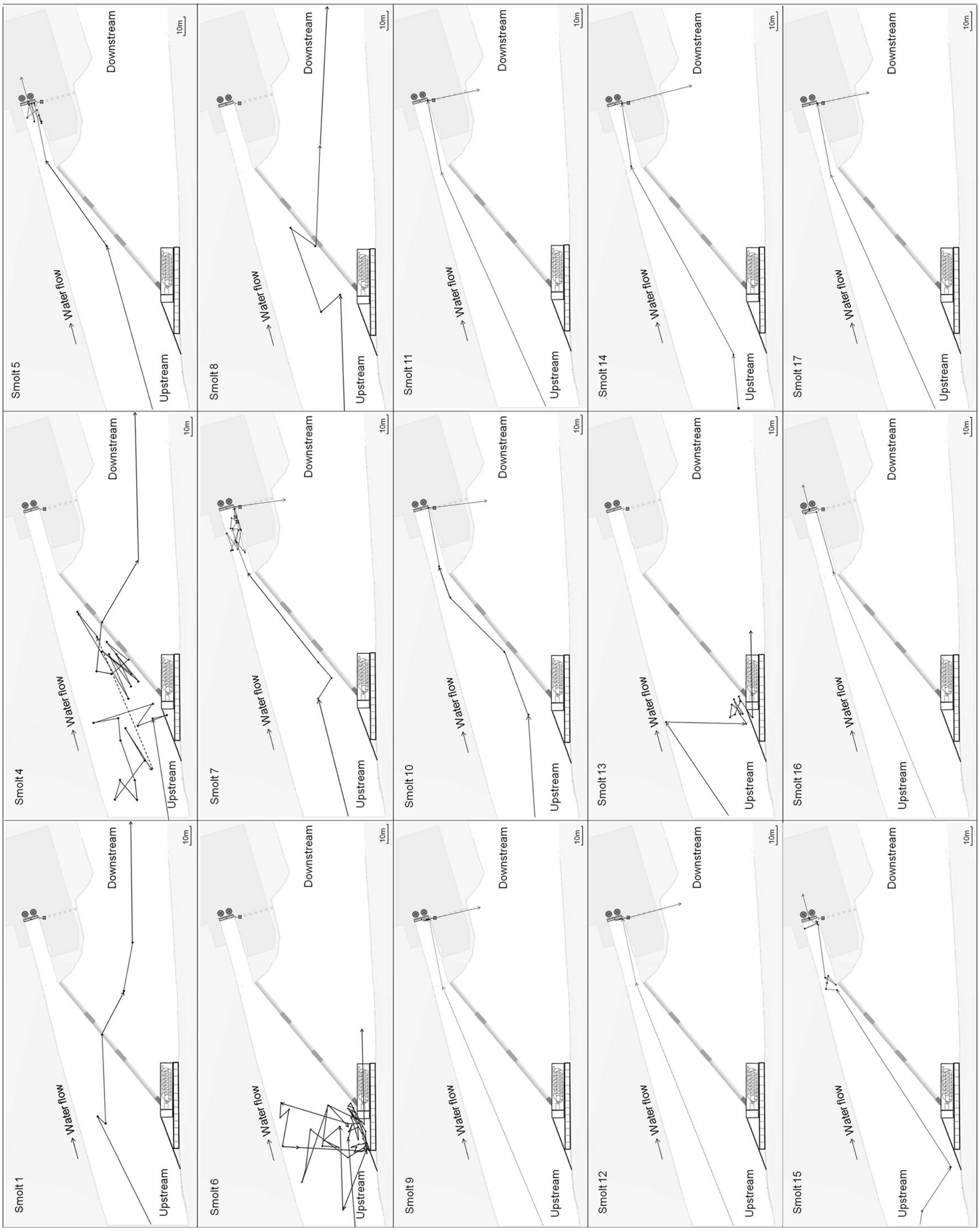

Fig. 3 Trajectories of n = 15 radio-tagged smolts at the approach of the hydropower station of Méry (W1)

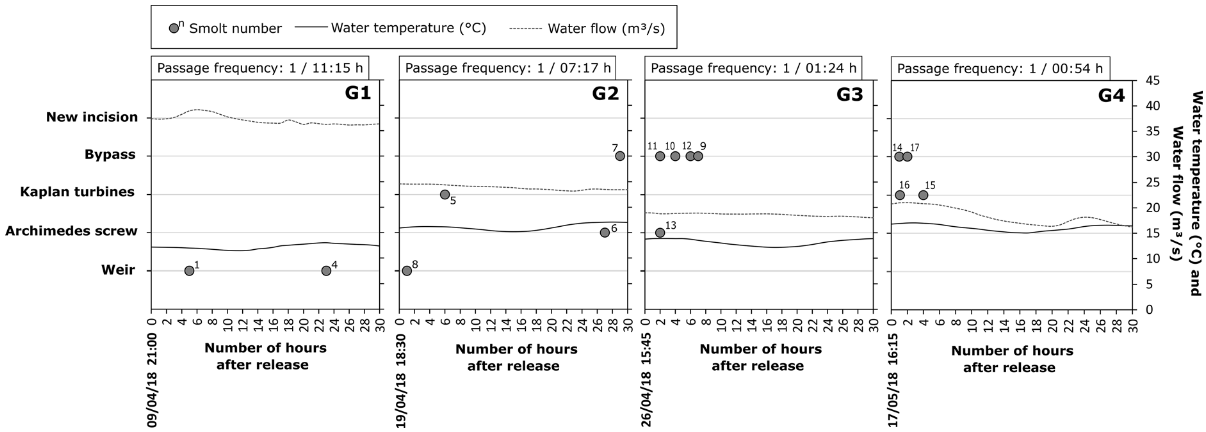

Fig. 4 Time to event representation of the choice of the migration routes in relation with the water temperature and flow by the radio-tagged smolts of each release group (G1 to G4)

flow, and use of the bypass mainly during lower flow for G3 and G4 (Fig. 4). The passage frequency progressively decreased during the study (G1: 1 passage/11:15 h and G4: 1 passage/00:54 h). The water discharge affected the radio-tagged smolts' choice of a migration route (Kruskal–Wallis test, $\chi^2 = 8.36$, df = 3, $P = 0.039$) and was significantly higher for the weir migration route than the bypass (Mann–Whitney test, $P = 0.022$). The highest average water discharge was related to the weir's use, with a median of 35.9 m^3s^{-1} (range 24.1–37.2 m^3s^{-1}) and the lowest was combined with the bypass with a median

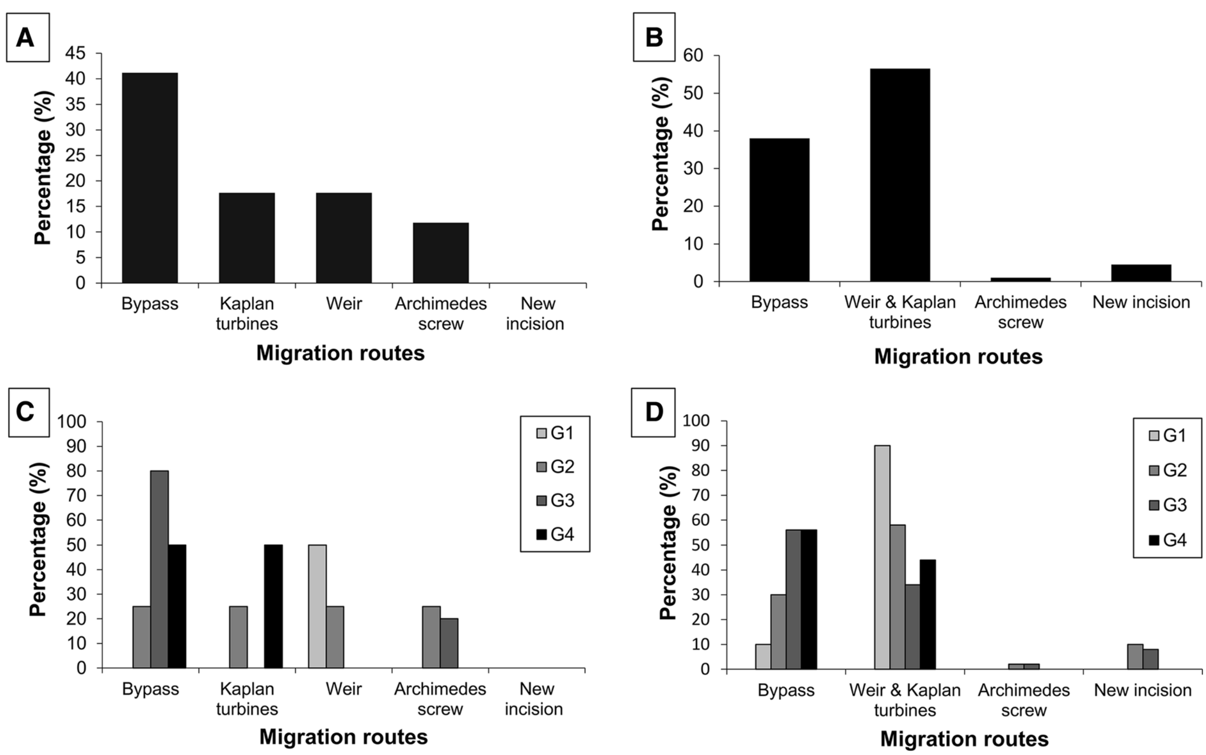

Fig. 5 Repartition of the different migration routes used by the tagged smolts. **A** Percentage of migration route used by the radio-tagged smolts. **B** Percentage of migration route used by the RFID-tagged smolts. **C** Percentage of use by release group of radio-tagged smolts. **D** Percentage of use by release group of pit-tagged smolts (**D**)

value of 19.1 m^3s^{-1} (range 18.0–22.9 m^3s^{-1}) (Fig. 5C). The proportion of RFID-tagged smolts choosing the bypass as their last migration route was significantly greater for G3 and G4 release groups than for G1 and G2, when the water discharge was lower (χ^2 tests, $\chi^2 = 27.50$, $P < 0.001$) (Fig. 5D). The average water discharge obtained for use of the bypass was 20.4 and 19.1 m^3s^{-1} for RFID-tagged and radio-tagged smolts, respectively. This was also the case for the use of the Archimedes screw, with 20.4 and 21 m^3s^{-1}. The water temperature did not significantly affect the smolts' choice of a migration route (radio-tagged smolts: Kruskal–Wallis test, $\chi^2 = 4.42$, df = 3, $P = 0.22$; RFID-tagged smolts: χ^2 tests, $\chi^2 = 2.12$, $P = 0.14$). The progression of the season did not significantly influence the use of the different migration routes of the radio-tagged smolts (Kruskal–Wallis test, $\chi^2 = 7.08$, df = 3, $P = 0.069$). The body length of smolts did not significantly differ among the migration routes used (Kruskal–Wallis, radio-tagged smolts: $\chi^2 = 4.33$, df = 3, $P = 0.23$; RFID-tagged smolts: $\chi^2 = 5.63$, df = 2, $P = 0.059$).

Downstream migration behaviour after the passage of the Méry hydropower station

Once the Méry hydropower station was crossed, most radio-tagged smolts (88.2%) continued their downstream migration towards the Meuse river with a variable speed (Fig. 6). One smolt was captured dead during the trap monitoring and another was lost. $N = 14/15$ of smolts were tracked at least up to the W3 weir and $n = 7/15$ smolts were recorded until the last weir (W6), upstream of the confluence with the Meuse, about 11,674 m downstream of the release site (Fig. 6). Between W1 and W3, the radio-tagged smolts migrated with a median speed of 0.48 ms^{-1} (mean = 0.46 ms^{-1}, range 0.07–0.99 ms^{-1}, $n = 13$ smolts) and between W1 and W6 with a median speed of 0.18 ms^{-1} (mean = 0.28 ms^{-1}, range 0.16–0.62 ms^{-1}, $n = 7$ smolts). No significant correlation was found between the body length and the migration speed of the smolts (Spearman correlation, $r_s = 0.025$, $P = 0.53$). The last migration route used did not significantly influence the migration speed downstream of the hydropower station (Kruskal–Wallis, $\chi^2 = 5.76$, df = 3, $P = 0.12$).

At stretch B, smolts migrated with the highest median speed of 0.52 ms^{-1} (range 0.05–0.84 ms^{-1}, $n = 14$). Only two smolts slowed down and/or paused in their downstream migration after crossing the W1 weir (Fig. 6 G3 Smolt 11 & G4, Smolt 14). At the W2 weir, the smolts were not slowed. At C, most smolts (64%) slowed and/or stopped their migration about 1000 m upstream of the W3 weir, reducing the median speed to 0.44 ms^{-1} (range 0.05–0.91 ms^{-1}, $n = 13$). After that, the median migration speed was, respectively, 0.17 ms^{-1} (range 0.06–3.08 ms^{-1}, $n = 5$), 0.42 ms^{-1} (range 0.02–0.80 ms^{-1}, $n = 3$) and 0.16 ms^{-1} (range 0.03–0.28 ms^{-1}, $n = 2$) in river stretches D, E and F. The migration speed of the smolts did not significantly vary among the different river stretches (Kruskal–Wallis, $\chi^2 = 5.67$, df = 5, $P = 0.34$).

Discussion

The re-establishment of quick and safe downstream fish migration is a major challenge in a highly fragmented river system, especially when old hydropower stations have to be equipped with retrofitted fish-friendly devices and when multiple migration routes are offered to fish. This study highlighted the diversity of individual behaviour expressed by Atlantic salmon smolts at the approach of a hydropower station before the final choice of a migration route. Most of the smolt pass the hydropower station using a safe migration route, but among the two types of turbines installed on the site, the retrofitted Archimedes screw (recognised as fish friendly turbine) was less used than the build-in Kaplan turbines (potentially unsafe). These results in a single study site put forward that fish-friendly turbines are not automatically attractive for smolts and suggest more broadly the importance of optimising their position to increase their attractiveness. This underlines the importance to conduct further studies to better understand the process of selection of a specific migration route by individual smolts.

Among the diverse set of methods suitable for fishway target setting and monitoring frameworks, biotelemetry is recognised as an efficient tool to quantify their efficiency with associated behavioural patterns (Ovidio et al., 2017b; Wilkes et al., 2018a). Our field approach was possible by use of accurate manual biotelemetry methods, allowing a qualitative analysis of smolt behaviour, which is important in fish

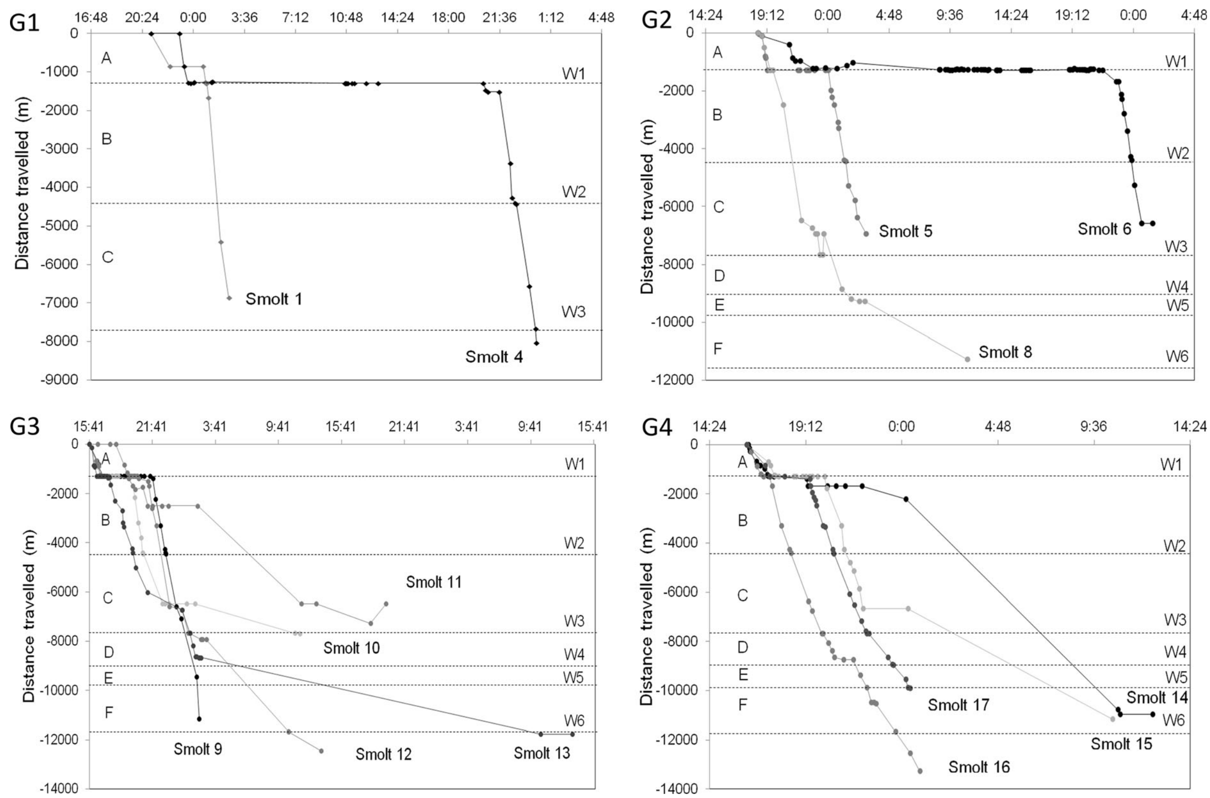

Fig. 6 Migration behaviours of the radio-tagged smolts (G1 to G4) after their passage of the hydropower station of Méry in relation with the presence of weirs. One dot represents one recorded position for one smolt

passage studies (Castro-Santos & Perry, 2012; Silva et al., 2018). We have tried to work under variable environmental conditions, but the results obtained in this study do not represent a complete vision of what would have happened during the entire migration season of smolts in the river Ourthe, especially under more extreme environmental conditions. Although the smolts released in the Ourthe river were hatchery fish, they all started the downstream migration after their tagging and release. As observed by Karppinen et al. (2014), hatchery smolts remained highly sensitive to the environmental cues triggering fish migration. However, the difficulty to work with wild populations did not allow investigating whether behavioural responses when approaching the hydropower station would differ from those expected in natural smolts.

Smolts are able to detect fluctuations in water velocity when they approach a hydropower station (Coutant & Whitney, 2000). Instinctively, smolts follow the main stream in order to minimise their energy cost (Coutant & Whitney, 2000; Serrano et al., 2009; Thorstad et al., 2012, 2017; Havn et al., 2017, 2018) and, consequently, the hydraulic configuration of the site and the typological characteristics of each migration route affect their behaviour and choice (Scruton et al., 2003; Ovidio et al., 2017a). Before reaching a potential route to cross the hydropower station, individual smolts expressed different trajectories upstream of the weir. Most smolts approached the intake channel of the Kaplan turbines relatively directly (within 35 min) and with simple trajectories, maybe because this route is located in the most downstream part of the study site. This underlines the importance of the first smolt movement trajectory at the approach of a hydropower station and the interest of establishing it as fish-friendly as possible to allow safe and rapid passage for a major part of the population. A first trajectory towards a potentially unsafe path would therefore be a very problematic situation, given that in our study, the smolts that first entered the intake channel of the Kaplan turbines did not turn around to exit. The intake channel was therefore similar to an impasse towards the Kaplan turbines and, fortunately, to alternative use of the downstream bypass as migration route in our study site. Some smolts expressed more complex movement trajectories and approached one or two potential migration routes before choosing a final one to cross the hydropower station. It is still unclear why some individuals expressed different behaviours/trajectories when approaching the hydropower station, as they originated from the same strain and were released at exactly the same place using the same methodology. It could be a result of the expression of behavioural syndromes with the potential existence of exploration and avoidance characteristics in individuals (Conrad et al., 2011). Different types of approach and entrance behaviours in migrating smolts were also described by Ovidio et al. (2017a) at a downstream bypass.

Despite the fish-friendly characteristics, the installation of an Archimedes screw in the study site did not result in a preferential orientation towards, and use of this migration route by smolts, as only 11.8% of the smolts used it to pass. Havn et al. (2017) showed a 43% use of an Archimedes screw when the main discharge was moving towards this turbine. Moore et al. (2018) highlighted minimal utilisation of an Archimedes screw (8.1%) by smolts in favour of the weir use (71.4%). Even if the discharge of the Archimedes screw was greater than that of Kaplan turbines (ratio: 116%), the latter has been used more often as a migration route by smolts. The low attractiveness and low use of the Archimedes screw in our study may be linked to its inappropriate position, in the upper part of the weir. It is also conceivable that the Archimedes screw may repulse and frighten smolts because its functioning is associated with important noises (e.g. slapping of water, smashing at crossbeam: Lashofer et al., 2012) whose impact on fish is still unknown. Piper et al. (2018) studied the effect of an Archimedes screw on the movement patterns and behaviour of five potamodromous species and the European eel [*Anguilla anguilla* (Linnaeus, 1758)] and highlighted the low attractiveness of the Archimedes screw for downstream migrating eels. Although adult seaward-migrating eels passed through the operating turbine, they rarely did so directly; more frequently, they milled and returned back upstream, thus contributing to delayed migration. The new incision gate installed near the Archimedes screw was sometimes approached but not used by the radio-tagged smolts and only used by 1% of the RFID-tagged smolt. The main existing old incisions in the weir were more attractive, probably because of their higher discharge.

The retrofitted downstream bypass was the most used migration route with 41.2% for radio-tagged and 38.0% for RFID-tagged). The adjusted bypass efficiency was 63.6% (radio-tagged smolt). Visual observations indicated that the smolts close to the entrance remained in negative rheotaxis indicating the perception of danger associated with an increase of accelerated velocity and turbulence at the entrance (Haro et al., 1998; Ovidio et al., 2017a). Other studies have shown that bypass performance varies widely depending on the site typology and can range from 16.5 to 95% (Scruton et al., 2007; Nyqvist et al., 2016; Havn et al., 2017, 2018; Ovidio et al., 2017a; Fjeldstad et al., 2018; Klopries et al., 2018; Tomanova et al., 2018) with retrofitted devices having lower performance than new built-in devices. The retrofitted bypass efficiency in our study site was not optimally configured and its performance could probably be improved according to Courret and Larinier (2008), who recommended a bar rack with a narrow bar spacing ($\leq$ 25 mm), an angle of inclination with respect to the horizontal below $\leq 26°$ or a rack orientation below $\leq 45°$, a normal flow speed ($\leq 0.5\ ms^{-1}$) and a functional flow from 2 to 10% of turbine discharge. Tomanova et al. (2018) showed very good bypass performance ($> 80\%$) in compliance with these recommendations.

The unsafe route represented by the Kaplan turbines was used by 17.6% of the radio-tagged smolts, which means that the majority of smolts used a potentially safe migration route to cross the hydropower station during the tested conditions. Different authors observed percentages of passage through non-fish-friendly turbines ranging from 0 to 94% (Scruton et al., 2007; Fjeldstad et al., 2014; Thorstad et al., 2017; Havn et al., 2018; Tomanova et al., 2018). However, Havn et al. (2017) demonstrated that smolts used a bypass instead of turbines more often than expected in relation to the proportion of water discharge, especially for larger smolts at lower discharge. We observed that variations in total water discharge affected smolts' migration route choice, which is in agreement with several authors (Serrano et al., 2009; Fjeldstad et al., 2012; Nyqvist et al., 2016). At higher water discharge, smolts used the weir instead, while at lower discharge (< 20 m^3s^{-1}), the water level above the weir was insufficient to enable the smolts to pass and the intake channel of the Kaplan turbines and the bypass was therefore more attractive. Water temperature and season progression did not affect the choice of a migration route in our study site.

The translocation of smolts from a hatchery to the river may have influenced the timing of their migration, but we observed that they started their downstream migration rapidly (± 1 h after release) and crossed the weir from the end of the day to the crepuscule period, and continued their migration until the middle of the night. This is in accordance with the literature, suggesting that downstream migration occurs mainly during the dusk and the night in temperate environments (Aarestrup et al., 2002; Riley et al., 2002; Scruton et al., 2007; Fjeldstad et al., 2012; Ovidio et al., 2017a). Brevé et al. (2014) observed a slight preference for Meuse smolts to migrate during the day. The smolts crossed the weir quite rapidly (median 58 min) and continued their downstream migration to the confluence with the Meuse river. In the literature, the median time required to cross a hydropower station with more than four potential migration routes varied between 30 min (Havn et al., 2017; for 6 migration routes), 1 h 30 min (Thorstad et al., 2017; for 6 migration routes) and 5 h (Havn et al., 2018; for 10 migration routes). Tomanova et al. (2018) have shown that 50% of the smolts required less than 18 min, 20 min and 1 h to cross three different complex hydropower stations (5 migration routes) using the associated ichthyo-compatible bypass. Nyqvist et al. (2016) and Tomanova et al. (2017) measured median time of 30 min and 7 h, respectively, to cross a hydropower station with three potential migration routes, but in a reservoir. This underlines that hydropower stations presenting multiple migration routes inevitably cause a wide range of delay for smolt migration, depending on their typology, but those equipped with built-in efficient ichthyo-compatible (see Tomanova et al., 2018) bypass seems much less impactful.

It is important to set ecologically realistic targets for passage effectiveness at barriers considering the diversity of life histories, swimming abilities and spatial ecologies (Wilkes et al., 2018a). For diadromous migratory species, whose critical habitats are clearly separated in space, it can be assumed that passage efficiencies should be greater than for the "non-migratory" species (Wilkes et al., 2018a). We observed that 82.3% of the radio-tagged smolts continue their downstream migration after crossing the hydropower station of Méry (W1) and would successfully reach the main course of the Meuse. They will then have to travel more than 300 km and pass four other hydropower stations before reaching the North Sea. Currently, it is not obvious if the observed passage success in our study site is sufficient to support the re-establishment of a self-sustaining population in the Meuse basin. Telemetry studies on a larger spatial scale, including successive hydropower stations, would be necessary to estimate the escapement success to the North Sea. We observed quite important changes in median migration speeds (v_{min} = 0.16 ms^{-1} and v_{max} = 0.52 ms^{-1}) between river stretches. Contrary to Havn et al. (2017) who showed an increase in the subsequent migration speed of the smolts using the Archimedes screw, the migration route used at Méry hydropower station did not influence the migration speed of the smolts downstream of the hydropower station. In the literature, median migration speed in impounded rivers is reported as about 0.03 ms^{-1}, 0.12 ms^{-1} to 0.78 ms^{-1} over a median distance of 15 km (Stich et al., 2015; Newton et al., 2018). Median migration speeds obtained in un-impounded stretches range from 0.06 ms^{-1}, 0.84 ms^{-1} to 1.53 ms^{-1} over 12 km (Stich et al., 2015; Thorstad et al., 2004; Havn et al., 2018; Newton et al., 2018).

The re-establishment of sustainable Atlantic salmon (and sea trout, *Salmo trutta* Linnaeus, 1758) populations in the international river Meuse basin is a challenging project starting in the beginning of the 1990s (Philippart et al., 1994). From 2000 to 2018, the number of returning Atlantic salmon and sea trout progressively increased, but not enough to achieve a self-sustainable population. Restocking with hatchery parrs and smolts is still necessary. The ecological state of the Meuse basin is greatly improved (physical and chemical quality of the water, construction of fishway for upstream movements of adults), but the downstream migration of the smolts and the associated escapement success remains one of the main problems, as is the case in many anthropised rivers (Marschal et al., 2011). In this context, improving passage performance at hydropower stations with multiple migration routes will be a big challenge in the future.

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