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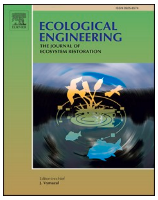

Trying to choose the less bad route: Individual migratory behaviour of Atlantic salmon smolts (*Salmo salar* L.) approaching a bifurcation between a hydropower station and a navigation canal

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ABSTRACT

Contrary to small- and medium-sized rivers, little attention has been paid to the downstream migration of Atlantic salmon smolts in large-sized rivers and the size-related impact of hydropower stations. From 2014 to 2016, we investigated the downstream migration of $n = 72$ acoustic-tagged smolts in the Meuse river at a bifurcation zone between a hydropower station equipped with three Kaplan turbines and a navigation canal. A hydrodynamic model that solves the depth-integrated shallow water equations on a Cartesian grid using a finite volume technique was used to infer the influence of water discharge and flow velocity on the smolts' behaviour upstream of the hydroelectric complex. Of the migrating smolts, 41.5% performed back and forth movements before approaching the complex for the first time, sometimes over long distances and at a slow pace, leading to significant delays (3–298 h). Beyond about 250 $m^3 s^{-1}$, the water flow direction changes towards the hydropower station with a gradual acceleration. A median water discharge of 161 $m^3 s^{-1}$ and associated median flow velocity of 0.14 $m s^{-1}$ tended to favour a more direct and downstream movement towards the hydropower station. On the other hand, the navigation canal was mainly approached at low water discharge (median 132 $m^3 s^{-1}$), due to a higher flow velocity (median 0.11 $m s^{-1}$) at the entrance. Of the released smolts, only 38.6% passed through the complex, of which 36.4% migrated by the navigation canal and 63.6% by the hydropower station, with a median research time of 04:44. Among all the released individuals, the escapement rate at the end of the study site was 2.9% by the canal and 8.3% by the Meuse river. This site, which offers two non-optimal, unattractive and unsafe migration routes, turns out to be problematic for successful downstream smolt migration.

1. Introduction

For several decades, rivers have been fragmented and homogenised to enable man-made activities, such as boat navigation, hydropower production, and water regulation (Parrish et al., 1998; Baras and Lucas, 2001; Nilsson et al., 2005), which have caused a drastic reduction and the extinction of several migratory fish species (Larinier and Travade, 2002; Katopodis and Williams, 2012). The Atlantic salmon (*Salmo salar* Linnaeus, 1758) is one of the most sensitive species due to the complexity of its life cycle, its important ecological requirements in freshwater and marine environments, the challenge of performing precise homing, and the extent of the downstream and upstream migrations at the smolt and adult stages (Parrish et al., 1998; Thorstad et al., 2012). Most populations are declining, and some strains have completely disappeared from European and American rivers during the last decades. Reintroduction efforts have been performed in some countries (e.g., France, Belgium, Germany, The Netherlands) with some success, but some major problems persist before the establishment of self-sustainable populations. In highly fragmented environments, the success of migrations is dependent on the performance of the up- and downstream fish-passage structures and mitigation and management measures to facilitate smolt and adult movements (Katopodis and

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Williams, 2012; Williams et al., 2012; Fjeldstad et al., 2018). Significant progress has been made in fishway design to restore the upstream migration of different fish species, including Atlantic salmon adults, with some that have demonstrated good performance (Benitez et al., 2018; Silva et al., 2018; Ovidio et al., 2020). On the other hand, the re-establishment of a successful and quick downstream migration often remains difficult and challenging in anthropised rivers (Holbrook et al., 2011; Fjeldstad et al., 2012; Newton et al., 2019; Ovidio et al., 2021). The escapement rate of smolts to the sea is often insufficient to expect further quantitative returns of adults (Thorstad et al., 2008).

In small- and medium-sized rivers, one of the most often encountered problems is the accumulation of physical migration barriers such as hydropower stations throughout the fish migration routes (Noatch and Suski, 2012; Katopodis and Williams, 2012; Haraldstad et al., 2018, 2019). Such structures cause considerable delays in migration and significant mortality notably due to energy expenditure (Marschall et al., 2011; Nyqvist et al., 2017; Ovidio et al., 2017), to predation close to the sites (Coutant and Whitney, 2000; Koed et al., 2002; Brevé et al., 2014) and turbine passage (Coutant and Whitney, 2000; Serrano et al., 2009; Fu et al., 2016; Pauwels et al., 2020). During their downstream migration, Atlantic salmon smolts, which face classical physical barriers to migration, will express different behavioural tactics to find a migration route to pass the site (Haraldstad et al., 2019; Renardy et al., 2020). Depending on the typology of the site, the final choice of a migration route may be influenced by a single or a combination of environmental or biological factors. Some authors have already mentioned the effect of water discharge (Fjeldstad et al., 2012; Cheng and Gallinat, 2004; Persson et al., 2019; Renardy et al., 2020), water temperature (Castro-Santos and Perry, 2012), the smolts' morphological and physiological state (Coutant and Whitney, 2000; Fjeldstad et al., 2012; Tetard et al., 2019), and the progression in time of the migration season (Tetard et al., 2019).

In large rivers, migrating fish may also encounter other additional types of man-made structures, such as diversions, navigation canals and navigation locks. Some authors have underlined their potential effects in terms of delays of downstream migration, mortality, and reduction of the seaward escapement rate for different fish species (Steel et al., 2013, Johnston et al., 2018, *Oncorhynchus tshawytscha* L.; Hondorp et al., 2017, *Acipenser fulvescens* L.; Vergeynst et al., 2019, *Anguilla anguilla* L. & *Salmo salar* L.). Despite their absence of physical effects, navigation canals and diversions may be in some situations favourable and in others unfavourable (Lin et al., 2020). Navigation canals can be a more direct migration route to the sea (Verhelst et al., 2018a), but they are regularly associated with low flow velocities, pumping stations, artificial water discharge, and flow direction changes. These artificial regulations may cause a discontinuous flow, which may induce fish disorientation (Verhelst et al., 2018a). In some particular places, smolts have to choose between a hydropower station and a navigation canal as two potential migration routes. This represents a challenging situation with a choice between two potentially inadequate routes to continue downstream migration. Knowledge of environmental factors that influence their choice, as well as the success in continuing downstream depending on the selected route is of great importance, but has not been investigated before.

The use of hydraulic modelling in combination with acoustic telemetry helps to understand the choice made by migrating fish, the passage success and their further behaviour afterwards (Vergeynst, 2018; Szabo-Meszaros et al., 2019; Silva et al., 2020). Combining detailed hydraulic modelling and precise behavioural analyses enabled a better visualization of the influence of hydrodynamic characteristics on smolts' behaviour upstream of migration barriers (Vergeynst, 2018; Silva et al., 2020) or the identification, by simulations, of the most suitable mitigation measures to favour a quick and safe migration (Szabo-Meszaros et al., 2019).

In the Belgian Meuse river, during their seaward migration, the migrating smolts will encounter a migration barrier offering two migration routes, a navigation canal and a hydropower station equipped with three Kaplan turbines, and without fish protection devices. This represents a complex situation to manage for the smolts during their route to the sea. By using acoustic-tagged Atlantic salmon smolts and numerical modelling of the hydrodynamic characteristics of the site, we investigated the downstream migration behaviour of smolts confronted with this site, to determine (1) the variability of smolts' individual research behaviour at the site, (2) the quantification of the migration routes used by the smolts, (3) the influence of the distribution of the flow velocity and its fluctuation on their orientation and route choices, and (4) the downstream migratory patterns of smolts after the selection of a migration route.

2. Materials and methods

2.1. Study area

The Meuse river is a 950 km long international river (Fig. 1A - source in France, flows across Belgium and has its estuary in The Netherlands) with a catchment area of 36,000 km^2. In the Belgian course, the Meuse river corresponds to a bream fish zone (Huet, 1949) and hosts 36 different species, of which 75% are cyprinids, such as the common bream (*Abramis brama* Linnaeus, 1758), the roach (*Rutilus rutilus* Linnaeus, 1758), and the chub (*Squalius cephalus* Linnaeus, 1758) (Benitez et al., 2018). The lower part of the Belgian Meuse river is highly anthropised, modified by navigation canals, with rectified and artificial banks, fragmented by dams and ship locks, water regulation, and hydropower production. The average annual temperature and discharge during the study, as measured in Liège, was 15.2 °C and 163.75 m^3 s^{-1}. The Ourthe river, a main tributary of the Meuse river, is a medium-sized river that is 235 km long and has a mean annual water temperature of 10.6 °C. The river is classified as a barbel zone (Huet, 1949) with the presence of 29 fish species also dominated by cyprinids.

The study site corresponds to the Meuse river stretch from the confluence with the Ourthe river to the Flemish and Dutch border (Fig. 1B) and includes two hydropower stations: the Monsin and the Lixhe hydropower stations (Fig. 1B; W1 & W2). The main study site is located in Liège, from the confluence with the Ourthe river to the Monsin dam and hydropower station on the one hand, and the entrance of the Albert navigation canal on the other hand (Fig. 1C). This stretch is approximately 4.5 km long and, on this stretch, the Meuse river is divided in two, with the so-called diversion flowing on the right of the main riverbed (Fig. 1C).

The Monsin dam regulates the water level along the entire study site, i.e., at the Albert Canal entrance and in the downstream part of the Ourthe river. An average annual water discharge of 36.5 m^3 s^{-1} is directed towards the Albert Canal, which modifies the natural watercourse of the Meuse river. Due to navigation locks in the Albert Canal, water discharge can sometimes be inverted. The other part is directed towards the hydropower station situated in the natural course of the Meuse river. The partition of water varies considerably depending on the upstream flow. The hydropower station next to the dam has a 225 m long intake channel that diverts water towards three Kaplan turbines with 3 × 150 m^3 s^{-1} nominal flows, a rotational speed of 65.2 rpm, a diameter of 13.83 m, and a head of 5.6 m. The dam is 180 m long and is equipped with six spillway gates, which were constantly closed during the surveys depicted in this study. A vertical slot fishway, with a water discharge of 0.8 m^3 s^{-1}, is located between the power station and the dam, and its performance was already assessed for upstream migrating fish (Benitez et al., 2018).

Currently, the Monsin hydropower station combined with the entrance of the Albert Canal is a zone where migrating smolt can choose two different migration routes towards the sea (Fig. 1D). In the direction of the main course of the Meuse river, the hydropower station of Lixhe is located 13 km downstream of the Monsin hydropower station and represents the border between Belgium and The Netherlands (Fig. 1B; W2).

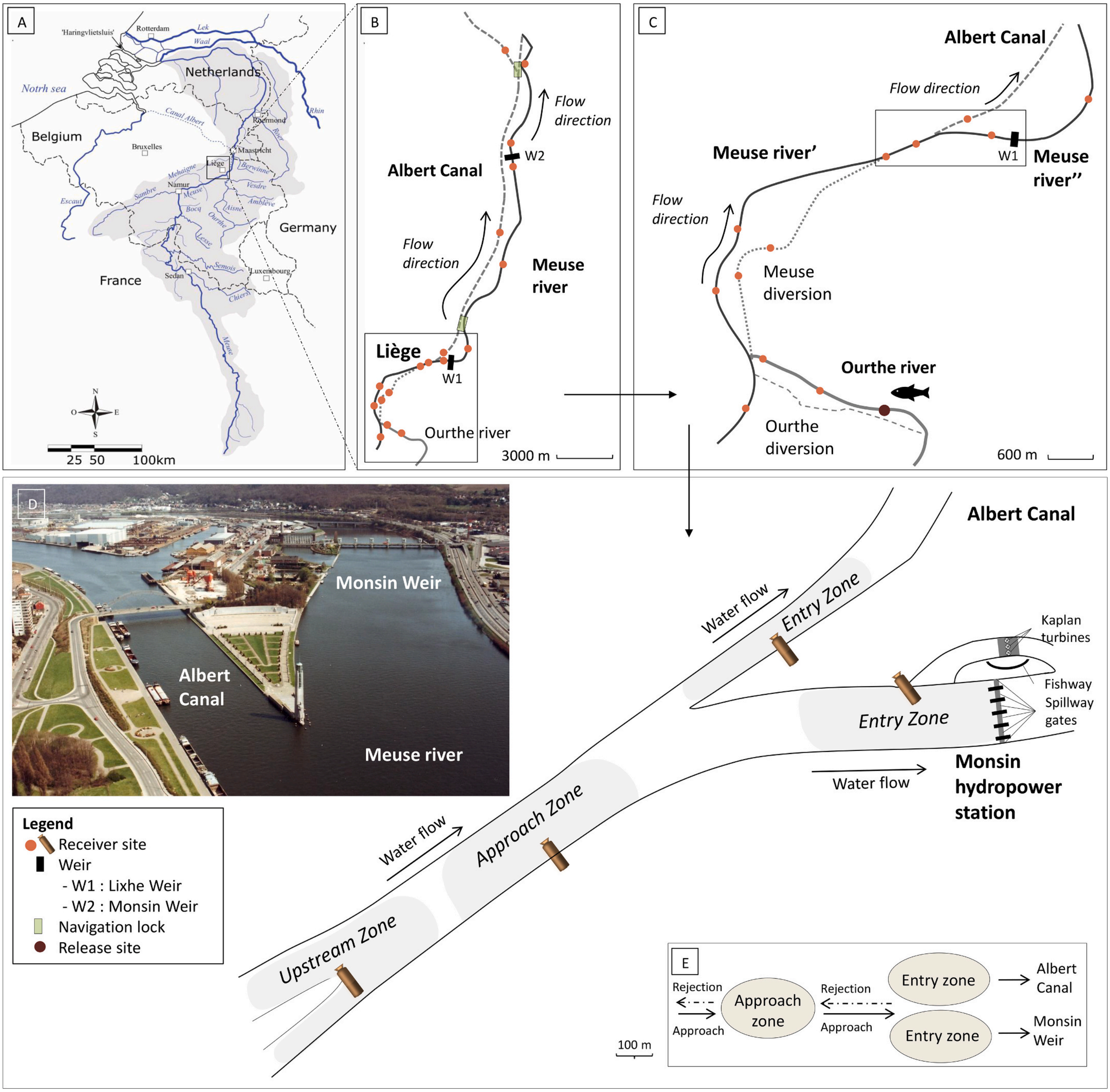

Fig. 1. Representation of the study site. (A) The international Meuse basin in France, Belgium, and The Netherlands. (B) The studied Meuse river and Albert Canal stretches with the locations of the most downstream acoustic receivers and two dams. (C) Meuse and Ourthe river stretches upstream of the Albert – Monsin site with the locations of the upstream acoustic receivers. (D) Photographic (©SPW-Direction des Voies Hydrauliques de Liège) and schematic representations of the Monsin hydropower station and the Albert Canal entrance. The study site is divided into four zones: the upstream zone, the approach zone, and the entry zones, which correspond to the detection area of 4 automatic receivers. (E) A schematic diagram showing the two entry zones (inspired by Nyqvist et al., 2017).

Downstream of the Lixhe hydropower station, there is still 323 km to the sea and seven migration barriers including two hydropower stations to cross. In the direction of the Albert Canal, 870 m upstream of the Monsin hydropower station, the distance to the sea is 129.5 km. The Albert Canal is equipped with two navigation locks, enabling the smolts to go back to the Meuse river, 2 km (Monsin navigation lock) and 17 km (Lanaye navigation lock) downstream of the entrance of the Albert Canal (Fig. 1B). If the fish do not branch off in the Meuse river, they can continue towards the port of Antwerp. Smolts will have to pass six navigation locks and will also face several canal bifurcations that could disorient them. In the Antwerp harbour, downstream migrating smolts can use one of the three maritime locks to reach the Scheldt estuary or might eventually migrate through the Scheldt-Rhine canal up to Dutch estuaries.

We divided the hydropower/canal complex into two zones: the *approach zone* and two *entry zones* (Fig. 1D). To pass this complex and to select a migration route, the smolts enter the *approach zone* and may choose between the *entry zone* of the Albert Canal or the *entry zone* of the Monsin hydropower station or to move back upstream (Fig. 1E). After accessing an *entry zone*, a smolt can continue to migrate downstream or

Table 1
Characteristics of the experimental conditions encountered by the tagged smolts.

Group	Date of release	N = reared/wild smolts	Mean fork length (mm) (min – max)	Mean body mass (g) (min - max)	Environmental conditions					Turbined discharge ($m^3 s^{-1}$) (number of turbines)
					Ourthe river	Meuse river		Albert Canal		
					Mean discharge ($m^3 s^{-1}$)	Mean discharge ($m^3 s^{-1}$)	Flow velocity ($m s^{-1}$)	Mean discharge ($m^3 s^{-1}$)	Flow velocity ($m s^{-1}$)	
G1	23–04-14 15:30	5/5	224.6 (185–263)	109.6 (63–171)	13.0	116.8	0.08	33.6	0.10	59.4 (1)
G2	12–05-14 15:30	9/1	244.9 (189–275)	165.5 (71–286)	16.0	117.8	0.13	33.0	0.10	60.8 (1)
G3	22–04-15 11:00	20/0	302.7 (268–321)	327.5 (204–409)	28.0	220.7	0.14	37.8	0.11	145.7 (1)
G4	27–04-15 09:20	20/0	299.7 (264–331)	312.9 (176–421)	21.6	183.4	0.14	38.7	0.11	115.1 (1)
G5	13–04-16 16:00	12/0	167.5 (166–171)	49.9 (46–55)	45.6	284.1	0.21	42.8	0.12	203.7 (2)

reject the zone by moving upstream.

2.2. Smolts tagging

We tagged a total of 72 one or two-years-old smolts during the three years of study (2014, 2015, and 2016). Sixty-six smolts came from the hatchery of Erezee (Public Service of Wallonia, Belgium) and six were captured at a bypass of the Mery hydropower station in the Ourthe river (description in Renardy et al., 2020). The hatchery-reared smolts had a mean fork length of 266.4 mm (range 166–331 mm) and a mean body mass of 238 g (range 46–286 g) (Table 1). The wild smolts had a mean fork length of 194.3 mm (range 185–208 mm) and a mean body mass of 72.3 g (range 63–88 g). The fork length and the body mass differed significantly between the hatchery-reared and wild smolts (Wilcoxon–Mann–Whitney tests, all $p < 0.01$).

For tagging, the smolts were first anaesthetised with 0.2 mL l-1 of eugenol, and after a 7 mm incision, they were surgically equipped with an acoustic transmitter in their body cavity (Vemco, Model Coded Tag V7; frequency 69 kHz; dimensions 7 mm × 20.25 mm; mass in water 0.7–1.0 g; expected lifetime 255 days). The incision was closed with two stitches using absorbable suture material (Renardy et al., 2020). After recovery, the tagged smolts were released into the Ourthe river.

2.3. Smolts tracking

The tagged smolts were divided into five groups (G1 to G5) spread over three years (2014, 2015, and 2016) and released at different periods in order to have contrasting environmental conditions (Table 1). Over the three periods of tracking, the water discharge of the Meuse river varied from 43.3 to 454.9 $m^3 s^{-1}$ (Table 1). The five groups were released 1965 m upstream from the confluence between the Ourthe river and the Meuse river (Fig. 1C). The smolts were passively tracked with 18 acoustic receivers (Vemco, Model VR2W; identifiable frequency 69 kHz; dimensions 308 mm × 73 mm; mass in water 50 g; battery expected lifetime 15 months), which were fixed at strategic locations in the study area and beyond from 1000 m downstream of the release site (Ourthe river) to 26,025 m (Meuse river) and 28,223 m (Albert Canal) downstream of the release site (Fig. 1B). The smolts were detected when they approached the acoustic receiver stations, at a distance of approximately 300 m. The number of detections per smolt was 2536 on average.

2.4. Smolt behavioural metrics

The smolt detections in the receiver network enabled the definition of several quantitative behavioural metrics useful to describe smolts' migration upstream of the Albert Canal – Monsin site.

Travel time

Hourly time required by the smolts to move from one point to another corresponding to the time between the last detection at the first receiver and first detection at the second receiver.

Hesitation time

Hourly time between the first and last detection in a studied zone (*upstream*, *approach* and *entry zones*) spent by the smolts before swimming downstream or upstream (Fig. 1D).

Arrival delay in reaching the approach zone

Hourly time needed for acoustically tracked individual smolts to reach the *approach zone* of the hydropower/canal complex. This *travel time* corresponds to the time between the release time and the first detection in the *approach zone.*

Approach zone detection rate

Number of recorded detections in the *approach zone* for each smolt (Fig. 1D).

Passage attempt

Movement of smolts from the *approach zone* to one of the *entry zones* (Fig. 1D).

Passage time

The last recorded detection (local hour) of the smolts in the *entry zones* before passing the hydropower/canal complex and indication of the period of the day (dusk, night, sunrise, and day).

Research time

Time required by the smolts to pass through the hydropower/canal complex. This corresponds to the time spent upstream of the site between the first location in the *approach zone* and last location in the *entry zones* (Fig. 1D).

Migration route used

The percentage of individual smolts using each migration route at the hydropower/canal complex in comparison with the tagged smolts that approached the site.

2.5. Hydrodynamic numerical modelling

Numerical modelling of the hydrodynamic conditions during the survey periods was performed using the WOLF2D software developed by the HECE research group at Liège University for more than 20 years. This software solves the depth-integrated shallow water equations on a Cartesian grid using a finite volume technique (Erpicum et al., 2009, 2010a).

The model was applied to the survey site depicted in Fig. 1, which was extended upstream and downstream to include gauging stations locations where boundary conditions can be prescribed. Bathymetry data were gained from a high-resolution digital elevation model with a 1 m horizontal resolution and 0.15 m vertical accuracy (Erpicum et al.,

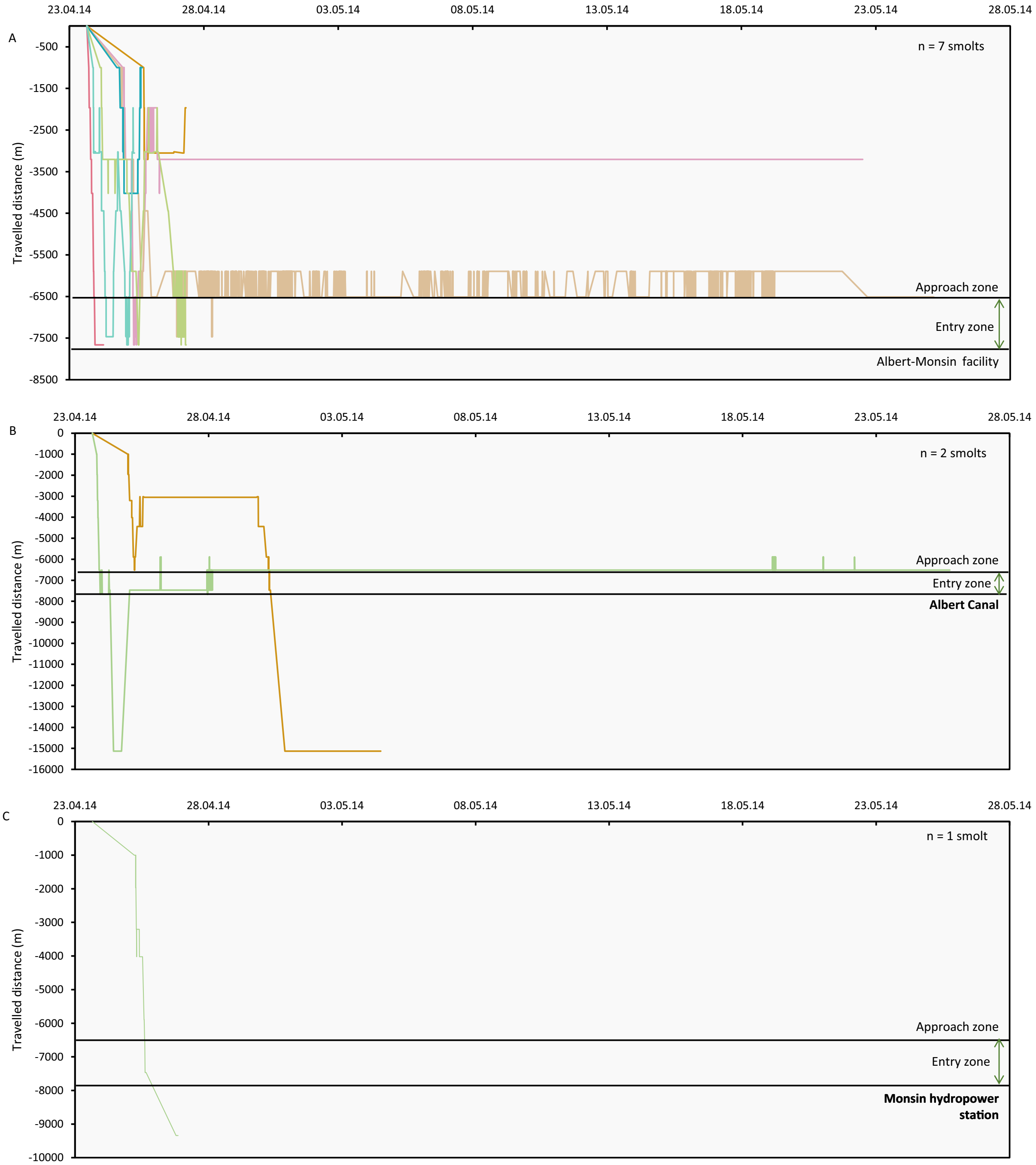

Fig. 2. Smolts migration patterns of the first release (G1). (A) Smolts that did not cross the Albert – Monsin site. (B) Smolts that migrated by the Albert Canal. (C) Smolts that migrated by the Meuse river.

2010b). The model was extended 8.6 km upstream in the Meuse river and 7.1 downstream of Liege in the Albert Canal to reach two gauging stations (the extreme parts of the modelled area are not represented in Fig. 1). The measured discharge was imposed as a boundary condition at these two locations and also in the Ourthe river. At Monsin, the discharge through the turbines was prescribed, while a constant water level boundary condition was used at the dam gates. The numerical model covered a total of 34.1 km of river stretches close to Liège in the Meuse and the Ourthe rivers and the Albert Canal.

Two sets of simulations were performed: a first one in hypothetical steady-state conditions with constant discharges in the Meuse river from 50 to 400 $m^3 s^{-1}$ with a step of 50 $m^3 s^{-1}$ and a mean constant discharge of 44 $m^3 s^{-1}$ in the Albert Canal. These values cover the whole range of discharge conditions observed during the telemetry surveys. The second set of simulations considered the real transient flow conditions faced by the smolts during the telemetry surveys using hourly basis records of discharges and water levels at the model boundaries.

Hydrodynamic results were analysed in terms of the averaged discharge and flow velocity, temporal velocity gradient and flow orientation in each automatic receiver estimated detection zone and during each smolt detection period.

2.6. Statistical analyses

Because the data violated the assumptions of normality (Kolmogorov–Smirnov, $p < 0.05$), non-parametric tests were used. To test the difference of the ratio of upstream and downstream movements between the groups, a Pearson's χ^2 test was used. The approach behaviour of tagged smolts described by *travel time*, *migration speed* and *hesitation time* was analysed and compared between the groups and the years by using Kruskal–Wallis (KW) tests and Mann–Whitney (U) tests. To observe the effects of water discharge ($m^3 s^{-1}$) and flow velocity ($m s^{-1}$) on the *approach zone* detection rate, we used Spearman correlations, and on *passage attempts*, we used *U* tests. The behaviour described by the *approach zone* detection rate, *passage attempts*, the *research time*, and the time spent in the *entry zones* was compared between the smolts that passed the site and those that did not with U tests. The effect of water discharge was tested with a Spearman correlation. The repartition of migration routes used by the smolts was compared between the years by using a Pearson's χ^2 test. The effects of water discharge and flow velocity on the migration route used were highlighted by using U tests. The migration speed was compared between the stretches, the groups and the years by using KW tests. All statistical analyses were performed using the software R (version 3.4.2), and the significance level was set at $p = 0.05$.

3. Results

3.1. Description of the general migration patterns

In 2014, 95% ($n = 19/20$) of the released smolts (G1 = 10/10 & G2 = 9/10) started their downstream migration (Figs. 2, 3, & 7). After reaching the Meuse river, downstream of the confluence with the Ourthe river, 42.1% of the smolts (G1 = 4/10 & G2 = 4/9) expressed hesitation behaviour by performing several back and forth movements, and sometimes even over long distances (up to 7 km). Of the smolts, 73.7% (G1 = 8/10 & G2 = 6/9) were recorded in the *approach zone* and 68.4% (G1 = 8/10 & G2 = 5/9) entered at least one of the two *entry zones*

Fig. 3. Smolts migration patterns of the second release (G2). (A) Smolts that did not cross the Albert – Monsin site. (B) Smolts that migrated by the Albert Canal.

Fig. 4. Smolts migration patterns of the third release (G3). (A) Smolts that did not cross the Albert – Monsin site. (B) Smolts that migrated by the Albert Canal. (C) Smolts that migrated by the Meuse river.

(Fig. 7). Once in the *entry zones*, 64.5% of the smolts (G1 = 5/8 & G2 = 3/5) expressed several back and forth movements between one of the *entry zones* and the *approach zone*. Only 23% (G1 = 2/8 & G2 = 1/5) of the smolts passed through the hydropower/canal complex, among which two smolts (G1 = 1/8 & G2 = 1/5) used the Albert Canal, one used the Monsin navigation lock to the Meuse river and one smolt via the hydropower station (G1 = 1/8) (Fig. 7). Out of the smolts that did not pass, 20% (G3 = 1/6 & G4 = 1/4) entered the Albert Canal but around 15,000 m downstream of the release site, they turned back to move upstream.

In 2015, 92.3% of the smolts (*n* = 37/40) started their downstream migration (G3 = 20/20 & G4 = 17/20) (Figs. 4, 5, & 7), and 43.2% (G3 = 11/20 & G4 = 5/17) expressed hesitation behaviour after entering the Meuse river by moving frequently back and forth. Among the 37 smolts, 8.1% (G3 = 2/20 & G4 = 1/17) stopped their migration probably due to exhaustion or disorientation before entering the *approach zone* (Fig. 7). Eighty-nine per cent (G3 = 17/20 & G4 = 16/17) were recorded in the *approach zone* and in the *entry zones* (Fig. 7), among which 60.6% (G3 = 12/17 & G4 = 8/16) expressed several back and forth movements. Among the 33 smolts, 36.4% (G3 = 6/17 & G4 = 6/16) passed through the complex: five by the Albert Canal (G3 = 3/6 & G4 = 2/6) and seven by the Monsin hydropower station (G3 = 3/6 & G4 = 4/6) (Fig. 7). Among the seven smolts that migrated by the Meuse river, five smolts (G3 = 2 & G4 = 3) crossed the Lixhe hydropower station and four

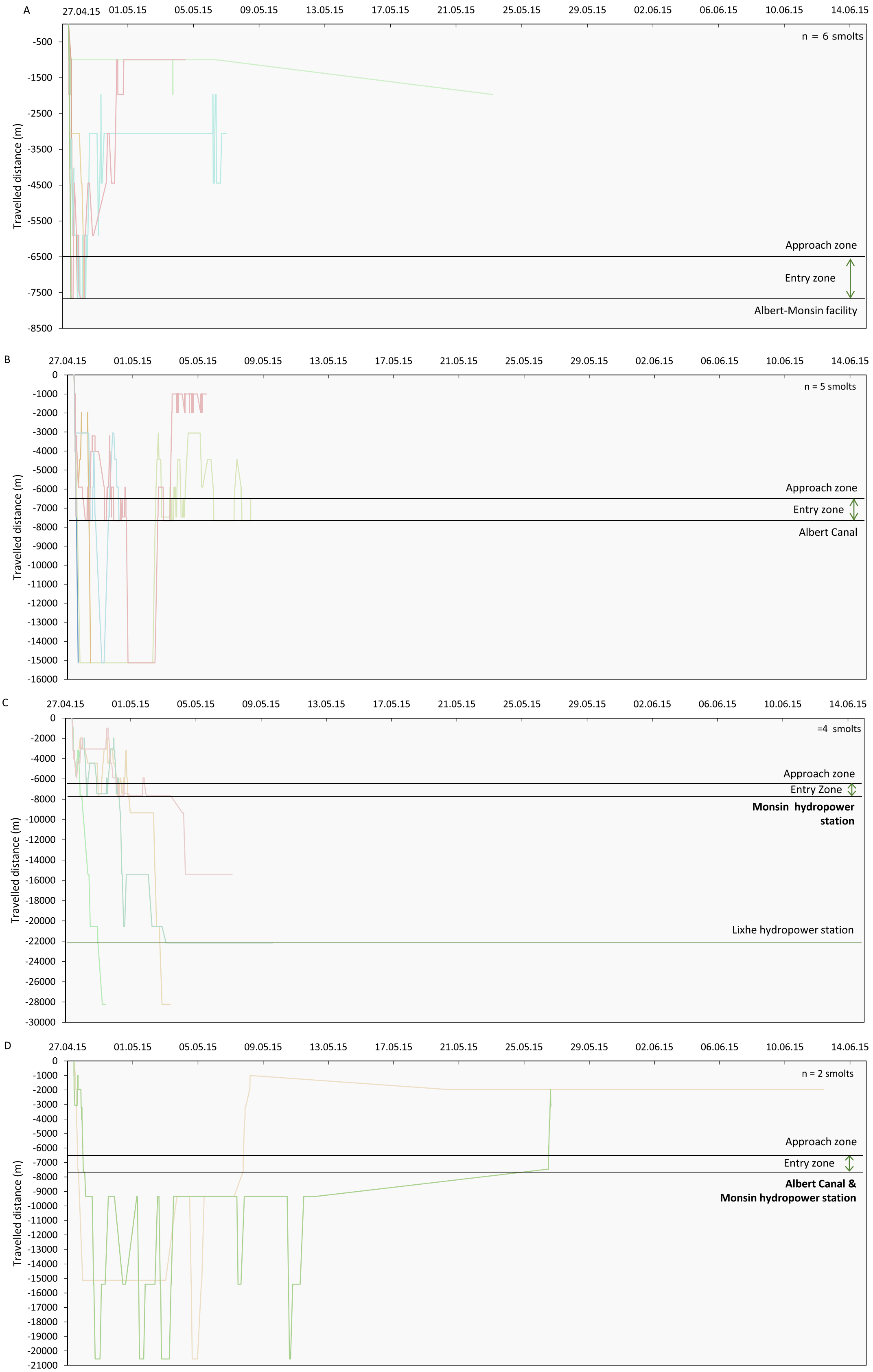

Fig. 5. Smolts migration patterns of the fourth release (G4). (A) Smolts that did not cross the Albert – Monsin site. (B) Smolts that migrated by the Albert Canal. (C) Smolts that migrated by the Meuse river. (D) Smolts that migrated by both the Meuse river and the Albert Canal.

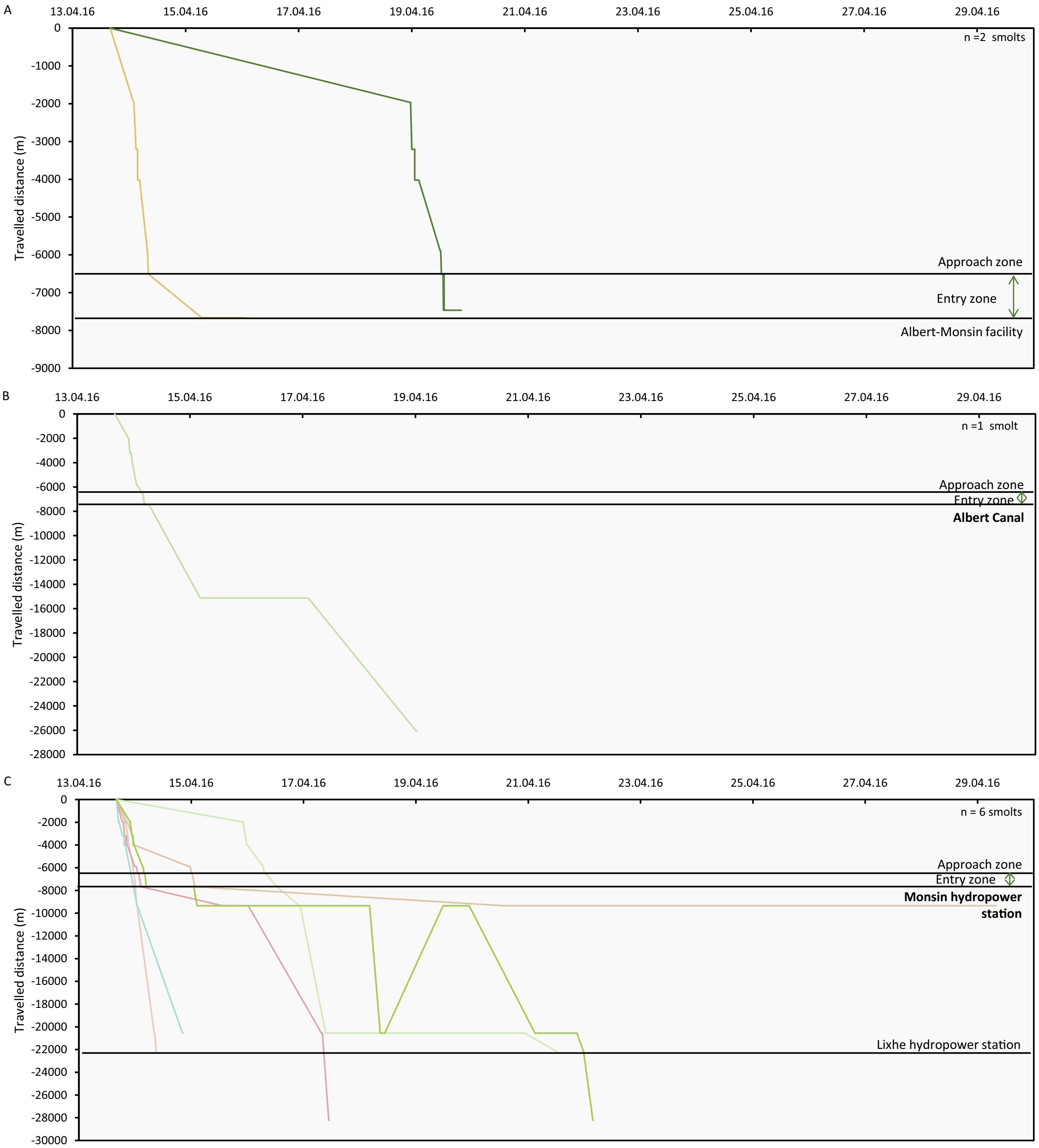

Fig. 6. Smolts migration patterns of the fifth release (G5). (A) Smolts that did not cross the Albert – Monsin site. (B) Smolts that migrated by the Albert Canal. (C) Smolts that migrated by the Meuse river.

continued their migration (G3 = 2 & G4 = 2) (Fig. 7). Regarding the other 67.6% of smolts (G3 = 14/20 & G4 = 11/17) that did not pass through the site, 18.9% (G3 = 3/20 & G4 = 4/17) migrated to the Albert Canal around 15,000 m downstream of the release site. Among these smolts, six turned back upstream to the *approach zone* and one reached the Meuse river and turned back upstream to the Monsin hydropower station.

In 2016, 75% (*n* = 9/12) of the smolts of the G5 initiated their downstream migration and were rapidly recorded in the *approach* and *entry zones* (Figs. 6 & 7). Only one performed a few back and forth movements before approaching the hydropower/canal complex. Among the nine smolts, 77.8% (*n* = 7/9) passed through the Albert – Monsin site without back and forth movements, six by the Monsin hydropower station, and one by the Albert Canal (Fig. 7). Among the six smolts that migrated by the Meuse river, four crossed the Lixhe hydropower station, and two continued their migration (Fig. 7). The other 22.2% of smolts did not pass through the site (*n* = 2/9).

3.2. Migration speed, hesitation time, and choice of migration route

Of the 72 released smolts of the five groups during the three years, 90.3% (G1 = 10/10, G2 = 9/10, G3 = 20/20, G4 = 20/20 & G5 = 9/12) started their downstream migration at a median speed of 0.14 m s^{-1} and reached the confluence with the Meuse river with a median *travel time* of 04:02 (range 00:15–127:14) (*n* = 64) (Table 2 & Fig. 8). Given the groups, the migration speed in the Ourthe river differed significantly

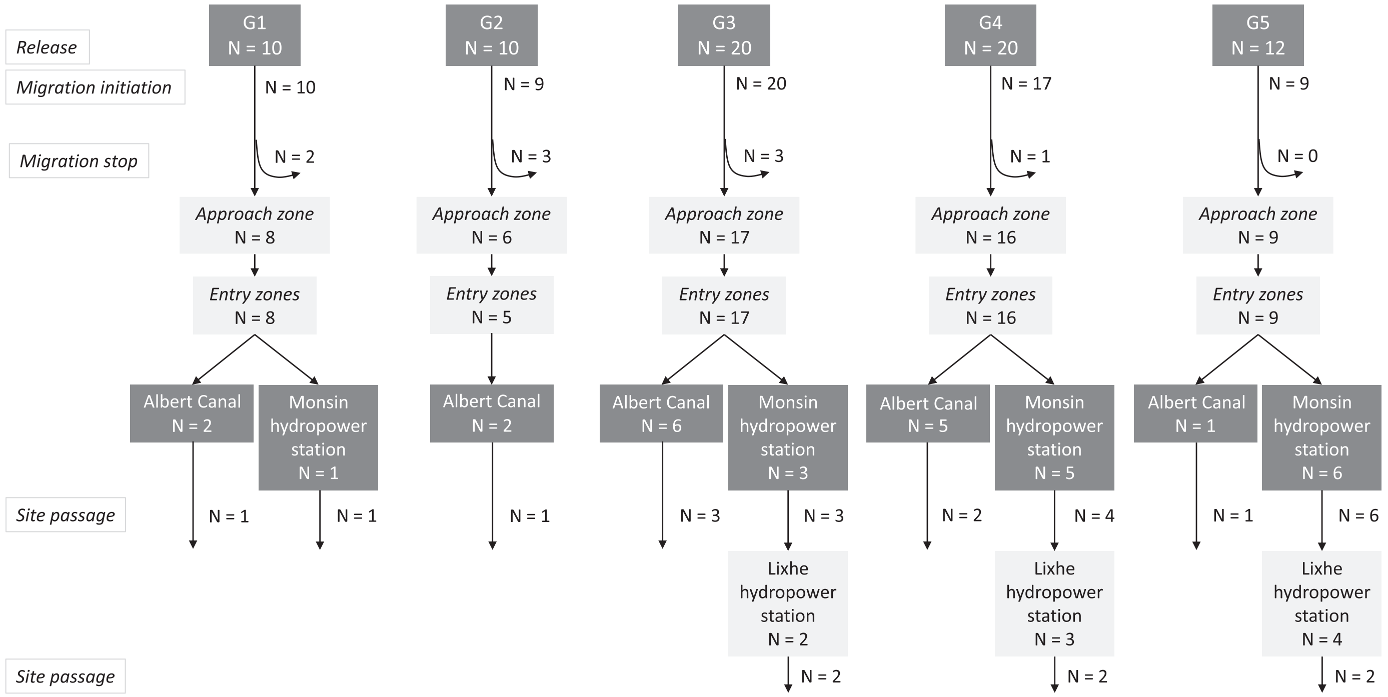

Fig. 7. Overview of smolts migration patterns of all groups (G1, G2, G3, G4, & G5) over the entire studied stretch.

Table 2
Downstream migration speed of the smolts in the different stretches of the river.

	Migration speed (m s^{-1})			
	2014	**2015**	**2016**	Mean
Ourthe river	0.13 (0.01–0.28)	0.16 (0.03–2.18)	0.1 (0.004–0.59)	0.14
Meuse river’ (upstream Meuse river)	0.21 (0.04–0.69)	0.16 (0.04–0.97)	0.21 (0.05–0.35)	0.17
Meuse river” (downstream Meuse river)	0.02	0.09 (0.02–0.42)	0.05 (0.0003–0.45)	0.14
Albert Canal	0.08 (0.02–0.13)	0.39 (0.16–0.87)	0.1	0.20

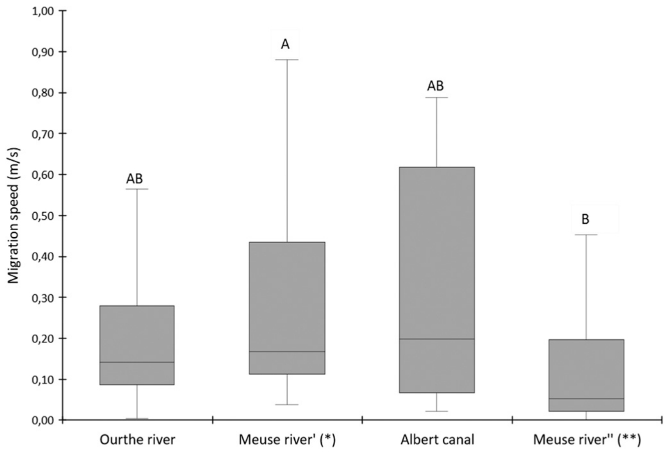

Fig. 8. Smolts migration speed in the Ourthe river, upstream, and downstream of the Albert – Monsin site. (*) Meuse river upstream & (**) downstream of the hydropower/canal complex. Values sharing at least one common superscript (a or b) do not differ at the 0.05 level of significance (KW test, $p = 0.02$).

(KW test, df = 4, $p < 0.0001$), with the highest median speed of 0.43 m s^{-1} for G4.

At the confluence with the Meuse river, smolts performed more or fewer back and forth movements, depending on the water discharge and flow velocities (Fig. 9). The mean Meuse water discharge varied from 116.8 m^3 s^{-1} for G1 to 284.1 m^3 s^{-1} for G5. At water velocities below 0.15 m s^{-1}, the smolts seemed to be disoriented by performing more upstream movements (Fig. 9B). The tendency to move downstream was favoured when the flow velocity was greater than 0.15 m s^{-1} and the downstream movements were even more pronounced at a flow velocity over 0.2 m s^{-1} (Fig. 9A).

Despite a gradual increase of the Meuse water discharge and flow velocities (Table 1), the proportions of downstream and upstream movements were similar for G1, G2, G3, and G4 (Pearson’s $\chi2$, $p = 0.34$) and did not differ significantly from a random distribution (Pearson’s $\chi2$, $p > 0.11$) (Fig. 10). However, for G5, the elevated water discharge and flow velocity (Table 1) stimulated the smolts to migrate downstream, which differed significantly from a random distribution (Pearson’s $\chi2$, $p < 0.0001$).

Once in the Meuse river, 86.2% of the smolts ($n = 57/65$) migrated downstream at a median speed of 0.17 m s^{-1} ($n = 57$) and took a median *travel time* of 07:30 to reach the *approach zone*, 6513 m downstream of the release site and upstream of the hydropower/canal complex (Table 2 & Fig. 8). The speed did not differ between groups (KW test, df = 4, $p = 0.76$) or years (KW test, df = 2, $p = 0.94$). The median *arrival delay in reaching the approach zone* was 13:43. With a median *research time* of 04:45 (range 00:33–473:16), only 38.6% ($n = 22/57$) passed through the hydropower/canal complex.

Out of the 14 smolts that migrated by the Meuse river”, 10 reached the Lixhe hydropower station with a median speed of 0.14 m s^{-1} ($n = 10$) (Table 2 & Fig. 8) and nine took a median *research time* of 10:48 (range 00:10–145:50) to cross the Lixhe hydropower station (situation in Fig. 1). In the Albert Canal, the median migration speed was 0.20 m s^{-1} (Table 2 & Fig. 8). The median migration speed of the smolts from the release site to the most downstream detection was 0.11 m s^{-1} (range 0.001–0.79 m s^{-1}), but the migration speed differed significantly between the stretches (KW test, df = 2, $p = 0.02$). Between the Meuse river’ and the Meuse river”, the speed was significantly higher in the *upstream*

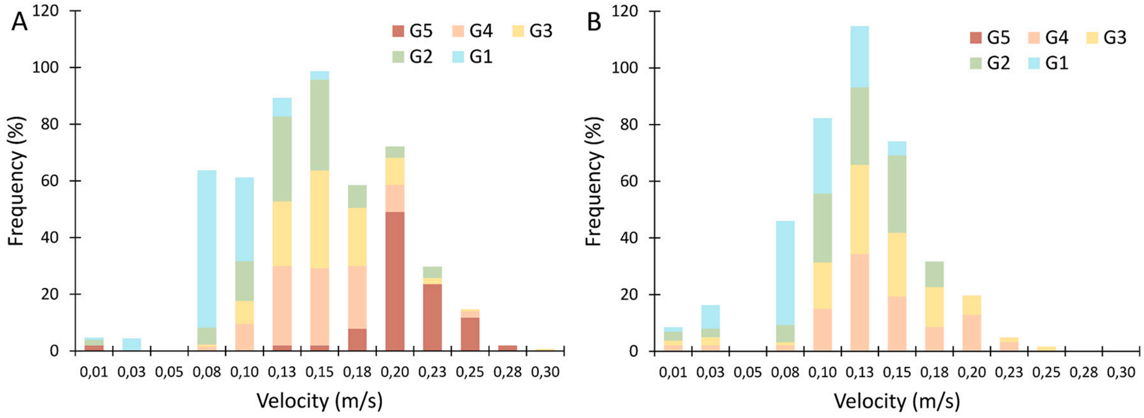

Fig. 9. Frequency distributions of flow velocities faced when the smolts choose to swim (A) downstream and (B) upstream.

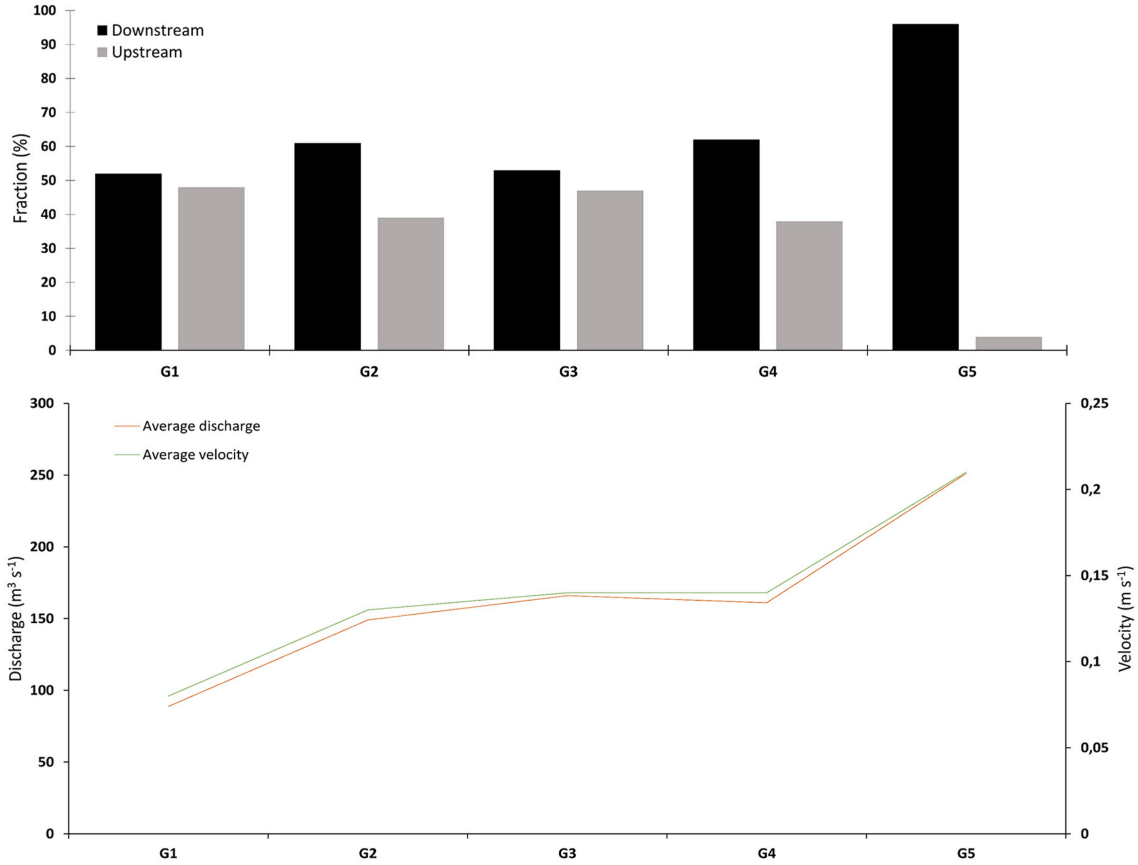

Fig. 10. Smolts' swimming orientations for each group (top) and associated average water discharge and flow velocity (bottom).

zone than downstream (*U* test, $p < 0.01$) (Fig. 8).

3.3. Fine-scale behaviour of smolts at the hydropower/canal complex

Among the 57 smolts detected in the *approach zone*, 56.1% were during dusk or the night (respectively: n = 10 and n = 22), 14% ($n = 8$) during sunrise, and 29.9% ($n = 17$) during the day (Fig. 11A). The distribution of detections between the four categories (dusk, night, sunrise, and day) was not significantly different from a random distribution (Pearson's $\chi 2$, $p = 0.23$). Comparing the migration period of the smolts between the groups, a significant difference was observed (Pearson's $\chi 2$, $p < 0.0001$), probably due to the time of release.

Before entering the *approach zone*, the smolts spent a median *hesitation time* of 00:12 in the *upstream zone* (Fig. 12). In the *approach zone*, the median number of detections was five (range 1–474). The Meuse water discharge and velocities had an effect on the *approach zone detection rate* (Spearman's correlation, both: Rho = −0.49, $p < 0.001$). An increase in the water discharge or water velocities in the *approach zone* was associated with fewer detections and therefore a reduction of back and forth movements. At every detection in the *approach zone*, the smolts made a passage attempt after a median *hesitation time* of 00:10 (Fig. 12), by the Albert Canal or the Monsin hydropower station, or returned towards the *upstream zone*; 54.4% ($n = 31/57$) of the smolts first approached the Monsin hydropower station, 36.8% ($n = 21/57$) approached the Albert Canal, and 8.8% (n = 5) moved back to the *upstream zone* without entering the *entry zones*. Fifty-six smolts were

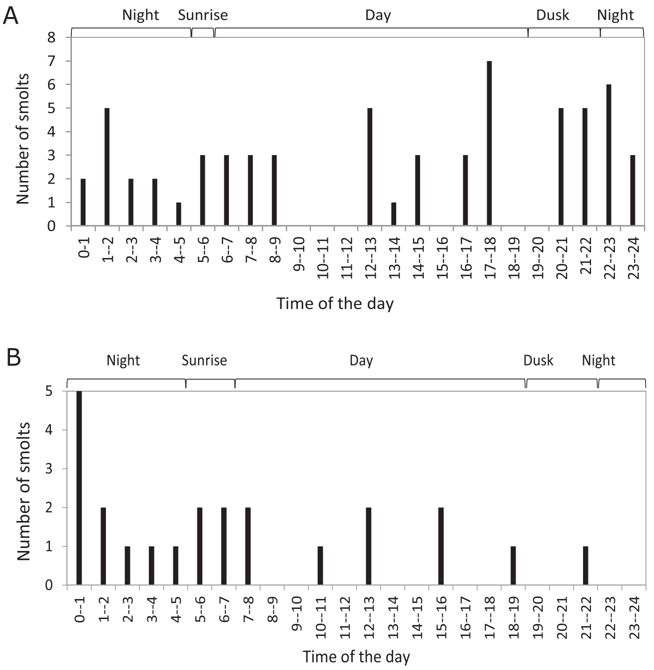

Fig. 11. A) First detection of the smolts in the approach zone according to the time of day. B) The passage of the Albert – Monsin site by the smolts according to the time of day.

detected in the *entry zones* and expressed a median of three *passage attempts* (range 1–36). The smolts expressed a median *hesitation time* of 00:38 upstream of the Monsin hydropower station and 00:20 at the entrance of the Albert Canal (Fig. 12). For the first passage attempt, 55.4% of the smolts (n = 31/56) followed the main flow, of which two smolts approached the Albert Canal, and 29 smolts approached the Monsin hydropower station. For the last passage attempt, 58.9% of the smolts (n = 33/56) followed the main flow, of which two smolts approached the Albert Canal, and 31 smolts approached the Monsin hydropower station. Considering all the choices expressed by the smolts in the *approach zone*, 37% were *passage attempts* towards the hydropower station and 36% towards the Albert Canal. The remaining 28% of choices were to return upstream of the *approach zone*.

Passage attempts towards a migration route were influenced by the Meuse water discharge (U test, $p < 0.0001$). The flow velocity in the *approach zone* and the flow velocity ratio between the Monsin station and Albert Canal had an effect on *passage attempts* towards a migration route too (U test, respectively: $p < 0.0001$ & $p < 0.001$). An increase of Meuse water discharge induces a change of water flow direction towards the Monsin hydropower station with a gradual acceleration of the flow velocity (Fig. 13).

Passage attempts via the Monsin hydropower station were associated with a median *approach zone* water discharge of 161 $m^3 s^{-1}$, a median flow velocity of 0.14 $m s^{-1}$, and a median velocity ratio of 0.92; whereas by the Albert Canal, the associated median *approach zone* water discharge was 132 $m^3 s^{-1}$, the median flow velocity was 0.11 $m s^{-1}$, and the median velocity ratio was 0.69 (Figs. 13 & 14). Between 0.1 and 0.14 $m s^{-1}$, which corresponds to a simulated water discharge varying between 150 and 200 $m^3 s^{-1}$ (Fig. 13), the smolts performed *passage attempts* towards both migration routes with similar frequencies (Fig. 14). The flow velocity in the Albert Canal also affected smolts' migration behaviour (Pearson's $\chi 2$, $p < 0.0001$). Eighty-eight per cent of the canal outputs to the *approach zone* were associated with a flow velocity below 0.15 $m s^{-1}$, and even sometimes associated with a negative flow velocity.

Among the 57 smolts detected in the *approach zone*, 38.6% (n = 22/57) passed through the hydropower/canal complex, of which 36.4% (n = 8) migrated by the Albert Canal, and 63.6% (n = 14) by the Monsin hydropower station. Depending on the year, the proportions of the migration routes used differed significantly (Pearson's $\chi 2$, p = 0.04), with a greater use of the Albert Canal in 2014, a balanced use between the Albert Canal and the Monsin hydropower station in 2015, and a greater use of the hydropower station in 2016. For nearly half of the smolts (45.4%), the *passage time* was during dusk or the night (respectively: n = 1 and n = 9), 18.2% (n = 4) during the sunrise, and 36.4% (n = 8) during the day (Fig. 11B). The distribution of detections between the four categories (dusk, night, sunrise, and day) was not significantly different from a random distribution (Pearson's $\chi 2$, p = 0.79). The median *research time* required to find a migration route was 04:45 (range 00:33–473:16). This differs slightly from the time spent by the smolts that did not cross the site, upstream of the complex (U test, p = 0.046). The smolts that did not pass the complex spent a median time of 23:23 (range 00:10–432:05). The *research time* varied significantly with the Meuse water discharge (Spearman's correlation, both: Rho = −0.43, p = 0.045), with a reduction of the required *research time* associated with an increase of water discharge.

Of the 57 smolts detected in the *approach zone*, 61.4% (n = 35/57) were not recorded downstream of the site, of which 7% (n = 4) were last recorded in the entrance of the Albert Canal, and 24.6% (n = 14) upstream of the Monsin hydropower station. The *approach zone detection rate* and the number of *passage attempts* differed significantly between the smolts that passed through the hydropower/canal complex and those that did not (respectively, U test, p = 0.002 and p = 0.008) (Fig. 15A & B). The median *approach detection rate* and *passage attempts* of the smolts that passed the site was 1.5 (range 1–11) and 1 (range 1–8), respectively. The median time spent in the *entry zones* was 04:37 (range 00:01–473:16) and differed significantly between the smolts that passed the hydropower/canal complex regardless of the migration route used

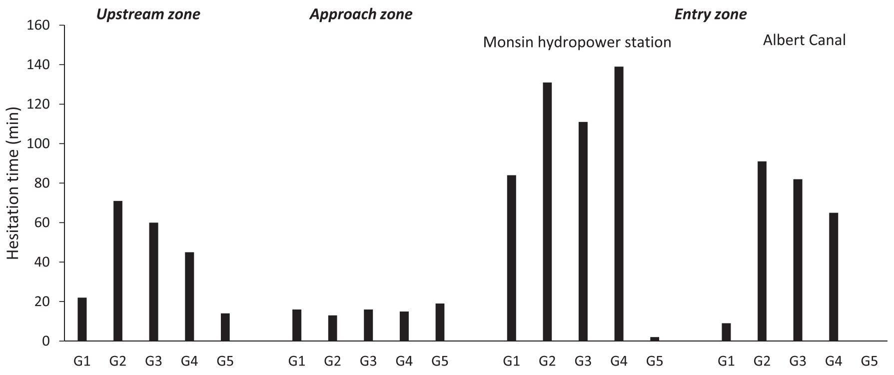

Fig. 12. Smolts' average hesitation time for each group in the different zones upstream of the hydropower/canal complex.

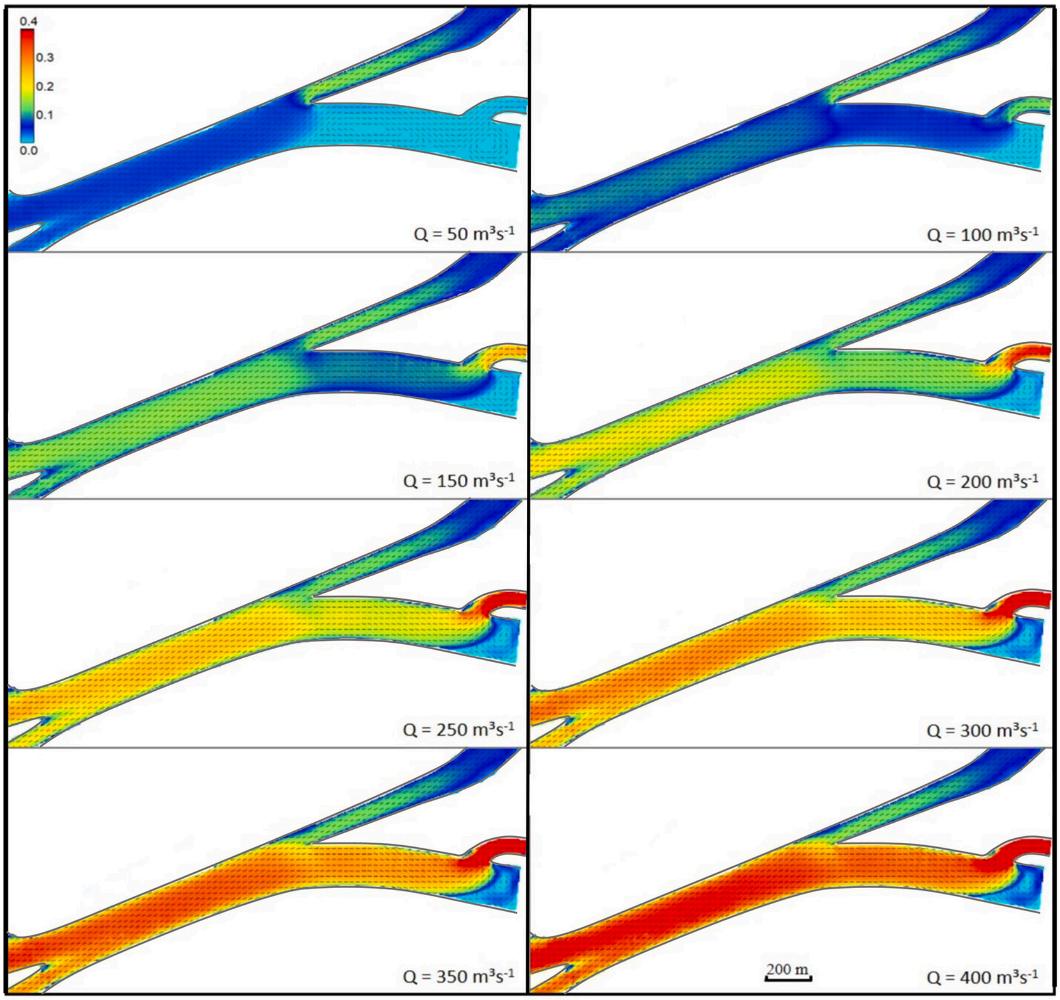

Fig. 13. Computed velocity fields between the confluence of the diversion and the main Meuse river upstream and the Albert Canal emergence and the Monsin weir/HPP downstream for global discharge from 50 to 400 m^{3}s^{-1} (80% of the discharge from the Meuse river and 20% from the Ourthe river). Flow from left to right. In colour: velocity value in ms^{-1}..

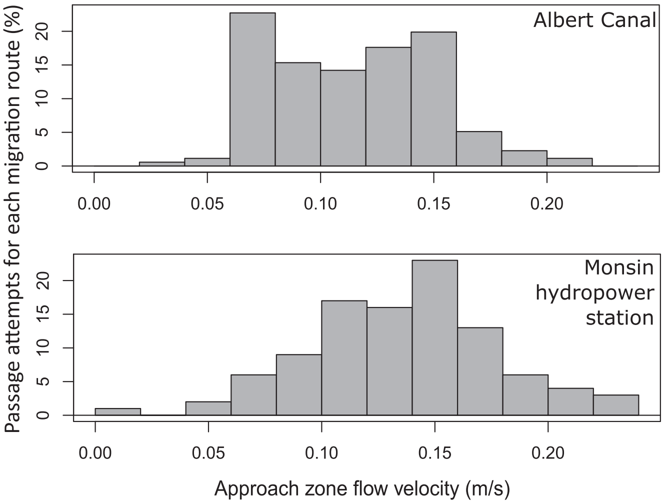

Fig. 14. All the passage attempts expressed by the smolts in the entry zones according to the approach zone flow velocity.

(median = 01:48) and those that did not (median = 07:35) (U test, p = 0.02) (Fig. 15B).

4. Discussion

In the present study, we coupled hydrodynamic modelling and acoustic telemetry to analyse the migratory behaviour of 72 Atlantic salmon smolts, over three consecutive years, at an experimental site that offers a bifurcation between two main migration routes: i) a hydropower station unequipped with a bypass and ii) the entrance of a navigation canal. This experimental site turned out to have a high impact and caused complex and uncommon research behaviour of the smolts, as well as definitive migration stops, associated with poor passage success. The modelling of the hydrodynamic characteristics enabled a better understanding of the influence of flow velocity and water discharge on smolts' behaviour and use of migration routes.

Over the three years of tracking, 41.5% of the migrating smolts performed back and forth movements before approaching the hydropower/canal complex for the first time. This behaviour was observed over long distances and extended over long periods, with a maximal delay of 298 h for one individual smolt. We observed that 13.8% of the smolts definitively stopped their migration before approaching the site.

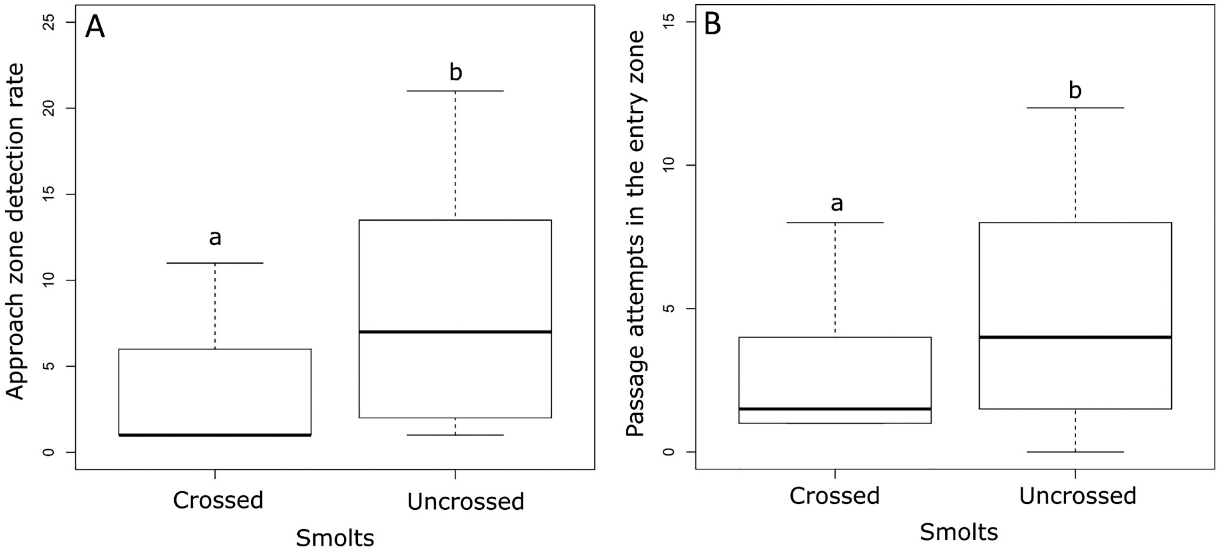

Fig. 15. Comparison between the smolts that crossed through the Albert – Monsin site and those that did not. (A) The approach zone detection number. (B) The passage attempts in the entry zones. Values that did not share a and b superscripts differ at a 0.05 level of significance (U test, respectively: p = 0.002 and p = 0.008).

Such large-scale round-trip behaviours are uncommon and are not supposed to be observed during downstream migration, which should be unidirectional (Davidsen et al., 2005). At the confluence between the Ourthe and Meuse rivers, this behaviour could be partly explained by two anthropogenic factors. Firstly, a low water discharge and associated low flow velocity (< 0.15 m s^{-1}) in the Meuse river may cause disorientation of the smolts and a loss of stimulation to move downstream (Coutant and Whitney, 2000; Fjeldstad et al., 2018). Secondly, the average temperature shift of 3.3 °C between the Ourthe tributary and the Meuse river might also disturb and slow down the downstream migration stimulation by reducing gill NKA, plasma GH, and cortisol levels. This would lead to a reduction of hypo-osmoregulatory capacities and a loss of seawater tolerance, with, in the worst case, a possible desmoltification (Duston et al., 1991; McCormick et al., 1999; Bernard et al., 2019, 2020). The median migration speed of the smolts from the release site to the most downstream detection was 0.11 m s^{-1}. The migration speeds mentioned in the literature vary between 0.09 m s^{-1} and 0.78 m s^{-1} (Stich et al., 2015; Newton et al., 2019; Renardy et al., 2020; Ovidio et al., 2021). Median migration speeds observed in un-impounded stretches ranged from 0.05 m s^{-1} to 0.84 m s^{-1} (Stich et al., 2015; Thorstad et al., 2004; Havn et al., 2018; Newton et al., 2019).

Smolt detections at the hydropower/canal complex were mainly during the dusk, night and sunrise periods. These findings are consistent with previous studies showing migration in smolts during darkness (McCormick et al., 1998; Scruton et al., 2008; Fjeldstad et al., 2012; Riley et al., 2014; Ovidio et al., 2021; Kärgenberg et al., 2020; Renardy et al., 2020). At the hydropower/canal complex, the smolts expressed different behavioural and research tactics, and most of them developed strong hesitating behaviour. The hesitation time differed greatly between the upstream and approach zones. The major hesitation times in the upstream zone were probably due to the smolts' anticipated perception of a bifurcation zone, which caused an increase of hesitating behaviour, mostly when the flow velocity was low. The hesitation time decreased with increasing flow velocity, in agreement with the observation of more frequent downstream movements. The approaching smolts were located a median of five times (range 1–474, $n = 57$) in the approach zone and performed a median of three passage attempts (range 1–36, $n = 56$) in the entry zones. The successful passage rate was 63.6% of the smolts after the two first passage attempts, whereas the 36.4% remaining smolts performed three to eight passage attempts. In smaller scale hydropower stations with multiple migration routes, Nyqvist et al. (2017) and Renardy et al. (2020) observed the same tendency, with a majority of passages during the first and the second attempts. The smolts spent a wide range of time in the approach and entry zones before passing through the site (median research time = 04:45, range 00:33–473:16). In the literature, the median research time was 00:30 for Havn et al. (2020), 00:58 for Renardy et al. (2020) and varied from 00:10 to 00:54 for Tomanova et al. (2018) in small and medium-sized rivers. The longer the smolts stayed upstream of the hydropower/canal complex, the less they were able to cross the site, possibly due to energy expenditure (Svendsen et al., 2011; Nyqvist et al., 2017) and disorientation (Coutant and Whitney, 2000; Scruton et al., 2008; Brevé et al., 2014; Fjeldstad et al., 2018).

At the hydropower/canal complex, the smolts had to choose between the hydropower station and the navigation canal to pass the site. However, most of them changed their decision over time, suggesting that both migration routes are potentially repulsive and unattractive. Migrating smolts may reject a migration route due to the perception of a danger or to inadequate configuration and associated hydrodynamic conditions and therefore may look for a safer migration route (Coutant and Whitney, 2000; Enders et al., 2009; Williams et al., 2012; Kerr and Kemp, 2019), which is sometimes associated with a lower water discharge at the entrance (Havn et al., 2017). Water discharge is a significant factor for smolts during migration by facilitating the crossing of migration barriers (Nyqvist et al., 2017; Thorstad et al., 2017; Persson et al., 2019). In our study, at the first passage attempt, 54.4% ($n = 31$) of the smolts followed the main flow, of which $n = 29$ approached the Monsin hydropower station. The main flow has rarely been directed towards the Albert Canal but in such circumstances, n = 2 smolts selected this route. The choice of the migration route with the main flow is consistent with the observations of Williams et al. (2012). However, we observed that 45.6% did not follow the main flow, as was also observed in some situations by Havn et al. (2017), Kärgenberg et al. (2020) and Renardy et al. (2020). The hydrodynamic characteristics of the river such as the flow velocity also influence smolts' behaviour, as observed by Kerr and Kemp (2019) and Silva et al. (2020). In our study, hydrodynamic modelling showed that the time evolution of the Meuse discharge leads to flow velocity variations in the approach zone. Discharge lower than 250 m^3 s^{-1} favoured flow velocities lower than 0.15 m s^{-1} and both upstream and downstream searching movements, while more oriented searching downstream movement was favoured by flow higher than 250 m^3 s^{-1} and associated flow velocities higher than 0.15 m s^{-1}.

Among the n = 57 smolts in the approach zone, only n = 22 succeeded in passing through the hydropower/canal complex to continue migration. Among them, at the last passage attempt, $n = 8$ used the Albert Canal and n = 14 the Monsin hydropower station. The smolts that crossed the hydropower station undoubtedly used the Kaplan turbines as a migration route in 2014 and 2015 as the spillway gates of the dam were closed. In 2016, it is not excluded that some used the flow over the gates as a migration route given the higher water discharge. After their passage, three smolts were last recorded downstream of the hydropower station and probably died after the passage through the Kaplan turbines. Depending on the properties of the turbine and the operating characteristics, the mortality rate varies from 0% (Vikström et al., 2020) to 20% (Larinier and Travade, 2002). In the present study, 32% of smolts detected in the approach zone, entered and migrated through the Albert Canal. Navigation canals may in some instances be a favourable migration route for salmonids, as suggested by Harnish et al. (2012) and Johnston et al. (2018). However, according to other studies, navigation canals turned out to be rather unfavourable notably due to fish disorientation (Hondorp et al., 2017, *Acipenser fulvescens*; Verhelst et al., 2018a and 2018b; Vergeynst et al., 2020, *Anguilla anguilla*). Of the smolts that entered the Albert Canal, 33.3% stopped their migration at a distance of 7.7 km downstream from the entrance, and 44.4% returned upstream of the hydropower station. These behaviours may be explained by the completely artificial nature of the Albert Canal, with an absence of distinct and constant natural water flow and a local widening of the watercourse that may induce a reduction of stimulation to migrate downstream. The median flow velocity in the Albert Canal was 0.10 m s^{-1} and might have resulted in the round-trip behaviour of smolts. Honkanen et al. (2021) observed that, in areas of standing waters, 49% of movements were in a direction opposite to the migration pathway. Slow-moving watercourses tend to be unattractive and prevent directional migration (Wolter and Vilcinskas, 1998; Honkanen et al., 2021). Moreover, navigation locks and boat navigation cause hydraulic disturbances with abnormal waves and currents and may further increase confusion in smolts, as observed by Wolter and Arlinghaus (2003), Verhelst et al. (2018a, 2018b), and Vergeynst et al. (2020). Migration through navigation canals also increases the risk of injuries and mortality due to potential collisions between fish and boats (Hondorp et al., 2017).

Out of the 57 smolts detected upstream of the site, 61.4% did not pass and probably died of exhaustion or predation, as stated above, after desperately searching for a migration route. The global mortality rate associated with our study site and flow conditions was therefore 66.7% ($n = 35$ non-passed & 3 passed smolts). As a consequence, exhaustion and predation were the major cause of mortality (55.3%) compared to passage through the turbines (7.9%). The remaining 36.8% were last recorded upstream of the Monsin hydropower station, and may have passed the hydropower station anyway but stopped their migration before being detected by the next acoustic receiver. This means that the impact of the hydropower station in terms of mortality has to be considered holistically, by adding the different forms of mortality, including those not caused by turbines. Nyqvist et al. (2017) showed the non-passage of 35% of the smolts detected upstream of a hydropower station in a medium-sized river and the possible predation of one-third of these smolts. Keefer et al. (2013) observed mortality rates of Chinook salmon smolts between 8 and 64% due to predation at large-sized dams. Thorstad et al. (2017) and Havn et al. (2018) highlighted that living, injured or dead smolts might be predated after passing hydropower stations. However, few studies have highlighted important mortalities due to exhaustion.

For the smolts that continued their migration in the Meuse river or the Albert Canal, the escapement rate towards the Flemish region or the Netherlands part of the Meuse river was very low: 2.9% by the Albert Canal and 8.3% by the Meuse river. Vis and Spierts (2011) and Brevé et al. (2014) highlighted a seaward escapement of up to 3% of the studied Atlantic salmon smolts in the Dutch part of the Meuse river after migrating more than 230 km from the Roer tributary (84 km downstream of the hydropower/canal complex considered here). Despite these low seaward escapement rates, the Meuse river probably remains the best way to reach the North Sea compared to the Albert Canal, but the migration conditions have to be improved.

Several management measures may be tested and achieved to improve smolts' downstream migration at the Monsin hydropower complex and along the Meuse river to increase seaward escapement. Upstream of the Kaplan turbines, the bar screen should be combined with a downstream bypass, which would favour successful passage of migrating smolts (Larinier and Travade, 2002; Fjeldstad et al., 2018). In addition, a combination of real-time smolt monitoring and the recently developed predictive model of smolt downstream migration (Teichert et al., 2020) may be useful when mitigation measures need to be implemented, such as the opening of the spillway gates or turbines shutdown. In some instances, spillway gates may be the preferred migration route (Calles et al., 2012; Katopodis and Williams, 2012). Navigation locks in the Albert Canal might also be at a standstill at night during smolt migration to avoid a flow increase in the canal. Furthermore, an adapted management of the repartition of water flow between the Albert Canal and the Meuse river during the smolt migration period might also be tested and simulated with our hydrodynamic model before being implemented to evaluate its potential efficiency, as suggested by Szabo-Meszaros et al. (2019). Simulations would make it possible to identify if a more elevated flow to the Meuse river, opened spillway gates, or turbines shutdown would favour the passage of smolts by increasing the attractiveness of the natural watercourse and direct the smolts towards a safe migration route. To increase their efficiency, these mitigation measures should be performed as a priority during dusk and at night, which are known to be the diel migration activity times in the Meuse river basin (Ovidio et al., 2021; Renardy et al., 2020). If mitigation measures turn out to be effective after simulations, a 2D—3D tracking evaluation would be useful after their implementation (Silva et al., 2020).

In conclusion, the present study highlighted the negative impact of a hydropower/canal complex site on smolts' downstream migration, by offering two suboptimal, unattractive and unsafe migration routes. The site caused disorientation and energy expenditure, which resulted in significant delays and mortality, and considerably affected the subsequent seaward escapement. The re-establishment of sustainable Atlantic salmon (and sea trout, *Salmo trutta* Linnaeus, 1758) populations in the international Meuse river basin is a challenging project that started at the beginning of the 1990s (Philippart et al., 1994). From 2000 to 2020, the number of returning Atlantic salmon and sea trout progressively increased, but not enough to achieve a self-sustainable population. The ecological state of the Meuse river basin was greatly improved in terms of the physical and chemical quality of the water and the construction of a fishway for upstream movements of adults, but the downstream migration of the smolts and the associated escapement success remains one of the main problems for the success of the reintroduction project.

Credit author statement

Séverine RENARDY: Formal analysis, data treatment, writing original draft, writing review and editing, validation, visualization. **Abderrahmane TAKRIET:** Formal analysis, data analysis and modelling. **Jean-Philippe BENITEZ:** Conceptualization, methodology, field work, formal analysis, paper proofreading. **Arnaud DIERCKX:** Conceptualization, methodology, field work, data monitoring. **Raf BAEYENS:** Conceptualization, methodology, field work, data monitoring, paper proofreading. **Johan COECK:** Supervision, project administration, funding acquisition, paper proofreading. **Ine S. PAUWELS:** field work, paper proofreading. **Ans MOUTON:** Conceptualization, methodology, field work, data monitoring, paper proofreading. **Pierre ARCHAMBEAU:** Development of the modelling software. **Benjamin DEWALS:** Development of the modelling software, paper

proofreading. **Michel PIROTTON:** Development of the modelling software. **Sébastien ERPICUM:** Development of the modelling software, data analysis and modelling, writing review and editing, paper proofreading. **Michaël OVIDIO:** Conceptualization, methodology, co-writing original draft, co-writing review and editing, supervision, project administration, funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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