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ORIGINAL ARTICLE

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Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in River Minho

Hugo Flávio[1] | Pablo Caballero[2] | Niels Jepsen[1] | Kim Aarestrup[1]

[1]National Institute of Aquatic Resources, Technical University of Denmark, Silkeborg, Denmark

[2]Xunta de Galicia, Dirección Xeral de Conservación da Natureza, Consellería de Medio Ambiente, Santiago de Compostela, Spain

Correspondence
Hugo Flávio, National Institute of Aquatic Resources, Technical University of Denmark, Silkeborg, Denmark.
Email: hdmfla@aqua.dtu.dk

Abstract

The Atlantic salmon (*Salmo salar*) population of the River Minho represents the southern natural distribution edge of the species. In line with the general trend for Atlantic salmon, this population has been declining over the years and is now at a critically low level. With river connectivity compromised by a large dam just 80 km upstream the River Minho's outlet, and an expected deterioration of climatic conditions, it is urgent to increase our knowledge of this population and identify survival bottlenecks that can be addressed. In this study, we used radio and acoustic telemetry to track Atlantic salmon smolts during their migration towards the sea and record both survival rates and possible causes of mortality. The recorded survival for the tagged migrating Atlantic salmon remained below 55% in the three studied years, indicating that the in-river loss of smolts is likely a strong constraint to this population. From the smolts to which a likely cause of mortality could be attributed (34%), most appear to have been removed from the river (25%), with two confirmed events of bird predation and one of mammal predation. Interestingly, eight tags were recorded moving back upstream, likely indicating predation by larger fish. Increasing predator populations (e.g. cormorants, *Phalacrocorax carbo*) and invasive predators (e.g. American mink, *Neovison vison*) lead to elevated predation pressure on this already strained Atlantic salmon population, and further studies quantifying their impact in more detail could prove crucial for future management considerations.

KEYWORDS

acoustic telemetry, climate change, fish migration, predation, radio telemetry, river barriers

1 | INTRODUCTION

Atlantic salmon (*Salmo salar*) is a species with a very high economic and cultural importance, with a natural distribution range encompassing the Baltic Sea and the northern part of the Atlantic Ocean. Pressured by multiple stressors that can impact survival in both the marine and freshwater life stages (e.g. habitat destruction, blocking of migratory paths, fishing, rising water temperatures), the Atlantic salmon populations have generally been in decline throughout their distribution range (Chaput, 2012; Gibson, 2017; ICES, 2018).

The seaward migration of the Atlantic salmon smolts represents a particularly hazardous life stage (Aarestrup, Nielsen, & Koed, 2002; Halfyard, Gibson, Ruzzante, Stokesbury, & Whoriskey, 2012; Thorstad et al., 2012), with high mortality rates caused by multiple interacting factors. For example, predator encounters (Blackwell & Juanes, 1998; Jepsen, Flávio, & Koed, 2019), the presence of barriers to migration (Birnie-Gauvin et al., 2018; Kärgenberg et al., 2020), or chemical pollution (Thorstad et al., 2013) can directly lead to mortality, or cause injuries that ultimately lead to the same fate. Increasingly, warm water temperatures (e.g. driven by climate change) can also impact migration timing (Otero et al., 2014), which in turn can impact the survival rates to adulthood (Antonsson, Heidarsson, & Snorrason, 2010).

During their seaward migration, Atlantic salmon smolts tend to increase their migration speed as they approach the shore (Davidsen et al., 2009; Moore, 1975). Additionally, the smolts tend to prefer to migrate during the night (Aarestrup et al., 2002; Moore, Potter, Milner, & Bamber, 1995), which likely allows them to avoid visual predators (Ibbotson, Beaumont, Pinder, Welton, & Ladle, 2006). However, this preference towards nocturnal migration may fade away during the later parts of the migration period, when smolts, to a greater extent, also move throughout the day (Thorstad et al., 2012).

While in the early life stages, the survival of young Atlantic salmon is dependent on the carrying capacity of the river (Gee, Milner, & Hemsworth, 1978). In other words, after a certain point, increasing the number of offspring does not translate into a higher number of fish produced, as regulation is exerted through competition for limited resources such as food or habitat (Milner et al., 2003). However, after this initial period, survival appears to be mainly density-independent, which implies that an increase in the number of successful out-migrating smolts translates directly into an increase in the number of returning adults (Crozier & Kennedy, 1993; Jonsson, Jonsson, & Hansen, 1998).

The Atlantic salmon population of the River Minho represents the southern natural distribution edge for the species (MacCrimmon & Gots, 1979) and is expected to suffer the most with the projected increasing temperatures in the coming decades. Despite the alarming situation of this population, little is known about the survival bottlenecks imposed to it, nor the respective sources of mortality. As such, it is essential that we expand our knowledge of this population so that management actions may be taken to stop its decline. Through the combined use of acoustic and radio telemetry, we aim to estimate the survival rates of Atlantic salmon smolts migrating through the rivers Tea and Minho, as well as unveil the respective sources of loss/mortality.

2 | METHODS

2.1 | Study area and experimental fish

The River Minho has a length of c. 310 km and a catchment of c. 17,000 km^2. The lowermost 79 km constitutes the border between Portugal and Spain. Popular records from the River Minho indicate that capturing over a thousand Atlantic salmon per year was common in the first half of the twentieth century, but catch records after 1950 show more modest values (200–400 fish per year). These values drop even further from 1990, with rarely over 100 captured fish per year being reported (Álvarez et al., 2010).

The Minho's longitudinal connectivity is broken by a large dam situated c. 80 km upstream from the river mouth (the Frieira dam), effectively reducing the accessible Atlantic salmon spawning grounds to c. 6% of the original area (Álvarez et al., 2010). Currently, returning adult Atlantic salmon are known to spawn in two tributaries: the River Tea and the River Mouro (Carlos Antunes, pers. comm.). Returning adults that get trapped downstream of the dam are captured and moved to hatchery facilities for spawning. The hatchery-reared juveniles are then released in the tributaries downstream of the Frieira dam, allowing them to grow and smoltify in natural conditions. One of these tributaries is the River Tea, where a wolf trap has been operational since 1999. The facilities at this location allow capture of smolts as well as counting of returning adults, showing a mean of 14 adults going up the river per year in recent years.

Downstream migrating smolts were captured in the Freixa trap, located in the River Tea, c. 14.7 km upstream of its confluence with the River Minho (Figure 1). Upon entering the River Minho, the smolts must swim c. 41.5 km before reaching the sea (totalling c. 56.2 km from the trap to the sea). The distance from the trap to the lowermost deployed automatic listening stations (ALS) was 44, 46.2 and 44 km in 2017, 2018 and 2019 respectively. However, the lowermost ALS in 2017 were lost, effectively reducing the covered distance in 2017 to 26.4 km.

At capture, smolts were selected for tagging based on morphological indicators (e.g. silvery appearance and streamlined body shape; Hoar, 1988). Fork length (L_f) and weight were measured before implanting the tag. Smolts measuring <13.5 cm L_f were not considered for tag implantation to ensure a low tag/body-weight ratio. The number of captured wild Atlantic salmon smolts of sufficient size (≥13.5 L_f) was low in 2018 and 2019 (n = 22 and 23) and sample sizes were supplemented by hatchery origin smolts in 2018 and with naturalised smolts in 2019 (Table 1). Naturalised smolts are fish that were born in a hatchery and were released as parr to the upper reaches of the river. These naturalised smolts were distinguished from wild smolts by the absence of the adipose fin, which was clipped when the juveniles were released.

Tagging dates varied between years (Table 1) due to early-spring high flows in 2018 (which prevented trap operation until later in the season) and due to inter-project constraints in 2019 (which forced tagging and release to be performed earlier than in 2017). Additional information on the temperature and flow profiles for river Tea during the tagging and release periods can be found in Figure S1.

2.2 | Acoustic telemetry

2.2.1 | Surgery

Smolts were anaesthetised in a 0.03 g/L solution of benzocaine until operculum rate became slow and irregular. Surgery was performed in a V-shaped surgical table, and the acoustic transmitter

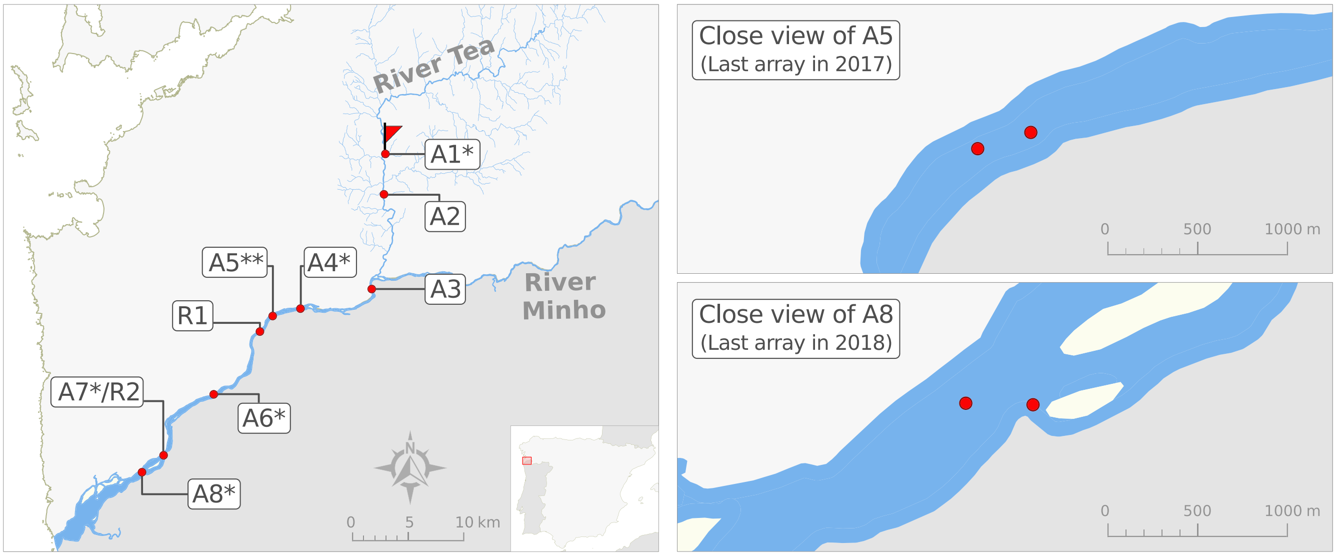

FIGURE 1 The River Minho and its tributary, the River Tea. The flag shows the release site (the Freixa trap). The acoustic automatic listening station arrays (ALS) are numbered A1 to A8, and the radio ALS are numbered R1 and R2. Arrays marked with * were only operational in 2018, while A5 (marked with **) was only operational in 2017. ALS were deployed at A7 in 2017, but were lost. All acoustic ALS arrays, with the exception of A7 in 2018, were composed of two receivers. The right-side panels show the positioning of the two ALS that composed A5 and A8, in 2017 and 2018 respectively

TABLE 1 Summary information on the tagged smolts per year

Year	Group	*n*	Fork length (cm)	Weight (g)	Tagging period
2017	Wild	50	16.5 (13.6–19.5)	44 (25–82)	14th of April to 4th of May
2018	Wild	22	14.7 (13.5–17.0)	30 (22–48)	2nd to 11th of May
	Hatchery	48	14.6 (13.7–16.1)	29 (23–37)	10th and 11th of May
2019	Wild	23	15.7 (14.1–17.8)	41 (28–61)	9th to 18th of April
	Natur.	9	17.7 (15.2–18.9)	56 (45–82)	9th to 18th of April

Note: The fork length and weight columns show the mean value with the ranges between parentheses. Note that in 2017 and 2018, the smolts were tagged with acoustic transmitters, and in 2019, they were tagged with radio transmitters. The numbers of fish released at each specific day during the tagging periods can be found in Figure S1.

was inserted into the body cavity through an incision slightly to the side of the mid-ventral line, anterior to the pelvic girdle. The incision was closed with two separate absorbable (Vicryl 4-0) sutures. The duration of the procedure varied between one and two minutes. All smolts tagged in each day were released at the same time just downstream of the trapping facilities, during the day, after showing full recovery from the handling and tagging procedure. The acoustic transmitters used were Thelma 7.3 mm tags (7.3 mm diameter, 17 mm length), weighing 1.8 g in air and 1.1 g in water, with a transmission rate of 20–60 s and an expected battery life of 98 days. Surgical implantation was performed by an experienced fish surgeon in compliance with local regulations.

2.2.2 | Tracking network

In 2017, eight ALS (Vemco VR2W) were deployed in four arrays (A2, A3, A5 and A7; Figure 1). Of these, the two lowermost ALS, which constituted array A7 (positioned c. 44 km downstream from release), were lost and the data could not be recovered, effectively shortening the covered river stretch to c. 26.8 km. In 2018, 13 ALS (Vemco VR2W) were deployed in seven arrays (A1 to A4, A6 to A8; Figure 1), covering c. 46 km downstream from release. None of the ALS deployed in 2018 were lost. All arrays, with the exception of A7 in 2018, were composed by two ALS. From these, in A6 the ALS were placed perpendicularly to the river, and in the remaining arrays, the ALS were placed in line with the river. At its largest, the river's width at the ALS locations was of c. 720 m (at the eastern ALS of array A8), with the remaining ALS positioned at places where the river had less than 500 m width.

In 2017, the detections in the two ALS at A5 were compared to one another to estimate intra-array efficiency. The same was done for array A8 in 2018 (relative ALS positions for both A5 and A8 can be seen in Figure 1). Additionally, manual tracking was performed by boat using a manual receiver (Vemco VR100) at the end of the study in 2017 to check for stationary tags. Manual tracking could not be performed in 2018.

2.3 | Radio telemetry

2.3.1 | Surgery

The surgery procedure was similar to that of the acoustic tag implanting. Additionally to that procedure, the radio antenna exits the body cavity posterior to the incision so that it trails back along the body of the fish. A hollow needle was used to puncture the lateral body wall, and the antenna was run through with the needle. The incision was closed with one absorbable (Vicryl 4-0) suture. Due to the reduced number of captures, fish were held up to five days and tagged in three different dates: 8th, 10th and 17th of April 2019 (n = 14, 9 and 12 respectively). From these, two of the fish tagged on the 8th of April and one of the fish tagged in the 10th were never detected and were thus removed from further analysis (i.e. valid n = 32). The radio tags used were ATS F1420 8 mm tags (7 mm diameter, 8 mm length), weighing 1.3 in air and 0.8 in water, with a pulse rate of 35 ppm and expected battery life of 39 days. Radio tagged smolts were kept in a recovery tank overnight to ensure full recovery and were released in the morning of the following day.

2.3.2 | Tracking network

Manual tracking was performed on a daily basis. Additionally, two radio ALS were deployed in the River Minho, 26.8 and 44 km downstream from the point of release. The radio ALS could not be deployed before the 15th of April (six days after the first batch of fish were released) due to transport complications.

2.4 | Data analysis

2.4.1 | Acoustic data validity and ALS efficiency

Raw acoustic detection data from 2017 and 2018 were checked for unlikely behaviour using the R package actel (https://github.com/hugomflavio/actel). Some examples of unlikely behaviour include skipping ALS arrays (e.g. being detected in the first and third array, but not in the second), or long upstream movements (e.g. being detected in an ALS array after being detected at one or several ALS arrays located further downstream). These events were analysed in detail so that false detections could be identified and removed.

Acoustic ALS detection efficiency was calculated through analytical CJS modelling (Perry, Castro-Santos, Holbrook, & Sandford, 2012) using the same R package. The most downstream ALS array in both years was composed of two ALS placed one after the other, within close proximity (c. 400 and 300 m in 2017 and 2018, respectively, Figure 1), which allowed the estimation of detection efficiency within the array itself (Perry et al., 2012).

2.4.2 | Effect of smolt origin and year on survival

The exploratory analysis revealed an (expected) high collinearity between the release dates and study year. As such, we decided to exclude the release date from the initial selection of explanatory variables. This implies that, should year be deemed to have a significant effect on survival, this effect could in fact be driven either by a year effect or a release date effect.

A Bernoulli generalised linear model (GLM) with logit link function was applied to test for effects of year (categorical, three levels), group (categorical, three levels) and length (continuous) on survival probability, measured either as registration in the last active acoustic ALS array for the acoustic studies or as detection in R2 during the radio study. Distance covered was included as an offset to compensate for the loss of the last ALS array in 2017, and ensure that any significant differences found were not an artefact of the difference in distances covered between years. Stepwise goodness-of-fit model selection was performed to determine which covariate combination would produce the best model.

The initial model's equation is as follows:

$$\text{Survival}_i \sim \text{Bernoulli}(\mu_i)$$

$$E(\text{Survival}_i) = \mu_i$$

$$\text{logit}(\mu_i) = \text{Year}_i + \text{Group}_i + \text{Length}_i + \text{offset}(\log(1/\text{Distance}_i))$$

It is important to note that, while we refer to survival as the response variable for simplification, the model is truly predicting the probability of a tag being detected at the last array (please read the considerations at the end of the discussion for the potential implications of this).

2.4.3 | Sources of smolt mortality

If a tagged smolt was not detected at the last receiver arrays, it was assumed that the smolt had died either by predation or due to unknown causes (two exceptions were made to this rule in 2019, more information available in Section 3.1). As such, tag movements recorded by the ALS or through manual tracking were investigated to identify the fate of each tagged fish. The following options were considered:

Acoustic studies:

1. A fish was presumed eaten by a terrestrial predator (i.e. mammal or bird) if the detections at the ALS arrays stopped and the tag could not be found during manual tracking within the lifetime of the tag;
2. A fish was presumed eaten by a larger fish or an otter if the tag started displaying long upstream movements with sequential detections in the ALS arrays;
3. A fish was presumed dead for unknown reasons if the detections at the ALS arrays stopped and the tag was later found stationary during manual tracking.

Radio study:

1. A fish was presumed eaten by a mammal if the tag was recovered with bite marks;
2. A fish was presumed eaten by a bird if the tag was recovered with no bite marks;
3. A fish was presumed eaten by a larger fish if the tag started displaying long upstream movements;
4. A fish was presumed eaten by a terrestrial predator (i.e. mammal or bird) if the tag disappeared before reaching the second radio ALS;
5. A fish was presumed dead for unknown reasons if the tag movement halted permanently in an inaccessible place and thus tag recovery was not possible.

2.4.4 | Smolt behaviour

Migration speed was calculated as the time from the first registration in one array to the time of first registration on the following array, divided by the shortest possible distance between the respective ALS. In the radio study, migration speed was calculated as the time between release and first registration on R1, and between first detection in R1 and first detection in R2, divided by the shortest possible distance between the two points. Migration speed was converted from metres per second to body-lengths per second (bl/s) using each individual fish's size, to standardise for fish length.

Diurnal/nocturnal migration patterns were assessed based on the time of first arrival at each ALS array. In the radio study, only the arrival times at the radio ALS were used for this calculation, because manual tracking was only performed once a day, during the day.

3 | RESULTS

3.1 | Acoustic data validity and ALS efficiency

In 2017, all ALS arrays successfully recorded all the fish detected further downstream (i.e. 100% efficiency; absolute numbers displayed in Table S1). In the last array for 2017 (A5), the eastern ALS recorded 27 tagged smolts, and the western ALS recorded 21 smolts, with 21 being detected in both ALS (i.e. 27 individual smolts were detected in the array as a whole). This implies a median estimated individual ALS efficiency of 100% and 78% respectively and an estimated combined efficiency of 100%.

In 2018, inter-array efficiency was high in arrays A1, A2, A3, A4 and A6 (ranging between median 86% and 100%; absolute numbers displayed in Table S1). Efficiency was lower in A7, with eight smolts passing through without being detected (62% median estimated efficiency). However, this array had no impact on fate assignment, and thus its lower efficiency had little impact on the study results. In the last array (A8), the eastern ALS recorded 17 tagged smolts, and the western ALS recorded 16 smolts, with 12 being detected in both ALS (i.e. 21 individual smolts were detected in the array as a whole). This implies a median estimated individual ALS efficiency of 76% and 71% for the eastern and western ALS respectively and an estimated combined efficiency of 93%. As such, the number of smolts estimated to have passed the last array is 22.58 (calculated as 21 detected fish divided by 0.93). Ultimately, potentially one or two smolts could have passed the last array undetected in 2018.

In 2019, 22 tags are known to have passed through the first radio ALS (R1), of which 20 were detected at the station, indicating a mean estimated efficiency of 92%. Efficiency could not be estimated for the second radio ALS (R2), because no manual tracking could be performed after that station. In total, four tags disappeared between R1 and R2, of which one was last detected c. 2 km downstream of R1 nine days after having passed that ALS, indicating that the fish likely did not succeed to migrate out. Assuming R2 had an efficiency similar to R1, it is possible for one of the three remaining tags to have passed through R2 undetected (c. 20% chance assuming 92% efficiency), but it is highly unlikely that more than one of those tags passed through R2 undetected (c. 2% chance). Additionally, it is important to mention that two fish were detected migrating quickly at the beginning of the study and may have moved out of the study area before the radio ALS could be set up (tags 71 and 180, Table S1). To adopt a conservative approach regarding mortality, these fish were considered to have survived.

3.2 | Effects of smolt origin and year on survival

The applied GLM showed that the three groups of tagged smolts (wild, naturalised and hatchery-reared) were equally likely to successfully move down through the study area (GLM, $X^2 = 0.829$, $p = .66$). Furthermore, year-to-year variation had no significant effect on survival (GLM, $X^2 = 1.198$, $p = .274$), with 27 smolts detected at the last ALS array in 2017 (54% of the released that year), 21 smolts detected at the last ALS array in 2018 (30% of the released that year) and 17 smolts considered to have survived in 2019 (53% of the released that year). Length, however, was revealed to have a significant effect on survival probability, with larger smolts being more likely to be detected at the last listening stations of the study area (GLM, $X^2 = 7.303$, $p = .007$, Figure 2).

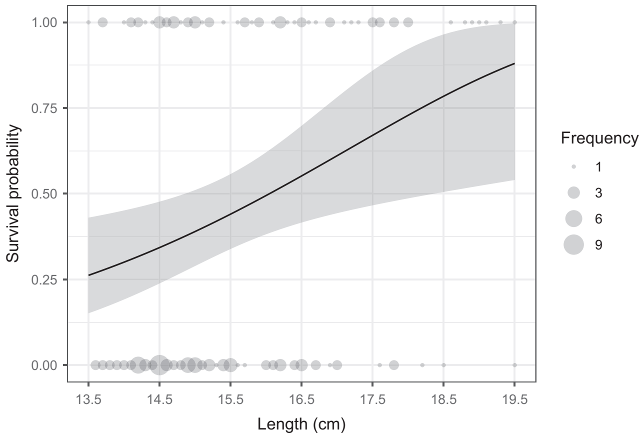

FIGURE 2 Survival probability as a function of fish length, assuming a distance travelled of 46.2 km. The circles at $y = 1$ and $y = 0$ show the recorded survivals/mortalities (respectively), distributed by the respective fish lengths. Survival was revealed to be highest for the larger Atlantic salmon smolts migrating through rivers Tea and Minho

3.3 | Sources of smolt mortality

In 2017, 15 tags were removed from the river, which is indicative of bird or mammal predation (Table 2). Eight tags were detected laying on the bottom during post-study manual tracking in 2017 (specific distances from release shown in Table S2). As the fish carrying these tags could have been predated or have died of other causes, the cause behind the death is unknown.

In 2018, long upstream movements were recorded for eight tags, which is indicative of predation by larger fish or otters and subsequent detection of this predator's movements (more details on the movements of each tag are available in Table S3). While these fish were considered successful migrants in the survival GLM, they are mentioned here as the behaviour indicates the fish were eventually eaten and the respective tags returned into the study area. The source of mortality for the remaining unsuccessful fish could not be determined because it was not possible to perform post-study manual tracking in 2018.

In 2019, one tag was recovered from the bank with bite marks and two without bite marks, indicating predation by a mammal and birds respectively. In addition, six tags were removed from the river (likely predated by a mammal or bird as well). Lastly, six tags remained stationary until the end of the study at different points in the river (specific distances from release shown in Table S2), and the respective fish were assumed to have died for unknown reasons (Table 2).

3.4 | Migration speed

In the three years, the migration speed tended to increase as the fish moved further away from the release site. The migration speed between the release site and the first array was very low (Figure 3a,b), indicating a tendency for the fish to remain stationary in the period immediately after release. This is particularly clear in 2018, where the differences in migration speed between release to A1 and A1 to A2 are remarkable (Figure 3b). The subsequent decrease in speed between A2 and A3 in 2018 could indicate a reluctance in moving from the River Tea to the larger River Minho. Also in 2018, six fish displayed particularly high speed in the stretches covering the River Minho (over 7.5 bl/s, Figure 3b). From these six fish, two completed the migration normally (i.e. last detection at A8), one came to a stop at A4, one was last detected after the high speed event (at A6), and two moved all the way to A8 and then started exhibiting upstream movements. The behaviour of the latter four tags could imply that the movement speeds recorded are that of a predator, rather than the salmon smolt. However, since it is impossible to determine the moment of predation, it is very hard to determine whether or not these measurements are valid. As such, we have decided to assume the fish were alive up until the point when the tags disappeared or started performing long upstream movements (i.e. a conservative estimation of mortality).

TABLE 2 Assigned fates of the unsuccessful tagged smolts in the three studied years

	2017	2018	2019	Total
Presumed mammal predation	–	–	1 (7%)	1 (1%)
Presumed bird predation	–	–	2 (13%)	2 (2%)
Presumed bird or mammal predation	15 (65%)	0[a]	6 (40%)	21 (22%)
Presumed larger fish or otter predation	0	8 (14%)[b]	0	8 (8%)
Unknown reason	8 (35%)	49 (86%)	6 (40%)	63 (66%)

Note: In 2017 and 2018, acoustic tags were used, while in 2019 radio tags were used instead. The percentage relative to the total number of lost tags is shown in between parentheses.

[a]Manual tracking for tags laying on the bottom could not be performed in 2018, and, as such, it was not possible to determine how many tags were removed from the river.

[b]Note that these fish were considered successful migrants during the mortality analysis, but have later on re-entered the river and moved a considerable distance upstream.

3.5 | Diel migration patterns

The migrating smolts showed a clear tendency to arrive at the first ALS arrays during the night period. In 2017, the average arrival time (of day) at A2 and A3 was 00:21 and 01:11 respectively, while the average arrival time at A5 was 05:36 (Figure 4a). In 2018, the night-arrival pattern was very clear in A1 to A4 (arrival times between 23:34 and 01:57), but seemed to fade as the fish moved closer to sea (Figure 4b). The average

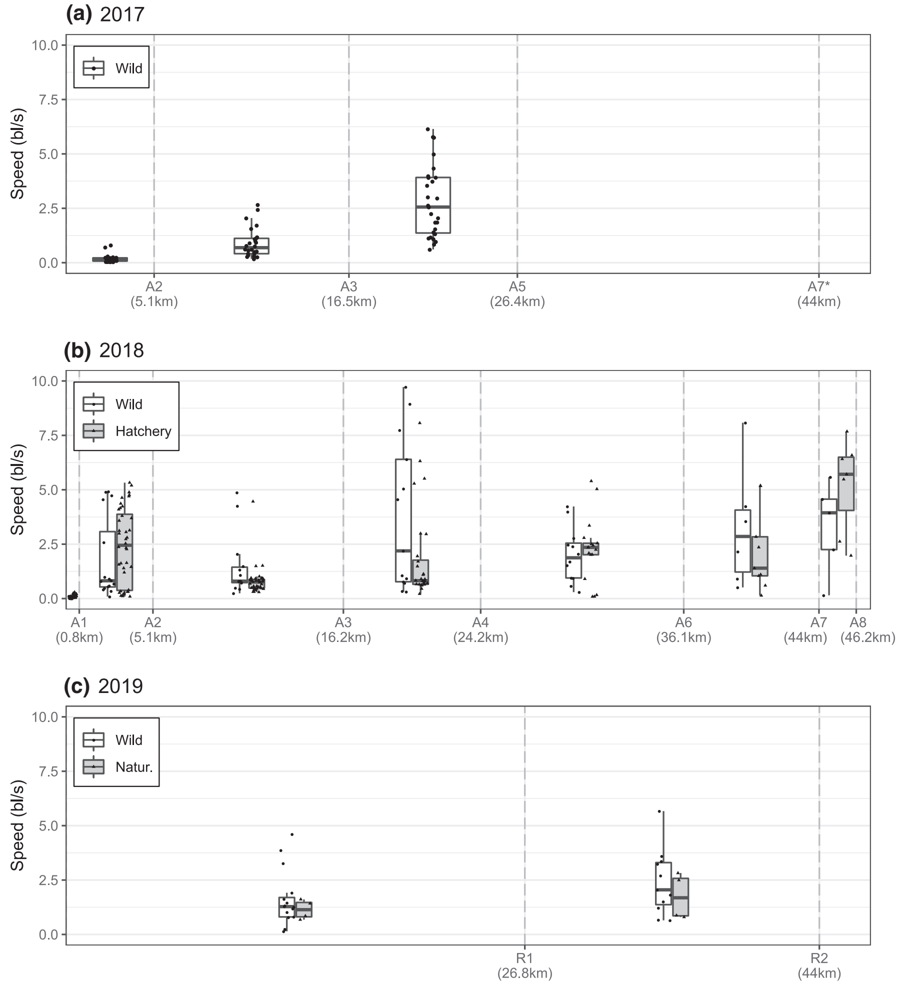

FIGURE 3 Migration speeds (in body-lengths per second) for smolts travelling through the acoustic and radio ALS arrays distributed through the rivers Tea and Minho. The distance from the release site for each array is noted between brackets, below the arrays' name. *No speeds could be calculated between A5 and A7 in 2017 because the ALS at A7 were lost

arrival times at A6, A7 and A8 were 08:33, 06:43 and 18:33 respectively. In 2019, average arrival time at both arrays fell within the night period (21:58 and 02:04 for R1 and R2, respectively, Figure 5).

4 | DISCUSSION

4.1 | Survival rates

The recorded survival for the tagged Atlantic salmon migrating through rivers Tea and Minho remained below 55% in the three studied years, with 2018 showing particularly bleak results (30% survival). This lower result for 2018 is expectable, as the average size of the tagged smolts was lower in this year. Additionally, high flows early in the smolt season prevented the trap operation and forced the tagging and release to be performed later in the season. This could imply that the most fit smolts had already migrated out during the high flows, and consequently that the sampling may have been biased, even though the model results did not show a clear effect of year on survival. The combination of confounding factors such as different release dates or the need to resort to hatchery-reared fish may have driven the exceedingly low survival results in 2018. While the recorded survival rates are not extraordinary low (Chaput et al., 2019; Flávio, Aarestrup, Jepsen, & Koed, 2019; Lothian et al., 2018; Thorstad et al., 2012), the high recorded in-river loss of smolts is likely a strong constraint to this population, which is already strained by loss of habitat, a prolonged decline and warming temperatures. Future research where the limitations revealed during the current study are addressed could help solidify the reported effects (or non-effects) of different factors on smolt survival in the River Minho. Importantly, detailed measurements of environmental variables along the study area could improve our understanding of the underlying drivers for the recorded smolt behaviour.

The statistical analyses revealed that larger sized smolts were more likely to successfully move down through the study area. Recent literature reports both cases where estimated survival is positively associated with length (Chaput et al., 2019; Davidsen et al., 2009; Flávio et al., 2019; Jepsen, Aarestrup, Økland, & Rasmussen, 1998), negatively associated with length (del Villar-Guerra, Larsen, Baktoft, Koed, & Aarestrup, 2019) and where no effect of smolt length was detected (Dempson et al., 2011; Persson, Kagervall, Leonardsson, Royan, & Alanärä, 2019; both of which tagged larger smolts on average), seemingly indicating that the impact of size on survival may be site-specific (Gregory, Armstrong, & Britton, 2018). Importantly, while it is not possible to entirely rule out tagging effects on survival, this difference in

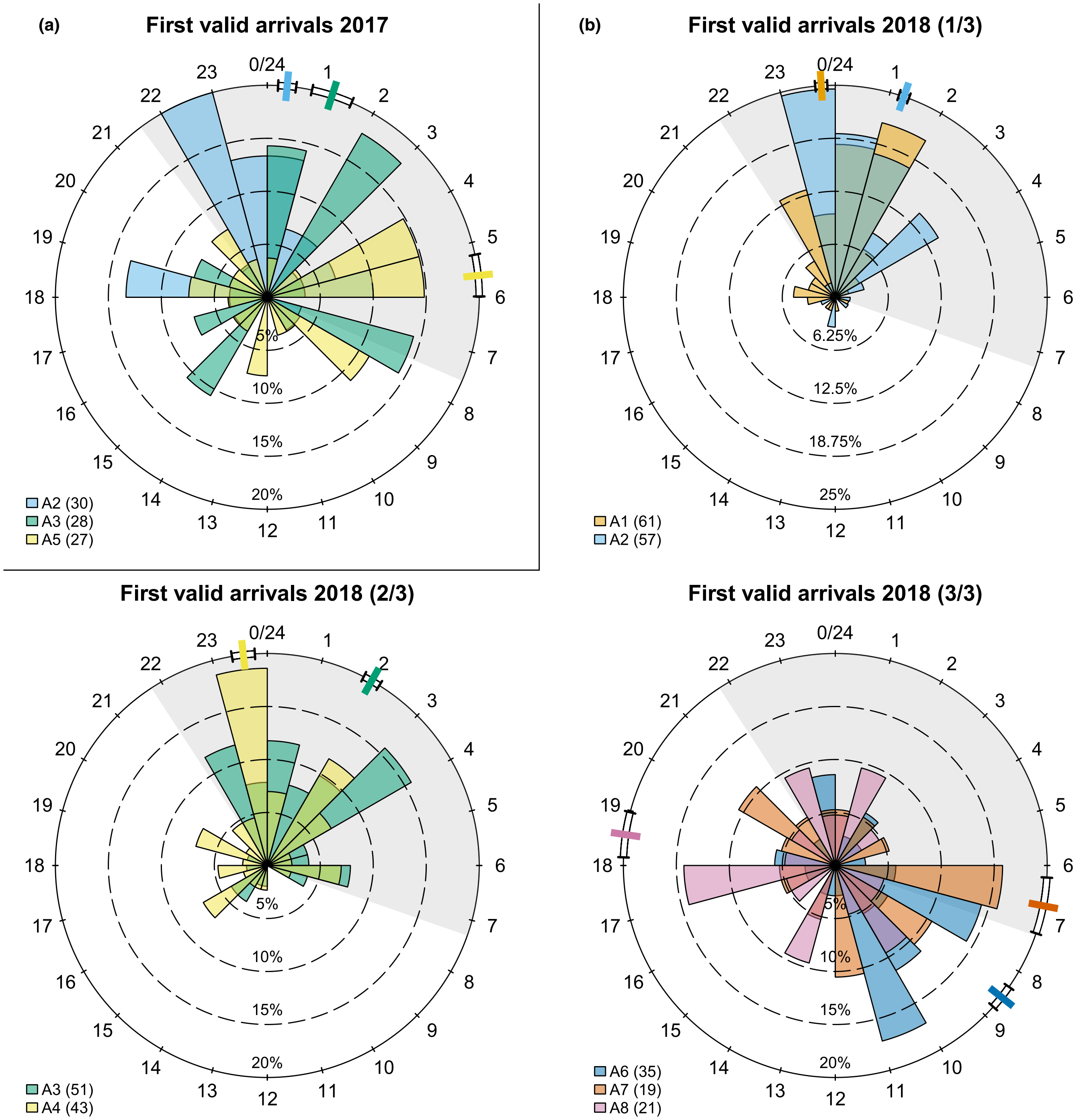

FIGURE 4 Arrival times at each of the acoustic receiver arrays in (a) 2017 and (b) 2018. The coloured markers in the outer circle indicate the mean value for the respectively coloured array. The ranges around each of the mean values show the SE. The shaded portion of the circle shows the average sunset-to-sunrise hours for the study period. The number of smolts that represent the pool of data for each array is presented between brackets in the respective caption. Each array's bars sum to 100%

survival rates between fish lengths is expected to reflect a true difference in fitness, as Newton et al. (2016) found no detrimental effect of tag burden on Atlantic salmon smolts of different lengths using similar acoustic tags (see also Jepsen, Mikkelsen, & Koed, 2008). It is possible that larger smolts migrate faster, and thus reduce the time during which they are vulnerable to predation. However, correlation tests between smolt size and the respective average speed at different sections of the study area revealed no significant correlations between these two variables. Alternatively, it is possible that smaller migrating smolts are vulnerable to predation by a wider range and number of predators, thus making the migration more hazardous.

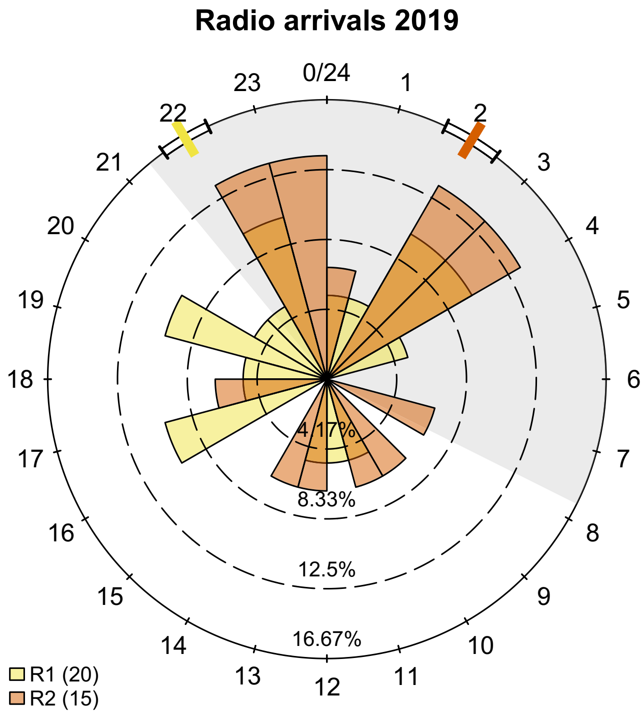

FIGURE 5 Arrival times at each of the radio stationary loggers deployed in 2019. The R1 and R2 radio stations were located 26.8 and 44 km downstream of the trap respectively (closest acoustic equivalents are A5 and A7). For more details on the graphic elements displayed, see the caption of Figure 4

4.2 | Sources of mortality

The study allowed to narrow down the likely sources of 34% of the recorded mortality (including the eight fish that likely died after crossing the study area). Most of the unsuccessful migrants appear to have been removed from the river (25% out of all recorded mortality), which is consistent with predation by terrestrial predators, such as birds or mammals. Indeed, the radio telemetry efforts in 2019 allowed to confirm two events of bird predation and one of mammal predation, all of which occurred within close proximity of the release site (c. 100 metres) and where tags were found on the river bank. The birds which are likely to predate on migrating smolts in these rivers are the grey heron (*Ardea cinerea*) and the great cormorant (*Phalacrocorax carbo*), the latter having markedly increased in numbers during the 90s (Conde, Filgueiras, & Malde, 2006). As cormorants are likely to shed tags away from the river (Jepsen, Klenke, Sonnesen, & Bregnballe, 2010), the tags found with no bite marks on the river bank have most likely been ingested by a heron. As for mammal predators, the main native predator of Atlantic salmon smolts in the rivers Tea and Minho is the Euroasian otter (*Lutra lutra*). However, American mink (*Neovison vison*) was also introduced in this area in the late 1980s (presumably escaping from fur farms in the south of Galicia; Vidal Figeroa & Delibes, 1987), and is currently expanding through the North of Portugal (Rodrigues et al., 2014). Exotic predators (such as the American mink; Heggenes & Borgstrøm, 1988) and predators whose numbers are rising markedly (such as cormorants; Jepsen et al., 2019; Källo, Baktoft, Jepsen, & Aarestrup, 2020) pose an additional pressure for Atlantic salmon smolts, as they increase the total number of predators present in the ecosystem and, therefore, the likelihood of predator-prey encounters.

The results from 2018 indicate that some smolts appear to be predated close to the River Minho's estuary, with the predator then moving back upstream following the water path. This most likely indicates predation by larger fish or otters. Sea bass (*Dicentrarcus labrax*) are known to be present in the Minho estuary, but since salt-water only intrudes up to 10 km inland (Moreno et al., 2005), it is unlikely that sea bass moved 20–30 km inland. As such, the only fish likely to be able to eat an Atlantic salmon smolt and move that far inland are sea trout (*Salmo trutta*). It is also important to note that otters' home ranges tend to remain below 20 km (Erlinge, 1967; Néill, Veldhuizen, de Jongh, & Rochford, 2009) and, as such, it is unlikely that the three tags which moved more than 20 km upstream were ingested by otters. Ultimately, further research would be required to be able to individually identify the predator(s) responsible for these upstream movements.

The causes behind a large proportion (66%) of the recorded mortality remain unknown. Pinpointing the sources of mortality with greater accuracy and determining whether or not there is an anthropogenic driver behind this mortality would allow a better assessment of management actions aiming to stop the decline of this strained population. This is particularly relevant considering that an increase in the number of smolts delivered to sea is likely to lead to a direct increase in the number returning adults (Crozier & Kennedy, 1993; Milner et al., 2003). The use of transmitters that can detect predation events (Daniels, Sutton, Webber, & Carr, 2019), which allow for a more accurate determination of the moment of predation, could prove a valuable method to further investigate the fates of those fish whose tags end up laying on the bottom for extended periods of time or start recording long upstream movements. These tags would also allow to confirm if the tag had passed through the gastrointestinal tract of predators before becoming stationary and allow for potential manual tracking of the predator while the tag is still inside it, to help identifying the predator. Similarly, quantitatively determining if fishing gear deployed during migration periods (of both juvenile and adult salmon) has an impact on the fish survival could also prove highly relevant for local management plans.

4.3 | Migratory behaviour

The tagged Atlantic salmon smolts showed behavioural patterns similar to that reported for other salmon populations in Europe. Specifically, the fish showed a tendency to move during the night period, with speeds increasing with proximity to the sea (as reported in other studies, e.g. Aarestrup et al., 2002; Moore et al., 1995; Thorstad et al., 2012).

4.4 | Considerations

When interpreting the results from this study, it is important to consider that telemetry methods have the inherent risk of recording the behaviour of a predator that has eaten the target fish (Gibson, Halfyard, Bradford, Stokesbury, & Redden, 2015; Klinard, Matley, Fisk, & Johnson, 2019). Tag ingestion by a predator is usually recognisable, as the tag starts recording unexpected behaviour (e.g. swimming long stretches upstream, stopping at a specific area, or going through multiple arrays undetected). However, should the predator's behaviour mimic the expected behaviour of an Atlantic salmon smolt, it would not be possible to detect the predation event, which would in turn lead to an erroneous fate assignment for the originally tagged fish. Such situations would lead to an overestimation of survival, which in turn reinforces the conclusions drawn from the recorded results (i.e. low survival of seaward migrating Atlantic salmon smolts).

Alternatively, a tagged fish could potentially pass through the last ALS array undetected. Should this happen, this fish would erroneously be classified as having died in the study area, when in fact it migrated out. The probability of this event depends on the efficiency of the last arrays, which can be challenging to measure. In 2017 and 2018, comparing the tags detected at the two ALS composing the last arrays revealed high estimated efficiency values, which reduces the risk of the issue mentioned above. In 2019 it was not possible to calculate an efficiency for the second radio station. As such, the recorded survival in this year corresponds to a minimum estimate.

5 | CONCLUSION

This study revealed that the seaward migration of Atlantic salmon smolts in the rivers Tea and Minho represents a hazardous period, with high mortality originating from various sources. Considering the historic decline of this population, it is urgent that we deepen our understanding of this population. Further studies in other tributaries of the River Minho accessible to Atlantic salmon (i.e. below the Frieira dam) will likely enable a more detailed assessment of the current conditions of this river's Atlantic salmon population.

The Atlantic salmon population of the River Minho is of high conservation and scientific relevance, as it may hold vital information regarding how the species is coping with climate change. Being the southernmost persisting Atlantic salmon population, this population is likely suffering the most with the warming temperatures and can be used to predict future shifts in the remaining populations at higher latitudes. Ultimately, it is fundamental that the cooperation between Portugal and Spain towards the recovery of Atlantic salmon and other migratory species in the River Minho continues, so that the agreed management actions can lead to an actual improvement in the size and resiliency of this particular population.

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AUTHORS' CONTRIBUTION

HF, PC, NJ and KA conceived and designed the investigation. HF and PC performed fieldwork. HF analysed the data. PC, NJ and KA contributed materials, reagents and/or analysis tools. HF led the manuscript writing, with contributions from PC, NJ and KA.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Hugo Flávio https://orcid.org/0000-0002-5174-1197
Pablo Caballero https://orcid.org/0000-0002-2541-7684
Niels Jepsen https://orcid.org/0000-0003-0927-6823
Kim Aarestrup https://orcid.org/0000-0001-8521-6270

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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