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Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment

Hugo Flávio[1] | Richard Kennedy[2] | Dennis Ensing[3] | Niels Jepsen[1] | Kim Aarestrup[1]

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

[2]Agri-Food & Biosciences Institute, Bushmills, Northern Ireland

[3]Agri-Food & Biosciences Institute, Belfast, Northern Ireland

Correspondence
Hugo Flávio, National Institute of Aquatic Resources, Technical University of Denmark, Silkeborg 8600, Denmark.
Email: hdmfla@aqua.dtu.dk

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Abstract

The River Bush (Northern Ireland) is an index river for the estimation of Atlantic salmon, *Salmo salar* L., stock size, population dynamics and marine survival rates. Marine survival estimates are based on the number of smolts counted at a trap 3.5 km upstream of the river outlet. The survival from release to coastal inshore waters for acoustic-tagged smolts released at the Bushmills trap varied between 32% and 68%, with both year and brightness during river exit playing a significant role in explaining the variations in survival. This constitutes an important survival bottleneck. Contrary to true marine mortality, this significant loss of smolts in the river and nearshore environments could be reduced by focused management actions. More studies on other rivers, where smolts are enumerated above the head of tide, could further partition smolt and post-smolt mortality, help differentiate true marine survival and help understand fluctuations in adult returns.

KEYWORDS

avian predation, diel cycle, management opportunity, *Salmo salar*, seaward migration, telemetry

1 | INTRODUCTION

The process of smoltification and the transition from freshwater to the marine environment represents a critical phase of the Atlantic salmon, *Salmo salar* L., life cycle (Hoar, 1976), which has been associated with increased mortality rates (Halfyard, Gibson, Ruzzante, Stokesbury, & Whoriskey, 2012). Thorstad et al. (2012) reviewed the available literature on Atlantic salmon smolt migration and found that mortality was often higher in river mouths and estuaries than in riverine or coastal areas. During this phase, salmon smolts are particularly vulnerable to physical (e.g. predation, barriers; Aarestrup & Koed, 2003; Handeland, Järvi, Fernö, & Stefansson, 1996; Jepsen, Klenke, Sonnesen, & Bregnballe, 2010) and chemical stressors (e.g. pollution; Thorstad et al., 2013). The downstream migration of Atlantic salmon smolts is believed to be highly influenced by light (e.g. Hansen & Jonsson, 1985; Riley, 2007), with the smolts preferring to move during the night (Aarestrup, Nielsen, & Koed, 2002; Moore, Potter, Milner, & Bamber, 1995). Nocturnal migration might allow the smolts to avoid visual predators (Ibbotson, Beaumont, Pinder, Welton, & Ladle, 2006; Thorstad et al., 2012). However, this preference to migrate during periods of darkness may change during the later parts of the migration period, when smolts, to a greater extent, move throughout the day (Thorstad et al., 2012).

The current context of decreasing Atlantic salmon stocks (ICES, 2018) has driven research efforts towards improving the ability to predict stock sizes and regulate both home-water fisheries and distant-water fisheries (Friedland et al., 2009; ICES, 2018; Potter et al., 2004). Modelling efforts rely on different parameters for predictions of pre-fisheries abundance, such as the number of returning adults or the smolt production or both (Crozier, Potter, Prévost, Schön, & Maoiléidigh, 2003; Potter et al., 2004). In particular, forecasting models rely, among other factors, on the number of smolts delivered to the sea. This number of outgoing smolts is most commonly estimated through mark–recapture methods (e.g. Cunjak & Therrien, 1998; Mäntyniemi & Romakkaniemi, 2002; Welch et al., 2008), partial trapping (e.g. Koed, Baktoft, & Bak, 2006; Lundqvist et al., 2010) or full trapping of the smolts migrating downstream (e.g. Armstrong, McKelvey, Smith, Rycroft, & Fryer, 2018; Jonsson, Jonsson, & Hansen, 1998; Shearer, 1990). Rivers where both the smolt run and the number of returning adults are estimated enable a direct comparison between the freshwater output and the adult return rates. These rivers play a crucial role in describing the developments in the Atlantic salmon stocks throughout their distribution range and under different fishing pressures. Rivers where this type of extensive work is done have been coined "index" rivers. However, there is an inherent risk of bias in these methods: smolts may be lost (e.g. predated) between the counting/estimation event and reaching the sea. Similarly, adults may be lost after returning to the river but before being counted.

One such index river is the River Bush (Northern Ireland). In this river, estimates of the number of smolts delivered to sea are based on direct counts made at a trap approximately 3.5 km upstream of the outlet to the sea (Crozier & Kennedy, 1993, 1994), with a parallel trap being used to count the returning adults. Processing of captured fish is mostly performed during the day, and also at night during the peak smolt emigration. Once counted, the fish are released to a recovery chamber that has a free opening to the river, for voluntary onwards migration. However, local observations suggest that smolts might suffer from avian predation pressure downstream of the trap (Kennedy & Greer, 1988), which might lead to overestimations of smolts delivered to sea. Additionally, seals, *Phoca vitulina* L., and harbour porpoises, *Phocoena phocoena* (L.), are sporadically sighted at Runkerry Bay, into which the river drains.

In comparison to more typically studied rivers that have long estuaries and fjords (e.g. Dempson et al., 2011; Hedger et al., 2008; Moore et al., 1995; Økland et al., 2006; Thorstad et al., 2012), the River Bush undergoes a transition from freshwater to full salt water over the length of a few metres. This absence of a gradual estuary represents one of the most abrupt transitional environments potentially experienced by emigrating smolts.

Exploring survival rates during early smolt migration may reveal bottlenecks that can be addressed more easily than factors operating at sea (Klemetsen et al., 2003). Furthermore, an increase in the number of smolts successfully reaching the sea is likely to translate to an increase in the number of returning adults, as there is a direct correlation between smolt output and returning adults (Crozier & Kennedy, 1993; Jonsson et al., 1998; Milner et al., 2003).

Using acoustic telemetry data from 2014, 2017 and 2018, interannual fluctuations in migration survival for Atlantic salmon smolts migrating through the River Bush were explored, including the survival from the trap to the river outlet and to the nearshore marine environment. As a secondary aim, smolts exiting the River Bush during the hours of darkness were assessed to determine whether they had an increased probability of survival compared to smolts leaving the river during daylight hours.

2 | METHODS

2.1 | Study area

The River Bush has a catchment area of approximately 340 km^2 and runs for 67 km before reaching the Atlantic Ocean, along the Antrim coast (Northern Ireland, Figure 1). This river has no estuary, opening directly to the sea across a stony beach (henceforth referred to as river outlet). During the 1970s, the Department of Agriculture for Northern Ireland set up traps at Bushmills, around 3.5 km upstream of the river outlet (55°12'10"N; 06°31'25"W). The same department also controls angling on the river through the provision of day tickets. Downstream migrating smolts are diverted from the River Bush

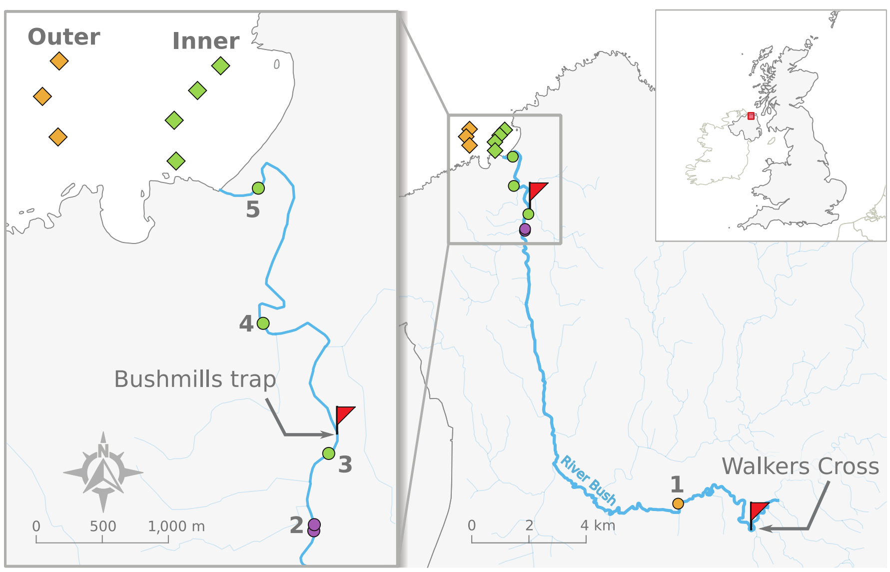

FIGURE 1 The River Bush in the northern coast of Northern Ireland. Diamonds represent the Runkerry Bay automatic listening stations (ALS), circles represent the river ALS, and flags represent the release sites. River arrays/ALS were numbered for ease of reference, while the Runkerry Bay arrays are referred to as "inner" or "outer." Orange ALS were operational during 2017 and 2018, purple ALS operational only during 2017 and green ALS were operational during the three studied years [Colour figure can be viewed at wileyonlinelibrary.com]

into a Wolf trap (Wolf, 1951) and are released back into the river after being counted.

2.2 | Experimental fish

Wild migrating smolts were captured at the Bushmills trap in all years and through fly-fishing upstream of Walkers Cross in 2014 and 2017. In 2018, 25 smolts captured at the Bushmills trap were transported to Walkers Cross and tagged and released there, as it was not possible to capture smolts through fly-fishing.

At capture, fish were selected for tagging based on morphological indicators (e.g. silvery appearance, enlarged eyes). Fork length (L_f) was measured for the selected smolts. Smolts with L_f <13 cm were not considered for tag implementation to ensure a low tag/body weight ratio.

2.3 | Tagging procedure

Atlantic salmon smolts were anaesthetised (2–4 min) in a 100 mg/L MS-222 solution until operculum rate became slow and irregular. The acoustic transmitter was inserted into the body cavity through a mid-ventral incision, posterior to the pelvic girdle. The incision was closed with one single absorbable suture (vicryl 4-0). Before release, fish were held in a tank with fresh stream water until full recovery. The duration of the procedure varied between 1 and 2 min, and the recovery time was 2–5 min. Surgical implantation was performed by an experienced fish surgeon in accordance with the guidelines described in the project licence PIL 2761 (U.K. Home Office Animals Scientific Procedures Act). All tagged smolts were released during the day at the same time, after showing full recovery from the handling and tagging procedure. In the Bushmills trap, the smolts were released into a recovery tank that has an exit pipe back into the river. At Walkers Cross, the smolts were released directly back into the river. All tagged fish appeared to be in good health at release. In 2014, the acoustic transmitters were Vemco V7-2L tags, weighing 1.6 g in air and 0.75 g in water. In 2017 and 2018, the acoustic transmitters used were Thelma 7.3 mm tags, weighing 1.9 g in air and 1.2 g in water. The transmitters had an expected operation time of 110 and 150 days (for Vemco and Thelma tags, respectively).

2.4 | Fish tracking

To enable the assessment of differences in mortality rates on river stretches both downstream and upstream of the Bushmills trap, tagged smolts were released both at the trap and at Walkers Cross, a site located 21 km upstream of the trap (Figure 1).

Automatic listening stations (ALS, Vemco VR2W) were distributed along the River Bush (in five strategic positions, listed in Figure 1), and in Runkerry Bay, into which the river drains. In 2014, four ALS were deployed in one single array covering the extent of the bay (referred to as the "inner bay array"). In 2017 and 2018, a second array with three ALS (Vemco VR2AR) was deployed further offshore, covering the area through which most smolts appear to migrate to the ocean (referred to as the "outer bay array"; Figure 1). This allowed the determination of the number of fish that: (a) disappeared before reaching the river outlet; (b) reached the river outlet but failed to reach the sea; and (c) successfully crossed the bay ALS arrays. In 2017 and 2018, an ALS was deployed 5 km downstream of the Walkers Cross release site to allow an earlier detection of migrating smolts.

ALS detection efficiency was measured by performing reverse checking of detected fish (Aarestrup et al., 2015). Specifically, inter-array ALS efficiency was measured by comparing the smolts detected in a given ALS array with the smolts detected in the arrays following it. In 2017 and 2018, the outer bay ALS array was used as a reference for the efficiency of the inner bay ALS array. In 2014, this calculation could not be performed due to the absence of the outer bay ALS array. Therefore, survival estimates in 2014 correspond to a minimum estimate.

2.5 | Data analysis

2.5.1 | Acoustic data validity

Raw acoustic data were checked for unlikely behaviour, such as back and forth movements (e.g. being detected in the river after being detected at the bay) or unrealistic speeds (i.e. moving from one ALS array to another much faster than the remaining tagged smolts). Unlikely events were analysed in detail so that flawed detections could be found and removed.

2.5.2 | Effects of year and release site on survival

After confirming the data validity and the absence of collinearity among the explanatory variables, a Bernoulli generalised linear model (GLM) with logit link function (i.e. a logistic regression) was applied to test for effects of year and release site on survival probability, measured as registration in one of the Runkerry bay ALS arrays. The model's equation is as follows:

$$Survived_i \sim Bernoulli\left(\mu_i\right)$$
$$E\left(Survived_i\right) = \mu_i$$
$$logit\left(\mu_i\right) = Year_i + ReleaseSite_i$$

Stepwise goodness-of-fit model selection was performed to determine which covariate combination would produce the best model. Post hoc analyses were performed using the multcomp package (Hothorn, Bretz, & Westfall, 2008) in R (R Core Team, 2018).

Mortality rates per kilometre (m/km) were calculated for both release sites as the quotient of the proportion of smolts lost in the river by the distance from the release site to the most seaward river

TABLE 1 Number of smolts released at each location and overall, per year. Fork length (L_f) values are displayed in millimetres

	Bushmills trap		Walkers cross		Overall	
	n	Avg. L_f (sd)	*n*	Avg. L_f (sd)	*n*	Avg. L_f (sd)
2014	28	159 (8.5)	12	145 (12.1)	40	155 (11.6)
2017	69	153 (9.6)	30	148 (10.7)	99	151 (10.2)
2018	25	159 (8.4)	25	157 (10.9)	50	158 (9.7)

ALS station (3.2 km for smolts released at the Bushmills trap and 24.5 km for smolts released at Walkers Cross).

Additionally, for the smolts released at Walkers Cross, the following were also calculated:

- In 2014, m/km was calculated between release and reaching the river ALS 3 (21 km stretch).
- In 2017 and 2018, m/km was calculated between release and the river ALS 1 (5 km stretch) and between this ALS and the river ALS 3 (16 km stretch).

2.5.3 | Effect of river exit time on survival

Only smolts detected at river ALS 5 (approximately 300 m upstream of the river outlet) were considered for this analysis. For these smolts, the time of the last detection at river ALS 5 was matched to the sunrise/sunset times (extracted from www.sunrise-and-sunset.com/en/sun/united-kingdom/bushmills/) of the respective day to determine whether the smolt left the river during the day or during the night. Finally, a Bernoulli GLM with logit link function (i.e. a logistic regression) was applied to test for effects of day/night departure and year on survival probability, measured as registration in one of the bay ALS arrays. Year was included on this model to account for potential inter-year fluctuations. The model's equation is as follows:

$$Survived_i \sim Bernoulli\left(\mu_i\right)$$
$$E\left(Survived_i\right) = \mu_i$$
$$logit\left(\mu_i\right) = DepartureLight_i + Year_i$$

Stepwise goodness-of-fit model selection was performed to determine which covariate combination would produce the best model. Additionally, a Mardia–Watson–Wheeler test was applied to further confirm differences in in-river exiting time between surviving and lost smolts. All statistical analyses were performed in R version 3.5.1 (R Core Team, 2018).

3 | RESULTS

3.1 | Tagging period and smolt length

In 2014, 40 smolts were captured on 28 and 30 April. In 2017, 99 smolts were captured between 24 April and 9 May. In 2018, 50 smolts were captured on 24 and 25 April. Detailed average length values and number of smolts released per site are shown in Table 1.

TABLE 2 Collated detection efficiency in the different sections of the study area

	River (%)	Sea (%)	In-river (%)
2014	100	—	90.9–100
2017	100	92.5	18.5–96.2[a]
2018	100	92.3	93.8–100

Note: Efficiency ranges for the ALS positioned inside the river can be seen on the last column.

[a]The large efficiency range in 2017 was caused by a single faulty ALS, with the remaining river ALS ranging between 94.2% and 96.2% detection efficiency.

3.2 | Acoustic data validity and ALS efficiency

One single case of reversed movement (i.e. detection in the river estuary after detection at the bay) was found in 2017. Upon detailed analysis, the fish was considered to have succeeded in migrating out to sea and was then likely predated by a bird that moved within detection range of river ALS 5. Therefore, for the aim of this study, this fish was considered as a successful migrant.

Detection efficiency was high throughout the study (Table 2). During the three years, all smolts detected at sea had also been detected in the river. In 2017, three smolts were detected at the outer bay ALS array without being detected in the inner bay ALS array (92.5% efficiency). In 2018, this only happened for one fish (92.3% efficiency). Efficiency within river ALS was overall high, with the exception of river ALS 4 in 2017, where only 18.5% of the passing smolts were detected. However, this station had no impact on fate assignment, and thus, its low efficiency had little impact on the overall study results. The efficiency of the remaining river ALS in 2017 was always above 94%.

3.3 | Effects of year and release site on survival

In 2014, 70% of the tagged smolts successfully crossed the study area, while in 2017 and in 2018 that percentage was reduced to 39% and 26%, respectively (Table 3).

The process of model selection revealed that release site had no significant effect in the survival probability for the smolts migrating out of the River Bush. However, year had a significant effect (GLM, $\chi^2 = 18.61$, $p = 9.084e^{-5}$, Figure 2; Table 4). Post hoc analysis revealed

TABLE 3 Number of surviving Atlantic salmon smolts in relation to the total of smolts released for each release site and study year

	Bushmills trap	Walkers cross	Overall
2014	19/28 (68%)	9/12 (75%)	28/40 (70%)
2017	27/69 (39%)	12/30 (40%)	39/99 (39%)
2018	8/25 (32%)	5/25 (20%)	13/50 (26%)

Note: Survival was measured as detection in the Runkerry Bay ALS arrays.

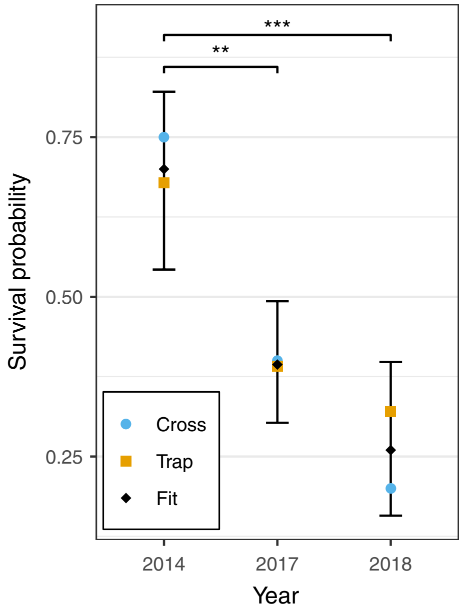

FIGURE 2 Effect of studied year on smolt survival probability. Smolts migrating in 2014 had a significantly higher survival probability than those migrating in both 2017 and 2018 (GLM, Tukey's Post hoc Test, $p < .005$ and $p < .0003$, respectively, represented by the '**' and '***' marks in the graphic). "Cross" shows the survival for the smolts released at Walkers Cross, "Trap" shows the survival for the smolts released at the Bushmills Trap, and "Fit" shows the combined survival, as estimated by the GLM [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Coefficients of the model testing for the effects of year on survival probability from release to the ALS arrays in Runkerry Bay

	Estimate	Std. error	Z value	Pr(>|z|)
Intercept	0.8473	0.3450	2.456	0.01406
Year 2017	−1.2781	0.4017	−3.182	0.00146
Year 2018	−1.8933	0.4722	−4.009	6.09e−05

that the year 2014 differed significantly from both 2017 and 2018 (GLM, Tukey's Post hoc Test, $p < .005$ and $p < .0003$, respectively).

3.3.1 | Mortality rates per kilometre

The mortality per km (m/km) differed greatly between release sites, with smolts released at the Bushmills trap consistently suffering

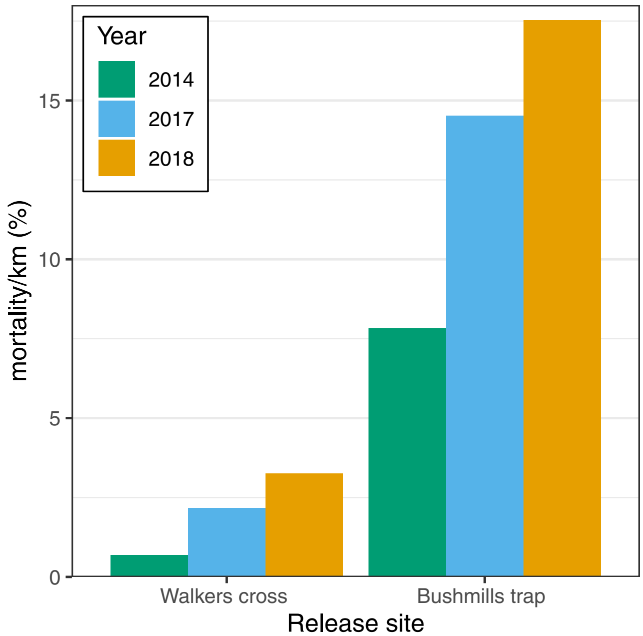

FIGURE 3 Mortality per kilometre (in percentage) for smolts released at the two sites. Smolts released at Walkers Cross must travel close to 24.5 km to reach the last river ALS while smolts released at Bushmills trap only need to travel approximately 3.2 km. The recorded differences seem to indicate a more hazardous environment downstream of the trap [Colour figure can be viewed at wileyonlinelibrary.com]

higher mortality per kilometre than those released at Walkers cross (Figure 3).

For the smolts released at the Bushmills trap, the major fraction of mortality occurred before reaching the first ALS (i.e. river ALS 4, approximately 1.4 km downstream). In 2014, the seven smolts lost in the river did not reach the first ALS. In 2018, this was the case for 13 out of the 14 smolts lost in the river. In 2017, this calculation could not be performed due to the low efficiency of river ALS 4 during that year.

For the smolts released at Walkers Cross, in 2014, only one out of 12 released smolts was lost before reaching river ALS 3 (0.4% m/km). In 2017, six of 30 released smolts disappeared before reaching river ALS 1 (4% m/km) and eight disappeared in the remaining stretch until river ALS 3 (2.1% m/km). In 2018, 13 of the 25 released smolts disappeared before reaching river ALS 1 (10.3% m/km) and a further four smolts disappeared before reaching river ALS 3 (2.1% m/km).

3.4 | Effect of river exit time on survival

In total, 96 smolts were detected at river ALS 5 (i.e. the last river ALS) across the three years (31 in 2014, 50 in 2017 and 15 in 2018), constituting the data pool used for the day/night river exit GLM. The process of model selection revealed that, for the smolts that reached river ALS 5, year had no significant effect in the probability of reaching the bay ALS arrays (i.e. there was no significant interannual

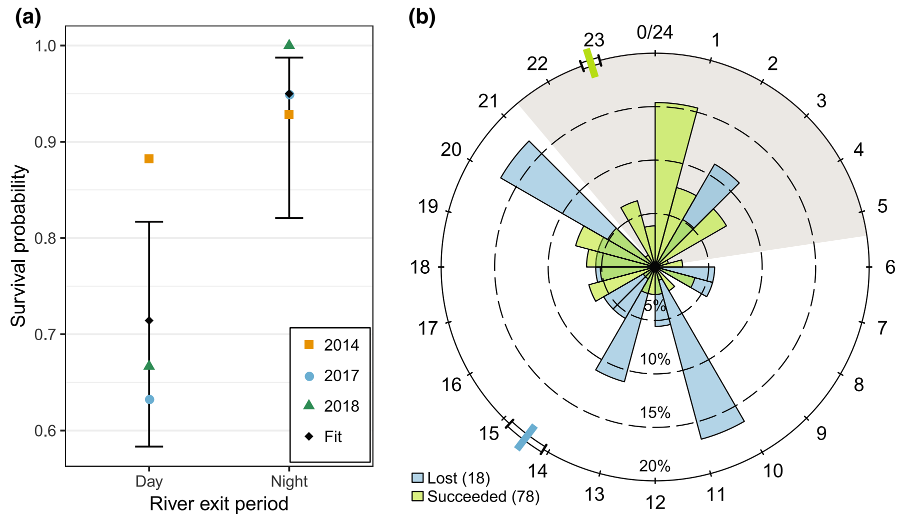

FIGURE 4 (a) Effect of day/night river exit on smolt survival probability. Detailed survival probabilities for each year are also presented. (b) Departure time for smolts that succeeded at reaching the bay automatic listening stations (ALS) arrays or were lost. Coloured lines on the outer circle indicate the mean value for each group, and the respective ranges show the SE. Each group's bars sum to 100%. The number of smolts in each group is presented between brackets in the legend. The shaded portion of the circle shows the average sunset-to-sunrise hours for the study period [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 5 Coefficients of the model testing for the effects of brightness on survival probability between the River Bush's outlet and the ALS arrays in Runkerry Bay

	Estimate	Std. error	Z value	Pr(>|z|)
Intercept	0.9163	0.2958	3.098	0.00195
Night	2.0281	0.7834	2.589	0.00963

variation in nearshore survival). However, day/night river exit had a significant effect on survival probability (GLM, $\chi^2 = 9.77$, $p = .0018$, Figure 4a; Table 5). On average, surviving smolts were last detected at the river at around 23:00, while smolts that were lost left the river at around 14:30 (Figure 4b). The Mardia–Watson–Wheeler test revealed that there was a significant difference in exit time of day between surviving and lost smolts ($W(2) = 6.8269$, $p = .0329$), which is in accordance with the GLM results.

4 | DISCUSSION

4.1 | Interannual fluctuations in survival

The analyses revealed a decreasing pattern in survival probability over the three years, with smolts from 2014 having a significantly higher chance of reaching the Runkerry Bay ALS than those from 2017 and 2018. The flow and temperature profiles of the study years did not reveal any extreme events (e.g. floods, droughts) that would be likely to drive these differences. However, flow was higher near the peak of the migration period for the tagged smolts in 2014 (see Supporting Information). This higher flow may have enhanced smolt survival either directly by the following: (a) a current assisted increase in net ground speed reducing the time in the river; (b) reducing visibility in the water column throughout the lower river; and/or (c) deepening the river mouth's channel section, or indirectly by increasing the number of smolts simultaneously migrating downstream (Hvidsten, Jensen, Vivås, Bakke, & Heggberget, 1995; Jonsson & Jonsson, 2009). The data suggest that the factors influencing survival operated both upstream and downstream of the trap. In 2014, a higher survival rate was also observed between Walkers Cross and the trap at Bushmills, just as the lower survival rates in 2017/2018 in the lower river were also reflected in the upstream part of the river.

In the three study years, most of the mortality for the tagged smolts released at the Bushmills trap occurred between the trap and the first ALS. These losses likely reflect predation and indicate major predation pressure on this river stretch. This predation pressure could be an indicator of predator habituation, caused by the recurrent smolt supply downstream from the trap outlet. This tendency for predators to aggregate at locations with higher prey abundance is expected and has been reported in numerous studies (e.g. Holling, 1959; Jepsen, Pedersen, & Thorstad, 2000; Kennedy, Rosell, Millane, Doherty, & Allen, 2018; Koed, Jepsen, Aarestrup, & Nielsen, 2002). During the study period, there was a considerable increase in the size of the local cormorant colonies, with the number of apparently occupied nests raising from 165 in 2014 to 240 in 2017 (Allen et al., 2015, 2018). This could partially explain the decreasing smolt survival in 2017 and 2018, as cormorants have been noted to represent strong predation pressure on migrating salmonids elsewhere (Jepsen, Flávio, & Koed, 2019). The potential effects of avian predators will be discussed in detail in a subsequent section.

The absence of an effect of release site on survival probability, together with the calculated m/km per release site, indicates a considerably higher predation pressure in the final 3.5 km river stretch. In a study with radio tagged Atlantic salmon smolts, Koed et al. (2006) reported higher mortality rates as smolts entered the estuary area of the River Skjern, as opposed to the 20-km stretch from release to the river mouth. Similarly, Serrano, Rivinoja, Karlsson, and Larsson (2009) reported high initial estuarine loss (35%–40%) for smolts migrating out of the River Testebo (Sweden). It is important to note that the River Bush differs from both examples above as it lacks a true estuary with a temperature and salinity gradient.

High smolt mortality in the final stretches of the river is particularly relevant if it is not accounted for during the estimation of marine survival and return rates. In the River Bush, the estimation

TABLE 6 Overview of the distance between the smolt counting site and the head of tide (HoT) for the rivers for which marine survival estimates of wild fish are given in the 2019 WGNAS report

River	Distance to HoT (km)
Imsa	0.1
Burrishoole	0.1
Corrib	0.1
Scorff	0.3
Ellidaar	0.7
North Esk	2.0
Bush	**3.5**
Nivelle	7.6
Vesturdalsa	8.1
Oir	8.2
Froome	9.1
Tamar	13.0
Bresle	16.1
Dee	40.0

Note: The rivers have been sorted by ascending distance to HoT, and the River Bush is highlighted in bold to show its positioning relative to the remaining rivers. Distances were rounded to the nearest hundredth metre.

of the number of smolts delivered to sea has historically been performed by counting the smolts passing through the trap (Crozier et al., 2003; Potter et al., 2004). Similarly, smolt counting facilities in 13 other rivers currently or historically used for estimation of marine survival by the Working Group on North Atlantic Salmon (WGNAS) are located between 100 m and 40 km upstream of the respective head of tide (Table 6). Importantly, in many of these rivers, the smolts must still successfully cross bays, lagoons or fjords before reaching the open sea. The results show not only that a considerable portion of the smolts may be lost before reaching the sea but also that the pressure in lower river stretches can be variable among years. High mortality in the lower river, below the smolt trap, could lead to an overestimation of marine mortality. This is of particular importance for index rivers used for stock assessments of Atlantic salmon and illustrates the need to understand the sources, extent and variability of freshwater mortality after the smolt monitoring location.

In 2014 and 2017, 28,814 and 18,466 migrating Atlantic salmon smolts were counted at the Bushmills trap. The estimated marine survival for one-sea-winter adults for the smolt cohorts of 2014 and 2017 was of 2.9% and 3.2% (i.e. 833 and 588 returning adults, respectively). However, by subtracting the mortality for the smolts released at the Bushmills trap for 2014 and 2017, the marine survival estimates would raise to 4.3% and 8.1%, respectively. Accounting for the number of smolts lost between the Bushmills trap and the sea ALS arrays shows that marine survival rates previously estimated to be similar could actually differ considerably from each other (nearly doubling from 2014 to 2017). Ultimately, this variable mortality pressure in the river stretch downstream of the smolt trap may help explain the potential variability in the overall return rates and improve the accuracy of marine survival estimates.

4.2 | Transitioning from river to sea

The tidal zone on the River Bush is extremely narrow, effectively limited to a single riffle where the channel disgorges across a steep, stony beach. The lack of any salinity or temperature gradient in the water column approaching the transitional zone, in conjunction with the steep nature of the river mouth, could imply that emigrating smolts in the River Bush have little or no environmental cue to signal the approach of the sea before dropping directly into salt water (Kennedy & Crozier, 2010). This may help explain the apparent random distribution in transitional timing found in this study, with the River Bush smolts leaving the river both during day and night periods. However, smolts attempting to cross the river–sea transition area during the night were significantly more likely to reach the Runkerry Bay ALS arrays (i.e. successfully reaching the sea). This result is in accordance with the observation of avian predators aggregating around the River Bush mouth during each study year, with cormorants, *Phalacrocorax carbo* (L.), being particularly evident during the smolt run period (Kennedy & Greer, 1988). Large flocks of seagulls (mostly *Larus argentatus*, Pontoppidan) were also noted standing in the current, facing upstream, and were on occasions observed to capture smolts from the shallow water (Peter Irvine, *pers. com.*) indicating the capability to opportunistically capture smolts when environmental conditions were suitable. These results also seem to indicate a limited predation pressure from seals and porpoises, which are likely to hunt both during day and night. Further, very few tagged fish which disappeared at the transition area in the River Bush were subsequently detected again, which is consistent with the complete removal of the tag by an avian predator.

The morphology of the River Bush outlet is highly dynamic, often changing shape, depth and course after heavy spate or storm events. In 2014, the river outlet was a single channel with the shallowest sections varying between 10 and 20 cm depth. In 2017 and 2018, the river outlet bifurcated across the beach and widened, with a mean depth of less than 5 cm in some places. The transition in depth between a relatively shallow river outlet and deeper coastal waters may also represent a hazardous navigation for migrating smolts. For example, Jepsen, Holthe, and Økland (2006) showed that the highest predation rate on tagged Atlantic salmon smolts in a coastal river mouth occurred where the depth changed rapidly from one to over 25 metres. By contrast, Lothian et al. (2018) demonstrated no predation loss on tagged smolts across a short (1 km) and shallow transitional zone on the River Deveron (North East Scotland), indicating that predation pressure may vary widely between rivers.

4.3 | Considerations

When performing telemetry studies, there is a risk that the recorded behaviour might not be that of the target animal, but of a predator having eaten the first (Gibson, Halfyard, Bradford, Stokesbury, & Redden, 2015). The main known sources of predation in the River Bush are mammals (i.e. otters) and birds (i.e. herons, cormorants, seagulls). In the case of predation by otters, it is unlikely that an otter would come within range of the Runkerry Bay ALS; thus, the recorded fate of the respective smolt would remain the same (i.e. died during migration). For the case of avian predation, particularly by seagulls or cormorants, it is possible for the predator to move within range of one or more of the ALS arrays after predating a smolt, leading to flawed detections. This would be particularly relevant if a smolt was predated in the lower river stretches and the predator subsequently moved within range of the Runkerry Bay ALS. Although special attention was paid to this when analysing the detected movements of the studied smolts, exceptional cases where the predator mimics the expected smolt behaviour would be undetectable. This behaviour, even if unlikely, would lead to an overestimation of survival, which would reinforce the conclusions drawn from the recorded results.

It is also important to note that it was only possible to perform manual tracking on the river stretch downstream of the trap. This showed that most of the missing tags had been removed from the river, with no tags found stationary on the river bed in 2014, and only five and three tags found stationary in 2017 and 2018, respectively. It was not possible to determine whether the smolts released from Walkers Cross and had never moved downstream of the trap had remained in the river, outside the range of the deployed ALS (either alive or dead). However, it is not expected that the tagging and handling would cause such a disturbance that would overturn the smoltification process and the migration instinct, and thus, it was assumed that those smolts have most likely been predated or have otherwise died due to another natural cause.

Lastly, it is relevant to consider that the transportation of the smolts from the Bushmills Trap to the release site at Walkers Cross in 2018 may have had a detrimental effect on their migration performance. Iversen, Finstad, and Nilssen (1998) found that capturing, loading and transporting Atlantic salmon smolts could lead to amplified stress responses, with the plasma cortisol levels of transported fish remaining high for periods over 24 hr. Therefore, it is possible that the estimated mortality rates for smolts released at Walkers Cross in 2018 was overestimated in comparison with the remaining years where smolts were captured locally.

5 | CONCLUSION

The marine survival of River Bush Atlantic salmon is monitored annually based on a full census of each emigrating smolt cohort, obtained through a smolt trap count, in conjunction with counts of subsequent returning fish from an adjacent adult trap. The current study demonstrated that the survival of smolts tagged with acoustic tags, released from the Bushmills trap, to coastal inshore waters varied between 68% (19 out of 28 smolts) in 2014 and 32% (8 out of 25 smolts) in 2018. Contrary to oceanic marine mortality, upon which it is difficult to act, this large percentage of smolts disappearing in the last river stretch could likely be reduced by focused management actions. For example, assuming that most of the smolt loss downstream of the Bushmills trap is caused by visual predators, ensuring the release of smolts during hours of darkness may reduce any initial predation. Similarly, management actions aimed at relieving the predation pressure on smolts migrating through the river outlet could lead to an increase in the number of smolts that truly reach the sea. This may lead to an increase in the number of smolts surviving to the sea and is likely to result in a direct increase in the number of returning adults, since marine survival is considered density-independent. Future research aimed at better understanding the mechanisms driving the recorded mortality for smolts migrating out of the River Bush would likely prove essential to improve the efficacy of local management actions and, thus, increase the number of smolts delivered to the sea.

More studies on other rivers, where the estimation of the number of smolts delivered to sea is performed similarly to River Bush, could help shed light on potential fluctuations in marine survival across populations. Importantly, discovering survival bottlenecks in the nearshore environments provides a crucial opportunity for targeted management actions that are less costly and more likely to succeed on a shorter timescale than actions aimed at ocean zones.

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ORCID

Hugo Flávio https://orcid.org/0000-0002-5174-1197
Richard Kennedy https://orcid.org/0000-0002-2239-6136
Dennis Ensing https://orcid.org/0000-0002-9639-7692
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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