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Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment

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Abstract

Long-distance migration of Atlantic salmon (*Salmo salar*) is known to result in high levels of mortality. For a species experiencing global population decline, it is thus vital to better understand migration behaviour, both in the river and marine stages. Atlantic salmon smolts (n = 50) were tracked using acoustic telemetry in the River Deveron, Scotland, and adjacent coastal area. Higher rates of mortality were observed in the river (0.77% per km) than the early marine stage of migration (0.0% per km). Mortality likely resulted from predation. Higher swim speeds were recorded in the early marine stage compared with the river (marine = 7.37 ± 28.20 km/day; river = 5.03 ± 1.73 km/day [mean ± *SD*]), a potential predator avoidance behaviour. The majority of smolts leaving the river did so in darkness and on a flooding tide. Overall river and marine migration success were linked to nights of lower lunar brightness. Marine migration speed decreased with increasing environmental noise levels, a finding with implications for fisheries management. The migration pathway in the early marine environment did not follow obvious geographical features, such as the coastline. Thus, we suggest that early marine environment pathways are more influenced by complex water currents. These findings highlight factors that influence smolt migration survival and behaviour, areas on which future research should focus.

KEYWORDS
acoustic, biotelemetry, marine, migration, salmon, smolt

1 | INTRODUCTION

Migration is a common life history strategy in animals (Alerstam, Hedenstrom, & Akesson, 2003; Roff, 1988). It is the directed movement of individuals from one habitat to another, enabling the exploitation of resources in a wider area to gain an evolutionary advantage (Alerstam et al., 2003; Dingle & Drake, 2007; Roff, 1988). The anadromous migration of Atlantic salmon (*Salmo salar*) from freshwater to saltwater enables individuals to access high ocean productivity, enabling increased growth, which results in higher fecundity and greater reproductive success (Fleming, 1996; Klemetsen et al., 2003). However, migration carries significant costs for the migrating individual, including increased energy expenditure, exposure to novel pathogens, predators and anthropogenic influences (Alerstam et al., 2003; Standen et al., 2002). As wild Atlantic salmon populations decline, with marine stage survival decreasing (e.g. from 12% to 2% in the last decade [Parrish, Behnke, Gephard, McCormick, & Reeves, 1998; Hannesson, 2003; Drenner et al., 2012; Thorstad, Whoriskey, et al., 2012]), a greater understanding of the migration process is required for effective management.

The seaward migration of Atlantic salmon begins with a transformation known as smolting. This results in behavioural, morphological and physiological changes in preparation for marine life (Hoar, 1976; Klemetsen et al., 2003; McCormick, Hansen, Quinn, & Saunders, 1998; Metcalfe, Huntingford, Graham, & Thorpe, 1989; Thorstad, Whoriskey, et al., 2012). The majority of Atlantic salmon migrate from rivers in spring and remain at sea for at least one winter (referred to as one sea winter fish), although individuals can remain at sea for a number of years (referred to as multi sea winter fish; Klemetsen et al., 2003), before returning to their natal rivers in the summer. Migration in this species allows individuals to access high-quality feeding areas. However, very little is known about the details of migration to marine feeding grounds, except that the movement to and from these feeding areas is typified by very high rates of mortality (Friedland, Hansen, Dunkley, & MacLean, 2000; Hvidsten & Møkkelgjerd, 1987; Jepsen, Holthe, & Økland, 2006; Thorstad, Whoriskey, et al., 2012; Vollset, Mahlum, Davidsen, Skoglund, & Barlaup, 2016). Although our knowledge of these migrations in recent years has improved, further information on the variables contributing to high mortality is still required.

The advent of telemetry, the tracking of animals using unique identifier tags, has enabled us to examine migration behaviour of Atlantic salmon in more detail (Drenner et al., 2012; Hussey et al., 2015). Studies on the seaward migration in Atlantic salmon smolts have shown that the migration is instigated by photoperiod and water temperature, but that timing of these cues may vary between catchments (Økland et al., 2006; Thorstad, Whoriskey, et al., 2012). Smolts initially exhibit a diel migration pattern, preferring to travel in hours of darkness. This is presumed to be a predator avoidance strategy (McCormick et al., 1998; Thorstad, Whoriskey, et al., 2012), but this effect becomes less distinct towards the end of the annual migration period when later emerging smolts actively swim with the river flow in hours of light and darkness (Hansen & Jonsson, 1985; Hvidsten, Jensen, Vivås, Bakke, & Heggberget, 1995; Thorstad, Whoriskey, et al., 2012).

To date, telemetry studies on riverine outmigration of smolts have reported considerable variation in migration mortality rate, ranging from 0.3% to 7.0% per km (Thorstad, Whoriskey, et al., 2012). River mortality is thought to be mainly the result of predators, for example pike (*Esox lucius*; Thorstad, Whoriskey, et al., 2012), Eurasian otter (*Lutra lutra*; Carss, Kruuk, & Conroy, 1990), American mink (*Neovison vison*; Heggenes & Borgstrom, 1988) and cormorants (*Phalacrocorax carbo*; Koed, Baktoft, & Bak, 2006; Jepsen, Klenke, Sonnesen, & Bregnballe, 2010). River motility may also be the result of environmental factors and anthropogenic obstacles, such as dams (Rand et al., 2006; Welch et al., 2008).

The relatively few studies of marine migration in Atlantic salmon have focused on long, deep estuaries and fjords (Dempson et al., 2011; Hedger et al., 2008; Økland et al., 2006) and have shown mortality rates ranging from 0.6% per km to 36% per km in estuaries and from 0.3% per km to 3.4% per km in the nearshore marine zone (Thorstad, Whoriskey, et al., 2012). Although Jepsen et al. (2006) noted high mortality at the mouth of the River Eira, Norway, few studies have investigated smolt behaviour around the river mouth and immediate marine environment in a system that discharges straight into the open sea. In addition, many previous migration studies have used hatchery-reared Atlantic salmon smolts because of the ease of obtaining them, and because their larger sizes are more reliable for tagging in comparison with wild smolts (Fried, McCleave, & Labar, 1978; Hansen & Jonsson, 1985; Thorstad et al., 2004; Vollset et al., 2016). Hatchery-reared smolts show differences in physiology and behaviour compared with wild smolts resulting from the differing mortality rates and selection pressures to which they are exposed (Pedersen, Koed, & Malte, 2008; Urke, Kristensen, Ulvund, & Alfredsen, 2013). They are therefore not a reliable proxy for understanding wild Atlantic salmon behaviour.

The main aim of the study presented here was therefore to quantify the speed, mortality and directional swimming behaviour of wild Atlantic salmon smolts in the coastal marine environment through the use of acoustic telemetry. A secondary aim was to quantify the riverine mortality rate of outward migrating smolts in a river system, adding to the current knowledge of river migration.

2 | MATERIALS AND METHODS

2.1 | Study site

The River Deveron, Northeast Scotland, has a catchment of 1,226 km^2 and is 96 km in length, flowing through Aberdeenshire and draining directly into the Moray Firth area through a bay at Banff (57°39′55.1″N, 2°30′48.2″W; Figure 1). The bay at Banff is approximately 1.3 km at its widest and has a maximum depth of approximately 8 m. The tidal zone of the River Deveron is restricted to the bay and approximately 1 km upstream of the river mouth. The bay has a mixed-semidiurnal, tidal pattern with two differing high and low tide events each day.

2.2 | Smolt capture and tagging procedure

Atlantic salmon smolts were caught using a rotary-screw trap located in the upper reaches of the River Deveron (57°02′44.1″N, 3°01′55.2″W) across 3 days in 2016; 14th, 18th and 21st April. Fifty smolts >120 mm in length (representative of the mean length distribution of fish in the Deveron) were selected for surgical implantation of a coded acoustic transmitter (7.3 × 18 mm, weight in air/water of 1.9/1.2 g, 69 kHz, 139 dB re 1 μPa at 1 m, ThelmaBiotel, Trondheim, Norway), to reduce any potential impacts of the transmitter size on the fish behaviour. Selected smolts were anaesthetised with clove oil (0.5 mg/L) mixed with river water. Once fully anaesthetised, fork length (mm) and mass (g) were recorded before a small incision (12–14 mm) was made along the ventral surface of the smolt anterior to the pelvic girdle. The transmitter was inserted into the peritoneal cavity through the incision. Two independent sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK) were used to close the incision. River water was used to aspirate the smolts throughout the procedure. Post-tagging smolts were left to recover in an aerated tank until fully recovered from the anaesthetic before being released into the river immediately downstream of the trap (Figure 1). Fish were released at 1200 hr on the 14th and 21st, and at 2100 hr on the 18th. This procedure was performed under UK Home Office licence.

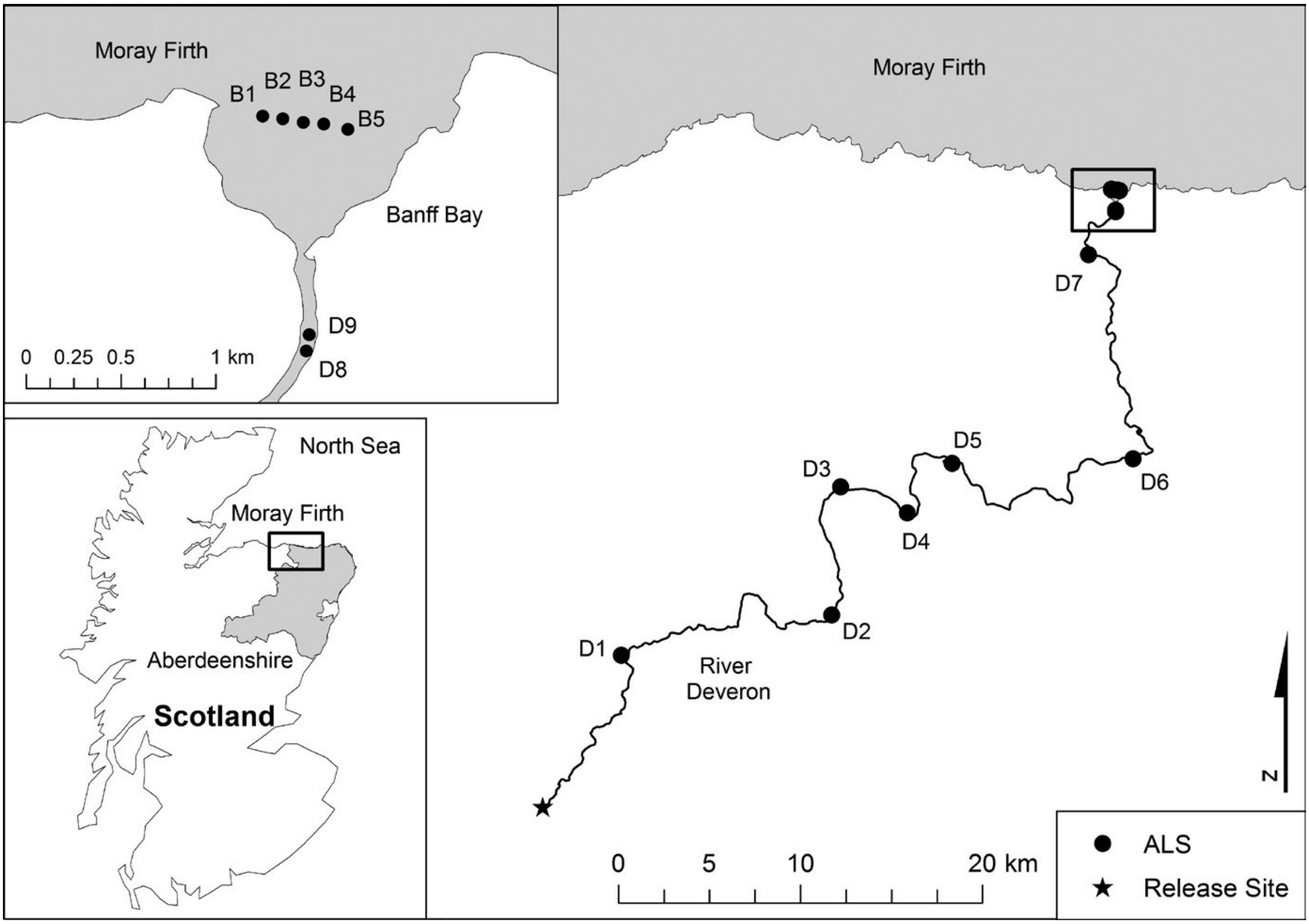

FIGURE 1 Automated listening stations (ALSs) along the river and in the bay at Banff (solid points). An enlarged map of the marine array is shown in the top-left corner. Names of individual ALSs are given next to ALS positions

2.3 | Automated listening station network

Automated Listening Stations (ALSs) were placed along the river and in the bay to detect smolt passage. Nine ALSs (D1–D9 (model VR2W, VEMCO, Nova Scotia, Canada); Figure 1) were placed along the river at deep, slow flowing sections with the aim of achieving high detection efficiencies. ALSs D1–D7 were positioned in the freshwater section of the river. D8 and D9 were positioned in the lower river, within 1 km of the river mouth (D1–D9 are henceforth referred to as the river array). Five further ALSs (B1, B3 and B5 (model VR2W); B2 and B4 (model VR2Tx, VEMCO, Nova Scotia, Canada); Figure 1) were placed linearly across the bay to maximise the likelihood of detecting a passing smolt (this group is henceforth known as the marine array). The two VR2Tx ALSs were also used to record water temperature (°C) in the marine environment every hour and environmental noise (measured as mV) every 15 min. All ALSs were deployed in early-April prior to smolt capture and extracted in mid-June after the depletion of implanted acoustic transmitter batteries.

A mark–recapture analysis was conducted using the RCapture package (Rivest & Baillargeon, 2014) in RStudio (v0.99.903; R Core Team, 2014), to estimate the probability of smolt detection for each ALS in the river. A continuous range test was also carried out to measure the detection efficiency across the ALSs in the marine array during the study period (Kessel et al., 2014). An acoustic transmitter in the ALS at B2 was activated to emit an acoustic pulse every 90 s. The detection efficiencies for each ALS were calculated by dividing the number of detected transmissions on each ALS by the number of known transmissions (n = 10) from B2 for each 15 min period.

2.4 | Statistical analyses

Successful river passage for a smolt was defined as when an individual completed riverine passage and was detected on the last river ALS. The proportion of fish achieving successful river passage was calculated as the number of successful smolts divided by the total number tagged. Mortality rate was expressed as a rate per distance travelled for both the river and early marine migration. This was performed by dividing the difference in the number of smolts detected at the upstream and downstream ALSs of interest by the distance between the two detection points. Time taken to migrate and the speed of migration were also calculated for those smolts that entered the river array. The river migration duration was determined as the time elapsed from the time of release until the first detection on the last river ALS, or the last detection obtained from a fish that failed to reach the last river ALS.

To test for the possibility of tag related mortality in migrating smolts, a binomially distributed General Linear Model (GLM; river escapement model) was created with transmitter burden (calculated as the ratio of transmitter length to fish fork length) and tagging date as explanatory variables, with fish migration success (successful migration = "1"; those that failed to successfully migrate = "0") as the response variable. All fish tagged in the study were included in this model. The significance of variables in the model was tested using a step-down approach, with the least significant variable being removed from the model. Model selection was based on a Likelihood Ratio Test (LRT) between nested models after variables were removed to obtain the significance of the removed variable in the model. This procedure was repeated, the final model selected being that where no further variable removal was possible without having a significant effect on the model. A *t* test comparing the ratio of transmitter weight to body weight for successful versus unsuccessful river passage groups was also carried out.

A second binomial GLM (passage success model) was created to model river passage success, with success denoted as either "1" or "0". Explanatory variables included in the model were time of release, transmitter burden and the overall mean ground speed of each fish, mean river height and mean lunar brightness from the first to the last detection for each fish. Data on river height (used as a proxy for river discharge) were gathered from the Scottish Environment Protection Agency (SEPA) monitoring station, Allt Deveron at Cabrach, upstream of the release site (SEPA, 2016). Lunar brightness was derived from online data (Lunar Calendar, 2016), which provided the maximum percentage lunar brightness for each night. Only those fish that were detected on the river ALSs were included in this analysis to allow for the river height and lunar brightness means to be calculated. Model selection was carried out using the simplification procedure outlined above.

A Generalised Linear Mixed Effect Model (GLMM) was used to model river migration speed. River migration speed was calculated for all fish that were detected on any river ALS, and was calculated for each river section (river sections separated by ALS positions). Explanatory variables included in the analysis were transmitter burden, time of smolt release and the means for river height, river temperature (also obtained from the SEPA monitoring station on the Allt Deveron at Cabrach) and lunar brightness for the duration that each smolt was in transit between two consecutive ALSs. Transmitter ID (unique to each tagged fish) was included as a random factor to account for pseudo-replication from multiple reported speeds for each fish resulting from multiple detections at successive receivers along the river. As with the river passage success GLM, only those fish that were detected within the river ALS were included in the analysis of swimming speeds. Model selection followed the same step-down and LRT procedure described above. Model diagnostics and quality were also assessed after the final model was selected.

Marine migration speed was calculated for each fish that left the river and was subsequently detected on any marine receiver. The time of entry into the marine environment was considered to be the time of last detection on the final river ALS, and migration in the marine environment examined in this study was deemed to be completed after the last detection at any receiver in the marine array (B1–B5). The speed of marine migration was compared with the river migration speed of fish that had successfully left the river using a Wilcoxon rank sum test. A similar test was used to compare the length of time that fish remained in range of a single ALS (henceforth referred to as residency time at an ALS) in both river and marine arrays. A GLM was created to investigate ground speed of smolts in the marine environment. Predictor variables included fish length, transmitter burden, date of release, length of time taken from release until first detection on any of the river ALSs (B1–B5), time of detection at the marine array (day or night at first detection of smolts on any of B1–B5), both mean river water height and mean lunar brightness (from last detection on D8 until first detection on any of B1–B5), mean bay water temperature and the mean environmental noise (to determine if noise influenced smolt behaviour) in the bay for the duration of fish transit from the last river ALS until first detection at the marine array. Model selection was performed using a step-down approach removing the least significant variable until only significant variables remained.

The average travel vector for fish entering the near coastal environment was also calculated. A Poisson distributed GLM was created to determine the influence of environmental variables on the travel vectors. The ALS in the marine array that first detected each smolt was used as the response variable. Explanatory variables included all those variables included in the marine ground speed GLM, in addition to the tide state (flooding or ebbing), and residency time in the bay. Model selection was determined with a step-down approach using chi-squared tests until the simplest model remained. Model diagnostics were also assessed for each model created.

A chi-squared test was performed on the frequency of detections recorded for each bay ALS to identify if smolt frequency of detection differed significantly from random. Three further chi-squared tests were carried out on the frequency of fish entry into the marine environment at three bay water temperatures ranges (7.5–8.5°C, 8.5–9.5°C and 9.5–10.5°C), at different tide states (flooding or ebbing) and at time of day (day or night). All analyses were conducted in RStudio. GLMM's were assessed using the lme4 package (Bates, Mächler, Bolker, & Walker, 2014).

3 | RESULTS

3.1 | Automatic listening station network efficiencies and range tests

Mark–recapture analysis indicated that ALSs D1 and D2 had low probabilities of detecting passing smolts (mean probability ± *SD* = 0.17 ± 0.20 and 0.03 ± 0.03 respectively). D3 was the first ALS downstream of the release site to have a high probability of detecting a smolt (1.00 ± 0.00; the probability of detecting a smolt that was confirmed as having passed this ALS by its detection at a subsequent ALS). As a result, data from D2 were removed from further analyses, and D1 detection data were only included in one specific analysis, to estimate mortality rate between D1 and D3. All ALSs downstream of D3, with the exception of D5, had detection probabilities of above .90. D5 had a detection probability of 0.56 ± 0.38, and thus, data from D5 were also removed from analyses. Although D9 had a detection probability of 0.95 ± 0.21, data from this ALS were also removed from analyses as D8 had a detection probability of 1.00 ± 0.00 and the ALSs in the marine array had detected all the fish that had been detected on D8. The mean (±*SD*) detection efficiency for B1–B5 in the bay during the study period was 0.76 ± 0.31 at 217 m (range = 0.00–1.00).

3.2 | Freshwater migration

Atlantic salmon smolts tagged in this study ranged in length from 121 to 141 mm (*n* = 50; mean ± *SD* = 128 ± 5.2 mm; number of fish tagged on each day of tagging: $n_{14} = 2$, $n_{18} = 41$; $n_{21} = 7$) and mass ranged from 18.0 to 26.0 g (*n* = 9; mean ± *SD* = 20.9 ± 2.8 g). Smolt river escapement success was not significantly predicted in the river escapement model by fish length (LRT: $\chi^2_1 = 0.02$, $p > .05$). Similarly transmitter burden on smolts did not have a significant influence on whether the fish successfully left the river or not (transmitter length:fork length ratio range = 12.8%–14.9%; mean ± *SD* = 14.0 ± 0.6%; LRT: $\chi^2_1 = 0.09$, $p > .05$; transmitter mass:body mass ratio range = 7.3%–10.6%, mean ± *SD* = 9.2 ± 1.2%; *t* test, *t* = 1.4, *df* = 4.5, *p* > .05). The smallest fish used in this study, 121 mm fork length, and thus with the highest transmitter burden (14.9% of length) was detected leaving both the river and marine arrays.

Thirty-four smolts were detected entering the river array at D3, indicating a mortality rate of 0.90% per km between the release site and the first operational ALS in the river. Of the eight fish detected on D1, six were also detected on D3, giving an estimated mortality rate between D1 and D3 of 1.05% per km. Overall mortality rate in the River Deveron from release site to D8, a distance of 81.5 km, was 0.77% per km, resulting in 40% (*n* = 20) of tagged fish exiting the river (Figure 2). Lunar brightness significantly explained smolt passage success in the river (LRT: $\chi^2_1 = 23.5$, $p < .001$), with those smolts migrating at times of lower lunar brightness, that is on darker nights (mean ± *SD* = 67.7 ± 14.7%, range = 47.2%–88.2%) having greater success than those moving on brighter nights (mean ± *SD* = 79.6 ± 10.9%, range = 52.7%–90.7%; Figure 3). The ground speed of smolt migration within the river was also significantly different between success groups (LRT: $\chi^2_1 = 23.5$, $p < .001$), with successful smolts having a higher ground speed (mean ± *SD* = 5.03 ± 1.73 km/day) than unsuccessful smolts (mean ± *SD* = 3.55 ± 1.47 km/day). No other variables in the river passage success model were significant.

The time taken for successful smolts to exit the river was 18.52 ± 7.70 (mean ± *SD*) days. River height was significant in the GLMM describing ground speed in the river (LRT: $\chi^2_1 = 95.9$, $p < .001$), being positively correlated with ground speed (Figure 4). No other variables were significant in the smolt river ground speed model. A qualitative assessment of the ground speed of smolts showed that their speed remained relatively constant throughout the riverine migration period; however, some smolts were observed to increase their speed towards the lower part of the river.

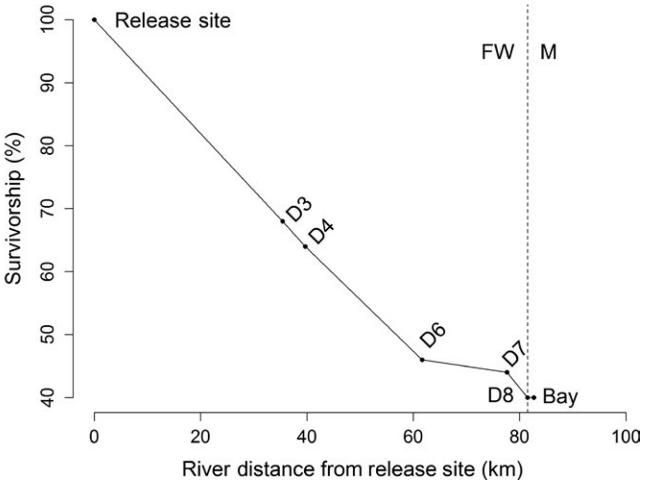

FIGURE 2 Survivorship of acoustically tagged Atlantic salmon smolts, in terms of the number of fish detected at each automated listening station (ALS) in the river array. ALSs are represented by solid points and labelled

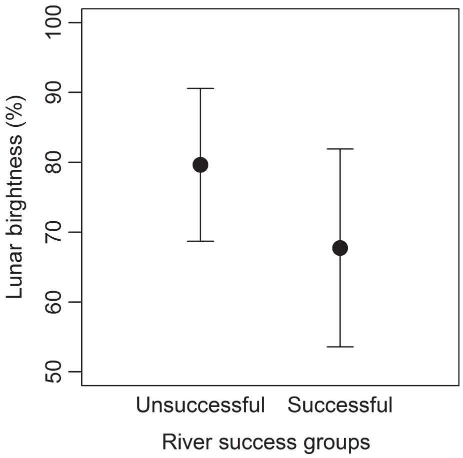

FIGURE 3 The lunar brightness (mean ± *SD*) during river migration for smolts that were unsuccessful and successful in exiting the river

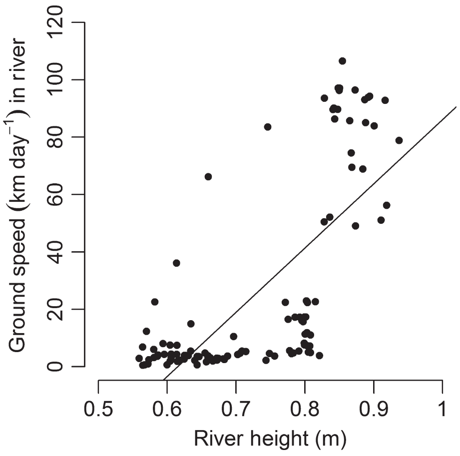

FIGURE 4 The relationship between ground speed (km/day) and river height (m; proxy for discharge) of each smolt between each consecutive automated listening station

3.3 | Marine migration

Twenty fish were detected on D8 at the downstream end of the river array, with all 20 being also detected on the marine array (1.2 km away) indicating 100% marine survival, significantly greater than that observed in river migration ($\chi^2_1=5$, $p = .02$). Smolts that had completed riverine migration had a significantly greater ground speed in the early marine stage of migration (mean ± *SD* = 37.37 ± 28.20 km/day) than they did in the river stage (mean ± *SD* = 5.03 ± 1.73 km/day; Wilcoxon rank sum test, $W = 19$, $p < .001$; Figure 5). The speed of smolt migration had a negative relationship with noise in the bay (GLM, $F_{1,\ 16} = 5.7$, $p = .03$; Figure 6). Smolts migrated with greater speed through the bay during the day (mean ± *SD* = 25.65 ± 28.10 km/day) than the night (mean ± *SD* = 10.56 ± 11.07 km/day; GLM, $F_{1,\ 16} = 9.3$, $p < .01$; Figure 7). The river height (a proxy for discharge) was weakly linked to smolt speed in the bay (GLM, $F_{1,16} = 3.6$, $p = .08$), where smolt speed tended to increase with river height. Smolts spent less time in range of an ALS in the bay (mean ± *SD* = 0.16 ± 0.12 hr) than they did in the river (mean ± *SD* = 0.67 ± 1.33 hr), but this difference was not significantly (Wilcoxon rank sum test, $W = 182$, $p > .05$). Smolts were detected significantly more frequently on B4 ($n = 108$ fish detections) than on the other bay ALSs ($n_{\mathrm{B1}} = 61$, $n_{\mathrm{B2}} = 94$, $n_{\mathrm{B3}} = 87$ and $n_{\mathrm{B5}} = 88$ fish detections; $\chi^2_4=12.7$, $p = .01$).

There was no clear single vector of travel used by all smolts as they moved into the bay. The median point of first detection for smolts reaching the marine array was, however, B4 (Figure 8). The distribution of smolts reaching the marine array was highest for B4 and B5, each detecting 6 smolts, with only two fish being detected on B1, four fish on B2 and two fish on B3 ($\chi^2_4=4.0$, $p > .05$; Figure 8). The first point of detection on the bay ALS was not significantly explained by any variable included in the travel vector GLM analysis. Fish showed a higher frequency of entry into the bay at lower temperatures between 7.5–8.5°C ($n = 15$), than at temperatures between 8.5–9.5°C ($n = 3$) and 9.5–10.5°C ($n = 2$; $\chi^2_2=15.7$, $p > .001$). More fish were detected entering the bay on a flooding tide ($n = 14$) rather than an ebbing tide ($n = 6$), this difference was close to statistical significance ($\chi^2_1=3.2$, $p = .07$). Significantly more smolts ($n = 15$) were first detected on ALSs in the bay at night, compared with during the day ($n = 5$) ($\chi^2_1=26.7$, $p < .001$). Of the 15 fish that entered the bay at night, there was no significant preference for lunar brightness at time of entry ($\chi^2_3=5$, $p > .05$), but no fish were detected entering during a full moon period.

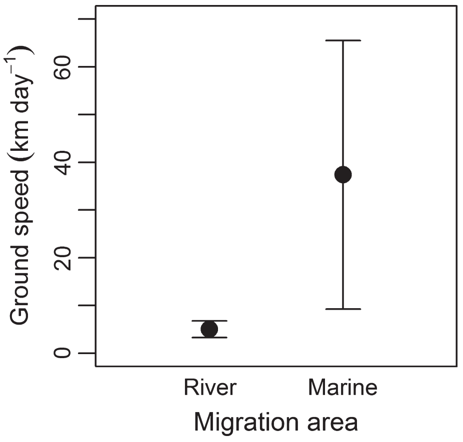

FIGURE 5 Ground speed (km/day; mean ± *SD*) of river and marine migration for Atlantic salmon smolts that exited the automated listening station arrays

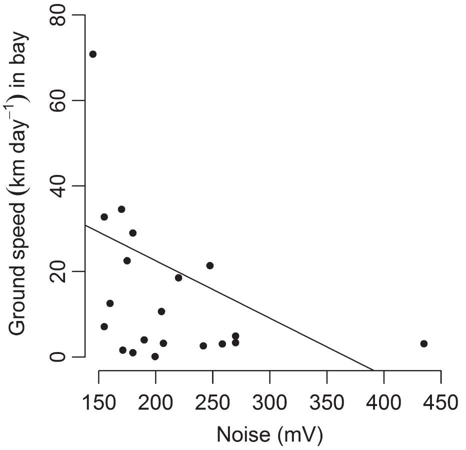

FIGURE 6 Relationship between ground speed (km/day) and environmental noise (mV) in the marine environment

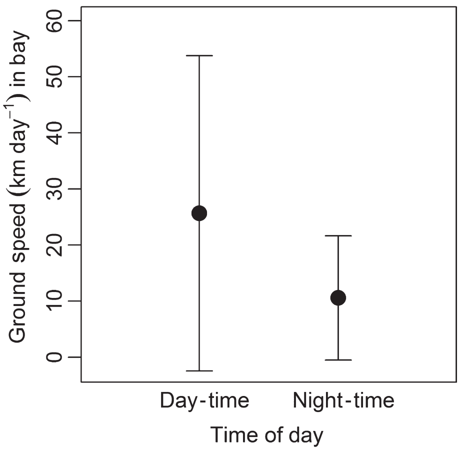

FIGURE 7 Ground speed (km/day; mean ± *SD*) in the bay compared between hours of daylight and during the night

4 | DISCUSSION

Overall survival rate of Atlantic salmon smolts in the River Deveron (40% survival) is lower than that reported in other salmon rivers (e.g. river survival reported as 97% in the River Conwy: Moore, Potter, Milner, & Bamber, 1995; and 89% in the River Skjern: Dieperink, Bak, Pedersen, Pedersen, & Pedersen, 2002). However the mortality rate per distance travelled is low (0.77% per km) compared to those reported in other Atlantic salmon smolt river migration studies (0.3–7.0% per km; Dieperink et al., 2002; Thorstad, Whoriskey, et al., 2012). The lower overall survival in this study may therefore

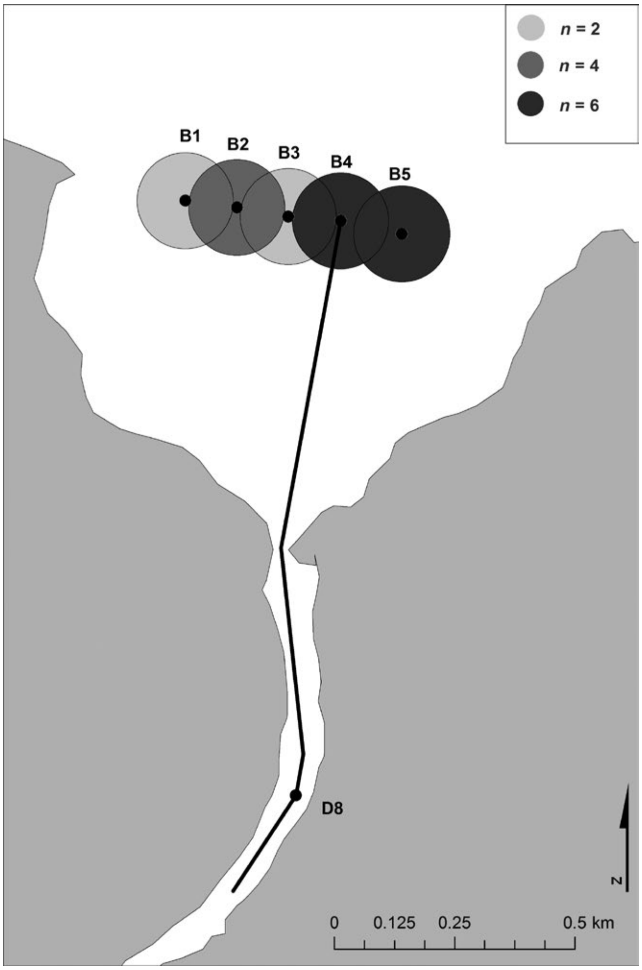

FIGURE 8 Median Atlantic salmon smolt travel vector into the bay (solid line), with the distribution of smolts upon first entry into the bay

be attributed to the relatively longer riverine migration distances over which fish were tracked in this study compared to the others. It is assumed that smolts not detected in the river array after tagging did not return to the upper reaches of the river, as the process of desmolting has not been observed in Atlantic salmon (McCormick et al., 1998). Once Atlantic salmon have begun smolting, they have a limited amount of time to exit the river (Hoar, 1976; McCormick et al., 1998). Therefore, as smolts were unlikely to move back upstream, and as tag failure is reported to be uncommon (Gauld, Campbell, & Lucas, 2013), a probable major cause for loss of fish detections is mortality.

There are several potential causes of mortality in tagging studies, these include tagging induced mortality, either from handling and tagging procedure itself (Jepsen, Schreck, Clements, & Thorstad, 2005) or as a result of the long-term effects of tag burden on the fish. A general "rule of thumb" when tagging fish has been the "2% rule," whereby the tag should not exceed 2% of the fish mass in air in order to allow the fish to behave naturally and prevent mortality through tagging (Winter, 1996). This tag limit, however, has been significantly challenged recently (Brown, Cooke, Anderson, & Mckinley, 1999; Newton et al., 2016; Rechisky & Welch, 2010; Welch, Batten, & Ward, 2007). In this study, there was no observed effect of the acoustic tag burden influencing successful river emigration, a finding that is similar to other studies using salmonid smolts of similar sizes (Rechisky & Welch, 2010; : Chinook salmon (*Oncorhynchus tshawytscha*), fish length range = 132–158 mm, mean burden (length) = 14.3%, fish mass range = 21.1–57.1 g, mean burden (mass) = 5.8%; Newton et al., 2016: Atlantic salmon, fish length range = 115–168 mm, mean burden (length) = 14.3%, fish mass range = 15–44 g, mean burden (mass) = 6.8%). Nor did tag burden influence the smolt ground speed in either the river or the marine environment. Although there was no difference in tag burden between fish that were successful and those that were not in this study, Welch et al. (2007) showed that mortality in steelhead trout (*Oncorhynchus mykiss*) presmolts resulting from a dummy transmitter (8 × 28 mm, 1.4 g in air) in a laboratory experiment increased with decreasing fish size, and that twenty per cent of the fish ranging from 120 to 140 mm in length died due to tag burden. As all fish in the study reported here were within the quoted size range used in the Welch et al. (2007) study (although a smaller tag was used in our study), it is thus conceivable that some of the fish that failed to leave the river did perish as a result of the transmitter burden.

Welch et al. (2007) also showed that 20% of the fish within the 120–140 mm size range ejected the dummy tag from their body. This effect could potentially bias mortality rate estimates. However, tag expulsion has been shown to occur after 140 days had elapsed following tagging (Lacroix, Knox, & McCurdy, 2004). In the study reported here the last smolt left the river 40 days after tagging, thus we conclude that it is unlikely that tag loss would result in mortality estimate bias.

Brown et al. (1999) provide evidence that a tag burden of up to 12% of fish body weight showed no significant effect on the critical swim speed of juvenile rainbow trout (*Oncorhynchus mykiss*). Although many authors highlight that there are no immediate consequences on fish performance, any tag burden has been observed to temporarily interrupt fish growth, although growth rate returns to normal when growth is eventually initiated (Lacroix et al., 2004; Welch et al., 2007). The long-term consequences of tagging were not considered in the presented study, but the smallest fish tagged was detected on the marine array, indicating that tag burden is not likely to be the main cause of fish loss in the study presented here.

Although the cause of mortality in this study was not determined directly, predation is known to be a major source of mortality in rivers (Carter, Pierce, Hislop, Houseman, & Boyle, 2001; Dieperink et al., 2002; Heggenes & Borgstrom, 1988; Hvidsten & Møkkelgjerd, 1987; McCormick et al., 1998; Thorstad, Whoriskey, et al., 2012). Several mammal species are known to prey on salmonid species in Scotland, such as the otter and the American mink, with studies indicating large increases in predation rates with the introduction of a mammal predator (Carss et al., 1990; Heggenes & Borgstrom, 1988). The River Deveron also supports a large population of goosanders (*Mergus merganser*) which is a more likely source of major predation than mammals, and a population of cormorants which have been observed to have a high (24%) predation rate on Atlantic salmon smolts (Jepsen et al., 2010). Large resident brown trout (*Salmo trutta*) are also known to be present in the River Deveron and may also heavily consume smolts, in a similar way to bull trout (*Salvelinus conflluentus*) binge-feeding on juvenile sockeye salmon (*Onchorhynchus nerka*) in western North America (Furey, Hinch, Mesa, & Beauchamp, 2016). All tags in this study were detected sequentially downstream or not at all, suggesting that tagged smolts were not consumed by a fish predator with a large home range. Brown trout often feed over small spatial ranges, and so may not make any long-distance movements along the river (Klemetsen et al., 2003), thus tags consumed by this predator would either show long-term, repeated detections on a single ALS or would not be detected again. However, expulsion of the tags by predators via regurgitation has been observed (Armstrong, Johnstone, & Lucas, 1992), which would also present as a continuous detection at one ALS or no detections at all.

The speed of Atlantic salmon smolt outward migration varies considerably between populations, with the main influences on speed being river discharge and photoperiod (Martin et al., 2012; McCormick et al., 1998; Rand et al., 2006; Thorstad, Whoriskey, et al., 2012). The ground speed of the River Deveron smolts at 4–5 km/day, is at the lower end of the range reported by other studies, from 0.2 to 60 km/day (Thorstad, Whoriskey, et al., 2012). As expected, smolt river migration speed in this study was heavily dependent on river discharge due to the passive displacement of smolts at higher flow velocities.

Migration success was linked to the lunar brightness, and entry into the marine environment occurred primarily at night. Nocturnal migration is thought to be a common predator avoidance strategy in outward migrating Atlantic salmon (McCormick et al., 1998; Thorstad, Whoriskey, et al., 2012) and European eel (*Anguilla anguilla*; Durif & Ellie, 2008; Barry et al., 2015), with movement on darker nights potentially hindering predator success (Barry et al., 2015; Thorstad, Whoriskey, et al., 2012; Urke et al., 2013). Some studies investigating early marine migration in Atlantic salmon have reported a less defined diel migration, with some suggesting a complete switch to more active swimming during the day (Dempson et al., 2011; Hedger et al., 2008; Koed et al., 2006). This is supported by the findings of this study where smolt ground speed in the marine environment was greater during hours of daylight than during the night. This is also a potential predator avoidance strategy. The change from nocturnal river to diurnal sea migration could therefore be the main migration strategy further out to sea. Further tracking of smolts throughout coastal waters would be necessary to determine this.

Unlike other studies, here there was no observed mortality during early marine migration. Suggested reasons for mortality at entry to sea have been predation and osmotic shock (Davidsen et al., 2009; Hvidsten & Møkkelgjerd, 1987; Thorstad, Uglem, et al., 2012; Thorstad, Whoriskey, et al., 2012; Urke et al., 2014; Vollset et al., 2016). The lack of an estuary in this study and the bay's shallow depth may have had a role in the absence of mortality through predation. Jepsen et al. (2006) reported that highest mortality at the mouth of the River Eira was in a region of rapidly increasing depth, where Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*) could prey on smolts from beneath, while birds such as gulls (*Larus* spp.) could prey on smolts from above. The lack of observed marine mortality in this study could also be due to the speed at which smolts were travelling through the bay, with the longest recorded residency within the bay being less than 30 min.

The observed speed of migration through the bay is greater than the reported values of early marine migration speeds in other Atlantic salmon populations (0.4–1.2 body lengths per s; Økland et al., 2006; Dempson et al., 2011; Thorstad, Whoriskey, et al., 2012) and greater than that exhibited in the river. The relatively short distance of travel (1.2 km) in the marine environment might have partly contributed to this in that river discharge may contribute to the relatively high speed of travel. However, the fact that fish were mostly entering coastal waters on a flooding tide would tend to suggest that a significant proportion of the higher speed of travel was the result of active swimming. No previous studies have observed an effect of environmental noise on smolt travel; this field might therefore be a fruitful area of future smolt migration and morality research. Background noise is very likely to be, at least partly, the result of strong winds and rain, and thus, the environmental conditions during poor weather may result in some level of disorientation. But background noise could also be increased by human activities within, or neat to, the coast. This information could influence future management decisions, for example instigating the exclusion of industrial activities along migration pathways during the smolt emigration.

The trajectory of smolts leaving the river was north-easterly, which is also the direction needed for fish to exit to the North Sea. On this swimming trajectory, it is important to note that the smolts remained closer to the centre of the bay than to the coast. This indicates that they do not follow geographical features but have a mechanism for navigation that does not include contouring coastal land features. One possibility is that they are following water currents created by river discharge (Lacroix & McCurdy, 1996; Thorstad, Whoriskey, et al., 2012).

This study increases current knowledge on wild Atlantic salmon smolt river migration and mortality of smolts entering directly into the marine environment without passing through an estuary. It also showed that Atlantic salmon smolts exhibited a higher mortality rate during river migration than during marine migration, a finding that has not been observed in other Atlantic salmon populations. Smolts also experienced a greater swimming velocity in the marine environment and exhibited a navigational ability exiting the river with a trajectory that would take them to the open sea. This is the first description of Atlantic salmon smolt behaviour and swimming trajectory in the nearshore marine phase of migration in Scotland. Future research should focus on determining the underlying mechanisms of smolt navigation.

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