



Riverine and early marine migration of Atlantic salmon *Salmo salar* L. smolts in the River Deveron, Scotland

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Abstract

Despite the many risks associated with migration, it is a common strategy for resource exploitation at different life stages exhibited throughout the animal kingdom. Atlantic salmon *Salmo salar* (L. 1758) are known for their long distance migration for resource exploitation and growth. *Salmo salar* migration has been intensively studied, with the cues for migration, swim speed and mortality in rivers is well documented. However, the early marine migration, an area thought to result in the highest migration mortality, is seldom reported. This study aims to increase understanding of wild *S. salar* outward migration, as well as presenting the first description of early marine behaviour in Scotland. It was hypothesised that 1) greater mortality would occur in the marine stage of migration than river stage, and 2) smolts would have a greater swim speed in the river stage than the marine. Smolts captured from the River Deveron ($n = 50$) were tagged with acoustic transmitters and tracked through the river and the immediate Moray Firth using Automatic Listening Stations. Overall survival of smolts in the River Deveron was 40%, with a higher observed mortality in the river ($0.77\% \text{ km}^{-1}$) than in the marine stage of migration ($0\% \text{ km}^{-1}$), resulting in a significantly higher survival rate in the marine stage than the river (100%; $\chi^2 (1) = 5, p = 0.02$). A greater swim speed was observed in the marine environment (mean \pm sd = $37.37 \pm 28.20 \text{ km day}^{-1}$) than in the river (mean \pm sd = $5.03 \pm 1.73 \text{ km day}^{-1}$; $W = 19, p < 0.001$). The main smolt trajectory leaving the river was north-easterly. Mortality in the river is most likely due to predation, although the exact cause cannot be determined. The absence of mortality in marine migration is uncommon; a potential result of the river mouth morphology. High swim speed of smolts in the marine environment could be due to passive displacement by high river discharge. But the trajectory of travel indicates an active swim, along with a potential innate navigational mechanism which should be the focus of future research.

Introduction

Migration, the act of moving between geographical regions, is a common life history strategy exhibited by terrestrial, airborne and aquatic animals (Roff, 1988; Alerstam *et al.*, 2003). It is often a result of differing resource requirement during changing seasons or at different stages of an animal's development, such as abundant nutrients for growth in juveniles and suitable breeding habitat for reproduction adults (Roff, 1988; Alerstam *et al.*, 2003; Dingle & Drake, 2007). There are several costs associated with migration, including habitat selection, mortality, energy expenditure, environmental stochasticity, novel pathogen exposure and anthropogenic influences (Standen *et al.*, 2002; Alerstam *et al.*, 2003; Wikelski *et al.*, 2003). Despite these risks, the benefits of migrating to a new habitat providing resource exploitation possibilities are far more advantageous.

Research has largely focused on terrestrial migration simply due to the relative ease for studying birds and mammals (Dingle & Drake, 2007). But with advancements in telemetry and tracking technologies over the last few decades, aquatic animal movements and behaviour can be studied in greater depth (Heupel *et al.*, 2006; Drenner *et al.*, 2012; Hussey *et al.*, 2015). The number of fish movement studies using acoustic and radio tracking techniques has increased dramatically since the 1970s, with a particular focus on economically important fishes, such as salmonids (Drenner *et al.*, 2012; Hussey *et al.*, 2015).

Atlantic salmon *Salmo salar* (L. 1758) migration is widely known and well-documented, with juveniles emigrating to grow and adults returning to reproduce (Fleming, 1996; Klemetsen *et al.*, 2003). *Salmo salar* migration is generally anadromous, whereby individuals undergo the arduous process of smolting, resulting in behavioural, morphological and physiological changes in preparation for marine life, before leaving freshwater rivers to reside in marine feeding grounds (Hoar, 1976; Metcalfe *et al.*, 1989; McCormick *et al.*, 1998; Klemetsen *et al.*, 2003; Thorstad *et al.*, 2012b). Their migration is often associated with sexual maturation, as *S. salar*

return to their natal rivers after several years to spawn with a higher reproductive fitness (Fleming, 1996). However, some individuals within populations, such as precocious males, mature prior to their outward migration and successfully reproduce (Gjerde, 1984; Fleming, 1996; Saura *et al.*, 2008). It is not common for females to mature before outward migration, but the occurrence of this is best described in the only known *S. salar* population that is entirely river-resident in the River Namsen (Sandlund *et al.*, 2014).

Initiation of migration in *S. salar* is due to temperature, river discharge and photoperiod cues (McCormick *et al.*, 1998; Thorstad *et al.*, 2012b). The speed of migration is variable, often depending on environmental factors, such as river discharge, and time of day (Rand *et al.*, 2006; Thorstad *et al.*, 2012b). Observed mortality rate within river migration varies temporally and spatially, but ranges from 0.3 to 7.0% km⁻¹ (Thorstad *et al.*, 2012b). Mortality is primarily due to predation by piscivorous animals, like brown trout *Salmo trutta* (L. 1758), and goosander *Mergus merganser* (L. 1758), but may also be attributed to physical trauma through collisions with obstacles (Jepsen *et al.*, 2006; Rand *et al.*, 2006; Thorstad *et al.*, 2012b). It is widely believed that the majority of *S. salar* migration related mortality occurs after the river phase, during the transition from freshwater to marine water, and in coastal regions (Hvidsten & Møkkelgjerd, 1987; Jepsen *et al.*, 2006; Thorstad *et al.*, 2012a; b; Vollset *et al.*, 2016). The few studies that quantify *S. salar* migration through the early marine stage have focused on long, deep estuaries and fjords, where mortality has been observed to be up to anywhere in the range of 0.6 to 36% km⁻¹ (Okland *et al.*, 2006; Hedger *et al.*, 2008; Dempson *et al.*, 2011; Thorstad *et al.*, 2012b). No studies have monitored *S. salar* early marine migration after leaving a river which drains straight into the sea without an estuary. Furthermore, many studies use hatchery-reared smolts to describe *S. salar* outward migration (Fried *et al.*, 1978; Hansen & Jonsson, 1985). However, hatchery smolts are not directly comparable with wild *S. salar* smolts as they often exhibit different behavioural and physiological traits (Pedersen *et al.*, 2008; Urke *et al.*, 2013). Only a greater focus on wild smolt migration will aid in conservation efforts for *S. salar*.

This study aims to expand on the current knowledge of wild *S. salar* river migration, by quantifying mortality and swimming speed through the use of acoustic telemetry. Migration parameters, such as swim speed, will also be explained with environmental data. The second aim of this study is to gain further understanding of marine migration, with the speed and mortality of *S. salar* smolts exiting a river directly into the sea being quantified. Lastly, *S. salar* behaviour during early marine migration will be described. This study contains two hypotheses. Firstly, it is hypothesised that a greater mortality rate will be observed in the early marine migration stage rather than the river migration as a result of osmo-regulatory shock and predation. The second hypothesis is that there will be a greater swim speed in the river stage of migration than the marine stage as smolts are aided by river flow.

Materials and Methods

Study Site

The study was conducted over three months from April to June, 2016, on the River Deveron, Northeast Scotland. The Deveron has a catchment of 1,226 km² and is 96 km in length, flowing through Aberdeenshire and draining directly into the Moray Firth through a bay at Banff (57°39'55.1"N, 2°30'48.2"W; Fig. 1). The bay at Banff is approximately 1.3 km at its widest at its mouth 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.

Smolt capture and Tagging Procedure

Salmo salar smolts were caught using a rotary-screw trap placed in the upper reaches of the River Deveron (57°02'44.1"N, 3°01'55.2"W) across three days in 2016; 14 April, 18 April,

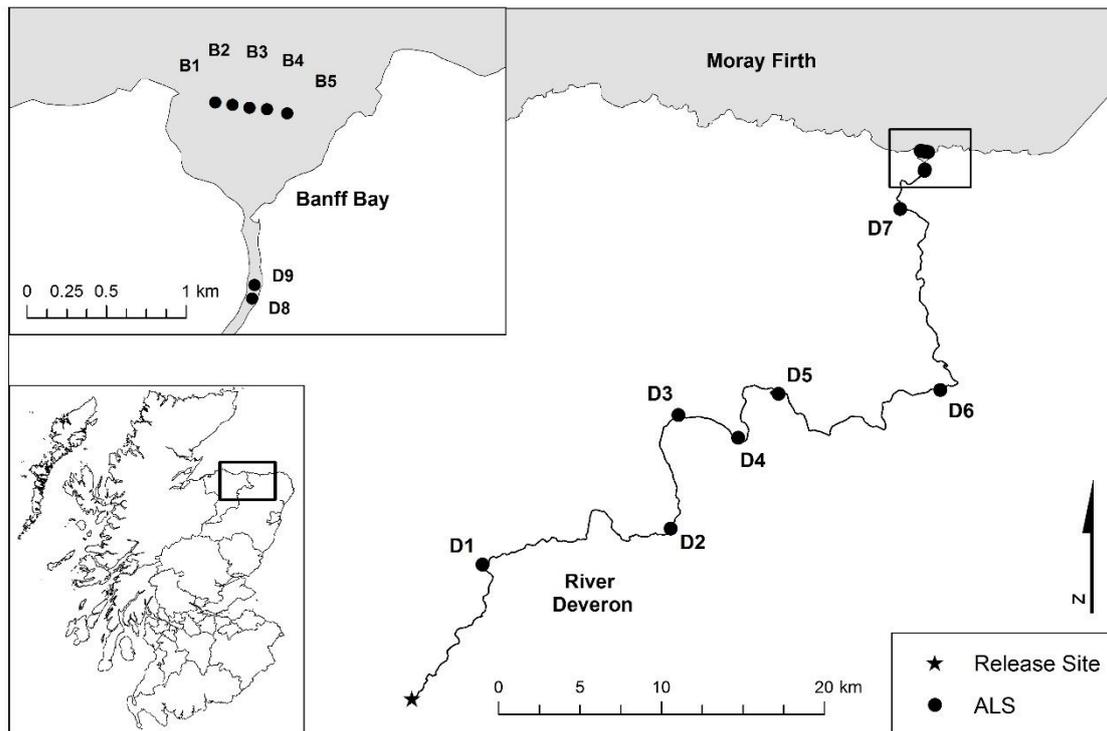


Fig. 1. Map of the River Deveron, showing the smolt release site (star) and the position of the Automatic Listening Stations (ALS) along the river and in the bay at Banff (solid points). An enlarged map of the marine array is shown in the top-left corner. Names of individual ALS are given next to ALS positions.

and 21 April. Fifty smolts greater than 120 mm in length were selected for surgical implantation of a coded acoustic transmitter (7.3x18 mm, weight in air/water of 1.9/1.2 g, 69 kHz, ThelmaBiotel, Trondheim, Norway). Selected smolts were anaesthetised with clove oil (0.5 mg l⁻¹) mixed with river water. Once fully anaesthetised, fork length (L_F , 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 passed into the peritoneal cavity through the incision. Two sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK) were used to close the incision. River water was used to aspirate the smolts during the procedure. Post-tagging smolts were left to recover in an aerated tank for a minimum of three hours before being released in the river immediately downstream of the trap (Fig. 1).

Automated Listening Station Network

Automatic Listening Stations (ALS) were placed along the river and in the bay to detect smolt passage. Nine ALS (D1-D9: VR2W, VEMCO, Nova Scotia, Canada; Fig. 1) were placed along the river at sections of narrower passage. D1-D7 were positioned in the freshwater section of the river (henceforth referred to as the river array). D8 and D9 were positioned in the lowest section within 1 km of the river mouth. Five further ALS (B1, B3, and B5: VR2W; B2 and B4: VR2Tx, VEMCO, Nova Scotia, Canada; Fig. 1) were placed linearly across the bay in order to maximise the likelihood of detecting a passing smolt (henceforth known as the marine array, including D8 and D9). All ALS were deployed in early-April prior to smolt capture and extracted in mid-June, after the depletion of implanted acoustic transmitter batteries.

Retrospective range tests on river ALS showed poor detection efficiency of D1 and D2, with maximum detection efficiencies equalling 17.65% ($n = 6$) and 2.78% ($n = 1$), respectively. Efficiency was determined by dividing the number of smolts detected on each ALS by the number detected on the next downstream ALS. D3 was assumed to have 100% ($n = 34$) detection efficiency as all smolts detected by D3 were also detected on downstream ALS. As a result D2 data were removed from further analyses, and D1 detection data were only included in one specific analysis. All ALS downstream of D3, with the exception of D5, had detection efficiencies above 90%. D5 had an efficiency of 52.17% ($n = 12$), with all but three smolts detected upstream of D5 also being detected on ALS downstream of D5. Thus data from D5 were also removed from analyses. Although D9 had a detection efficiency of 90.0%, data from it were also removed from analyses as D8 and the ALS in the bay had 100% efficiencies. Data obtained by D9 did not provide any extra information to smolt early marine migration.

A continuous range test was carried out across the bay ALS in the marine array during the study period to ensure that all fish that left the river were detected by the ALS array (Kessel *et al.*, 2014). An acoustic transmitter in B2 was activated to emit a sound every 90 seconds. 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 minute period. The mean \pm sd detection efficiency in the bay during the study period was $76.15 \pm 31.0\%$ at 217 m (range = 0 – 100%).

Statistical analyses

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). To account for the possibility of tag related mortality in migrating smolts, a comparison of the transmitter burden between fish that successfully exited and those that failed to exit the river was carried out. Transmitter burden was calculated in two ways: the ratio of transmitter length to fork length and the ratio of transmitter weight to body weight.

All tagged smolts were used in calculations for successful river passage. This was achieved by dividing the number of successful smolts by the total number tagged. Successful smolts were recognised as those that had completed riverine passage by being detected on D8. Mortality rate was determined for both the river and early marine migration. Time taken to migrate and the speed of migration was also calculated for those smolts that entered the river array at D3. Initial time of migration was considered to be time of release at the release site and the conclusion of river migration was considered as the first detection on D8 or the last detection obtained from a fish that failed to reach D8. Time taken until river migration was completed and the speed of migration was calculated for both fish that succeeded and failed to leave the river. A Welch two sample t-test was used to compare the mean river migration speed for both groups of fish.

A generalised linear mixed effect model (GLMM) was used to model river migration speed. This was performed in the lme4 package (Bates *et al.*, 2014) in R.Studio (v0.99.903; R Core Team, 2014). Explanatory variables included in the analysis were river height, the intensity of

lunar brightness, and smolt fork length (L_F). An interaction between river height and lunar brightness was included in the global model to account for potential collinearity in the explanatory variables. Transmitter ID was included as a random factor to account for pseudo-replication from multiple detections along the river. 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 until the final model was selected with LRT showing each remaining variable was important in explaining variation in swim speed.

A second GLMM was created to explain successful river passage. The response variable was binary, either 0 for failed or 1 for successful. The explanatory variables included were fork length, swim speed, river height, and delay at each ALS. Delay was calculated as the time that smolts were in range of each ALS. An interaction was included between swim speed and river height to account for potential collinearity and transmitter ID was included as the random factor. Significance of variables and model selection was tested in the same as the previous GLMM.

Marine migration speed was calculated for each fish that left the river. The time of entry into the marine array was considered to be from the last detection on D8, and marine migration was deemed to be completed after the last detection within the marine array. 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 carried out comparing the length of time in hours that river completest fish remained in range of ALS in both river and marine arrays.

The average travel vector for fish entering the near coastal environment was calculated. A General Linear Model (GLM) was created in R.Studio to determine the influence of environmental variables on the travel vectors. The longitudinal coordinate of the ALS that first

detected each smolt was used as the response variable. Explanatory variables included discharge and lunar brightness. Model selection was determined with a step-down approach using Chi-squared tests in R.Studio until the simplest model remained.

Environmental data

Data on river height was gathered from the Scottish Environmental Protection Agency (SEPA) monitoring station Allt Deveron at Cabrach, upstream of the release site. Lunar brightness was accessed from online sources (Lunar Calendar), which provide the maximum percentage lunar brightness for each night.

Results

Freshwater Migration

Salmo salar smolts tagged in this study ranged in length (L_F) from 121 to 141 mm ($n = 50$; mean \pm sd = 128 ± 5.2 mm) and mass ranged from 18.0 to 26.0 g ($n = 9$; mean \pm sd = 20.9 ± 2.8 g). Comparison of length between fish that left the river and those that failed to showed no significant difference (t -test, $t = -0.3$, d.f. = 40.2, $p > 0.05$). Transmitter burden on smolts did not have a significant influence on whether the fish exited the river or not (transmitter length:fork length (L_F) range = 12.8 – 14.9%, mean \pm sd = $14.0 \pm 0.6\%$; t -test, $t = 0.3$, d.f. = 40.3, $p > 0.05$; transmitter mass:body mass range = 7.3 – 10.6%, mean \pm sd = $9.2 \pm 1.2\%$; t -test, $t = 1.4$, d.f. = 4.5, $p > 0.05$). The smallest fish, $L_F = 121$ mm, was detected exiting both the river and marine arrays.

Thirty-four smolts were detected entering the river array at D3, indicating a mortality rate of $0.90\% \text{ km}^{-1}$ 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, equalling a mortality rate between D1 and D3 of

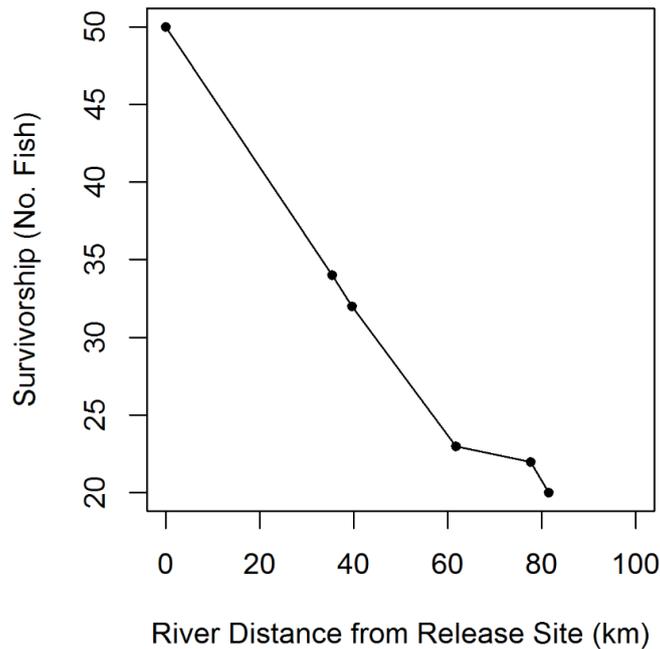


Fig. 2. Survivorship of acoustically tagged *S. salar* smolts, in terms of the number of fish detected at each ALS in the river array. ALS are represented by solid points.

1.05% km⁻¹. Overall mortality rate in the River Deveron from release site to D8 was 0.77% km⁻¹, resulting in 40% of tagged fish exiting the river (Fig. 2).

Time taken for smolts to exit the river was 18.52 ± 7.70 (mean \pm sd) days, with smolts travelling at a ground speed of 5.03 ± 1.73 (mean \pm sd) km day⁻¹. Smolts that did not complete riverine migration moved significantly slower (mean \pm sd = 3.55 ± 1.47 km day⁻¹) than those that did (*t*-test, $t = -2.6$, d.f. = 30.7, $p = 0.01$). The GLMM predicting smolt ground speed through the river showed that the interaction between the river height and lunar activity was significant, with increases in both variables leading to an increase in speed (LRT: $\chi^2(1) = 24.5$, $p < 0.001$). Smolt fork length (L_F) was not significant in the model predicting ground speed (LRT: $\chi^2(1) = 2.2$, $p > 0.05$). No variables were found to be significantly related to smolt river passage success.

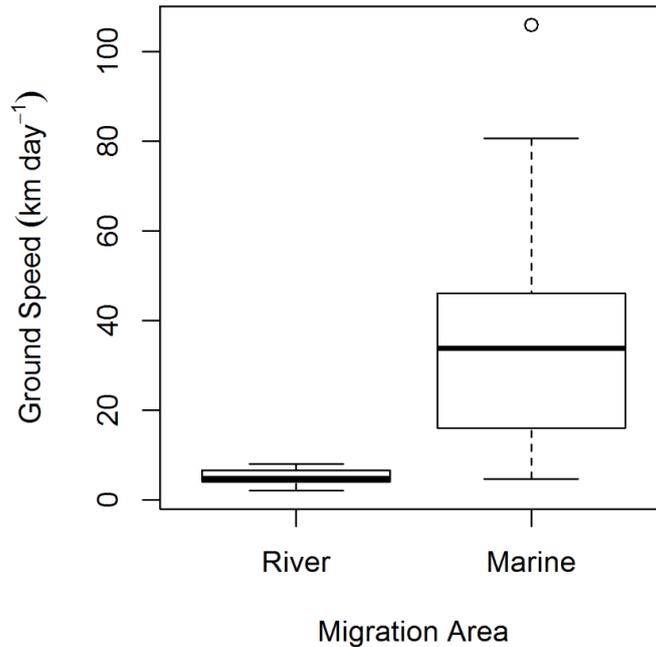


Fig. 3. A boxplot depicting the difference in ground speed during the river and marine migration for *S. salar* smolts that exited the river.

Marine Migration

Twenty fish were detected on D8 with all 20 being detected on ALS in the bay, indicating 100% marine survival, significantly greater than that observed in river migration ($\chi^2(1) = 5, p = 0.02$). Smolts that had completed riverine migration had a significantly greater ground speed in the early marine stage of migration (mean \pm sd = 37.37 ± 28.20 km day⁻¹) than in the river stage (Wilcoxon rank sum test, $W = 19, p < 0.001$; Fig. 3). Smolts spent less time in range of an ALS in the bay (mean \pm sd = 0.16 ± 0.12 hours) than in the river (mean \pm sd = 0.67 ± 1.33 hours), but not significantly different (Wilcoxon rank sum test, $W = 182, p > 0.05$).

There was no clear single vector of travel used by all smolts as they moved into the bay. The median point, however, of first detection for smolts entering the bay was east of B4 (Fig. 4). Two fish were detected on B1, four fish on B2, two fish on B3, six fish on B4, and six fish on B5 (Fig. 4). Significantly more smolts ($n = 15$) were first detected on bay ALS at night, with the rest ($n = 5$) being detected during the day ($\chi^2(1) = 5, p = 0.03$). The first point of detection

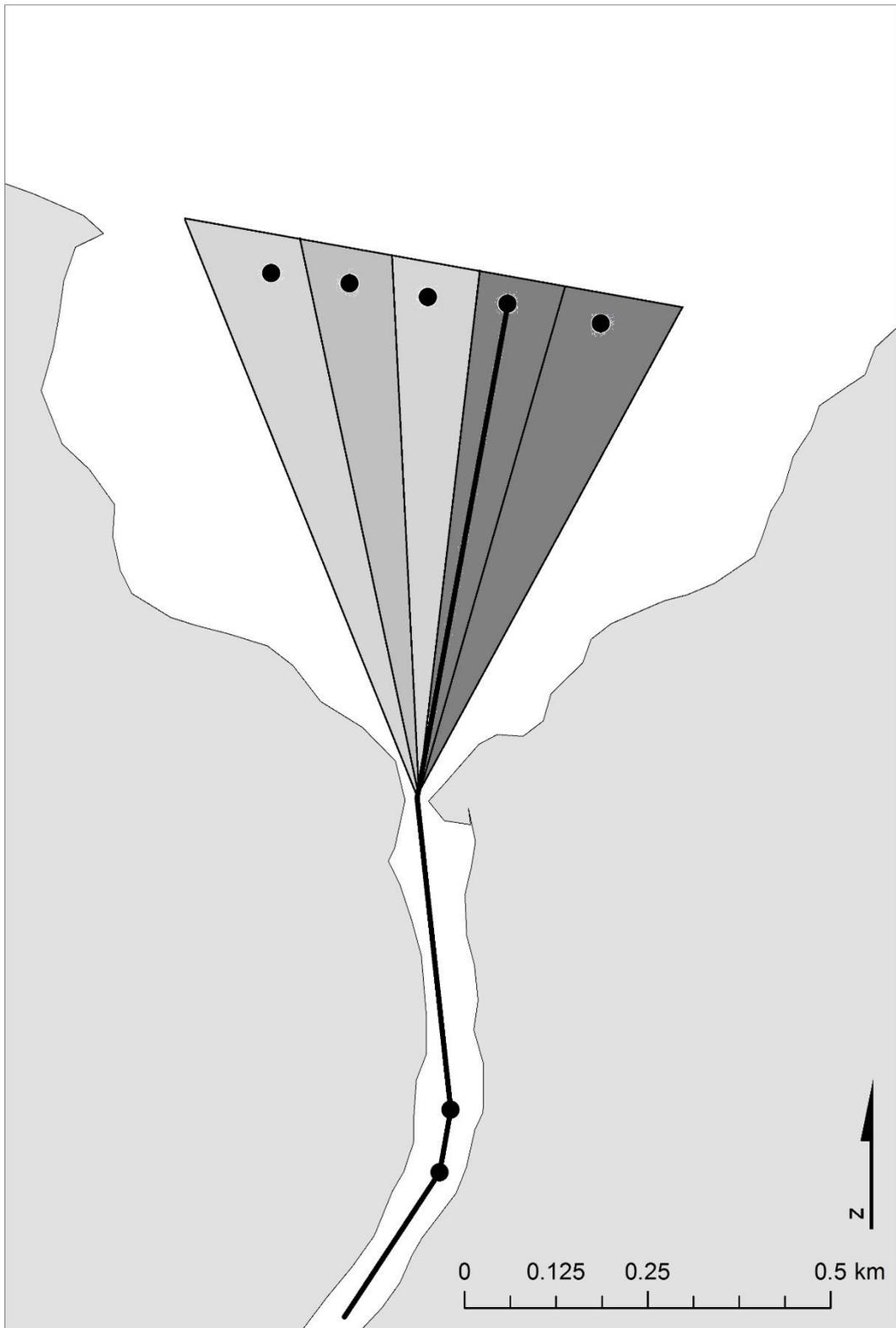


Fig. 4. The median *S. salar* smolt travel vector into the bay (solid line) with distribution of smolts upon first entry into the bay - light grey represents two smolts (B1 and B3), medium grey represents four smolts (B2) and dark grey represents six smolts (B4 and B5).

on the bay ALS was partly but only marginally significantly explained by the river height (GLM, $F_{1, 18} = 3.6, p = 0.07$), with smolts being detected on the most easterly ALS (B4 and B5) at times of greater river height.

Discussion

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 de-smolting has not been observed in *S. salar* (McCormick *et al.*, 1998). Once *S. salar* have begun smolting they have a limited amount of time to exit the river (Hoar, 1976; McCormick *et al.*, 1998). As there was no observed effect of the transmitter influencing whether fish left the river or not, a finding similar to other studies using salmonid smolts of similar fish sizes (Welch *et al.*, 2007; Rechisky & Welch, 2010; Newton *et al.*, 2016), along with the smallest tagged fish being detected on the marine array, death of those fish not detected within the river array cannot be directly associated with tagging. The most likely cause for smolt death before the first river array ALS is from natural causes. This is also supported by the similarity between the observed mortality rates from the release site to D3 and from D1 to D3.

Overall survival rate of the River Deveron is lower than that in other similar rivers (Moore *et al.*, 1995; Thorstad *et al.*, 2012b). Despite this, the rate of mortality in the Deveron is within the range reported in other *S. salar* seaward migration studies (Dieperink *et al.*, 2002; Thorstad *et al.*, 2012b). Although the cause of mortality in this study cannot be determined, predation is known to be a major source for mortality in rivers (Hvidsten & Møkkelgjerd, 1987; Heggnes & Borgstrom, 1988; McCormick *et al.*, 1998; Carter *et al.*, 2001; Dieperink *et al.*, 2002; Thorstad *et al.*, 2012b). Several mammal species exist in Scotland that are known to prey on salmonid species, such as the otter *Lutra lutra* (L. 1758) and the American mink *Neovison vison* (Schreber 1777). The River Deveron is host to a large population of *M. merganser* which is a

more likely source of major predation than mammals. Predation by either of these bird or mammal predators would prevent the tags from being detected downstream. This is due to the low frequency transmissions of the tags which prevent effective sound wave propagation through air (Melnychuk & Walters, 2010; Gjelland & Hedger, 2013; Hussey *et al.*, 2015).

There is also a long history of large resident *S. trutta*, a species which have been shown to feed heavily on *S. salar* smolts as they migrate downstream (Furey *et al.*, 2016), in the River Deveron. As the tag would remain in the water, further detections may be possible as *S. trutta* move through the river. However, no abnormal directional movements were recorded, with all tags being detected sequentially downstream or being removed altogether. River resident *S. trutta* often feed in particular sections of rivers, and so may not make any long-distance movements along the river (Klemetsen *et al.*, 2003). Therefore, *S. salar* smolts consumed by *S. trutta* between ALS may not be detected again due to the restricted *S. trutta* feeding ranges.

Speed of *S. salar* outward migration varies considerably between populations, with the main influences on speed being river discharge and photoperiod (McCormick *et al.*, 1998; Rand *et al.*, 2006; Martin *et al.*, 2012; Thorstad *et al.*, 2012b). The ground speed of the River Deveron smolts is at the lower end of the range reported by other studies, from 0.2 to 60 km day⁻¹ (Thorstad *et al.*, 2012b). Smolt river migration speed in this study was heavily dependent on river discharge and lunar brightness, indicating that smolts had increased speeds at times of elevated water velocity and bright nights. Nocturnal migration is a common predator avoidance strategy in outwardly migrating *S. salar* (Thorstad *et al.*, 2012b; Urke *et al.*, 2013), and so swimming on bright nights aids in fish's ability to see while being concealed from predators. Therefore, as expected, the majority of the river complete smolts in this study entered the bay at night. Some studies investigating early marine migration have reported a less defined diel migration, with some suggesting a complete switch to more active swimming during the day (Koed *et al.*, 2006; Hedger *et al.*, 2008; Dempson *et al.*, 2011). This could be the case after the

initial entry into the marine environment, and could therefore be the main migration strategy further out in the Moray Firth. Further tracking of smolts throughout coastal waters would be necessary to determine this.

Unlike other studies, there was no observed mortality during early marine migration. Suggested reasons for mortality have been predation and osmotic shock (Hvidsten & Møkkelgjerd, 1987; Davidsen *et al.*, 2009; Thorstad *et al.*, 2012a; b; Urke *et al.*, 2014; Vollset *et al.*, 2016). The lack of an estuary in the River Deveron and the bay's shallow depth may be the reasons for the absence of mortality through predation. Jepsen *et al.* (2006) reported that highest mortality at the river mouth of the River Eira was in a region of rapidly increasing depth, where the predators Atlantic cod *Gadus morhua* (L. 1758) and saithe *Pollachius virens* (L. 1758) could prey on smolts from beneath. *Salmo salar* smolts exiting the River Eira were also heavily preyed on by birds such as gulls *Larus spp.* (Jepsen, *et al.* 2006), but there was no observed predation by birds on tagged smolts in the bay of the River Deveron. This could 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 increased speed of smolts travelling through the bay may suggest that they were forced out of the river and through the bay by passive displacement of high river discharge (McCormick *et al.*, 1998; Rand *et al.*, 2006). But a more likely possibility may be that smolts actively left the river at a high discharge to make use of a potential freshwater wedge that would increase access to the bay before exposure to full-salinity marine water (Janardanan *et al.*, 2015; Nebra *et al.*, 2016). The speed through the bay is also within the limits of early marine migration speeds as seen in other populations (Okland *et al.*, 2006; Dempson *et al.*, 2011; Thorstad *et al.*, 2012b). The trajectory of smolts leaving the river was north-easterly which is also in line with the mouth of the Moray Firth and the way to the North Sea, indicating smolts actively swam out of the river and bay. Along with this swimming trajectory, it is important to note that the

smolts remained closer to the centre of the bay than to the coast, showing that they do not follow geographical features but have a greater mechanism for navigation, possibly by following water currents created by the high river discharge (Lacroix & McCurdy 1996; Thorstad *et al.* 2012b).

Conclusion

This study aimed to increase current knowledge on wild *S. salar* smolt river migration and the mortality of smolts entering directly into the marine environment without passing through an estuary. This study also aimed to describe the behaviour of smolts during the early marine migration phase. Both hypotheses, that marine mortality will be greater than river mortality and speed of migration in the river will be greater than marine migration speed, were rejected. *Salmo salar* smolts exhibited a higher mortality rate during river migration than in marine migration, a finding that has not been observed in other *S. salar* populations. Smolts also experienced a greater swimming velocity in the marine environment, exhibiting an innate navigational ability exiting the river with a trajectory aimed at the mouth of the Moray Firth. This is the first description of *S. salar* smolt behaviour and swimming trajectory in the early marine phase of migration in Scotland. Future research should focus on determining the underlying mechanisms of smolt navigation, as well as increasing the understanding of smolt behaviour in the early marine phase of migration.

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