

River Deveron 'Missing Salmon Project' 2019



**The Deveron, Bogie & Isla
Rivers Charitable trust**



Report compiled by the Scottish Centre for Ecology and the Natural Environment, University of Glasgow & Atlantic Salmon Trust

Contents

Executive Summary.....	3
River Deveron Highlights.....	4
Introduction.....	6
Materials and Methods.....	8
Results and Discussion.....	11
Next Steps.....	20
References.....	26
Appendix.....	28

Acknowledgements

We would like to express our thanks to all our financial partners for helping to fund the project, the six District Salmon Fishery Boards / Fishery Trusts in the Moray Firth and Marine Scotland. Without their help the project would not have been possible.

Executive Summary

In the spring of 2019, the largest acoustic telemetry project in Europe, the Moray Firth “Missing Salmon Project”, was initiated. The Moray Firth project partnership, led by the AST, comprises Glasgow University, the six District Salmon Fishery Boards / Fishery Trusts in the Moray Firth and Marine Scotland. Over 340 acoustic receivers were deployed from the headwaters of the rivers out into the open sea within the Moray Firth. Fish were captured in seven river systems (Deveron, Spey, Findhorn, Ness, Conon, Oykel, Shin) which all flow into the Moray Firth. Three tagging teams successfully captured and tagged 850 migrating smolts. The core aim of the project was to: 1) Identify how successfully smolts move down the main stem and into the transitional waters of the estuary and 2) Identify the marine migration routes.

All acoustic receivers were deployed prior to any fish being tagged and released. The majority of acoustic receivers were deployed in the marine environment by the MRV Alba Na Mara, funded by Marine Scotland Science. Fish were captured through close collaboration between tagging teams and local fishery boards who aided in the capture and pre-sorting of smolts ready for tagging. Smolts were tagged with Vemco V7 Acoustic Transmitters and were allowed to fully recover following tagging. The smolts were released a minimum of 45 minutes post- tagging. The tags used have a battery life in excess of 90 days.

Overall, year 1 of the project proved very successful. Recovery of acoustic receivers commenced in June and was completed in October 2019. A total of ~95 % of the receivers were recovered. Data downloaded from the receivers comprised of over 15million detections recorded throughout the study period, a significant amount of data. This report details the **initial analysis** of information so far gleaned from the data. Subsequent scientific reports will provide a detailed, quantitative analysis of the results. The aim of this report is to present descriptive data for the overall project but also focusing on river specific information.

The first year of the project has provided information on where fish losses in the seven rivers of the study occurred, during the first part of their ocean migration. From these initial analyses, it is clear that salmon migration through freshwater habitats during the migration

of the salmon is risky. On average, across all seven river systems, confirmed escapement (fish detected leaving the river, including Oykel and Shin tidal environments), was 49.2%. with a range of 9%-79%. Overall, for the Deveron, loss rate in freshwater was 0.75 %km⁻¹. This is well within the range of other rivers in the study, from 0.52% (Shin) to 5.95 % (Findhorn) fish per km.

Future analysis of the 2019 results will aim to better understand the factors governing the smolt migration, including variables such as environment, genetics and morphology. In 2020 the project will develop additional (complimentary) research themes in order to examine the in-river smolt migration phase more closely

River Deveron highlights

- Throughout the smolt run, a total of 125 smolts; 100 salmon smolts and 25 sea trout were tagged with acoustic tags (Vemco V7) over a 17-day period (13/4/19 to 30/4/19).
- Of the salmon tagged, 75 were standard acoustic tags and 25 predator tags.
- The Atlantic salmon smolts had a mean fork length of 133.6 mm and a mean weight 23.5 g. The mean tag burden (% of body weight) was 6.8%. The sea trout smolts sampled had a mean fork length of 162.1 mm and a mean weight 4313 g. The mean tag burden (% of body weight) was 3.94% (SD ± 0.98).
- Of the 100 salmon smolts, 38 smolts were estimated to have reached the furthest downstream receivers at the river mouth and 34 smolts reached the receivers in Banff Bay, giving a confirmed survival rate of 38% to the mouth and 34% to the sea.
- Overall, freshwater loss rate in freshwater was 0.75 %/km. The loss rate varied between 0.12%/km (Lower receiver) to 1.2%/km (Huntly Receiver).

- Freshwater receiver efficiency (proportion of the total number of tagged fish correctly detected at a receiver) averaged 99.4%. Six of the receivers operated at over 98% efficiency.
- The median ground speed for confirmed successful migrant was 0.05 m/s for river travel, 0.39 m/s for the travel to the Banff Bay, and 0.28 m/s for the travel to the Fraserburgh array.
- Confirmed successful migrant smolts took a median of 15.5 days to travel from the release site to the most downstream river receiver and 0.04 day from the most downstream receiver to the Banff Bay. They took 1.8 days to reach the Fraserburgh array from Banff Bay.
- Upon entering the sea, the salmon smolts showed strong directional movement, heading east, north east.

Introduction

Smoltification and extensive migration characterise the anadromous Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta*). Migration from a freshwater to saline environment is essential for individuals to rapidly grow in the richer feeding grounds offshore, optimising their growth rate and future reproductive output. When salmon parr reach a threshold size, they undergo physiological pre-adaptations to life in a saline environment through a process called smoltification (Kennedy and Crozier, 2010; Hvidsten *et al.*, 1995). The smolt run, occurring in spring, marks the mass migration of smolts to the sea. Smoltification and migration present numerous risks, which include an increased risk of predation, increased nutrient competition amongst smolts and stress as they undergo physiological adaptation to deal with the osmotic pressures once they reach their new environment (Kennedy and Crozier, 2010). Numerous studies have reported these risks as having resulted in high mortality rates during the run. A review by Thorstad *et al.* (2012) reported the mortality rates started at 0.3%, and rose as high as 7.0%/km (averaging 2.3%/km). High variation in mortality rates occurs due to the differentiating river conditions (Thorstad *et al.*, 2012) and predatory hotspots (Juttila, Jokikokko and Julkunen, 2005). In Scotland, similar scenarios have been observed, for example, higher rates of mortality were observed in the Deveron river (0.77% per km) than the early marine stage of migration (0.0% per km) (Lothian *et al.* 2018).

There is increasing concern over the declining marine survival rates of Atlantic salmon being recorded from most North East and South East Atlantic monitored populations since 1980 (ICES, 2019). In recent years, wild salmon marine survival from Scottish rivers is generally believed to be below 5%, and this represents a notable decline in survival now compared to recorded return rates of over 10% in the 1990s. In a fitting setting under 2019s 'International Year of the Salmon', the Missing Salmon Project launched the largest acoustic tracking project in Europe. The project planned to tag 800 salmon smolts and 50 sea trout smolts across 7 river catchments in the Moray Firth to identify what is happening to salmon and halt this decline.

This report outlines the overview of the **initial analysis** of data for fish tagged in the River Deveron and their downstream migration to the Moray Firth. Currently detailed modelling, and investigation of other factors in the study are ongoing and outlined in the Next Steps section.

This report will refer to detection of fish as 'confirmed survival,' Hence the data here refers to that of only fish which have been detected. A smolt that has not been detected does not necessarily imply that it has died, there are several other reasons possible for non-detection, including that the smolt may have been missed by the acoustic receiver. Efficiency and range testing will be subsequently used to model potential missed detections of fish and thus provide more robust estimates on confirmed survival estimates.

Materials and methodology

Nine acoustic receivers were deployed at six locations, at various intervals along the river, and a further three at Banff (Figure 1a). Where possible, receivers were positioned in deep, slow moving pools, which provide the most suitable conditions for detecting tagged fish as they move downstream.

Smolts were captured via two rotary screw traps, located in the Blackwater (grid reference 57.3622, -3.0321) and Allt Deveron (57.3636, -3.0317). Smolts of suitable size (>130mm Fork Length [nose to 'V' of the tail]) were selected for tagging thus limiting any tag burden effects. Throughout the run a total of 124 smolts were tagged, 100 salmon smolts and 25 sea trout smolts. Of the salmon tagged, 74 were standard acoustic tags (Vemco V7; 1.6 g air weight) and 25 predator tags (Vemco V7D; 1.7 g air weight). The acoustic tags emitted a 'ping' which is a unique ID, randomly every 15-35 seconds. Each tag was checked to confirm its activation. Fish were tagged over a 17-day period from 13/4/19 to 30/4/19.

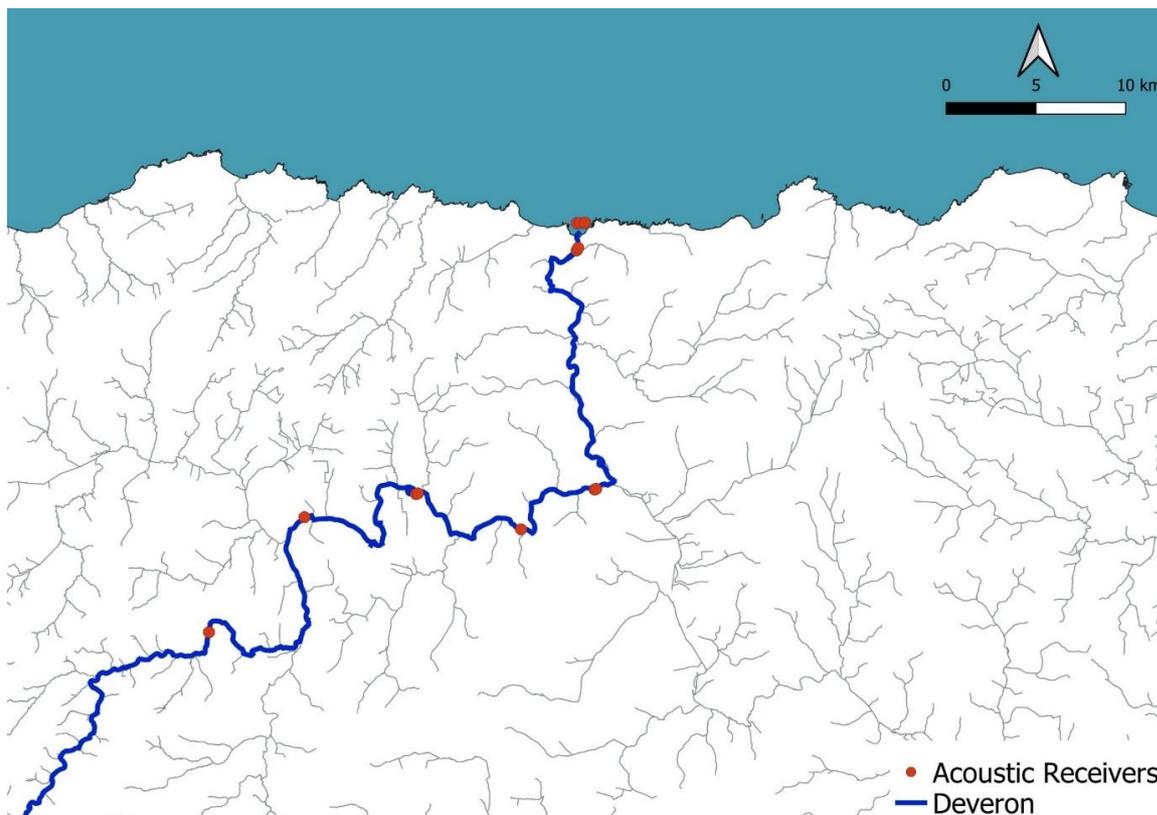


Figure 1a. Locations of the acoustic receivers along the River Deveron. Could we label them as follows us-ds: 1. Huntly, 2. Avochie, 3. Bridge of Marnoch, 4. Lower Netherdale, 5. Muiresk & 6. Banff.

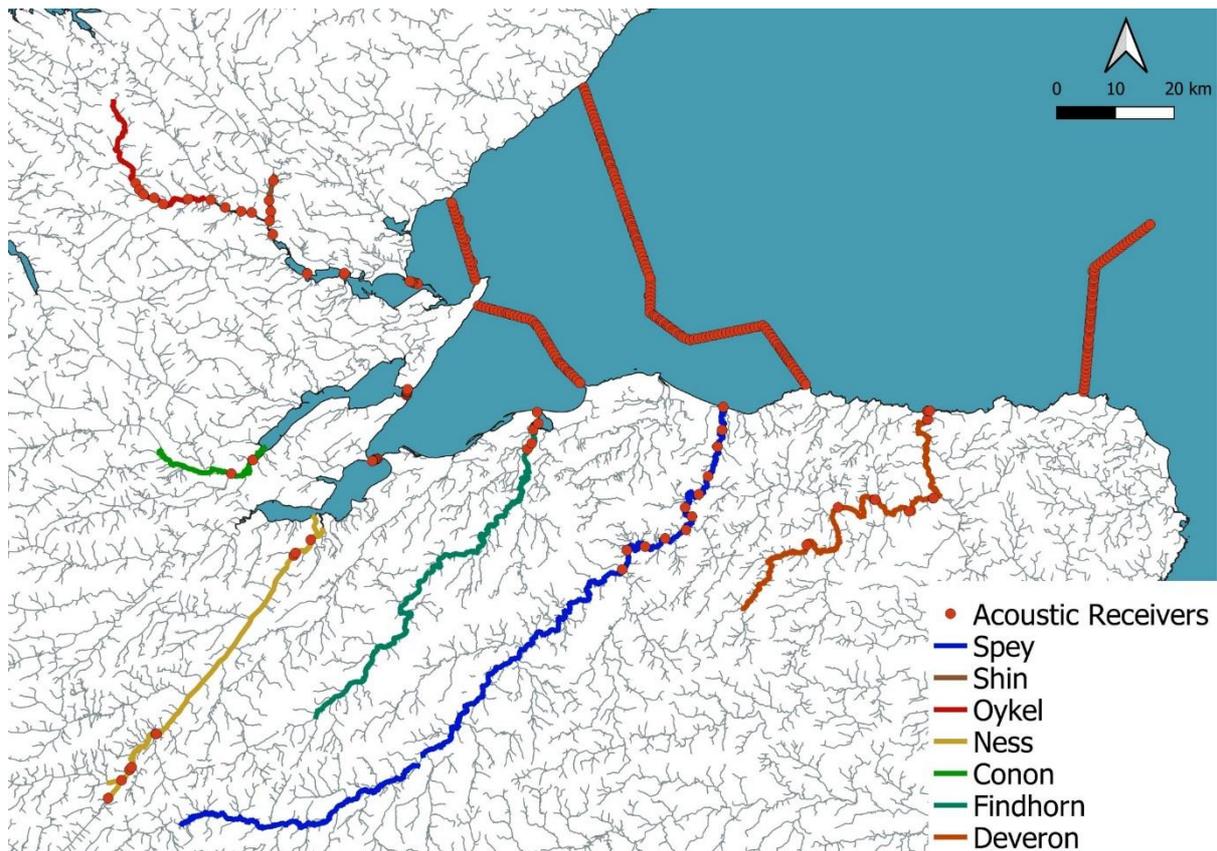


Figure 1b. Locations of the acoustic receivers across the Missing Salmon Project.

So as to mimic the progression of the natural smolt migration pattern as far as possible, the sampling teams tried to tag a number of fish each day that was proportional to the number sampled in the trap. In some situations the decision was taken to tag fish of an appropriate size opportunistically in order to try to keep sample sizes consistent from all the rivers.

Prior to tagging, acoustic tags were sterilized in absolute ethanol and rinsed in distilled water. Fish were anesthetized (MS222: 0.1g to 1L of water). Their fork length (mm) and mass (g) were measured and a photograph recorded for later morphometric analysis (Figure 2). Fish were placed on a v-shaped surgical pillow with their abdomen side up. A small incision (10-13mm in length) was made anterior of the pelvic girdle where the tag was inserted. The incision was closed with two interrupted absorbable sutures (Ethicon VICRYL). All fish were oxygenated initially with 100% river water throughout the procedure, a 50% anesthetic dilution was used to maintain anesthesia if the fish showed signs of recovery. Finally, a fin clip (adipose fin) was collected from the fish and stored in absolute ethanol for later genetic analysis. The fish were then placed in a bucket containing aerated river water and allowed to

fully recover (approx. 5 minutes), groups of tagged fish were then held within a recovery box (0.5m.sq perforated holes) and placed in the river, within an area of gentle flow and allowed to acclimatize for a minimum of 45 minutes prior to release. Fish were released approximately 200 meters downstream of the smolt trap in an effort to avoid recaptures.



Figure 2. A morphometric photograph was recorded for each tagged smolt

Receivers and manual tracking

In addition to the 9 acoustic receivers (Figure 1a), a Vr100 and omnidirectional hydrophone were deployed throughout the period of 19/6/19 to 21/6/19. Manual tracking took place from downstream of the tagging sites to 5 river miles upstream of the first receiver (at Huntly), whereas each pool along the river were sampled.

Results and Discussion

Length and weight frequencies

The mean fork length of the tagged Atlantic salmon smolts encountered over the course of the study in the River Deveron was 133.6 mm and the mean weight of the tagged smolts was 23.5 g. Salmon smolts over 130mm in length represent a small percentage of the smolt population from the upper tributaries (5.4% of Blackwater smolts and 6.4% of Allt Deveron smolts in 2019). The tags weigh 1.6 g which results in an average tag burden (% of body weight) of 6.8% (SD \pm 0.71). The range of salmon smolt sizes and weights among rivers in the study varied from 133.6 mm (Deveron) to 140.3 mm (Ness) and from 23.5 g (Deveron) to 28.8 g (Ness).

The mean length of the tagged sea trout smolts was 162.1 mm and the mean weight was 43.1 g. The tags weigh 1.6 g which results in an average tag burden (% of body weight) of 3.94% (SD \pm 0.98). The range of sizes and weight among rivers in the study varied from 151.0 mm (Findhorn (n=1)) to 162.1 mm (Deveron) and from 29.4 g (Findhorn (n=1)) to 43.3 g (Deveron).

A primary concern in migration behaviour studies that incorporate telemetry is that the implant of acoustic tags may impact fish behaviour and buoyancy compensation, impairing their swimming ability. The generally accepted '2% rule' states tag burden should not exceed 2% of dry body weight in salmonids. However, further studies have reported transmitters up to 7% (Smircich and Kelly, 2014) and as high as 12% body weight (Brown *et al.*, 2011) as having negligible impacts on swimming ability. In this study the tag burden did not exceed 8% of wet weight.

Survival

Of the 100 salmon smolts released, 38 individuals (38.0%) were detected leaving the River Deveron at Banff and 34 individuals (34.0%) were detected in the sea between Banff and Macduff. Overall there was a decrease in the detection rates of smolts further downstream with an overall loss rate of 0.75 % fish per km (Figure 3 and Table 1). This is well within the range of other rivers in the study, from 0.75% (Deveron) to 5.95 % (Findhorn) (Figure 4; Appendix 1).

Receiver Efficiency

Receiver efficiency was calculated by determining the number of individuals which were detected on receivers downstream of the specific receiver that was being used. Freshwater receiver efficiency averaged 99.4%, with six receivers operating at over 98% efficiency (Figure 3 and Table 1).

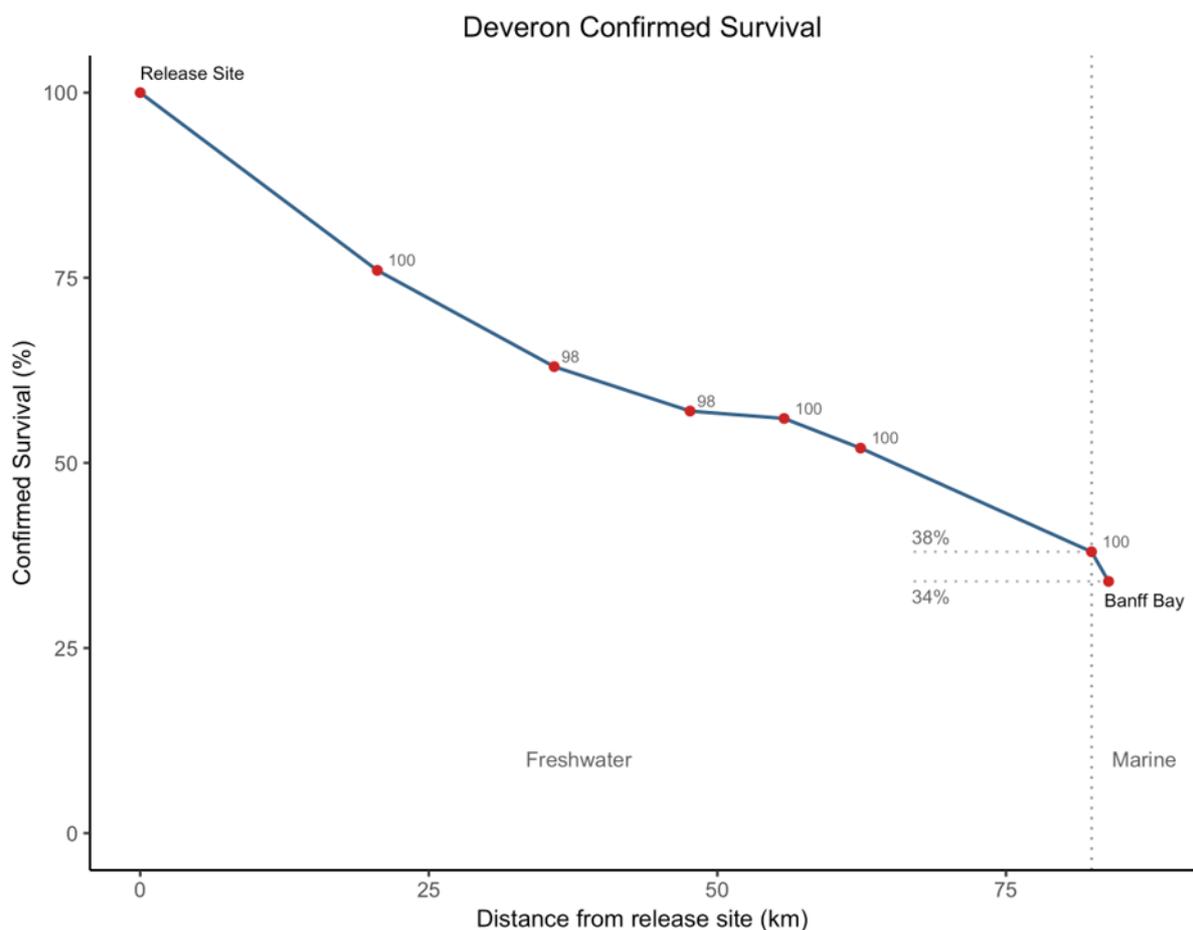


Figure 3. Confirmed survival (%) of smolts at increasing distance from the release site on the Deveron River. Red dots represent receivers, and detection efficiency (%) of each freshwater receiver is provided. *Please note that the marine array efficiencies are not complete as the Fraserburgh array was a partial array and not a fully closed array. The efficiencies of the marine arrays will be determined through modelling and simulations (see Next Step section).

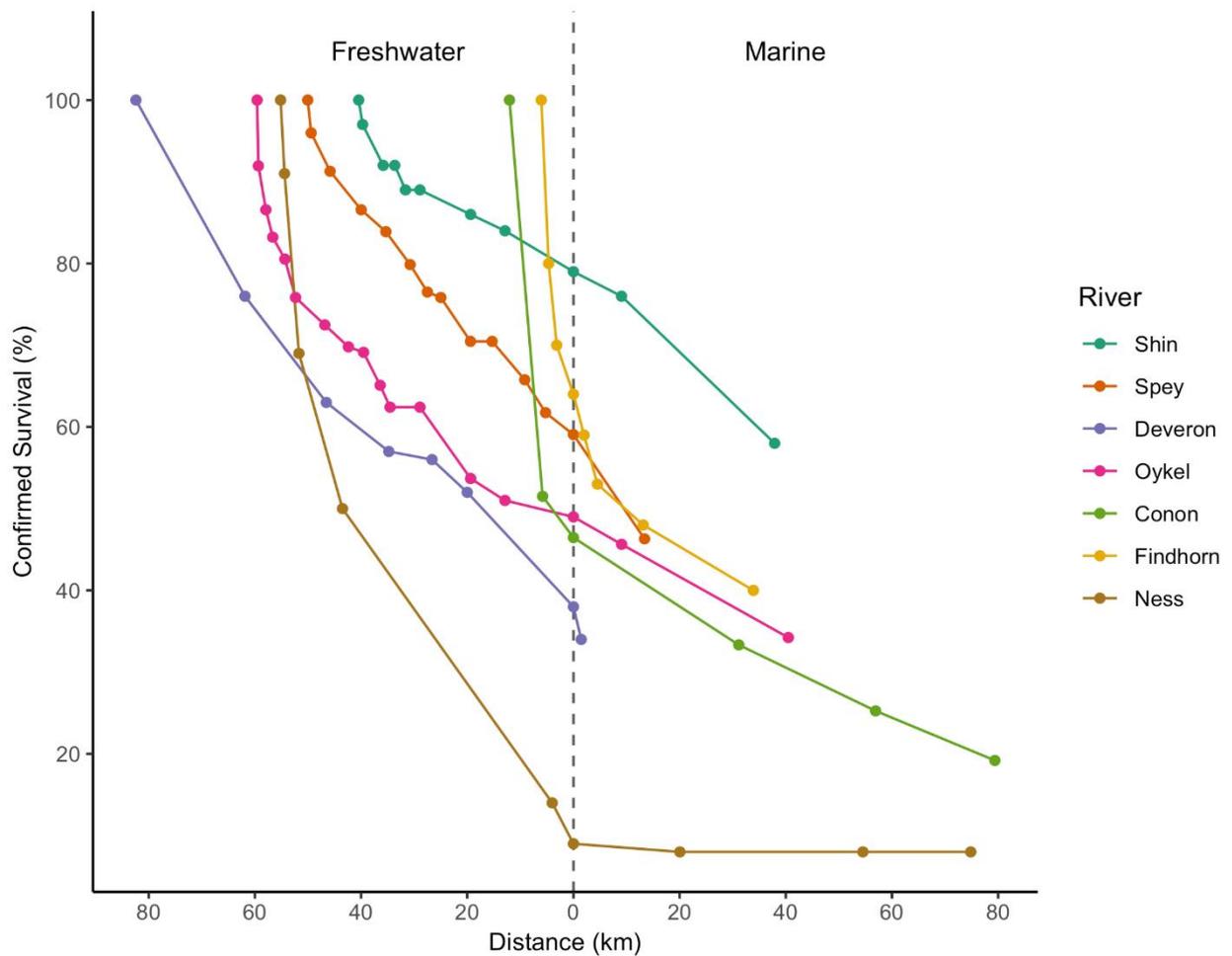


Figure 4. Confirmed survival (%) of salmon smolts for the seven rivers of the Moray Firth, with distance of smolt migration undertaken. Both freshwater and marine environments are included.

Rate of Movement (ROM)

To determine speed of migration, medians are given (in place of means) as due to the nature of the data, estimates of means can be skewed by the behavior of a small number of fish. Confirmed successful migrant smolts took a median of 15.5 days to travel from the Deveron release site to the most downstream river receiver, 0.04 days from the most downstream receiver to the Banff Bay, and 1.8 days to reach the marine Fraserburgh array (Figure 5). This represents a median ground speed of 0.05 m/s for river travel, 0.39 m/s for the marine environment travel to the Fraserburgh array, and 0.28 m/s (Figure 6).

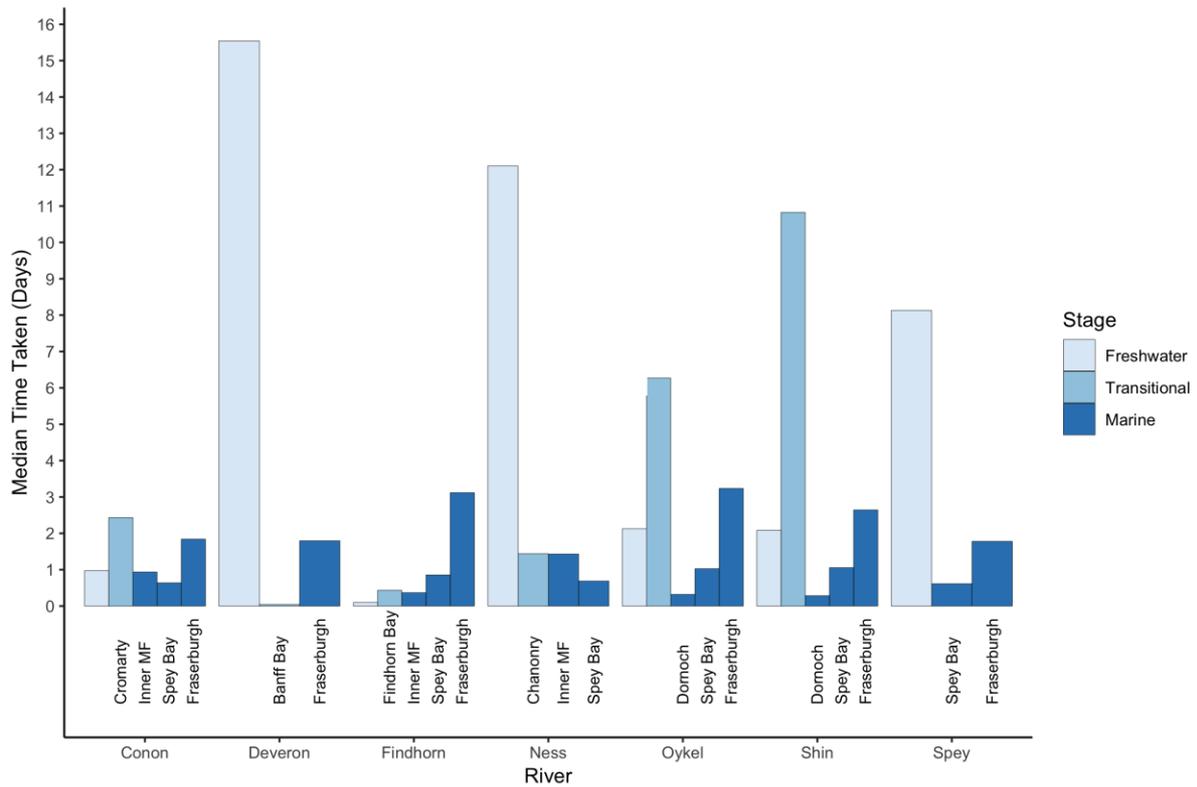


Figure 5. Median time taken by smolts to travel from the release site, to the mouth of the river, and then to each marine arrays. *Please note these values are only for fish that successfully migrated from release site to the Fraserburgh marine array. Distance travelled is not taken into consideration (see Figure 6 for standardised values among rivers).

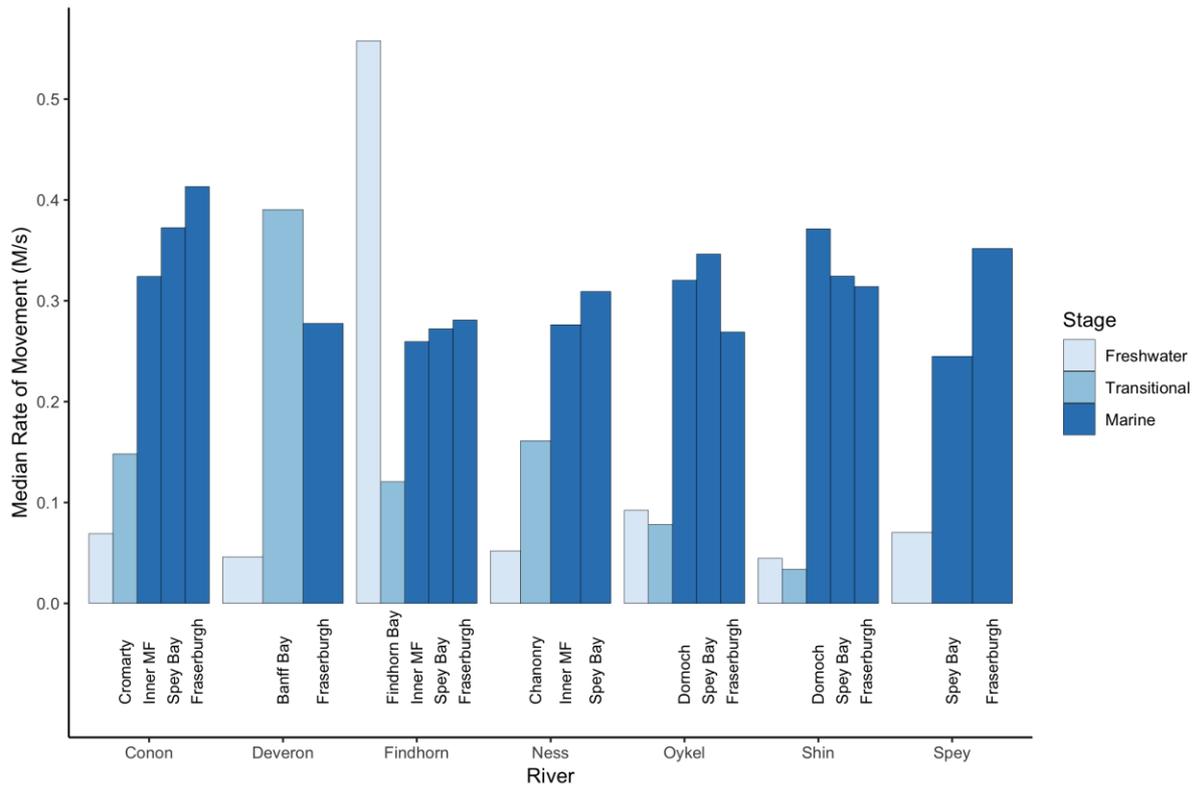


Figure 6. Median speed of smolts from all rivers travelling from the release site, to the mouth of the river, and then to each marine arrays. *Please note these values are only for fish that successfully migrated from release fish to the Fraserburgh marine array.

Residency Times

For residency time, medians are given (in place of means) as due to the nature of the data, estimates of means can be skewed by the behavior of a small number of fish. The residency time, is the total time an individual fish spent at a single receiver. A new residency event was assigned if the fish went undetected for a period of 12 hours (e.g. to correspond with the day vs. night migrating timeline) thus fish could have multiple residency events at a single receiver (although this was rare). In general, residency times of tagged fish were low on the River Deveron (Figure 7 and Table 1) and in the marine environment (Table 1). For the Deveron River, the higher residencies were found at Muiresk and Banff Bay receivers.

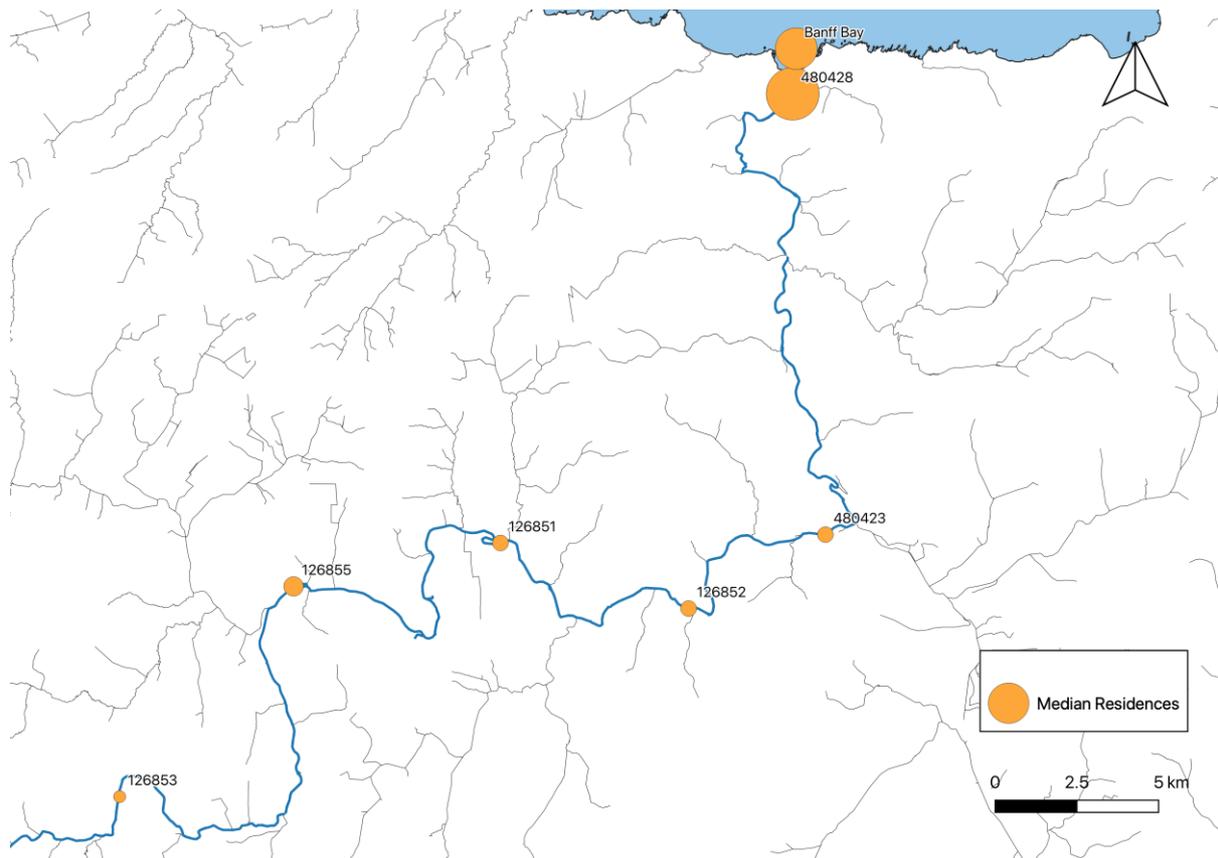


Figure 7. Median residency time of smolts on the Deveron River, moving downstream. Larger Symbols indicate longer residency times

Marine migration route/direction

Salmon smolts did not appear to show shoaling behavior when exiting the mouth of the river for the marine environment. However, as the movement of the majority of the (un-tagged) smolt population was not recorded this should be treated with caution. A split pattern of direction was detected when smolts exited the mouth of the river, with two spatial clusters. Overall, the salmon smolts showed strong directional movement, heading east, north east (Figure 8). This is well within the range of patterns expressed by the other rivers in the study (Figure 10). Sea trout generally also showed a similar directional movement to salmon smolts when exiting the mouth of the river for the marine environment. This contrasts with the generally non-directional movement recorded in other rivers (Figure 9 and 11).

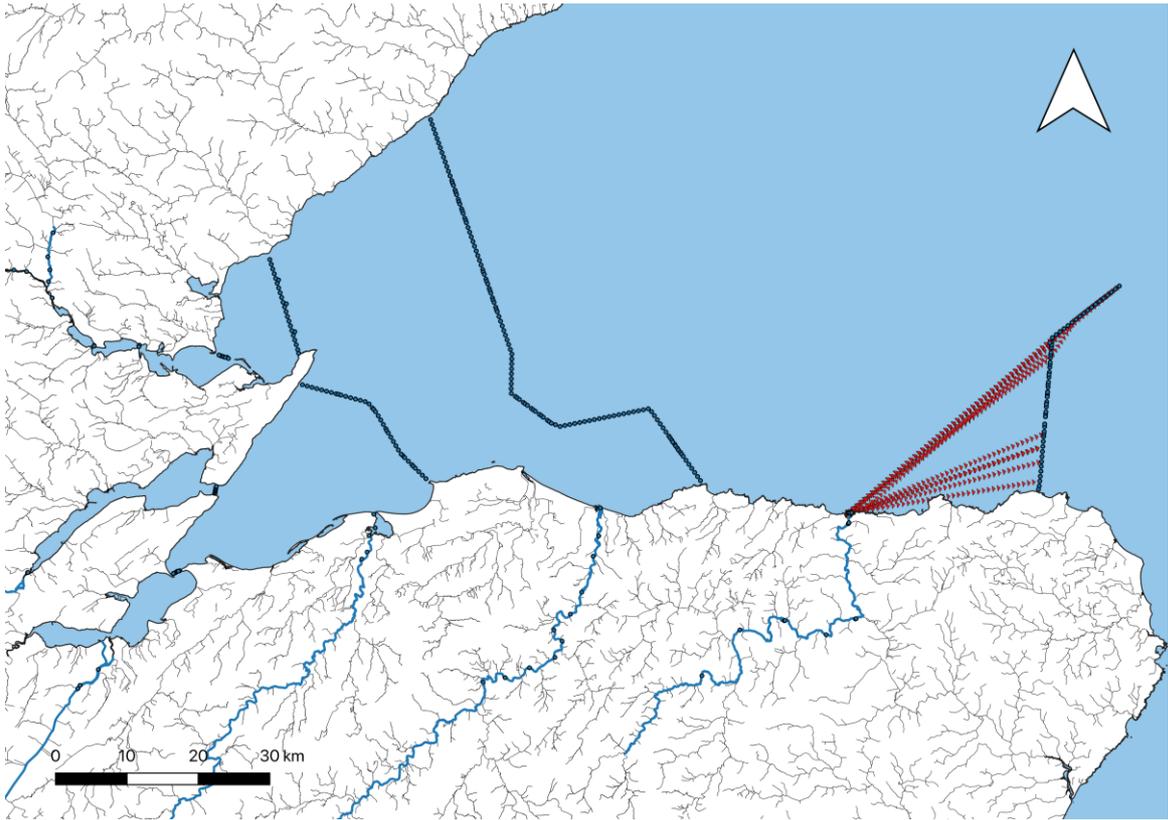


Figure 8. Marine migration direction of salmon smolts exiting the Deveron River, moving towards the Fraserburgh array.

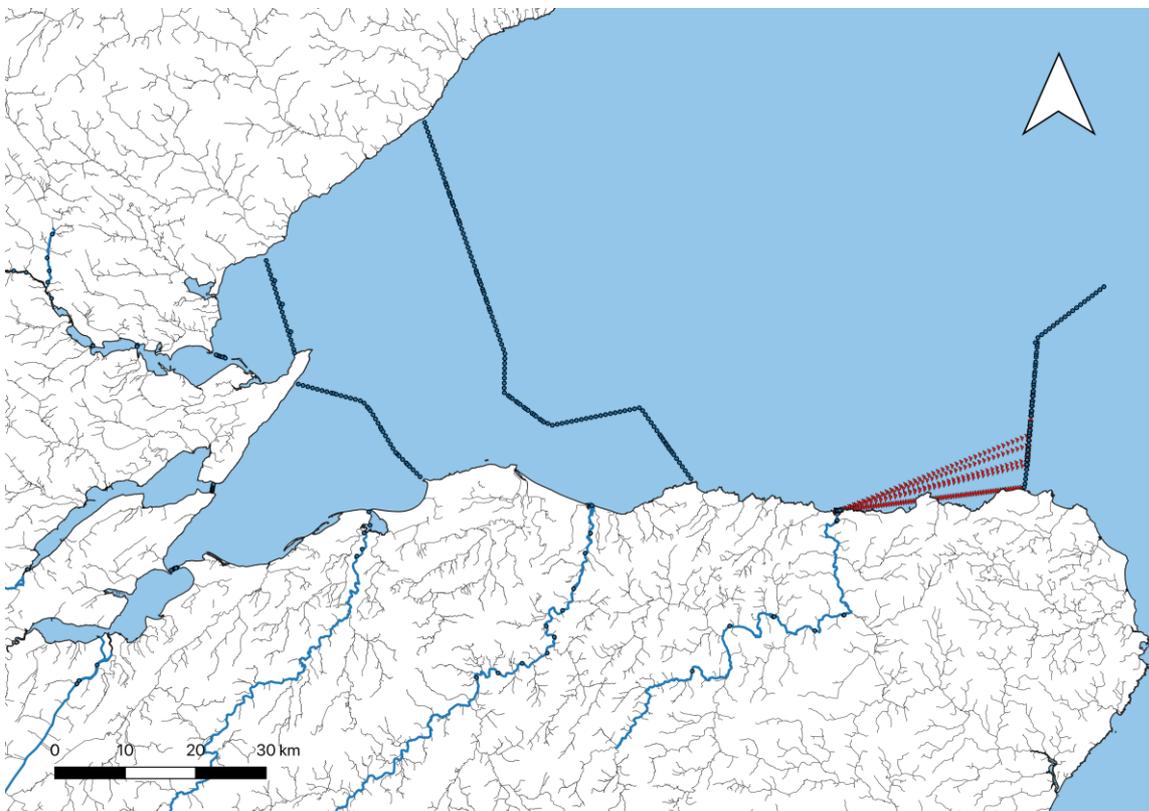


Figure 9. Marine migration direction of sea trout smolts exiting the Deveron River, and recorded at the Fraserburgh array.

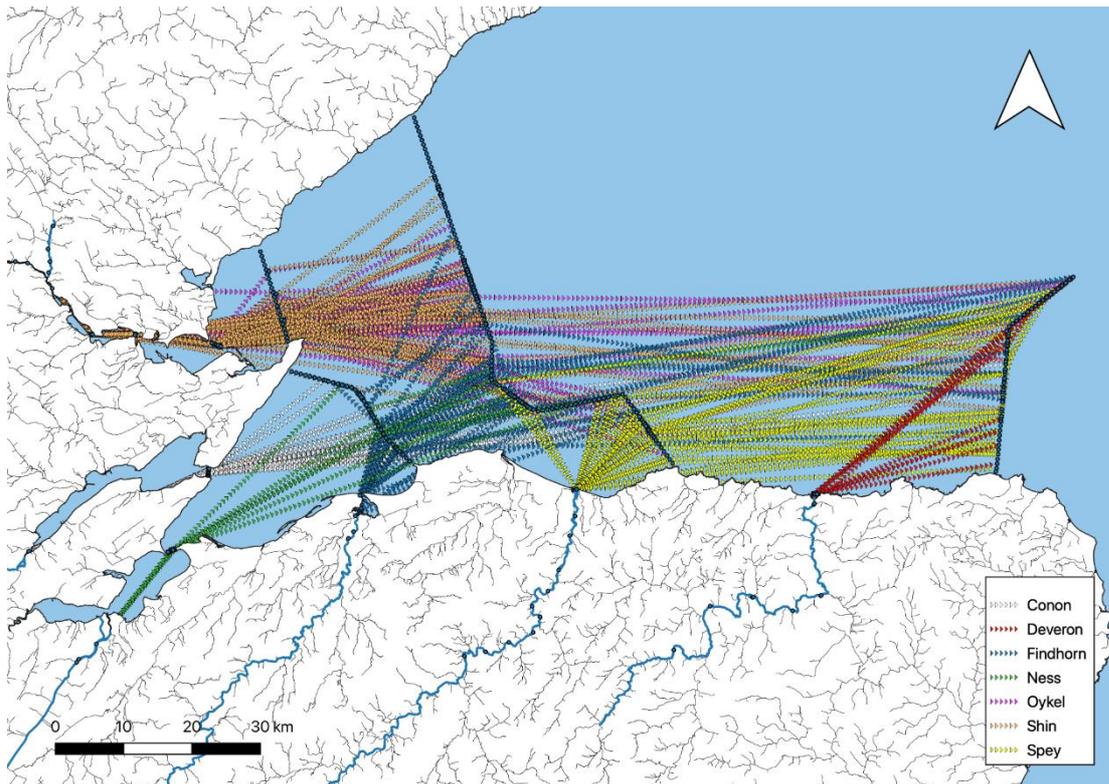


Figure 10. Marine migration direction of salmon smolts for the seven rivers of the Moray Firth, moving towards the Spey Bay and Fraserburgh arrays.

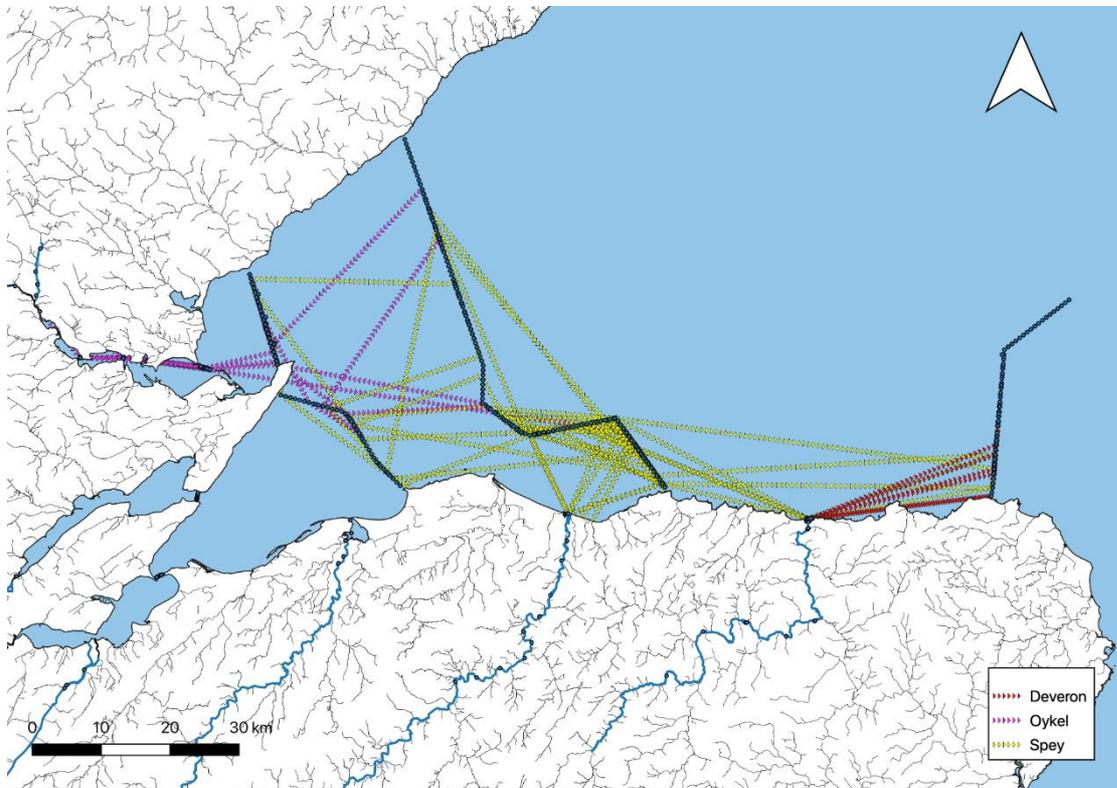


Figure 11. Marine migration direction of sea trout for three rivers of the Moray Firth, moving towards the Spey Bay and Fraserburgh arrays.

Table 1. Metrics of tagged fish that were detected at the reach scale (between two receivers) in the Deveron River. Values are for all fish detected at least one time.

Receiver	Distance (km)	Distance Diff. (km)	Efficiency (%)	Confirmed Survival (%)	% losses per km	Median residences (mins)**	Median ROM (m/s)	Median duration (secs)
Release Site	0	0	NA	100	NA	NA	NA	NA
126853	20.54	20.54	100	76	1.17	1.72	0.06	335454.5
126855	35.86	15.32	98.4	63	0.85	7.11	0.09	179627
126851	47.63	11.77	98.2	57	0.51	5.15	0.12	94885
126852	55.78	8.15	100	56	0.12	4.28	0.10	80289.5
480423	62.4	6.62	100	52	0.60	4.29	0.04	161203
480428	82.41	20.01	100	38	0.70	27.03	0.08	253730
Banff Bay	83.884	1.474	NA	34	2.71	19.18	0.39	3775.5
Fraserburgh	118.145	34.261	NA	NA	NA	6.20	0.28	155013

*Please note that the marine array efficiencies are not fully tested because Fraserburgh array was a partial array and not a closed array. Efficiencies of marine arrays will be determined through modelling and simulation (see Next Step section).

Next Steps

2019 Quantitative Data Analysis (University of Glasgow and AST)

For a more thorough understanding of the data, a variety of statistical models will be used to explore a potentially more complex set of questions. We will include all data from smolt migration across all rivers so as to provide a robust and thorough analysis of 2019 data. Some of the areas which will be investigated are:

-Determine efficiencies of marine arrays through modelling and simulation.

-Migration direction/success – How do smolts decide on their migration routes using the cues they have available?

A range of factors that could impact on the migration patterns will be examined in the analyses, including:

- Marine migration directionality; vector of travel (river and marine environments)
- Does marine migration directionality affect survivorship?
- Morphology (body shape / proportions) – what makes a successful migrating fish? Can we find characteristics that may affect confirmed survival (morphology is likely to vary among the rivers and may be among years)?
- Are there Sex differences in survival and behaviour? Genetics analysis, currently underway, will allow us to determine the sex of individual smolts. – is there a difference in survival between sexes; in river or marine migration?
- Timing – are fish arriving at the marine arrays at roughly the same time? Is there evidence of migration synchronicity? Are smolts from different rivers merging into groups in the marine environment?
- Do different river types show different patterns of migration passage from freshwater into the marine arrays, here we will compare rivers that open directly to the sea (e.g., Deveron) and rivers and that have sea loch type estuaries (e.g., Conon, Shin, and Oykel)?
- Are fish congregating before entering the marine environment?

- Do fish that migrate through the same areas compared with those fish that take alternative routes, show different migration success?
- Incorporate the temporal and environmental aspects into our analyses (e.g. day vs night, tidal events, precipitation, flow, temperature)?
- Looking at the migration patterns, grouping and temporal aspects we can try to visualise this by animating all the movement (e.g. day vs night, tidal events, precipitation, flow, temperature).

Freshwater Study 2020

As the rivers are the priority areas for understanding where fish are being lost the number of receivers in freshwater will be doubled in the second year of the study to increase the resolution at which the problem can be examined. A minimum of 700 salmon will be tagged across the seven rivers, as a repeat of the 2019 work. Alongside the tagging work, a predator pilot study will be conducted, as described below.

Marine Study 2020

The Spey Bay to Brora marine array will be reinstated in the 2020 study, as the work in 2019 indicated a very high efficiency in detecting tagged fish and acceptable losses of receivers from fishing activities. This configuration of the array for 2020 will allow for estuarine and coastal mortality information to be collected in a comparable way to 2019.

Buoyancy Ocean Glider

In addition to the above, there will be a trial of a buoyancy glider to track smolt migration outside of the Moray Firth. This will add to the limited knowledge on Scottish smolt migration routes beyond in near coast and will provide additional information to help validate the Marine Scotland smolt dispersal model. The exact route of the glider is currently being determined with the University of East Anglia and Marine Scotland. However, it is likely to be the offshore area to the north east of the Moray Firth.

The key deliverables of the 2020 programme will be:

1. Build on the success of the 2019 programme to ensure the results are valid between years.
2. Begin to understand the reasons for the high loss of salmon smolts in the freshwater environment (see predation study below).
3. Increase our understanding of smolt migration routes by locating them further out to sea and validating the smolt dispersal model.
4. Support the Likely Suspects Framework by providing key information on domains and associated pressures / mortality factors.

Genetics study (AST, Hull University, and University of Glasgow)

The ability to tag and track individual salmon will uncover where and when salmon are being lost on their journey downstream. But understanding why they disappear is more difficult. By extracting the DNA from fin clips of fish with a known migration pattern, and success rate and by studying the genomes of the missing individuals compared to the successfully migrating ones, we may be able to identify why some fish and not others disappear.

Fish from two rivers will be used to:

- Compare immune response genes to understand the role parasite viral or bacterial burden, might play in migration success.
- Associate genetic types with migration success and body shape.
- Identify genomic signatures for different populations from different tributaries.
- DNA fingerprint successful individuals to track their eventual return as adults (after the battery in the tag has run out of power)

This will allow us to look for genomic associations between migratory traits, migration success and genetic regions, while also allowing us to demonstrate differences between populations from closely related tributaries, should there be any. It is possible that there are different processes affecting fish from different rivers, and this focussed strategy should give us the

power to detect that. Ideally, given a successful outcome, we could then scale our study up across all rivers.

Predator study (AST and University College Dublin)

Predation of smolts by birds, fish and mammalian predators has the potential to substantially impact juvenile and smolt survival. This reduced survival may, in turn, negatively affect adult returns to freshwater systems. However, both the scale and the timing of predation by these is little known, and largely subject to anecdotal claims. Indicative results from Moray Firth 2019 tracking project suggest higher than expected losses of smolts in-river and so there is a need to direct efforts to determine why this is happening. The following research questions are proposed as the guiding aims for a programme of predation studies in the Moray Firth in 2020 (and 2021).

1. Are predators responsible for the majority of smolt losses during in-river migration period?
2. If predation is responsible for the loss of a high proportion of the smolts in-river for the loss of smolts, what can be done about it?
3. If predation is responsible for losses of smolts during the in-river migration, does this actually lead to a correspondingly reduced adult return rate?
4. What groups of predators are responsible, and what proportions of the smolt run are lost to each group?
5. If predation is responsible for the loss of a high proportion of the smolts in-river then how does smolt tag burden influence the predation rate?
6. If predation is responsible for the loss of a high number of smolts in-river then how does smolt size, timing of migration and river conditions influence the severity of this pressure?

Clearly, advancing all of these in 2020 is not possible, and we acknowledge that Marine Scotland Science is planning a programme of predator research in 2020 and 2021. The research outlines presented here will compliment these plans and we aim to work collaboratively with MSS in this important area of research.

1. Avian predator abundance and distribution on rivers

In order to advance our knowledge about the distribution of avian predators within the Moray Firth rivers, one basic information requirement is a robust method for assessing population size and distribution at various times of the year. Canoe and ground based surveys have their limitations for counting birds but aerial survey methods may be possible and improve accuracy. Drone technology is advancing rapidly and missions in the UK can currently be flown 1km from an operator and up to 120m in height. Thermal imaging cameras can be carried and are coupled with regular cameras to provide a range of resolution options for warm-blooded targets, which will alter depending upon the height and also the width of the river corridor being surveyed.

2. Use of predator scat (faeces) and eDNA analysis as a quantitative tool to determine predation on salmon smolts

Molecular analysis of fresh avian and mammalian predator scat (faeces) can provide a non-invasive and accurate metric for estimating the composition of fish species that are consumed. Importantly, it may allow the estimation of the proportion of salmon and also the other fish in predator diets (otter, mink, heron, various gulls, cormorant and goosander / mergansers) throughout a season, or from particular locations (hotspots). The scat also contains genetic material from the predator that can be fingerprinted to identify species and potentially an individual. The suite of new techniques offer potential to use scat to investigate if the salmon predator population is made up of salmon specialists or mobile opportunists. The programme of work will focus on describing temporal and spatial changes in the pattern of salmon parr and smolt predation through the year.

3. Radio tracking of juvenile salmon to determine predation impacts

With the indications from tracking in 2019 suggesting considerable smolt losses in-river, there is now an urgent requirement to find out what is actually happening to the fish. Radio telemetry for fish is limited to use in freshwater systems, but can enable a higher level of spatial resolution for tag location than is possible using the current acoustic tagging system and static receivers. By using radio tags (or small acoustic tags and mobile receivers if tests

prove them to be more suitable) the fate of individual fish can be determined more clearly during their in-river migration. An important refinement to this tracking study will be to differentiate if smolts lost from the migrating population are being removed from the water, or if they remain in the river. This will allow refinement of estimates of the proportion of smolts that are lost to avian or aquatic predators during in-river migration, and an assessment of factors that influence severity.

References

Brown, R. S., Cooke, S. J., Anderson, W. G., McKinley, R. S. (2011). Evidence to Challenge the “2% Rule” for Biotelemetry. *North American Journal of Fisheries Management*. 19(3). [online] Available at: [https://afspubs.onlinelibrary.wiley.com/doi/abs/10.1577/1548-8675\(1999\)019%3C0867:ETCTRF%3E2.0.CO;2](https://afspubs.onlinelibrary.wiley.com/doi/abs/10.1577/1548-8675(1999)019%3C0867:ETCTRF%3E2.0.CO;2)

Hvidsten, N. A., Jensen, A. J., Vivås, H., Bakke, O., Heggberget, T. G. (1995). Downstream Migration of Atlantic Salmon Smolts in Relation to Water Flow, Water Temperature, Moon Phase and Social Interaction. *Nordic Journal of Freshwater Research*. 70.

ICES. 2019. Working Group on North Atlantic Salmon (WGNAS). ICES Scientific Reports. 1:16. 368 pp. <http://doi.org/10.17895/ices.pub.4978>

Jutila, E., Jokikokko, E., Julkunen, M. (2005). The smolt run and postmolt survival of Atlantic salmon, *Salmo salar* L., in relation to early summer water and temperatures in the northern Baltic Sea. *Ecology of Freshwater Fish*. 14(1). [online] Available at: <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1600-0633.2005.00079.x>

Kennedy, R. J., Crozier, W. W. (2010). Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology*. 76(7). [online] Available at: <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1095-8649.2010.02617.x>

Lothian, A.J., Newton, M., Barry, J., Walters, M., Miller, R.C. and Adams, C.E., 2018. Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. *Ecology of Freshwater Fish*, 27(2), pp.549-558.

Smirich, M. G., Kelly, J. T. (2014). Extending the 2% rule: the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. *Animal Biotelemetry*.

2(16). [online] Available at:

<https://animalbiotelemetry.biomedcentral.com/articles/10.1186/2050-3385-2-16>

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*. 81(2). [online] Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1095-8649.2012.03370.x>

Appendix 1.

Metrics of among the seven rivers of the Moray Firth 2019 tracking project. Values for tagged fish that were detected, at the reach scale (between two receivers). Values encompass all fish detected at least one time.

River	Receiver	Distance (km)	Distance Diff. (km)	Confirmed Survival %	Efficiency %	% losses per km	Median residences (mins)	Median ROM (m/s)	Median duration (sec)
Conon	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Conon	481433	6.23	6.23	51.52	100.00	7.78	13.67	0.02	311034.0
Conon	480419	12.05	5.81	46.46	100.00	0.87	15.89	0.07	84119.0
Conon	Cromarty	43.19	31.14	33.33	100.00	0.42	10.88	0.15	210135.0
Conon	Inner MF	68.97	25.78	25.25	92.00	0.31	8.53	0.32	80902.0
Conon	Spey Bay	91.43	22.46	19.19	NA	0.27	4.03	0.37	55202.5
Conon	Fraserburgh	152.93	61.50	NA	NA	NA	2.43	0.41	159015.5
Shin	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Shin	481450	0.74	0.74	97.00	100.00	4.03	6.79	0.01	119326.0
Shin	480409	4.62	3.88	92.00	36.96	1.29	0.90	0.08	72141.5
Shin	480417	6.79	2.17	92.00	100.00	0.00	5.22	0.04	59004.0
Shin	481426	8.81	2.02	89.00	98.88	1.49	2.03	0.24	8426.0
Shin	480408	11.53	2.72	89.00	100.00	0.00	73.78	0.03	86385.0
Shin	481435	21.07	9.54	86.00	93.02	0.31	238.40	0.07	141907.5
Shin	481444	27.55	6.48	84.00	96.43	0.31	14.11	0.51	12590.0
Shin	483468	40.45	12.89	79.00	78.48	0.39	10.63	0.28	46759.0
Shin	Dornoch	49.50	9.05	76.00	92.11	0.33	11.76	0.37	24642.0
Shin	Spey Bay	78.34	28.84	58.00	NA	0.62	5.99	0.32	91235.0
Shin	Fraserburgh	148.01	69.67	NA	NA	NA	8.45	0.31	228432.5
Deveron	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Deveron	126853	20.54	20.54	76.00	100.00	1.17	1.72	0.06	335454.5
Deveron	126855	35.86	15.32	63.00	98.41	0.85	7.11	0.09	179627.0
Deveron	126851	47.63	11.77	57.00	98.25	0.51	5.15	0.12	94885.0
Deveron	126852	55.78	8.15	56.00	100.00	0.12	4.28	0.10	80289.5

Deveron	480423	62.40	6.62	52.00	100.00	0.60	4.29	0.04	161203.0
Deveron	480428	82.41	20.01	38.00	100.00	0.70	27.03	0.08	253730.0
Deveron	Banff Bay	83.88	1.47	34.00	NA	2.71	19.18	0.39	3775.5
Deveron	Fraserburgh	118.15	34.26	NA	NA	NA	6.20	0.28	155013.0
Spey	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Spey	126845	0.65	0.65	95.97	98.60	6.20	3.17	0.02	34678.0
Spey	480407	4.22	3.57	91.28	98.53	1.32	1.33	0.75	4729.0
Spey	480410	10.07	5.85	86.58	99.22	0.80	3.62	0.07	86022.0
Spey	482008	14.72	4.65	83.89	61.60	0.58	3.43	0.06	83146.0
Spey	482012	19.29	4.57	79.87	97.48	0.88	3.98	0.05	87996.0
Spey	131694	22.54	3.25	76.51	98.25	1.03	3.68	0.82	3987.0
Spey	482007	25.07	2.53	75.84	93.81	0.27	1.72	0.66	3836.5
Spey	482006	30.65	5.58	70.47	88.57	0.96	1.02	0.07	74765.5
Spey	126849	34.73	4.08	70.47	98.10	0.00	9.01	1.16	3530.0
Spey	482010	40.88	6.15	65.77	70.41	0.76	0.88	0.75	8226.0
Spey	131693	44.80	3.92	61.74	96.74	1.03	0.81	0.26	17095.5
Spey	483473	50.05	5.25	59.06	98.86	0.51	6.43	1.02	5157.0
Spey	Spey Bay	63.44	13.39	46.31	NA	0.95	6.93	0.24	53113.0
Spey	Fraserburgh	118.03	54.60	NA	NA	NA	8.93	0.35	153771.5
Findhorn	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Findhorn	131691	1.38	1.38	80.00	100.00	14.49	5.63	0.00	291313.0
Findhorn	480427	2.90	1.52	70.00	78.57	6.58	0.97	0.47	3240.0
Findhorn	483276	6.05	3.15	64.00	100.00	1.90	10.18	0.64	4953.0
Findhorn	126850	8.05	2.00	59.00	72.88	2.50	5.18	0.25	8104.0
Findhorn	480411	10.57	2.52	53.00	60.38	2.38	20.48	0.27	9166.0
Findhorn	Inner MF	19.20	8.63	48.00	85.42	0.58	11.40	0.26	31798.0
Findhorn	Spey Bay	39.95	20.75	40.00	NA	0.39	6.03	0.27	74000.0
Findhorn	Fraserburgh	115.43	75.49	NA	NA	NA	9.05	0.28	269472.0
Ness	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Ness	480432	0.75	0.75	90.00	100.00	13.42	94.60	0.01	119760.0

Ness	483488	3.45	2.71	69.00	100.00	7.75	113.35	0.36	9662.0
Ness	483492	11.66	8.21	50.00	100.00	2.31	237.23	0.10	84935.0
Ness	483460	51.16	39.49	14.00	100.00	0.91	33.18	0.05	780018.0
Ness	483458	55.16	4.00	9.00	100.00	1.25	204.90	0.05	74611.0
Ness	Chanonry	75.21	20.05	8.00	100.00	0.05	10.98	0.16	124367.0
Ness	Inner MF	109.68	34.47	8.00	87.50	0.00	6.92	0.28	123733.0
Ness	Spey Bay	130.00	20.32	8.00	NA	0.00	7.10	0.31	59467.5
Ness	Fraserburgh	206.91	76.91	NA	NA	NA	8.33	0.25	308927.0
Oykel	Release Site	0.00	0.00	100.00	NA	NA	NA	NA	NA
Oykel	480422	0.25	0.25	91.95	100.00	32.47	4.25	0.00	183032.0
Oykel	131692	1.67	1.42	86.58	100.00	3.78	5.47	0.29	4913.0
Oykel	480415	2.96	1.29	83.22	100.00	2.60	11.40	0.30	4365.0
Oykel	480414	5.25	2.29	80.54	100.00	1.17	2.53	0.28	8260.0
Oykel	482009	7.25	2.00	75.84	100.00	2.35	15.45	0.03	60862.0
Oykel	480431	12.76	5.51	72.48	100.00	0.61	13.38	0.18	31042.0
Oykel	480413	17.21	4.45	69.80	100.00	0.60	26.05	0.34	13251.5
Oykel	481428	20.06	2.85	69.13	100.00	0.24	37.46	0.25	11281.5
Oykel	480424	23.18	3.12	65.10	100.00	1.29	69.80	0.43	7244.0
Oykel	480420	25.06	1.88	62.42	100.00	1.43	126.96	0.43	4348.0
Oykel	480408	30.68	5.62	62.42	100.00	0.00	37.63	0.04	137651.0
Oykel	481435	40.22	9.54	53.69	95.00	0.91	89.95	0.08	117823.0
Oykel	481444	46.70	6.48	51.01	93.42	0.41	11.82	0.58	11111.0
Oykel	483468	59.59	12.89	48.99	73.97	0.16	6.27	0.30	43680.0
Oykel	Dornoch	68.66	9.06	45.64	92.65	0.37	9.62	0.32	27706.0
Oykel	Spey Bay	100.06	31.41	34.23	NA	NA	9.07	0.35	88764.5
Oykel	Fraserburgh	177.96	77.90	NA	NA	NA	9.60	0.27	279448.5