River Spey 'Missing Salmon Project' 2019

Spey Fishery Board

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

Contents

Acknowledgements

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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. 850 migrating smolts were trapped and selected for tagging by the District Salmon Fishery Boards and successfully tagged by three tagging teams. 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, and during the first part of their ocean migration. From these initial analyses, it is clear that salmon smolt 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 only 49.2%.

Future analysis in 2020 will aim to better understand the factors governing this part of the smolts migration, including variables, such as environment, genetics and morphology. Building on the 2019 results, the next two years of the project will focus on identifying the key factors involved in smolt losses in freshwater.

Spey River highlights

- Throughout the smolt run, a total of 170 smolts; 149 salmon smolts and 21 sea trout were tagged with acoustic tags (Vemco V7) over a 20-day period (13/04/2019 – 02/05/2019).

- The Atlantic salmon smolts had a mean fork length of 134.5 mm and a mean weight 24.0 g. The mean tag burden (% of body weight) was 6.7%. The sea trout smolts sampled had a mean fork length of 161.0 mm and a mean weight 43.3 g. The mean tag burden (% of body weight) was 3.7%.

- Of the 149 tagged salmon smolts, 88 smolts were estimated to have reached the downstream receivers and 69 smolts reached the Spey Bay array. The confirmed survival rate were 59.1% and 46.3% respectively.

- Overall, losses rate in freshwater was 0.82 %/km. The losses rate varied between 0.27%/km (receiver 131694) and 6.2%/km (receiver 126845).

- Freshwater receiver efficiency averaged 91.6%. Six receivers operating at over 98% efficiency.

- The median speed for confirmed migrants (e.g., smolts that were detected when crossing Fraserburgh array) was 0.07 m/s for the river travel, 0.24 m/s for the marine travel to the Spey array, and 0.35 m/s for the marine travel to the Fraserburgh array.

- Confirmed successful migrant smolts took a median of 8.1 days to travel from the release site to the most downstream river receiver, and 0.6 day from the most downstream river receiver to the marine Spey array. They took 1.8 days to reach the Fraserburgh array from the Spey array.

- Overall, the salmon smolts showed strong directional movement, heading east, north east.

Introduction

Smoltification and extensive migration characterise the anadromous Atlantic salmon (*Salmo salar*) and sea trout (*Salmon 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 pre-determined physiological threshold, determined by a combination of genetic and environmental controls, 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" refers to the mass migration of these pre-adapted salmon out towards the marine environment. Smoltification and migration present numerous risks including physiological stress (osmotic changes) and exposure to an increased risk of predation (Kennedy and Crozier, 2010). Numerous studies have reported smolt mortality during the in-river migration. A review by Thorstad *et al.* (2012) reported river mortality rates for wild smolts ranging from 0.3% km^{-1} to 5.0%km^{-1} The high variation in mortality rates is influenced by the river conditions (Thorstad *et al.,* 2012) and also possibly the presence of predatory hotspots (Jutila, Jokikokko and Julkunen, 2005).

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 the 2019 '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, aiming to identify what is happening during the smolt run and provide information to support management action to boost wild smolt survival.

This report provides an overview of the **initial analysis** of data for fish tagged in the River Spey and their downstream migration pattern to the Moray Firth. Currently detailed modelling, and investigations of other factors in the study are ongoing. These are outlined in the Next Steps section of the report. This report will refer to detection of fish as 'confirmed survival,' Hence the data here refers only to smolts which have been detected. A smolt that has not been detected may not necessarily have died. There are several other possible reasons for non-detection of the tagged fish, including non-detection by the acoustic receivers. Efficiency and range testing will be used to model potential missed detections of fish and thus provide more robust estimates of confirmed survival estimates. This is most likely to affect marine detections, where if any change occurs it would be a positive effect (i.e. an increase in survival).

Materials and methods

Twelve acoustic receivers were deployed throughout the River Spey at approximately 5km intervals. The uppermost receiver was positioned at Ballindalloch (downstream of the confluence of the Spey and Avon) and the lowest receiver was sited in the mouth of the river at Spey Bay (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.

Salmon smolts were captured via rotary screw traps on the lower River Avon within the Ballindalloch Estate (Lat Long 57.4160, -3.3767). 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 smolt run a total of 170 smolts; 149 salmon smolts and 21 sea trout smolts were tagged with acoustic tags (Vemco V7; 1.6g 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 20-day period (13/04/2019 – 02/05/2019). So as to mimic the natural smolt migration pattern, the number of fish tagged each day was proportional to the number of fish caught in the trap.

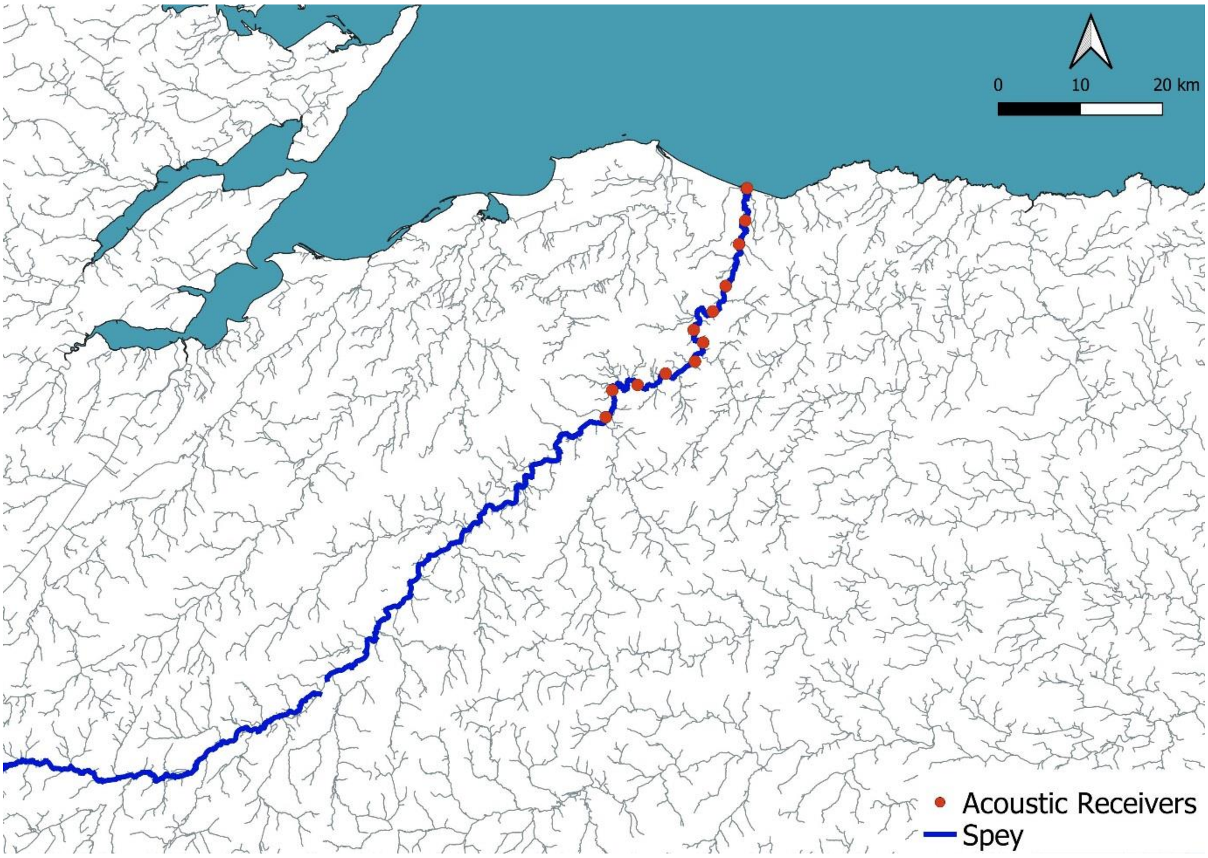

Figure 1a. Locations of the acoustic receivers along the River Spey.

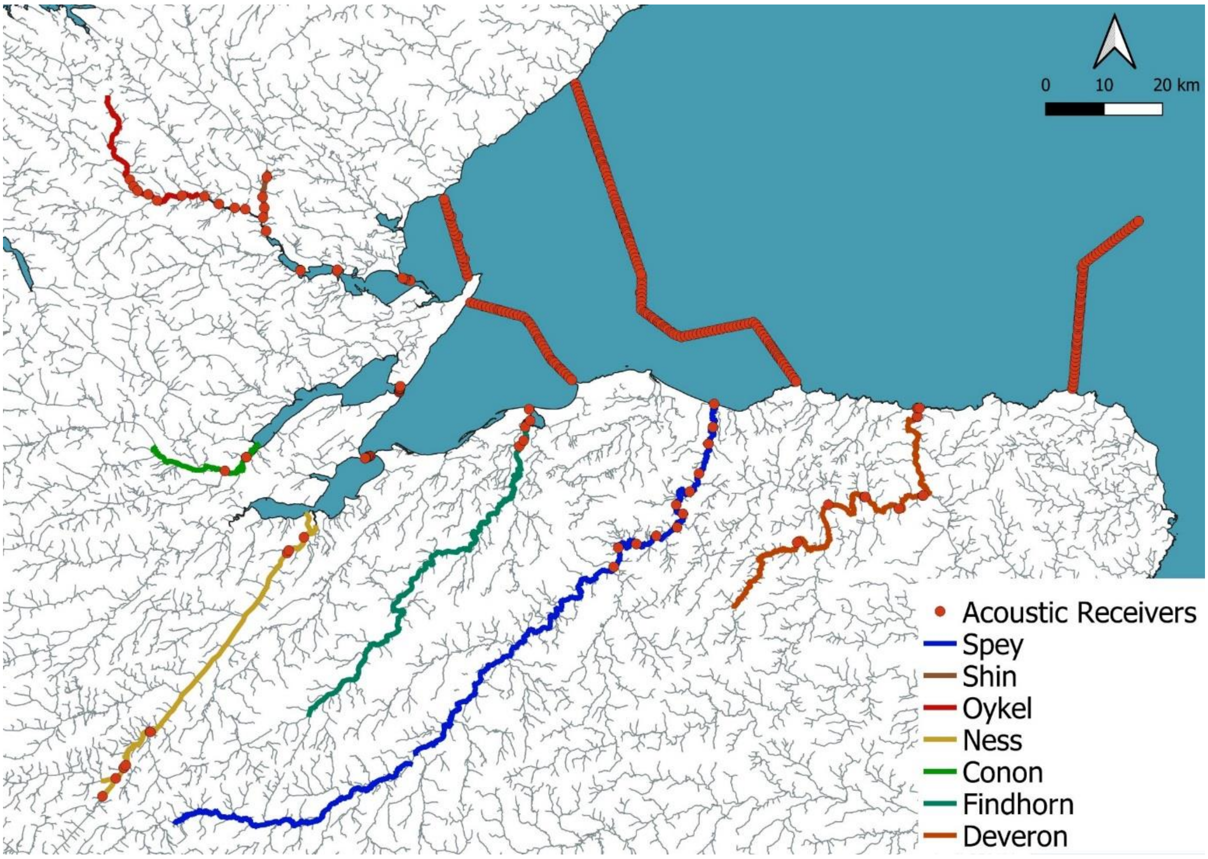

Figure 1b. Locations of the acoustic receivers across the Missing Salmon Project.

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 to avoid recaptures.

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

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 Spey River was 134.5mm and the mean weight of the tagged smolts was 24.0g. The tags weigh 1.6g which results in an average tag burden (% of body weight) of 6.7%. The range of smolt sizes and weights among rivers in the study varied from 133.6 mm (Deveron) to 140.3mm (Ness) and from 23.5g (Deveron) to 28.8g (Ness). The mean fork length of the tagged sea trout smolts was 161.0 mm and the mean weight of the tagged smolts was 43.3g. The tags weigh 1.6g which results in an average tag burden (% of body weight) of 3.7%. The range of sizes and weight among rivers in the study varied from 151.0mm (Findhorn (n=1)) to 162.1mm (Deveron) and from 29.4g (Findhorn (n=1)) to 43.3g (this river).

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.

Survival

Of the 149 salmon smolts released, 88 (59.1%) individuals were detected leaving the River Spey for the marine environment and 69 individual confirmed to survive at the Spey Bay array (46.3%). Overall there was a decrease in the detection rates of smolts further downstream with an overall freshwater loss rate of 0.82 % fish per km (Figure 3 and Table 1). This is well within the range of other rivers in the study, from 0.52% (Shin) 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 91.6%, with six receivers operating at over 98% efficiency (Figure 3 and Table 1).

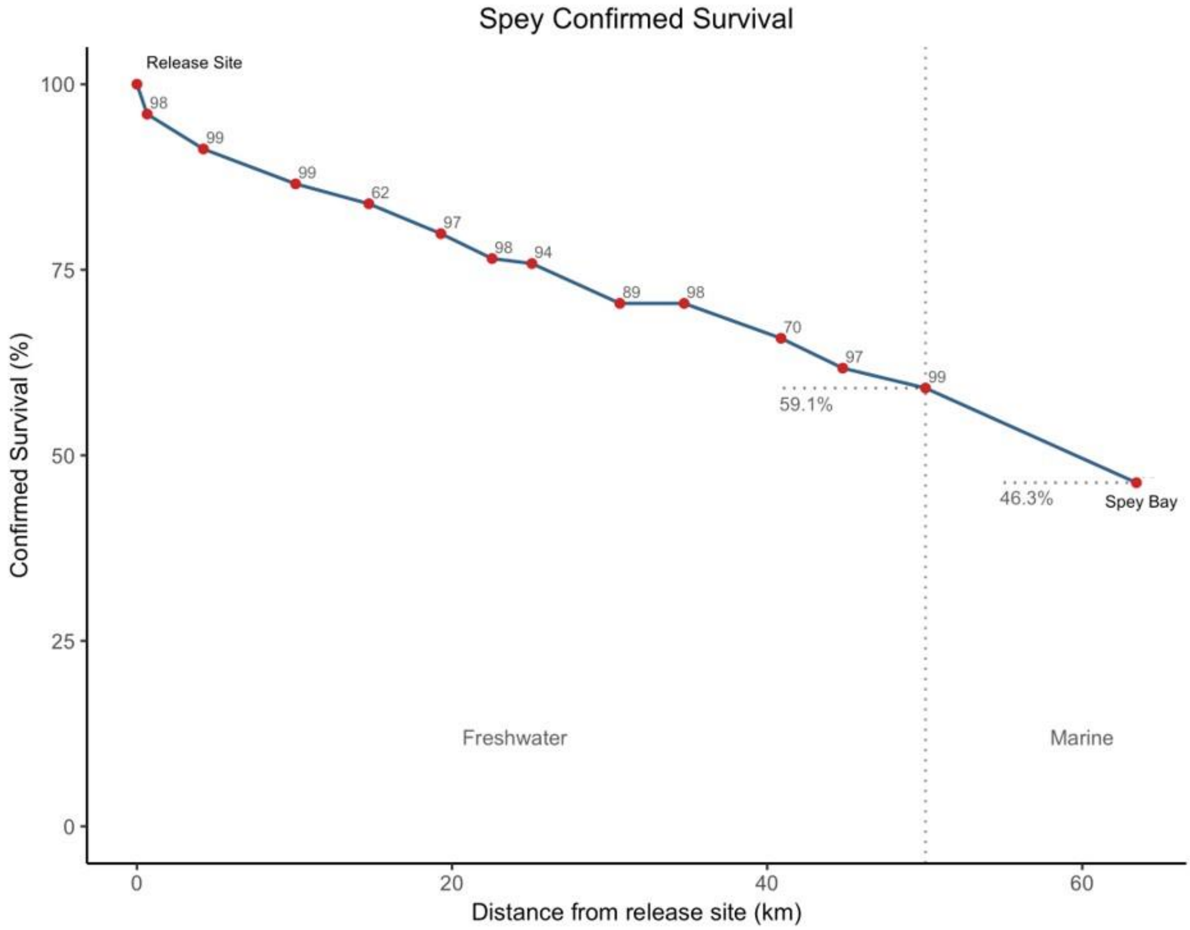

Figure 3. Confirmed survival (%) of smolts at increasing distance from the release site on the River Spey. Red dots represent receivers, and detection efficiency (%) of each freshwater receiver is provided. *Please note that the marine array efficiencies are not complete as the Fraserburgh array was 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).

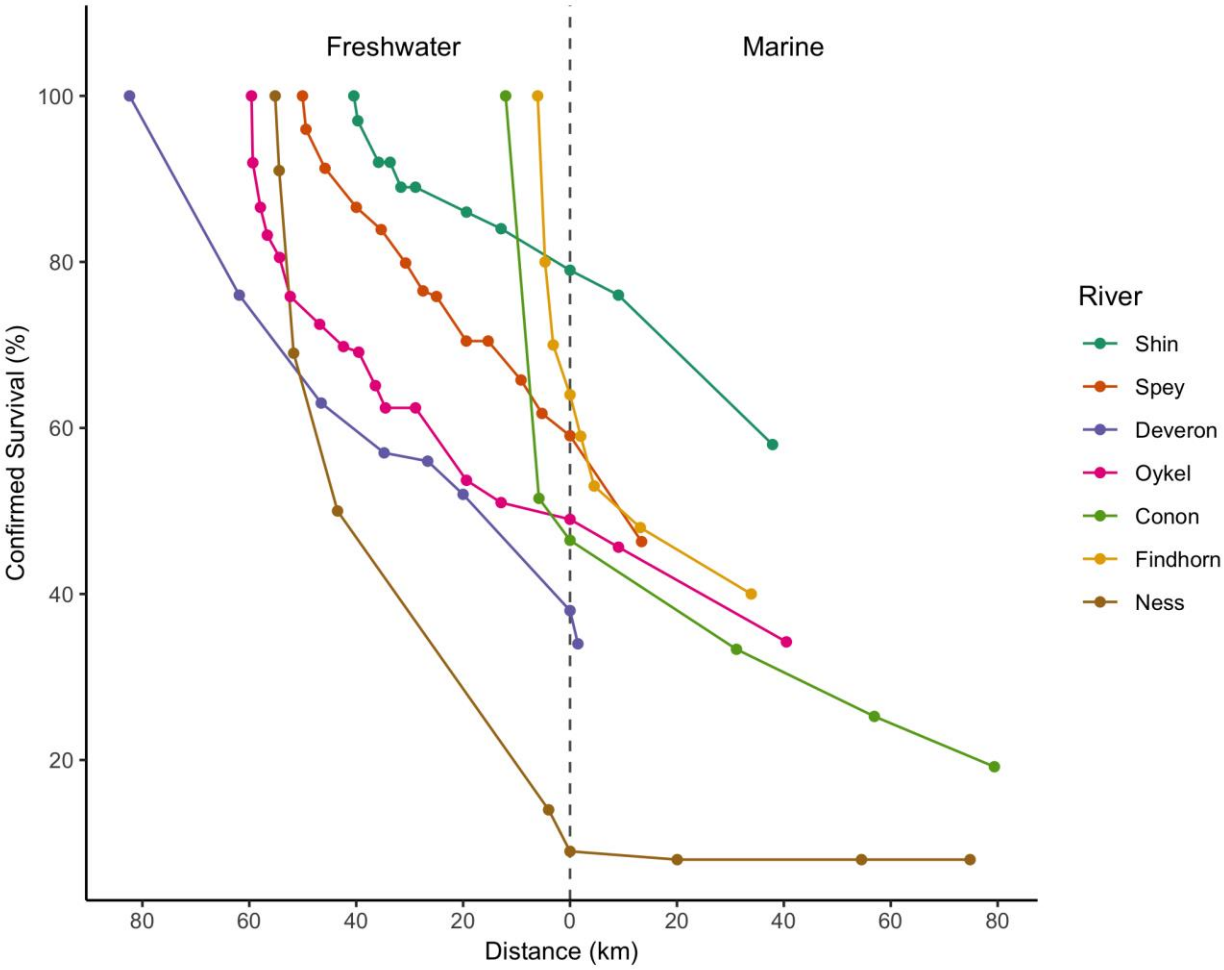

Figure 4. Confirmed survival (%) of salmon smolts for the seven rivers of the Moray Firth, with distance of smolt migration undertaken. Both freshwater and marine environments are included. The migration distance has been standardized so that the dotted line represents entry to marine water on each river system.

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 8.1 days to travel from the release site to the most downstream river receiver, 0.6 days from the most downstream receiver to the marine Spey array, and 1.8 days to reach the marine Fraserburgh array (Figure 5). This represents a median ground speed of 0.07 m/s for river travel, 0.24 m/s for the marine travel to the Spey array, and 0.35 m/s for the marine travel to the Fraserburgh (Figure 6).

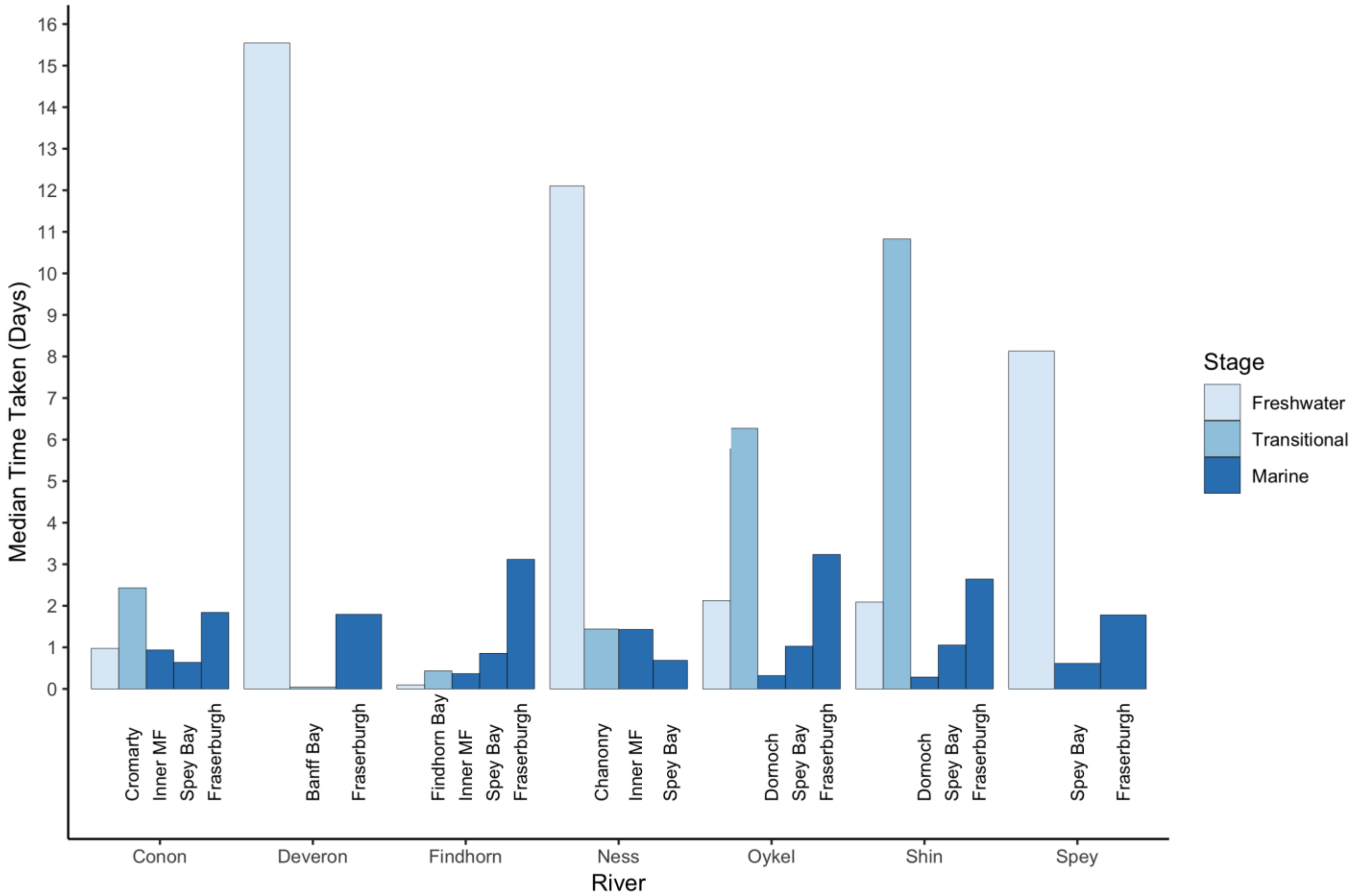

Figure 5. Median time taken by smolts to travel from the release site, to the mouth of the river, and then to each marine arrays. *Please note these values are only for fish that successfully migrated from release site to the Fraserburgh marine array. Distance travelled is not taken into consideration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

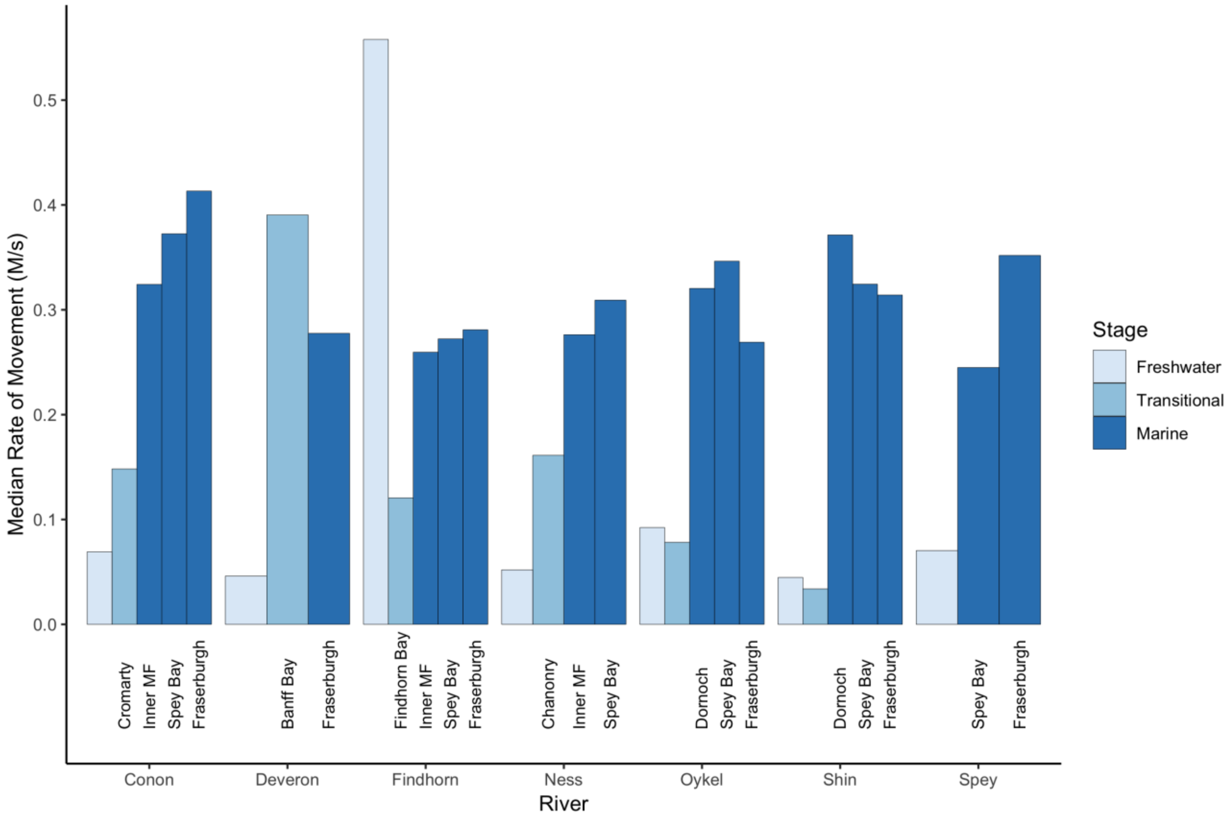

Figure 6. Median speed of smolts from all rivers travelling from the release site, to the mouth of the river, and then to each marine arrays. *Please note these values are only for fish that successfully migrated from release fish to the Fraserburgh marine array.

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 Spey (Figure 7 and Table 1) and in the marine environment (Table 1). For the Spey River, the higher residencies were found at receivers 126849 (Orton) and 483473(Spey Bay)

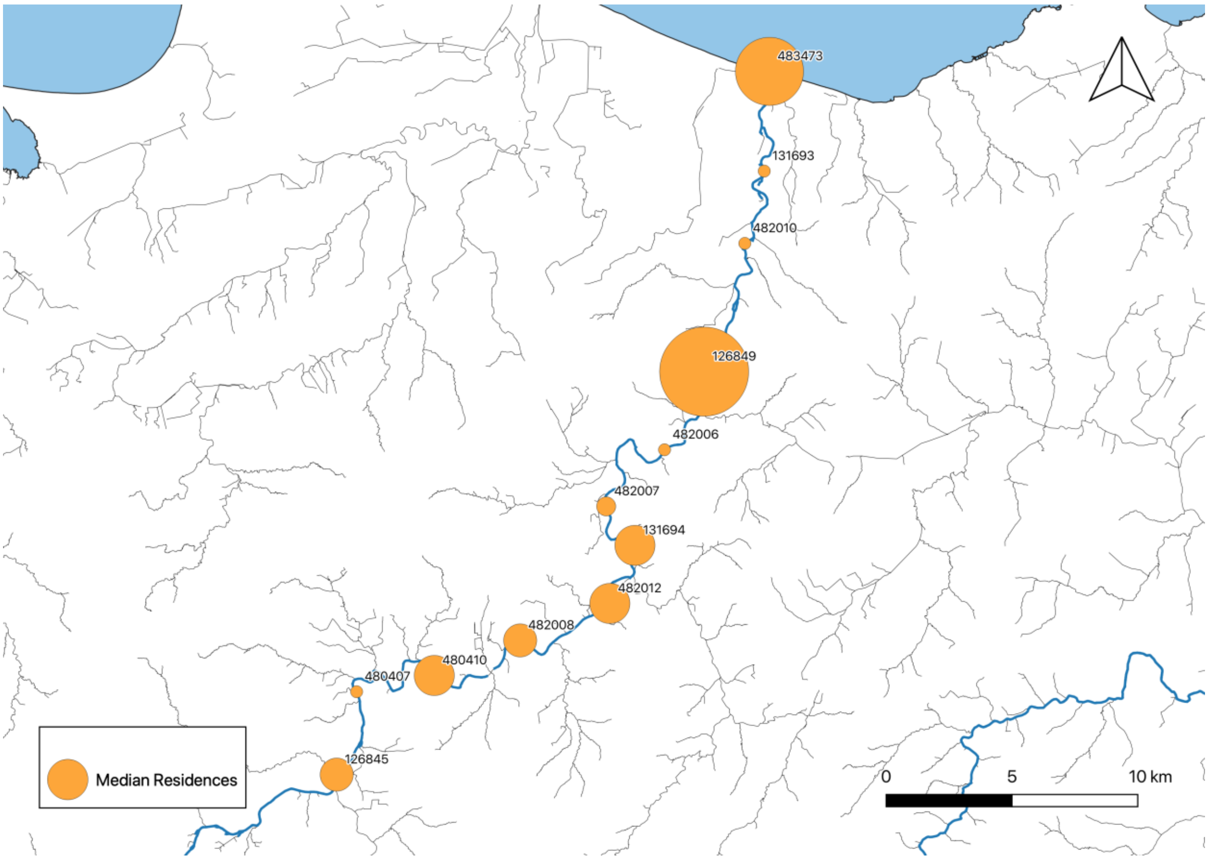

Figure 7. Median residency time of smolts on the River Spey, moving downstream.

Marine migration route/direction

Salmon smolt did not show shoaling behavior when exiting the mouth of the river for the marine environment. However, a split pattern of direction was detected when smolts exited the mouth of the river, with two spatial clusters. From the Spey Bay array, the migration directions begin to spread out spatially, with smolts recorded crossing the Fraserburgh array at multiple points along its length. Overall, the salmon smolts showed strong directional movement, heading east, north east (Figure 8). In comparison, sea trout showed non-directional movement when exiting the mouth of the river for the marine environment (Figure 9). This is well within the range of patterns expressed by the other rivers in the study (Figure 10 and 11).

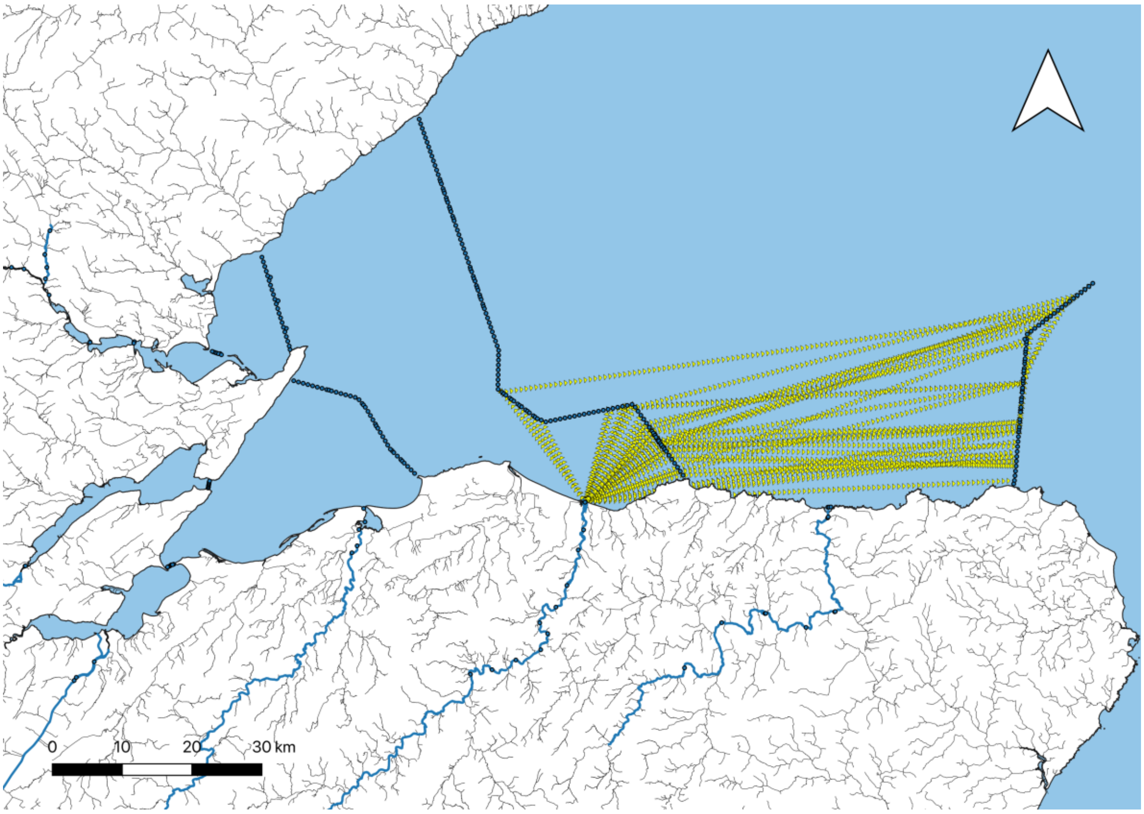

Figure 8. Marine migration direction of salmon smolts exiting the River Spey, moving towards the Spey Bay and Fraserburgh arrays.

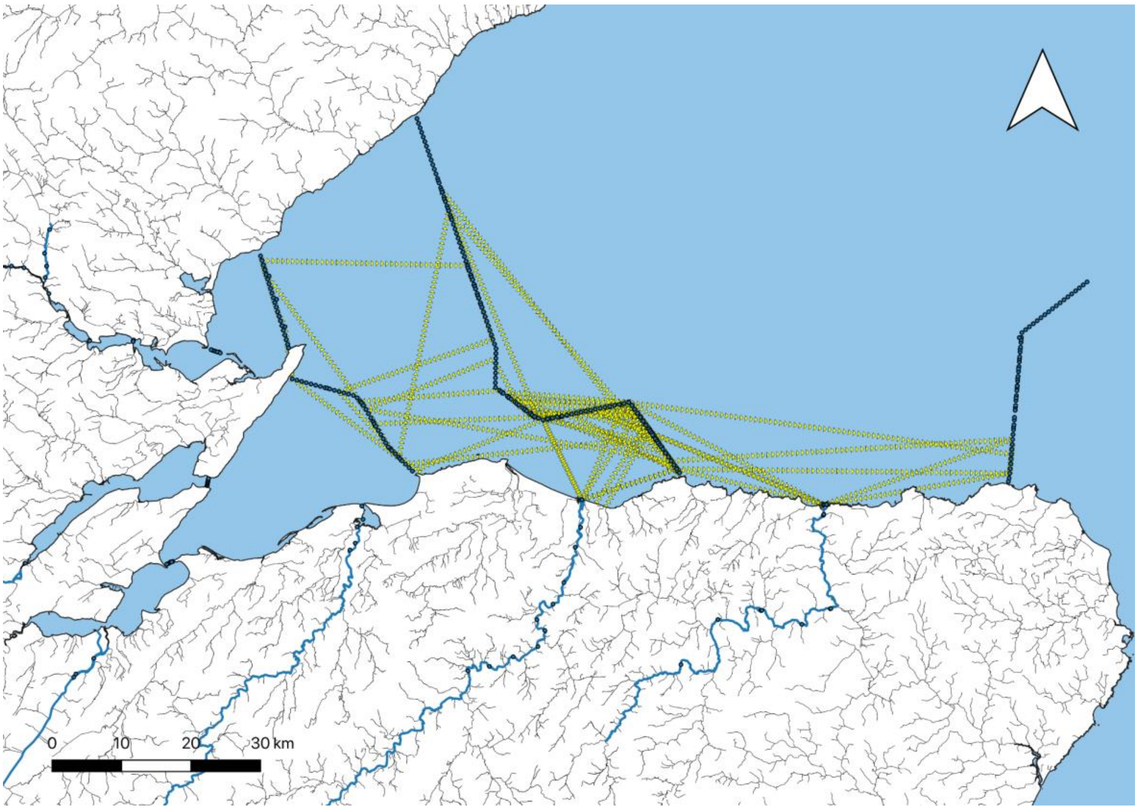

Figure 9. Marine migration direction of sea trout smolts exiting the River Spey, moving towards the Spey Bay and Fraserburgh arrays.

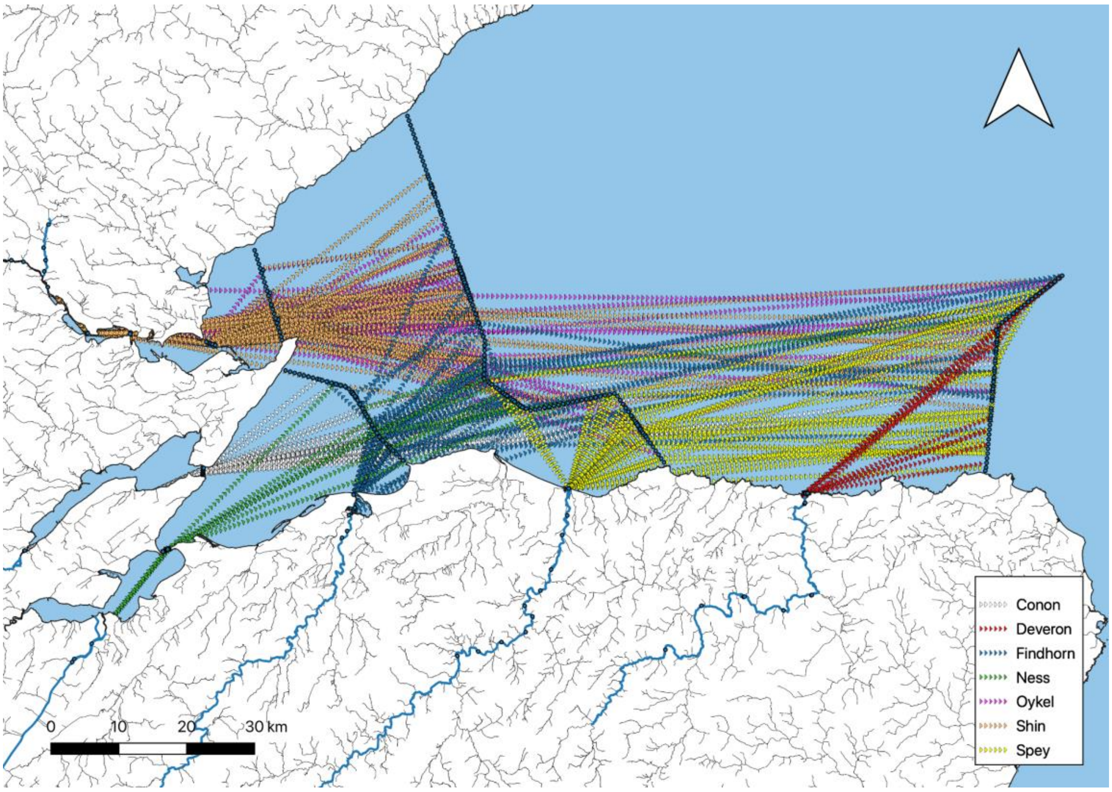

Figure 10. Marine migration direction of salmon smolts for the seven rivers of the Moray Firth, moving towards the Spey Bay and Fraserburgh arrays.

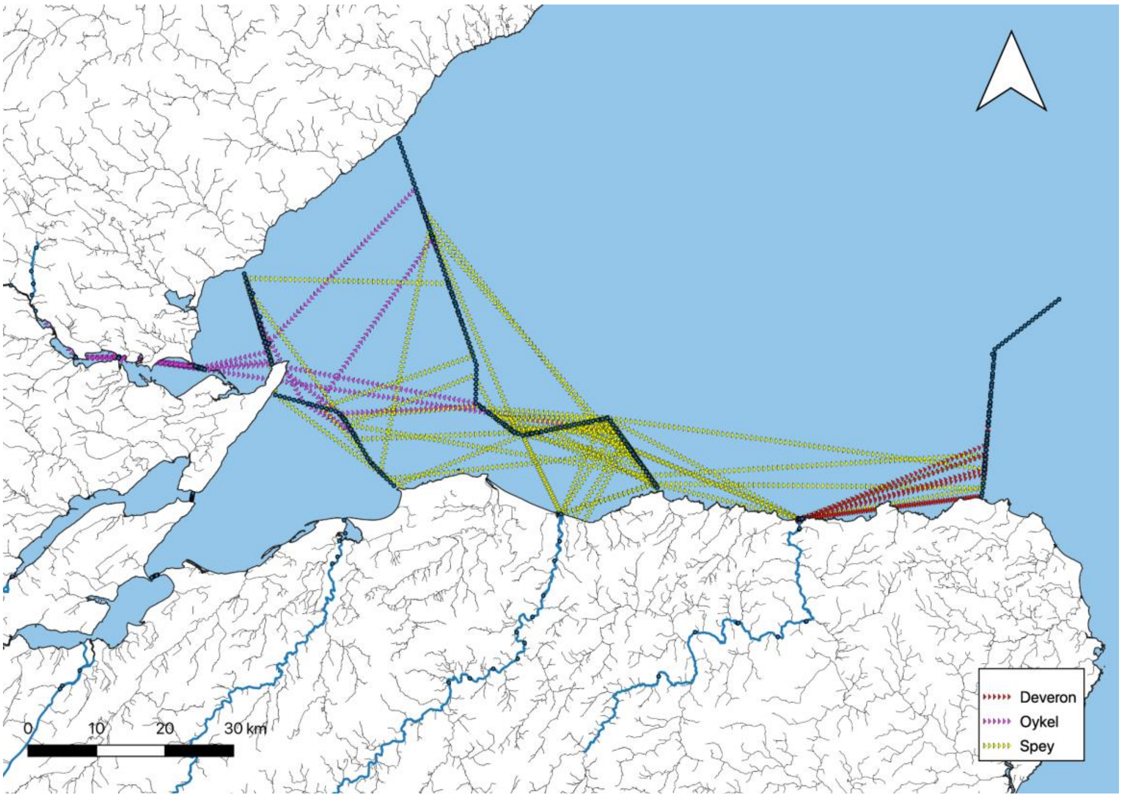

Figure 11. Marine migration direction of sea trout for three rivers of the Moray Firth, moving towards the Spey Bay and Fraserburgh arrays.

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

Receiver	Beat	Distance (km)	Distance Diff. (km)	Efficiency (%)	Confirmed Survival (%)	% losses per km	Median residences (mins)	Median ROM (m/s)	Median duration (secs)
Release Site	Ballindalloch	0.00	0.00	NA	100.00	NA	NA	NA	NA
126845	Ballindalloch	0.65	0.65	98.60	95.97	6.20	3.17	0.02	34678.00
480407	Lower Pitchroy	4.22	3.57	98.53	91.28	1.32	1.33	0.75	4729.00
480410	Carron & Laggan	10.07	5.85	99.22	86.58	0.80	3.62	0.07	86022.00
482008	West Elchies	14.72	4.65	61.60	83.89	0.58	3.43	0.06	83146.00
482012	Macallan	19.29	4.57	97.48	79.87	0.88	3.98	0.05	87996.00
131694	Easter Elchies	22.54	3.25	98.25	76.51	1.03	3.68	0.82	3987.00
482007	Arndilly	25.07	2.53	93.81	75.84	0.27	1.72	0.66	3836.50
482006	Delfur	30.65	5.58	88.57	70.47	0.96	1.02	0.07	74765.50
126849	Orton	34.73	4.08	98.10	70.47	0.00	9.01	1.16	3530.00
482010	Brae 5	40.88	6.15	70.41	65.77	0.76	0.88	0.75	8226.00
131693	Cumberlands Ford	44.80	3.92	96.74	61.74	1.03	0.81	0.26	17095.50
483473	Mouth	50.05	5.25	98.86	59.06	0.51	6.43	1.02	5157.00
Spey Bay		63.44	13.39	NA*	46.31	0.95	6.93	0.24	53113.00
Fraserburgh		118.03	54.60	NA*	NA	NA	8.93	0.35	153771.50

*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

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 increased in the second year of the study to increase the resolution at which the pattern of fish movement can be recorded. The exact positions of receivers to be deployed in each river will be determined in partnership with the relevant fishery board or trust (Spey Fishery Board). 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 Berriedale 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 hopefully provide additional on migration routes taken by smolts outwith the Moray Firth as well as providing 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 mechanisms responsible for the 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 assisting with validating the smolt dispersal model.
4. Support the Likely Suspects Framework by providing evidence on pressures / mortality factors.

Genetics study (partnership amongst 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. Understanding the reasons why they disappear is more difficult. Using the DNA from fin clips of smolts that have been tracked downstream to record both their in-river migration pattern and migration "success" (as indicated by their detection at the outermost marine receiver array) we may be able to identify genetic markers that suggest why some fish are successful and some are not.

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)

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.

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 both have their limitations for counting birds and can be resource intensive. 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. This project will pilot methods and trial the various imaging options to assess if avian predator counts can be assisted in the future using this technology.

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.

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

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

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	7z5.84	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