The benefits of merging two tracking approaches: passive acoustic telemetry combined with active acoustic tracking by transects provide new insights into riverine migration by salmonid smolts.

Louise Chavarie*[1,2], Hannele M. Honkanen[2], Matthew Newton[2], Jessie M. Lilly[2], Hannah R. Greetham[2], and Colin E. Adams[2]

[1] Norwegian University of Life Sciences, Faculty of Environmental Sciences and Natural Resource Management, Ås, Norway

[2]Scottish Centre for Ecology and the Natural Environment, IBAHCM, University of Glasgow, Rowardennan, Loch Lomond, Glasgow G63 0AW, UK

Running title: Passive and active tracking of smolts

Key words: Acoustic tags, Telemetry, Atlantic salmon, Sea Trout, predation, mortality, small-scale behaviour, social network, morphology, phenotype, river, anadromous.

*Corresponding author:

louise.chavarie@nmbu.no

Abstract

The process of smolting is a critical phase in the life-cycle of anadromous salmonids and it has been associated with substantial rates of mortality. Survival during freshwater and marine migration is known to have population level effects, thus an understanding of the patterns of mortality has the potential to yield important insights into population bottlenecks. Despite important advancements in tracking techniques, the specifics of mortality events in anadromous salmonids during their initial migration to sea remains somewhat elusive. Here, we develop a framework combining spatial and temporal detections of smolt riverine migration from two tracking techniques, which enable inferences to be made about mortality locations, causes, and rates. We embed this framework into a fine-scale behaviour study of migration and social structure. In this study, we demonstrate that during their initial riverine transitional phase, smolts were particularly vulnerable to predators. Specifically, avian predation appeared to be the main cause of mortality (42%), although piscine predation events were not trivial (14%). Our results suggested some direct and indirect tagging-induced mortality (e.g., through increased predation vulnerability), which highlights the importance of determining tagging mortality in a telemetry study to ensure adequate interpretation of migration success. There is evidence that predation induced selection on smolt morphology. Unsuccessful river salmon migrants with a phenotype comprising a shorter head and jaw and smaller eye had a higher probability of mortality in the later parts of riverine migration where avian and aquatic predation mortality dominated. In contrast, mortality earlier in river migration was independent of phenotype, most likely a result of tagging effects. Successfully river migrants were found to be interacting with each other, often in a pair or as a trio, indicating that a few individuals of Atlantic salmon and sea trout formed notable intra- and interspecific social associations. However, the heterogeneity of the social associations of

successful migrants did not support the assumption that social network features attributed any clear specific benefits of reduced predation risk. Overall, by estimating migration loss and its variability, our study framework should help to guide management actions to mitigate the widespread population declines these species are currently facing.

Introduction

Atlantic salmon (*Salmo salar*) and sea trout (the anadromous form of the brown trout complex; *Salmo trutta*) are salmonid species of biological, cultural, and economic importance, but these species have experienced dramatic declines in recent decades (ICES 2011, ICES 2018). Despite various attempts to mitigate anthropogenic stressors and mortality rates, Atlantic salmon and sea trout populations throughout most of geographic range of these fish are currently at or near record low abundances (ICES 2017, 2018). The anadromous life-history tactic of both species results in migration between freshwater and marine habitats, which exposes individuals to multiple threats (e.g., migration barriers, diseases, pollution, overexploitation, parasites, climate change, and aquaculture impacts; Parrish et al. 1998, Forseth et al. 2017). Smolts (the seaward migrating stage of the life cycle) are particularly vulnerable during their first migration to sea because they are increasingly mobile and traverse a high-risk landscape that exposes them to predators (Ward et al. 2008, Ward and Hvidsten 2011). However, the location, timing, and relative proportion of the total mortality attributable to Atlantic salmon and sea trout populations during their initial migration remains elusive (Chaput et al. 2018). This lack of an understanding of migration losses is highly challenging for practical management and for policy development. To add to the complexity of our understanding, there is substantial variability among populations, indicating that causes of mortality, loss rates and mechanisms to mitigate predation risk, such as swamping predators with high densities (e.g., through schooling behaviour and social networks) can be system- and habitat-specific (Thorstad et al. 2012, Furey et al. 2016, Thorstad et al. 2016).

Recent advances in the development of electronic tags that transmit information that enables tracking of animals across broad- and fine- spatial and temporal scales have made significant contributions to the understanding of salmonid behaviour and migration (Drenner et al.

2012, Hussey et al. 2015). Our ability to track aquatic organisms often varies with the species studied and the habitat they inhabit. There are trade-offs among operating requirements, transmission quality, and tracking capabilities in the devices used to track animals; these become more complex in species that migrate between freshwater and marine systems (Leander et al. 2019). Currently, electronic tags are the leading technology to track fish with high temporal and spatial resolution in the wild (Hussey et al. 2015). Radio telemetry has been commonly used in rivers, since it allows the determination of fine-scale movements and mortality (Jepsen et al. 2019). However, radio telemetry cannot be used to track animals in salt water or deep-water environments, which is a major limitation when studying an anadromous migration (Cooke et al. 2013).

When freshwater and marine migrations by anadromous salmonids are investigated, passive acoustic telemetry offers a good alternative. The main issue with passive acoustic telemetry is that tagged individual must move within the detection range of an acoustic receiver to be detected (Both et al. 2012, Bruneel et al. 2020). This issue can be overcome by deploying a sufficient number of receivers to achieve complete coverage of a given area. For example, when the direction of migration is known or constrained in certain areas, using an array of receivers in a grid positioning system in relatively enclosed study areas (e.g., lakes and estuaries) or by using by an array of receivers organised as a gate through which fish are likely to travel, have both been proved to be efficient methods to detect organisms (Heupel et al. 2006, Roy et al. 2014, Kraus et al. 2018). Despite being well suited for marine or lake environments, these solutions to increase the resolution of the data do not necessarily work well in rivers systems. Rivers are often shallow, sinuous, frequently with fast-flowing water that results in a noisy environment that makes tag detection challenging; thus increasing the number of receivers for better detection resolution is not

necessarily feasible (Bergé et al. 2012). Combining approaches with different trade-offs (e.g., using PIT tagging or radio telemetry along with acoustic telemetry) may circumvent some of the challenges of tracking in riverine systems, but would require double tagging individuals or running programs in parallel (Furey et al. 2016, Schwinn et al. 2017, Dainys et al. 2018, Jepsen et al. 2019).

As a result of some of these shortcomings from passive acoustic telemetry associated with rivers, we revisited the concept of active acoustic tracking in association with passive acoustic telemetry. Active acoustic tracking is not a new concept (e.g., Halfyard et al. 2012, Gauld et al. 2016). Active acoustic tracking has been considered to be a detection method with some advantages, it is likely to provide: 1) a high frequency of detections of animal positions, 2) position estimates are not limited to areas that are in range of fixed receiver stations, and 3) relatively precise animal positions (Brownscombe et al. 2019). However, because active tracking is labour intensive and as it often restricts the sample size compared to a passive tracking approach (e.g., frequently only one animal can be tracked at a time and the duration over which animals can be tracked is usually limited), methods using fixed acoustic receivers have been favoured in telemetry studies (Fetterplace et al. 2016, Brownscombe et al. 2019). Novel active tracking techniques have been recently developed, such as autonomous robotic technology or receivers attached to large, free ranging animals to enable detection of individuals of the target species (Carlon 2015, Ennasr et al. 2020), none of which are currently suitable for most rivers. Thus, to counter the limitations of existing passive telemetry in small to moderate sized riverine systems and enhance the collected information on smolts during their freshwater migration phase, we developed a novel framework that integrates fixed acoustic receivers and active tracking by systematic canoe transects. The purposes of our study were to: 1) test the relative efficiency of each tracking methodology (i.e., passive and active) separately and together, 2) use the combined active-passive approach to define

and quantify the locations, causes, and rates of mortality of salmonid smolts during their riverine migration phase, 3) examine if phenotypic characteristics (i.e., morphology and fish length) influence smolt success during riverine migration and 4) determine the fine-scale behaviour and social structure related to riverine migration of salmonid smolts.

Material and methods

Study Site and Tagging Procedures

The River Endrick (Scotland) is a major inflowing tributary to Loch Lomond, a medium sized lake in the catchment through which fish must migrate to reach the sea (Fig. 1). Atlantic salmon and sea trout smolts were captured using a 1.2 m diameter rotary screw trap in the middle reaches of the River Endrick, 12.33 km upstream of the river mouth (56 º 2´ 58´´N; 004 º 26´ 27´´ W) where it discharges into Loch Lomond. Between April 13th and 20th 2020, a total of 135 Atlantic salmon and 23 sea trout smolts were tagged with VEMCO V7-2L 69kHz (VEMCO Ltd, Halifax, Canada) tags. To minimize the tag burden, only smolts in excess of 130 mm fork-length were tagged. Smolts were anaesthetised using 0.1gram/litre (g/L) of tricaine methanesulfonate; measured for weight (g), length (fork length, mm) and a photograph was taken for morphometric analysis. A minimum recovery period of one hour was allowed before fish were released at the tagging site.

Passive Acoustic Tracking Design

To assess smolt migration through the River Endrick, four 69 kHz acoustic receivers (VEMCO VR2W and VR2Tx VEMCO Ltd.) were deployed in the river between March 24th and April 14th 2020. The first receiver was located 800 m downstream from the trapping/release zone and the last receiver was placed at the mouth of river, to detect smolts entering Loch Lomond (#1,

5, 6, and 7; Fig. 1). On May 21st 2020, three additional acoustic receivers (VR2Tx; VEMCO Ltd.) were deployed in the river when the environmental conditions in the river (i.e., the lack of precipitation) resulted into a total obstruction of the smolt migration due to an exposed sandbank at the junction of the river mouth and Loch Lomond. These three additional acoustic receivers (#2-4) were deployed in the mid-section of the river to expand detection coverage from the trapping zone to the mouth of the river (Fig. 1). All receivers were attached to a steel bar welded onto a 20kg weight, which was then anchored to the shore with a rope or chain (Fig. A1).

Active Acoustic Tracking Design

The active tracking programme consisted of a number of transects of 13.5 km, undertaken by canoe that began ~200 m upstream of the rotary screw trap, downstream into Loch Lomond (Balhama Pier; 56 º 08’ 36’’N; 004 º 54’ 79’’ W). Tags were detected during the passage downstream using a VR100 receiver (VEMCO Ltd.; normal filter setting), designed for manual tracking from small boats, coupled with an omni-directional hydrophone which was attached to the canoe. The operator could adjust the length of the cable to prevent the trailing hydrophone hitting the substrate. Canoe transects were completed daily, beginning three days after tagging commenced, for seven days (that is the April 16th to the 23rd 2020) and every two weeks after that (i.e., April 24th to the June 6th 2020), for an overall total of 10 active tracking surveys. The last canoe transect, completed on June 6th 2020, was started further upstream near a waterfall that acts as a natural barrier for smolts and parr upstream movements. This barrier is ~ 3.7 km upstream of the release site, resulting in a transect of ~17. 2 km. This longer transect ensured coverage of all possible upstream sites into which fish may have moved and thus reduced the possibility of undetected tags (see Table 1).

Detection efficiency

All data were initially compiled in Vemco VUE software and all analyses were conducted in R version 3.5.0 (R Core Team 2016), except if stated otherwise. For calculating detection efficiency of fixed receivers (with the exception of the last receiver downstream), fish detections at a downstream receiver were compared to those from the next upstream receiver, i.e. all fish detected at receiver #2 must have passed receiver #1, providing a detection efficiency measure for receiver #1. Fixed receivers #1, #5 and #6 were included in this analysis (due to their earlier deployment, receiver #2-4 were excluded from this assessment). We also calculated the efficiency of fixed receivers by combining passive and active tracking data; this allowed for the detection of fish between receivers, improving the estimates of fixed receiver detection efficiency. Active tracking detection efficiency was estimated by combining data from active tracking and fixed receivers. Fixed receivers were used to assess which tagged individuals remained within the study area (i.e., those that had not exited the river) and the percentage of these individual detected by active tracking were calculated.

Sources of smolt riverine migration failure

The pattern of detection of individuals from active and passive acoustic tracking were used to infer the fate of each fish. In the process of evaluating this, we relied on two common assumptions. 1) Tag failure (e.g., through early battery discharge or mechanical failure) was assumed to be minimal. Failure of the tags used in this study is generally under two percent (H. H. Honkanen, Unpublished data; Newton et al. 2019). 2) Tag expulsion from the fish was assumed to be inconsequential. This study accumulated data from fish over a few days to a few weeks and where it has been examined, tag expulsion is thought to occur over a longer period (i.e., 40 days; Lacroix et al. 2004, Brunsdon et al. 2019). In addition, to infer an ultimate fate to each tagged fish, we followed postulations used in other recent studies (for example, see Gerber et al. 2017, Flávio et

al. 2020a, Klinard and Matley 2020, Villegas-Ríos et al. 2020, Weinz et al. 2020), with some modifications for the local study area, to infer nine categories of riverine migration outcomes from tag detection patterns (see Table 1 and A1 for more details). A Chi-squared test (Zar 2010) was used to determine if the of number of migration failures was spatially randomly distributed throughout the River Endrick by dividing the river into 1 km sections.

Telemetry analyses

Because the data deviated from normality (Shapiro-Wilk; p-values <0.001), the non-parametric Wilcoxon rank tests, implemented by the kruskalmc function from the pgirmess package (Giraudoux 2012) were used for all telemetry analyses. The four fish with fate categorized as 'unknown' were excluded from these analyses and analyses were done separately on salmon and sea trout smolts. The duration of residency events, defined as the time that a fish spent detected at a single receiver, was compared between fish that were successful and unsuccessful river migrants and among receivers. The rate of movement, measured as the detected distance moved over time elapsed between fixed receivers, of all fish was determined and the difference between successful and unsuccessful migrants and among different river sections (between fixed receivers) were tested with a Kruskal-Wallis chi-squared. To look for diurnal patterns of fish movement and any changes in these patterns, we recorded the time of day that a smolt was first detected at a receiver. Finally, the effects of fork length and tag burden on smolt migration success were assessed.

Morphology

To determine if the fate of tagged smolts was influenced by phenotypic traits, twenty-one landmarks were digitized on whole-body images to calculate linear morphometric measurements (Fig. A2). Landmarks were digitized in x and y coordinates using TPSDig2 software

(http://life.bio.sunysb.edu/ecotype). Digitized landmarks and semi-landmarks were processed in a series of Integrated Morphometrics Programs (IMP) version 8 (http://www2.canisius.edu/;sheets/ecotypesoft), using partial warp scores, which are thin-plate spline coefficients. Morphological methods and programs are described by Zelditch et al. (2012) and specific procedures were described by Chavarie et al. (2013). TMoprhGen (IMP) was used to calculate fin- and body-length measures based on paired coordinate measurements (BCs). All morphological measurements were standardised to remove the effect of body size, the residuals of regressions of the morphological measure on fish centroid size (Zelditch et al. 2012).

MANOVAs on linear measurements were performed to test for differences between successful and unsuccessful individuals, for Atlantic salmon and sea trout, separately. Principal component analysis (PCA) of the linear measurements was used to visualize morphological variation between successful and unsuccessful river migrants of Atlantic salmon and sea trout. To look for a continuum of an effect of morphology on migration failure, the last detection downstream (calculated from lat. and long. of last detection) of unsuccessful river migrants of Atlantic salmon smolts (sea trout were excluded because of sample size) was used to create a heat map of the first principal component (PC1) of the morphological traits of the unsuccessful river migrants. The last detection point was assumed to be the maximum distance of migration of fish which were unsuccessful in reaching the end of the river and which probably died at this point. A PCA was done on the head measurements solely among unsuccessful Atlantic salmon migrants because it was the main morphological variation detected previously (Table A4). The PC1 scores of head measurements were regressed on the furthest detection downstream of each Atlantic salmon individual inferred as “dead” within the river and linear regressions were tested for differences from 0.

Social Network Analyses

The gambit of the group hypothesis is based on temporal or spatial proximity of individuals. In this study we conducted social network analysis on combined tagged salmon and sea trout smolts to test if they were likely to associate within and between species during the study. Individual associations were defined by co-occurrences of successful Atlantic salmon and sea trout river migrants at fixed acoustic receivers (Whitehead and Dufault 1999, Guttridge et al. 2009) using the R package spatsoc (Robitaille et al. 2019). Unsuccessful river migrants were not included due to the induced temporal and spatial bias resulting from loss of detections and its effect on the social network analyses (Whitehead 2008, Stehfest et al. 2013). The active tracking dataset was also excluded from this analysis due to the single data point generated each day by this tracking method.

Co-occurrence strength can be determined from the frequency of co-occurrences at acoustic receivers (Stehfest et al. 2013, Lilly et al. 2020). Based on a sensitivity analyses (Armansin et al. 2016) of the detections of individuals at fixed receivers, associations between individuals across interval periods stabilized at an interval period of five minutes (Fig. A3). Using spatsoc with a multilevel algorithm detection method (Yang et al. 2016), smolts detected within that five minute period at the same location (i.e., at a single acoustic receiver) were deemed to have been associated with each other and assigned to the same group. We initially pooled all detection data for the social network analysis to ensure an adequate sample size, but we also conducted these analyses on the fish from the last three tagging dates separately ($n > 20$ of tagged fish per day, April 18-20th; Table A2), to ensure an equal opportunity for fish from the time of release to form associations with tagged conspecifics.

Using the asnipe package (Farine 2013), the strength of co-occurrences was estimated using the Simple Ratio Index (SRI; Cairns and Schwager 1987, Mourier et al. 2019). This index varies between zero and one, where zero indicates that smolts were never detected within the same group and one indicates that they are always detected within the same group (Farine and Whitehead 2015). To test whether Atlantic salmon and sea trout smolt co-occurrences were due to chance, we compared the coefficient of variation (CV; standard deviation divided by the mean) of the observed network to the CV of permuted networks (n= 40 000; Farine and Whitehead 2015, Findlay et al. 2016). Observed CV values that are greater than the 95% confidence interval of the permuted CV networks were indicative of individuals exhibiting preferential co-occurrences within the network (Machado et al. 2019). A multiple regression quadratic assignment procedure was used to determine if weight, fork length, species, and tagging date were predictors of strength associations using the asnipe package (Farine and Whitehead 2015). Both fork length and weight were binned into 0.5 cm/g bins for comparison and the observed network was permuted 10,000 times (Lilly et al. 2020).

In order to determine if Atlantic salmon and sea trout form distinct groups, the modularity (Q; which ranges between 0-1) of the networks was calculated using the modularity-optimisation community detection method, with values near one indicating strong group division (Newman 2006, Shizuka et al. 2014). The cluster leading eigenvector method was used to determine modularity (i.e., a measure of the structure of networks) as it resulted in the highest Q value of all the group detection algorithms available in the package igraph (Csardi and Nepusz 2006). We tested the observed modularity against those calculated from 1,000 permutations, which empirical derived modularity values of the Simple Ratio Index were considered statistically significant if they fell outside the 95% confidence interval of the randomized distributions (Mourier et al. 2019).

Finally, we used PCAs of linear morphology measurements (see morphology section above for more details) to visualize if successful individuals were interacting socially with similar phenotypes using the Simple Ratio Index above 0.1 (spending at least 10% of their time together; see Croft et al. 2009, Lilly et al. 2020), for all smolts detected during our study but also for individuals tagged during the three last days, to determine if associations were driven by release time.

Results

Detection efficiency

Detection efficiency using the fixed receivers #1, #5, and #6 (Fig. 1) was 98.7%, 100%, and 100%, respectively. When active tracking data were added to efficiency measures, fixed receivers #1, #5, and #6 had a detection efficiency of 95.6%, 100%, and 100%, respectively. For active tracking alone, efficiency increased with time, from 38.5% to 95.2% (Table 2). Overall, 93% (53/57) of the successful migrants, 69% (67/97) of the unsuccessful migrants, and 100% (4/4) of the unknown were detected by active tracking.

Sources of smolt riverine migration failure

In our study, 36.1 % of the Atlantic salmon and sea trout smolts from the River Endrick were assumed to have made a successful river migration, that is, the tag was detected having left the River Endrick. Successful river migration for Atlantic salmon was 36.3%, (n=49; Fig. 2) and for sea trout 34.8% (n=8). 61.4 % of the tagged smolts failed to migrate successfully and were inferred as dead (see Table 1 and A1). For Atlantic salmon, failed river migration was 63.7% (n=86) and for sea trout 47.8% (n=11; see Table 1 and A1). Four sea trout smolts (17.4%), had their migration success categorized as unknown fate (see Table 1 and A1).

Of the salmon assumed dead (sea trout excluded due to sample size, see Fig. 2 and Table 1 and A1), 25.6 % were never detected by both methods (n=22; inferred as avian predation shortly after release, near the trap) and 16.3% of smolts suddenly stopped being detected (n=14; inferred as avian predation). Thus, 41.9% of tagged salmon were thought to have been preyed upon by birds. 9.3% of the Atlantic salmon smolts (n=8) were consistently detected at the same place, close to the fish release site and did not move, we infer these to be fish lost as tagging mortality. 14.0 % of the Atlantic salmon smolts (n=12) displayed a pattern of detection indicating a change of behaviour that gave a strong indication of piscine predation. The continuous detection patterns for 26.7% of the smolts (n=23) could not be classified but displayed stationary detections indicative of mortality within the river, which we categorized as river mortality - unknown. 1.2% of Atlantic salmon smolts (n=1, Table A1) were categorized as unknown mortality due to a stationary tag but the detection pattern resulted in a number of possible inferences. 21% Atlantic salmon smolts (n=18) were detected upstream of the release site. Of these, 6 individuals (7%) never initiated a downstream migration, and thus they were classified as upstream mortality. The remaining 12 individuals comprising both successful and unsuccessful migrants, subsequently detected downstream of the release site (see Table A1; Fig. 2).

Finally, mortality inferred events were not randomly distributed along the River Endrick (X^2 =220.54, *df*=13, *P* <0.001; Fig. A4), the highest failure of migration was observed in the first kilometer from the release site.

Telemetry

Overall, successful river migrants of Atlantic salmon spent on a median of 3.99 days (interquartile range (IQR): 2.82-5.22) in the River Endrick, whereas sea trout spent 23.04 days (IQR: 13.98-37.75). For Atlantic salmon, the median duration of all residency events was 1156

seconds (IQR: 544-4109). The duration of residency events was significantly shorter for successful salmon (996 seconds; IQR: 500-2197) compared with unsuccessful river migrant smolts (1926 seconds; IQR: 635-6221; W = 56346, *P* <0.01). A similar but non-significant pattern was found for sea trout, with successful river migrants having shorter residency events (888.5 seconds; IQR: 486.5-2724.3) than unsuccessful river migrants (3431 seconds; IQR: 586-8842; W = 535.5, p = 0.32). The duration of residency events also varied among receivers (Kruskal-Wallis chi-squared = 29.12, *P* <0.01; Table A3), with smolts of Atlantic salmon displaying the longest residency around receiver #1. There were no differences in residency event durations among receivers for sea trout (Kruskal-Wallis chi-squared = 6.34, *P* = 0.096).

For salmon, the successful river migrants had a higher rate of movement (median: 0.11 $m.s^{-1}$; IQR: 0.05-0.64) than unsuccessful river migrants (0.04 $m.s^{-1}$; IQR: 0.03-0.10; W = 730, *P* <0.01). For sea trout, there was no difference in the rate of movement between successful (median: 0.25 $m.s^{-1}$; IQR: 0.08-0.65) and unsuccessful river migrants (0.09 m/s; IQR: 0.04-0.36 $m.s^{-1}$; W = 61, *P* = 0.53). For both species, rate of movement differed among river sections (salmon: Kruskal-Wallis chi-squared = 105.95, df = 2, *P* <0.01; sea trout: Kruskal-Wallis chi-squared = 16.65, df = 2, *P* <0.01), with the movement rate increasing with distance downstream for both species (i.e., the highest movement rate being at the final section of the river, between receiver #6 and #7). For most of the migration, trout had higher rate of movement than salmon, except for the final section (between receivers #6 and #7) whereas salmon had higher median rate of movement than trout (0.84 and 0.71 $m.s^{-1}$, respectively). During their migration, smolts of Atlantic salmon and sea trout passed the first receiver at all hours of the day, whereas by receivers #6 and #7, most movement was during daytime hours (Fig. 3).

Although successful river migrants had a slightly larger for-length for both species (salmon: 145.3 ± 14.5 mm; trout: 169.6 ± 31.1 mm) than unsuccessful ones (salmon: 141.6 ± 8.9 mm; trout: 168.9 ± 36.3 mm), these size differences were not significant for either species (salmon: W = 1782, P = 0.14; trout: W = 41, P = 0.87). Additionally, there were no significant differences in tag burden between successful river migrants (salmon: 5.60 ± 1.2%; sea trout: 4.04 ± 1.9%) and unsuccessful river migrants (salmon 5.72 ± 1.0%; trout: 4.05 ± 1.6%; salmon: W = 2156, P = 0.82; sea trout: W = 44, P = 1).

Morphology

No differences were observed in linear measurements of morphology between successful and unsuccessful river migrants for Atlantic salmon (MANOVA, F= 1.3, P = 0.2; Fig. A5) or for sea trout (Manova, F= 0.73, P = 0.7; Fig. A5). The first two principal components of linear measurements explained 24.16% and 14.75 % of variation in morphology for salmon and 25.04% and 22.82% of variation for sea tout (Fig. A5; Table A4). For unsuccessful river migrating Atlantic salmon categorized by mortality causes, the first two principal components of linear measurements explained 26.40 % and 15.02% of the variation (Fig. 4). Taken together, there were no differences in morphology among individuals from each of the seven inferred mortality groups. Accordingly, the heat map of phenotype (PC1) allocated to different mortality categories showed random assortment of phenotypes mortality in the river nearest to the release site (Fig. 4). However, as distance from the release site to the river mouth increased, individuals with a shorter head, jaw, and eye length showed evidence of higher mortality. Thus, there was a positive linear relationship between PC1 scores of head measurements and the maximum distance downstream that a migrant was recorded for the events classified as piscine predation (R^2=0.39, P =0.03, Fig. 4). A similar but non-significant pattern was found for avian predation (R^2=0.18, P =0.1, Fig. 4).

Social Network Analysis

When all fixed receiver data were combined, the number of associations (i.e., frequency with which two individuals are found together) of successful river migrants smolts was 5.23 ± 4.18 (mean ± SD; Table 3). The average interactions strength was below 0.1 (indicating 10% of their time together) suggesting that Atlantic salmon and sea trout smolts exhibited weak associations in the River Endrick (Table 3). However, the coefficient of variation was significantly higher than chance for Atlantic salmon and sea trout smolts, which indicated that smolts exhibited preferred co-occurrences (i.e., not random co-occurrence). Only capture date was a significant predictor of the formation of associations during our study (Table A5). The modularity of the smolt networks exceeded the 95% confidence interval for the permuted networks indicating that smolts formed distinct groups in the River Endrick (Table 4, Fig. 5).

The social networks of Atlantic salmon and sea trout based on each tagging day, during the period April 18th-20th, were variable in terms of number of associations, Simple Ratio Index, and modularity (Table 3 and 4). Atlantic salmon and sea trout were found to co-occur with the most individuals during April 19th and 20th whereas the 18th had a lower number of associations (19-20th: 3.41 ± 3.42 and 18th: 1.71 ± 1.64; Table 3). The average association strength was below 0.1 (but April 18th was close to an average of 0.1) suggesting that a tagged smolt did not generally exhibit strong co-occurrences with another individual in the River Endrick. However, the coefficient of variation was significantly higher than chance for Atlantic salmon and sea trout smolts tagged on two out of the three dates, indicating that a proportion of smolts exhibited preferred co-occurrences within and between species. The modularity of the smolt networks was found to be higher than the 95% confidence interval for the permuted networks suggesting that

smolts formed distinct groups within the River Endrick (Table 4; Fig. 5). Modularity were higher for April 19th and 20th than April18th.

The two first PCs from a PCA of successful salmon and trout together, combined explained 47.14% of the variation (Fig. 6). The Simple Ratio Index above 0.1 (10% of their time spent together) between individuals on PCAs showed that individuals were interacting with a range of phenotypes and between species (Fig. 6).

Discussion

We provided evidence that the success of river migration by smolts in the River Endrick was low with only 36% of tagged smolts exiting the mouth of the river. This seems to be a trend emerging across rivers in Scotland (Adams, Unpublished data; Lothian et al. 2018, Honkanen et al. 2021) but also elsewhere (Gibson et al. 2015, Jepsen et al. 2019, Flávio et al. 2020a, Flávio et al. 2020b). Undeniably, the process of smolting is a critical phase in the life-cycle of anadromous salmonids and has been associated with substantial mortality rates (Halfyard et al. 2012, Thorstad et al. 2012). Accordingly, one of the pressing requirements to better understand anadromous fish population dynamics is to be able to identify the location, the cause, and the rate of mortality smolts are facing during their first seaward migration. Here, we produced a framework combining spatial and temporal measures of smolt riverine migration to detect and estimate mortality events using acoustic telemetry. By combining active and passive tracking techniques, we were able to refine the spatiotemporal pattern detection scale, which allowed inferences to be made about mortality location, causes, and rates that would not have been possible using fixed position acoustic receivers solely. The lack of ability to detect fish between two fixed receivers introduces uncertainties that can prevent reasonable inferences from being drawn.

Despite the importance of the smolting phase in anadromous salmonids, the migration from freshwater to marine habitats has been generally less intensively studied than adult spawning migration (Drenner et al. 2012, Furey et al. 2020). The spatial and temporal patterns of migration failure (e.g., mortality rates, and location) during the smolt riverine migration have the potential to yield important insights into population bottlenecks for anadromous salmonids. In this study we demonstrated that during their initial riverine transitional phase, smolts were particularly vulnerable to predators whilst migrating through that high-risk landscape (Ward et al. 2008, Ward and Hvidsten 2011). The main cause of mortality of tagged smolts in this study were interpreted as avian predation (mammalian predators is thought to be low in this study area), however, piscine predation was also substantive. Predation can be a major driver of population dynamics and demography (Jonsson et al. 2017) by exerting a strong selective pressure (Ward and Hvidsten 2011), but other factors can act concomitantly (e.g., environmental factors, hydropower, etc.; Thorstad et al. 2012, Lothian et al. 2018). Our finding that avian predation rates were particularly high immediately near the release site suggests that there was a concomitant interaction between the effects of trapping/tagging and vulnerability to predation for smolts. Thus, the high percentage of individuals that were never detected by either method after release could be a result of either: 1) a learned response by avian predators to the numerical increase in prey near the release site (grey herons (Ardea cinerea) and goosanders (Mergus merganser) were regularly observed close to the release site; pers. comm.; Ward et al. 2008, Flávio et al. 2020a, Wargo Rub and Sandford 2020) and/or 2) individuals were more susceptible to predation following tagging (e.g., trapping, anaesthesia, fish handling; higher residency were observed near the trap; Thedinga et al. 1994). Nevertheless, other explanations independent of trapping/tagging induced effects, such as a naturally high predation level in that specific area, cannot be ruled out.

A contentious point of using telemetry has always been to estimate the direct effect of tagging on smolt fate, which has been mostly tested experimentally or using models, but rarely in the wild (Hueter et al. 2006, Newton et al. 2016, Klinard and Matley 2020, Vollset et al. 2020). This study suggests some tagging-induced mortality, but it was unrelated to tag burden. The varying skills of the tagger when inserting tags surgically have been shown to have an effect on the outcome of the tagging process (Cooke et al. 2003) but environmental factors, such as elevated water temperature, can also have an effect on tagging outcomes (Brownscombe et al. 2019). One way or the other, this result highlights the urgent need to determine direct and indirect effects of surgically implanted tags in telemetry studies to ensure adequate interpretation of the results.

Because migration is known to be costly for salmonid smolts (e.g., high mortality level when migration is initiated; Ward and Hvidsten 2011, Thorstad et al. 2012), the eco-evolutionary dynamics of migration success are likely to result in selection pressures for populations (Hindar et al. 2011, Tamario et al. 2019). The morphological phenotype of an individual can affect its functional performance during migration, and ultimately survival and fitness (Blob et al. 2008, Lagarde et al. 2018). Atlantic salmon is considered to display relatively little pronounced discrete intraspecific morphological differences within a population, yet among-individual variation does exist (Adams, Unpublished data; Riddell and Leggett 1981). In this study, there was some evidence pointing to selection pressure on unsuccessful migrant shape, downstream from the release site. Individual salmon smolts with a shorter head, jaw, and eye appear to be more vulnerable to piscine predation (and to a certain extent, avian predation). In addition to functional performance influenced by morphology and body size (e.g., swimming, feeding; Webb 1984, Robinson and Parsons 2002), a shorter head might correlate with a smaller brain and lower cognitive ability, which may influence predator response capabilities and individual's vulnerability to predation

(Mason 2020, Møller et al. 2020). In contrast, mortality earlier in river migration was independent of phenotype. The high mortality near the release site (first 800 m) could explain the lack of discrepancy of morphological differences between successful and unsuccessful migrants, with direct and indirect tagging effects appeared to select regardless of the phenotype.

The fine-scale social structure of a population can also play a central role in ecological and evolutionary processes, with behavioural phenotypes influencing individual vulnerability to predation (van Oers et al. 2004, Croft et al. 2009). Shoaling tendency, predator inspection, and boldness are among behavioral traits that can influence the social network of a population and in turn individual fish survival (Wilson et al. 2014). In our study, we observed heterogeneity in the number and strength of interactions among successful smolts and there were no specific social associations based on morphological attributes or size. The heterogeneity of social associations of successful smolts did not support the assumption of the social network features attributing any specific adaptive benefits into reducing predation risk (e.g., schooling and shoaling; Krause et al. 2002, Croft et al. 2009, Ward and Hvidsten 2011). However, successful individuals interacting strongly with each other were often in a pair or as a trio, which demonstrated that some Atlantic salmon and sea trout smolts formed notable intra- and interspecific social associations. These associations appear to have been driven by social preferences over a tendency for aggregation during the smolt riverine migration (Jacoby et al. 2014), which could be related to predation risk or resource use (Haak et al. 2020).

Tagged smolts showed migratory behavioral patterns that were both similar and distinct to other migratory salmonid populations experiencing high predation risks. Residence period and rate of movement of smolts while migrating indicated that a shorter time spent within the river was related to migration success, corroborating the notion that the River Endrick is a high-risk

landscape for salmonid juveniles (Furey et al. 2016, Honkanen et al. 2018, Furey et al. 2021). Despite the evidence of high predation pressure found in the river, smolts travelled during the day, especially as they moved further downstream. Typically, smolts travel during the night as a behavioural predation risk-reduction mechanism (Ibbotson et al. 2006, Furey et al. 2016, Flávio et al. 2020b). Diurnal travelling is counterintuitive to predation avoidance, particularly in a river with visual predators, and thus migration during the night should lead to lower mortality. However other studies have also found a diurnal pattern (Fängstam et al. 1993, Thorstad et al. 2012), indicating the occurrence of daytime migration could be related to other factors (e.g., the predator community of a river, latitude, and how early or late in the period of the smolt migration period the fish is).

Upstream movements are considered unlikely for migrating Atlantic salmon smolts and downstream movements are assumed to be ubiquitous (Gauld et al. 2013, Lothian et al. 2018). Yet, movements of the smolts in the River Endrick offered a diverse range of upstream movements, with a variation in time and final direction (downstream or upstream). Salmon telemetry studies rarely link upstream movements to tag effects or handling and to mortality events occurring upstream after tagging (Frank et al. 2009). These complex behaviours could also be induced from exploratory movements (Keefer et al. 2008), seeking alternative routes, waiting for appropriate conditions (Holbrook et al. 2009), disorientation in certain hydraulic conditions (Honkanen et al. 2021), or varying sensitivity in distinct migratory phases (Mäkinen et al. 2000). The amount of upstream movement and mortality found in this study highlight the importance to monitoring these movements to ensure adequate interpretation of the results of telemetry studies.

Important considerations:

A few caveats should be noted that could alter interpretations in this study. Despite our best efforts, some uncertainties persisted when mortality sources and rates were untangled and

inferred. For example, a number of uncertainties are related to the detection patterns of “never been detected” or “sudden stop in detections”, which were inferred as avian predation. Other factors could induce these patterns, i.e., undetected long-distance upstream movements (no fixed receivers were positioned upstream), mammal predation, and/or tag malfunctioning/expulsion that could result in an overestimation of the avian predation. Although bias in the precision in estimating the proportion of fish in any inferred mortality category is probable; regardless of the uncertainties in our estimations, the main point remaining here is that by far the most substantive detection pattern points to a high percentage of avian predation events.

Our result bias can also be related to underestimating mortality events, which is likely to occur in the delineation of piscine predation events. Due to the difficulty of characterizing a change of behavior, we included only the most obvious patterns from our detections. Most likely, a number of piscine predation mortality events were classified as river mortality – unknown because of the difficulty of distinguishing predator from prey behaviors (vice versa is also possible, a prey behavior could have been quantified as a predator behavior, although less likely due to the strong unidirectional downstream migration patterns displayed by Atlantic salmon). There are also uncertainties associated with the location and timing of these piscine predation events (i.e., where and when the smolt was predated). The use of predation tags (Weinz et al. 2020), which can detect predation events, coupled with active tracking, could be a valuable method to further refine mortality events of smolts. Finally, due to our strict temporal and spatial assumptions around mortality near the release site, the inferred tagging mortality rate might be an underestimation. In reality, mortality events associated with tagging could take place downstream and upstream of the release site and/or after seven days; in this paper, these events have been classified as river mortality or upstream mortality.

There was a learning curve associated with the active tracking methodology, mostly linked to the disruptive code collisions (i.e., detection interference as a result of several transmissions echoes being heard simultaneously; Binder et al. 2016). Because 53 of 57 successful migrants were detected by active tracking, the increase of detection efficiency over time appears to be linked to the gained experience of handling tag transmission collisions than differences of detection between alive and dead individuals. Even with the poor performance of active tracking at the start of the study, detection efficiency of active tracking improved and refined the scale of detection when those data were combined with fixed receivers.

Despite these caveats, the aim of this paper was to disentangle some aspects of the location, cause, and rate of mortalities occurring and influencing riverine migration success based on several published assumptions with their associated uncertainties (enumerated above). These assumptions are frequently used by studies to target specific mortality causes independently (e.g., avian and piscine predation). Combining spatial and temporal metrics allowed us to attempt to improve the resolution of the tagged smolt fates, while we are acknowledging some uncertainties surrounding identifying location, cause, and rate of mortality events remain. As more studies refine active tracking combined with fixed receivers as a tracking methodology in the riverine environment, assigning location, cause, and rate of morality more precisely is anticipated.

Conclusion

Active tracking combined with fixed acoustic receivers provided considerable insights into the patterns of migration failure and their causes that could not be identified by relying solely on fixed acoustic receivers. Refining the temporal and spatial scale of the mortality location enabled the causes and rates to be inferred, which we embedded this into a behaviour and movement study. Thus, we provided a case study of a methodology, applicable to any small-moderate riverine

system, which should stimulate further use in an emerging research theme and provide insights to help to guide management actions (Flávio et al. 2020a, Klinard and Matley 2020, Villegas-Ríos et al. 2020). The extended spatial and temporal characteristics of salmonid migration means that factors acting over long periods and broad geographic scales may all contribute, both cumulatively and synergistically, to the currently depressed populations (Thorstad et al. 2012). Thus, the freshwater and marine survival of anadromous salmonids are known to be intertwined at the population level, although our knowledge of the relationship between the two is limited (McCormick et al. 2009). Anadromous salmonid marine mortality is considered to be density-independent (Jonsson et al. 1998, Flávio et al. 2019), which implies that the number of juvenile individuals, the smolts, entering seawater will broadly determine the number of adults that return from sea to spawn (McCormick et al. 2009). Thus, success in the early stages of migration to sea success is likely to have far reaching effects on population dynamics. Considering the major declines of anadromous salmonid worldwide (Chaput 2012), anadromous salmonid populations are of high conservation and scientific relevance, and identifying bottlenecks during their freshwater transition to the marine environment should allow specific management actions to mitigate these losses.

Acknowledgements

This is a SeaMonitor project funded by the European Union INTERREG VA Programme award number IVA5060. We thank the Loch Lomond Angling Improvement Association, Megan-Rose MacDonald, and Adam Wright for their valuable help with fieldwork and logistics. We thank Matthew Faust for his thoughtful comments on the manuscript. Loch Lomond Angling Improvement Association.

Declarations:

Authors' contributions

LC conceived the study. AC funded the study. LC, HH, JL, HG, and CA carried out the field work. LC, HH, JL, MN participated in the data analyses. LC wrote the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets supporting the conclusions of this article are included within the article. Raw data will be available on Dryad upon manuscript acceptance.

Funding

SeaMonitor (https://www.loughs-agency.org/managing-our-loughs/funded-programmes/current-programmes/sea-monitor/)

Bibliography:

Armansin, N. C., K. A. Lee, C. Huveneers, and R. G. Harcourt. 2016. Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. Animal Behaviour **115**:245-258.

Bergé, J., H. Capra, H. Pella, T. Steig, M. Ovidio, E. Bultel, and N. Lamouroux. 2012. Probability of detection and positioning error of a hydro acoustic telemetry system in a fast-flowing river: Intrinsic and environmental determinants. Fisheries Research **125-126**:1-13.

Binder, T. R., C. M. Holbrook, T. A. Hayden, and C. C. Krueger. 2016. Spatial and temporal variation in positioning probability of acoustic telemetry arrays: fine-scale variability and complex interactions. Animal Biotelemetry **4**:4.

Blob, R. W., W. C. Bridges, M. B. Ptacek, T. Maie, R. A. Cediel, M. M. Bertolas, M. L. Julius, and H. L. Schoenfuss. 2008. Morphological selection in an extreme flow environment: body shape and waterfall-climbing success in the Hawaiian stream fish Sicyopterus stimpsoni. Integrative and Comparative Biology **48**:734-749.

Both, A., M. Duckham, P. Laube, T. Wark, and J. Yeoman. 2012. Decentralized Monitoring of Moving Objects in a Transportation Network Augmented with Checkpoints. The Computer Journal **56**:1432-1449.

Brownscombe, J. W., E. J. I. Lédée, G. D. Raby, D. P. Struthers, L. F. G. Gutowsky, V. M. Nguyen, N. Young, M. J. W. Stokesbury, C. M. Holbrook, T. O. Brenden, C. S. Vandergoot, K. J. Murchie, K. Whoriskey, J. Mills Flemming, S. T. Kessel, C. C. Krueger, and S. J. Cooke. 2019. Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. Reviews in Fish Biology and Fisheries **29**:369-400.

Bruneel, S., P. Verhelst, J. Reubens, J. M. Baetens, J. Coeck, T. Moens, and P. Goethals. 2020. Quantifying and reducing epistemic uncertainty of passive acoustic telemetry data from longitudinal aquatic systems. Ecological Informatics **59**:101133.

Brunsdon, E. B., J. Daniels, A. Hanke, and J. Carr. 2019. Tag retention and survival of Atlantic salmon (Salmo salar) smolts surgically implanted with dummy acoustic transmitters during the transition from fresh to salt water. ICES Journal of Marine Science **76**:2471-2480.

Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indices. Animal Behaviour **35**:1454-1469.

Carlon, R. 2015. Tracking tagged fish using a wave glider. Pages 1-5 *in* OCEANS 2015-MTS/IEEE Washington. IEEE.

Chaput, G. 2012. Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. ICES Journal of Marine Science **69**:1538-1548.

Chaput, G., J. Carr, J. Daniels, S. Tinker, I. Jonsen, and F. Whoriskey. 2018. Atlantic salmon (Salmo salar) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. ICES Journal of Marine Science **76**:1107-1121.

Chavarie, L., K. L. Howland, and W. M. Tonn. 2013. Sympatric polymorphism in lake trout: the coexistence of multiple shallow-water morphotypes in Great Bear Lake. Transactions of the American Fisheries Society **142**:814-823.

Cooke, S. J., B. D. S. Graeb, C. D. Suski, and K. G. Ostrand. 2003. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. Journal of Fish Biology **62**:1366-1380.

Cooke, S. J., J. D. Midwood, J. D. Thiem, P. Klimley, M. C. Lucas, E. B. Thorstad, J. Eiler, C. Holbrook, and B. C. Ebner. 2013. Tracking animals in freshwater with electronic tags: past, present and future. Animal Biotelemetry **1**:5.

Croft, D. P., J. Krause, S. K. Darden, I. W. Ramnarine, J. J. Faria, and R. James. 2009. Behavioural trait assortment in a social network: patterns and implications. Behavioral Ecology and Sociobiology **63**:1495-1503.

Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. InterJournal, complex systems **1695**:1-9.

Dainys, J., S. Stakėnas, H. Gorfine, and L. Ložys. 2018. Mortality of silver eels migrating through different types of hydropower turbines in Lithuania. River Research and Applications **34**:52-59.

Drenner, S. M., T. D. Clark, C. K. Whitney, E. G. Martins, S. J. Cooke, and S. G. Hinch. 2012. A Synthesis of Tagging Studies Examining the Behaviour and Survival of Anadromous Salmonids in Marine Environments. PloS one **7**:e31311.

Ennasr, O., C. Holbrook, D. W. Hondorp, C. C. Krueger, D. Coleman, P. Solanki, J. Thon, and X. Tan. 2020. Characterization of acoustic detection efficiency using a gliding robotic fish as a mobile receiver platform. Animal Biotelemetry **8**:32.

Fängstam, H., I. Berglund, M. Sjöberg, and H. Lundqvist. 1993. Effects of size and early sexual maturity on downstream migration during smolting in Baltic samon (Salmo salar). Journal of Fish Biology **43**:517-529.

Farine, D. R. 2013. Animal social network inference and permutations for ecologists in R using asnipe. Methods in Ecology and Evolution **4**:1187-1194.

Farine, D. R., and H. Whitehead. 2015. Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology **84**:1144-1163.

Fetterplace, L. C., A. R. Davis, J. M. Neilson, M. D. Taylor, and N. A. Knott. 2016. Active acoustic tracking suggests that soft sediment fishes can show site attachment: a preliminary assessment of the movement patterns of the blue-spotted flathead (Platycephalus caeruleopunctatus). Animal Biotelemetry **4**:15.

Findlay, R., E. Gennari, M. Cantor, and D. P. Tittensor. 2016. How solitary are white sharks: social interactions or just spatial proximity? Behavioral Ecology and Sociobiology **70**:1735-1744.

Flávio, H., K. Aarestrup, N. Jepsen, and A. Koed. 2019. Naturalised Atlantic salmon smolts are more likely to reach the sea than wild smolts in a lowland fjord. River Research and Applications **35**:216-223.

Flávio, H., P. Caballero, N. Jepsen, and K. Aarestrup. 2020a. Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in River Minho. Ecology of Freshwater Fish **n/a**.

Flávio, H., R. Kennedy, D. Ensing, N. Jepsen, and K. Aarestrup. 2020b. Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. Fisheries Management and Ecology **27**:92-101.

Forseth, T., B. T. Barlaup, B. Finstad, P. Fiske, H. Gjøsæter, M. Falkegård, A. Hindar, T. A. Mo, A. H. Rikardsen, E. B. Thorstad, L. A. Vøllestad, and V. Wennevik. 2017. The major threats to Atlantic salmon in Norway. ICES Journal of Marine Science **74**:1496-1513.

Frank, H. J., M. E. Mather, J. M. Smith, R. M. Muth, J. T. Finn, and S. D. McCormick. 2009. What is "fallback"?: metrics needed to assess telemetry tag effects on anadromous fish behavior. Hydrobiologia **635**:237-249.

Furey, N. B., S. G. Hinch, A. L. Bass, C. T. Middleton, V. Minke-Martin, and A. G. Lotto. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. Journal of Animal Ecology **85**:948-959.

Furey, N. B., E. G. Martins, and S. G. Hinch. 2020. Migratory salmon smolts exhibit consistent interannual depensatory predator swamping: Effects on telemetry-based survival estimates. Ecology of Freshwater Fish **n/a**.

Furey, N. B., E. G. Martins, and S. G. Hinch. 2021. Migratory salmon smolts exhibit consistent interannual depensatory predator swamping: Effects on telemetry-based survival estimates. Ecology of Freshwater Fish **30**:18-30.

Gauld, N. R., R. N. B. Campbell, and M. C. Lucas. 2013. Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. Science of the Total Environment **458-460**:435-443.

Gauld, N. R., R. N. B. Campbell, and M. C. Lucas. 2016. Salmon and sea trout spawning migration in the River Tweed: telemetry-derived insights for management. Hydrobiologia **767**:111-123.

Gerber, K. M., M. E. Mather, and J. M. Smith. 2017. A suite of standard post-tagging evaluation metrics can help assess tag retention for field-based fish telemetry research. Reviews in Fish Biology and Fisheries **27**:651-664.

Gibson, A. J. F., E. A. Halfyard, R. G. Bradford, M. J. W. Stokesbury, A. M. Redden, and J. M. Jech. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Canadian Journal of Fisheries and Aquatic Sciences **72**:728-741.

Giraudoux, P. 2012. pgirmess: Data analysis in ecology. R package version **1**:617.

Guttridge, T. L., S. H. Gruber, K. S. Gledhill, D. P. Croft, D. W. Sims, and J. Krause. 2009. Social preferences of juvenile lemon sharks, Negaprion brevirostris. Animal Behaviour **78**:543-548.

Haak, C. R., F. K. C. Hui, G. W. Cowles, and A. J. Danylchuk. 2020. Positive interspecific associations consistent with social information use shape juvenile fish assemblages. Ecology **101**:e02920.

Halfyard, E. A., A. J. F. Gibson, D. E. Ruzzante, M. J. W. Stokesbury, and F. G. Whoriskey. 2012. Estuarine survival and migratory behaviour of Atlantic salmon Salmo salar smolts. Journal of Fish Biology **81**:1626-1645.

Heupel, M. R., J. M. Semmens, and A. J. Hobday. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Marine and Freshwater Research **57**:1-13.

Hindar, K., J. A. Hutchings, O. H. Diserud, and P. Fiske. 2011. Stock, recruitment and exploitation. Atlantic salmon ecology:299-332.

Holbrook, C. M., J. Zydlewski, D. Gorsky, S. L. Shepard, and M. T. Kinnison. 2009. Movements of Prespawn Adult Atlantic Salmon Near Hydroelectric Dams in the Lower Penobscot River, Maine. North American Journal of Fisheries Management **29**:495-505.

Honkanen, H. M., D. L. Orrell, M. Newton, S. McKelvey, A. Stephen, R. A. Duguid, and C. E. Adams. 2021. The downstream migration success of Atlantic salmon (Salmo salar) smolts through natural and impounded standing waters. Ecological Engineering **161**:106161.

Honkanen, H. M., J. R. Rodger, A. Stephen, K. Adams, J. Freeman, and C. E. Adams. 2018. Counterintuitive migration patterns by Atlantic salmon Salmo salar smolts in a large lake. Journal of Fish Biology **93**:159-162.

Hueter, R. E., C. A. Manire, J. P. Tyminski, J. M. Hoenig, and D. A. Hepworth. 2006. Assessing Mortality of Released or Discarded Fish Using a Logistic Model of Relative Survival Derived from Tagging Data. Transactions of the American Fisheries Society **135**:500-508.

Hussey, N. E., S. T. Kessel, K. Aarestrup, S. J. Cooke, P. D. Cowley, A. T. Fisk, R. G. Harcourt, K. N. Holland, S. J. Iverson, J. F. Kocik, J. E. Mills Flemming, and F. G. Whoriskey. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. Science **348**:1255642.

Ibbotson, A. T., W. R. C. Beaumont, A. Pinder, S. Welton, and M. Ladle. 2006. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. Ecology of Freshwater Fish **15**:544-551.

ICES. 2017. Report of the working group on North Atlantic salmon (WGNAS).

ICES. 2018. Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST), 20–28 March 2018, Turku, Finland.:369.

ICES, C. S. 2011. Report of the working group on North Atlantic salmon. ICES Document CM/ACOM **9**.

Jacoby, D. M. P., L. N. Fear, D. W. Sims, and D. P. Croft. 2014. Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. Behavioral Ecology and Sociobiology **68**:1995-2003.

Jepsen, N., H. Flávio, and A. Koed. 2019. The impact of cormorant predation on Atlantic salmon and sea trout smolt survival. Fisheries Management and Ecology **26**:183-186.

Jonsson, B., M. Jonsson, and N. Jonsson. 2017. Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (Salmo salar). Canadian Journal of Zoology **95**:581-587.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon Salmo salar. Journal of Animal Ecology **67**:751-762.

Keefer, M. L., C. C. Caudill, C. A. Peery, and C. T. Boggs. 2008. Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system. Journal of Fish Biology **72**:27-44.

Klinard, N. V., and J. K. Matley. 2020. Living until proven dead: addressing mortality in acoustic telemetry research. Reviews in Fish Biology and Fisheries **30**:485-499.

Kocik, J., J. P. Hawkes, T. F. Sheehan, P. A. Music, and K. F. Beland. 2009. Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the Narraguagus River, Maine using ultrasonic telemetry. Pages 293-310 *in* American Fisheries Society Symposium.

Kraus, R. T., C. M. Holbrook, C. S. Vandergoot, T. R. Stewart, M. D. Faust, D. A. Watkinson, C. Charles, M. Pegg, E. C. Enders, and C. C. Krueger. 2018. Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival. Methods in Ecology and Evolution **9**:1489-1502.

Krause, J., G. D. Ruxton, G. Ruxton, and I. G. Ruxton. 2002. Living in groups. Oxford University Press.

Lacroix, G. L., D. Knox, and P. McCurdy. 2004. Effects of Implanted Dummy Acoustic Transmitters on Juvenile Atlantic Salmon. Transactions of the American Fisheries Society **133**:211-220.

Lagarde, R., G. Borie, R. W. Blob, H. L. Schoenfuss, and D. Ponton. 2018. Intra- and inter-specific morphological diversity of amphidromous gobies influences waterfall-climbing performance. Journal of Zoology **306**:243-251.

Leander, J., J. Klaminder, M. Jonsson, T. Brodin, K. Leonardsson, and G. Hellström. 2019. The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (Salmo salar) smolt and European eel (Anguilla anguilla) around hydropower facilities. Canadian Journal of Fisheries and Aquatic Sciences **77**:177-187.

Lilly, J., M. F. McLean, M. J. Dadswell, I. Wirgin, P. Comolli, and M. J. W. Stokesbury. 2020. Use of social network analysis to examine preferential co-occurrences in Atlantic Sturgeon Acipenser oxyrinchus oxyrinchus Mitchill, 1815. Animal Biotelemetry **8**:14.

Lothian, A. J., M. Newton, J. Barry, M. Walters, R. C. Miller, and C. E. Adams. 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**:549-558.

Machado, A. M. S., M. Cantor, A. P. B. Costa, B. P. H. Righetti, C. Bezamat, J. V. S. Valle-Pereira, P. C. Simões-Lopes, P. V. Castilho, and F. G. Daura-Jorge. 2019. Homophily around specialized foraging underlies dolphin social preferences. Biology Letters **15**:20180909.

Mäkinen, T. S., E. Niemelä, K. Moen, and R. Lindström. 2000. Behaviour of gill-net and rod-captured Atlantic salmon (Salmo salar L.) during upstream migration and following radio tagging. Fisheries Research **45**:117-127.

Mason, J. 2020. Predation Effects on the Evolutionary Trajectory of Brain Morphology in the Threespine Stickleback Fish (Gasterosteus aculeatus). M.S. Clark University, Ann Arbor.

McCormick, S. D., D. T. Lerner, M. Y. Monette, K. Nieves-Puigdoller, J. T. Kelly, and B. T. Björnsson. 2009. Taking it with you when you go: how perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. Pages 195-214 *in* American Fisheries Society Symposium. Citeseer.

Møller, A. P., K. Hongisto, and E. Korpimäki. 2020. Predation risk in relation to brain size in alternative prey of pygmy owls varies depending on the abundance of main prey. PloS one **15**:e0236155.

Mourier, J., L. Ballesta, E. Clua, and S. Planes. 2019. Visitation patterns of camouflage groupers Epinephelus polyphekadion at a spawning aggregation in Fakarava inferred by acoustic telemetry. Coral Reefs **38**:909-916.

Newman, M. E. J. 2006. Modularity and community structure in networks. Proceedings of the National Academy of Sciences **103**:8577.

Newton, M., J. Barry, J. A. Dodd, M. C. Lucas, P. Boylan, and C. E. Adams. 2016. Does size matter? A test of size-specific mortality in Atlantic salmon Salmo salar smolts tagged with acoustic transmitters. Journal of Fish Biology **89**:1641-1650.

Newton, M., J. Barry, J. A. Dodd, M. C. Lucas, P. Boylan, and C. E. Adams. 2019. A test of the cumulative effect of river weirs on downstream migration success, speed and mortality of Atlantic salmon (Salmo salar) smolts: An empirical study. Ecology of Freshwater Fish **28**:176-186.

Parrish, D. L., R. J. Behnke, S. R. Gephard, S. D. McCormick, and G. H. Reeves. 1998. Why aren't there more Atlantic salmon (Salmo salar)? Canadian Journal of Fisheries and Aquatic Sciences **55**:281-287.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riddell, B. E., and W. C. Leggett. 1981. Evidence of an Adaptive Basis for Geographic Variation in Body Morphology and Time of Downstream Migration of Juvenile Atlantic Salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences **38**:308-320.

Robinson, B. W., and K. J. Parsons. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. Canadian Journal of Fisheries and Aquatic Sciences **59**:1819-1833.

Robitaille, A. L., Q. M. R. Webber, and E. Vander Wal. 2019. Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. Methods in Ecology and Evolution **10**:1203-1211.

Roy, R., J. Beguin, C. Argillier, L. Tissot, F. Smith, S. Smedbol, and E. De-Oliveira. 2014. Testing the VEMCO Positioning System: spatial distribution of the probability of location and the positioning error in a reservoir. Animal Biotelemetry **2**:1.

Schwinn, M., K. Aarestrup, H. Baktoft, and A. Koed. 2017. Survival of Migrating Sea Trout (Salmo trutta) Smolts During Their Passage of an Artificial Lake in a Danish Lowland Stream. River Research and Applications **33**:558-566.

Shizuka, D., A. S. Chaine, J. Anderson, O. Johnson, I. M. Laursen, and B. E. Lyon. 2014. Across-year social stability shapes network structure in wintering migrant sparrows. Ecology Letters **17**:998-1007.

Stehfest, K. M., T. A. Patterson, L. Dagorn, K. N. Holland, D. Itano, and J. M. Semmens. 2013. Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. Animal Behaviour **85**:839-848.

Tamario, C., J. Sunde, E. Petersson, P. Tibblin, and A. Forsman. 2019. Ecological and Evolutionary Consequences of Environmental Change and Management Actions for Migrating Fish. Frontiers in Ecology and Evolution **7**.

Thedinga, J. F., M. L. Murphy, S. W. Johnson, J. M. Lorenz, and K. V. Koski. 1994. Determination of Salmonid Smolt Yield with Rotary-Screw Traps in the Situk River, Alaska, to Predict Effects of Glacial Flooding. North American Journal of Fisheries Management **14**:837-851.

Thorstad, E., F. kland, B. Finstad, R. Sivertsgrd, P. Bjorn, and R. McKinleyd. 2004. Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. Environmental Biology of Fishes **71**:305-311.

Thorstad, E. B., C. D. Todd, I. Uglem, P. A. Bjørn, P. G. Gargan, K. W. Vollset, E. Halttunen, S. Kålås, M. Berg, and B. Finstad. 2016. Marine life of the sea trout. Marine Biology **163**:47.

Thorstad, E. B., F. Whoriskey, I. Uglem, A. Moore, A. H. Rikardsen, and B. Finstad. 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**:500-542.

van Oers, K., P. J. Drent, P. de Goede, and A. J. van Noordwijk. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proceedings of the Royal Society of London. Series B: Biological Sciences **271**:65-73.

Villegas-Ríos, D., C. Freitas, E. Moland, S. H. Thorbjørnsen, and E. M. Olsen. 2020. Inferring individual fate from aquatic acoustic telemetry data. Methods in Ecology and Evolution **11**:1186-1198.

Vollset, K. W., R. J. Lennox, E. B. Thorstad, S. Auer, K. Bär, M. H. Larsen, S. Mahlum, J. Näslund, H. Stryhn, and I. Dohoo. 2020. Systematic review and meta-analysis of PIT tagging effects on mortality and growth of juvenile salmonids. Reviews in Fish Biology and Fisheries **30**:553-568.

Ward, D. M., and N. A. Hvidsten. 2011. Predation: compensation and context dependence. Atlantic salmon ecology:199-220.

Ward, D. M., K. H. Nislow, and C. L. Folt. 2008. Predators reverse the direction of density dependence for juvenile salmon mortality. Oecologia **156**:515-522.

Wargo Rub, A. M., and B. P. Sandford. 2020. Evidence of a ⍰dinner bell⍰ effect from acoustic transmitters in adult Chinook salmon. Marine Ecology Progress Series **641**:1-11.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist **24**:107-120.

Weinz, A. A., J. K. Matley, N. V. Klinard, A. T. Fisk, and S. F. Colborne. 2020. Identification of predation events in wild fish using novel acoustic transmitters. Animal Biotelemetry **8**:28.

Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press.

Whitehead, H., and S. Dufault. 1999. Techniques for analyzing vertebrate social structure using identified individuals. Adv Stud Behav **28**:33-74.

Wilson, A. D. M., D. P. Croft, and J. Krause. 2014. Social networks in elasmobranchs and teleost fishes. Fish and Fisheries **15**:676-689.

Yang, Z., R. Algesheimer, and C. J. Tessone. 2016. A Comparative Analysis of Community Detection Algorithms on Artificial Networks. Scientific Reports **6**:30750.

Zar, J. 2010. Biostatistical analysis. Pearson Education. Pearson Education Inc

New Jersey.

Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric morphometrics for biologists: a primer. Academic Press.

Table 1. The fate of each tagged fish was inferred following postulations used in other recent studies (for example, see Gerber et al. 2017, Flávio et al. 2020a, Klinard and Matley 2020, Villegas-Ríos et al. 2020, Weinz et al. 2020), with some modifications for the local study area. Riverine migration outcomes from tag detection patterns were inferred as: successful river migrant, unknown fate, and unsuccessful river migrants that were classified into seven migration failure categories. A detailed movement pattern and justification of our criteria for each fish inferred as dead or as an unknown fate is provided in table A1.

	Inferred Riverine Migration Outcomes	**Movement Patterns Criteria for Inference**	**Species-specific**
	Successful	A successful river migration was assumed if tags were detected during active tracking and/or on sequential accoustic receivers downstream, to the last river receiver at the mouth of the river (Kocik et al. 2009, Lothian et al. 2018, Honkanen et al. 2021).	No
	Unknown fate	Countinuous upstream and downstream movements until the end of the study among tagged sea trout; the inference of migration failure (e.g., piscine predation) could not be distinguished from alternative fates (e.g., delayed migration; Thorstad et al. 2004) due to the nature of their behaviour (Klinard and Matley 2020, Villegas-Ríos et al. 2020, Weinz et al. 2020).	Yes, sea trout only
Unsuccessful river migrants: Migration Failure Categories	Avian predation shortly after release	If no detections were recorded by either tracking technique between the release site and the first receiver, the fish was presumed to be consumed by an avian predator. The lack of detections indicate that the tag was removed from the river system (Flávio et al. 2020a, Klinard and Matley 2020); the incidence of piscivorous mamalian predators in this river is known to be low (Malcolm MacCormick *pers. comm.*).	No
	Avian predation	A tagged smolt was assumed to be predated by an avian predator if sequential detections from a migration downstream was followed by a sudden loss of detections by both techniques. The lack of detections indicate that the tag was removed from the river system (Flávio et al. 2020a, Klinard and Matley 2020, Villegas-Ríos et al. 2020). If no detections were recorded by both fixed acoustic receivers and active tracking for an extended period, followed by the sudden reappeareance of the tag with stationary detections, recorded by either techniques, the fish was presumed to have been consumed by avian predators (i.e., removed from the river) and the tag defecated into the river (i.e., stationary signal been recorded afterward). Three tags were classified as they were defecated by avian predators, with specific detection patterns in locations or/and elapsed time to support theses conclusions (see Table A1).	
	Upstream mortality	Detection of a stationary tag upstream of the trap was classified as upstream mortality. In this case the cause of the death could not be inferred, only the location of inferred mortality could be determined.	No
	Tagging mortality	Early detection (i.e., within the first seven days post-release) of a consistently stationary tag within 800 m of the release site (upstream of the fixed receiver #1), was classified as tagging mortality (Villegas-Ríos et al. 2020). Loss is infered as direct or indirect tagging mortality from the tagging and trapping processes, the anaestetic, or/and handling.	No

Piscine predation	Inferred from an abrupt change in recorded behavior of a detected tag, often an upstream movement following the initial consistent downstream movement, we assumed an Atlantic salmon smolt was consumed by a fish predator (Flávio et al. 2020a, Klinard and Matley 2020, Villegas-Ríos et al. 2020, Weinz et al. 2020). This assumption was not made for sea trout smolts due to the nature of their behaviour (e.g., Thorstad et al. 2004).	Yes, salmon only
River mortality - unknown	Where a tag was countinously detected as stationary at a location along the river, several possibilities for the fate of that fish exist: piscine defecated tag, tag expulsion, tagging mortality, or natural mortality. The mortality of the smolt was assumed (due to the stationary detection) but was classified as "river unknown" because the cause could not be infered. The consistent tag detection implies that the tag was not removed from the river (as might be the case for avian predation) but the detection patterns were outside of the range established by our other criteria to infer a cause of loss (Jepsen et al. 2019, Flávio et al. 2020a, Klinard and Matley 2020).	No
Unknown mortality	Detections of a consistently stationary tag infer mortality but the cause of death could not be inferred (e.g., pattern of detections outside of the range established by our other criteria, often avian with other detection patterns cannot be distinguished) (Jepsen et al. 2019, Flávio et al. 2020a, Klinard and Matley 2020).	No

Table 2. Efficiencies of active tracking, fixed receivers and fixed receivers encompassing active tracking data (see methods) in the River Endrick.

Active tracking efficiency (%)		**Fixed receiver efficiency (%)**		**Fixed receiver efficiency (%) - active tracking**	
April 17th	48	#1	98.7	#1	95.6
April 18th	47.4	#5	100	#5	100
April 19th	45.1	#6	100	#6	100
April 20th	38.5				
April 21th	42.1				
April 22th	67.5				
April 23rd	64.9				
May 8th	82.6				
May 21th	86				
June 4th	95.2				

Table 3. Results from Social Network Analysis conducted on successful Atlantic salmon and sea trout tagged between April 18th and April 20th 2020 and all fixed receiver data. The total number of dyads, their Simple Ratio Index (SRI) and degree (average number of dyad formations per individual) are included in the table. Results from the Multiple Regression Quadratic Assignment Procedure including the observed coefficient of variation (CV) and the mean CV of the permuted SRI networks.

Main variable	**# Salmon**	**# Sea trout**	**# dyads**	**Mean SRI (± SD)**	**Mean degree (± SD)**	**Obs. CV**	**Mean perm. CV**	***P***
20-04-18	13	1	14	0.09 ± 0.09	1.71 ± 1.64	4.03	2.08	0.002
20-04-19	13	1	14	0.07 ± 0.1	3.41 ± 3.42	3.99	3.42	0.07
20-04-20	11	1	12	0.07 ± 0.11	3.41 ± 3.42	3.50	1.39	0.0002
All Time	49	8	57	0.07 ± 0.1	5.23 ± 4.18	5.49	2.03	0.0003

Table 4. Information on the social networks of successful Atlantic salmon and sea trout tagged between April 18th and April 20th 2020 and all fixed receiver data. The number of individuals included in each group, the modularity scores of the observed networks and the 95% confidence interval of the modularity of the permuted networks are provided.

Date	Modularity (Q)	# individuals	95 % CI Permuted Modularity
20-04-18	0.52	14	0.27 – 0.28
20-04-19	0.73	14	0.262 – 0.268
20-04-20	0.19	12	0.061 – 0.064
All Time	0.68	57	0.137 – 0.139

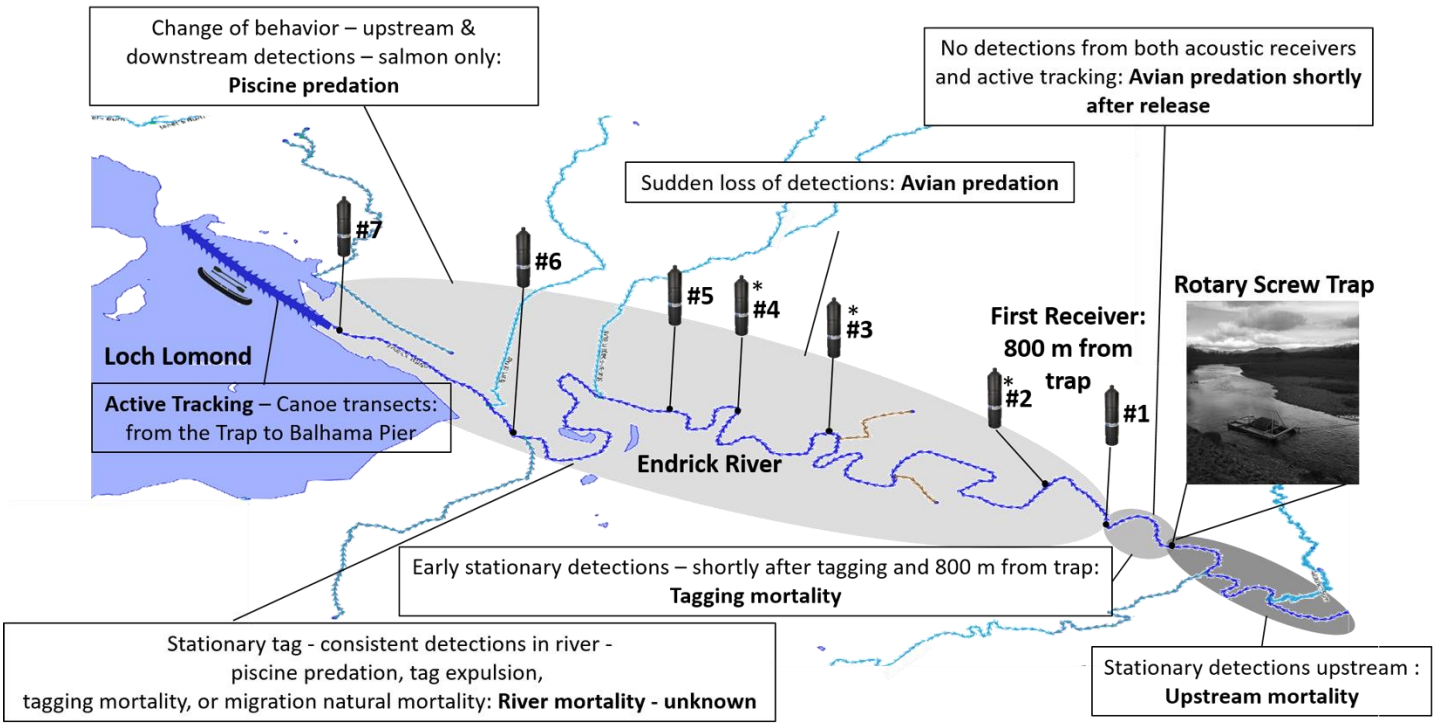

Fig. 1. Schematic of the study area and the combined passive and active tracking methodology developed to monitor Atlantic salmon and sea trout smolt migration. The passive acoustic design includes four VR2W receivers initially installed between March 24th and April 14th 2020 (that is prior to fish tagging). Three additional receivers were installed on May 21th 2020, which are represented by *. The active tracking design consist of a canoe transect commencing ~200 m above the rotary screw trap (and the release site) down river to Balhama Pier, beyond the mouth of the river, using a VR100 portable acoustic reciever. The River Endrick is represented in dark blue. The inflows to the River Endrick are represented in light blue, whereas the outflows are in yellow. Inferences drawn from the patterns of detections (or the lack of detections) from the combined active and passive accoustic receivers led to six plausable migration outcomes for each fish (beside the "unknown"). These inferences are presented in Table 1 and A1.

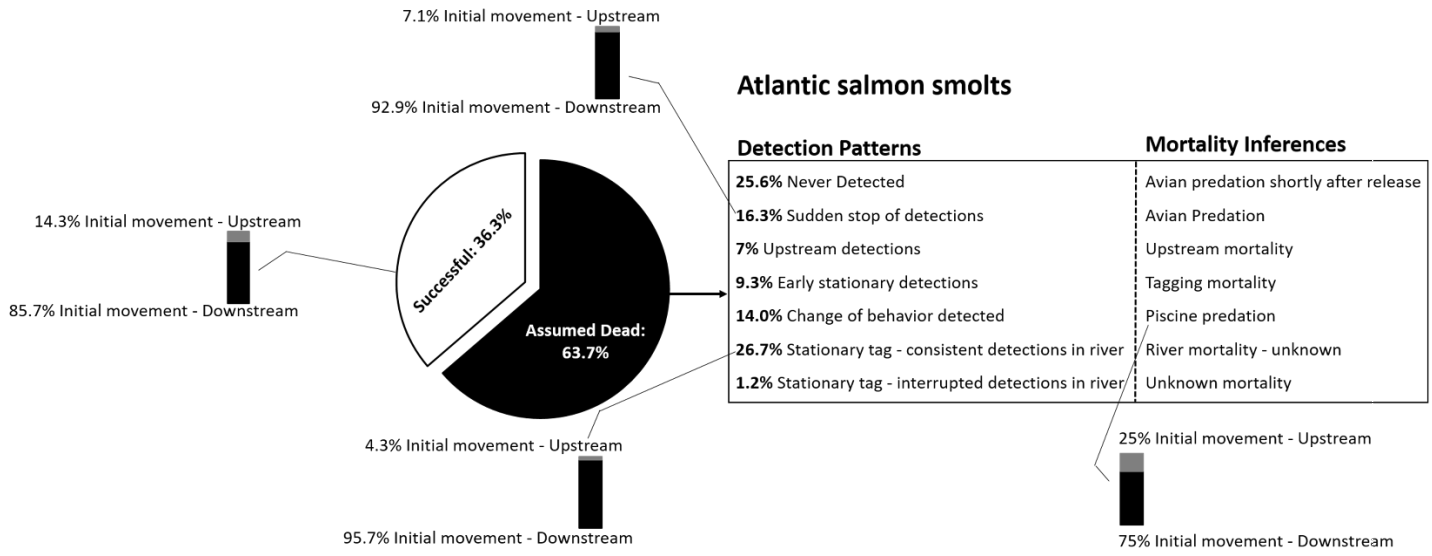

Fig. 2. Tags movements of Atlantic salmon recorded with fixed acoustic and active tracking techniques led to the determination of detection patterns that allowed the inference of the fate for each fish (see Table A1 for details). Seven detection patterns were defined to lead to a specific cause of mortality inference (see source of mortality section, table 1 and A1). Initial upstream movement detected were reported with a bar graph.

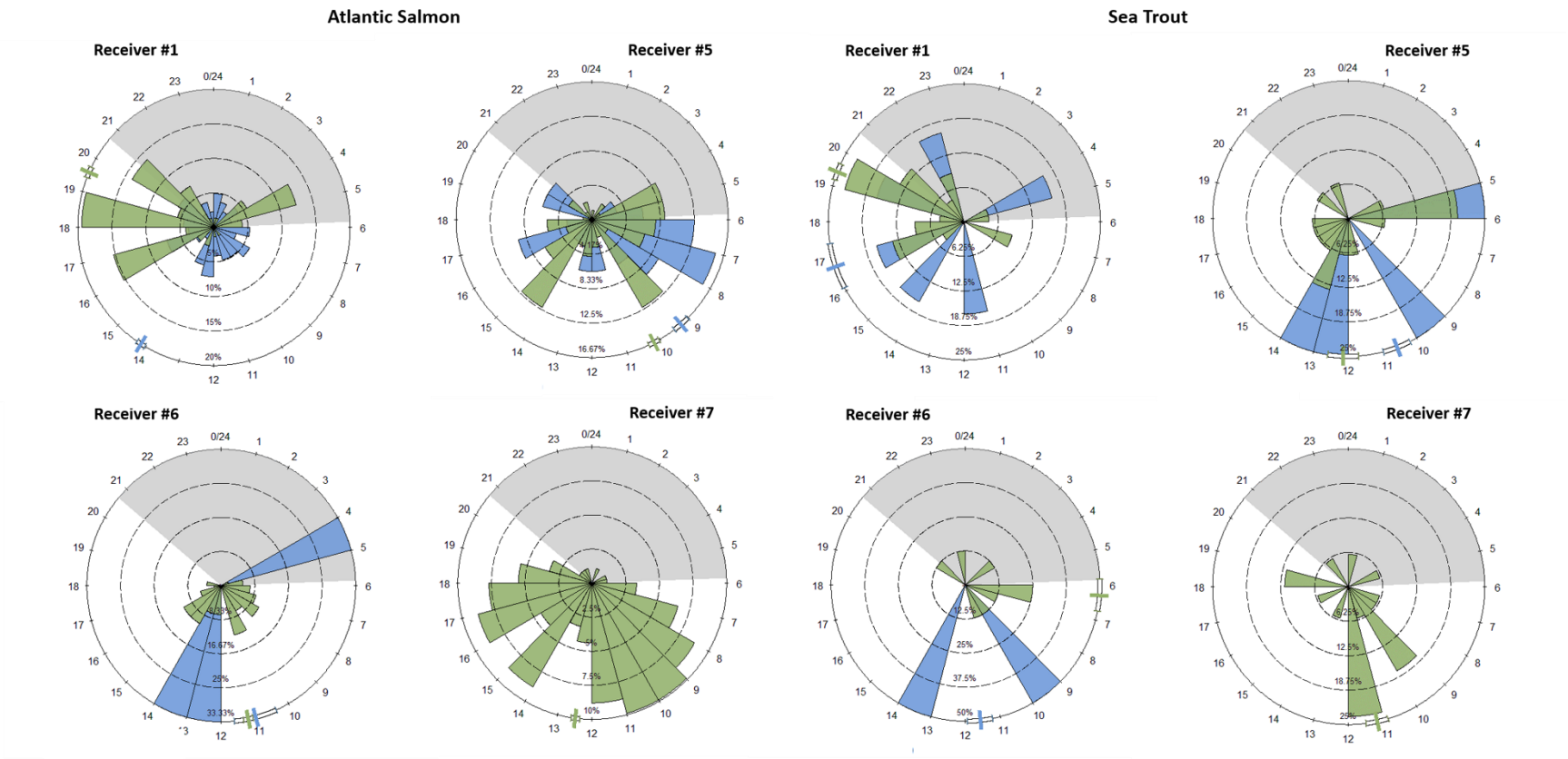

Fig 3. Arrival time at each fixed receiver in the River Endrick showing when Atlantic salmon and sea trout smolts are moving and whether the pattern changes during their migration downstream. Successful (green) and unsuccessful (blue) river migrant smolts are represented at each receiver and each array's bar sum to 100%. The coloured markers in the outer circle indicate the mean value respectively to the coloured category (i.e., successful and unsuccessful river migrants). The shaded portion of the circle shows the average sunset-to-sunrise hours for April.

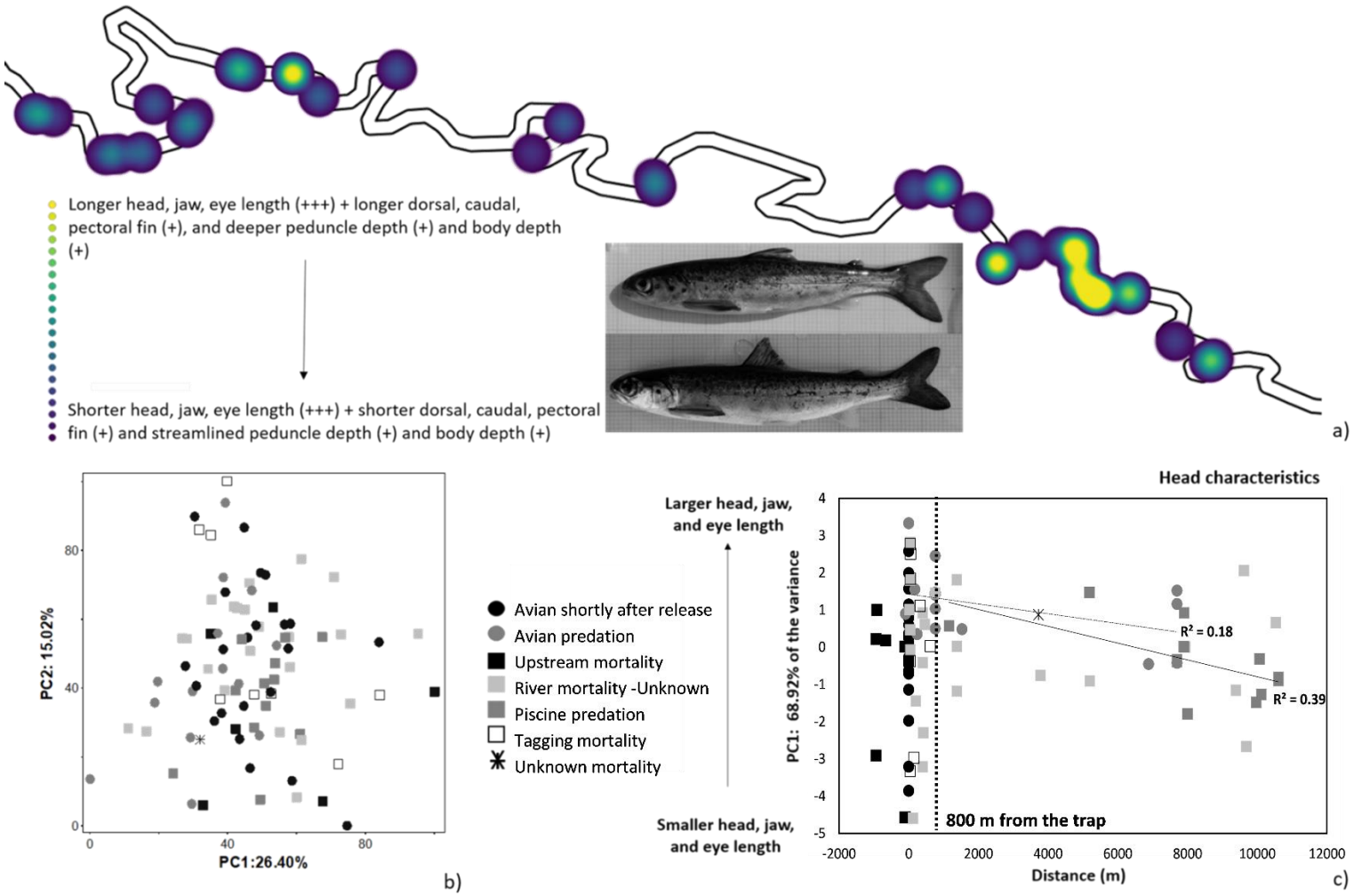

Fig. 4. Morphological differences of tagged Atlantic salmon along the River Endrick. In a), a heat map of fish morphology (PC1 scores of linear measurements) of unsuccessfully migrating fish plotted on their furthest downstream detection in the River Endrick. In b), PC1 and 2 scores morphology of unsuccessful migrants used in a), categorized into seven inferred causes of mortality. In c), the PC1 scores of head measurements only of unsuccessful migrants, allocated into the seven causes of inferred mortality, regressed against their furthest downstream detection in the River Endrick. The 800 m from the trap was illustrated in c) to illustrate a criterion we used to identify mortality close to the trap.

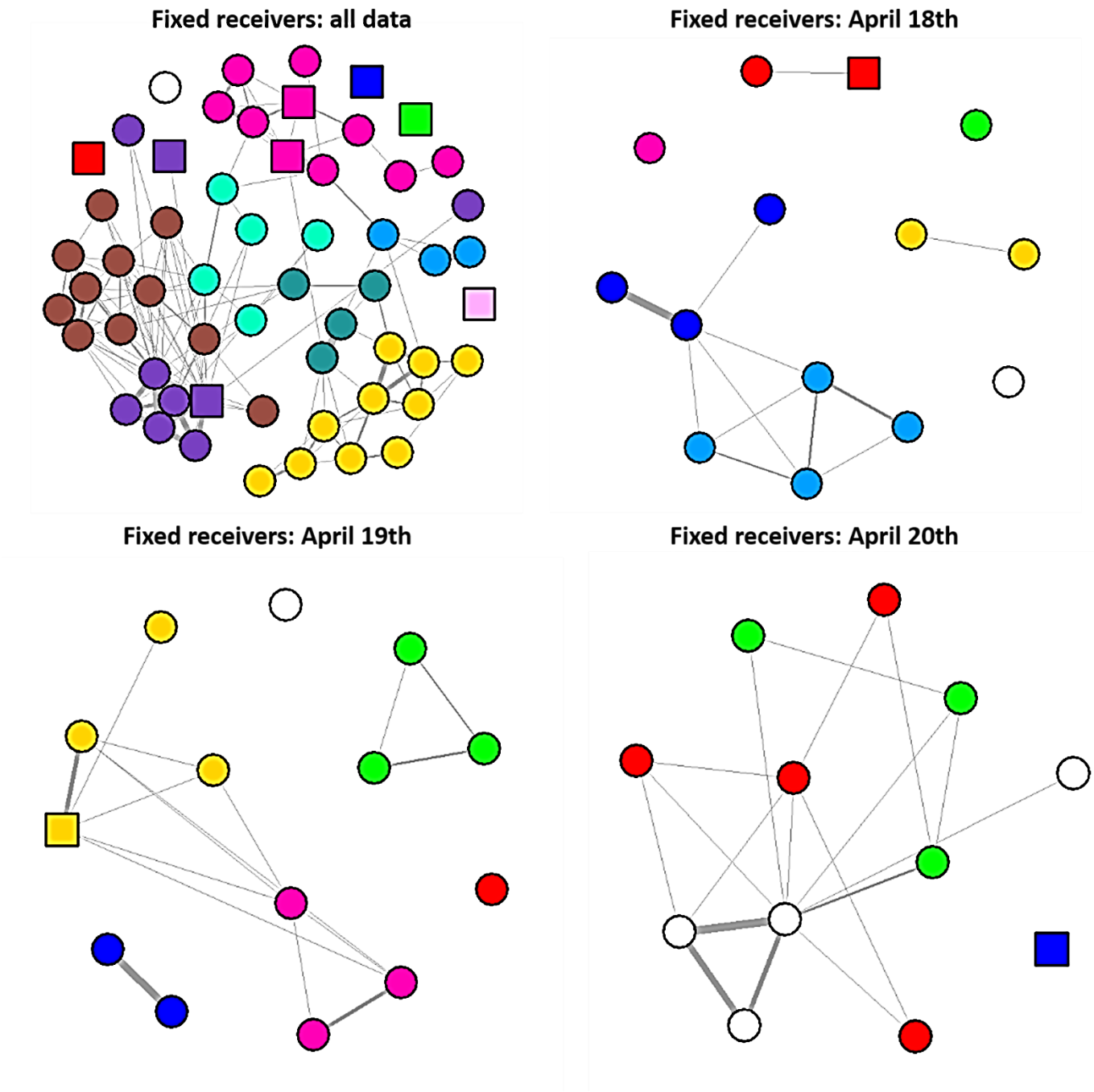

Fig. 5. Social networks representing the formation of co-occurrences of successfully migrating Atlantic salmon and sea trout within the River Endrick from all fixed receivers data and smolts tagged on April 18th - 20th 2020. The nodes represent unique individuals and the thickness of the edges refer to the strength (weighted degree) of the Simple Ratio Index (SRI) between a dyad. The networks are colour coded to reflect the different social modules and Atlantic salmon are represented by circles, and sea trout by squares.

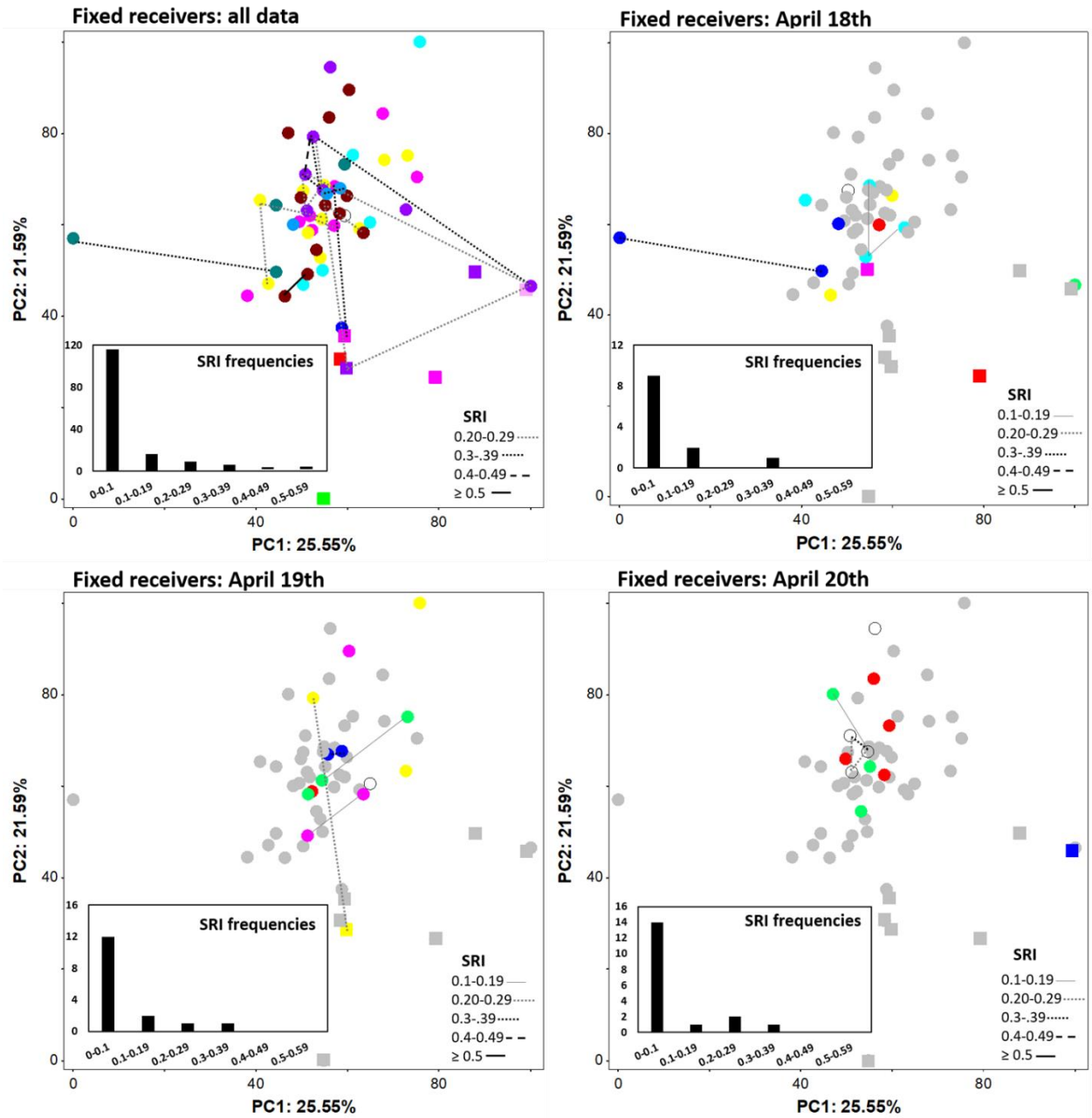

Fig. 6. PC1 and 2 scores of linear measurements of all (salmon and trout combined) sucessfully migrating smolts detected during the study and sucessfully migrating smolts tagged during the last three days. Lines represent the strength of interactions (SRI) between individuals (SRI; % of their time togheter). Strength of interaction frequencies are also given (inset graphs). Colours reflect the different social modules from network analysis represented in Fig. 4, Atlantic salmon and sea trout are represented by circles and squares respectively. For the three last tagging days PCAs, tagged individuals were represented coloured symbols, where all other successful smolts tagged during the entire season are represent with grey symbols.