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A comparative study of the alternative life history of iteroparous salmonids

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Abstract

The kelt phase of anadromous iteroparous salmonid life history remains mysterious, particularly aspects of their habitat use and factors influencing survival. Atlantic salmon and sea-run brown trout were captured in the estuary during their return migration to the Vosso River, Norway, tagged with acoustic transmitters, and tracked in the watershed and estuary in three different years (2020–2023). We found a relatively narrow window of river exit timing among trout that survived overwinter, whereas salmon tended to leave during a more protracted period. Trout preferred overwintering in lakes within the river system, which provided for lower locomotor activity than fish that overwintered in pools in the river according to data from tri-axial accelerometer transmitters. In contrast, Atlantic salmon tended to spend surprisingly little time in lakes even though the energy expenditure in this habitat is was seemingly lower for salmon that did overwinter in the lake. Our results demonstrate different use of habitat during overwintering and could suggest that measures to protect iteroparous life history strategies of salmonids will differently impact these two iteroparous salmonids.

KEYWORDS
acoustic telemetry, anadromy, freshwater ecology, kelt, repeat spawning, winter biology

1 | INTRODUCTION

Within and between species, Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) can exhibit remarkable plasticity in how they maximise lifetime fitness (Birnie-Gauvin et al., 2021). Salmonid species in the Atlantic exhibit broad phenotypic plasticity in life histories that may reflect adaptive responses to variable environmental conditions that they encounter (Hutchings & Myers, 1994) and the need to optimise reproductive output via investment in one ultimate or several repeat spawning events (Birnie-Gauvin et al., 2023; Crespi & Teo, 2002; Einum & Fleming, 2007). Most Pacific salmon (*Oncorhynchus* spp.) are semelparous spawners that are highly invested in one spawning instance, whereas the *Salmo* species are iteroparous and can spread the reproductive output across multiple occasions as long as they survive the intervening time (Birnie-Gauvin et al., 2023).

A key aspect for maximising fitness via this alternative life history strategy is the post-spawning behaviour, the late autumn, and winter period during which salmon and trout must persist in order

to make it back to sea to recondition and have a chance to spawn again. Habitat characteristics and availability that provide winter refuge is an important bottleneck in repeat spawner survival rates (Birnie-Gauvin et al., 2023; Bordeleau et al., 2020). After spawning, persisting through the winter is challenging for iteroparous salmonids across life stages (e.g., Cunjak et al., 1998). In many locations, the "kelts" that have completed spawning have minimal energy remaining after migration and reproduction (Jonsson et al., 1997) and they may leave the river altogether rather than remain in freshwater (Halttunen et al., 2013). Salmon expend about 70% of their somatic energy after they stop feeding at sea to after spawning (Jonsson et al., 1997), including digestion of the red and white muscle (Bombardier et al., 2010) and the skeleton (Kacem et al., 2000), leaving a small margin of energy for survival over winter. A few studies of other salmonid species have revealed the use of lakes as overwintering habitats, with evidence of thermoregulation by sea-run brown trout (Lunde, 2015) and colder temperatures for Arctic charr in lakes of northern Canada (Mulder et al., 2018). Although neither of those studies investigated activity during winter, Monsen (2019) estimated that sea-run charr and brown trout in a lake were moving extensively in the lakes during winter, which is an energetically inefficient strategy to wait out the winter given the finite energy they have available.

Repeat spawning can be critically important for brown trout and Atlantic salmon populations, which requires a more thorough understanding of the overwintering period and how it may affect the potential for repeat spawning. Many Atlantic salmon kelt studies have focused on tagging fish after winter (Bøe et al., 2019; Halttunen et al., 2013; Hubley et al., 2008; Jacobs, 2011), limiting our understanding of the post-spawning behaviour of salmonids expressing this strategy. We adopted a comparative approach to track the overwinter ecology of iteroparous adult salmon and trout following spawning. Using acoustic transmitters implanted during the summer before spawning, we followed trout and salmon through the full migration in freshwater and contrasted survival, river exit timing, habitat use, and locomotor activity between species, and across time. Tracking data from an array of acoustic receivers were used to compare the selection of overwintering areas between the two species and their fate for up to three separate migrations per individual. Transmitted locomotor activity data (based on tri-axial accelerometer sensors) were additionally compared for the two species to determine whether total activity differed during winter for the two species. Based on fate determinations made from the tracking data, these variables were tested to determine whether habitat selection was a determinant of overwinter survival for salmon or trout in the river system.

2 | METHODS

2.1 | Study site

We studied the Atlantic salmon and sea-run brown trout of the Vosso River in western Norway. Vosso was once one of the premier rivers in the world for salmon fishing but the population underwent a collapse in the late 1980s, and salmon production has failed to recover despite interventions including hatchery supplementation with a gene bank program. No supplementation has been attempted to enhance production of the brown trout, but abundance is also low. Only a few hundred wild salmon return to Vosso every summer, migrating from the ocean into the Osterfjord system, continuing through the small fjord arm Bolstadfjord, and into the river system that includes the Bolstad River, Evangervatnet Lake, Vosso River, Vangsvatnet Lake, and Strandaelva River (where the hatchery is located, Figure 1). Vosso has one high-head power generating station that discharges mountain water from a lake down to nearly sea level in Evanger Lake. The hypolimnetic water from the power station cools the water in the lake and lower reaches of the river during spring and summer and provides a bit of warming during winter relative to the surface waters of the system. However, temperature loggers on the acoustic receivers provided information about the river temperatures throughout the study period in each part of the system, suggesting relatively limited thermal variation within the system during the study period. Using the longest deployed receivers from the system and the 2 years when they were deployed year-round, calculated average temperatures were 0.7–17.4°C in the lower river (2021) and 1.1–11.5°C (2022) and in the upper river, −0.2 to 20°C (2021) and −0.2 to 16.1°C (2022). Ice coverage was not monitored, but there is ice on the lakes usually from December to March and occasionally shelf ice on parts of the river, which was most prominent in January–February 2021.

2.2 | Experimental design

We tagged Atlantic salmon and sea-run brown trout during June–September 2020 and 2021, and additional salmon during June–August 2022. Fish were captured using rod and reel, traditional Norwegian wedge nets (aka kilenot), or large fyke nets in Bolstadfjord, the last fjord arm in the Osterfjord system of western Norway before reaching the Vosso River system. In 2020, Atlantic salmon of both wild and hatchery origin were tagged (determined based on absence or very small adipose fin relative to the body size of salmon of hatchery origin). The Vosso River system is formally divided into three rivers and two exorheic lakes: Bolstad River, Evangervatnet Lake, Vosso River, Vangsvatnet Lake, and Strandaelva River. Tags were Thelma Biotel LP13-T (in 2020, 13 mm × 30 mm, 9.7 g in air, S64K protocol, 60–120 s transmit interval, battery life of 1560 days) or LP13-AT (in 2021–2022, 9.3 g, 13 mm × 33 mm, S64K protocol, 60–120 s transmit interval, battery life of 793 days). Captured fish were held for 0–24 h in a keepnet prior to tagging. Any captured fish were rejected if they had sustained visible injuries from being captured. Tagging was conducted according to protocols approved by the Norwegian Food Safety Authority (Mattilsynet). Each fish was anaesthetised, and a transmitter was placed intraperitoneally using a surgical scalpel. Tools and the transmitter were disinfected with chlorhexidine. The wound was closed using 4/0 braided nylon or monofilament interrupted sutures. The wound site in 2021–2022

FIGURE 1 (a) Map of the Vosso River watershed and the connection to the Osterfjord system. Vosso comprises the Bolstad River, Evangervatnet Lake, Vosso, Vangsvatnet Lake, and Strandaelva River. (b) Acoustic receiver deployment locations within the river for 2020–2021 and 2022–2023 (orange points). Receiver locations shifted slightly due to unexpected losses during flooding and additional placements in the second half of the study.
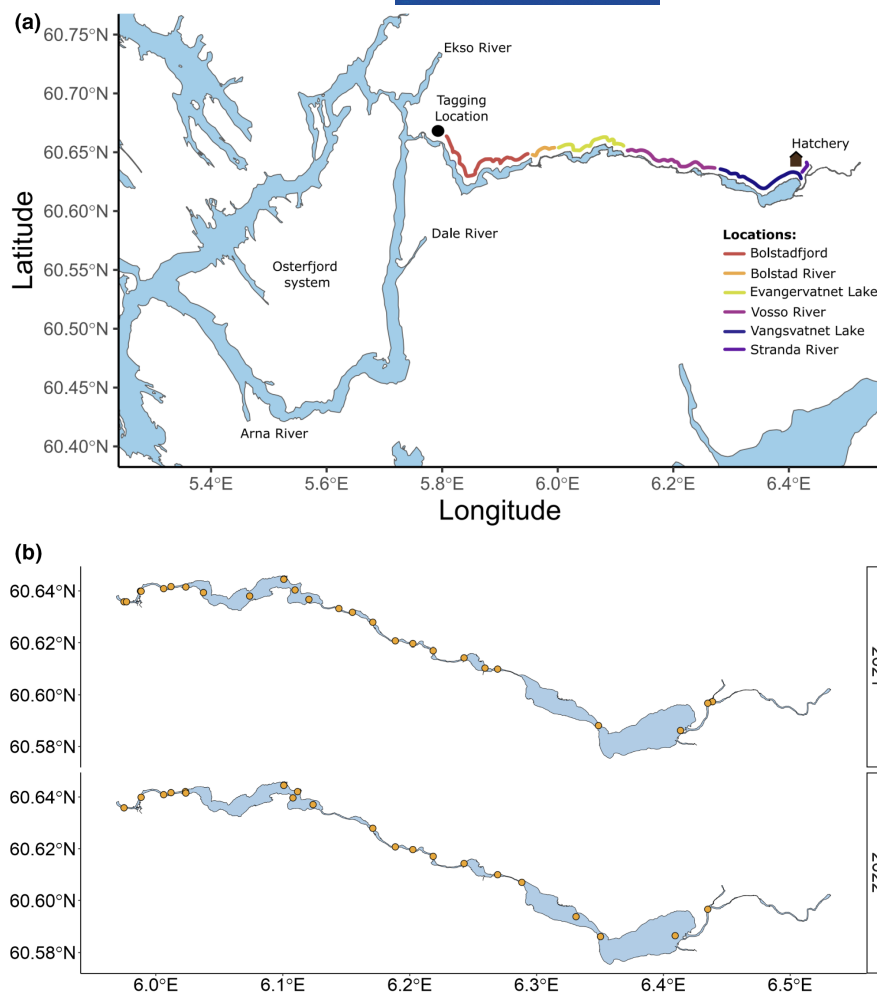
was disinfected with a smear of iodine. Fish recovered in a keep net for 5–10 min before being released back to the fjord. Trout (516 ± 112 SD mm) were generally smaller than salmon (785 ± 123 SD mm); we did not record the sex of the fish because external determination is generally inaccurate.

Fish were tracked using an array of passive acoustic receivers deployed in 2020 before the first round of tagging occurred. The array configuration changed slightly across years as new opportunities arose to add units to the study area, enhancing coverage. Receivers were Thelma Biotel TBR700 (8-month battery life), TBR700L (16-month battery life), or TBR800 (24-month battery life). Receivers were mostly placed on the river bottom using concrete anchors and rebar moorings, and in the lakes and the fjord using the same anchors attached to ropes to surface buoys about 1.5 m below the surface during winter to avoid ice. A gate of receivers was placed on the Nordhordland Bridge about 70 km from the river mouth at the end of the Osterfjord to track egress from the study area out of the inner Osterfjord area and to the outer areas. Additional opportunistic detections were made on Thelma Biotel TBR800 acoustic release receivers placed around the outer fjord and the city of Bergen and from a neighbouring array of Thelma TBR700 units in the Hardangerfjord about 100 km south by water (Figure 1).

Winter does not have a consistent definition and may be defined by daylight hours, thermal regimes, or other variables (Sutton et al., 2021). We used data beginning at the end of the spawning period for salmon and sea trout, which is mostly in November and may in some years extend into December, with sea trout spawning before Atlantic salmon generally. Overwintering for salmonids means persisting between cessation of spawning and reconditioning in the spring and in this study we explore the different life history strategies employed by salmon and trout to cope with this cold, dark, and minimally productive period by moving, or not moving, within and between habitats available to them.

2.3 | Data analysis

Data were analysed using R (R Core Team, 2022). Only fish that entered the Vosso River system, the main river of interest, and that remained there during the winter were kept for data analyses. Those fish that entered Vosso and then exited before the winter, never entered the river and remained in the fjord or migrated towards the sea, were detected on receivers placed in nearby rivers, or were detected on neighbouring arrays were excluded for the data analyses. For salmon and trout that entered Vosso to spawn, we extracted

timing of river entry and exit from the detection histories and, if necessary, estimated the time of death and ascribed it as pre-spawn or post-spawn mortality based on a presumed spawning time around November 1, which is about the end of spawning for trout and about the start for salmon. Individuals for which the tracking data from receivers showed no movement or, if the transmitter had an acceleration sensor, the acceleration sensor permanently went to zero, their fate were determined as dead (although this could also be due to tag expulsion). Fish that ceased to be detected were also defined as dead at the time of last detection. For fish that returned for a subsequent migration in another year (i.e., as a repeat spawner), additional river entry and exit times were recorded as a new migration event.

2.3.1 | River exit

We used tracking data from the onset of winter through springtime, based on the earliest and latest dates of river exit, to identify where in the river each fish was in the system and when it exited the river. River exit was determined by a detection in the fjord immediately at the end of the river mouth. The timing of river exit was therefore calculated for any fish that successfully exited the river. Date of river exit was converted to a time interval from November 4 of the spawning year (the minimum date of river exit in our dataset). Days until river exit was an integer and fitted to a negative binomial regression due to overdispersion of the Poisson model, and fit with the *glm.nb* function in MASS (Venables & Ripley, 2002). The model used only the species and the migration year as fixed factors. Random effects were not included because so few fish had multiple migrations observed, meaning that repeated migrations in different years for the same fish were assumed as independent. Hatchery and wild Atlantic salmon were grouped together because of a relatively small sample size of hatchery fish. To verify results of the more complex model and because there appeared to be differences in the distribution of exit timing between trout and salmon, a non-parametric Kolmogorov–Smirnov test was used to compare days to exit for trout and salmon.

2.3.2 | Overwintering

Until river exit, we determined where each fish spent each day based on the detections within the Vosso system. A fish was inferred to be in the river or lake based on presence detections, and data were interpolated for fish that were not detected based on the most recent detection. Data were downsampled to daily data to establish the number of days spent in each habitat prior to river exit based on data interpolated for each year for each fish that survived overwintering with days from November 4 each year (the earliest date of exit in the dataset) through to each individual's date of river exit. There are two lakes (Evanger and Vangsvatnet) and three main river reaches (Bolstad and Vosso) in the system, which were collapsed into river or lake habitat. For each overwintering day starting with

November 4, the number of salmon and trout in lakes was calculated each year. A generalised additive model with Poisson distribution was fit to the count of individuals in either lake or river habitats, with overwintering date as a smooth effect ($K=5$) and species and year as fixed factors using the *gam* function in mgcv (Wood, 2004, 2011). The total number of fish was incorporated as a log offset to account for the potential number of trout and salmon that could have been in the lake on that day for each year.

2.3.3 | Activity

We compared the accelerometer-derived activity of trout and salmon based on available detection data from within the river and lake overwinter. Raw acceleration data were transmitted as numbers from 0 to 255 and converted to acceleration by multiplying the transmitted value by 3.465 and dividing the product by 255. To test how active trout and salmon were in the different habitats during the overwintering period, a GAM was fitted to the data using the *bam* function in the R package mgcv (Wood, 2004, 2011). Fish that died were included, but any acceleration data following the presumed date of death were excluded. The model was fitted with a Gamma family and log link function because root mean square (RMS) acceleration is non-negative. Because the acceleration sensors provide high-resolution data, there was extremely high temporal autocorrelation in the measurements, so the first time point for each fish in 12h windows was drawn for modelling. Habitat was included as a factor with an interaction with species, overwintering day as a smooth effect interacting with $K=4$, and a random effect of individual and receiver, to account for some of the potential for repeated measures. Data were included until the date of river exit and only for detections in the freshwater system (including the lakes) and not the fjord.

3 | RESULTS

One hundred thirty-eight salmon (wild $N=57$, hatchery $N=20$) and sea-run brown trout ($N=61$) were tagged and tracked from 2020 to 2023, which accounted for 156 migration events when considering salmon and trout that completed a full freshwater cycle in Vosso and those that attempted at least one additional migration to freshwater. Exclusions included fish that died before exiting the river and 14 trout that never entered the river and remained around the inner fjord area where there is an estuarine spawning ground (Gabrielsen et al., 2021). Interestingly, two wild salmon tagged in 2021 also remained at the estuarine spawning area, one departed from the fjord in November and the other apparently overwintered in the fjord before migrating out to sea in spring; these fish were also excluded because they did not use the river for spawning. Thirteen of the 77 tagged salmon (13%) turned away from the river and were either detected in nearby rivers (1 in Ekso, 1 in Arna, 1 in Dale), were detected moving into an adjacent fjord by a neighbouring array (1 in

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Hardangerfjord), or were detected moving out of the fjord and never detected again. This was the case for only one trout. Three salmon were removed by hatchery staff for broodstock, two in Vosso and one in Dale (it was never detected by the receiver in Dale). After excluding migration events that did not generate usable data, 120 migration events remained: 39 wild salmon, 18 hatchery-origin salmon, and 62 sea-run brown trout. Among these, there were 40 of 58 (69%) successful salmon migrations (i.e., they exited the river and returned to the fjord) compared to 38 of 62 (61%) successful sea-run brown trout migrations. Post-spawning mortality (after November 1) was 18% for salmon and 16% for trout.

Thirteen of 38 trout survived their first migration and returned to the river once more (34%), and four of those nine trout returned again for a third migration event. One salmon returned from the 2020 tagging group as an alternate repeat spawner in 2022. One salmon from the 2020 tagging group was detected in Sørfjorden in 2021 near Trengereid (~44 km from the river mouth) but was not detected elsewhere; it was then detected at Stanghelle about 30 km from Vosso in Veafjorden four times, on June 29, July 1, July 2, and July 20, suggesting that it had remained in the inner fjord. Considering only the 58 tagged salmon that apparently used Vosso as their spawning river, the repeat spawning rate was 2%.

3.1 | River exit

Seventy-eight successful Vosso River exits were recorded for the two species during the 3 years. It seemed that trout exited the river during a relatively narrow timing window compared to salmon (Figure 3). Although there appeared to be some differences between wild and hatchery salmon, hatchery salmon were only tagged in 2020 and the sample size was too small for a three-way comparison so salmon data were pooled. By average, salmon exited 116 ± 60 days after November 4, whereas trout exited 142 ± 24 days after this date. The date interval until exit was an integer and could not be negative,

so we initially used a Poisson distribution to model the days until exit; however, the Poisson model was overdispersed, and a negative binomial model was therefore the preferred option. The negative binomial model did not identify significant differences between trout and salmon in the number of days until river exit ($z = 1.45$, $p = .15$). There were also no differences between 2020 and 2021 ($z = -0.11$, $p = .91$) or between 2020 and 2022 ($z = -1.36$, $p = .17$) in the interval until river exit. A Kolmogorov–Smirnov test identified weak evidence that the exit timing of salmon and trout were drawn from different distributions ($D = 0.03$, $p = .06$).

3.2 | Overwintering

Some salmon exited the river early in winter rather than overwintering, but many stayed in the river (Figure 2). Trout appeared to be more lake resident than salmon with many individuals exclusively overwintering in the lake (Figure 3). Atlantic salmon appeared to overwinter in areas throughout the system, presumably close to their spawning grounds (Figure 3). The main overwintering area for trout was a lake, where 75% of individuals were tracked through the whole winter compared to 24% of salmon; this was mostly lake Evanger with only a few individuals overwintering in Vangsvatnet (Figure 3). The Poisson model with sample size log offset provided a significant difference between lake use by trout and salmon ($z = 25.12$, $p < .01$; Figure 4). Both 2021 and 2022 appeared to be different from the baseline factor level, 2020 (both $z > 10$, both $p < .01$). The smooth function indicated a general increase in the proportion of fish in lakes with increasing overwinter date (Figure 4).

3.3 | Activity

Salmon and trout generally had higher levels of locomotor activity in the river (salmon: 0.55 ± 0.45 SD m/s^2, trout: 0.40 ± 0.20 SD m/s^2) while overwintering compared to when in the lake habitat (salmon:
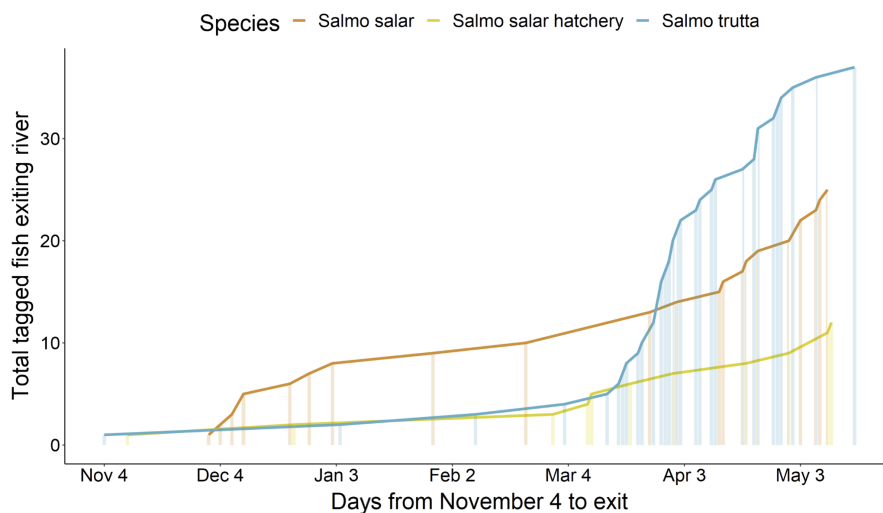

FIGURE 2 Timing of river exit for sea-run brown trout and Atlantic salmon tagged in the Vosso River system from 2020 to 2022. Dates are aggregated across years. Curves indicate the cumulative sum of fish exiting the river across the study. The minimum date (November 4) was selected because it was the first date of river exit recorded in the series. Note that dates are aggregated across years and include the same fish multiple times if it completed multiple migrations.
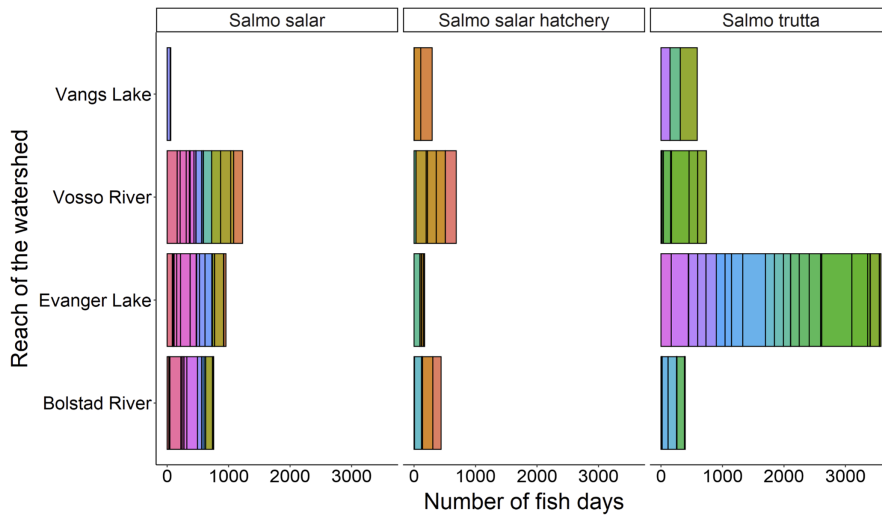
FIGURE 3 Cumulative number of overwintering days spent in different segments of the river. Coloured bands represent individual fish-year combinations.
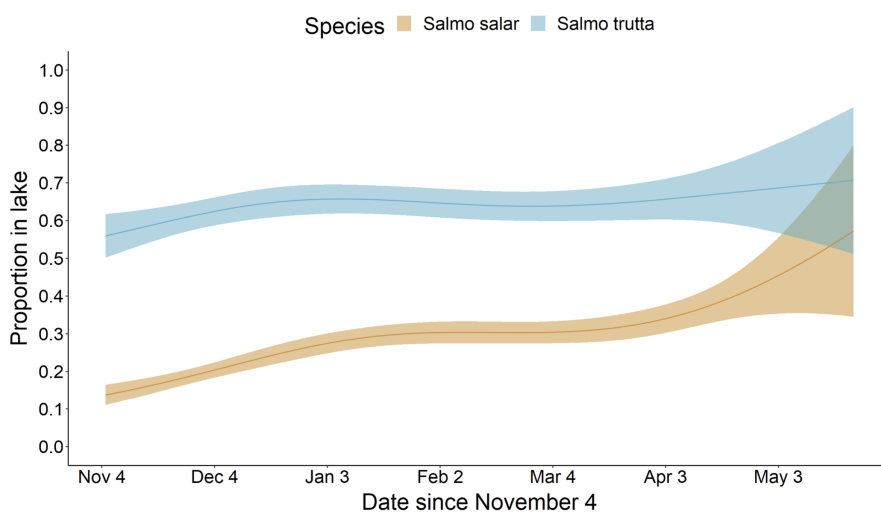

FIGURE 4 Poisson model predicted time spent in lake habitat (either Evangervatnet or Vangsvatnet) during the overwintering period, including upper and lower confidence boundaries as shaded areas for brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). For modelling, hatchery and wild salmon were combined. Model predictions excluded effects of interannual variation for illustration purposes by excluding year from the function.
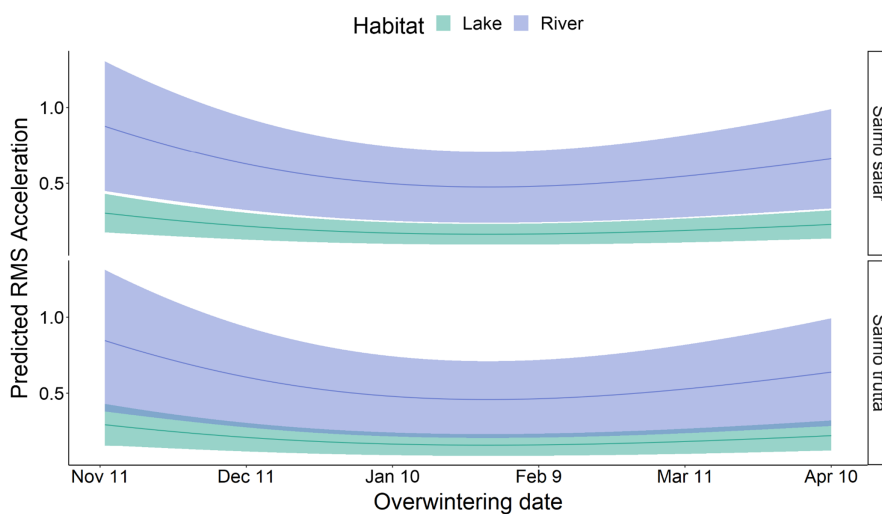

FIGURE 5 Predicted acceleration (m/s^2) for Atlantic salmon and sea-run brown trout during the overwintering period in Vosso in two habitats, lakes and river. Ribbons indicate the range of the standard error of the additive model predictions.

$0.19 \pm 0.27\,\text{m/s}^2$, trout: $0.15 \pm 0.18\,\text{m/s}^2$). The smooth effect for overwintering day indicated lower locomotor activity in the middle of the overwintering period with increasing activity at the beginning of winter when fish were perhaps still spawning or finding overwintering territory, and at the onset of spring when migratory instincts may have set in ($F = 15.23$, $p < .01$; Figure 5). There was no difference in acceleration between trout and salmon ($t = -0.43$, $p = .67$), but there was a clear difference between river and lake

habitats such that accelerometer-derived locomotor activity was higher in the river areas than in the lakes ($t = 3.59$, $p < .01$; Figure 5).

4 | DISCUSSION

Alternative life histories allow salmon to maximise lifetime fitness via multiple potential pathways. Whereas Pacific salmonids have a life history where they reproduce only once during their lifespan (Crespi & Teo, 2002), Atlantic salmon and brown trout display more variability in their life histories (Birnie-Gauvin et al., 2023), including the ability to spawn again after returning to sea to recondition (Bendall et al., 2005; Halttunen et al., 2013). Repeat spawning Atlantic salmon and brown trout tend to be large and fecund and can be disproportionately large contributors to the spawning production in rivers, acting as a buffer against poor smolt year classes (Halttunen, 2011). As Atlantic salmon conservation becomes increasingly dire (Thorstad et al., 2021), repeat spawners become more important to ensure the viability of many populations. Post-spawning behavior of iteroparous Atlantic salmon and brown trout may act as a bottleneck for fish to express the alternative life history, and we found that there were key differences between trout and salmon in several aspects of their post-spawning ecology as well as differences in the incidence of repeat spawning based on tracking multiple migrations of the two species. Most of the fish that spawned in the Vosso River spent some time after the spawning period in freshwater before exiting in spring. Importantly, salmon and trout appeared to distribute themselves a bit differently during winter, with trout mostly using the lake Evanger to overwinter while the salmon appeared to overwinter in both river and lake sections.

We expected Atlantic fish to leave Vosso soon either after spawning or during spring (e.g., Halttunen et al., 2013). Most trout and salmon left the river during spring and although salmon seemed to leave more during winter months, there was ultimately no strong evidence for a species-level difference in the outmigration timing based on the negative binomial regression model. Several studies have observed the outmigration of Atlantic salmon kelts tagged in the spring, which would miss the share of fish that exit the river during winter months (e.g., Bøe et al., 2019; Halttunen et al., 2013; Hubley et al., 2008; Jacobs, 2011). The seaward migration of salmon kelts contrasted with trout that more reliably exited year after year during a few weeks in the springtime from about mid-March through mid-April. Trout were generally smaller than salmon in our sample, yielding some collinearity between species and size. Larger fish are expected to deplete more energy than small fish and therefore have lower survival (Jonsson et al., 1997). However, there was no evidence that the larger salmon were leaving earlier than the smaller trout, so differences appeared to be more related to species-specific behaviour and physiology. Bordeleau et al. (2019) found that nutritional status was a strong predictor of migration timing, overwinter survival, and repeat spawning, which may explain some of the variance that we observed. The outmigration window in Vosso was notable to us because of work conducted on the Atlantic salmon smolts from the same river, with tagging mostly occurring in mid-late April and May yielding very high incidence of smolt predation in the lakes, including direct observations of trout consuming smolts in April and May (Hanssen et al., 2022; Nash et al., 2022). An alternative explanation for this pattern is that there are ecotypes of trout that specialise in foraging on prey fish in lakes, such as smolts, that are not well represented among our tagged fish (Lennox, Espedal, et al., 2019).

Few studies have actually observed overwintering habitat of salmonids using telemetry, and there are no systematic descriptions of lake use by trout and salmon during overwintering (Lennox et al., 2021). Komadina-Douthwright et al. (1997) tracked salmon kelts in New Brunswick and found most were used in the estuary and only one of five overwintered in the river. Suitable habitat for overwintering seems to be important for rivers to have healthy salmon populations (Bardonnet & Baglinière, 2000); therefore, we expected to observe high rates of lake use for overwintering, in part because other salmonids prefer or even depend on lakes for overwintering (Clarke et al., 2003; Mulder et al., 2018, 2019). Clarke et al. (2003) compared Atlantic salmon, Arctic charr, and brook charr in a Canadian river and found the three species overwintering in distinct areas. Dahlmo et al. (2023) suggested that lakes allow energetic savings for trout in the lead-up to spawning. Similarly, we identified a strong signal in our acceleration data that lakes provided an opportunity to reduce activity during the overwintering period. Mulder et al. (2019) estimated resting behaviour for Arctic charr to be represented by acceleration values of $0.29 \pm 0.11 \, \text{m/s}^2$, slightly higher than what we observed for trout and salmon in the lake, but lower than mean values recorded in the river; both values were lower than the active swimming values reported for charr by Mulder et al. (2019): $1.28 \pm 0.25 \, \text{m/s}^2$. In contrast, acceleration data from rivers (Dahlmo et al., 2023) indicated a higher level of activity, which suggests that salmon and trout must spend more energy to maintain their position in the river during overwintering. Lakes can also be expected to provide refuge from predators such as Eurasian otters (*Lutra lutra*) that are recolonising areas of western Norway, while they may be more vulnerable to predation when overwintering in pools (Landa & Guidos, 2020; Sortland et al., 2023). It may be that the energetic savings in lakes are nominal at the cold temperatures the fish experience during winter, and perhaps we incorrectly assume that animals will always know how to optimise their resources and allocate them efficiently (Lennox et al., 2016). However, the clear differences in lake use by the two salmonids represent an important finding when considering the overall ecology of the species with iteroparous life histories.

There were clear differences in habitat use during overwintering between the two species, such that salmon spent less time in the lakes than trout. Salmon and trout coexisting in rivers have different spawning areas and spawning times, although there is some overlap and it likely differs among rivers based on available habitat (Heggberget et al., 1988). For example, radio-tracking studies of salmon and trout during the upriver migration have revealed some

differences in the migration pattern including timing and speed (Finstad et al., 2005). However, the trout's choice to migrate into the lake Evanger for overwintering is most likely not a matter of availability or competition with salmon because densities of individuals are probably low and distances to lakes are short. Had we tracked only salmon in isolation, we may have concluded that the lake habitat was a less suitable habitat for overwintering for salmonids in the system. However, tracking of both species in the same system provided evidence that the choice to overwinter in the lake or river must be a consequence of the life history difference between the two salmonid species. Future comparative studies linking activity data of kelts to energy expenditure in swim tunnels could provide evidence for this hypothesis.

The sea-run brown trout mostly returned to the river each year if they survived the summer feeding migration, but only one Atlantic salmon was confirmed to return to spawn multiple times. Brown trout are generally held as being more likely to spawn repeatedly and are thought to return to overwinter in fresh or estuarine water each year rather than remain in the sea. However, only about 34% of the trout that entered Vosso in the tagging year attempted another migration in a future year. This is similar to the 30–50% rate of return calculated by Haraldstad et al. (2018) and greater than the 10% suggested by Eldøy et al. (2019) and 18% return rate observed by Bendall et al. (2005).

Only one of the hatchery salmon and none of the wild salmon returned as a repeat spawner (2%). Jacobs (2011) tagged 100 Miramichi River salmon kelts in May 2008–2009 and recorded seven consecutive (7%) repeat spawners and four alternate (4%) repeat spawners. Bøe et al. (2019) detected 33% of Campbellton River and 16% of Conne River salmon kelts returning as consecutive repeat spawners. Bordeleau et al. (2020) detected 22% of tagged salmon kelts returning as alternate repeat spawners. Salmon tagging in Vosso provided a very low rate of iteroparity for the population despite high overwinter survival that should allow the fish to express the alternative life history tactic. Such a small incidence of iteroparity recorded is concerning for the population because iteroparous fish are large and experienced individuals that can make a substantial contribution to the effective population size. It is unlikely that the tagging had a negative impact on iteroparity and a long-term series of PIT tagging data does not provide for a higher estimate of multiple spawners in Vosso (B. Barlaup Unpublished Data). Recent pop-up satellite archival tagging data from Atlantic salmon post-kelts originating from other rivers throughout Europe suggest that the Vosso salmon probably migrate quickly north from Vosso through the Bergen-Shetland corridor toward the Barents Sea to feed (Rikardsen et al., 2021). Strøm et al. (2019) had PSAT data from Atlantic salmon that suggested predation by toothed whales and endothermic fishes like tunas could be a factor limiting return rates for these potential repeat spawners, and high predation of kelts has been flagged as a concern for an endangered population of salmon in Canada (Lacroix, 2014). However, other stressors such as food availability and habitat fragmentation may also be affecting survival and merit

further scrutiny to better understand what might be limiting survival for these fish (Birnie-Gauvin et al., 2023).

We deployed receivers in the lakes and most of the major pools in the system, but there were gaps in our coverage that did not allow us to completely describe all the areas where salmon and trout were overwintering. For this reason, we used interpolation to fill gaps when a fish was not detected on a given date assuming that it was in the same reach until it was detected in a new reach. Using the passive telemetry data collected from the array, we had sufficiently thorough data that we could identify the timing of river entry and exit, estimate the overwintering areas, and even assign mortalities of some fish that died during the migration. Leaving the acoustic receivers through the winter was not without risks, and several of our moorings were crushed by nearly a metre of ice that formed over the Vosso River during winter 2020–2021, fortunately not affecting any receivers. A couple of receivers were lost to the very deep lakes (max depth ~130m) that had steep slopes. Sinking the buoys in the lakes during winter allowed us to recover all the receivers in springtime, but a 10-year flood that occurred in autumn 2022 resulted in some attrition of our array and loss of data near the end of the study, leaving some gaps in the middle of the lake Vangsvatnet in 2021–2022; however, it seemed that there were relatively few trout and no salmon in that area in those years from the receivers that were recovered. The vast majority of the receivers survived multiple spring and autumn floods and ice to provide data year after year.

Transmitted acceleration data from acoustic tags (Lennox et al., 2021) offered insight into animal ecology that is not possible from traditional acoustic telemetry and is challenging to recover from higher resolution accelerometer loggers (Wilmers et al., 2015; Wright et al., 2014). The accelerometer data from trout and salmon in this study were not calibrated to each individual (Brivio et al., 2021), which may have been valuable to better understand how minor differences in tag placement affected the measurements. However, fish were released immediately, and there was no such opportunity. Future applications could include calibrations of the tags (Mulder et al., 2019). To measure acceleration, we used a relatively long sampling window (27s) during which time the three-dimensional acceleration measurements were summarised to root mean square, averaged, and transmitted. The long sampling window was selected to capture the general activity of the fish during the migration without being excessively battery demanding. Shorter sampling windows are more common programming for similar transmitters and consume less battery life (Lennox et al., 2021) and might be considered in the future, but investigators keen to make comparisons with our study should be careful to match the specifications of these tags.

5 | CONCLUSIONS

Salmon and trout transitioning from spawning to overwintering must make trade-offs in order to be among those that make it back to spawn again. Repeat spawning can be a rare but valuable fitness benefit for salmon and trout that make the right decisions and come

back to spawn again (especially rare for salmon). Our results suggest that river managers must consider lakes and in rivers as important overwintering habitat for trout and that although springtime is the most important outmigration time for salmon kelts, they may exit throughout the winter and will require connectivity year-round to complete the life history. Our results do not suggest any fine-scale influences of habitat on winter survival and potential iteroparity, but future research should consider what can be done to improve post-spawning survival, especially in rivers with barriers that might limit migration, particularly temporally if barriers are lowered during spring, which may be too late for some salmon that would prefer to leave during wintertime (e.g., Baktoft et al., 2020; Leander et al., 2020). Greater focus on the full life cycle of iteroparous salmonids is needed to determine how conservation actions can contribute to providing the necessary protections for kelt survival. For sea-run brown trout and Atlantic salmon, small improvements to the survival rate to repeat spawning could provide major benefits at the population level (Birnie-Gauvin et al., 2023).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors wish to declare that their interests are not conflicting with this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in ocean tracking network at http://www/oceantrackingnetwork.org.

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