


Impacts of predation by Eurasian otters on Atlantic salmon in two Norwegian rivers

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Abstract

1. The return of the Eurasian otter (*Lutra lutra*) to western Norway has sparked human–predator conflicts because otters prey on vulnerable Atlantic salmon (*Salmo salar*) populations. Although predation may not be the ultimate cause of salmon population declines, otters that kill adult salmon in rivers before they spawn impact the salmon spawning stock, with potential consequences for stock recruitment and ecosystem services (especially fisheries).
2. To gain insight into impacts of otter predation on salmon populations, we quantified the predation by otters on adult salmon in two rivers in western Norway using a combination of radiotelemetry and temperature loggers. We tagged 30 salmon in Aureelva and 30 salmon in Søre Vartdalselva, and tracked the salmon until they died or left the river.
3. This method identified the fates of 95% of tagged salmon. Estimated predation rates on adult salmon were 32% in Aureelva and 95% in Søre Vartdalselva. The salmon stock in Søre Vartdalselva was well below the spawning target, partly attributable to putatively additive mortality from predation by otters. Notwithstanding, we found no evidence that otters selectively killed salmon based on sex, length, health status, or activity level.
4. Salmon in Søre Vartdalselva had greater predation risk compared to salmon in Aureelva, possibly due to differences in habitat types such as availability of holding pools. The presence of more holding area in Aureelva probably provided predation refuges for adult salmon that buffered the effectiveness of otter predation.
5. Our findings emphasise that management decisions should be guided by river-specific evaluations of impacts of predation on salmon. Otters are a very visible predator operating at the final phase of the life cycle before spawning, so predation is liable to be controversial given that salmon are now Red Listed in Norway.

KEYWORDS

additive mortality, migration, selection, spawning, telemetry

[Correction added on 31 May 2023, after first online publication: The copyright line was changed.]

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1 | INTRODUCTION

Natural mortality is a major driver of fish population dynamics and is therefore an essential parameter used in stock assessments and underlying stock management strategies (Clark, 1999; Maunder et al., 2023). A key component of natural mortality is predation; however, it can be challenging to estimate the share of natural mortality attributable to predation because predation may be the proximate but not the ultimate cause of death. For instance, predators may attack and eat fish sick from infectious agents that would probably have killed them if they were not eaten (i.e., compensatory mortality; e.g., Furey et al., 2021). Alternatively, predators can kill fish that otherwise would have survived to spawn and thereby influence stock recruitment (i.e., additive mortality; Ward & Hvidsten, 2011). Thus, selective predation can in some cases generate compensatory mortality. Other factors that may influence predation risk include activity level of prey (i.e., more active animals are more likely to encounter predators; Ciuti et al., 2012), sex of prey (e.g., salmonid males move more during spawning and may therefore be more exposed to predators than females; Carss et al., 1990), and size of prey (e.g., bears target larger salmonids to maximise food intake with fewer kills; Quinn & Kinnison, 1999; Gende et al., 2001). Understanding the underlying mechanisms driving natural mortality of fish stocks can benefit from a more synoptic view of predation mortality and the contextual factors underlying predation.

Predators are controversial; lauded for the ecosystem services that they provide (Estes et al., 2011; Ritchie et al., 2012), but disdained for the impacts they are purported to have on domesticated animals (Allen & Hampton, 2020; Schiess-Meier et al., 2007), harvestable populations (Yodzis, 2001), and human health and safety. As biodiversity conservation efforts support the rebuilding of some key predator populations, there is increased potential for conflicts and a need for evidence to underpin effective and acceptable management (Marshall et al., 2016). In Norway, the Eurasian otter (*Lutra lutra*) is an apex predator that feeds predominantly on culturally and economically valuable fish species, particularly Atlantic salmon (*Salmo salar*, hereafter termed salmon). After decades of extirpation, otters are now recolonising the Atlantic coast of Norway, instigating conflict between conservation of salmon and otters (van Dijk et al., 2020). Much like seals (e.g., *Phoca vitulina*) and other predators (e.g., cormorants *Phalacrocorax carbo sinensis*), otters may be disliked or even persecuted to preserve spawning salmon (Klenke et al., 2011). However, the impacts of otter predation on Norwegian spawning salmon populations have not been well documented. Consequently, the need for and effectiveness of potential management interventions is uncertain. Removing otters could only improve the status of salmon stocks in streams where the predation is a source of additive and not compensatory mortality (Ward & Hvidsten, 2011), but evaluating the effect of predation on salmon populations is not possible without quantitative data on both predation and salmon abundance.

Electronic tagging is a key tool for studying natural mortality of animals in the wild (Hightower et al., 2001; Strøm et al., 2019). There is an increasing number of tools available to detect mortality

caused by predation (Lennox et al., 2023), including the use of acid-based (Halfyard et al., 2017), tilt-based (Lennox et al., 2021), and temperature-based (Strøm et al., 2019) tag sensors that can help infer the fate of tagged animals (see also Klinard & Matley, 2020; Lennox et al., 2022). To better understand the effect of predation on salmon populations in small streams, this study implemented a novel combination of radio transmitters and temperature loggers. We used individual tracking of salmon to quantify predation by otters and test the following hypotheses and associated predictions: (1) otters kill salmon selectively based on sex, length, health status, and activity level, such that males, larger fish, fish with suboptimal health status, and more active individuals are more likely to be predated; and (2) otter predation affects the ability of salmon populations to reach their spawning target because salmon are killed prior to spawning.

2 | METHODS

2.1 | Study area

2.1.1 | Aureelva

River Aureelva is located in Sykkylven municipality in western Norway and has a spawning target of 323 kg female salmon set by the Norwegian Scientific Advisory Committee for Atlantic salmon (hereafter referred to as VRL; Figure 1; Vitenskapelig råd for lakseforvaltning, 2022a). VRL evaluates the status of Norwegian salmon populations and importance of threats, and gives science-based advice on attainment of the spawning target, i.e., the biomass of females necessary to attain the carrying capacity for each population (Forseth et al., 2013). The lower stretch of Aureelva runs 4.2 km from the lake Andestadvatnet to the sea (Figure 1), and the main spawning areas are located downstream from the lake (Kambestad et al., 2020). Average slope of Aureelva from Andestadvatnet to the sea is 1.6%, with a mean annual discharge by the river mouth of 2.7 m³/s (Kambestad et al., 2020; van Dijk et al., 2020). The habitat of the lower river consists of a mixture of rapids, pools, and riffle stretches (Kambestad et al., 2020). A smaller and steeper river (Aurdalselva) runs into the lake, with an anadromous stretch of c. 1.5 km. The salmon population in Aureelva reached its spawning target from 2015 to 2018, whereas the population reached approximately 75% and 84% of its target in 2019 and 2020, respectively (Vitenskapelig råd for lakseforvaltning, 2022a). Based on the spawning target attainment between 2015 and 2019, VRL (2022a) considers the population of Aureelva to be in moderately good condition and fishing remains open.

2.1.2 | Søre Vartdalselva

Søre Vartdalselva is a river located in Ørsta municipality in western Norway, with a spawning target of 324 kg female salmon (Figure 1; Vitenskapelig råd for lakseforvaltning, 2022b). According to the local angling community, salmon mainly use the lowermost 5 km of

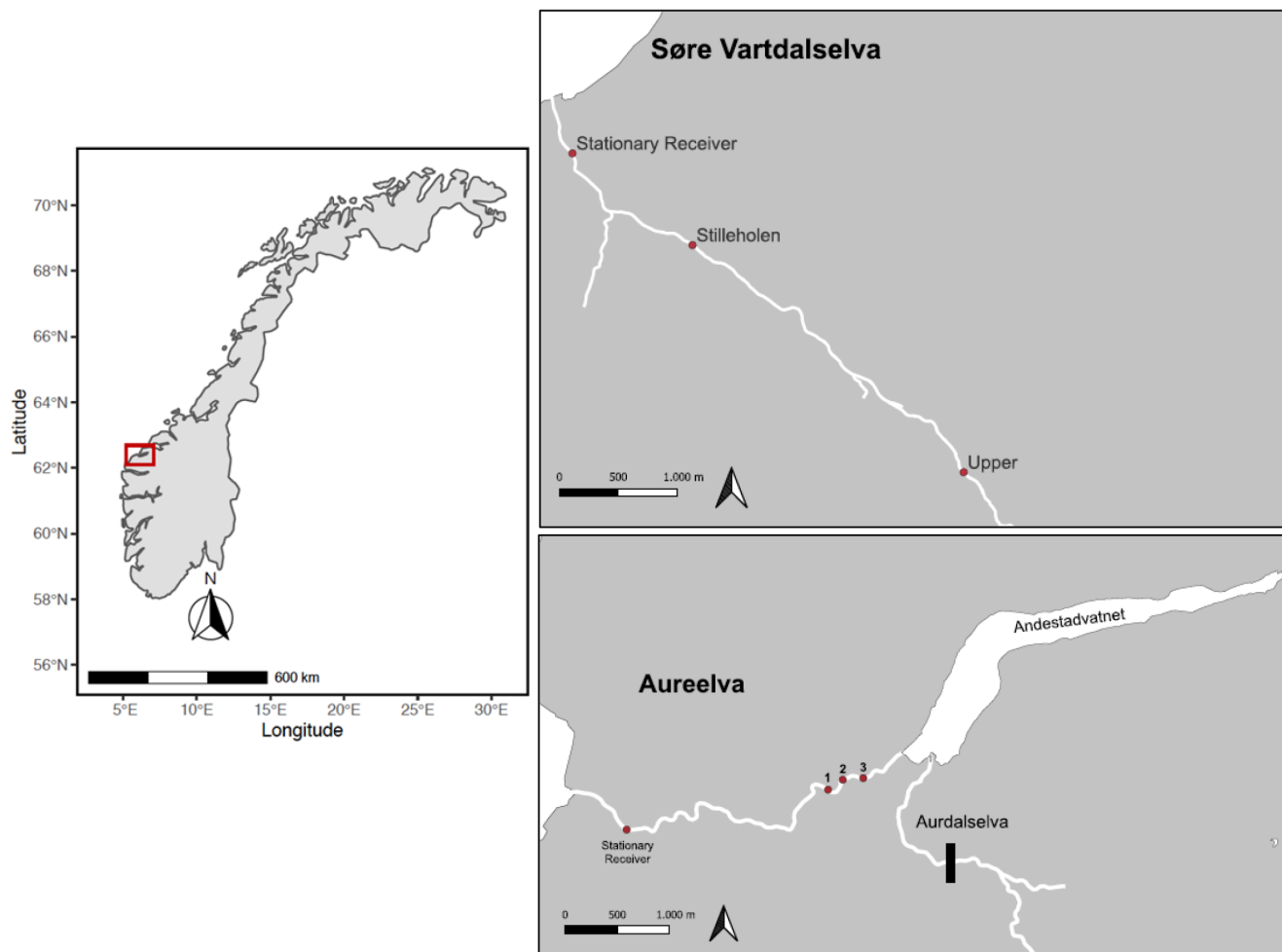


FIGURE 1 The rivers Søre Vartdalselva and Aureelva in Sunnmøre, Norway (red box). Søre Vartdalselva: red points indicate locations of stationary receiver, Stillehølen (*Stilleholen*; capture and tagging site), and maximum upriver migration by a tagged individual (*Upper*). Aureelva: red points indicate locations of stationary receiver, capture and tagging sites: (1) Sjellarhølen; (2) Fløtvøren; (3) Lyshol. Black line indicates the upper limit of the anadromous stretch in Aurdalselva.

the river (Figure 1), which has an average slope of 2.7% (Kambestad et al., 2020). A fish ladder is located 2 km from the sea (by Stillehølen; Figure 1), and there are no lakes in the anadromous stretch. Stillehølen is the only relatively large pool, and the river mainly consists of rapids and shallow riffle habitat. Mean annual discharge by the river mouth is $3.4 \text{ m}^3/\text{s}$. The salmon population in Søre Vartdalselva has had poor spawning target attainment after 2017 (Vitenskapelig råd for lakseforvaltning, 2022b). Based on the spawning target attainment between 2015 and 2019, VRL (2022b) considers the population of Søre Vartdalselva to be in very poor condition. Consequently, fishing was closed from 2020 and since 2019 a maximum of 50 adult salmon have been caught each year to establish a live genebank to prevent extinction of the population (Kambestad et al., 2020).

2.2 | Capture method

Thirty adult salmon were caught and tagged in Aureelva on 3 September 2020. Catch locations in Aureelva included the three

major pools Lyshol, Sjellarhølen and Fløtvøren (Figure 1). In Lyshol, a seine net was deployed by two divers to catch the salmon. In Sjellarhølen and Fløtvøren, all salmon were caught with dip nets.

Thirty adult salmon were caught and tagged in Søre Vartdalselva between 5 and 28 August 2021. Salmon were caught with dip nets in the fish ladder (Stillehølen in Figure 1) and in the pools and riffles downstream of the fish ladder. The salmon were given a minimum of 15 min to recover from capture in submerged cages before the tagging procedure. All salmon were tagged at the capture locations (Figure 1).

2.3 | Tagging procedure

The salmon were anaesthetised in benzocaine water (0.15 mL/L) for approximately 3 min. Once properly anaesthetised, the sex, weight (g), fork length (mm), and total length (mm) of each salmon were recorded. In Søre Vartdalselva, weight was not recorded. Individuals were categorised into optimal or suboptimal health status based on external

damages (bite/scratch marks, salmon louse [*Lepeophtheirus salmonis*] damage) observed during tagging. Individuals with gill parasites (e.g., gill maggot; *Salmincola salmoneus*) and gross pathology (ulcerative skin lesions, skin haemorrhages, and fin erosions) that could affect their fitness or swimming abilities were categorised as having suboptimal health status ($n=24$), whereas individuals with no external damage (gross pathology) or mild superficial marks (e.g., scratch marks) were categorised as having optimal health status ($n=36$). The salmon were held supine using a foam tagging trough in Aureelva and a tagging tube in Søre Vartdalselva. A tube with flowing benzocaine-medicated water (0.8mL/10L) was inserted into the salmon's mouth to keep the fish subdued and oxygenated throughout the procedure. Water temperatures ranged from 13°C to 15°C during tagging in Aureelva, and from 13°C to 16°C in Søre Vartdalselva.

For the tagging procedure, an incision was made in the ventral side between the pelvic and pectoral fins. A surgical cannula 1.1 mm in diameter was passed through the skin posterior to the incision. The radio tag antenna was passed through the cannula so that it trailed on the ventral side of the fish. The radio tag was inserted into the ventral cavity of the fish and the incision was closed with sutures. Tagged fish were transferred to submerged cages for recovery, from which they were released after regaining equilibrium and tail grab reflexes. Except for five individuals in Søre Vartdalselva that were released approximately 100 m above the fish ladder, all individuals were released at the tagging location. No fish under 1 kg or 50 cm total length were tagged to keep tag burden under 2% of the body weight to minimise impact on fish physiology and swimming abilities (e.g., Smircich & Kelly, 2014). Because salmon weight was not recorded in Søre Vartdalselva, the weight was estimated using Fulton's condition factor formula (Robinson et al., 2008) assuming $K=1$. Tag burdens were a maximum of 1.7% of body weight.

Thirty individuals in Aureelva and 30 individuals in Søre Vartdalselva were tagged. Total length of tagged salmon ranged from 510 to 810 mm in Aureelva and from 502 to 890 mm in Søre Vartdalselva, with an average total length of 644.5 ± 102.3 mm (SD) and 658.0 ± 102.6 mm (SD) respectively. Eighteen females and 12 males were tagged in Aureelva, and 13 females and 17 males in Søre Vartdalselva.

2.4 | Radiotelemetry

2.4.1 | Electronic tags

Each salmon was tagged with a radio transmitter (Advanced Telemetry Systems: Model F1835C) and a temperature logger (iButtonLink LLC: DS1922L-F5# Thermochron 8K Data Points-40/85C) package. Temperature loggers were glued to the tags and the package was covered in brightly coloured Plasti Dip. The tag package will hereafter be referred to as a tag. The weight of the tag was 17 g. The radiotransmitter had an estimated battery life of 280 days in Aureelva and 465 days in Søre Vartdalselva. The temperature loggers recorded the temperature every hour. Stationary temperature loggers were placed in the river and on land to compare data with the temperature loggers in the fish.

For some tags situated under water in Aureelva, it was difficult to assess whether the tagged fish were dead or alive during tracking. Thus, a radio transmitter (Advanced Telemetry Systems: Model F1835C) with a motion-based mortality sensor was used in Søre Vartdalselva to determine whether the fish were alive or dead with greater certainty. The mortality sensor in the radio transmitter doubled the pulse rate of signals when the tag had not moved for 24 h, indicating that the tagged animal had died (Advanced Telemetry Systems, 2022).

2.4.2 | Tracking tagged salmon

Tagged salmon were manually tracked using a handheld ATS R4500C radio receiver connected to an antenna until the salmon died or left the river. During tracking, date and geographic position of each salmon were recorded and tags from dead salmon were recovered. A stationary radio receiver (ATS R4500C) was placed near the river mouth above the high tide mark to record tagged salmon that left the river (Figure 1). A range test was performed prior to tagging to ensure that the stationary receiver registered passing tagged salmon.

From September 2020 to March 2021, the salmon tagged in Aureelva were tracked for a total of 20 days. From September until the start of spawning (20 October), 1–3 days of tracking was conducted every 2–3 weeks. We tracked the fish twice for 4 and 3 days during the spawning period (20 October to 15 November). After spawning, tagged salmon were tracked once every month from December 2020 to March 2021, with the last tracking day on 7 March 2021.

In Søre Vartdalselva, tagged salmon were tracked every 10–14 days from August to November 2021 for a total of 11 tracking days. One exception occurred in September–October, when 23 days passed between two tracking trips. Last tracking was conducted on 12 November 2021, as all salmon were dead or had left the river at this time.

2.5 | Data analysis

All statistical models and figures were produced using Rstudio Version 1.4.1103 (RStudio Team, 2021).

2.5.1 | Fates of tagged salmon

Fates of salmon were determined using a decision-tree (Figure 2) based on two sources of information: (1) location where tags were found; and (2) when the individual died or last showed signs of being alive. Salmon whose tags were recovered on land were categorised as killed by otters (step 1; Figure 2). To identify time of death from temperature loggers (step 2), we plotted river temperature, air temperature, and tag temperature over time using *ggplot* within the *tidyverse* package (Wickham et al., 2019). A temperature change in the tags moving from river to land indicated time of death. The river

temperature logger in Søre Vartdalselva was lost due to a flood. Therefore, the temperature data from individuals with the longest survival time were used as a proxy for river temperature. For the salmon that died last, tag temperatures were compared to each other and to land temperature to estimate time of death.

For salmon whose tags had remained in the river until they were recovered or tags that were never recovered (step 1), time of death or time of last sign of being alive was used to categorise fate (step 2). For tags recovered in the river or in puddles on land without temperature data to indicate time of death, the time an individual stopped moving or the time the mortality sensor turned on (only in Søre Vartdalselva) were used to estimate time of death. Upriver or downriver movements towards spawning grounds that occurred at the same time as conspecifics were considered signs that the individual was alive (hereafter termed *sign of life*). For salmon in Søre Vartdalselva, uninitiated mortality sensors were also considered a sign of life. Because adult Atlantic salmon in freshwater usually have high survival until spawning (Havn et al., 2015; Jensen et al., 2010;

Lennox et al., 2015; Thorstad et al., 2003, 2007; Whoriskey et al., 2000), individuals that died before or during the spawning period were considered killed by otters. There are no other predators known to kill adult salmon in freshwater in this region of western Norway, except harbour seals (*Phoca vitulina*) in larger rivers. Salmon can have high mortality after spawning (Bardonnet et al., 2000; Cunjak et al., 1998). Therefore, individuals that died after spawning were categorised as having unknown cause of death, unless the tag was recovered on land, which suggests predation by otters.

Individuals last registered on the stationary receiver were categorised as having left to sea pre- or post-spawning (Figure 2). Individuals in the river with signs of life up until the last tracking day were categorised as overwintering kelts. Because tagged salmon may be affected by the tagging procedure for some time after tagging and thus experience higher predation risk than untagged conspecifics (Brown et al., 2011; Raby et al., 2014; Wilson et al., 2017), salmon that died less than 1 week after tagging were excluded from data analysis.

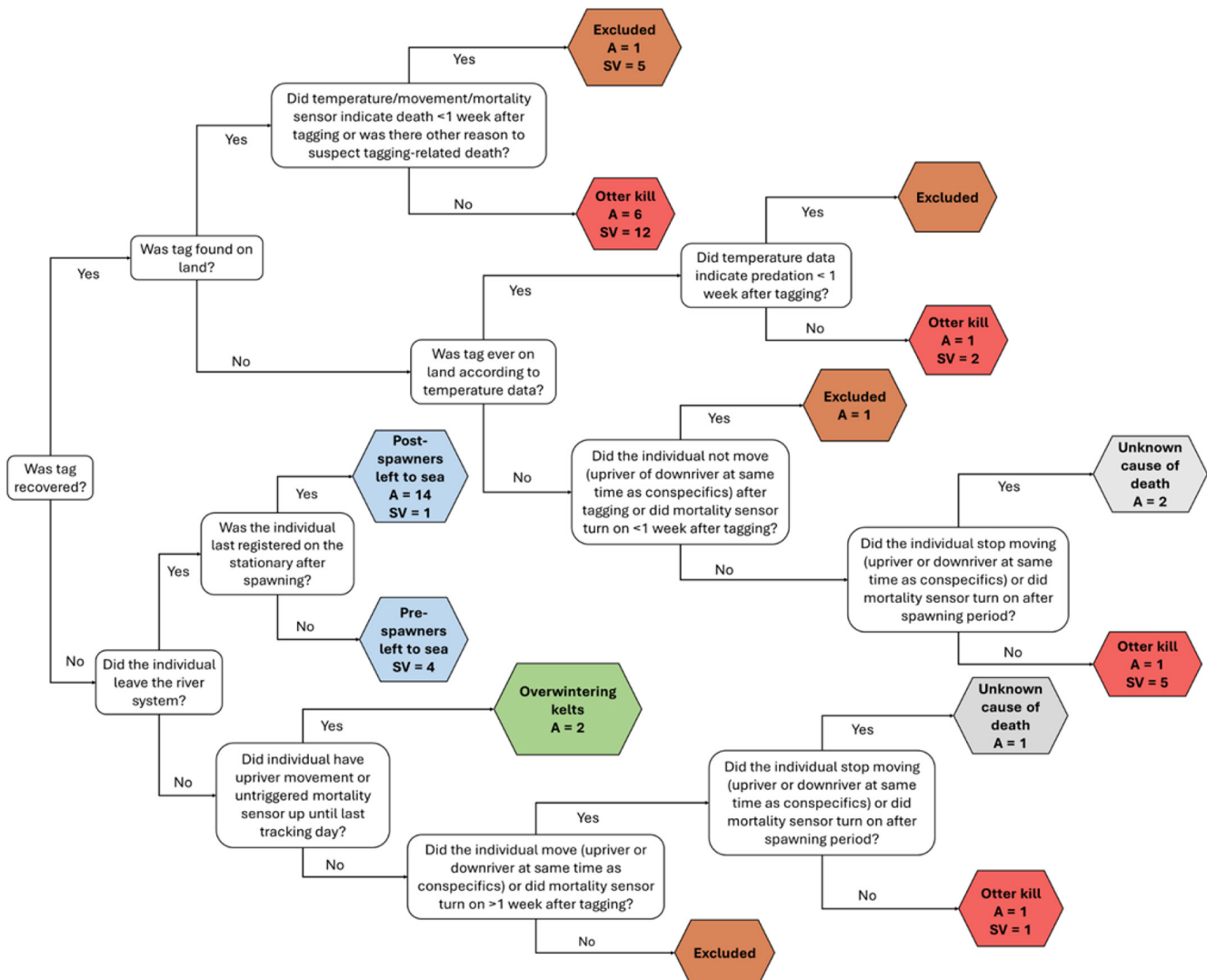


FIGURE 2 Decision-tree used to categorise the fate of tagged salmon. Only fish in Søre Vartdalselva had mortality sensors as a criterion for categorisation of fates. "A" and "SV" indicates the number of salmon categorised from Aureelva and Søre Vartdalselva, respectively.

2.5.2 | Predator selectivity

To visualise differences in survival probability over time, the non-parametric likelihood estimator of the survival probability $S(t)$ was plotted using *ggplot* in the tidyverse package (Wickham et al., 2019). Survival probability $S(t)$ is the probability that a salmon survives from tagging to a specified time t (Clark et al., 2003). The non-parametric likelihood estimator of the survival probability was estimated for each river using the function *ic_np* in the icenREG package (Anderson-Bergman, 2017).

To test whether otters selectively killed salmon based on sex, length, health status, or activity level, a semi-parametric Cox proportional hazards (PH) model (Cox, 1972) was fitted using the function *ic_sp* in the icenReg package (Anderson-Bergman, 2017). The

$$ic_sp(\text{cbind(left, right)} \sim \text{River} + \text{Length} + \text{Sex} + \text{Health_status} + \text{Activity}, \text{Model 1}) \text{ model} = "ph", \text{bs_samples} = 100)$$

Cox PH model is a survival regression model that tests for association between time-to-death (i.e., survival time), expressed by the hazard function $h(t)$, and explanatory variables. The hazard function (hereafter called predation risk) is the instantaneous probability of dying at a given time (Bradburn et al., 2003). The semi-parametric nature of the Cox PH model means that the baseline hazard is not specified, and the survival times are not assumed to follow a particular distribution (Bradburn et al., 2003). The regression coefficients were estimated non-parametrically through 100 bootstrap samples, which was deemed sufficient as estimators did not change with larger bootstrap samples.

Because death was only known to have occurred between two tracking dates for some salmon, the survival times were registered as time intervals with lower (left) and upper (right) limits. We censored individuals whose time of death was not observed on a specific day or never experienced death. Censoring means that the individual's exact time of death is unknown. This study includes two types of censoring. Individuals that exited the river or were alive by the end of the study were right-censored, meaning that it was only known that the true time of death occurred after a given date. Thus, right-censored individuals were registered to have died between the last tracking day or time of leaving the river (left) and infinity (right) (Anderson-Bergman, 2017). Individuals that were known to have died between two tracking dates were interval-censored; the tracking date before last sign of life was set as the lower limit (left), and the upper limit (right) was set as the tracking date after which no further sign of life was detected (see Section 2.5.1). Individuals that were known to have died on a specific day were uncensored, meaning that the lower (left) and upper (right) limit of the survival time occurred on the same day.

Explanatory variables in the model included river (Aureelva/Søre Vartdalselva), sex (male/female), total length (mm), activity level, and health status (optimal/suboptimal; see Section 2.3). Distance travelled per tracking day (m) was used as a proxy for activity level. For the calculation of activity, the shapefiles with spatial data of the study sites were reformatted into rasters using the function *rasterize*

in the raster package (Hijmans & van Etten, 2021). To calculate the minimum distance between the GPS points, a transition matrix was created using the *transition* function within the *gdistance* package (van Etten, 2017). The shortest path between GPS points within the river system was found using the *shortestPath* function in the *gdistance* package (van Etten, 2017), and the length of each path segment was measured using *gLength* in the *rgeos* package (Bivand & Rundel, 2021). Total distance travelled by each individual fish was found using the *sum* function in base R, and number of tracking days was summarised using the *count* function in the *dplyr* package (Wickham et al., 2021). Activity was then calculated by dividing total distance travelled (metres) with the number of tracking days for each individual.

The final model was:

The validity of the proportional hazard assumption was confirmed using the *diag_covar* function within the *icenReg* package. The no multicollinearity assumption was confirmed using the function *ggpairs* within the *GGally* package (Schloerke et al., 2021).

2.5.3 | Predation impact on spawning stock

Finally, we calculated whether the salmon populations would have reached their spawning targets without predation from otters in the two rivers. Because the spawning target is based on female biomass, only female salmon were included in this analysis. Estimates of actual female spawner biomass were obtained from the Norwegian Scientific Advisory Committee for Atlantic Salmon (Vitenskapelig råd for lakseforvaltning, 2022a) for Aureelva and from Hanssen et al. (2022) for Søre Vartdalselva and reported as female biomass (kg) during the spawning period. Forty salmon were removed from Søre Vartdalselva by angling between 8 June and 12 September 2021 for gene bank purposes and were not included in estimates of spawning target attainment. To estimate female spawner biomass in the absence of otter predation, we divided the estimated female spawner biomass by the proportion of tagged females that survived until the spawning period:

$$\text{No predation (kg)} = \frac{\text{Actual female spawner biomass (kg)}}{(1 - \text{proportion of females killed by otters})}$$

where *No predation* is the female spawner biomass (kg) if there had been no otter predation, *Actual female spawner biomass* is the estimated attainment of spawning target (kg) after predation, and *proportion of females killed by otters* is the proportion of tagged female salmon that were killed by otters before spawning.

Pre-spawners that left the river system were not included in the female sample when calculating the proportion killed by otters before spawning. The remaining sample included 28 salmon in Aureelva (17 females and 11 males) and 21 salmon in Søre Vartdalselva (nine

females and 12 males). Salmon killed by otters before spawning or during the first half of the spawning period (Aureelva: 20 October–2 November; Søre Vartdalselva: 25 October–1 November) were assumed not to have spawned, whereas salmon killed during the last half of the spawning period (Aureelva: 2–15 November; Søre Vartdalselva: 2–9 November) or after spawning were considered to have spawned. Spawning periods were set based on observations of spawning activity during snorkelling in the rivers and information from locals.

3 | RESULTS

3.1 | Movements of tagged salmon

The majority of tagged salmon in Aureelva resided in pools near tagging sites (Sjellarhølen, Fløtvøren, and Lyshol; Figure 1) before the spawning period. Six salmon in Aureelva migrated into the lake and moved more compared to the salmon that stayed in the river. Fourteen tagged salmon left the river after spawning between 16 and 23 November, and two left in December. On the last tracking day, two salmon were registered as overwintering in the lake and five salmon in the river had died, from which four tags were retrieved.

In Søre Vartdalselva, six individuals left the river in mid- to late August, of which two individuals returned later. One of the returners was captured by a local angler and kept in a genebank tank for 6 days, after which it was released at the river mouth and later ascended the river. Three individuals migrated upstream from Stillehølen pool after tagging, of which two migrated approximately 1.3 km upstream

of the fish ladder and one migrated approximately 3.9 km upstream from the fish ladder. Most salmon resided in Stillehølen (Figure 1) until 28 September, after which seven individuals were found closer to or at spawning grounds downstream from Stillehølen on 21 October. One individual migrated out of the river system on 9 November, after the spawning period.

3.2 | Fates of tagged salmon

Except for three salmon that died of unknown causes in Aureelva, fates of all tagged salmon were determined. One individual in Aureelva and four in Søre Vartdalselva died within a week of tagging and were excluded from further analysis. Additionally, two individuals were excluded, one in each river, because they were found dead by locals with no signs of otter predation. Of the 28 remaining tagged salmon in Aureelva, three died after spawning with unknown cause of death (*Unknown cause of death*), 14 migrated to the fjord after the spawning period (*Post-spawners left to sea*), nine were killed by otters (*Otter kill*), and two resided in the lake by the end of the study (*Overwintering kelts*; Figure 3). Of the remaining 25 tagged salmon in Søre Vartdalselva, four migrated to the fjord before the spawning period (*Pre-spawners left to sea*), one left after the spawning period (*Post-spawners left to sea*), and 20 were killed by otters (*Otter kill*).

For step 1 in resolving fates, most tags were found on land or were not recovered, with some tags retrieved in the river (Table 1 and Figure 2). Most tags were found without salmon carcasses or adjacent to small remnants of fish (Box 1). For step 2 in resolving fates, temperature data was the most used tool to estimate the time of last

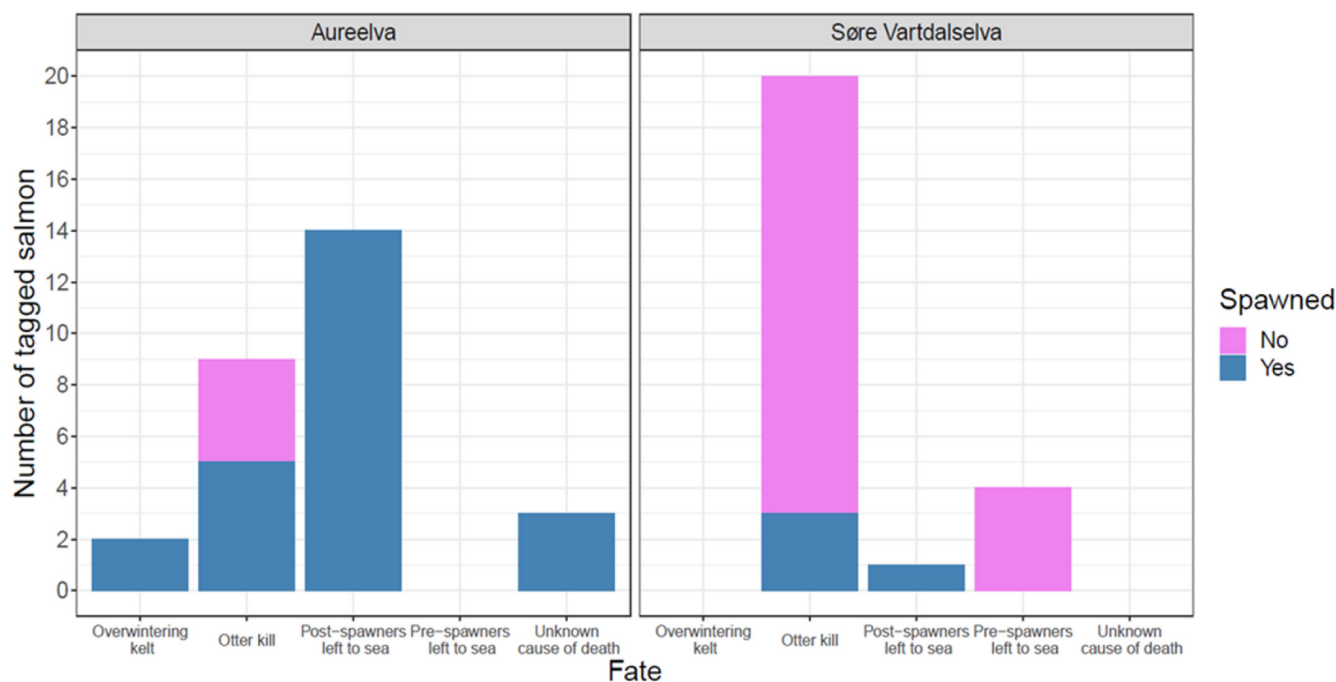


FIGURE 3 Fates of tagged salmon, $n=28$ in Aureelva and 25 in Søre Vartdalselva.

TABLE 1 Number of tagged salmon whose fates were inferred based on a combination of (1) location where tag was found and (2) last sign of life inferred from temperature data, movement data, stationary receiver data, or mortality sensors in Aureelva and Søre Vartdalselva.

Location found	Tool used to determine last sign of life	Søre Vartdalselva	Aureelva
Land	Temperature data	11	6
Land	Mortality sensor	3	0
Land	Movement data	2	0
River	Movement data	1	4
River	Temperature data	2	1
River	Mortality sensor	4	0
Unrecovered	Movement data	0	4
Unrecovered	Mortality sensor	1	0
Unrecovered	Stationary receiver	5	14

Note: Two individuals (one in each river) found by locals in poor condition are not included in the table.

sign of life (Figure 4), followed by stationary receivers, movement data, and mortality sensors.

3.3 | Predator selectivity

The survival times of 16 individuals in Aureelva (14 post-spawners left to sea and two overwintering kelts) and five individuals in Søre Vartdalselva (four pre-spawners and one post-spawner left to sea) were right-censored. Seven individuals in Aureelva and 12 individuals in Søre Vartdalselva remained uncensored. Five individuals in Aureelva and eight in Søre Vartdalselva were interval-censored. In total, the data contained 21 right-censored, 19 uncensored, and 13 interval-censored observations.

Individuals in Aureelva had a higher survival probability throughout the study period compared to individuals in Søre Vartdalselva (Figure 5). Length ($Z=0.04$, $p=0.97$), sex ($Z=0.60$, $p=0.55$), activity level ($Z=0.15$, $p=0.88$), and health status ($Z=1.41$, $p=0.16$) were not associated with predation risk (Table 2). River was significantly associated with predation risk after accounting for length, sex, activity level, and health status ($HR=5.58$, $SE=0.59$, $p<0.01$). At any moment in time, individuals from Søre Vartdalselva had 5.581-times higher predation risk than individuals from Aureelva.

3.4 | Predation impact on spawning stock

Nine tagged salmon were killed by otters in Aureelva, including three that were killed before, two during, and four after the spawning period. One of the salmon that were killed during the



spawning period was killed during the first half of the spawning period and had probably not spawned, whereas the other was killed during the last half of the spawning period and probably had spawned (Figure 6). Thus, otters killed 14.3% ($n=4$ of 28) of the pre-spawners. Two of the killed pre-spawners were females and two were males, implying that otters killed 11.8% ($n=2$ of 17) of the female pre-spawners. Based on rod catches during the summer of 2020 and a drift dive count of salmon spawners on 16 November 2020 (139 adult salmon were observed; NINA, 2022), attainment of the spawning target was estimated to be 84% (Vitenskapelig råd for lakseforvaltning, 2022a). We estimate that the spawning target attainment in Aureelva would have been 95% (Table 3) in the absence of otter predation.

In Søre Vartdalselva, 20 tagged salmon were killed by otters, including 14 that were killed before and six during the spawning period. Three of the salmon that were killed during the spawning period were killed during the first half of the spawning period and had probably not spawned, and three were killed during the last half of the spawning period and probably had spawned (Figure 6). Thus, 81.0% ($n=17$ of 21) of the total sample of pre-spawners was determined to have been killed by otters. Seven of the killed pre-spawners were females and 10 were males, implying that otters killed 77.8% ($n=7$ of 9) of the female pre-spawners. Based on a drift dive count of salmon spawners on 2 November 2021 (41 adult salmon were observed; Hanssen et al. (2022)), attainment of the spawning target was estimated to be 21% (Hanssen et al. (2022)). We estimate that the spawning target attainment in Søre Vartdalselva would have been 94.6% (Table 3) in the absence of otter predation.

4 | DISCUSSION

With freshwater ecosystems under extreme pressure around the world (Reid et al., 2019), we need knowledge on how freshwater and terrestrial ecosystems are connected by ecosystem interactions, such as predation. This study aimed to investigate the impacts of predation across the terrestrial-freshwater interface using adult salmon and the predator Eurasian otter as model species. A combined use of loggers and radio transmitters provided the fates for 95% of tagged salmon in this study and demonstrated that semi-aquatic predators comprise a major source of natural mortality for migrating salmon in these systems. Otters killed nine (32%) tagged salmon in Aureelva and 20 (95%) in Søre Vartdalselva. Body length, sex, activity, and health status were not associated with predation risk. However, salmon in Søre Vartdalselva had significantly higher predation risk compared to salmon in Aureelva, indicating that habitat features might be a major contributor to these predator-prey dynamics in freshwater ecosystems. We estimate that otter predation reduced the population of females from 95% to 84% of the spawning target in Aureelva and from 95% to 21% of the spawning target in Søre Vartdalselva.

BOX 1 Circumstantial evidence that indicates otter predation on Atlantic salmon in Aureelva (VRL, 2022a) and Søre Vartdalselva (VRL, 2022b).

Type of evidence	Example of evidence
Carcasses	
Local observations	
Camera trap	



Only in a few cases did we find carcasses of tagged salmon.

However, several carcasses of untagged salmon were found in both rivers during the study period. Anterior muscles and eggs were eaten, as is typical of otter predation (see Carss et al., 1990).

Left: tagged salmon found on land in Aureelva on 15 November, 2020.

Right: untagged salmon carcass found by locals in Søre Vartdalselva in 2020.

In both rivers there were multiple reported sightings of otters in the study period, including an otter catching a salmon in Søre Vartdalselva and an otter attempting to steal a live salmon hooked by an angler in Aureelva. An otter family was observed in Aureelva on 9 September 2020.



A camera trap stationed by Søre Vartdalselva has documented otter activity during and after the study period, including almost daily otter presence by the camera trap in the summer and autumn of 2021. A family of four otters were recorded during the 2021 study period. See @tammytheotter on twitter.

Type of evidence

Example of evidence

Carcass remains
indicating otter
predation



Although carcasses were rarely found, other signs of predation such as fins, eggs, and scales were common. Left: Fins found on the river bank in Aureelva. Middle: Eggs located near a tag recovered in the river in Søre Vartdalselva. Right: Tag found on land with fish scales scattered around it.

Otter scats



Multiple scats (i.e. spraints) containing fish remnants were found along Aureelva. The picture shows a scat containing fish bones, found on a rock by Aureelva on 10 November 2020.

Bite marks on living
salmon



During a drift dive count in November 2021, 32% of observed salmon in Søre Vartdalselva had tail bite marks compatible with otter attacks. The picture is an example, taken in the River Ramstaddalselva in the same region.

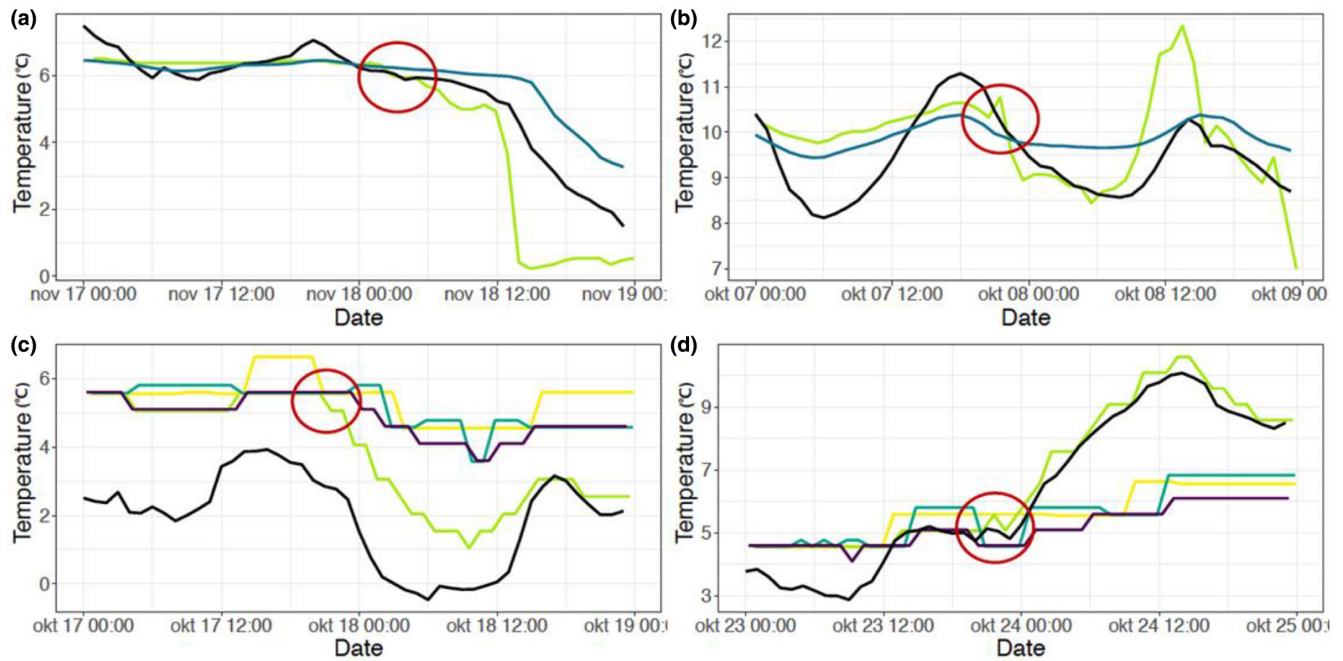


FIGURE 4 Temperature data used to determine time of death (red circle) for two individuals from Aureelva (A and B) and two individuals from Søre Vartdalselva (C and D). In Aureelva, time of death was determined to be when the tag's temperature (green) changed from following river temperature (blue) to land temperature (black). In Søre Vartdalselva, time of death was determined to be when the individual's temperature (green) stopped following the same trend in temperature as conspecifics (yellow, blue, and purple) and started following land temperature (black) more closely.

4.1 | Fates of tagged salmon

Other studies have used core temperature differences in tagged animals and predators to identify predation events in aquatic environments (e.g., Gallagher et al., 2021; Strøm et al., 2019). In this study, we used temperature loggers in water, on land, and in tags to pinpoint time of death for tagged salmon. Not all predation events could be identified from temperature data in the current study. Tags recovered in the river were probably jettisoned into the water by an otter, resulting in temperature data following river temperature with no indication of a predation event. This was also the case for some tags recovered in puddles on land along Søre Vartdalselva. Nevertheless, three tags recovered in the river contained temperature data indicating predation events, which highlights how temperature loggers can be important for discerning predation events from other natural mortality.

Tags recovered on land could have been flushed up on land in flood events. However, based on tag position and discharge levels in the study period, this was deemed unlikely for the majority of tags found on land. Furthermore, flooding was unlikely to have been responsible for killing adult salmon. Therefore, flooding did not influence predation estimates in this study.

Analyses of movement patterns is a valuable tool for assigning fates in biotelemetry studies (e.g., Schwinn et al., 2018; Villegas-Ríos et al., 2020), but movement data alone can be prone to misinterpretation. For instance, dead fish or tags can drift downstream and be misidentified as live fish (Havn et al., 2017), which also could have occurred in the present study for salmon that were last registered by

the stationary receiver. Furthermore, salmon predominantly remain stationary in pools until spawning, and the tags used in Aureelva were not equipped with mortality sensors. This made it hard to determine whether salmon in holding pools were alive or dead during tracking. Five individuals in Aureelva were for weeks or months misinterpreted as overwintering salmon and not discovered to have died before the tags were found by diving on the last tracking day. If mortality sensors had been used in Aureelva, it is likely that tags from dead salmon in the river would not have been mistaken for overwintering kelts and thus the last sign of life could have been determined with greater precision. The mortality sensors that were added to the radio transmitters in Søre Vartdalselva provided a quicker and more precise identification of the fate of salmon and was a successful addition to the project protocol.

A drawback of using radiotelemetry and temperature loggers is the inability to discern among predator species. To estimate the impact of specific predators in an ecosystem with several predators, other methods would be necessary (e.g., Ganz et al., 2023). Several lines of evidence indicated otter activity and predation on salmon in the two rivers (Box 1), supporting the assumption that tags found on land were evidence of otter kills. Locals observed otters hunting and killing salmon before and during the study period in both rivers. Several salmon carcasses or remains, such as eggs, scales, and fins were found along both rivers (for untagged and tagged salmon). Otter scats containing fish bones and vomit containing fish eggs were also found several places along Aureelva. Two tags recovered on land, one in each river, were found with chew marks, probably

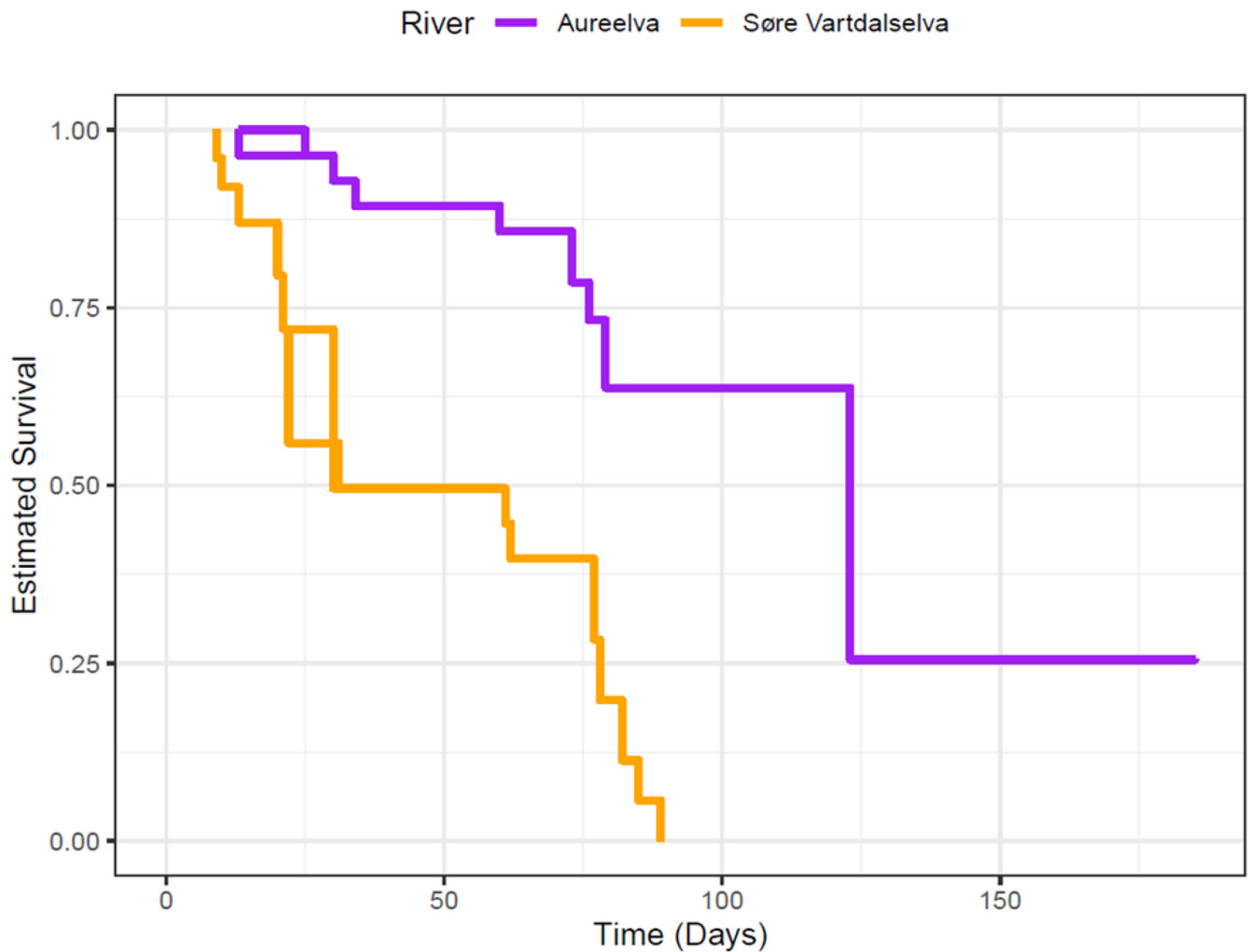


FIGURE 5 Non-parametric likelihood estimator survival curves for Aureelva (purple) and Søre Vartdalselva (orange). Because the data contains interval-censored observations, each river's survival curve is represented by two lines; any curve that lies between the two lines of a group (i.e., River) maximises the likelihood associated with the group (Anderson-Bergman, 2017).

TABLE 2 Summary of the Cox proportional hazards model output.

Cox PH model, bootstrap samples = 100					
	Estimate	Exp(Est)	SE	Z value	p-Value
RiverSøre Vartdalselva	1.72	5.58	0.59	2.93	<0.01
Length	0.00	1.00	0.00	0.04	0.97
SexMale	0.45	1.57	0.75	0.60	0.55
Health_status Optimal	0.90	2.46	0.64	1.41	0.16
Activity	0.00	1.00	0.00	0.15	0.88

from otters. Lastly, a camera trap stationed in Søre Vartdalselva has recorded high otter activity during and after the study period (see @tammytheotter on twitter). Furthermore, there are no bears (*Ursus arctos*) in this region (Bevanger, 2015), and predation by sea eagles (*Haliaeetus albicilla*) and American mink (*Neovison vison*) on adult salmon is assumed to be negligible (as observed by locals). Therefore, otters are the only predators known to be killing adult salmon in the studied rivers. Collectively, the aforementioned lines of evidence supports that tagged salmon that died during the study

were killed by otters (with the exception of fish categorised as having died of unknown reasons).

4.2 | Predator selectivity

Selective predation may remove weak individuals that die or fail to spawn (i.e., compensatory mortality) or, alternatively, kill animals that would have otherwise survived and spawned (i.e., additive

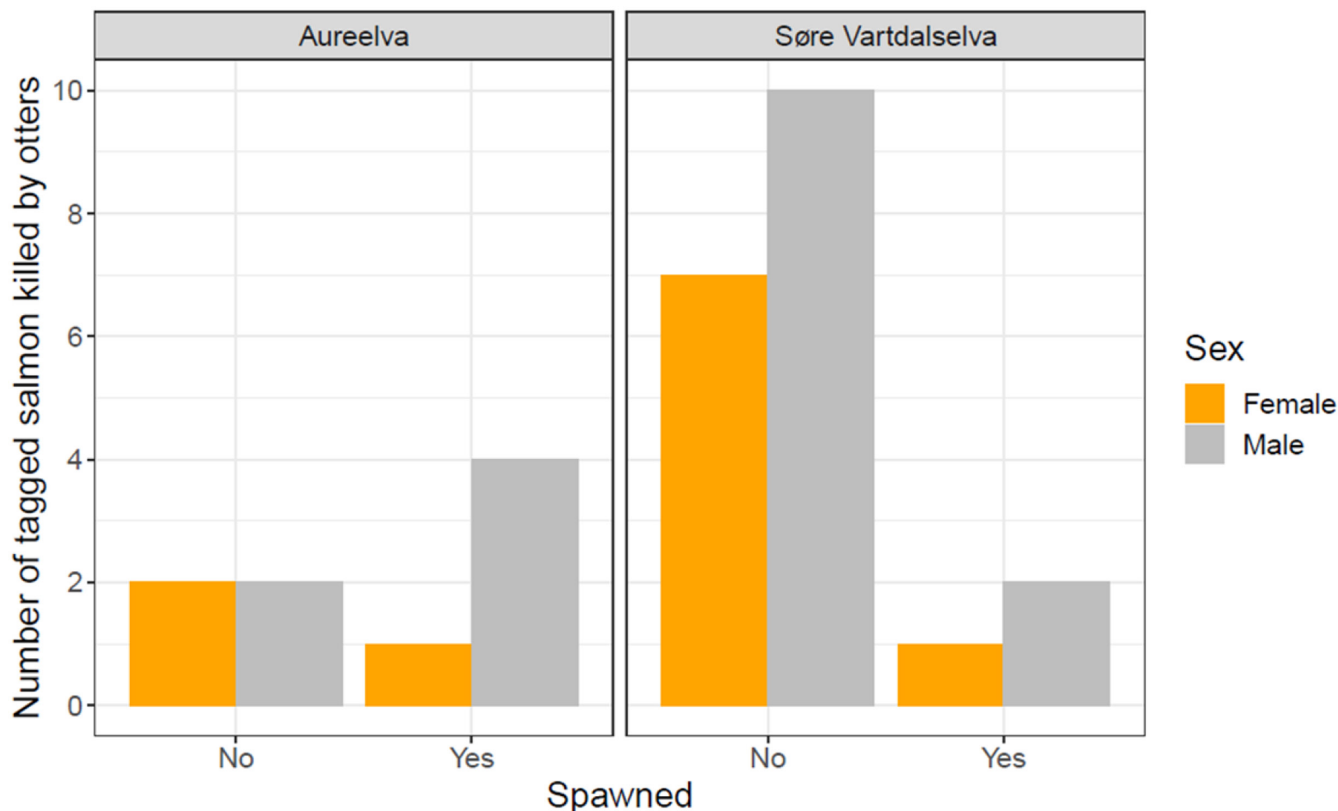


FIGURE 6 The number of male and female salmon killed by otters and whether they probably had spawned before they were killed.

TABLE 3 Calculations for attainment of spawning target without otter predation in Aureelva (VRL, 2022a) and Søre Vartdalselva (VRL, 2022b).

River	Spawning target (kg)	Attainment of spawning target (%)	Estimated female spawning stock (kg)	Estimated predation mortality (%)	Spawning stock without predation (kg)	Attainment of spawning target without predation (%)
Aureelva	323	84 (VRL, 2022a)	271.3	11.8	307.6	95.2
Søre Vartdalselva	324	21 (Hanssen et al., 2022)	68.0	77.8	306.5	94.6

mortality). Potential positive impacts of predator selectivity include the removal of sick individuals, which can result in healthier populations (i.e., compensatory mortality; Furey et al., 2021). By contrast, otters targeting larger salmon or female salmon might impact stock recruitment more than if they were killing indiscriminately via additive predation. This is because large females have the greatest reproductive output, males can spawn with multiple females, and large males spawn with more females than smaller males do (Fleming, 1996). Previous studies have suggested that male salmon are more vulnerable to otter predation because they tend to move more extensively than females during the spawning period (Carss et al., 1990; Cunningham et al., 2002). However, we found no evidence to support the hypothesis that otters killed salmon selectively based on sex, length, activity level, or health status. Assessment of health status only included externally visible traits (i.e., injuries, skin disease etc.) as seen during tagging and we were not able to test if otters selectively killed asymptomatic individuals carrying disease

or parasites. Lack of evidence for selective predation suggests that other factors than prey traits were important in determining predation risk, that selection gradients were small, or that predation was random.

River was the only explanatory variable associated with predation risk, which suggests that river characteristics are an important determinant of predation risk for salmon. Differences in the number and size of holding pools might explain the higher predation risk in Søre Vartdalselva compared to Aureelva. Stillehølen is the only relatively large pool in Søre Vartdalselva, whereas Aureelva contains several large holding pools. The lake and the large holding pools in Aureelva probably provided adult salmon with better opportunities to escape otter attacks, which probably influenced the ability of otters to select preferred prey. This is supported by studies on habitat preferences by otters, which indicate that otters prefer to hunt in shallow and narrow stretches of streams that facilitate easier capture (Almeida et al., 2012; Cho et al., 2009). Also, findings by

Sittenthaler et al. (2019) suggest that larger stream dimensions (i.e., discharge, depth, and width) and deep pools reduce predation risk of salmonids by otters.

Population size and demographics of the otters living around Aureelva and Søre Vartdalselva could have influenced the predation risk of salmon in this study. A larger population of otters require more food than a smaller population. Also, the age–sex composition of the otter populations could have influenced the predation on adult salmon. For instance, Lanszki et al. (2014) found that diet composition of otters differed by sex and age group, where males preyed more on larger fish than females, and juveniles preyed on invertebrates to a greater extent than adults and sub-adults. Information about the sex and age structure of the otter populations around the studied rivers is not available. However, it is reasonable to assume that demographic fluctuations in the otter populations cause varying salmon predation rates among years.

4.3 | Predation impact on spawning stocks

Otter predation reduced the salmon spawning stock in Aureelva and Søre Vartdalselva, with both populations being below their spawning targets during the spawning period. There was no evidence that otters selectively killed individuals based on visually assessed health status, which suggests that predation on female pre-spawners was a source of additive mortality. Thus, our findings support the hypothesis that otter predation affected the ability of the salmon populations in Aureelva and Søre Vartdalselva to reach their spawning targets. However, both populations would have been slightly below their spawning targets during the study years even without otter predation. Thus, factors besides otter predation have probably also contributed to reducing the spawning stocks in Aureelva and Søre Vartdalselva during the study years. Potential factors reducing the viability of salmon populations in Norway include genetic introgression of farmed escaped salmon, transmission of diseases and parasites from nearby fish farms, reduced survival and growth at sea, overharvesting, and physical alterations of freshwater habitats (Forseth et al., 2017; Vollset et al., 2022). Reduced recruitment due to predation on adult salmon in previous generations may also have reduced the size of the 2020 and 2021 spawning stocks. However, the current study only investigated the direct effects of predation on pre-spawners during the same year as the spawning stock assessment. Thus, any additive effect of predation on consecutive generations was not estimated.

The magnitude of predation-induced mortality on the female spawning stock was low in Aureelva compared to Søre Vartdalselva. The large proportion of pre-spawners killed in Søre Vartdalselva contrasts findings by Carss et al. (1990), who found that most otter predation occurred after the spawning period. Cunningham et al. (2002) reported more predation on pre- or part-spawned female salmon than Carss et al. (1990), with predation mortality of 5%–10% for females, which is similar to the predation mortality found in Aureelva. The otter predation of spawners in Søre Vartdalselva represents to our knowledge the highest published predation mortality on adult

salmon by otters. However, comparisons with previous studies are not straightforward, due to differences in methodology. Previous attempts to quantify otter predation have used carcass counts (Carss et al., 1990; Cunningham et al., 2002), which can underestimate predation if carcasses quickly disappear due to scavengers (van Dijk et al., 2020).

4.4 | Limitations and future opportunities

Handling and tagging may influence predation risk so that tagged salmon are not representative of the full population. However, Keefe et al. (2022) found that tagged salmon had high survival up until spawning, with no difference in survival between salmon tagged with external or internal radio transmitters. Also, Hubbard et al. (2021) found no negative effects of internal acoustic telemetry tagging on the survival, growth or body condition of lake trout (*Salvelinus namaycush*) over a 12-year period. Lastly, Thorstad et al. (2000) found that tagging adult Atlantic salmon with body-implanted radio transmitters did not influence swimming performance or blood physiology. Therefore, we assume tagging effects to be minimal in our study. We nevertheless excluded fish that died within a week of tagging in an attempt to reduce the influence of short-term handling and tagging effects. Long-term effects on behaviour and predation risk still cannot be excluded. For example, stress induced by handling and tagging can cause salmon to make down-stream movements, delay migration, or even abandon upriver migration (Havn et al., 2015; Mäkinen et al., 2000). Six salmon left Søre Vartdalselva prior to spawning, which may potentially have been attributable to handling or tagging effects. Alternatively, some salmon could have originated from a different river and strayed into Søre Vartdalselva, which could explain why four of the six salmon did not return to Søre Vartdalselva. Pre-spawners that left the rivers without returning were excluded from the spawning stock sample as these could have been killed if they remained in the river, and thus did not affect predation rate estimates.

Habitat has a large influence on salmon predation risk by otters. Previous studies suggest that certain river habitats, such as deep pools, are predation refuges for adult salmon (Day et al., 2015; Sittenthaler et al., 2019). Moreover, Martínez-Abraín et al. (2020) found that otters had greater hunting success in a dry year compared to a year with average amounts of rainfall, which suggests that fish are easier prey when water levels are low. Identifying how habitat types influence predation risk can aid management in identifying salmon populations that are more vulnerable to impacts of otter predation. There is also little information on the density and behaviour of otters in Norwegian rivers and how the density varies among years and among seasons. For instance, we lack information on whether the behaviour (i.e., functional response) and density (i.e., numerical response) of otters are influenced by changes in salmon density. Thus, future studies should investigate otter behaviour, density, and patterns of predation on salmon in different habitat

types of several rivers across multiple years, using tools such as faecal analysis, camera traps, and tracking of salmon and otters using telemetry.

4.5 | Management implications

Although predation is a major driver of mortality, data on predation mortality for adult salmon prior to spawning is scarce, and not taken into consideration in evaluation of spawning target attainment in Norway (Hindar et al., 2007, 2019). Thus, estimates of spawning stocks may be biased if there is considerable mortality between the time of stock assessment and spawning. Several studies have shown that tagging salmonids with internal transmitters does not influence survival (Hubbard et al., 2021; Jepsen et al., 2008; Keefe et al., 2022) and that natural mortality for Atlantic salmon before spawning is infrequent (Havn et al., 2015; Jensen et al., 2010; Lennox et al., 2015; Thorstad et al., 2003, 2007; Whoriskey et al., 2000). Therefore, tagging salmon with internal transmitters can be a valuable tool to quantify predation and provide estimates of predation mortality that can be used in stock assessments and reduce the risk of overharvesting. Furthermore, evidence of impacts of predation can guide management decisions to resolve local predator–human conflicts. Finally, the differences in predation mortality observed in this study highlights the importance of river-specific assessments to evaluate impacts of otter predation on salmon populations.

5 | CONCLUSION

Lack of evidence for selective predation in this study suggests that predation by otters on pre-spawning salmon was a source of mostly additive mortality, thereby reducing the number of spawning fish and the recruitment to the next generation. Both Aureelva and Søre Vartdalselva would have been closer to reaching their spawning targets in the absence of otter predation. However, the magnitude of predation impact varied greatly between the two rivers. The difference in predation risk is hypothesised to be attributable to habitat types, such as availability of deep holding pools, which are probably predation refuges for adult salmon (Sittenthaler et al., 2019). This study highlights the need for more detailed knowledge to assess the impacts of otter predation on salmon populations as the number of otters is increasing and the number of salmon is decreasing in Norway. The tools refined in this study provide management with a method for estimating local predation mortality, which can aid in reducing risk of overharvesting vulnerable salmon populations and provide guidance on how to holistically manage freshwater ecosystems.

AUTHOR CONTRIBUTIONS

Conceptualisation: M.K., R.J.L., L.K.S., G.V., K.W.V. Developing methods: M.K., R.J.L., L.K.S. Conducting the research: L.K.S., M.K., R.J.L. Data analysis: L.K.S., R.J.L., G.V., K.W.V. Data interpretation:

L.K.S., R.J.L., M.K., G.V., K.W.V. Preparation of figures and tables: L.K.S., R.J.L. Writing: L.K.S., R.J.L., M.K., G.V., K.W.V.

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DATA AVAILABILITY STATEMENT

Data will be made available on the Zenodo server.

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