Predation by Eurasian otters on adult Atlantic salmon


Photo: Vegard Lødøen

by

Lene Klubben Sortland

Supervisors: Robert James Lennox (NORCE Norwegian Research Centre), Knut Wiik Vollset (NORCE) & Gaute Velle (Department of Biological Sciences, University of Bergen & NORCE)

Thesis submitted in partial fulfilment of the requirements for the degree of:

Master of Science in Biology - Biodiversity, Evolution and Ecology

Department of Biological Sciences
University of Bergen, Norway
April 2022

Acknowledgements

This master thesis would not have been possible without all the great assistance from my supervisors, Robert James Lennox, Knut Wiik Vollset and Gaute Velle. Thank you for always providing advice whenever I came knocking on the door, even if I had already asked perhaps too many questions. I am especially grateful for Robert, who have built up my confidence in both writing and R skills, and was available 24/7 if I struggled with anything. Throughout my masters I have been provided amazing opportunities to join fieldwork, write academic papers, and go to conferences. I would also like to give a shoutout to the project leader of my thesis work, Marius Kambestad, for all the help in the field and checking my writing for errors (nothing gets past you). I am also grateful for all the amazing people at LFI. Meeting Bjørn Barlaup in the office at Saturdays made it a much nicer experience to go to the office during the weekends. I would also like to thank Helge Skoglund and Knut for making difficult predator-prey ecology concepts understandable. And of course, thank you Gaute for introducing me to this field of biology, your passion for freshwater ecology is what started this all.

My deepest gratitude goes out to my family and friends for boosting my mood whenever the thesis work became overwhelming. Lunching together reminded me that we are all equally confused about our thesis work. Thanks to my roomies for always cheering me up however late I got home, you have made my everyday a wonder. Especially thank you to Cecilie and Lotte, who provided amazing help with fieldwork, R-code, and made my studentlife at LFI 100 % better. And lastly, thank you to mom and dad, who always, no matter how many times I had already called, was available to talk when I needed a mood boost.

Table of Contents

Abstract

The return of the Eurasian otter to western Norway has sparked human-predator conflicts as otters prey on vulnerable Atlantic salmon populations. Although predation may not be the direct cause of salmon population declines, otters that kill salmon in rivers before they spawn may impact the salmon spawning stock, with potential consequences for stock recruitment. Concerns of local people and stakeholders suggest that otter predation inhibits recovery of salmon populations. However, there is limited information on mortality caused by otter predation on adult salmon. To gain insight into impacts of otter predation on salmon populations, I quantified the predation by otters on adult salmon in two rivers in Western Norway using a novel combination of radiotelemetry and temperature loggers. I tagged 45 salmon in Aureelva and 30 salmon in Søre Vartdalselva and tracked the salmon until they died or left the river. This method identified the fates of 95 % of tagged salmon. Otters killed 9 tagged salmon in Aureelva and 20 tagged salmon in Søre Vartdalselva. I found no evidence that otters selectively killed salmon based on sex, length, health status or activity level, which suggests that predation mortality on pre-spawners was additive. Otter predation contributed in reducing both salmon populations below their spawning targets, and without otter predation both populations would have been closer to reaching their spawning targets. However, the magnitude of predation differed greatly between rivers. Salmon in Søre Vartdalselva had greater predation risk compared to salmon in Aureelva, possibly due to differences in the number of holding pools between the two rivers. The findings from this study emphasise that management decisions should be guided by river-specific evaluations of impacts of otter predation on salmon, for which the combination of radiotelemetry and temperature loggers can provide a valuable tool.

1. Introduction

Competition between humans and predators over mutual resources is a recurring topic of conflict in many ecosystems. Resolving human-predator conflicts is challenging for management, which has to consider both the social and biological side of conflicts (Treves & Karanth, 2003). Predators can directly impact people's source of food, economy, or recreational activity and sense of place (Thirgood *et al.*, 2000; 2005). However, predators also have important roles in structuring ecosystems through top-down effects by altering the density and behaviour of prey (Terborgh *et al.*, 2001; Berger *et al.*, 2001; Baum & Worm, 2009; Kuijper *et al.*, 2013). Predators' abilities to influence ecosystems and maintain biodiversity have been one of the major motivations for predator conservation (Ritchie & Johnson, 2009; Ritchie et al., 2012). However, the recovery of predator species has also generated conflicts when predators kill protected prey or compete with humans for prey (Marshall *et al.*, 2016). A prime example has emerged in Western Norway where the return of the Eurasian otter (*Lutra lutra*) and conservation of Atlantic salmon (*Salmo salar*) have recently come into conflict.

Atlantic salmon (hereafter referred to as salmon, unless otherwise specified) is an anadromous fish that undertakes large-scale migrations between freshwater systems and the Atlantic Ocean, during which they experience predation by multiple predators, including humans (Strøm *et al.,* 2019). Atlantic salmon are currently experiencing declines throughout their distribution, with the number of Norwegian salmon reduced to half of its abundance since the 1980s (Thorstad *et al.*, 2021; Vitenskapelig Råd for Lakseforvaltning (VRL), 2021). As of 2021, Atlantic salmon has been listed as "near threatened" on the Norwegian red list (Artsdatabanken, 2021). Ensuring that a large number of wild smolts in good condition leave the river to the ocean has been proposed as the best strategy to minimise the impacts of changing ecosystems and low marine survival (Thorstad *et al.,* 2021). Thus, Norwegian salmon populations are managed according to spawning targets for female biomass, which maximises recruitment of smolts during the freshwater phase (Forseth *et al.,* 2013).

The Eurasian otter (hereafter called otter) was previously exterminated from most of Norway by humans, however, since their protection in 1982, the otter has expanded and re-established its range from refuges in Northern Norway (van Dijk *et al.*, 2021). This means otters have returned as predators of salmon in rivers in Western Norway (van Dijk *et al.,* 2020). Although salmon have a long history of coexisting with predators, predation on salmon populations already reduced in numbers can suppress recovery by maintaining the salmon population at low density-equilibriums known as a predator pit (Smout *et al.*, 2010). There is a growing concern that otters killing adult salmon will negatively impact population dynamics, especially in populations that are below their spawning target (van Dijk *et al.,* 2020).

Predation is a major driver of natural mortality, which is an important parameter in fisheries stock-assessments. Predation mortality and other sources of mortality such as disease and injury make up natural mortality. Together with fishing mortality, natural mortality constitutes total mortality of a stock (Tyrrell *et al.*, 2011). In many fisheries, natural mortality is difficult to estimate. Typically, natural mortality has to be estimated through indirect methods, such as using models integrating several types of data (Lee *et al.*, 2011). The share of natural mortality attributable to predation can be challenging to estimate because predation may be the direct but not the underlying cause of death. For instance, predators may attack and eat salmon sick from infectious agents that likely would have killed them if they were not eaten (e.g., Furey *et al*., 2021). At high abundance, prey recruitment may also be limited by density-dependent effects such as competition, in which case predation mortality may be compensated by higher survival due to reduced competition. When predation mortality compensates for other sources of mortality, it is termed compensatory mortality (Ward & Hvidsten, 2011). Thus, selective predation can generate compensatory mortality. Alternatively, if predation mortality adds on to other sources of mortality so that total prey survival is reduced, it is called additive mortality and can be a major driver of population dynamics (Ward & Hvidsten, 2011). Predation impacts on prey populations can be viewed as a gradient from compensatory to additive mortality (Payton *et al.*, 2020).

Predation can be quantified through non-invasive methods, like carcass counts, or use of more invasive methods by tagging and tracking animals with telemetry. Otter predation has previously been quantified by carcass counts (Carss *et al.,* 1990; Cunningham *et al.,* 2002). However, carcasses often quickly disappear due to scavengers and thus require frequent site visits to get realistic estimates of predation levels (van Djik *et al.,* 2020). Tagging prey with electronic tags and tracking their movements have allowed researchers to quantify predation in terrestrial and aquatic environments. Methods used to identify predation events include the use of temperature loggers, records of vertical and horizontal movements, and finding and inspecting carcasses (e.g: Brodie *et al.,* 2013; Strøm *et al.,* 2019; Gallagher *et al.,* 2021). Most of the aforementioned methods are only applicable in either aquatic or terrestrial environments, which poses a challenge for quantifying predation by semi-aquatic predators, such as otters, where carcass counts can be too work-intensive (van Dijk *et al.*, 2020). However, applying temperature loggers on salmon to quantify predation by otters has never been attempted, but holds promise given that salmon eaten are pulled onto land, which should generate detectable temperature changes.

This study attempts to quantify otter predation on adult salmon using a novel combination of radio transmitters and temperature loggers in an area of Norway where the conflict between conservation of salmon and predation by otters is ongoing and the impacts of predation remain uncertain (van Djik *et al.*, 2020). Important questions for management are (1) whether or not salmon removed by otters would have survived and spawned (additive or compensatory mortality), and (2) whether the removal of these fish would lead to a reduction of spawner abundance below the spawning target, thereby reducing the numbers of salmon smolts produced in the next generation. To investigate the impact of otter predation on salmon populations, I tagged adult salmon in two Norwegian rivers with a radio transmitter and temperature logger package and tracked them until they died or left the river. I hypothesise that (1) tagging salmon with radio transmitters and temperature loggers allows one to determine the fates of tagged salmon, (2) otters selectively kill salmon based on sex, length, health status, or activity level, and that (3) otter predation affects the adult salmon population's ability to reach its spawning target.

2. Methods

2.1 Study Area

2.1.1 Aureelva

Aureelva is a river located in Sykkylven municipality in Western Norway, with a spawning target of 323 kg female salmon (Figure 1A; Kambestad *et al.*, 2021; VRL, 2022a). The main river of Aureelva runs 4.2 km from the lake Andestadvatnet to the sea (Figure 1C; van Dijk *et al.*, 2020), with the main spawning areas being located downstream from the lake (Kambestad *et al.,* 2021). Average slope of Aureelva from Andestadvatnet to the sea is 1.6 %, with a mean annual discharge by the river mouth of 2.7 m^3/s (van Dijk *et al.*, 2020; Kambestad *et al.*, 2021). The habitat of the main river consists of a mixture of rapids, pools, and riffle stretches (Kambestad *et al.*, 2021). A smaller and steeper river (Aurdalselva) runs into the lake, with an anadromous stretch of ca. 1.5 km. The salmon population in Aureelva reached its spawning target from 2015 to 2018, with some poorer attainment in 2019 and 2020 (VRL, 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 1A; Kambestad *et al.,* 2021; VRL, 2022b). The local angling community estimates that the salmon mainly uses the lowermost 5 km of the river stretch (Figure 1B), which has an average slope of 2.7 % (Kambestad *et. al.,* 2021). A fish ladder is located 2 km upriver (by Stillehølen; Figure 1B), and there are no lakes in the part of the river available to salmon. 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 m^3/s. The salmon population in Søre Vartdalselva reached its spawning target from 2015 to 2017, but had poor attainment after 2017 (VRL, 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 in an attempt to prevent extinction of the population (Kambestad *et al.*, 2021).

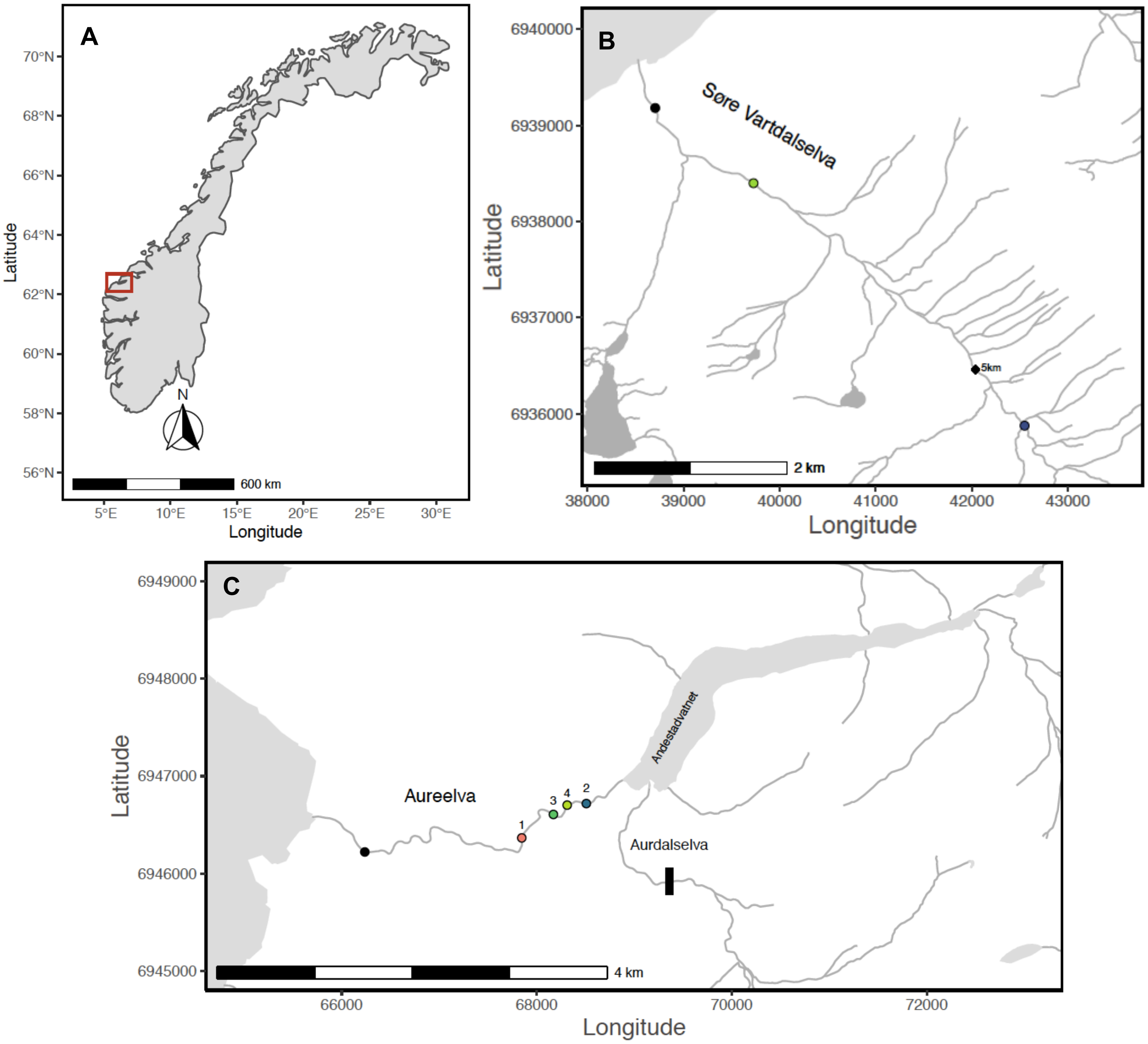


Figure 1: Map (A) red box indicates study area (Sunnmøre) in Norway. Map (B) illustrates Søre Vartdalselva with location of stationary receiver (black), Stillehølen (green), maximum upriver migration by a tagged individual (purple), and the lowermost 5 km of the river (black rhombus). Map (C) illustrates Aureelva with location of stationary receiver (black) and capture locations in chronological order: (1) Storhølen (pink); (2) Lyshol (blue); (3) Sjellarhølen (dark green); (4) Fløtvøren (light green). Black line indicates the upper limit of the anadromous stretch in Aurdalselva. UTM, being a metres-based projection, is used for higher precision in the zoomed-in maps B) and C), whereas longitude-latitude is used for the primary map A).

2.2 Capture method

Forty-five adult salmon were caught and tagged in Aureelva in September 2020. Water temperatures ranged from 13 to 15 degrees Celsius during the tagging. Catch locations in Aureelva included the four major pools Storhølen, Lyshol, Sjellarhølen and Fløtvøren (Figure 1C). In Storhølen and Lyshol, a seine net was deployed by two divers to catch the salmon. The salmon caught in Storhølen were visibly stressed from the seine net being deployed several times. Therefore, the seine net was only deployed once in Lyshol. Due to higher mortality for salmon tagged at Storhølen compared to the other sites, possibly due to the capture method, this group (n = 15) was excluded from data analysis to avoid overestimation of predation impact. In Sjellarhølen and Fløtvøren, all salmon were caught with dip nets.

Thirty adult salmon were caught and tagged in Søre Vartdalselva in August 2021. Salmon were caught with dip nets in the fish ladder (Stillehølen in Figure 1B) and in the pools and riffles 0-500 m downstream of the ladder. The salmon were given a minimum of 15 minutes to recover from capture in submerged cages before the tagging procedure was performed. Water temperatures ranged from 13-16 degrees Celsius during tagging. All salmon were tagged at capture location (Figure 1B & C).

2.3 Tagging procedure

The salmon were anaesthetized in benzocaine water (1.5 mL/10L) for approximately three minutes. Once properly anaesthetized, the salmon`s weight (g), fork length (mm) and total length (mm) was recorded. I also noted injuries to the fish (bite/scratch marks, salmon louse (*Lepeophtheirus salmonis*) damage) and sex based on external traits. In Søre Vartdalselva, weight was not recorded. Individuals were categorised into perfect or imperfect health status based on damages observed during tagging. Individuals that had damage that could affect their swimming abilities (e.g., missing a fin), energetics (e.g., gill parasites, skin disease) or potentially make them more visible to otters (e.g., red coloured skin from infection) were categorised as imperfect (n = 24), whereas individuals with no external damage or mild superficial marks (e.g., scratch marks) were categorised as being in perfect 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 in the salmon's mouth so that the salmon remained subdued and oxygenated throughout the procedure.

For the tagging procedure, an incision approximately 4 cm long was made in the ventral side between the pelvic and pectoral fin. 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 (Appendix 1). 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. With the exception of 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 were tagged to keep tag burden under 2 % of the bodyweight, which studies indicate minimises impact on fish physiology and swimming abilities (e.g., Smircich & Kelly, 2014). Because salmon weight was not recorded in Søre Vartdalselva, the size limit was translated from weight (g) to total length (cm) using Fulton's condition formula (Robinson *et al.*, 2008) and no fish with total length below 500 mm were tagged. Tag burdens were at maximum 1.7 % of body weight. All handling and tagging were done according to animal welfare regulations and was approved by the Norwegian Food Safety Authority FOTS application 24390.

The final sample size used for data analysis was 30 individuals in Aureelva and 30 individuals in Søre Vartdalselva. Total length of tagged salmon ranged from 510 - 810 mm in Aureelva and 502 - 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. There were 18 females and 12 males 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 an implanted 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 subsequently covered in Plasti Dip (Appendix 1). Combined weight of the radio transmitter and temperature logger was 17 grams. The combination of radio transmitter and temperature logger will hereafter be referred to as tag. Tags had an estimated battery life of 280 days. The temperature loggers implanted in the salmon 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 and establish time of death. It was difficult to assess whether some individuals in the river were dead or alive during tracking in Aureelva. Thus, a coded radio transmitter (Advanced Telemetry Systems: Model F1835C) with a motion-based mortality sensor was used in Søre Vartdalselva so that it could be determined whether the tracked fish were alive or dead with greater certainty than in Aureelva. The mortality sensor in the radio transmitter doubled the pulse (beep) rate of signals when the tag had not moved for 24 hours, 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 was recorded and tags from dead salmon on land or in the river 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 1B & C). A range test was performed prior to tagging to ensure the stationary receiver registered any tagged salmon passing.

From September 2020 to March 2021, the salmon tagged in Aureelva were tracked on a total of 20 unique non-consecutive days. From September until the start of spawning (October 20th), one to three days of tracking was conducted every two-three weeks. Two tracking trips were made during the spawning period (October 20th - November 15th, 2020), each trip included four to five days of tracking. After spawning, tagged salmon were tracked once every month from December 2020 to March 2021, with the last tracking day on March 7th, 2021.

In Søre Vartdalselva, tagged salmon were tracked approximately every 10-14 days from August to November 2021 on a total of 11 unique non-consecutive tracking days. Last tracking day was conducted November 12th 2021 as all salmon were either dead or had left the river.

2.5 Data analysis

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

2.5.1 H1: Fates of tagged salmon

Fates of salmon were determined based on 1) location where tags were found, and 2) when the individual died or last showed signs of being alive (Figure 2). The second step was important to determine whether individuals died within a week after tagging, or if individuals died before or after spawning. Because tagged salmon may be affected by anaesthesia, handling, or tagging procedure for some time after tagging and thus experience higher predation than untagged conspecifics (Brown *et al.*, 2011; Raby *et al.,* 2014; Wilson *et al.,* 2017), salmon determined to have died less than one week after tagging were excluded from data analysis.

Because otters remove salmon from rivers to feed, salmon whose tags were recovered on land were categorised as killed by otters (Figure 2). To identify time of death from temperature loggers (step 2), I plotted temperature over time in the river, on land, and as measured by the tag 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. In 2021, the river temperature logger in Søre Vartdalselva was lost due to extreme flooding. Therefore, the temperature data from individuals with the longest survival time were used as reference 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 found or tags that were never recovered (step 1), when the individual died or had its 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, when the individual stopped moving or when mortality sensor turned on (only in Søre Vartdalselva) was used to estimate time of death. Upriver movements or downriver movements towards spawning grounds at the same time as conspecifics were considered signs of the individual being alive (hereafter termed "sign of life"). For salmon in Søre Vartdalselva, uninitiated mortality sensors were also considered a sign of life. As adult salmon in freshwater usually have high survival until spawning (Havn *et al.*, 2015), individuals that died before or during the spawning period were considered killed by otters. Individuals that died after spawning were categorised as having an unknown cause of death, unless the tag was recovered on land, suggesting it was taken by an otter after having spawned. Salmon can have high natural mortality after spawning, thus tags found in the river could have been from individuals that died of other causes after spawning (Bardonnet *et al.*, 2000; Cunjak *et al.*, 1998).

Individuals last registered on the stationary receiver were categorised as having left the river system pre- or post-spawning (Figure 2). Individuals in the river system with signs of life up until the last tracking day were categorised as overwintering kelts.

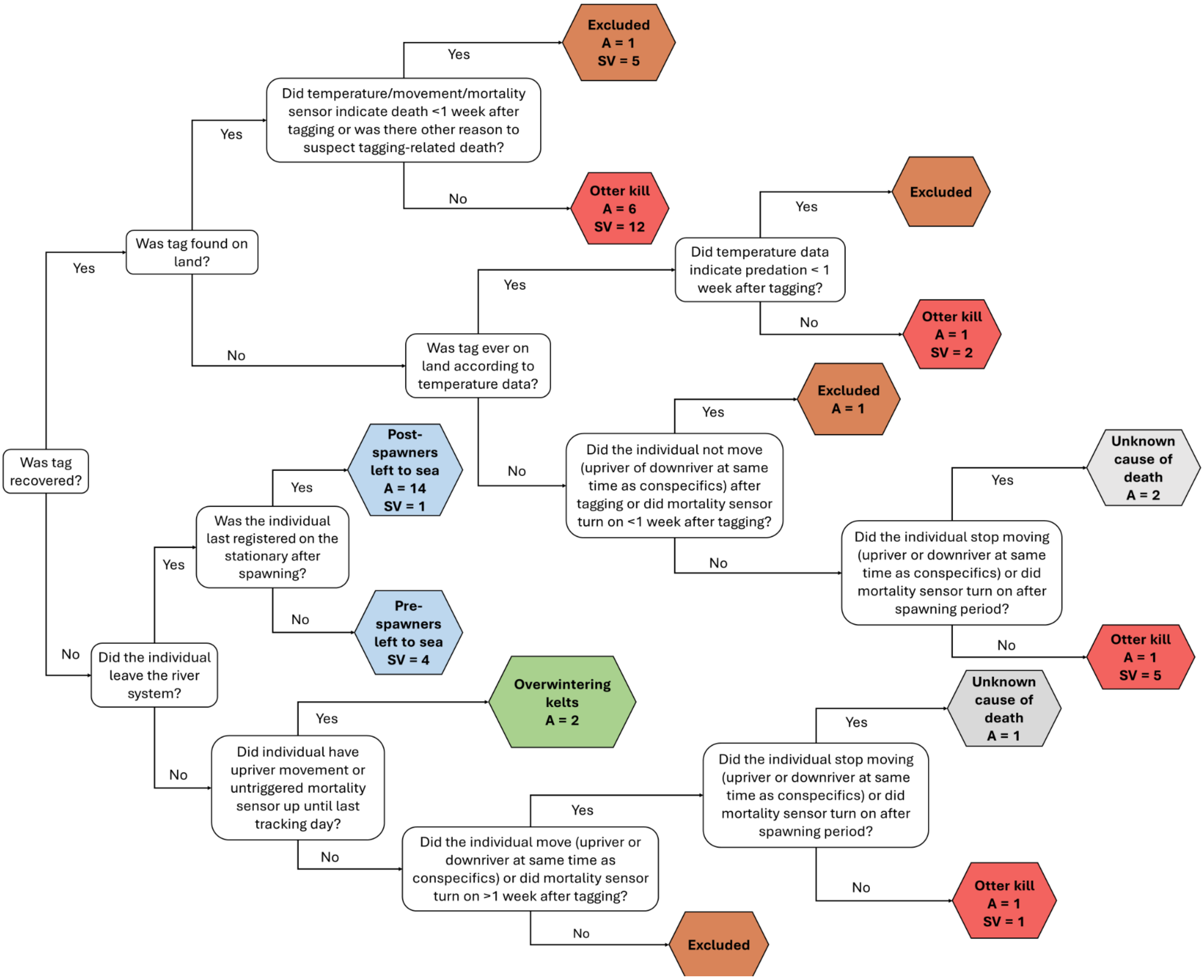


Figure 2: Decision-tree used to categorise the fate of tagged salmon in Aureelva and Søre Vartdalselva. Only fish in Søre Vartdalselva had mortality sensors as a criterion for categorization of fates.

2.5.2 H2: Predator selectivity

The remaining sample after exclusion of potential tagging-related deaths was 28 salmon in Aureelva (17 females and 11 males) and 25 salmon in Søre Vartdalselva (10 females and 15 males).

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

To test if otters selectively killed salmon based on sex, length, health status, or activity level, a semi-parametric Cox propotional hazards (PH) model (Cox, 1972) was used. The 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 bootstrap samples (n = 100). Associations were considered statistically significant if $p \leq 0.05$.

Because death was only known to have occurred between two tracking dates for some salmon, the survival times were registered as time intervals with a lower (left) and upper limit (right). Individuals whose time of death was not observed on a specific day or never experienced death were censored. Censoring means the individual's exact time of death is unknown. My study contains 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 was beyond the study time Thus, right-censored individuals were registered to have died between the last registered tracking day (left) and infinity (right) (Anderson-Bergman, 2020). Individuals that were known to have died between two tracking dates were interval-censored; the tracking date before its last sign of life was set as the lower limit (left), and the upper limit (right) was the tracking date after which it had no further sign of life (see section 2.5.1). Individuals that were known to have died on a specific day were uncensored, meaning the same day was registered as the lower (left) and upper (right) limit of the survival time interval.

Explanatory variables included in the model were river (Aureelva/Søre Vartdalselva), sex (male/female), total length (mm), activity level (metres travelled per tracking day), and health status (perfect/imperfect; 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 *et al.,* 2021). The coordinate reference system (CRS) of the study site raster was set using the *proj4string* function in the raster package. The GPS points from tracking were transformed into spatial objects using the *coordinates* function in the sp package (Pebesma *et al.,* 2021), and transformed into the same projection system as the study site raster using the function *spTransform* in sp. 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, and the length of each path segment was measured using *gLength* in the rgeos package (Bivand *et al*., 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.

A Cox-PH model was fitted using the function *ic_sp* in the icenReg package, which allowed for analysis of interval-censored data:

ic_sp(cbind(left, right) ~ River + Length + Sex + Health_status + Activity, **(Model 1)**
model="ph", bs_samples=100)

In Model 1, “left” and “right” represent lower and upper limit of the survival time interval, “River” is Aureelva or Søre Vartdalselva, “Length” is total length (mm) of tagged, “Sex” is male or female, “Health_status” is visually assessed health status (perfect/imperfect), and “Activity” is activity level of tagged salmon, “ph” is proportional hazards, and “bs_samples” is the number of bootstrap samples.

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 H3: Predation impact on spawning stock

To investigate if otter predation affected the salmon populations` ability to reach their spawning target by being a source of additive mortality, I calculated whether the population would reach their spawning target if predation from otters had been absent. Estimates of attainment of spawning target was obtained from VRL (2022a) for Aureelva and from Hanssen *et al*. (in prep) for Søre Vartdalselva and reported as female biomass (kg) during the spawning period. Forty salmon were removed from Søre Vartdalselva between June 8th and September 12th for gene bank purposes and were not included in estimates of spawning target attainment. To estimate what the female spawner biomass would have been without otter predation for the two salmon populations, I divided the estimated attainment of spawning target by the proportion of female spawners that I estimated to have spawned:

$$No\ predation\ (kg) = \frac{Attained\ spawning\ target\ (kg)}{(1 - proportion\ of females\ killed\ by\ otters)}$$

, where "No predation" is the female spawner biomass (kg) if there had been no otter predation, "Attained spawning target" is the estimated attainment of spawning target (kg) after predation, and "(1 – females killed by otters)" is the proportion of female salmon that survived to spawn based on estimated predation mortality among tagged females in my study. Attainment of spawning target (kg) if there had been no otter predation ("No predation" in the equation above) was thereafter divided by the spawning target (kg) to calculate estimated percentage attainment of spawning target without otter predation.

Pre-spawners that left the river system were not included as a part of this female sample. The remaining sample was 28 salmon in Aureelva (17 females and 11 males) and 21 salmon in Søre Vartdalselva (9 females and 12 males). Salmon killed by otters before spawning or during the first half of the spawning period (Aureelva: October 20th – November 2nd; Søre Vartdalselva: October 25th – November 1st) were considered to most likely not have spawned, whereas salmon killed during the last half of the spawning period (Aureelva: November 2nd – November 15th; Søre Vartdalselva: November 2nd - 9th) or after spawning had most likely spawned. Spawning periods were set based on observations of spawning activity during snorkelling in the rivers (M. Kambestad, pers. comm.).

3. Results

3.1 Movements of tagged salmon

No tag batteries expired during the study period, that is until the fish either had died or left the study area. The majority of tagged salmon in Aureelva resided in pools in the river near tagging sites (Stillehølen, Sjellarhølen, Fløtvøren, and Lyshol; Figure 1) with little movements before the spawning period. Six salmon in Aureelva migrated into the lake and had greater movements compared to the salmon who resided in the river pools. Fourteen tagged salmon left the river after spawning between November 16th and 23rd, and two left in December. On the last tracking day, five salmon in the river were determined to have died and four tags were retrieved in the river, whilst two salmon were overwintering in the lake.

In Søre Vartdalselva, six individuals were registered to have left the river by the stationary receiver mid to late August, of which two individuals later returned. One of the returners was captured by a local rod fisherman and kept in a gene bank tank adjacent to the river from September 10th to 16th. It was thereafter released at the river mouth, after which it migrated upriver and remained near spawning grounds. Three individuals migrated upstream from Stillehølen after tagging, past the fish ladder and resided in upstream areas. Two of these fish migrated approximately 1.3 km upstream of the fish ladder, whereas one migrated approximately 3.9 km upstream from the fish ladder. Most salmon resided in the Stillehølen pool (Figure 1C) until September 28th, after which seven surviving individuals were found closer to or at spawning grounds downstream from Stillehølen on October 21st. One individual migrated out of the river system after spawning on November 9th.

3.2 H1: 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 individuals 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 by locals in poor condition. The remaining 28 salmon tagged in Aureelva had the following fates (Figure 3): Three individuals died after spawning with unknown cause of death; 14 individuals migrated to the fjord post spawning (Post-spawners left to sea); nine individuals were killed by otters

(Otter kill); and two individuals resided in the lake by the end of the study (Overwintering kelts). The remaining 25 salmon tagged in Søre Vartdalselva had the following fates (Figure 3): Four individuals left the river system before the spawning period (Pre-spawners left to sea); one individual left post spawning (Post-spawners left to sea); and 20 individuals 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 found in the river (Table 1 & Figure 2). Most tags were found without salmon carcasses. For step 2 in resolving fates, temperature data was the most used tool to estimate the last sign of life (Figure 4), followed by stationary receiver, movement data, and mortality sensor. Interval for time of death ranged between 5 and 53 days for movement data, 0 to 11 days for mortality sensor, and 0 days for temperature data (within two hours of predation event).

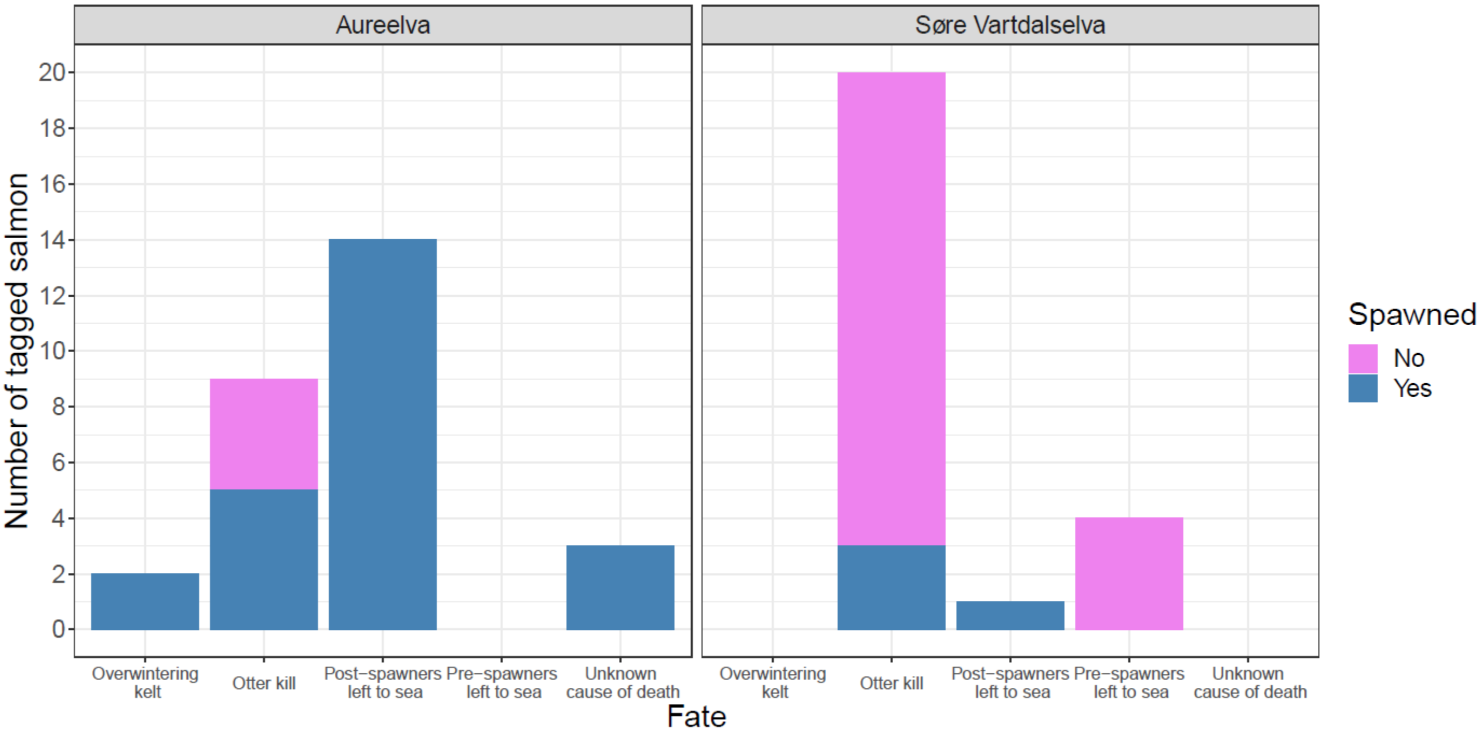


Figure 3: Fates of tagged salmon. Bars indicate number of tagged salmon assigned the following fates: overwintering kelts, otter kill, post-spawners left to sea (i.e., individuals who left the river after spawning), pre-spawners left to sea (i.e., individuals who left the river prior to spawning), and unknown cause of death. n = 28 in Aureelva and 25 in Søre Vartdalselva.

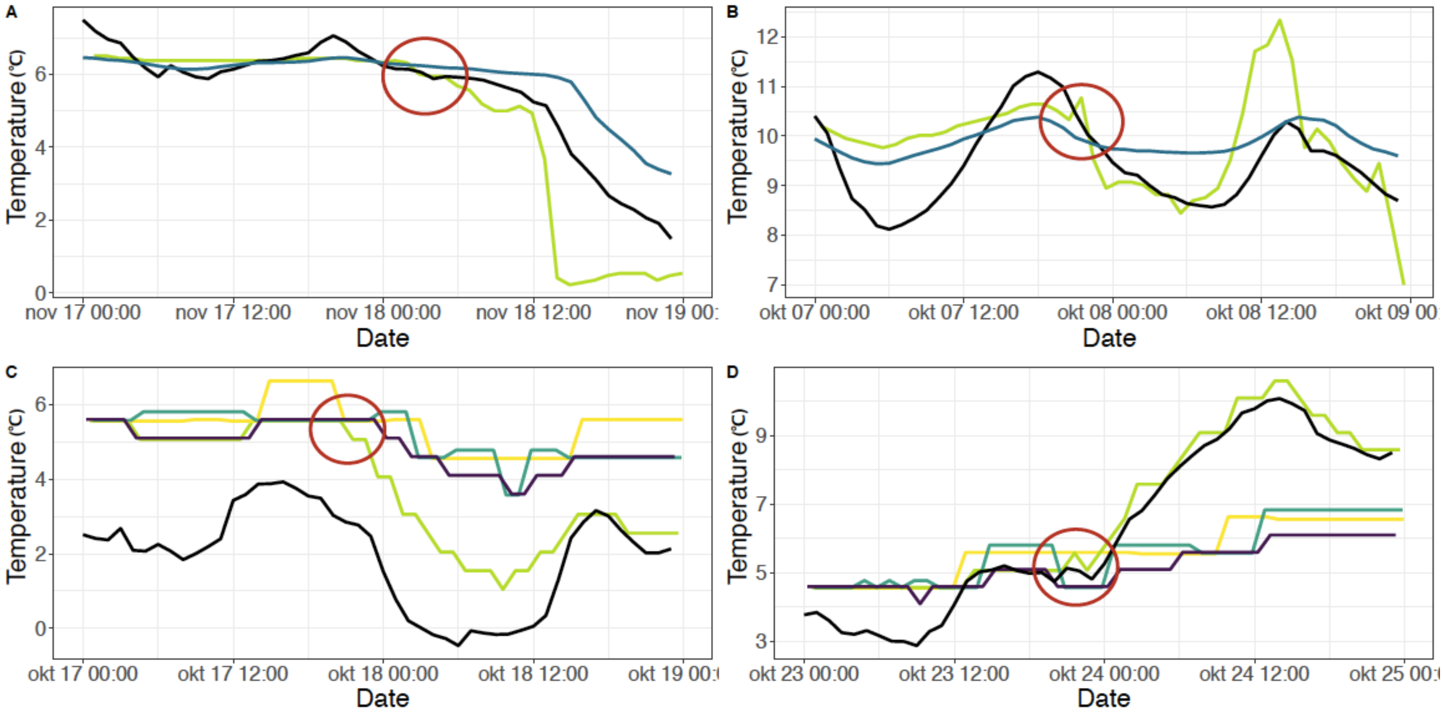


Figure 4: Line plots illustrating time of death (red circle) for two individuals from Aureelva (A and B) and two individuals from Søre Vartdalselva (C and D). In Aureelva, time of death was determined to be when the salmon`s temperature (green) changed from following river temperature (blue) to land temperature (black). For individuals 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. Temperature is in degree Celsius (°C).

Table 1: Number of tagged salmon whose fates were inferred based on 1) location where tag was found and 2) last sign of life estimated from temperature data, movement data, stationary receiver data or mortality sensor in Aureelva and Søre Vartdalselva. Two individuals were found by locals in poor condition and are not represented in the table.

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

3.3 H2: 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 individuals 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 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 = 5.581, std. Error = 0.586, p = 0.003). At any moment in time, individuals from Søre Vartdalselva had 5.581 higher predation risk than individuals from Aureelva.

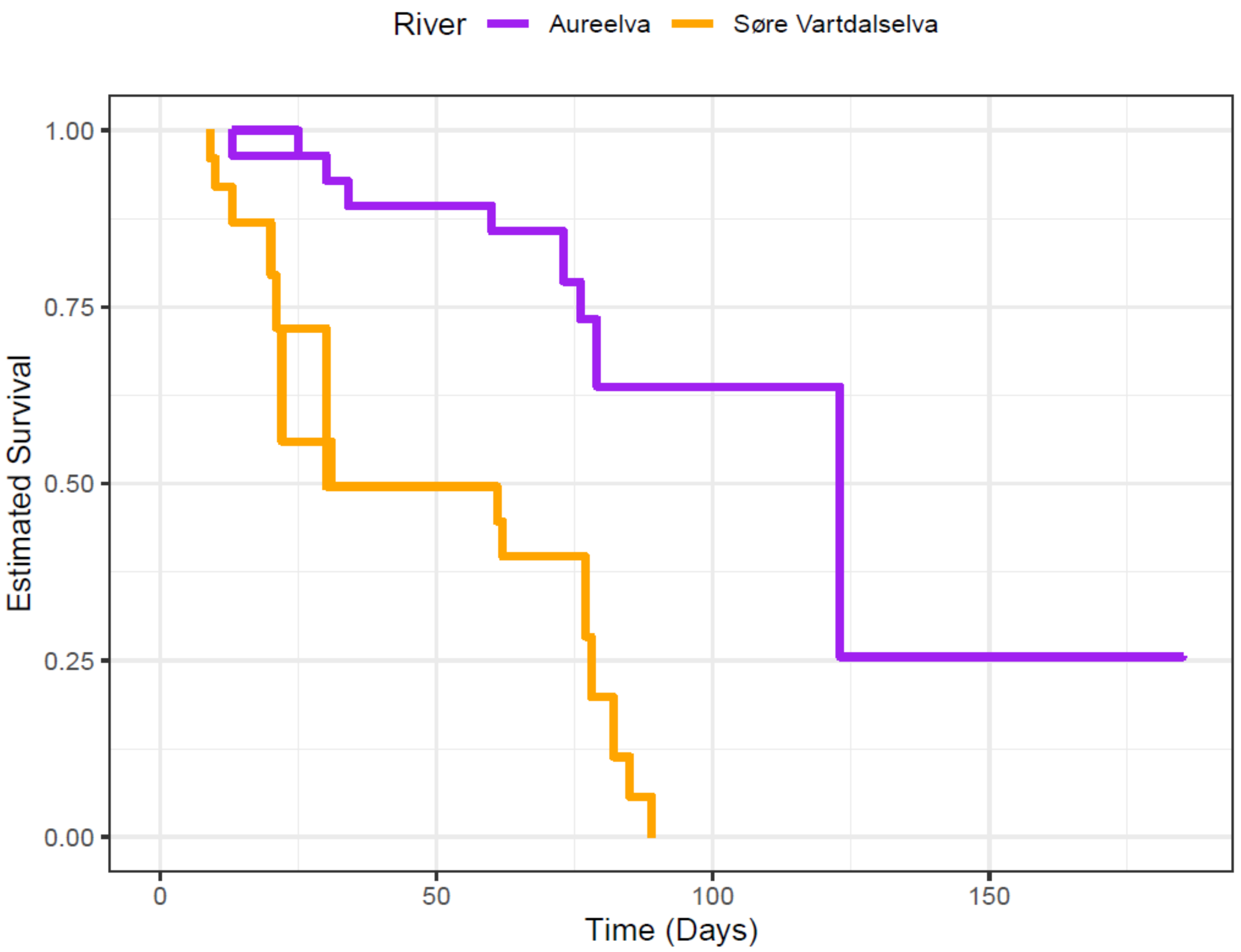


Figure 5: NPMLE survival curves for Aureelva (purple) and Søre Vartdalselva (orange). Because the data contains interval-censored observations, each river`s survival curve is represented by two lines; any curve that lies between the two lines of a group (i.e., River) maximises the likelihood associated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

Table 2: Summary of the Cox Proportional Hazards model output with 100 bootstrap samples.

	Cox PH model, bootstrap samples = 100				
	Estimate	**Exp(Est)**	**Std.Error**	**Z value**	**p - value**
RiverSøre Vartdalselva	1.719	5.581	0.586	2.932	0.003
Length	0.000	1.000	0.004	0.041	0.967
SexMale	0.452	1.572	0.751	0.602	0.547
Health_status Perfect	0.898	2.455	0.635	1.414	0.157
Activity	0.000	1.000	0.001	0.151	0.880

3.4 H3: Predation impact on spawning stock

In Aureelva, nine tagged salmon were killed by otters. Four individuals were killed before or during the first half of the spawning period and most likely had not spawned, whereas five individuals were killed during the last half or after the spawning period and most likely had spawned (Figure 6). Thus, otters were estimated to have killed 14.3 % pre-spawners (n = 4) of the total sample (n = 28). Among the pre-spawners killed, two were females and two were males. Otter predation on female pre-spawners was estimated to be 11.8 % (n = 2) of the total female sample (n = 17). Rådgivende Biologer (NINA, 2020) counted 139 adult salmon during drift dive counts on November 16th 2020. Based on the salmon count and rod catches during the summer of 2020, attainment of the spawning target was estimated to be 84 % (VRL, 2022a). If there had been no otter predation, spawning target attainment in Aureelva was estimated to have been 95.2 % (Table 3).

In Søre Vartdalselva, 20 tagged salmon were killed by otters. Seventeen individuals were killed before or during the first half of the spawning period and thus likely had not spawned, whereas three individuals were killed during the last half of the spawning period and most likely had spawned (Figure 6). Thus, otter predation on pre-spawners was estimated to be 81.0 % (n = 17) of the total sample (n = 21). Of the pre-spawners killed, seven were females and ten were males. Otter predation on female pre-spawners was estimated to be 77.8 % (n = 7) of the total female sample (n = 9). Hanssen *et al.* (in prep.) counted 41 salmon during drift dive counts November 2nd 2021. Based on the salmon count, attainment of the spawning target was estimated to be 21 % (Hanssen *et al.*, in prep.). If there had been no otter predation, spawning target attainment in Søre Vartdalselva was estimated to have been 94.6 % (Table 3).

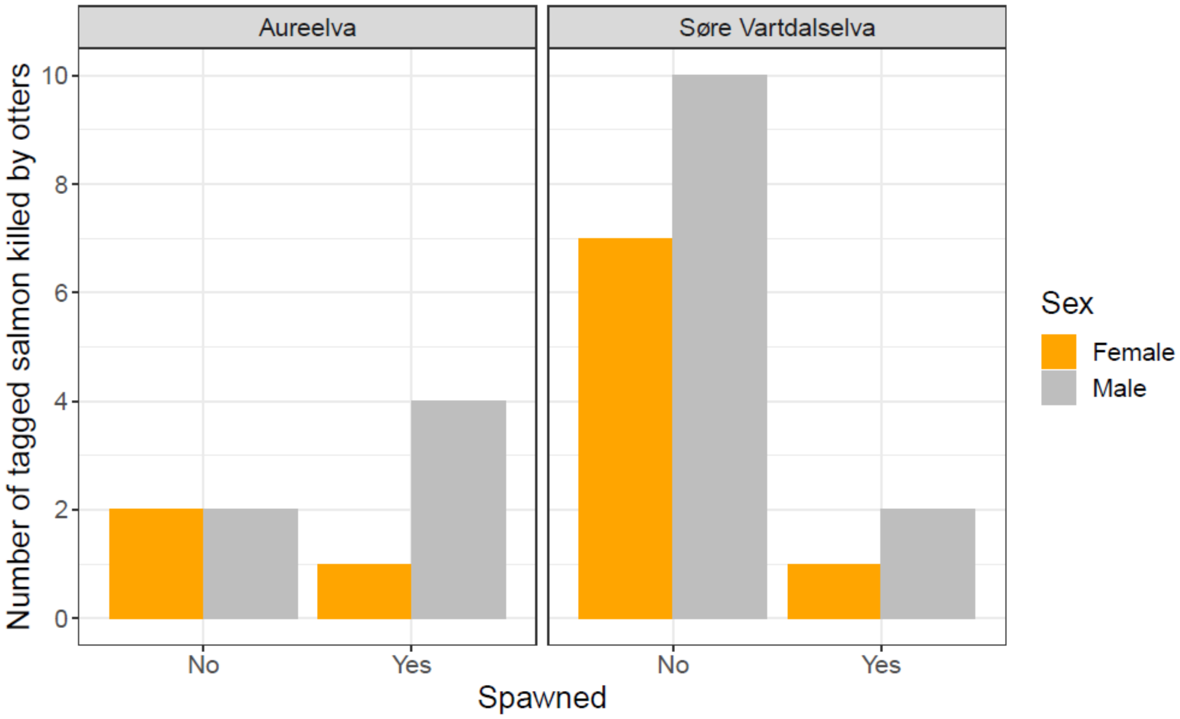


Figure 6: The number of male and female salmon killed by otters and whether they had spawned before they were killed.

Table 3: Calculations for attainment of spawning target without otter predation in Aureelva (2020) and Søre Vartdalselva (2021).

River	**Spawning target (kg)**	**Attainment of spawning target (%)**	**Estimated female spawning stock (kg)**	**Predation mortality (%)**	**Spawning stock without predation (kg)**	**Attainment of spawning target without predation (%)**
Aureelva	323	84	271.3	11.8	307.6	95.2
Søre Vartdalselva	324	21	68.0	77.8	306.5	94.6

4. Discussion

This study aimed to investigate the impacts of otter predation on adult salmon populations in two rivers in Norway. This is the first study to use radiotelemetry combined with temperature loggers to determine fates of spawning salmon and quantify predation on salmon by otter. The novel combination of loggers and transmitters provided the fates of 95 % of tagged salmon in this study. Fates were resolved based on 1) location where tags were found, and 2) last sign of life determined by temperature data, movement data or mortality sensors. Most tags were found on land or were unrecovered, with a few found in the river (Table 1). Temperature data were the most frequently used tool to determine fates based on last sign of life (Table 1), and provided the most precise estimates of time of death compared to mortality sensors and movement data from manual tracking. The stationary receiver data identified all salmon that left the study system and was the second most important tool to resolve fates based on the last sign of life. Otters killed 9 tagged salmon in Aureelva and 20 tagged salmon in Søre Vartdalselva. Length, sex, activity level, and health status were not associated with predation risk. However, individuals in Søre Vartdalselva had significantly higher predation risk compared to individuals in Aureelva. Otter predation on female pre-spawners was 11.8 % of the total female sample in Aureelva and 77.8 % of the total female sample in Søre Vartdalselva, with both populations falling below their spawning target in the study years. Without otter predation, I estimated that both Aureelva and Søre Vartdalselva would have reached 95 % of their spawning targets.

4.1 H1: Fates of tagged salmon

The first aim of this study was to evaluate how to best resolve fates of tagged salmon using radiotelemetry and temperature loggers. Locating tags on land was the most important criteria resolving fates for salmon killed by otters, which was the case for 22 of 60 tagged salmon (Figure 2). Temperature data added confidence in fates by providing time of death estimates within two hours of predation (Table 1). This aided in identifying exclusions, because four individuals in Søre Vartdalselva died less than a week after tagging. Other studies have used temperature loggers to identify predation events in fully aquatic environments by the use of core temperature differences in tagged animals and predators (e.g., Strøm *et al.,* 2019, Gallagher *et al.,* 2021). However, this is the first study to use temperature difference between river and air to identify predation by otters. Not all predation events could be identified from temperature data. Several tags recovered in the river or along the riverbank were probably jettisoned into the water by the otter, resulting in temperature data following river temperature throughout the study with no indication of predation event. This was also the case for some tags recovered on land in Søre Vartdalselva that were found in puddles. Thus, loggers recording temperature once per hour was not sufficient to detect all predation events by temperature data alone. However, more frequent registrations would have filled the logger memory too quickly to be viable for this study. Nevertheless, three tags recovered in the river contained temperature data indicating predation events, which highlights how temperature loggers in some cases can be important for discerning predation events from other natural mortality.

Stationary receiver, movement data from tracking, and mortality sensors were important tools for resolving fates of unrecovered tags or tags recovered in the river with no temperature data to indicate predation (Table 1). The stationary receiver was most important for resolving fates of salmon that left the river system (Figure 2 & 3), whereas movement data and mortality sensors identified fates for individuals that remained in the river system (note mortality sensors were only used in Søre Vartdalselva). Although movement patterns have proved to be a valuable tool for assigning fates in telemetry studies (e.g, Schwinn *et al.,* 2018, Villegas-Ríos *et al.,* 2020), movement alone does not produce as accurate estimates for time of death as temperature loggers and can be prone to misinterpretation. For instance, dead fish or tags can drift downstream and be misinterpreted as live fish (Havn *et al.,* 2017). Tagged salmon registered to leave the river system by the stationary receiver could have been dead salmon or tags drifting downstream, and their fates could not be controlled with tracking because radiotransmitter signals are lost in saltwater. There was greater confidence in the fate determination of the post-spawners that exited from Aureelva, because these individuals migrated together and it was unlikely that a large number of carcasses would float downstream undetected by locals.

There was a limitation with estimating time of death for dead salmon that had remained stationary in river pools over a longer time in Aureelva. The lack of mortality sensors in the radio-transmitters used in Aureelva made it harder to determine whether individuals in the river were dead or alive, because salmon most of the time resided stationary in pools until spawning, a behaviour known as "holding" (Thorstad *et al.,* 2008). After spawning, the same pools could have been suitable habitats for overwintering. Consequently, tags from fish that died could have remained in holding and overwintering pools so that the fate of the fish were not determined before the last tracking day (March 7th, 2021). For these salmon, time of death had to be estimated based on recent upriver movements. Although this introduces some uncertainty in time of death estimates, the more frequent tracking during the spawning period reduced uncertainty as to whether these salmon died before or after spawning, which was the main criterion used to determine fates for these salmon (Figure 2).

The mortality sensor added to the radio-transmitters in Søre Vartdalselva aided in locating dead salmon quicker and provided greater certainty in whether individuals were alive or dead during tracking. 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 salmon. The addition of the mortality sensor was therefore an effective refinement to the project protocol.

A drawback of using radiotelemetry and temperature loggers is the inability to discern among predator species. In this study, I assume that otters are the only predators killing adult salmon in the studied rivers, which likely is the case because 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 in these rivers (local observations). If a study needs to estimate the predation impact of a certain predator species in an ecosystem with several predators, one would need to inspect the carcasses for signs that can distinguish predators, such as claw marks from eagles or distinctive eating marks of otters (e.g., Cunningham *et al.*, 2002; Brodie *et al.*, 2013). I was not able to inspect predation marks, because most carcasses were gone by the time the tag was located. van Dijk *et al.* (2020) also reported that carcasses quickly disappeared, most likely due to scavenging by red fox (*Vulpes vulpes*), hooded crow, and other animals. Thus, the application of this method is limited to river systems with one predator species or several species of predators with distinguishable predation marks.

The combination of radiotelemetry, temperature loggers, and motion-based mortality sensors allowed for fate determination of 95 % (n = 57) of the total sample, while the remaining 5 % (n = 3) had unknown cause of death in Aureelva. My findings support the hypothesis that radiotelemetry and temperature loggers can be used to determine fates of adult salmon if used in combination with mortality sensors.

4.2 H2: Predator selectivity

I found no evidence to support the hypothesis that otters killed salmon selectively based on sex, length, activity level, or visually assessed health status. Selective predation may compensate or exacerbate impacts of predation. Potential positive impacts of predator selectivity include the removal of sick individuals, which can result in healthier populations (Furey *et al.,* 2021). On the other hand, otters targeting larger salmon or female salmon might impact stock recruitment more than if killing indiscriminately, because large females have the greatest reproductive output and males can spawn with multiple females (Fleming, 1996). Previous studies have suggested that male salmon are more vulnerable to otter predation because they tend to move more extensively than female salmon during the spawning period (Carss *et al.*, 1990; Cunningham *et al*., 2002). However, neither sex nor activity level were associated with predation risk in this study. Health status included visible traits (i.e., injuries, skin disease etc.) as seen during tagging and I was not able to test if otters selectively killed individuals carrying disease and parasites not detectable to the human eye. Lack of evidence for selective predation suggests that other factors than prey traits were important in determining predation risk.

River was the only explanatory variable that significantly influenced predation risk, which suggests that river characteristics might be an important determinant of predation risk of salmon. Differences in the number of holding pools might explain why individuals in Søre Vartdalselva had higher predation risk compared to individuals in Aureelva. Large holding pools provide adult salmon with better ability to escape otter attacks, which likely influences the ability of otters to select preferred prey. This is supported by findings on habitat preference by otters, which indicate that otters prefer to hunt in shallow and narrow stretches of streams that facilitates easier capture (Cho *et al.*, 2009; Almeida *et al.*, 2012). Also, findings by Sittenthaler *et al.* (2019) suggested that higher stream dimensions (i.e., discharge, depth, and width) and deep pools reduced predation risk of salmonids and prey selection by otters. Stillehølen is the only relatively large pool in Søre Vartdalselva, whereas Aureelva contains several large holding pools. Thus, the habitat in Aureelva likely is better suited for predator evasion. Because Søre Vartdalselva has fewer deep pools compared to Aureelva, one might expect selective predation in Søre Vartdalselva and not in Aureelva. However, I found no evidence for selective predation by otters, which might be explained by there being too few salmon returning to Søre Vartdalselva for otters to make a selection.

4.3 H3: Predation impact on spawning stock

Otter predation reduced the female spawning stock in Aureelva and Søre Vartdalselva, with both populations ending the season below their spawning targets. There was no evidence that otters selectively killed individuals based on visually assessed health status, which suggests the predation on female pre-spawners was a source of additive mortality. Without predation, both Aureelva and Søre Vartdalselva would have been close to reaching their spawning targets. Thus, my 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, even if there had been no otter predation, both rivers would still not have reached their spawning targets. Thus, factors other than otters have also reduced the spawning stock in Aureelva and Søre Vartdalselva.

The magnitude of predation-induced mortality on the female spawning stock was low in Aureelva compared to Søre Vartdalselva. The large number 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 between 5 and 10 % of available females, a proportion similar to the predation level found in Aureelva. Therefore, the otter predation of spawners in Søre Vartdalselva represents the highest reported predation mortality on adult salmon by otters measured in the literature. The low predation mortality reported in previous studies compared to this could be due to differences in methodologies. 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 as reported by van Dijk *et al.* (2020).

Density-dependent mechanisms such as resource limitations (e.g., shelter from predators, food) restrict the survival of salmon juveniles for populations that are near or above the spawning target of a river (Jonsson *et al*., 1998). Populations reduced well below their spawning target have greater growth potential than populations near their spawning target, because juveniles produced will experience less competition and have more resources available, thereby increasing individual survival. Thus, predation has a larger impact on stock recruitment in populations far below their spawning target compared to populations close to their spawning target. Because Aureelva was close to its spawning target with 84 % attainment, predation on female pre-spawners likely affected stock recruitment less than in Søre Vartdalselva, which only had 21 % attainment of spawning target. Also, otters killed a small proportion of pre-spawners in Aureelva. Thus, otter predation likely had a modest impact on recruitment in Aureelva. This is supported by previous findings in Aureelva, where there was no evidence of decrease in salmon fry densities following a year with a high number of salmon carcasses from otter kills found along the river (Hellen 2014; Kambestad 2016; Kambestad *et al.,* 2021; Kambestad pers. comm.).

4.4 Methodological issues and limitations

There is always a possibility that handling and tagging influences predation risk so that tagged salmon do not represent untagged conspecifics. Excluding individuals that died within a week of tagging reduced the risk of short-term handling and tagging effects. However, long-term effects from handling and tagging could have influenced behaviour and predation risk of individuals. Stress induced by handling and tagging can cause salmon to make downstream movements, delay migration, or even abandon upriver migration (Mäkinen *et al.,* 2000; Havn *et al*., 2015). The six pre-spawners that left Søre Vartdalselva prior to spawning, two of which later returned, could have left due to handling or tagging effects. Another possibility is that the salmon originated from a different river and strayed into Søre Vartdalselva, which could explain why four individuals did not return to Søre Vartdalselva. The pre-spawners that left permanently were accounted for in the analysis of predator selectivity (H2) by registering their death as later than their last tracking day (i.e., right-censoring) and were excluded from the analysis of predator impact on spawning stock (H3). Thus, the pre-spawners that left permanently did not influence the data analysis. The individuals who remained in the study system could have had greater predation risk than conspecifics due to long-term handling and tagging effects. However, Thorstad *et al.* (2000) found that tagging adult Atlantic salmon with body-implanted radio transmitters did not influence swimming performance or blood physiology of tagged salmon. Thus, the predation mortality reported in this study is likely a representative estimate.

After potential tagging-effect deaths were excluded, the remaining sample included 28 salmon in Aureelva and 25 salmon in Søre Vartdalselva. Small sample sizes can make it difficult to transfer findings from sample to population level and challenges analysts to identify small effect sizes in data. During the spawning period, 139 salmon were counted in Aureelva (NINA, 2022) and 41 salmon were counted in Søre Vartdalselva (Hanssen *et al.*, in prep.). Thus, my sample likely represented a substantial proportion of the populations, providing valuable insights into the mechanisms of predation by otters on the salmon populations in these rivers.

This study investigated predation on the populations of Aureelva and Søre Vartdalselva during one spawning period, which makes it hard to conclude if the predation mortality represents a general pattern that can be extrapolated to other years and river systems. Multiple factors can influence capture success and predation levels of otters, consequently predation mortality can vary between years. For instance, Martínez-Abraín *et al.* (2019) found that otters had greater hunting success in a dry year compared to a year with standard amounts of rainfall, which suggests that fish are easier to capture when water levels are low. Thus, rainfall and water level can influence estimates of predation mortality. Temporal differences in weather could have influenced the difference in predation levels between Aureelva and Søre Vartdalselva, which were sampled in different years.

4.5 Future research

Atlantic salmon are iteroparous and can return to rivers to spawn multiple times (Niemelä *et al.*, 2006). Predation can therefore impact this life-history trait, i.e. the number of times a salmon can spawn. Repeat spawners often have a larger average body size and thus contribute more eggs in stock recruitment compared to a first-time spawner (Ward & Hvidsten, 2011). Some post-spawners killed by otters could have returned during subsequent years to spawn, thus the predation could have impacted long-time recruitment. However, post-spawning survival at sea is low and often less than 10 % of the spawning stock returns to spawn again (Fleming, 1996). Nevertheless, the number of repeat spawners can vary greatly between rivers and years (Niemelä *et al.*, 2006; Reid & Chaput, 2006). Future studies should therefore investigate the importance of repeat-spawners in rivers with otter predation.

Habitat can be an important driver of salmon predation risk by otters. Previous studies suggest that certain habitat typologies of rivers, such as deep pools, provide opportunity for predator refuge for adult salmon (Day *et al.*, 2015; Sittenthaler *et al.,* 2019). Thus, salmon in rivers with fewer large pools, such as Søre Vartdalselva, might have a greater predation risk than others. Identifying how habitat types influence predation risk can aid management in identifying salmon populations more vulnerable to impacts of otter predation. Habitat types can also influence the ability of otters to select preferred prey. Selective predation can compensate (e.g., removal of sick individuals) or exacerbate impacts of otter predation (e.g., kill larger female salmon) (Fleming, 1996; Furey *et al*., 2021). Thus, future studies should study the magnitude and pattern of otter predation in different habitat types of several rivers.

The shape of an otter`s functional response, i.e., how predation behaviour of an individual otter changes with abundance of salmon, has important implications. For instance, whether otters switch to other prey at low salmon densities, termed a type III functional response, or still prey opportunistically on salmon, termed a type II functional response (Ward & Hvidsten, 2011). The type II functional response will have a greater impact on salmon population dynamics than the type III functional response, because at low densities the proportion of salmon killed per otter will be larger than at high salmon densities. The functional response of otters likely depends on the availability of other prey species in the river system and nearby coastal areas (Smout *et al.*, 2010). Kleptoparasitism may also influence the functional response of otters. For instance, sea eagles are known to steal salmon from otters (van Dijk *et al*., 2020), thus otters may have to kill more salmon. Therefore, future studies should consider impacts of otter predation in a community context.

The abundance of otters may impact the predation on salmon. There is little information on the density of otters near Norwegian rivers and how this may vary between years or seasons. It is important to know whether otter populations are affected by decreases in salmon abundances, i.e., the numerical response. If otter populations do not respond to changes in salmon abundances, predation rate can remain high at low salmon densities. Generalist predators, such as otters, may be less affected by changes in one prey species because they can feed on other prey items (Ruiz-Olmo *et al.,* 2009). Thus, opportunistic predation on salmon at low densities can maintain salmon populations at low-density equilibriums known as a predation pit, which can repress recovery (Smouth *et al.*, 2010). Therefore, future studies should investigate the density of otters near rivers with salmon by faecal analysis, camera traps, and tracking otters using telemetry**.**

4.6 Management implications

As otters in Norway continue to recover from overexploitation and expand their range into new rivers (van Dijk *et al.,* 2021), conflicts between otter predation and conservation of salmon are likely to become an increasing problem for management. As observed in this study, impacts of predation can vary greatly between rivers, which emphasises the importance of river-specific assessments to evaluate impacts of otter predation on salmon populations. The method of radiotelemetry and temperature loggers refined in this study can be used to quantify predation on pre-spawners. Evidence of impacts of predation can guide management decisions to resolve local predator-human conflicts. If predation mortality is additive, short-term removal of predators might aid in recovery for salmon populations that are maintained at low densities due to predation (i.e., known as a predator pit). However, otters are parts of complex food webs and attempts to remove them might have unexpected outcomes through indirect effects, such as potential meso-predator release of mink (Guidos, 2019). Removing otters from established territories can open up for immigration of several new individuals (Erlinge, 1968), which can increase predation until territories are claimed by new otters. Thus, predator-removal is likely only beneficial for short-term recovery to increase salmon abundance to a level where predation impact is negligible, but may not have lasting benefits on the salmon population size.

Although predation is a major driver of mortality, data on predation mortality used in stock assessments are scarce (Hindar *et al.,* 2007; 2019). Thus, estimates of natural mortality of adult salmon in rivers might not hold true as predators, such as otters, increase in abundance due to conservation. As otters recolonise rivers, natural mortality included in stock assessments should reflect the increase in predation mortality, which likely is different depending on how long otters have been present (i.e., as otters establish territories; Erlinge, 1968). Underestimating the magnitude of predation mortality within natural mortality can lead to stock estimates that are overly optimistic (Tyrrell *et al.*, 2011). By avoiding overly optimistic estimates of spawning target attainment, correct assessment of predation mortality can be used to reduce the risk of overharvesting.

5. Conclusion

This study aimed to provide insight into patterns and impacts of otter predation on the spawning salmon populations in two rivers in Norway. This is the first study to utilise radiotelemetry in combination with temperature loggers to identify predation events and infer fates. I found this method to be well suited to determine the fates of tagged salmon. Adding mortality sensors increased confidence in whether tracked individuals were alive or dead, and allowed for quicker location of dead salmon. There was no evidence for selective predation on salmon by otters, however only sex, length, activity, and visually assessed health status of salmon were included in the model and I could not test if otters preferentially killed individuals carrying diseases that were not evident by external examination. At the present sample size, only large effect sizes could be expected to be detected by the model, so we cannot exclude the possibility that further studies will reveal more evidence of selection. Lack of evidence for selective predation suggests that predation on pre-spawners was a source of additive mortality, killing individuals that would otherwise have spawned and reducing both populations' spawning stock, egg deposition, and progress towards meeting the spawning target. If there had been no otter predation, both Aureelva and Søre Vartdalselva would have been closer to reaching their spawning targets. However, the magnitude of predation impact on salmon varied greatly between the two rivers, and individuals in Søre Vartdalselva had greater predation risk compared to Aureelva. The difference in predation risk might be due to habitat types, such as availability of deep holding pools, which are better suited for predator refuge for adult salmon (Sittenthaler *et al.,* 2019). This study highlights the need for river-specific studies to assess the impacts of otter predation on salmon populations. The tools refined in this study can provide management with a method for estimating predation mortality, which can aid in reducing risk of overharvesting

6. References

Advanced Telemetry Systems. (2022). *Select a Program for Your Transmitters.* atstrack. https://atstrack.com/customer-support/how-to-select-a-program-for-your-transmitter.html

Almeida, Barrientos, R., Merino-Aguirre, R., & Angeler, D. G. (2012). The role of prey abundance and flow regulation in the marking behaviour of Eurasian otters in a Mediterranean catchment. *Animal Behaviour*, *84*(6), 1475–1482. https://doi.org/10.1016/j.anbehav.2012.09.020

Anderson-Bergman C (2017). "icenReg: Regression Models for Interval Censored Data in R." _Journal of Statistical Software_, *81*(12), 1-23. doi: 10.18637/jss.v081.i12 (URL: https://doi.org/10.18637/jss.v081.i12).

Artsdatabanken (2021, 24. november). Norsk rødliste for arter 2021. https://www.artsdatabanken.no/lister/rodlisteforarter/2021

Bardonnet, A., & Baglinière, J. L. (2000). Freshwater habitat of Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(2), 497-506.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of animal ecology*, *78*(4), 699-714.

Berger, J., Stacey, P. B., Bellis, L., & Johnson, M. P. (2001). A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications*, *11*(4), 947-960.

Bevanger K (2015). Brunbjørn Ursus arctos Linnaeus, 1758. www.artsdatabanken.no/Pages/180928. Downloaded 03.04.2022.

Bivand, B. & Colin Rundel, C. (2021). rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.5-9. https://CRAN.R-project.org/package=rgeos

Bradburn, M. J., Clark, T. G., Love, S. B., & Altman, D. G. (2003). Survival analysis part II: multivariate data analysis–an introduction to concepts and methods. *British journal of cancer*, *89*(3), 431-436.

Brodie, J., Johnson, H., Mitchell, M., Zager, P., Proffitt, K., Hebblewhite, M., ... & White, P. J. (2013). Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. *Journal of Applied Ecology*, *50*(2), 295-305.

Brown, R. S., Eppard, M. B., Murchie, K. J., Nielsen, J. L., & Cooke, S. J. (2011). An introduction to the practical and ethical perspectives on the need to advance and standardize the intracoelomic surgical implantation of electronic tags in fish. *Reviews in Fish Biology and Fisheries*, *21*(1), 1-9.

Carss, D. N., Kruuk, H., & Conroy, J. W. H. (1990). Predation on adult Atlantic salmon, Salmo salar L., by otters, Lutra lutra (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology*, *37*(6), 935-944.

Chaput, G., & Jones, R. A. (2006). Reproductive rates and rebuilding potential for two multi-sea-winter Atlantic salmon (Salmo salar L.) stocks of the Maritime provinces. Moncton, New Brunswick: Fisheries and Oceans Canada, Science.

Cho, H. S., Choi, K. H., Lee, S. D., & Park, Y. S. (2009). Characterizing habitat preference of Eurasian river otter (Lutra lutra) in streams using a self-organizing map. *Limnology*, *10*(3), 203-213.

Clark, T. G., Bradburn, M. J., Love, S. B., & Altman, D. G. (2003). Survival analysis part I: basic concepts and first analyses. *British journal of cancer*, *89*(2), 232-238.

Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, *34*(2), 187-202.

Cunjak, R. A., Prowse, T. D., & Parrish, D. L. (1998). Atlantic salmon (Salmo salar) in winter:" the season of parr discontent"?. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 161-180.

Cunningham, P. D., Brown, L. J., & Harwood, A. J. (2002). Predation and scavenging of salmon carcasses along spawning streams in the Scottish Highlands. Final report for the Atlantic Salmon Trust, 3-6.

Day CC, Westover MD, Mcmillan BR. 2015. Seasonal diet of the northern river otter (*Lontra canadensis*): what drives prey selection? *Can J Zool* 93: 197–205.

Erlinge, S. (1968). Territoriality of the otter Lutra lutra L. Oikos, 81-98.

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in fish biology and fisheries, 6(4), 379-416.

Forseth, T., Fiske, P., Barlaup, B., Gjøsæter, H., Hindar, K., & Diserud, O. H. (2013). Reference point based management of Norwegian Atlantic salmon populations. *Environmental conservation*, *40*(4), 356-366.

Furey, N. B., Bass, A. L., Miller, K. M., Li, S., Lotto, A. G., Healy, S. J., ... & Hinch, S. G. (2021). Infected juvenile salmon can experience increased predation during freshwater migration. Royal Society open science, 8(3), 201522.

Gallagher, C. P., Storrie, L., Courtney, M. B., Howland, K. L., Lea, E. V., MacPhee, S., & Loseto, L. (2021). Predation of archival tagged Dolly Varden, Salvelinus malma, reveals predator avoidance behaviour and tracks feeding events by presumed beluga whale, Delphinapterus leucas, in the Beaufort Sea. *Animal Biotelemetry*, *9*(1), 1-17.

Gibson, A. J. F., Halfyard, E. A., Bradford, R. G., Stokesbury, M. J., & Redden, A. M. (2015). Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Canadian Journal of Fisheries and Aquatic Sciences, 72(5), 728-741.

Guidos, S. A. (2019). *Interactions between Eurasian otters (Lutra lutra) and American mink (Neovison vison) in western Norway: A camera trap study over space and time* (Master's thesis, The University of Bergen).

Hanssen, E. M., Wiers, T., Normann, E. S., Landro, Y., & Kambestad, M. (in prep.). Bestandsovervåking av laks og sjøørret i elver på Sunnmøre høsten 2021. NORCE LFI, technical report.

Havn, T. B., Uglem, I., Solem, Ø., Cooke, S. J., Whoriskey, F. G., & Thorstad, E. B. (2015). The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon Salmo salar during spawning migration. Journal of Fish Biology, 87(2), 342-359.

Havn, T. B., Økland, F., Teichert, M. A., Heermann, L., Borcherding, J., Sæther, S. A., ... & Thorstad, E. B. (2017). Movements of dead fish in rivers. *Animal Biotelemetry*, *5*(1), 1-9.

Hellen, B.A. 2014. Fiskebiologiske undersøkelser i Aureelva, Sykkylven 2013. Rådgivende Biologer AS, rapport 1851, 23 s.

Hijmans, R.J. (2021). raster: Geographic Data Analysis and Modeling. R package version 3.4-13.https://CRAN.R-project.org/package=raster

Hindar, K., Diserud, O., Fiske, P., Forseth, T., Jensen, A. J., Ugedal, O., Jonsson, N., Sloreid, S.-E., Arnekleiv, J. V., Saltveit, S. J., Sægrov, H. & Sættem, L. M. 2007 Gytebestandsmål for laksebestander i Norge. - NINA Rapport 226. 78 s.

Hindar, K., Diserud, O.H., Hedger, R.D., Finstad, A.G., Fiske, P., Foldvik, A., Forseth, T., Forsgren, E., Kvingedal, E., Robertsen, G., Solem, Ø., Sundt-Hansen, L.E. & Ugedal, O. 2019. Vurdering av metodikk for andregenerasjons gytebestandsmål for norske laksebestander. NINA Rapport 1303. Norsk institutt for naturforskning.

Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon Salmo salar. *Journal of Animal Ecology*, *67*(5), 751-762.

Kambestad, M. 2016. Ungfiskundersøkelse i Aureelva i oktober 2016. Rådgivende Biologer AS, notat, 4 s.

Kambestad, M., Hanssen, E.M., Wiers, T., Postler C., & Normann, E.S., 2021. Bestandsovervåking av laks og sjøørret i elver på Sunnmøre høsten 2020. NORCE, LFI rapport 417, 105 sider, ISSN 2535-6623.

Kuijper, D. P. J., De Kleine, C., Churski, M., Van Hooft, P., Bubnicki, J., & Jędrzejewska, B. (2013). Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography*, *36*(12), 1263-1275.

Lee, H. H., Maunder, M. N., Piner, K. R., & Methot, R. D. (2011). Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. *Fisheries Research*, *109*(1), 89-94.

Mäkinen, T. S., Niemelä, E., Moen, K., & Lindström, R. (2000). Behaviour of gill-net and rod-captured Atlantic salmon (Salmo salar L.) during upstream migration and following radio tagging. Fisheries Research, 45(2), 117-127.

Marshall, K. N., Stier, A. C., Samhouri, J. F., Kelly, R. P., & Ward, E. J. (2016). Conservation challenges of predator recovery. Conservation Letters, 9(1), 70-78.

Martínez-Abraín, A., Santidrián Tomillo, P., & Veiga, J. (2020). Otter diet changes in a reservoir during a severe autumn drought. *Journal of Mammalogy*, *101*(1), 211-215.

Niemelä, E., Erkinaro, J., Julkunen, M., Hassinen, E., Länsman, M., & Brørs, S. (2006). Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. *Journal of Fish Biology*, *68*(4), 1222-1240.

NINA. (2022). Overvåkning av gytebestander av laks og sjøørret. NINA. https://bestand.nina.no/#/

Payton, Q., Evans, A. F., Hostetter, N. J., Roby, D. D., Cramer, B., & Collis, K. (2020). Measuring the additive effects of predation on prey survival across spatial scales. *Ecological Applications*, *30*(8), e02193.

Pebesma, E.J., R.S. Bivand, 2005. Classes and methods for spatial data in R. R News 5 (2), https://cran.r-project.org/doc/Rnews/.

Raby, G. D., Packer, J. R., Danylchuk, A. J., & Cooke, S. J. (2014). The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish and Fisheries*, *15*(3), 489-505.

Reid, J. E., & Chaput, G. (2012). Spawning history influence on fecundity, egg size, and egg survival of Atlantic salmon (Salmo salar) from the Miramichi River, New Brunswick, Canada. *ICES Journal of Marine Science*, *69*(9), 1678-1685.

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G., & McDonald, R. A. (2012). Ecosystem restoration with teeth: what role for predators?. *Trends in ecology & evolution*, *27*(5), 265-271.

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology letters*, *12*(9), 982-998.

Robinson, M. L., Gomez-Raya, L., Rauw, W. M., & Peacock, M. M. (2008). Fulton's body condition factor K correlates with survival time in a thermal challenge experiment in juvenile Lahontan cutthroat trout (Oncorhynchus clarki henshawi). *Journal of Thermal Biology*, *33*(6), 363-368.

RStudio Team (2021). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Ruiz-Olmo, J., & Jiménez, J. (2009). Diet diversity and breeding of top predators are determined by habitat stability and structure: a case study with the Eurasian otter (Lutra lutra L.). *European Journal of Wildlife Research*, *55*(2), 133-144.

Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg, A., & Crowley, J. (2021). GGally: Extension to 'ggplot2'. R package version 2.1.2. https://CRAN.R-project.org/package=GGally

Schwinn, M., Baktoft, H., Aarestrup, K., Lucas, M. C., & Koed, A. (2018). Telemetry observations of predation and migration behaviour of brown trout (Salmo trutta) smolts negotiating an artificial lake. *River research and applications*, *34*(8), 898-906.

Sittenthaler, M., Koskoff, L., Pinter, K., Nopp-Mayr, U., Parz-Gollner, R., & Hackländer, K. (2019). Fish size selection and diet composition of Eurasian otters (Lutra lutra) in salmonid streams: Picky gourmets rather than opportunists?. *Knowledge & Management of Aquatic Ecosystems*, (420), 29.

Smircich, M. G., & Kelly, J. T. (2014). Extending the 2% rule: the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. *Animal Biotelemetry*, *2*(1), 1-7.

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. PloS one, 5(5), e10761.

Strøm, J. F., Rikardsen, A. H., Campana, S. E., Righton, D., Carr, J., Aarestrup, K., ... & Thorstad, E. B. (2019). Ocean predation and mortality of adult Atlantic salmon. *Scientific reports*, *9*(1), 1-11.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., ... & Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. Science, 294(5548), 1923-1926.

Thirgood, S., Redpath, S., Newton, I., & Hudson, P. (2000). Raptors and red grouse: conservation conflicts and management solutions. Conservation Biology, 14(1), 95-104.

Thirgood, S., Woodroffe, R., Rabinowitz, Al. (2005). The impact of human-wildlife conflict on human. People and wildlife, conflict or co-existence?, 9, 13.

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M., ... & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(9), 2654-2665.

Thorstad, E. B., Økland, F., Aarestrup, K., & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, *18*(4), 345-371.

Thorstad, E. B., Økland, F., & Finstad, B. (2000). Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. Journal of fish biology, 57(2), 531-535.

Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation biology, 17(6), 1491-1499.

Tyrrell, M. C., Link, J. S., & Moustahfid, H. (2011). The importance of including predation in fish population models: implications for biological reference points. *Fisheries Research*, *108*(1), 1-8.

van Dijk, J., Kambestad, M., Carss, D.C. & Hamre, Ø. 2020. Kartlegging av oterens effekt på bestander av laks og sjøørret – Sunnmøre. NINA Rapport 1780. Norsk institutt for naturforskning

van Dijk, J., Sægrov, H. Fjellstad Israelsen, M., & Rosvold, J. 2021. Bestandsutvikling for oter, laks og sjøørret ut fra historiske data på Sunnmøre. NINA Rapport 1982. Norsk institutt for naturforskning

van Etten, J. (2017). R package gdistance: Distances and routes on geographical grids. Journal of Statistical Software, 76(1), 1–21. https://doi.org/10.18637/jss.v076.i13

Villegas-Ríos, D., Freitas, C., Moland, E., Thorbjørnsen, S. H., & Olsen, E. M. (2020). Inferring individual fate from aquatic acoustic telemetry data. *Methods in Ecology and Evolution*, *11*(10), 1186-1198.

Vitenskapelig råd for lakseforvaltning 2021. Status for norske laksebestander i 2021. Rapport fra Vitenskapelig råd for lakseforvaltning nr 16, 227 s.

Vitenskapelig Råd for Lakseforvaltning (VRL). (2022a). Status for norske laksebestander. Vitenskapsradet. https://www.vitenskapsradet.no/VurderingAvEnkeltbestander/#/report/84

Vitenskapelig Råd for Lakseforvaltning (VRL). (2022b). Status for norske laksebestander. Vitenskapsradet. https://vitenskapsradet.no/VurderingAvEnkeltbestander/#/report/78

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

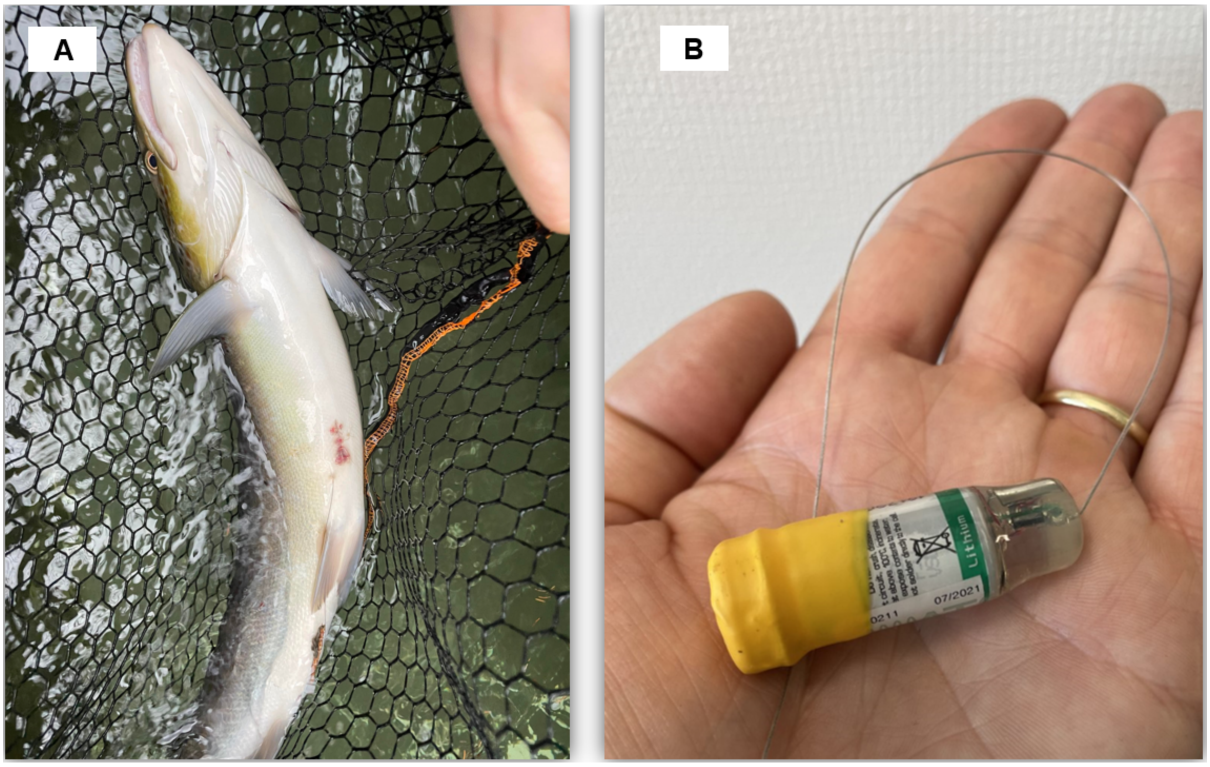
Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019). "Welcome to the tidyverse." *Journal of Open Source Software*, **4**(43), 1686. doi: 10.21105/joss.01686.

Wickham, H., François, R., Henry, L., and Müller, K. (2021). dplyr: A Grammar of Data Manipulation. R package version 1.0.7. https://CRAN.R-project.org/package=dplyr.

Wilson, A. D., Hayden, T. A., Vandergoot, C. S., Kraus, R. T., Dettmers, J. M., Cooke, S. J., & Krueger, C. C. (2017). Do intracoelomic telemetry transmitters alter the post-release behaviour of migratory fish?. *Ecology of Freshwater Fish*, *26*(2), 292-300.

7. Appendices

Appendix 1:



Appendix 1: A: Tagged salmon seen from ventral side with antennae trailing posterior to incision. B: Temperature logger glued onto radiotransmitter (white) using plastidip (yellow).

Appendix 2:

Appendix 2: Relevant information on the 30 tagged salmon in Aureelva and 30 tagged salmon in Søre Vartdalselva. "Salmon ID" is the identification of each fish, "River" is where tagged salmon came from, "Tag date" is date of tagging, "TL" is total length in mm, "Sex" is either male or female based on visual assessment, "left" and "right" is lower and upper limit of survival time interval, "Health status" is visually assessed health status based on observations during tagging ("Comment health status").

Salmon ID	River	Tag date	TL (mm)	Sex	Fate	left	right	Health status	Comment health status
092-9	Aureelva	03.09.2020	810	Female	Unknown	90	143	Perfect	Minor scratches
044-9	Aureelva	03.09.2020	630	Male	Post-spawner sea	81	Inf	Perfect	Scratches on head
083-75	Aureelva	03.09.2020	740	Female	Tagging	2	12	Imperfect	Larvae on gills
024-9	Aureelva	03.09.2020	800	Female	Post-spawner sea	76	Inf	Perfect	
092-75	Aureelva	03.09.2020	540	Female	Otter	73	90	Perfect	
013-11	Aureelva	03.09.2020	600	Male	Post-spawner sea	106	Inf	Imperfect	Big claw marks
013-13	Aureelva	03.09.2020	750	Female	Otter	60	60	Perfect	
024-11	Aureelva	03.09.2020	550	Male	Lake	185	Inf	Imperfect	Gill parasite
072-75	Aureelva	03.09.2020	530	Male	Otter	79	79	Perfect	

052-13	Aureelva	03.09.2020	530	Male	Lake	185	Inf	Perfect	
092-8	Aureelva	03.09.2020	760	Female	Post-spawner sea	74	Inf	Perfect	
052-8	Aureelva	03.09.2020	750	Female	Post-spawner sea	76	Inf	Imperfect	Fresh bite wounds. Gill parasites.
062-11	Aureelva	03.09.2020	510	Male	Post-spawner sea	76	Inf	Perfect	
083-13	Aureelva	03.09.2020	600	Male	Otter	30	30	Perfect	
003-13	Aureelva	03.09.2020	730	Female	Post-spawner sea	80	Inf	Imperfect	Gill parasites
013-8	Aureelva	03.09.2020	530	Female	Unknown	90	143	Perfect	
072-9	Aureelva	03.09.2020	570	Female	Post-spawner sea	94	Inf	Imperfect	Bite mark tail
083-11	Aureelva	03.09.2020	710	Female	Post-spawner sea	79	Inf	Imperfect	Scar after hook on mouth. Gill parasites.
034-75	Aureelva	03.09.2020	690	Female	Post-spawner sea	77	Inf	Imperfect	Scratch marks. Open wound on ventral side.

003-9	Aureelva	03.09.2020	670	Female	Post-spawner sea	76	Inf	Imperfect	Lots of gill parasites
083-9	Aureelva	03.09.2020	710	Female	Post-spawner sea	76	Inf	Imperfect	Lots of gill parasites
052-11	Aureelva	03.09.2020	740	Female	Post-spawner sea	75	Inf	Perfect	Minor scratches
062-9	Aureelva	03.09.2020	510	Female	Otter	13	25	Perfect	Minor scratches on head
034-8	Aureelva	03.09.2020	550	Male	Otter	123	123	Imperfect	Gill parasites
092-11	Aureelva	03.09.2020	565	Female	Post-spawner sea	79	Inf	Imperfect	Gill parasites
024-13	Aureelva	03.09.2020	560	Male	Otter	34	34	Perfect	
034-11	Aureelva	03.09.2020	760	Male	Otter	73	73	Perfect	
072-8	Aureelva	03.09.2020	530	Female	Unknown	68	73	Imperfect	Gill parasites. Open wound. Bitten lower cuddle fin. Scale loss. sea sealice scars.
003-8	Aureelva	03.09.2020	610	Male	Tagging	3	3	Perfect	Scratches on the side.
003-75	Aureelva	03.09.2020	800	Male	Otter	76	76	Perfect	Fin fray lower cuddle.

033-14	Søre Vartdalselva	05.08.2021	583	Male	Otter	22	31	Perfect	Scrapemarks
062-75	Søre Vartdalselva	05.08.2021	774	Female	Pre-spawner sea	22	Inf	Perfect	Held in air for a while during capture in sling with no water
083-14	Søre Vartdalselva	05.08.2021	855	Female	Otter	77	84	Imperfect	Otter bite damage (open flesh wound) + Went out of water at the end of the operation
014-14	Søre Vartdalselva	05.08.2021	612	Male	Pre-spawner sea	14	Inf	Imperfect	Fungus on operculum + Kicked during gill sampling collection, stabbed in gill
003-12	Søre Vartdalselva	06.08.2021	748	Female	Otter	21	30	Imperfect	Scars below pelvic fin
092-14	Søre Vartdalselva	06.08.2021	502	Male	Pre-spawner sea	16	Inf	Perfect	
072-9	Søre Vartdalselva	06.08.2021	621	Male	Otter	30	41	Imperfect	Damage to right eye

092-9	Søre Vartdalselva	06.08.2021	544	Female	Otter	21	21	Imperfect	Red marks, looks like skin infection
062-14	Søre Vartdalselva	06.08.2021	661	Male	Otter	89	89	Imperfect	Bite marks
052-9	Søre Vartdalselva	06.08.2021	705	Male	Otter	78	78	Imperfect	Missing its right pectoral fin
044-9	Søre Vartdalselva	06.08.2021	574	Female	Otter	85	85	Perfect	Kicked into scalpel so it stapped itself during incision on ventral side
062-8	Søre Vartdalselva	06.08.2021	649	Male	Otter	21	30	Perfect	Scratches
103-14	Søre Vartdalselva	06.08.2021	589	Male	Otter	20	20	Perfect	Peduncle scar
072-14	Søre Vartdalselva	06.08.2021	606	Male	Pre-spawner sea	17	Inf	Perfect	
014-9	Søre Vartdalselva	15.08.2021	555	Female	Tagging	6	6	Perfect	
044-8	Søre Vartdalselva	15.08.2021	695	Female	Otter	12	21	Perfect	

052-8	Søre Vartdalselva	17.08.2021	640	Male	Otter	19	30	Perfect	Some scratches
003-9	Søre Vartdalselva	17.08.2021	675	Male	Otter	62	62	Imperfect	Two extra sutures, blurry eye
083-12	Søre Vartdalselva	17.08.2021	570	Male	Otter	10	10	Perfect	Some scratches
014-8	Søre Vartdalselva	17.08.2021	573	Male	Otter	61	61	Perfect	
033-8	Søre Vartdalselva	17.08.2021	816	Female	Otter	65	77	Perfect	
052-14	Søre Vartdalselva	18.08.2021	796	Female	Otter	82	82	Perfect	Scratches on side
033-12	Søre Vartdalselva	18.08.2021	603	Female	Tagging	5	5	Imperfect	Bite and scratches + Sutures less than ideal
014-12	Søre Vartdalselva	18.08.2021	750	Female	Tagging	2	2	Imperfect	Big lice wounds near tail
092-12	Søre Vartdalselva	18.08.2021	890	Female	Otter	9	9	Perfect	Some scratches
072-12	Søre Vartdalselva	18.08.2021	680	Male	Otter	77	77	Perfect	

062-9	Søre Vartdalselva	18.08.2021	640	Male	Otter	13	13	Perfect	
072-8	Søre Vartdalselva	18.08.2021	530	Male	Tagging	3	3	Perfect	
024-9	Søre Vartdalselva	28.08.2021	769	Female	Post-spawner sea	73	Inf	Perfect	"Slight snout damage, split breast fins and chewed anal find"
024-12	Søre Vartdalselva	22.08.2021	535	Male	Tagging	7	7	Imperfect	Redness, skinny

Appendix 3:

Appendix 3: This appendix includes the main code used to produce figures and model testing in Rstudio.

```
#Hypothesis 1: Fates of tagged salmon.
Survival <- read.csv("C:/Users/bruker/OneDrive/Masteroppgave/Feltdata/Survival.csv",
sep=";")

#Figure 3:
Survival %>%
  dplyr::filter(Fate=="Lake"| Fate=="Post-spawner sea"| Fate=="Pre-spawner sea"|
Fate=="Otter"|Fate== "Unknown") %>%
  group_by(Spawned, River, Fate) %>%
  summarize(n=n()) %>%
  ggplot(aes(Fate, n, fill=Spawned))+
```

```
  geom_col(position="stack") +
  scale_y_continuous(breaks=c(0,2,4,6,8,10,12,14,16,18,20),
labels=c(0,2,4,6,8,10,12,14,16,18,20))+
  ylab("Number of tagged salmon") +
  facet_wrap(~River)+
  scale_fill_manual(values=c(
    "violet","steelblue")) + #Green then blue
  theme_bw()+
  theme(text=element_text(size=18))+
  theme(axis.text.x = element_text(size = 9.5, hjust = .5, vjust = .5))+
  scale_x_discrete(labels=c("Overwintering\n kelt", "Otter kill", "Post-spawners\n left to sea",
"Pre-spawners\n left to sea", "Unknown\n cause of death"))




#Code to produce Figure 4:
#Code to plot temperature in river and on land for Aureelva:

p02413 <- aur %>%
  dplyr::filter(Freq.id=="024-13") %>% #Change Freq-id for different salmon
  dplyr::filter(lubridate::month(dt)==10, #Change month and day to zoom in
              lubridate::day(dt)==7|lubridate::day(dt)==8) %>%
  group_by(Freq.id) %>%
  arrange(dt) %>%
  ggplot(aes(dt, temp))+
  geom_line(colour="#B8DE29FF", size=1)+ ##B8DE29FF for fishes
  scale_colour_viridis_c() +
  geom_line(data=Land %>%
            mutate(dt=lubridate::ymd_hms(paste(Date, Time))) %>%
            dplyr::filter(lubridate::month(dt)==10,
                   lubridate::day(dt)==7|lubridate::day(dt)==8),
          aes(dt,Temperature),
          inherit.aes=F, size=1)+
```

```
  geom_line(data=Elv %>%
            mutate(dt=lubridate::ymd_hms(paste(Date, Time))) %>%
            dplyr::filter(lubridate::month(dt)==10,
                          lubridate::day(dt)==7|lubridate::day(dt)==8),
          aes(dt,Temperature),
          inherit.aes=F, colour="#2d708EFF", size=1)+
  labs(x="Date",y="Temperature")+
  theme_bw()+
  theme(text=element_text(size=18))

#Søre Vartdalselva:
p148 <- tempvart %>%
  dplyr::filter(Freq.id=="062-14"|Freq.id=="072-12"|Freq.id=="052-14"|Freq.id=="014-8")
%>%
  dplyr::filter(lubridate::month(dt)==10,
              lubridate::day(dt)==17|lubridate::day(dt)==18) %>%
  group_by(Freq.id) %>%
  arrange(dt) %>%
  ggplot(aes(dt, temp, colour=Freq.id)) +
  geom_line(size=1) +
  geom_line(data=Landsv %>%
            rename(dt=Dato) %>% #new name = old name
            mutate(dt=paste(dt, klokke, sep=" ")) %>%
            mutate(temp=gsub(",", ".", temp)) %>% #replacing the commas with dot
            mutate(dt=lubridate::dmy_hms(dt)) %>%
            dplyr::filter(lubridate::month(dt)==10,
                          lubridate::day(dt)==17|lubridate::day(dt)==18) %>%
            mutate(temp=as.numeric(temp)) %>%
            dplyr::select(-klokke),
          aes(dt,temp),
          inherit.aes=F, colour="black", size=1)+ #Landtemp is black
  labs(x="Date",y="Temperature")+
  scale_color_manual(values=c("#B8DE29FF", "#fde725", "#1f9e89", "#440154"))+ #Green
first, yellow, blue, purple
```

```
  theme_bw()+
  theme(legend.position = "none")+
  theme(text=element_text(size=18))

#The four example plots were combined using cowplot:
plot_grid(p00375, p02413, p148, p529, labels = c('A', 'B', 'C','D'), label_size = 12)



#H2: Predator selectivity


#Figure 5:
#Fitting non-parametric estimator (NPMLE) for each group (river):
np_fit <- ic_np(cbind(left, right)~River, data=Survival)

np_fit$scurves$Aureelva$S_curves %>%
  as_tibble %>%
  ggplot(aes(1:nrow(.), baseline))+
  geom_line()+
  geom_line(data=np_fit$scurves$`Søre Vartdalselva`$S_curves %>%
               as_tibble,
             aes(1:15, baseline), colour="red")

scurve<-np_fit$scurves$Aureelva$Tbull_ints %>%
  as_tibble %>%
  bind_cols(np_fit$scurves$Aureelva$S_curves) %>%
  mutate(r="Aurelva") %>%
  bind_rows(np_fit$scurves$'Søre Vartdalselva'$Tbull_ints %>%
               as_tibble %>%
               bind_cols(np_fit$scurves$'Søre Vartdalselva'$S_curves) %>%
               mutate(r="Søre Vartdalselva"))

#Survival curve based on Turnbull intervals extracted from the np_fit.
scurve %>% mutate(lower=case_when(lower==185~190, T~lower)) %>%
  ggplot(aes(lower, baseline, colour=r))+
```

```
  geom_step(size=1.2)+
  geom_step(data=scurve,
            aes(upper, baseline, colour=r), lty=1, size=1.2)+
  theme_bw()+
  scale_x_continuous(limits=c(0, 185))+
  scale_colour_manual(values=c("purple", "orange"))+
  xlab("Time (Days)") + ylab("Estimated Survival")+
  labs(colour = "River")+
  theme(legend.position="top")


#Cox Proportional Hazards model:
fit_ph1 <- ic_sp(cbind(left, right)~River+Length+Sex+Externaltraits+speed, model="ph",
#ph = proportional hazards model
                 bs_samples=100, data=Survival)

summary(fit_ph1)


#H3: Predation impact on spawning stock

Survival <- read.csv("C:/Users/bruker/OneDrive/Masteroppgave/Feltdata/Survival.csv",
sep=";")
Survival <- Survival %>%
  dplyr::filter(Fate=="Otter"|Fate=="Lake"|Fate=="Sea"|Fate=="Unknown")

#Figure 6:
Survival %>%
  dplyr::filter(Fate=="Otter") %>%
  group_by(Sex, River, Spawned) %>%
  summarize(n=n()) %>%
  ggplot(aes(Spawned, n, fill=Sex))+
  geom_col(position="dodge") +
  scale_y_continuous(breaks=c(0,2,4,6,8,10), labels=c(0,2,4,6,8,10))+
```

```
ylab("Number of tagged salmon killed by otters") +
facet_wrap(~River)+
scale_fill_manual(values=c(
  "orange", "grey")) + #pink then blue
theme_bw()+
theme(text=element_text(size=18))
```