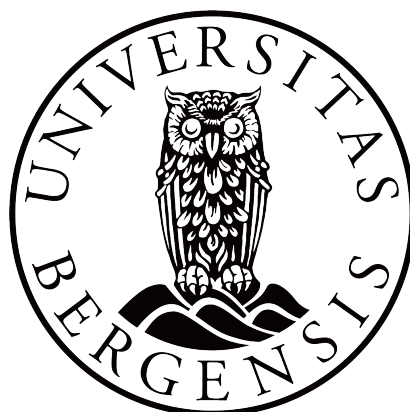


**Novel telemetry predation sensors and mechanistic models  
reveal the tribulations of Atlantic salmon (*Salmo salar*)  
smolts migrating through lakes**



**Thesis submitted in partial fulfilment of the requirements for the degree of:  
Master of Science in Marine Biology**

**by  
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# Abstract

More than one third of Norwegian rivers have lakes, yet the use of lakes by Atlantic salmon (*Salmo salar*) during their migration is poorly understood. The limited research on the subject suggests that passive migration ceases when salmon smolts encounter lakes and that salmon may suffer high rates of mortality in lakes. However, the mechanisms of mortality are uncertain. The innovation of acoustic transmitters with predation sensors has the potential to greatly advance our understanding of the behaviour and fate of smolts in lakes. We conducted a laboratory validation test of the predation sensor tags for this purpose along with a field study in Lake Evangervatnet, Voss, Norway. Survival was low compared to riverine survival rates, with only 40 % successfully migrating through the lake. Half of the mortalities were attributed to predation by trout (*Salmo trutta*). The surviving *Salmo salar* smolts were slow to traverse the 6.5-kilometer lake, with progression rate between lake entry and exit on average 0.01 m/s over a mean  $11 \pm 6.4$  (SD) days. Acoustic detections revealed a consistent pattern of nocturnal migration by smolts. Smolts made extensive movements within the lake, and several displacements upstream towards the lake inlet were observed, seemingly non-directed movements. A series of correlated random walk models suggested that behavior of the smolt was similar to model with a completely random swimming pattern, suggesting that they lack the ability to efficiently navigate through lakes, instead swimming at random until they reached the lake outlet. Acoustic transmitters outfitted with predation sensors can offer improved resolution for tracking the behavior and fate of smolts and can help us conduct better mitigation efforts by allocating survival bottlenecks and separating natural mortality from predation.

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# 1.0 Introduction

Wild Atlantic salmon (*Salmo salar*) populations across the northern Atlantic Ocean have been experiencing drastic declines the past decades (Parrish et al. 1998, Chaput 2012). Across Europe and North America, wild populations of salmon are Endangered or even Extinct in numerous rivers (Jonsson 1999, WWF 2001). Finding the cause has proven difficult because several factors are simultaneously contributing to the decline, such as hydropower, pollution, escaped farmed salmon, overfishing, acid rain, and habitat modification/loss (Forseth et al. 2017). In Norway, the number of salmon returning to their natal river has more than halved in the past 35 years (Thorstad and Forseth 2019). The western region is experiencing the worst decline, with a 66% reduction in returning salmon over the same period (Thorstad and Forseth 2019). Being a species of historical, cultural, and economic importance, extensive mitigation efforts have taken place, yet many populations are still below critical conservation thresholds (Thorstad and Forseth 2019). Understanding salmon ecology is crucial to identify threats, identify the best mitigation methods, and restore salmon populations.

Throughout their anadromous life cycle, salmon encounter a great variety of threats and survival bottlenecks, and one of the most vital is the smolt and post-smolt migration phase (Thorstad et al. 2012b). The downstream migration of smolts towards the sea generally occurs in springtime and is triggered by environmental cues such as water discharge and temperature (Jonsson and Ruud-Hansen 1985, Whalen et al. 1999). It is believed that smolts mostly migrate downstream by passively drifting with the currents, although studies also suggest that active migration may account for some of the downstream movement (Fångstam 1993). Although the riverine migration phase is well studied (Jonsson and Ruud-Hansen 1985, Hansen and Jonsson 1985, Ibbotson et al. 2006, Davidsen et al. 2009, Persson et al. 2019), hydrography of rivers differs, and many include segments containing artificial reservoirs or impoundments. Less research focus has been put on migration through natural lakes, and knowledge about behavior, migration patterns, predation, and other mechanisms of migration through lakes is limited (Thorstad et al. 2012b).

Downstream migration through lacustrine environments is poorly understood, yet a third of Norwegian rivers contain such areas. Studying these habitats is therefore vital for further conservation actions and to better understand the decline of Atlantic salmon (Thorstad et al. 2012b). Upon entering large lakes, smolts must depend on active migration to successfully transit because the flow will not carry them through. Complicated flow patterns

caused by large water masses in inlets and outlets of a lake can make it especially demanding for an actively migrating fish to navigate. Inefficient navigation through lakes can prolong exposure to predators, increase energetic expenditure, and desynchronize migration with optimal conditions at sea, negatively impacting smolt fitness (Rikardsen et al. 2004). Studying this phase is challenging, but with the advances in acoustic telemetry technology, the knowledge gap is closing (Thorstad et al. 2012b). Among the few studies on smolt migration through lakes and reservoirs, most report high mortality rates and attribute this mortality to predation (Jepsen et al. 1998, Honkanen et al. 2018, Kennedy et al. 2018). In the river Vosso, acoustic telemetry revealed high mortality rates from Lake Vangsvatnet, via Lake Evangervatnet, and the estuary Bolstadfjorden (Haugen et al. 2017). The highest rates were observed in Lake Evangervatnet, ranging from 49 to 82 %, and they attributed most of the mortality to predation, but could not verify this due to lack of predator behavior data (Haugen et al. 2017). Additionally, Haugen et al. (2017) observed high mortalities downstream from the outlet of a hydro power station in Lake Evangervatnet, and attributed this in part to environmental effects from the power plant.

Identification of predation events has long been a frontier in telemetry science (Mech 1967, Gibson et al. 2015, Schultz et al. 2015) Many post-hoc methods have been developed to identify if a tag has been eaten by other animals based on sensors that detect changes in temperature, depth, activity, or simply based on changes in tag behaviour (Thorstad et al. 2012a, Berejikian et al. 2016, Strøm et al. 2019) The common denominator for all the quantitative methods is that they require the subjective interpretation of behaviour from telemetry detection data to conclude if a predation event took place or not (Gibson et al. 2015, Daniels et al. 2019) To make this decision, movement patterns of the predator need to be ascertained, which can be both time-consuming and costly. According to Daniels et al. (2019), most classification methodologies can only identify if a predation event took place, not what time it occurred, leading to a subjective identification of predation occurrence, or removal of that individual's detections from the data. Smolts and post-smolts can be subjected to frequent predation from various predators during migration including marine and terrestrial mammals, birds, and other fish (Thorstad et al. 2012b). If a tagged smolt is eaten by a piscivorous predator, the tag will still emit pings from the gastrointestinal tract of the predator (Schultz et al. 2015). The time between an observed predation event and the excretion of the tag by the predator is termed the retention time (Halfyard et al. 2017). Retention time of tags can reach up to 194 days (Klinard et al. 2019), however this is expected to vary depending of the size and shape of the tag (Gibson et al. 2015, Schultz et al. 2015). If detecting the

predation event fails, the study data will exhibit predation bias (Gibson et al. 2015), leading to a type II error.

There is a clear discrepancy between the number of rivers having lakes and the level of knowledge about smolt behaviour in this habitat. The few studies that have observed smolts in lakes report deviant behavior and high mortality rates, therefore there is a need for research that focus on mechanisms for migrating Atlantic salmon smolts in lakes. By utilizing novel predation sensor technology never tested in this setting, we aimed to improve the understanding of smolt biology by being able to exclude smolts that were eaten, isolating analyses to living smolts to attain better estimates of smolt behaviour and survival in lakes. To achieve this, we tagged 35 wild smolts with acoustic tags containing predation sensors, split in a field study in Lake Evangervatnet (N=20) and two laboratory studies to evaluate tag burden from these transmitters (N=5) and to test the predation sensor (N=10). The study aimed to (1) validate the novel predation tag technology for this application, (2) apply it to evaluate the role of predation and survival through a lake, (3) concurrently gather information on smolt behavior in lacustrine areas and (4) use a mechanistic model to explore spatial and temporal aspects of smolt migration in Lake Evangervatnet.

## 2.0 Methods

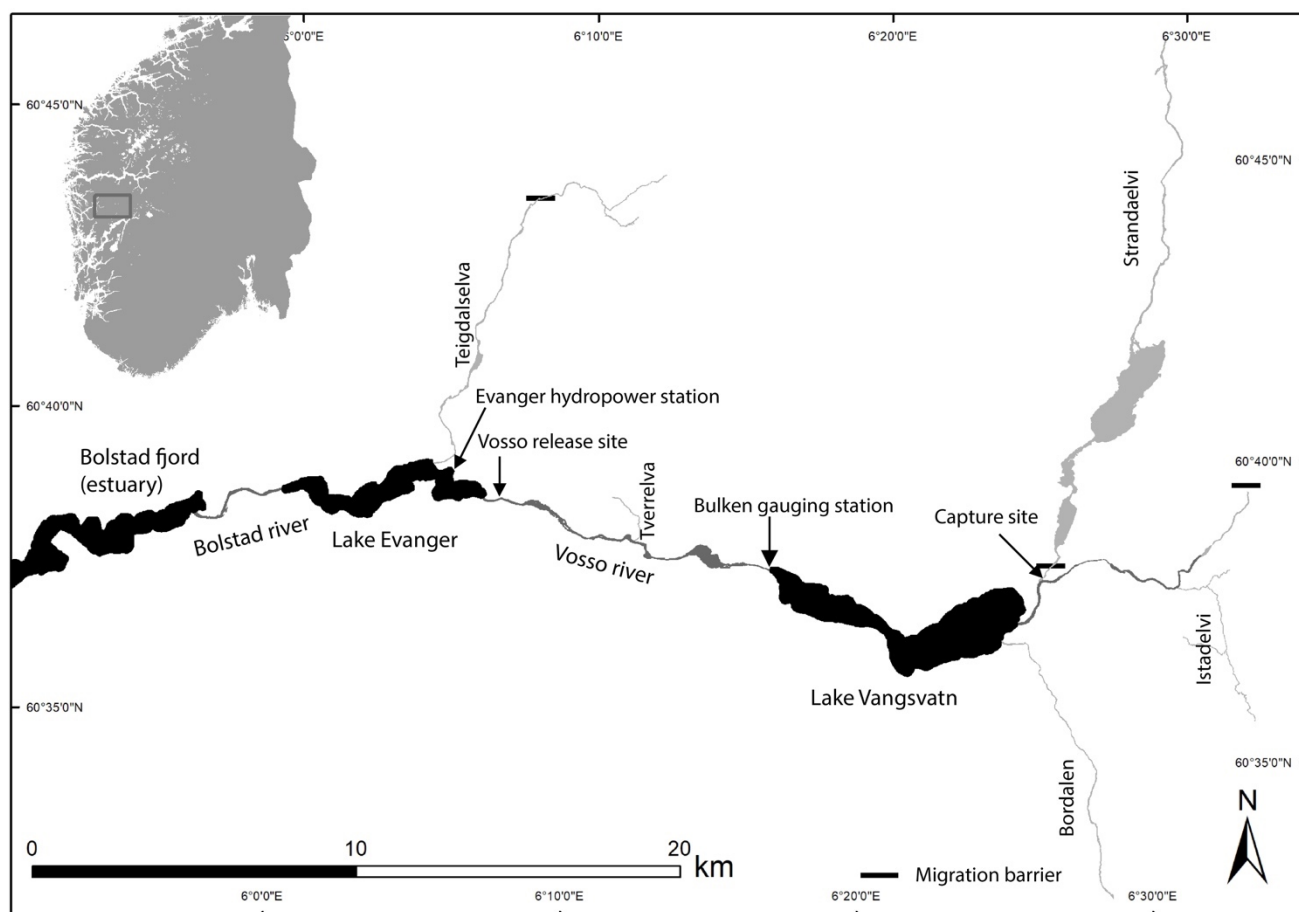
### 2.1 Study site

The research was carried out during a period of five months (May – September) in 2019, with the smolt migration occurring in May and early June (thus defining study period as: 7<sup>th</sup> May-14<sup>th</sup> June) in the Vosso River system in Vestland County, Norway (Figure 1). The River Vosso was once one of the most productive salmon rivers in Norway, having an annual catch of up to 10 tons. During the 1980s, the population collapsed, and has not since recovered. The reasons for the population's lack of recovery remain uncertain. The salmon stock is now composed of wild spawned fish, fish originating from hatchery eggs planted in the substrate, as well as hatchery-reared fish that are towed out from Bolstadfjorden and released in the outer fjords.

The total Vosso catchment is the largest in western Norway (1,497 km<sup>2</sup>) (Barlaup et al. 2018) with 18 of the 35-kilometer anadromous stretch consisting of the two lakes; Lake Evangervatnet and Lake Vangsvatnet. Lake Evangervatnet covers an area of approximately 3



km<sup>2</sup> and has a maximum depth of 114 meters. The lake stretches from Vassenden in the west to Evanger in the east. At the narrowest part, the width is 186 meters. At the confluence of river and lake in the east, Vosso has its outlet and becomes the Bolstad River with a mean annual discharge of 71 m<sup>3</sup>/s (Barlaup et al. 2018). During the study period (7<sup>th</sup> May-14<sup>th</sup> June), the mean discharge was 117 m<sup>3</sup>/s (min/max 25-244). Teigdalselva also drains into Evangervatnet at a rate of 1 m<sup>3</sup>/s (Gabrielsen et al. 2011). In the inner part of a small bay, Evanger Hydropower Station (EHS) discharges water abstracted from Teigdalselva and Eksingdalen through a tunnel at a mean rate of 23.6 m<sup>3</sup>/s (2009-2019), increasing annual discharge and contributing to a change in temperature regimes in the Bolstad River downstream of Lake Evangervatnet (Raddum and Gabrielsen 1999) (Figure 1). During the study period the station had a mean discharge of 16.9 m<sup>3</sup>/s (range: 0-50).



**Figure 1:** The Vosso catchment system. Showing capture, release and study site (Lake Evangervatnet). Anadromous part ends at the black “Migration barrier” lines.

## 2.2 Experimental design

Atlantic salmon smolts were captured and divided into three experimental groups. Five smolts were allocated to a tag effect study, examining how surgical implantation and retention of tags impact survival and physiology. Ten smolts were needed to validate the predation sensor technology, and after euthanasia and tagging with transmitters each was force-fed to a trout and kept in a tank in the Dale hatchery building. The last 20 smolts were tagged and released the same day for a field test of the tag technology and to gain novel insights of smolt migration through lakes.

## 2.3 Sampling and tagging

The capture of wild smolts took place in the uppermost anadromous section of Strandaelvi at a wolf trap, which captures smolts migrating downriver from Strandaelva (Figure 1). A total of 35 Atlantic salmon smolts were collected at wolf traps for utilization in this study. In order to cause as little harm as possible to the smolts, and to make sure the smolts utilized for this study had started downstream migration, electrofishing in the rivers was eschewed. Twenty of the smolts were captured during their downstream migration on May 6<sup>th</sup> and 7<sup>th</sup> in the Vosso wolf trap (see section 2.1). They were kept in a container with continuous flow of freshwater sourced from Vosso River, keeping them in the same temperature as before capture (7 °C), and with an O<sub>2</sub>-concentration of 106%. A minimum size limit for smolts was set to 12.0 cm (Table 1), and they were tagged and released on May 7<sup>th</sup>. An additional 15 smolts were caught in a separate wolf trap (60.5826 N, 5.8127 E) in the Dale river in Vaksdal municipality. Five of the smolts were collected on May 6<sup>th</sup>, and ten on June 13<sup>th</sup>. After capture, they were moved to the Dale hatchery building, in immediate proximity of the Wolf trap. The individuals were graded to be within the same size range (12.9-15.8 cm) as the fish from the field study. Brown trout (*Salmo trutta*) >35 cm total length were also collected from Dale in a trap net in Dalevågen, Vaksdal municipality (60.5759 N, 5.7683 E). The fish (N=10) were collected during the period between the 30<sup>th</sup> of May and 12<sup>th</sup> of June. They were transported (trip 10 minutes) in plastic bags to the Dale hatchery facility and placed in separate tanks from the smolts. They were not fed during the time in the tank prior to the experiment.

The smolts were tagged with Vemco V5 tags (or dummy-tags for the five tag effect smolts). The fish were checked for abnormalities and deemed healthy before surgery. The tagging procedure started by anesthetizing the smolts in 100 mg L<sup>-1</sup> MS-222 Tricaine Methanesulfonate, buffered with 100 mg L<sup>-1</sup> sodium bicarbonate. The smolts were held in 10

L containers with water and anesthetics for 2-3 minutes. The 10 smolts utilized for the validation study were euthanized prior to tagging. Weight and total length were recorded prior to surgery. The fish were placed on a v-shaped operation table made of foam and microfiber cloths. The cloths were saturated with water to best protect the slime layer of the smolts. Before making the surgical incision, a tube with continuously flowing water with half the anesthetic dosage was placed in the mouth of the smolt, providing continuous sedation and oxygen over the gills. All the equipment was disinfected with chlorhexidine ( $1\text{mg mL}^{-1}$ ) and rinsed in distilled water before and between surgeries, and the surgeon used plastic gloves. A 7-9 mm incision was made on the ventral side anterior to the pelvic girdle, at an offset of 1-2 mm from the linea alba, with a pointed scalpel. The tag was then inserted in the peritoneal cavity and pushed in a slight posterior direction compared to the incision site. The incision was closed with one suture (Ethilon suture EH7144H 4-0 FS2 45cm) at the middle of the incision. After handling, fish were placed in a large container with fresh water. Equilibrium was regained after 3-4 minutes. After the procedure, the fish were monitored for some time to check for abnormal activity/effects. The main output metrics for the study fish can be seen in table 1.

**Table 1.** Atlantic salmon (AS) and Brown trout (BT) measures in the Tag effect, Validation and Field study. All lengths in cm, weights in g, tag burden is the tag weight relative to fish weight in air ( $\text{tag burden} = \text{tag weight}/\text{fish weight} * 100$ ). S.D. is standard deviation.

Study	Species	Sample size	Length mean $\pm$ S.D.	Weight mean $\pm$ S.D.	Tag burden mean $\pm$ S.D.	Length range	Weight range	Tag burden range
Tag effect	AS	5	13.9 $\pm$ 1.0	18.0 $\pm$ 2.6	3.8 $\pm$ 0.5	12.9-15.2	14.8-21.6	3.1-4.53
Validation	AS	10	14.3 $\pm$ 0.9	21.8 $\pm$ 4.6	3.2 $\pm$ 0.7	12.9-15.8	15-30	2.23-4.47
Validation	BT	10	43 $\pm$ 7.0	813.5 $\pm$ 530	N/A	36-55	448-1922	N/A
Field	AS	20	14.3 $\pm$ 1.2	21.7 $\pm$ 5.7	3.1 $\pm$ 0.7	12.8-17	16-37	1.81-4.18

## 2.4 Acoustic telemetry

### *2.4.1 Acoustic tags*

V5D 180-kHz Predation Tags (Vemco Ltd., Halifax NS, Canada) were employed for this study. The tags weighed 0.68 grams in air and measured 12.7x5.6x4.3 mm. Tags were coded to emit unique signals at random intervals between 60 and 120 s, and also contain a biopolymer sensor. If a fish would be predated, stomach acid (low pH) in the gastrointestinal tract of the predator would react with the biopolymer. This reaction flips an internal switch that changes the signal communicated by the tag to the receiver, indicating predation (Halfyard et al. 2017).

### *2.4.2 Passive acoustic receivers*

Acoustic VR2W-180 kHz receivers (Vemco Ltd., Halifax NS, Canada) were deployed to track the smolts in the lake. These receivers are battery-powered and programmed to record Vemco coded transmitters at 180 kHz. The receiver detects a transmitter using an omnidirectional hydrophone, decodes the signal, logs ID-number, time and if the fish is predated.

## 2.5 Effect of tagging on smolts

In order to get an indication of the surgery and tag effect on smolt survival and physiology, five smolts were tagged with dummy (i.e. same size and weight as the Vemco predation tags, but with inactive components) tags. They were kept in a container with continuous flow of water from Dale river (temperature on average 12 °C). The fish were kept in this container for 38 days. The field study was concluded within this time, and they were therefore euthanized at this timepoint to look at the wound healing and tag effect. The smolts were euthanized with blunt force to the head, resulting in immediate death and the opportunity to do the necropsy with no damage or changes to the inner organs. They were immediately frozen.

### *2.5.1 Necropsy of smolts*

The necropsy was conducted on October 25<sup>th</sup>. The necropsy started by examining the exterior. Especially the incision site was examined, looking at degree of healing (incision closed or open). Any bulging or external signs of tag was also recorded. After the external check, a cut with the scalpel to open the abdominal cavity was made. We examined damage to inner organs, tag placement and encapsulation, wound healing, hemorrhaging, inflammation, and

adhesion between body wall and internal organs (peritoneal adhesion to the muscle wall). The necropsies were performed by another person than the surgeon.

## 2.6 Validation of Vemco V5 predation tag

Due to the novelty of the predation tag and the fact that the tags had not been tested for these species (neither Atlantic salmon as prey nor brown trout as predator), a validation study to monitor function of tags in a controlled environment was conducted.

### *2.6.1 Force-feeding of trout with tagged smolts*

After euthanized smolts were implanted with tags and the incision closed with suture, they were force fed to brown trout that had been anesthetized (see section 2.3 for procedure). To identify which trout was fed a specific smolt, they were tagged with an exterior floy tag in the dorsal fin. Time of the procedure was recorded for each test subject and ranged between 190 sec and 425 sec (Appendix 1). The trout were then monitored for two hours to look for expulsions and other abnormalities. The tank was monitored daily for 22 days to look for tag expulsions.

Three main metrics were measured during the experiment, using similar procedures as reported in Halfyard et al. (2017); false negatives, signal lag, and retention time. False negatives were defined as a failure to shift signal from pre- to post-predated during predation event. Signal lag was measured as time between predation event and shift of signal. Time between predation and expulsion of tag was termed tag retention.

## 2.7 Field study

In order to test the tag in a natural environment, and to get more knowledge about smolt migration through lakes, a field study was conducted. Tag ID, length and weight measures for the field study smolts can be seen in Appendix 2.

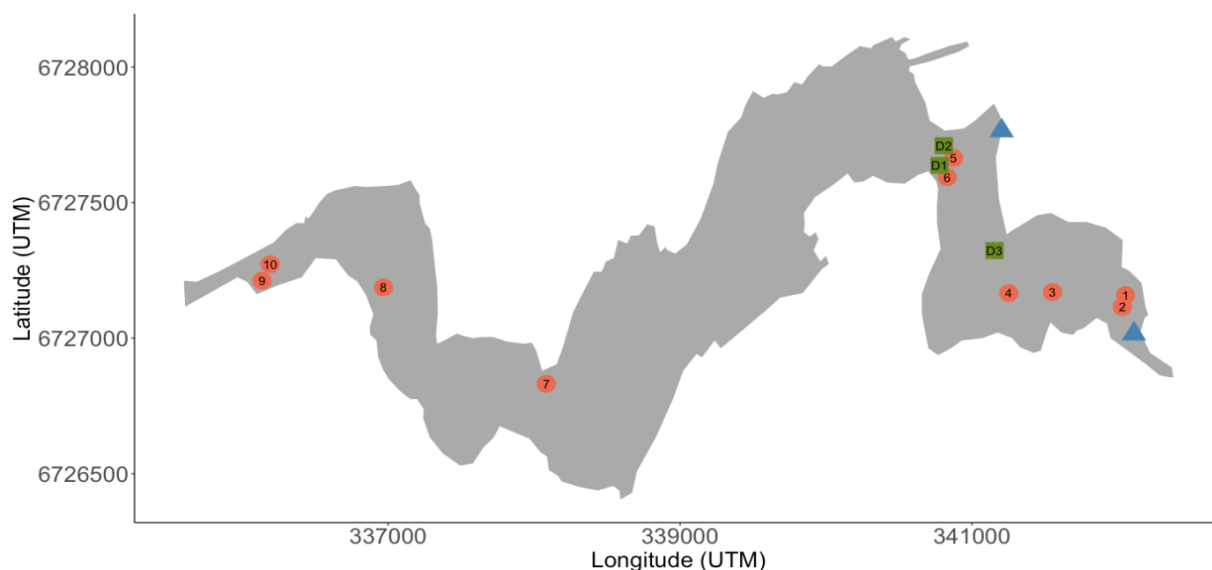
### *2.7.1 Smolt release*

Smolts were returned to the container (temp: 7.2 °C and 106 % O<sub>2</sub>) after tagging and kept for 5-7 hours to recover prior to transportation. The smolts were transferred with a plastic colander (to minimize handling and damage to the fish) into two separate plastic bags with oxygenated river water (300 % O<sub>2</sub>) and transported by car for 30 minutes, translocated downstream their migratory route 18 km to “Vosso release site” (see section 2.1, Figure 1).

From the car, the fish were carried down to the riverbank and released 50 minutes after transportation start. The release was conducted by letting water flow into the plastic bag (2 min) so that the fish would acclimatize with the Vosso water. Thereafter, the 20 smolts were released in two groups, a couple of meters apart, during dark (23:14), to maximize probability of survival (Vollset, Barlaup, and Normann, 2017).

### 2.7.2 Measuring equipment

Temperature and flow were measured during the entire study period on five locations and ten acoustic receivers were positioned in the lake (Figure 2).



**Figure 2:** Location of receivers (red circles, numbered 1-10), temperature loggers (blue triangles) and flow/temperature loggers (green squares).

#### 2.7.2.1 Discharge

Water discharge from Vosso and Evanger Hydropower Station (EHS) were measured daily during the study period. The Vosso discharge measures were collected from the Norwegian Water Resources and Energy Directorate (NVE) at Bulken gauging station (nr 62.5.0) (See section 2.1, Figure 1), and the hydropower discharge measures were received from Bergenhalvøens Kommunale Kraftselskap (BKK).

#### 2.7.2.2 Temperature

Water temperature at circa 1-meter depth was recorded every 10 minutes, using Vemco (Halifax, NS, Canada) Minilog-II-T temperature data loggers. The loggers measured temperature in the first basin of Lake Evangervatnet (located together with flow measurement

equipment), the Vosso water and the water from the outlet of EHS.

#### 2.7.2.3 Flow measurements

Flow data were logged for 60 seconds every 10 minutes, at three separate stations, with an Aquadopp Current Profiler 400 kHz (Nortek, Norway). Flow measurements were recorded at 5.5 and 13.5 meters depth, based on observed depth use by smolts in the lake (Haugen et al. 2017). The Aquadopp is an acoustic doppler instrument designed to measure flow direction and velocity. The SeaReport (Nortek, v.1.1.1), Surge (Nortek, v.1.14.01) and SD6000 (Morten Hammersland Programvare, v.4.6.3.49) software were utilized for analysis and quality control of equipment.

#### 2.7.2.4 Acoustic receivers - deployment and range testing

An array of ten passive acoustic receivers was positioned in Lake Evangervatnet (Figure 2) on May 5<sup>th</sup> and retrieved on September 13<sup>th</sup> 2019. Two receivers were deployed in the mouth of the lake, upstream, and two at the end of the lake, downstream. This was to ensure information about when smolts entered, and when they made it through the lake. Additional receivers were positioned throughout the lake; six were deployed strategically to monitor progress of smolt migration through the lake. The first basin and the area around the hydropower plant received greatest coverage, as earlier study indicates that a large proportion of acoustically tagged fish disappear here (Haugen et al. 2017).

Receivers were attached to a rebar with cable ties, and the rebar was embedded in a concrete weight (25-30 kgs). The weights were attached by mooring rope to a buoy and placed in a way that made sure the receivers stayed in an upright position. Depth of receivers were measured using a portable depth sounder (Hondex PS-7 LCD digital sounder). The receivers were deployed in depths ranging from 13.1 to 27.5 meters (see section 2.7.2.6, Table 2).

To get an approximation of the range for each receiver, range tests were conducted at several timepoints throughout the study period, ensuring testing during varying flow and temperature conditions. A range test tag (V5-1x-180k-3, Vemco, NS, Canada) with similar transmission power and function as the V5D tags was attached to a rope and placed two meters behind a boat, submerged 1 meter below surface. The range tag emitted a signal every 3 seconds. In the boat, a GPS-tracker was continuously recording position. Post data-collection, the GPS tracks were matched with the range test detections from the receivers and 95 % kernel density estimation (kde) was calculated for all receivers, using the adehabitatHR

package (Calenge and Fortmann-Roe 2020) in RStudio (Rstudio-Team 2016). Kernel density estimation is a statistical method to calculate an estimation of distribution based on clusters of spatial data points (Worton 1989). A total of six days was spent range testing, predominantly in May.

#### 2.7.2.5 VR100

A manual tracking acoustic receiver, Vemco VR100 with a VH180 (180 kHz) omnidirectional hydrophone, was used to track smolts throughout the entire study period. The hydrophone was deployed from a boat, monitoring at intervals of five minutes, throughout the lake. When a tag was within the range of the VR100, the ID, decibel, and location were recorded. This tracking was utilized to get more data on tags outside of the range of the receivers. After the smolt run, the lake was scanned with the manual receiver to look for missing tags.

#### 2.7.2.6 Field study receiver detections

The raw dataset from the receivers consisted of 622 922 detections from the 20 tagged smolts (Table 2).

**Table 2.** Detections between May and September (total detections) and during the study period (May 7<sup>th</sup> – June 14<sup>th</sup>), placement (Latitude and Longitude in decimal degrees) and depth (m) of receivers 1-10.

Receiver	Total detections	Total detections study period	Depth	Latitude	Longitude
1	58 788	5 128	13.1	60.64895	6.110867
2	15 736	13 085	13.9	60.64855	6.1105
3	18 896	18 114	19.6	60.64885	6.1017
4	215 828	30 652	27.5	60.6487	6.09625
5	36 919	11 691	18.1	60.653017	6.088933
6	17 331	12 139	15.8	60.652367	6.0882
7	1 502	1 502	21.6	60.644433	6.03865
8	116 578	10 262	26.6	60.647167	6.017983
9	104 294	13 803	23.7	60.64705	6.002783
10	36 820	10 969	20	60.647617	6.00375



### 2.7.3 Predator sampling

To obtain an indication of the size range, spatial distribution, and species of predators, rod and reel fishing was employed between May 7<sup>th</sup> and September 9<sup>th</sup> (N=9 days), for a total of 40 rod hours. Fishing was conducted predominantly during daytime. Artificial lures (Rapala, Finland) between 7-12 cm imitating smolts were utilized during fishing. Coordinates, fishing depth, and length of fish were recorded (Appendix 3). The different areas of the lake were fished with approximately the same effort, with increased effort around the first basin, outlet of Teigdals River, and the outlet of the lake. All fish were released except one, which was bleeding. The same procedure was conducted during May and June 2016 with a total of 36 rod hours, and these data are included in the results, however coordinates of capture was not documented in 2016. Additionally, during the fishing, avian predators observed on the lake were identified and counted.

## 2.8 Statistical analysis

All statistical analyses and visualizations of data were conducted in R-studio 1.1.456 (Rstudio-Team 2016). Before any data analysis was conducted false detections were removed. False detections were defined as detections of the same individual with a time interval shorter than the emitted signal interval (i.e. under 60 seconds) or ID-codes of fish other than those utilized in this study.

### *2.8.1 Validation of Vemco V5 predation tag*

To test if smolt or trout weight had an effect on retention time and signal lag, a linear regression model (*lm* function in R) was fit to the data, using trout or smolt weight as predictor and retention time and signal lag as response. A potential relationship between false negatives (i.e. if the tag switched signal from pre- to post-predated) and smolt and trout length was tested using a generalized linear model with binomial distribution, with false negatives as response and weight as predictor.

### *2.8.2 Field study*

#### 2.8.2.1 Survival

Smolts were assumed dead if the tag changed signal from pre to post-predated, if the tag disappeared within the lake, or if the tag was detected at a single receiver for the rest of the

study period. The location of tag switch was defined as the site of mortality for predated fish, whereas tags that stayed resident or disappeared at a given receiver was designated this location as site of mortality. Because there was almost complete overlap between receivers 5 and 6, and 9 and 10, these stations were pooled as receiver 5 and 10 respectively. To test if smolt weight or length had an effect on survival, a generalized linear model (*glm*; binomial family) was used.

#### 2.8.2.2 Survival per km

To estimate survival per kilometer through the lake, the progression in kilometers for a given smolt was defined as distance between inlet (Receiver 1) and the most downstream receiver (subset of receivers that covered the whole lake: 1,4,5,7,8 and 10) they were detected at. If a fish was last detected at the outlet (Receiver 10), it was defined as successful migrant. If a smolt was registered as predated, the most downstream receiver detection of the pre-predated signal was used. To get an estimation of bias included as a result of predator movement, two datasets were created. The naïve dataset included movements of live and post-predated smolt. The sensor-enhanced dataset only included movements of live smolts. Thus, a comparison between the information gathered using standard telemetry tags (naïve dataset) and predator tags (sensor-enhanced dataset) can be made. This difference is termed predation bias (Daniels et al. 2019). To compare the added information gathered by utilizing the predation tag, survival per km was calculated for both the naïve and sensor-enhanced dataset.

#### 2.8.2.3 Smolt behavior

Lake entrance was defined as the first observation at the lake inlet. Lake exit was defined as the last observation on the most downstream receiver near the lake outlet, if this was the last observation of that individual within the lake. Within the receiver array in Lake Evangervatnet, the longest section between receivers was between Receiver 5 and 7, reaching a distance of approximately 2900 meters. Because receiver detections overlap within the first basin of Lake Evangervatnet, and smolts often got detected at an almost continuous scale, the temporal movements were hard to define. Thus, to look at in-lake movement, the section between 5 and 7 was chosen. To investigate movement in this area, the last detection at Receiver 5 and the corresponding first detection at Receiver 7 was used. Because this indicates when the fish migrates away from Receiver 5, and when the fish enters the range of Receiver 7, it gives a good view of in-lake movements of smolts

Progression rate was defined as the speed between the first detection at the inlet receiver and a given downstream receiver in the lake. To calculate the progression rates for the 20 smolts, the most downstream receiver all smolts reached was used (i.e. Receiver 5). Progression rates for the surviving smolts was estimated using the first detection at the inlet receiver and the first detection at the last receiver (maximum net progression rate) or the first detection at the inlet receiver and the last detection at the outlet receiver (minimum net progression rate). To test if progression rate had an effect on survival, a generalized linear model (*glm*; binomial family) was used.

#### 2.8.2.4 Diel migration

To estimate diel horizontal migration, the R-package *suncalc* (Agafonkin and Thieurmel 2019) was used to download the sunset and sunrise-times for Lake Evangervatnet (60.6484 N, 6.0957 E). Based on sunrise and sunset times, days were split into three groups; nighttime (between sunrise and sunset), dim period (interval of two hours after sunrise and before sunset) and daytime (between the dim period). Thus, a 24-hour day was disproportionate split, where nighttime represented a mean of 27.5%, dim-period 16.7 % and daytime 55.8 % of the day.

Via Rayleigh test of uniformity, the diel migration of smolts into, within and out of the lake was tested, by utilizing the *r.test* within the *CircStats* package (Lund and Agostinelli 2018). Time of day in hours was transformed into radians by multiplying hour by 12 divided by  $\pi$ .

#### 2.8.3 Mechanistic model

To get an estimate of total distance travelled by smolts and to investigate if smolts could be moving randomly throughout the lake before they reach the outlet, we simulated 20 000 correlated random walks (CRW) bounded within Lake Evangervatnet using R and the *glatos* package (Holbrook et al. 2017). Correlated random walks entail that the direction of each step is correlated with direction of the previous step, thus mimicking an animal's tendency to continue moving forwards (Codling et al. 2008). Over time, this direction declines, meaning that the movement on large scale is multidirectional, but locally occurs in a straight fashion. One simulation results in a two-dimensional virtual track of a smolt through Lake Evangervatnet. By running simulations with varying parameter input ( $\sigma$  and step length, see below) and comparing simulated travel time data with observed field travel time data, the best fit model was identified.

To simulate from our CRW, we made several assumptions regarding the distributions of the step lengths and turning angles in accordance with the *crw\_in\_polygon* function in the *glatos* package (Holbrook et al. 2017). Specifically, we fixed the start and end positions, as well as the initial swimming direction. We assumed that the turning angle,  $\theta$ , followed a Gaussian distribution with mean  $\mu$  and standard deviation  $\sigma$ . Step lengths were assumed to be constant (i.e., no variability) and to occur regularly in time. For each track, we additionally indicated the number of steps to be simulated, thus implicitly fixing the duration of each track. Start point was set as the coordinates of Receiver 1 (inlet receiver) and symbolized the start location of the simulation. The initial direction of the first step was set west, because the water flow direction at this point goes westerly. The end line was set to the “west coordinate” of Receiver 10 (outlet receiver). If the simulation path crossed this line (i.e. was located more to the west than the west coordinate), the smolt was defined as through the lake and simulation terminated. Step length was set to 50 meters based on a sensitivity analysis, and one track was generated with a maximum of 5000 steps. In order to fit a correlated random walk, the mean turning angle  $\mu$  was set to 0 in all simulations. The strength of the correlation varied depending on  $\sigma$  which took one of four values (1,5,10, and 20 °), distributed in four respective simulation groups (see below).

Each two-dimensional track generated from a simulation represented an individual smolt, and this was run 5000 times for each of the set  $\sigma$  of  $\theta$ . Thus, in total 20 000 simulations were run distributed in the four groups, 5000 for each value of  $\sigma$ . The total distance travelled for one simulated smolt track was calculated using total number of steps for that simulation, and this was done for all simulations utilizing Equation 1:

$$d = Nsteps * StepLength \quad (1)$$

Where *Nsteps* denotes total number of steps for one simulated track, *StepLength* was set to 50 meters in all simulations and *d* was the total distance travelled for one simulated smolt in meters.

Mean swim speed for simulated smolts was calculated using Equation 2:

$$v = body\ length\ s^{-1} * L_m \quad (2)$$

Where  $v$  denotes mean swim speed in m/s, *body length*  $s^{-1}$  was derived from paper by (Thorstad et al. 2004) where hatchery post-smolts were recorded having a mean swim speed 1.2 body length  $s^{-1}$  and  $L_m$  was mean length (0.143 m) of smolts utilized in the field study. Using Eq.(2) the mean speed all simulated smolts swam with was 0.17 m/s.

To calculate total travel time for a simulated smolt to migrate through the lake, Equation 3 was utilized for every simulated track:

$$t = \frac{d}{v} \quad (3)$$

Where  $t$  denotes time in seconds and thereafter converted to days,  $d$  was calculated from Eq.(1) and  $v$  from Eq.(2). However, riverine smolt movement mostly occurs at night (Thorstad et al. 2012b). Based on the observations from Lake Evangervatnet, where smolts mainly migrated during night and dim period (44.2 % of a 24 hour day), a comparison where movement only occurs during this period (rounded up to 50 % of a 24-hour day for simplicity) was made, by dividing Eq.(3) by 2.

By utilizing Eq.(1), Eq(2) and Eq(3), salmon trajectories in the lake were calculated for all 20 000 simulations, and thus the output of the model was threefold: paths of individual salmon, total distance travelled, and time spent to traverse the lake. For reference, a track of the shortest path possible between start point and end line was made, using the *shortestPath* function in the *gdistance* package (Van Etten 2017) in R.

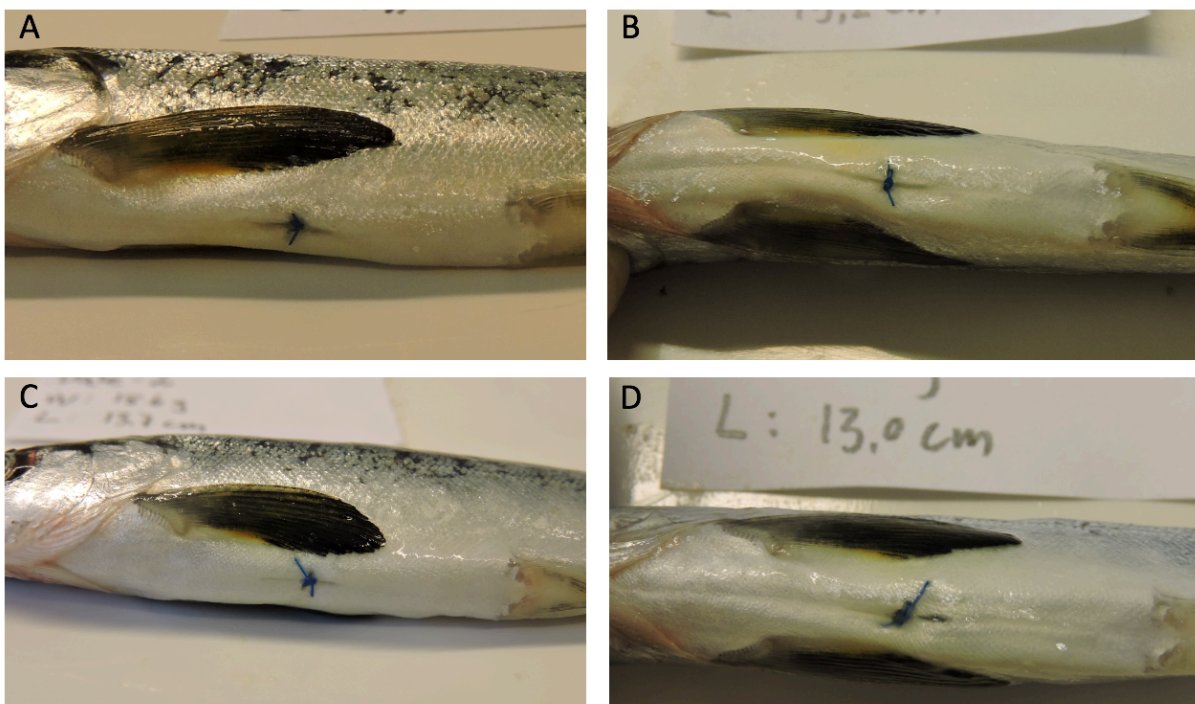
A quantitative sum of squared distances was calculated to compare the simulated travel time means for each of the four groups ( $\sigma=1,5,10$  and  $20^\circ$ ) and observed travel time mean and to find the best fit model. The observed travel time mean was based on the time difference between the first detection at the inlet receiver (Receiver 1) and the first detection at the outlet receiver (Receiver 10) by the smolts in the field study.

Multiple assumptions are made in the correlated random walk model. First, it assumes that migrating individuals move independently of each other. The second assumption is that the smolts move continuously at the same speed at a constant rate (either 12 or 24 hours a day). For the simulated smolts moving only at night (12 hours), an assumption was that the orientation (direction of movement) of the smolt was the same before and after the 12 hour stop. The fourth assumption was that the smolts move randomly through the lake, without flow, temperature, or other stimuli to guide them. Fifth, the smolts were assumed to move forwards (i.e. not turn and swim in random directions between steps).

## 3.0 Results

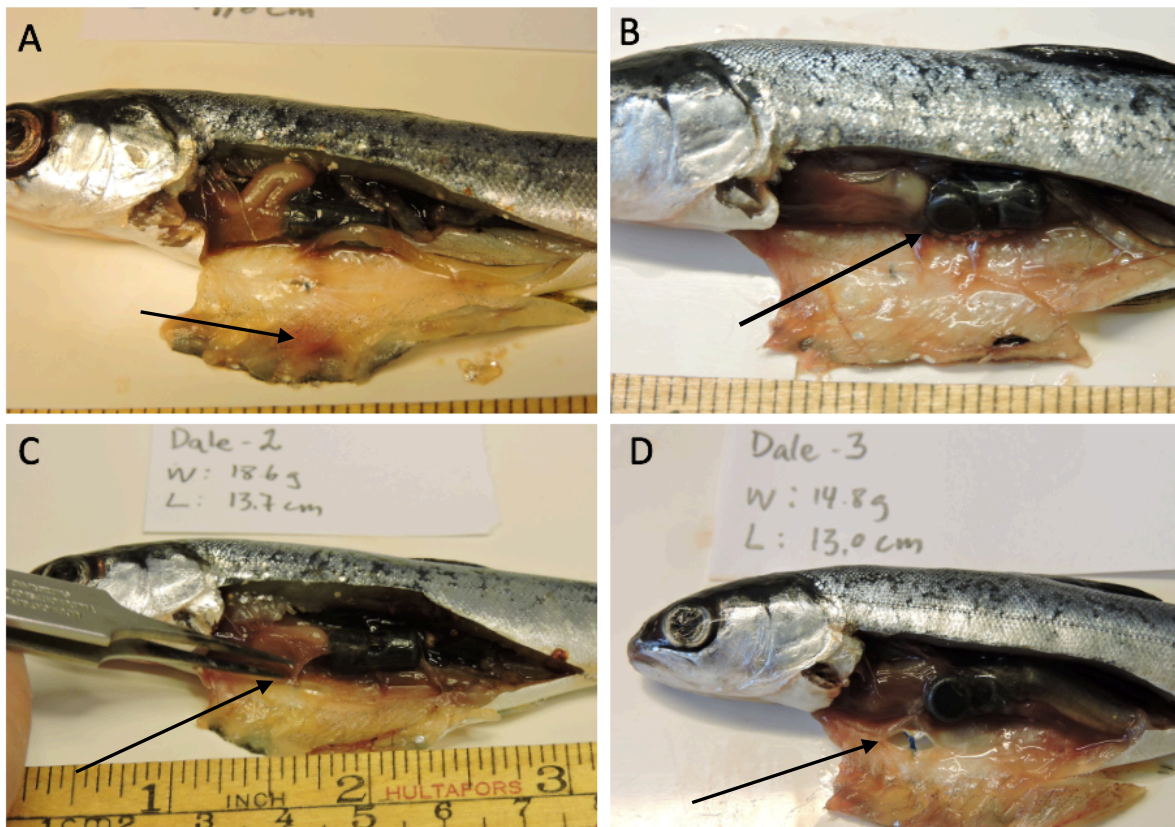
### 3.1 Effect of tagging on smolts

All five of the dummy-tagged fish survived surgery and showed no signs of abnormal behavior during the full monitoring period (38 days). An external inspection showed no sign of fungus or fin damage on any of the smolts. Wounds had healed perfectly in four of five fish, and no sign of bulging was observed. In one smolt, the tag was causing bulging and a small(1mm) opening in the epidermis (Figure 3, D), however the peritoneum in the peritoneal cavity was closed.



**Figure 3.** Macroscopic external view of incision site for four of the five dummy-tagged smolts.

Internal tag placement in all fish was posterior to the suture site, ventral to internal organs, and within the peritoneal cavity, encapsulated in a transparent tissue (Figure 4, B arrow). One incision ruptured when cutting open the abdominal cavity (Figure 4, D arrow). There were no signs of inflammation or hemorrhage in the muscle tissue around the incision site in four of the five fish. One smolt exhibited mild inflammation (Figure 4, A arrow). Adhesion between the muscle wall and peritoneal tissue was observed (Figure 4, C arrow), but no adhesion between nor damage to internal organs were detected. Because the smolts were frozen and then defrosted months later, some discoloration was seen.



**Figure 4.** Macroscopic internal necropsy of four of the five dummy tagged smolts. Arrows point at A: mild inflammation from surgery, B: tag encapsulated in transparent tissue, C: adhesion between muscle wall and peritoneal tissue, D: rupture after surgically opening of peritoneal cavity.

### 3.2 Validation of Vemco V5 predation tag

The validation studies was conducted in water temperatures ranging from 10.6 to 12.9 °C (mean=11.8° C). The number of false negatives for the ten experimental predation events was 50%, meaning that the tag shifted signal from pre-predated to post-predated in five out of ten trials (Appendix 1). Retention time of tags in the gastrointestinal tract of the trout ranged from 2 to 22 days, with a mean of 9.8 ( $\pm 6$  SD). Of the five successful events, signal lag time ranged from 13 to 61 hours, with a mean of 35.4 ( $\pm 17.7$  SD).

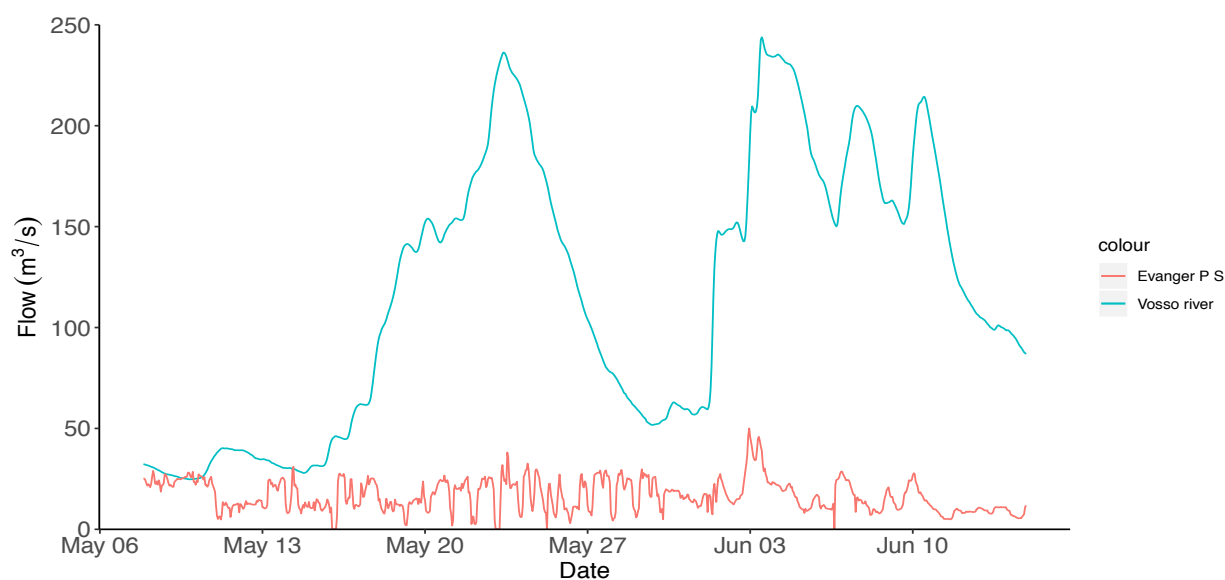
There was no significant effect of smolt nor trout weight on retention time (smolt weight,  $F_{1,8}=0.28$ ,  $p=0.6$ ; trout weight,  $F_{1,8}=2.28$ ,  $p=0.16$ ). Neither did smolt or trout weight affect false negatives (smolt weight,  $z_{1,8} = -1.1$ ,  $p = 0.28$ ; trout weight,  $z_{1,8} = 0.3$   $p = 0.76$ ). For the five experimental predation events that were successful, no significant effect from smolt

or trout weight on signal lag was observed (smolt weight,  $F_{1,3}=0.001$ ,  $p=0.93$ ; trout weight,  $F_{1,3}=1.63$ ,  $p=0.29$ ).

### 3.3 Field study

#### *3.3.1 Water discharge*

Water discharge from the Vosso river varied from 25 to 244 m<sup>3</sup>/s (mean=116 m<sup>3</sup>/s) and at the Evanger Power Station between 0 and 50 m<sup>3</sup>/s (mean=17 m<sup>3</sup>/s) during the study period (Figure 5). At three timepoints the discharge from the power station was bigger than from Vosso, all before the 14<sup>th</sup> of May.

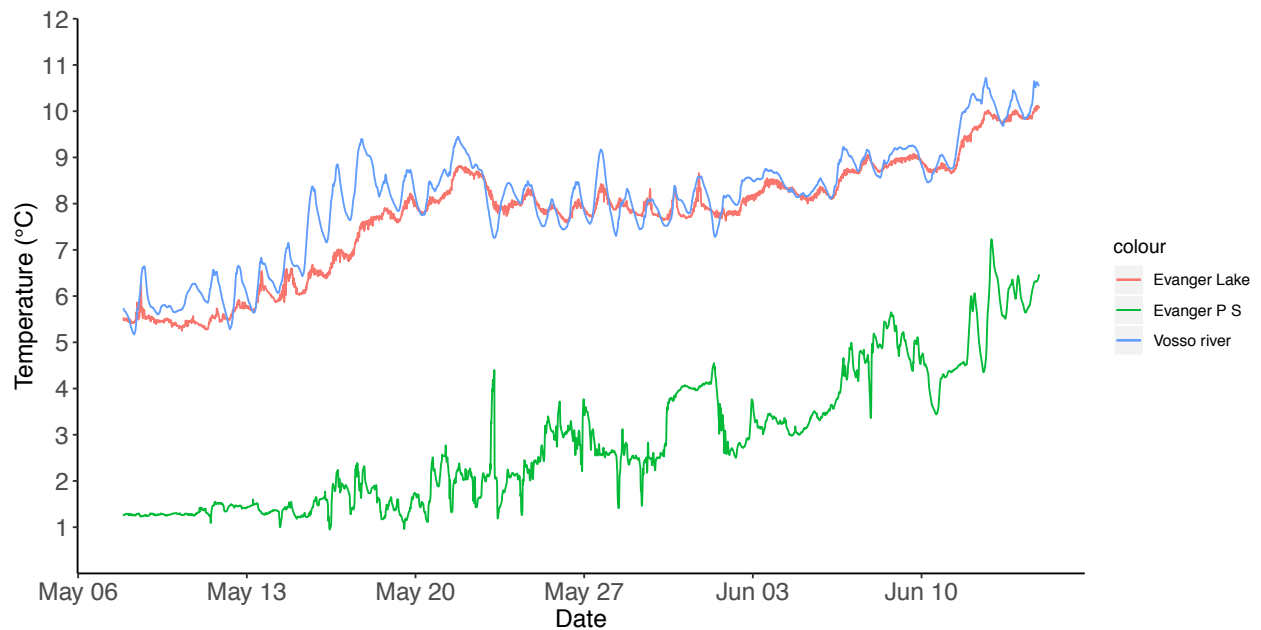


**Figure 5:** Discharge from Evanger Power station (red) and Vosso river (blue) during the study period (May 7<sup>th</sup>-June 14<sup>th</sup>).

#### *3.3.2 Temperature*

Water temperature increased throughout the study period at all locations (Figure 6). The water from Evanger Power Station (mean = 2.9 °C) was on average 4.9 °C colder than the water from Vosso and within Lake Evangervatnet (mean = 7.8 °C).

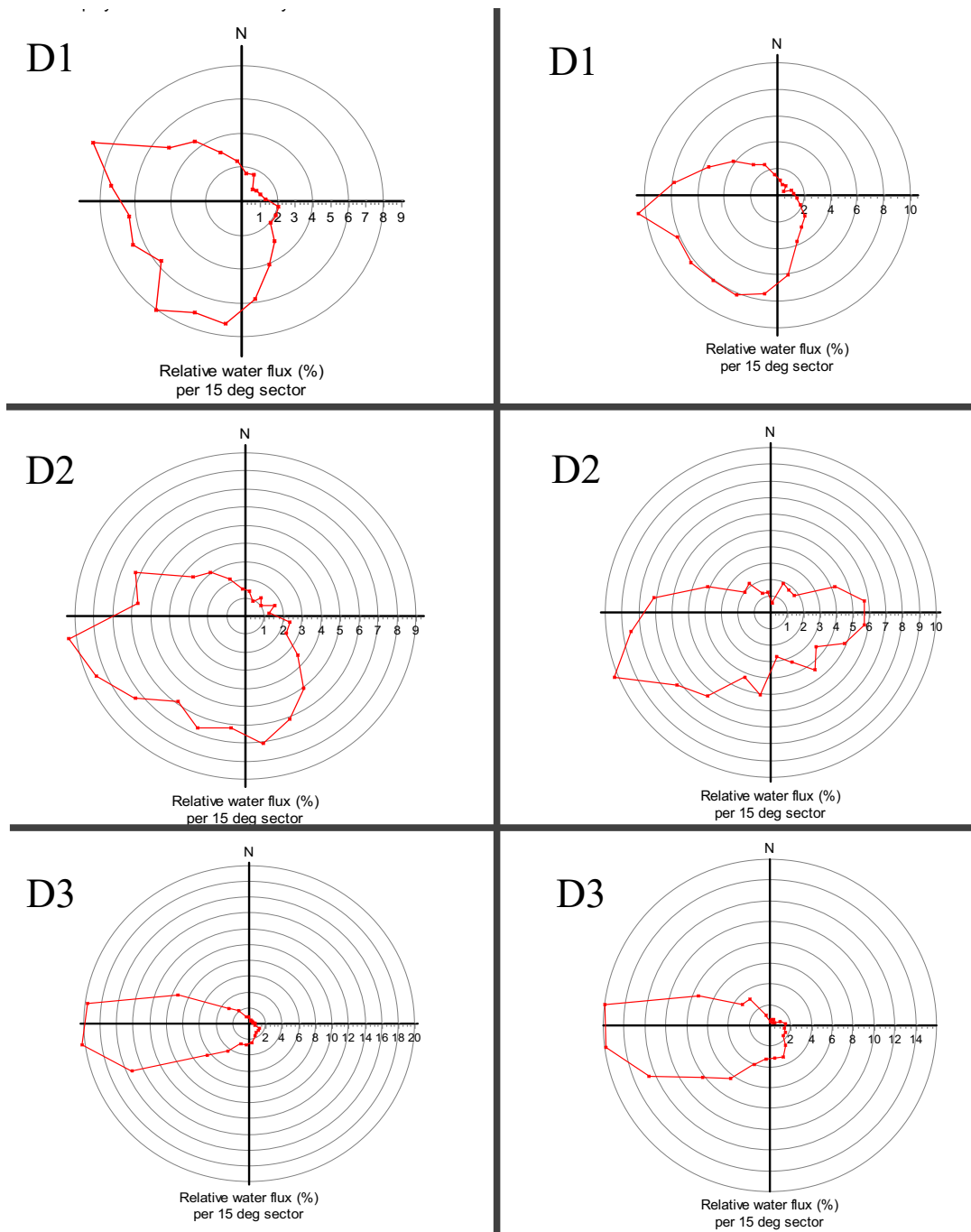




**Figure 6:** Temperature in the Vosso river water (blue), Evanger power station (green) and in the first basin of Lake Evangervatnet (red) during the study period (07.05.2019-14.06.2019).

### 3.3.3 Flow measurements

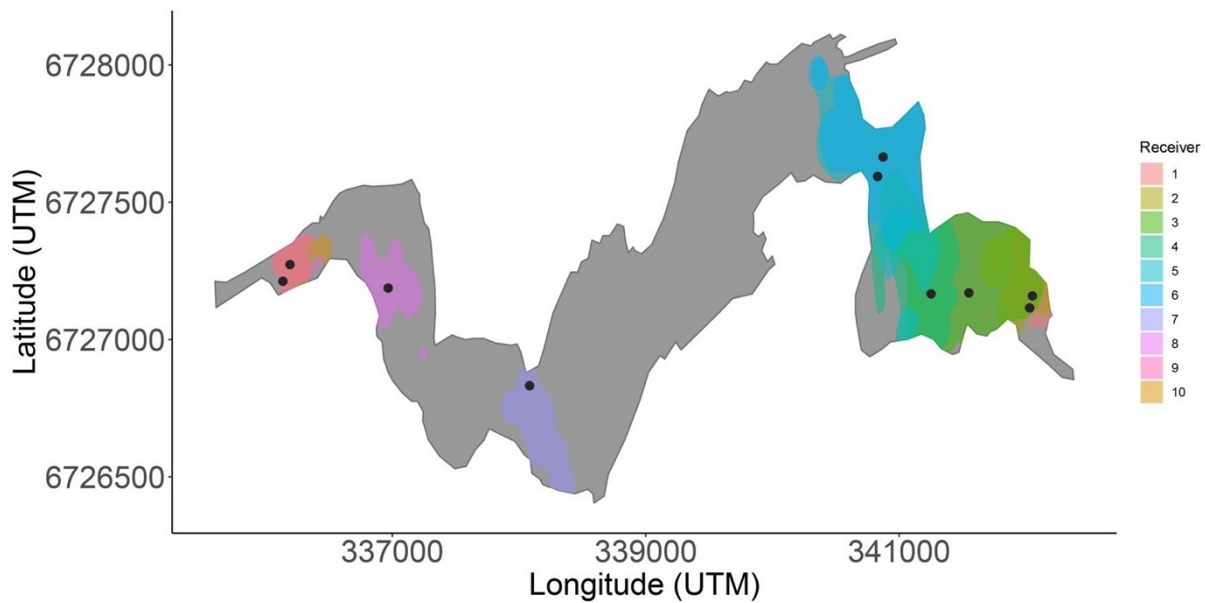
Flow was mostly southerly or westerly directed at both 5.5- and 13.5-meters depth at the three measuring stations. The measuring station placed closest to the outlet (D3) recorded predominantly western current with speeds of 0.084 m/s at both depths. However, the two stations in the narrow sound (D1, D2) recorded currents in both western (ca. 0.06 m/s) and southern (ca.0.06 m/s) directions at both depths. Before the 17<sup>th</sup> of May, the flow tended to go in a southern direction. This was due to an eddy that was formed within the first basin of Lake Evangervatnet. After 17<sup>th</sup>, the eddy disengaged, and the flow went in a western direction (Figure 7).



**Figure 7.** Average relative water flux (function of direction and velocity of water) during the period 8<sup>th</sup> of May to 20<sup>th</sup> of May at 5.5 m (left) and 13 m (right) depth at station D1, D2, and D3.

### 3.3.4 Receiver range

Receiver detection cover varied from 0.05 km<sup>2</sup> to 0.56 km<sup>2</sup> (Figure 8). Range of the receivers in the first basin (East in Figure 8) overlapped, giving almost 100 % cover. Receiver 7,8,9 and 10 had sufficient coverage, ensuring almost complete cover of the width of the lake at their mooring positions.



**Figure 8.** Range of the 10 receivers in Lake Evangervatnet. The black points give the receiver locations, the colors are coded for each receiver. Total range is the size of colored kernel home range density polygons.

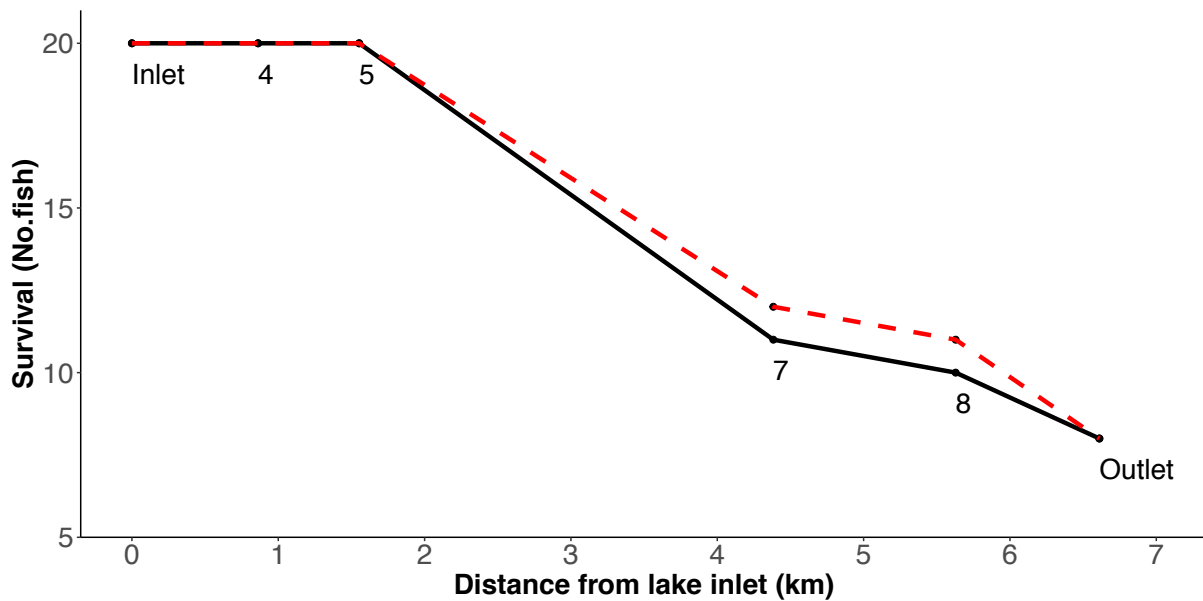
### 3.3.5 Smolt survival and predation

Migration success through Lake Evangervatnet was low, with eight smolts (40%) successfully transiting the lake. The remaining 12 (60%) died in the lake, with six of these mortalities positively registered as predation. The other six smolts were identified as dead, as the tags either disappeared within the lake (N=3) or were detected at a single receiver for the rest of the study period (N=3). Half of smolts died within the first 2 kilometers (first basin) of the lake.

The cumulative survival per kilometer through the lake showed that all smolts were detected at least once 1.5 kilometer from the inlet (Receiver 5). Based on the sensor-enhanced dataset, only 11 (55%) smolts successfully migrated minimum distance of 4.4 km, and 10 (50%) migrated minimum distance 5.6 km. A small difference in in-lake survival per km was observed for the naïve dataset, where 12 (60%) successfully migrated minimum distance of

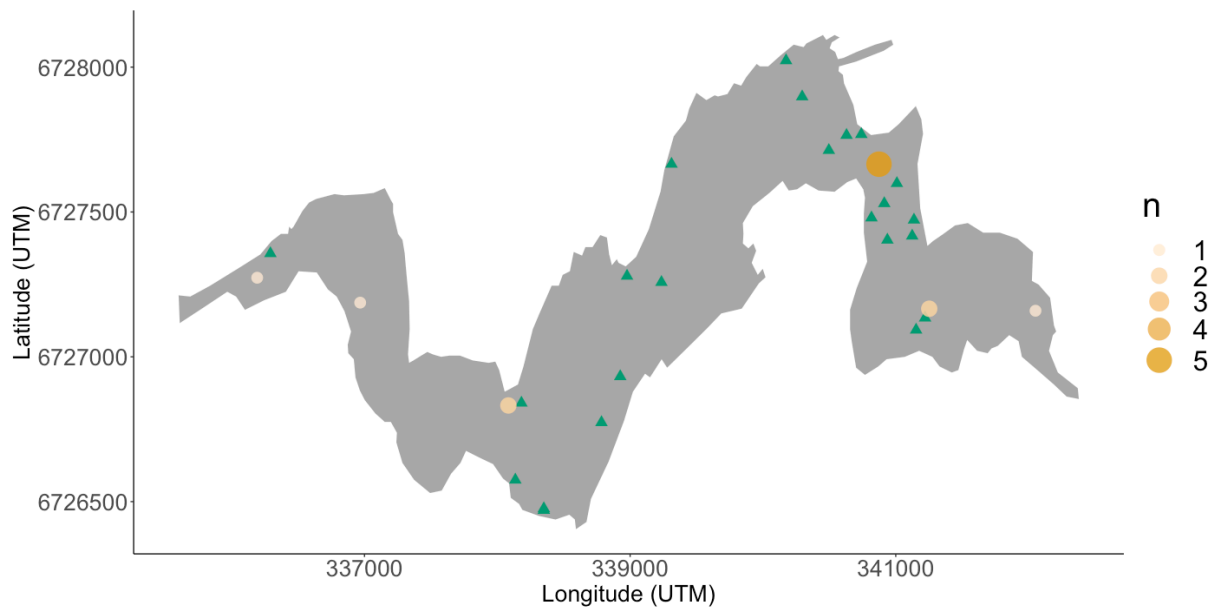
4.4 km, and 11 (55%) migrated minimum distance of 5.6 (Figure 9). No difference between naïve and sensor-enhanced dataset was observed for the total survivorship through the lake.

Neither length nor weight had an effect on smolt survival through Lake Evangervatnet (smolt weight,  $z_{1,19} = -0.98$ ,  $p = 0.33$ ; smolt length,  $z_{1,19} = 1.12$ ,  $p = 0.23$ ).



**Figure 9.** Survival per km through Lake Evangervatnet for the 20 smolts. Black line representing sensor-enhanced dataset (i.e. information included from predator tags), and dotted red line representing naïve dataset (i.e. no information included from predator tags). Line corresponding numbers indicate receiver ID.

Mortality occurred throughout the lake. Highest mortality rates were observed approximately 1.5 kilometers downstream, around the narrowest part of Lake Evangervatnet (Figure 10). Of the six positive predation events, one was located in the first basin, two around the narrow sound, two approximately four kilometers downstream and one at the lake outlet.



**Figure 10.** Map showing mortality of smolts throughout Lake Evangervatnet (circles indicating smolt mortality location, size indicating count), and capture sites of trout from rod and reel fishing 2019 (green triangles).

### 3.3.6 Predator sampling

Trout capture sites can be seen in Figure 10. Only brown trout (*Salmo trutta*) were caught during the rod and reel fishing, both in 2016 and 2019. Size ranged from 25 to 90 cm (mean=37 cm) (Appendix 4). The stomach of the trout that was euthanized because of bleeding was screened, and a salmon smolt was found in the stomach (trout: 46.5 cm, smolt: 11 cm). Catch-per-unit-effort (CPUE) was 1.27 fish/hour in 2016 and 0.58 fish/hour in 2019. There was no change in CPUE over time within the years. Of avian predators, the most numerous species was red-breasted merganser (*Mergus serrator*)(n=25), but also herring gull (*Larus argentatus*) (n=4), mew gull (*Larus canus*) (n=3), great cormorant (*Phalacrocorax carbo*) (n=7) and white-tailed eagle (*Haliaeetus albicilla*)(n=2) were observed.

### 3.3.7 Smolt behavior

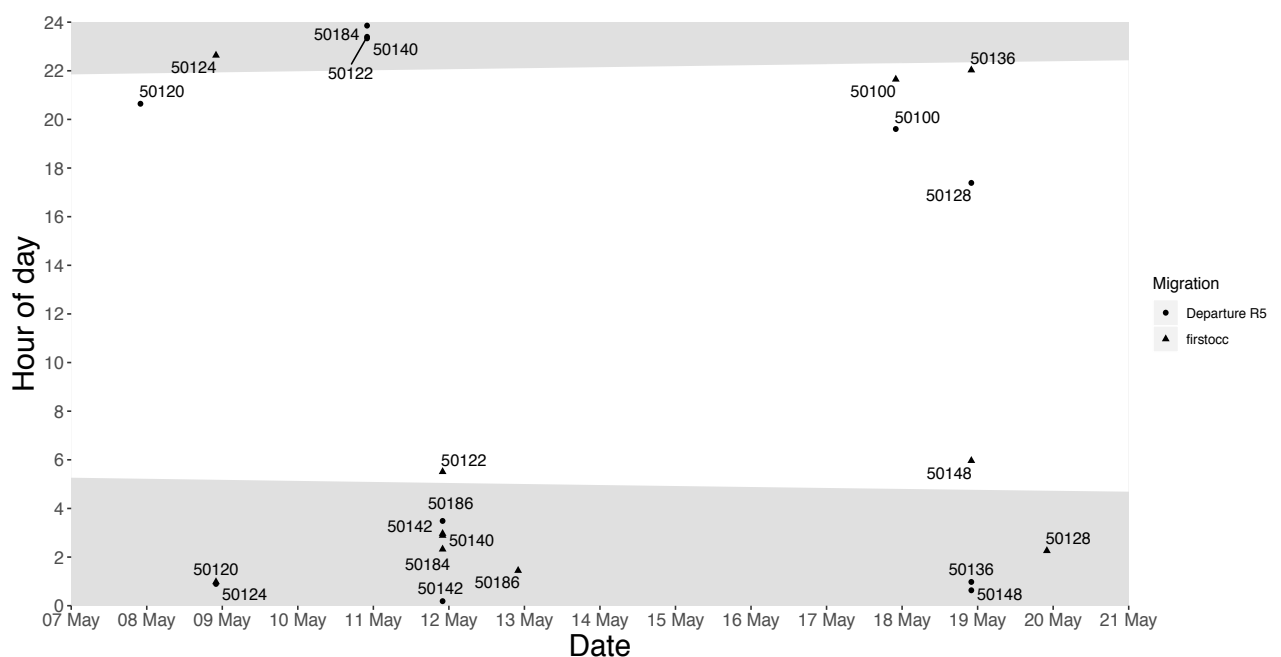
#### 3.3.7.1 Progression rates

Progression rates (calculated between inlet and 1.5 km downstream) for the 20 salmon smolts varied from 0.018 to 0.38 m/s (mean  $0.15 \pm 0.12$ ) and had no effect on survival ( $z_{1,19} = -0.7$ ,  $p=0.48$ ).

To reach the outlet, the eight surviving smolts spent between 3 and 17 days (mean  $7.9 \pm 6.2$  SD). Progression rates between lake entry and outlet ranged from 0.004 to 0.028 m/s (mean  $0.016 \pm 0.001$ ). Smolts did not exit the lake upon reaching the outlet but spent a mean three days around the lake exit before continuing the downstream migration. To exit the lake, survivors spent between 3 and 22 days (mean  $11.1 \pm 6.4$  SD). Thus, progression rate from lake entry to lake exit varied from 0.0035 to 0.026 m/s (mean  $0.01 \pm 0.007$ ).

#### 3.3.7.2 In lake diel movement

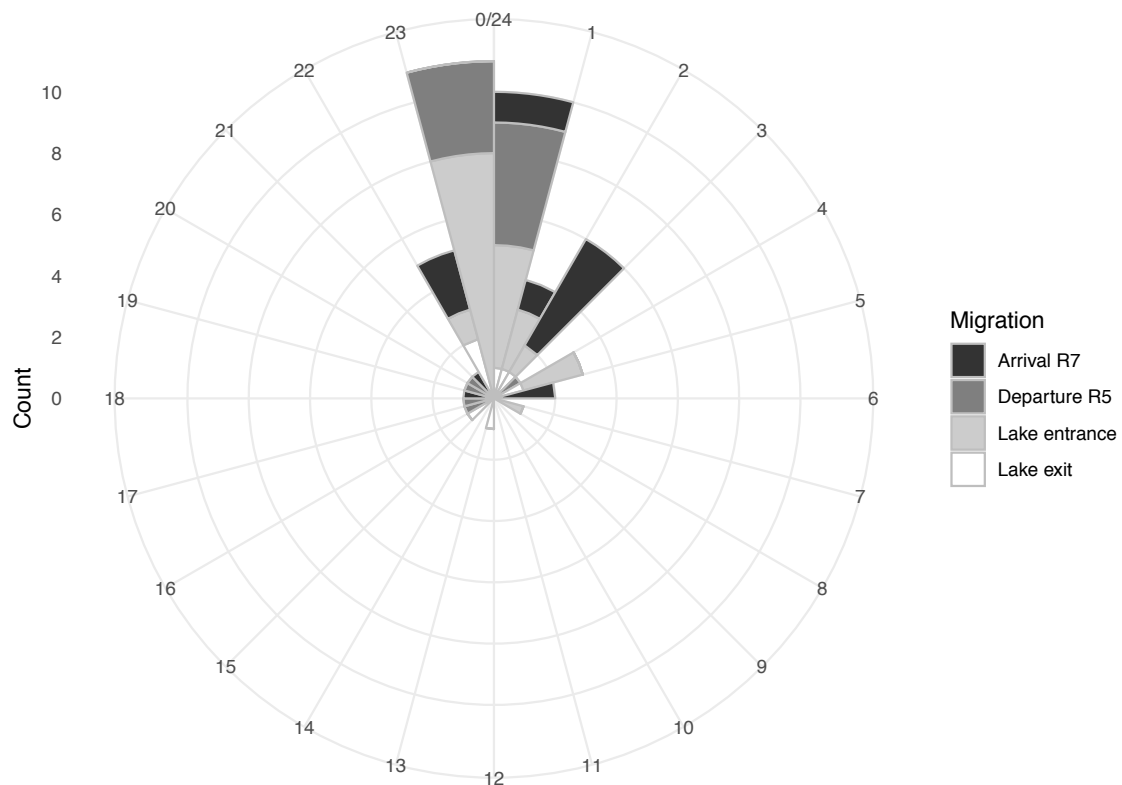
Of the 20 smolts in this study, eleven made it to Receiver 7, approximately 4.3 km downstream in the lake. The smolts exhibited a nocturnal in-lake migration pattern, with 68 % of arrival/departure times occurring at night, 23 % during the dim-period and 9 % during daytime (Figure 12). The smolts spent between 2 and 22 hours to traverse the 2.9 km stretch between receiver 5 and 7. A pattern was observed, in which smolts either migrated the whole distance through one night or departed one night and arrived the following night.



**Figure 12.** Smolt migration between receiver 5 and 7. Date on x-axis and time of day in hours on x-axis. Hour 0 and 24 both symbolize midnight. The shaded area at the top and bottom of

*the figure indicates dark (after sunset and before sunrise). Circular points symbolize the last detection at receiver 5 and the triangular points symbolize the first detection at receiver 7. The number at each point is ID of smolt.*

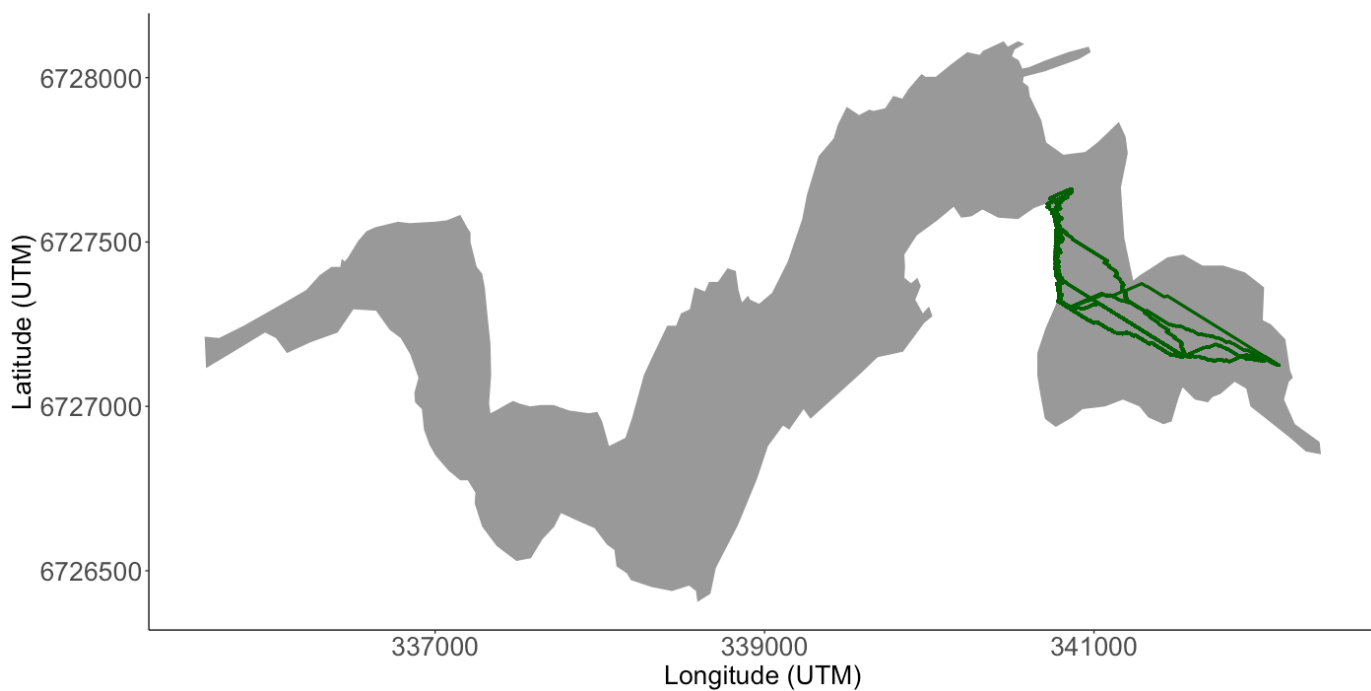
Similarly, migration into, within and out of Lake Evangervatnet was nocturnal ( $\bar{r} = 35.4$ ,  $p < 0.01$ ; Figure 13). Most of the smolts entered the lake within 6 hours after release, and 95 % of them entered the lake during nighttime. Lake exit was also primarily at night, with 75% of smolts leaving during dark.



**Figure 13.** Polar histogram showing time of diel migration into, within and out of Lake Evangervatnet for Atlantic salmon smolts. In-lake migration is represented by records of last detection at receiver 5 (Departure R5) and corresponding first detection at receiver 7 (Arrival R7). Radial distance (count) represents number of movement events.

### 3.3.7.3 Smolt movement

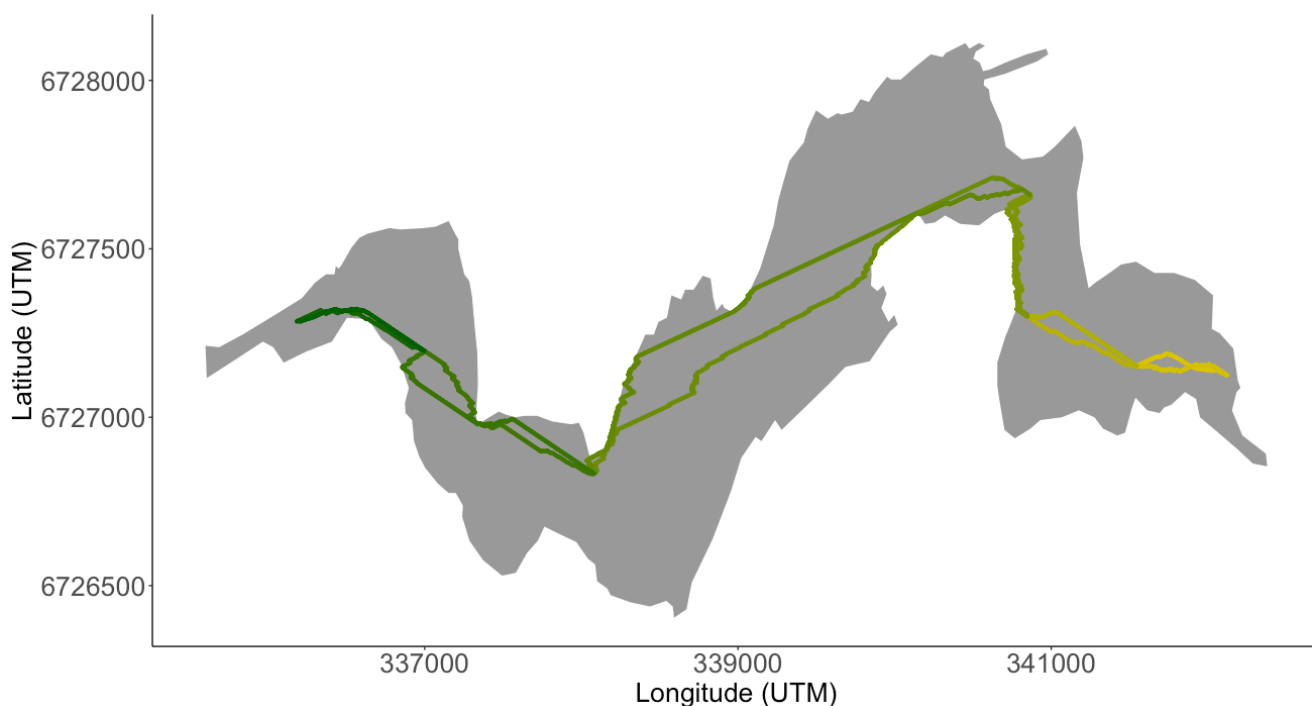
The Atlantic salmon smolts movement in the lake was not unidirectional, where smolts progressed consistently westward to the lake outlet. Many smolts spent a long time in the first basin before dying (Figure 14) or getting out into the main part of the lake.



**Figure 14.** Example of smolt (ID=50126) within the first basin unable to progress out of the first basin. The lines show movement between receivers and consist of shortest paths (shortestPath function in gdistance package) between temporally ordered detections. This individual was located in the first basin for 24 days before being eaten.



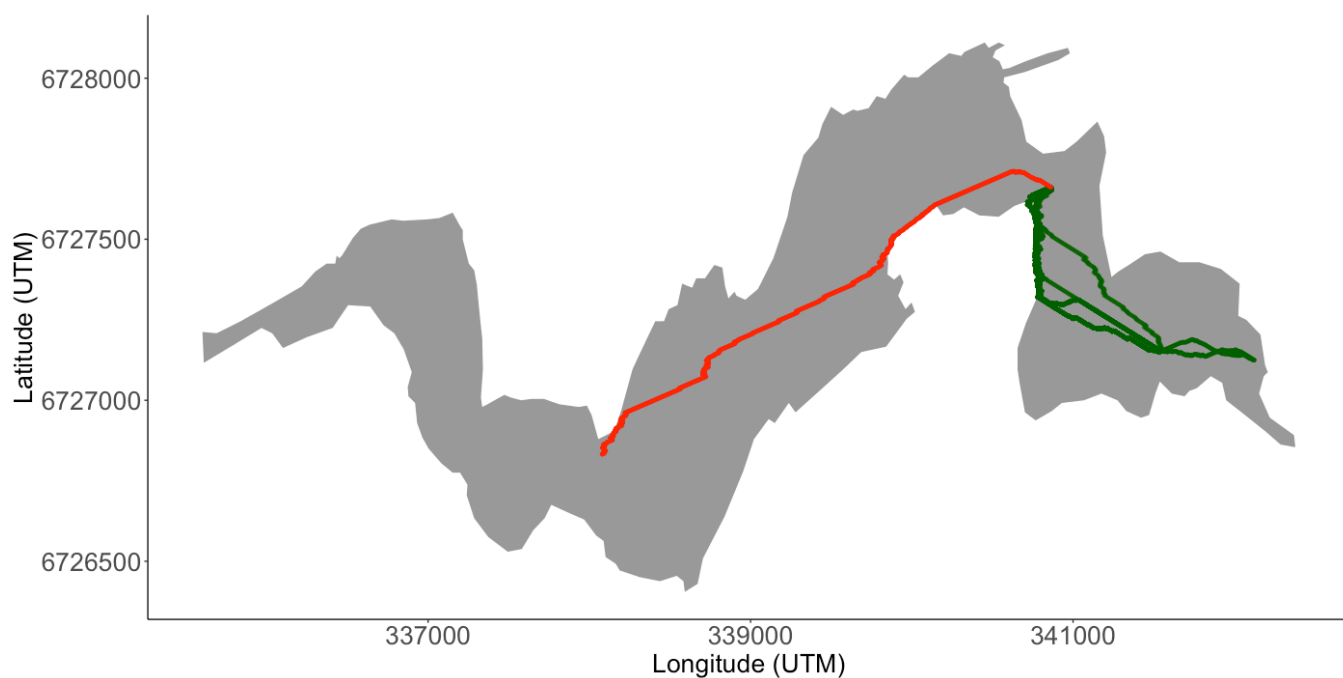
Among the smolts that made it past the first basin, ten (90 %) exhibited several periods of eastward movement, opposite the lake outlet (Figure 15). Several smolts reached the outlet, only to turn east again, swimming at random back and forth between receivers up to 10 times before exiting the lake.



**Figure 15.** Movement for one of the surviving smolts (ID = 50124) in Lake Evangervatnet (ID=). The lines show movement between receivers and consist of shortest path (shortestPath function in gdistance package) between temporally ordered detections. The progressing color-change of the track symbolize time, where yellow is early (07.05.2019) and dark green is late (25.05.2019) in the smolt's lake-residency. This smolt was quick out of the first basin, but made several long-distance movements away from the lake outlet in the main part of Lake Evangervatnet.

### 3.3.7.4 Predator movement

Trout could move with the tag in the gastrointestinal tract (retention time) for over 50 hours, and showed high mobility within the lake, moving distances of 3 km (Figure 16) with a progression rate of 0.27 m/s before expulsion of tag.



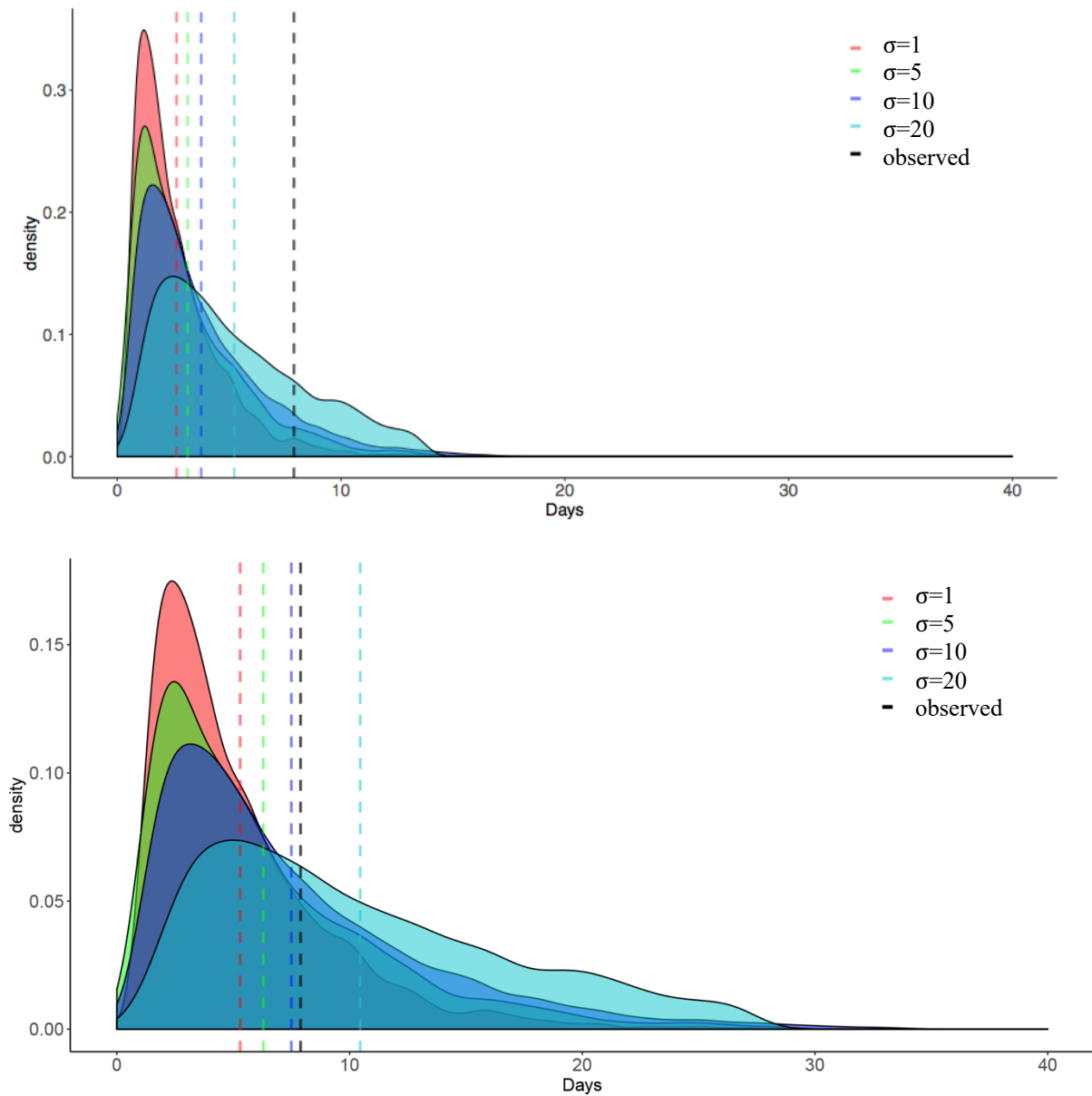
**Figure 16.** Movement for one of the eaten smolts (ID=50146) in Lake Evangervatnet. The lines show movement between receivers and consist of shortest path (shortestPath function in gdistance package) between temporally ordered detections. Green lines represent the smolt and red line represent the trout movement after having eaten the smolt. This smolt got eaten after two days in the lake, around the narrow sound in the lake.

### 3.3.8 Mechanistic smolt movement model

#### 3.3.8.1 Density distribution of travel length and time within the lake

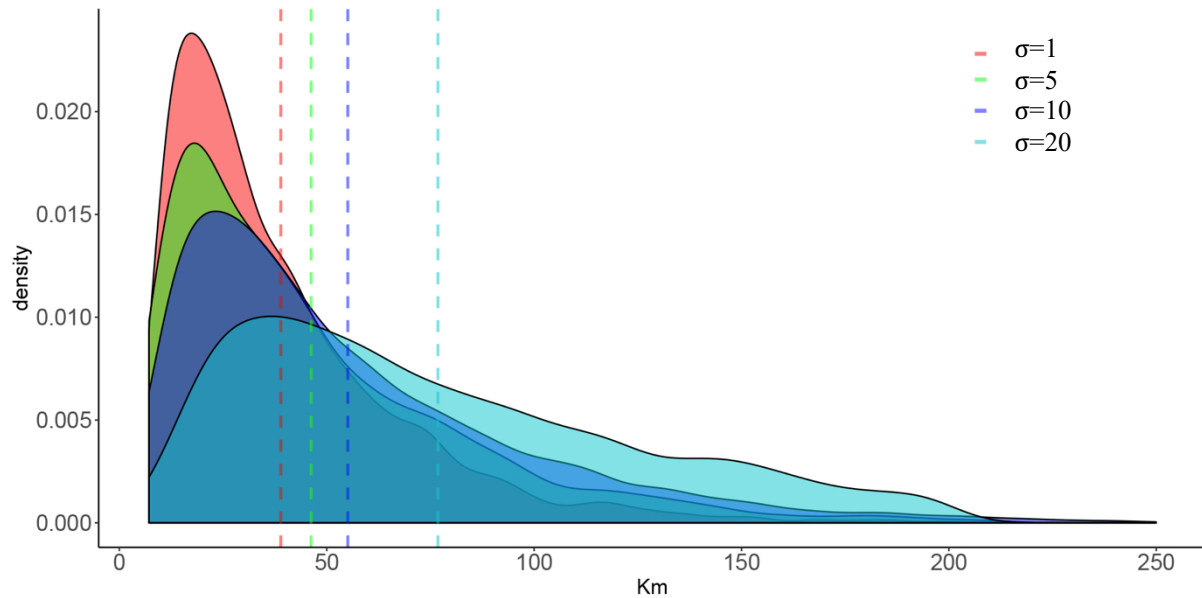
The simulated mean time spent to progress through lake varied among the four simulation groups. The smaller the value of  $\sigma$ , the faster they progressed through the lake. Assuming the simulated smolts moved constantly through a 24 hour day, the simulation output was skewed to the left compared to the observed values for all  $\sigma$  (Figure 17, top plot). By

accounting for diel migration at night, and no horizontal movement during the day, the mean time spent through the lake doubled, and was also more similar to the observed data (figure 17, bottom plot).



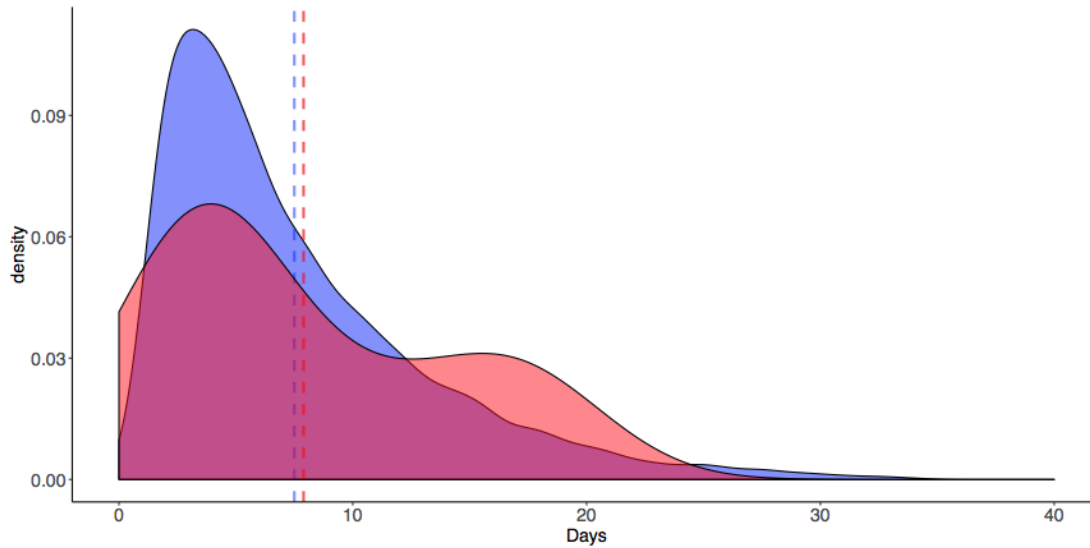
**Figure 17.** Plots of travel time density distribution in days for four  $\sigma$  (SD of turning angle). Top plot illustrates constant movement at day and night at 0.17 m/s speed. Bottom plot illustrates constant movement at night (12 hours of a 24-hour day) and stand-still at day, with speed of 0.17 m/s speed. Different color of density distribution represents different  $\sigma$ . Dashed lines indicate the mean number of days to traverse the lake for the four simulations with different  $\sigma$  (colors), and the black dashed line represent the mean of the observed data.

The total distance travelled by the simulated smolts within the 6.5 km lake inherited the same pattern, where the smaller standard deviation of theta decreased the total travel distance (Figure 18). Three of the simulation outputs ( $\sigma$ : 1,5,10) estimated mean travel distances of around 50 km, whereas the  $\sigma=20$  output mean was 76 km.



**Figure 18.** Plot of total distance travelled density distributions for the four simulations with varying  $\sigma$  (SD of turning angle). Dashed lines represent mean distance travelled for the different simulations. Distance travelled is constant whether smolts move 12 or 24 hours a day.

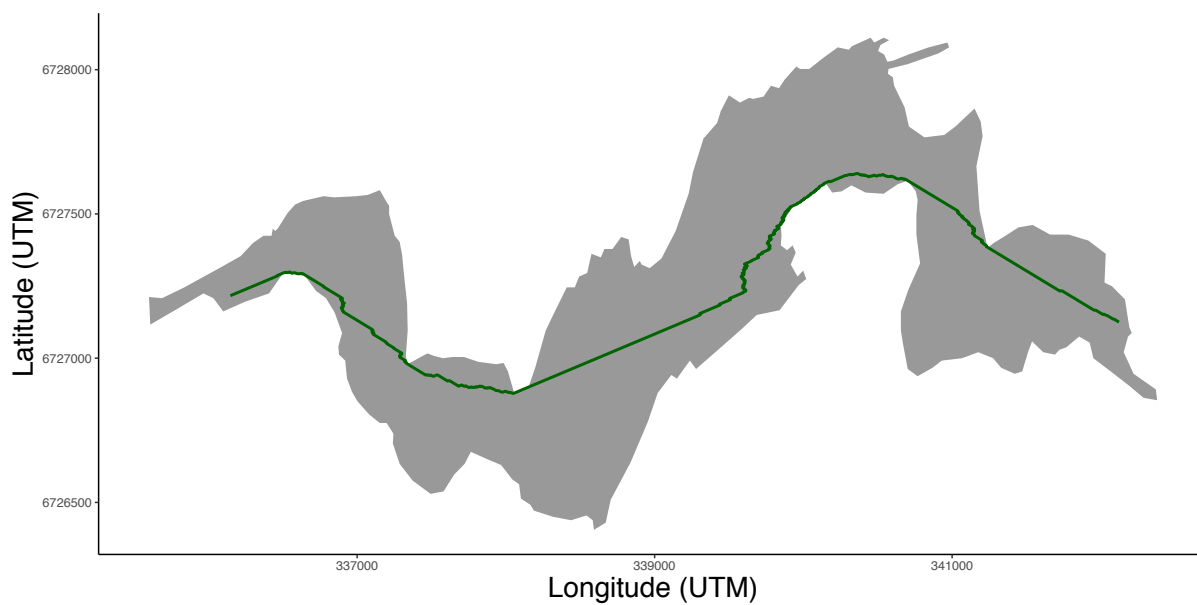
The model that best fit the observed data had a  $\sigma$  of 10 and nocturnal migration (Figure 19). Assuming these parameters are valid for in situ smolts in this study, the mean distance travelled within Lake Evangervatnet was 57 km with a nocturnal swim speed of 0.17 m/s and stand-still at day.



**Figure 19.** Plot showing the best fit model with  $\sigma = 10$  and movement for 12 (nighttime) hours a day (blue) and the observed values (red). Dashed lines indicate the means of the data.

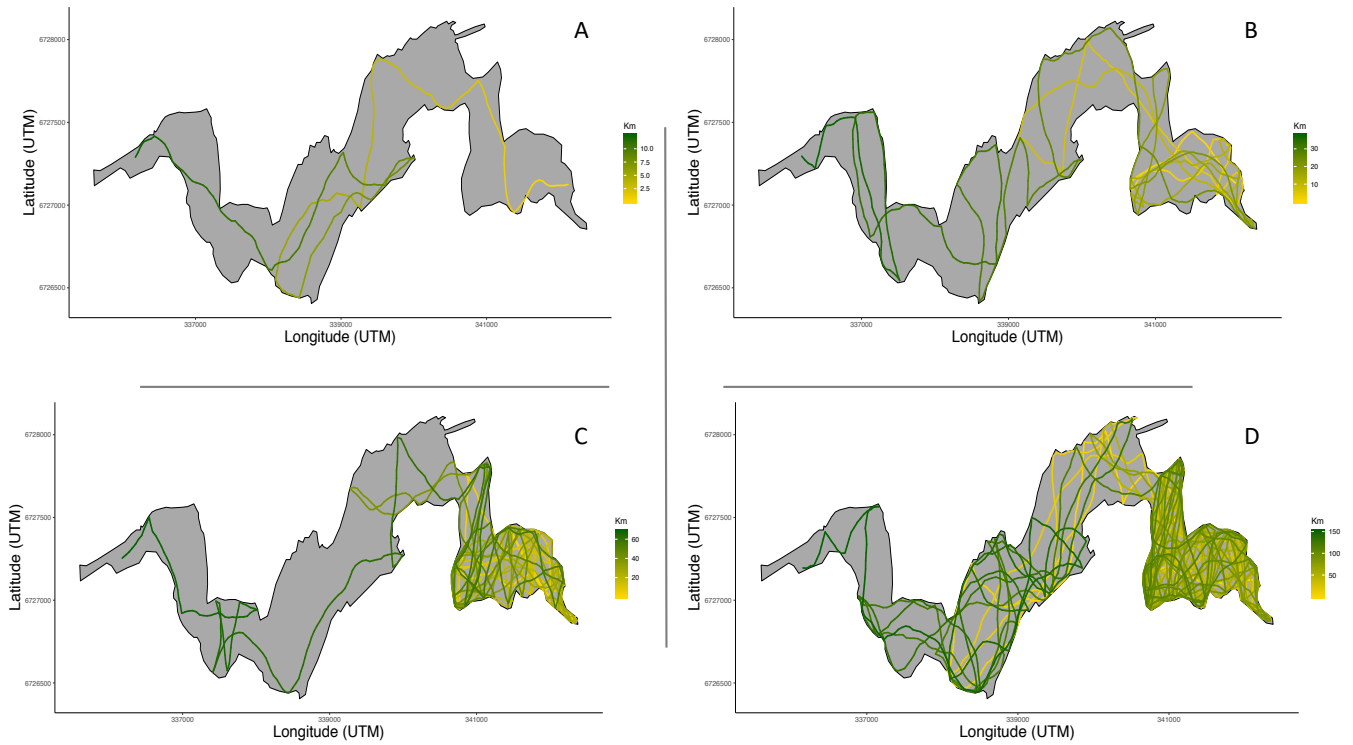
### 3.3.8.2 Simulated smolt tracks in the lake

Assuming smolts followed the most direct track, they would use 10.6 hours to traverse the 6.5 kilometer lake at a speed of 0.17 m/s (Figure 20). However, simulated smolts made extensive movements throughout the lake, concurring with what was observed from the field data (see section 3.3.7.3).



**Figure 20.** Simulation showing smolt track as the most direct track through Lake Evangervatnet from receiver 1 (inlet) to receiver 10 (outlet).

A pattern observed from the simulations was that virtual smolts often spent a good deal of time to transit the first basin (east) of the lake. Four simulated smolt tracks of the model with  $\sigma = 10$  can be seen in Figure 21.



**Figure 21.** Example of simulated tracks for four smolts moving at 0.17 m/s for 12 hours (nocturnal) a day. Yellow indicating start of track, green indicating end and successful passage through the lake. A: Simulated smolt travelled 12 km and used 1.7 days to exit the lake. B: Simulated smolt travelled 30 km and used 5 days to exit the lake. C: simulated smolt travelled 63 km and used 8.5 days to exit the lake. D: Simulated smolt travelled 150 km and used 21 days to exit the lake.

## 4.0 Discussion

This is the first study to directly investigate predation of migrating Atlantic salmon smolts in a lake environment, an area that has previously been recognized as a bottleneck for smolt survival (Honkanen et al. 2018, Kennedy et al. 2018). The novel predation sensor telemetry tag was validated in laboratory experiments and deployed in a field test in Lake Evangervatnet, Vosso, Norway. Surgical implantation and retention of tags did not affect survival of smolts, and tag effects were mild. During the experimental predation events, only 50% of the tags switched from pre- to post-predated, revealing limitations of this technology. The wild smolts in the field study exhibited low survival through the lake, with predation accounting for at least 50% of mortalities. Smolt movement within the lake was predominantly nocturnal, with slow progression rates and high in-lake residency time, probably caused by a multitude of seemingly random upstream movements. A mechanistic simulation model revealed potential spatiotemporal movement patterns of smolts in the lake, where simulated smolts travelled the lake nine times (mean) its length and exhibited non-directional movement in concurrence with field data, resulting in similar travel time distributions for both simulated and observed smolts.

### 4.1 Effect of tagging on smolts

The light weight and small size of the V5 tags make the tags suitable for tagging of wild Atlantic salmon smolts. All smolts implanted with dummy tags survived in our study, and only mild effects from the surgical procedure and negligible damage to inner organs from the tag were observed, although no control group was utilized for comparison of non-tagged smolts. Tag burden, effect the tag has on behavior, physiology, or survival of study fish, is often assumed to be insignificant in telemetry studies (Brownscombe et al. 2019). Yet, a number of studies show adverse effects of tags (Cooke et al. 2011, Jepsen et al. 2015). To increase reliability of results from acoustic telemetry research, information on tag effects of the specific tag on the specific species and size range should be available (Brownscombe et al. 2019). No research exists relating to tag effects from the V5 transmitters, and thus the tag effect study provides novel insights on this field. A common way to measure tag burden is with the tag weight relative to smolt weight (tag weight ratio), and upper limits between 2 and 10 % are suggested (Jepsen et al. 2002). In general, the lower the tag weight ratio, the less tag



effects (Brown et al. 2010), and injectable miniature tags for salmon smolts exist (Deng et al. 2015), though as of yet not with a predation sensor. Tag weight ratio is expected to have varying effect depending on the surrounding environment of the fish, and a smolt in a riverine or marine area will face dissimilar conditions than a smolt in a lacustrine area. In deeper waters, the tag can affect the individual's capability to remain neutrally buoyant and reduce likelihood of survival (Wright et al. 2019, Oppedal et al. 2020). In saline waters, the buoyancy of smolts increases, and thus the tag effect on buoyancy decreases. Hence, deep lacustrine areas such as our study site are where tag weight probably has highest potential for negative effects. Therefore, a lower tag weight ratio was proposed by (Wright et al. 2019) at around 2 %, keeping the observed tag burdens in this study of ~3 % at a similar level and the tag usable for smolt studies.

In the current study, the observed tag effects were minor, and all dummy-tagged smolts survived. Yet the tag impact on behavior was not examined. Capture, handling, sedation, and tagging procedure of smolts can induce stress and selective mortality of fish in a poorer condition (Armstrong et al. 1990, Cooke et al. 2016, Brownscombe et al. 2019). This in turn might affect the results of the study, by tagged smolts being more prone to predation or higher mortality than untagged individuals. Additionally, the small sample size utilized in the laboratory and field tests reduces the statistical power and increase the uncertainty of the results. The smolts were kept in shallow tanks where buoyancy compensation was not investigated, and studies have shown that both volume and weight of tags can impact buoyancy in smolts (Macaulay et al. 2020). Knowing the impacts tags have on smolts is essential when interpreting results, and future research should investigate the buoyancy effect of different weighted tags in lacustrine areas.

#### 4.2 Validation of Vemco V5 predation tag

Experimental predation events revealed important aspects for consideration when interpreting the field data. The novel predation tag can positively identify predation of Atlantic salmon smolts by piscine predators, concurrently revealing behavioral aspects of the predator, although limitations in this sensor technology were revealed. The predation sensor reacts with gastric acid in the predator stomach, corroding a biopolymer that induces the signal switch. Little is known about the effects of temperature on gastric acid production nor the difference in production between largemouth bass utilized by Halfyard et al. (2017) and brown trout and the effect this could have on tag efficiency. The observed false negatives (i.e.

tag failure to switch signal from pre- to post-predated after predation event) of 50% is significantly higher than the 6 % reported by Halfyard et al. (2017), and the findings will hopefully assist in refining the performance of the sensor. In the case of signal switch failure, an unregistered predation event can lead to bias, because detections will be classified as smolt not predator. However, this is most likely to impact the fine-scale temporal and spatial analysis, given that predators expelled the tags within the study array over one/two days (Daniels et al. 2019). The high number of false negatives observed in laboratory trials might have been impacted by the force-feeding procedure. In contrast to the methods by (Halfyard et al. 2017) where predators were actively feeding on smolts, the procedure in this study might have induced stress, further impacting the digestion of trout (Olsen et al. 2005) and the observed results. On the contrary, false-positives (i.e. tag switch signal from pre- to post-predated without predation occurring) may overinflate the predation estimate by tags shifting to post-predation without predation occurring and this was observed on average 47 days post-tagging (Halfyard et al. 2017), thus not likely to influence results from our field study.

Laboratory tag retention times (time between predation event and expulsion of tag) in trout averaged 9.8 days at 12 °C , longer than what has been observed in striped bass (*Morone saxatilis*) at 23 °C (mean 1.8 days) and largemouth bass (*Micropterus salmoides*) at 12 °C (mean 8 days) (Schultz et al. 2015, Halfyard et al. 2017). The prolonged retention times observed in this study might be due to species specific differences in metabolism and digestion by predators, size of prey, or prey species (Hayward and Bushmann 1994, He and Wurtsbaugh 2011, Schultz et al. 2015). This is not likely to drastically alter the results in this study, because all the tags from the positive predation events in the field study was sedentary (i.e. expelled by predator) after a maximum of three days post signal switch, indicating a shorter retention time in situ. Similar retention times were estimated by Daniels et al. (2019), who reported limited movement by striped bass (*Morone saxatilis*) post-predation in the Miramichi river, Canada. Within field studies, the period of retention before signal switch (signal lag) could lead to bias, where predator movements are classified as smolt behavior before tag switch. For instance, there is a possibility of anadromous trout with a tagged smolt in the gastrointestinal tract migrating up- or downstream out of the array during signal lag, though this is unlikely because predators in this study stayed within the receiver array, and no upstream movement out of the lake was observed from trout nor smolts. Signal lag time in our experimental validation study was on average 35.4 hours, longer than the 22 and 9 hours (tag generation 1 and 2 respectively) observed by Halfyard et al. (2017) at the same temperatures (12°C). The temperatures utilized in predation trials by Halfyard et al. (2017) and in the

current study were all 12 °C or above, whereas lake temperature in the field study was on average 7.8°C. Whether the cooler temperatures in the lake prolong signal lag time is unknown; Halfyard et al. (2017) modelled a regression indicating increasing retention and signal lag time with decreasing temperature but the coldest temperature in their study was 12°C. The predation sensor tags have therefore not been tested at these temperatures, and little is known about these processes at cold temperatures other than they have the potential to influence observations. Future studies at cold temperatures should consider additional tag validation studies.

By being able to segregate surviving and predated fish, interpretation of migration behavior and movements will be more valid (Gibson et al. 2015), however the added information by utilizing the predation tags did not appear to add as much as anticipated. For example, it seems from the results that no eaten smolts (i.e. trout with smolt and tag in stomach) left the lake, skewing the survival estimates that would have been observed by utilizing normal tags. Inclusion of the tag validation experiment was crucial when interpreting the field data, because conclusions about predation and natural mortality would be very different if we assumed the observed field data to be true. For instance, we observed high mortality (stationary tags in the lake without predation sensor switch) around the hydro power station that would be interpreted as natural mortality. The same mortality pattern was observed by Haugen et al. 2017, leading to questions asked about the influence of the outlet water on survival. Even though this might still have an effect, we also observed substantial predation in this area, and knowing of the tag limitations, the mortalities might be caused by predation and this narrow area being a bottleneck for the migrating smolts. Therefore, validation of the tag technology increases the confidence in the findings, and improves interpretations of the field observations (Brownscombe et al. 2019).

#### 4.3 Field study – smolt survival and behaviour

Smolt survival through Lake Evangervatnet was low compared to riverine survival rates (Thorstad et al. 2012b), with 40 % successfully traversing the lake. Half of mortalities were attributed to predation by trout (*Salmo trutta*). Because the only fish caught during research fishing was trout, it was believed to be the only piscine predator in the lake, and the large size of trout indicate piscivory. Both resident and anadromous trout are opportunistic predators, and upon reaching 13-15 cm they can start fish feeding (L’Abee-Lund et al. 1992). When they reach a size of >31 cm they primarily feed on fish (Keeley and Grant 2001).

Additionally, three smolts disappeared within the lake, possibly to avian predation by mergansers (*Mergus serrator*) or cormorants (*Phalacrocorax carbo*) (Aas et al. 2011) observed in Lake Evangervatnet. Assuming the rate of false negatives in the lab experiment reflected the performance in the field study, the number of predation events observed is most likely a minimum estimate. Mortality was highest during the first two kilometers of the lake, in concordance with similar studies by Kennedy et al. (2018), which reported a mean 31.2 % mortality per km in lake-river confluences for Atlantic salmon smolts. Kennedy et al. (2018) assumed predation by pike to be the main cause of mortality, however this was based on the assumption that sedentary tags that aggregated around high-density pike areas were indicative of predation. Similarly, smolts in Loch Lomond had 40 % mortality during lake migration, assumed to be from predation (Honkanen et al. 2018), without empirical evidence or *a priori* decision criteria for attributing predation. Haugen et al. (2017) also reported high mortality rates in Lake Evangervatnet, with mortality rates for wild smolts of 49 and 82 %, with the difference between the two groups the tag weight ratio of 6.5% and 8.2% respectively. Haugen et al. (2017) concluded predation by trout to account for most of the mortality. Because quantifying predation from telemetry is inherently complicated (Hightower et al. 2001), and identifying predation occurrence both spatially and temporally by use of behavioral analysis might not be accurate enough (Gibson et al. 2015) the novel predation tag technology has the potential to offer more reliable predation estimates, yet refinement of the technology is still needed. Because we were still able to attribute half of mortalities to predation utilizing the new sensor technology, this is the first study to directly investigate predation in a lake environment.

The wild smolts exhibited nocturnal movement in Lake Evangervatnet, and 95 % of smolts entered, whereas 75 % exited during night. Given that smolts were released after dark and most entered the same night, this could bias the entrance results. Four of the smolts did not enter the lake the first night, but still entered at night on the successive days, thus supporting the hypothesis of nocturnal lake entrance. Within the lake, highest activity was also observed at night, with only 9 % of smolt migration occurring diurnally. Nocturnal migration is well documented in riverine smolt migration (Moore et al. 1998, Ibbotson et al. 2006), and is thought to be a strategy for predator avoidance (Thorstad et al. 2012b). However, nocturnal migration in lakes is only documented once before, in Loch Voil Scotland (Thorpe et al. 1981). Most smolts migrated between the furthest receivers during one night, though a fraction of smolts exhibited migration over consecutive days. These smolts could in theory migrate the distance also during day with a slower progression rate but seeing

as smolts entered the downstream gate at night, and not at random throughout a 24-hour day, we inferred that smolts ceased migration during daytime. Other studies have shown smolts migrating in lakes to have long diurnal periods of inactivity (Honkanen et al. 2018), fitting well with our observed nocturnal migration pattern. Of the limited activity observed during the day in the field study, most was recorded at the end of the field study. Similar results were reported by Ibbotson et al. (2006) and Thorpe et al. (1994), who observed increased daytime migration later in the season induced by warming temperature. Increased activity during daytime was mainly observed after lake temperature reached 7 °C on the 17<sup>th</sup> of May, fitting well with the findings by Thorpe et al. (1994) who reported the same 7 °C threshold for change in diurnal migration in rivers. I argue that these findings suggest that Atlantic salmon smolts follow the same environmental cues in both riverine and lacustrine environments. With smolt migration in lakes being a topic of limited knowledge (Thorstad et al. 2012b), this offers new knowledge of smolt behavior in lakes and provides valuable insights for further mitigation efforts in the Vosso River system.

The surviving smolts were slow to migrate through the 6.5 km long lake, with a mean progression rate (i.e. minimum speed of displacement between two locations, including active and passive movement) between entry and lake exit of 0.01 m/s. Migration in riverine segments is relatively expeditious, and is known to consist of both passive movement and active swimming (Thorstad et al. 2012b), with reported mean progression rates of 0.03 m/s (Davidsen et al. 2009), 0.04 m/s (Spicer et al. 1995), and 0.14 m/s (Martin et al. 2009). In rivers, smolts can passively drift or actively follow the current, leading them downstream towards the estuary. Lakes contain more complicated flow patterns and sections of still water, and of the limited studies on wild smolt migration through natural lakes, only one reports progression rate, with a mean of 0.02 m/s (Hansen and Jonsson 1985). Despite the old conceptions of passive smolt migration through lakes (Thorpe et al. 1981), several studies have now shown active movement to be the main cause of displacement (Bourgeois and O'Connell 1988, Honkanen et al. 2018). Because the range of the receivers in the lake overlapped in the first basin, tracking smolt movement in this area was difficult. Given that receivers had good range, there will be bias in distance and speed measures, because a smolt moving between two receivers will in fact move between the range edge of receivers, and receiver range is in turn impacted by environmental factors (Kessel et al. 2014). Yet, the slow progression rate observed in this study and by Hansen and Jonsson (1985) are indicative of smolt moving inefficiently through lakes.

#### 4.4 Revelations of smolt behavior by mechanistic model

The mechanistic model simulating smolt movement through Lake Evangervatnet assuming nocturnal migration provided realistically timed tracks, suggesting that their movement could be close to a correlated random walk. The model parameters are biologically sensible (Zabel and Anderson 1997), derived from literature on smolt movement (Thorpe et al. 1981, Thorstad et al. 2004, Honkanen et al. 2018) and applicable for other studies researching smolt migration through lakes. Even though smolts exhibited slow progression rates in this study, the mean swimming speed within the lake was faster, because smolts made extensive movements in the lake, both downstream and upstream, before eventually reaching the lake outlet. Laboratory experiments have shown that Atlantic salmon smolts can swim at speeds of up to 0.54 m/s for a sustained period of time (Tang and Wardle 1992), and Thorstad et al. (2004) reported in situ mean swimming speeds of post-smolts of 0.17 m/s. If the smolts followed the shortest path through the lake with a speed of 0.17 m/s, they could in theory traverse the lake in under 11 hours. Instead, surviving smolts spent a mean of 11 days in the lake with a multitude of random movements. These results correspond with those of Honkanen et al. (2018), where random movement of smolts through Loch Lomond were observed, with smolts migrating distances of up to nine times the length of the lake. Thorpe et al. (1981) also observed random displacements of smolts in Loch Voil, with smolts shown to change direction frequently. Additionally, Honkanen et al. (2018) reported several periods of inactivity up to 12.6 hours, perhaps corresponding to the nocturnality observed in Lake Evangervatnet although the timing of movements was not detailed. Regardless, this supports the reasoning for 12-hour breaks in the model. Thus, we argue that the slow progression rates observed was most likely an effect of the environment and navigational difficulty, and not the physiological capabilities.

The simulation is a simplification of reality, and even though it explains travel times and behavior of smolts well, all models have limitations. Firstly, assuming individual movement of smolts might be inaccurate as smolts can form schools during downstream migration (Riley et al. 2014). Further, the simulation assumes the lake to be homogenous, whereas observations show that the lake has complicated flow patterns, especially in the first basin where an eddy is formed before temperatures reach 7 °C (Isaksen et al. 2019). Because smolts are negatively rheotactic (McCormick et al. 1998), currents moving in other directions than the downstream direction might confuse and delay the smolts. Additionally, the Evanger Hydropower Station outlet can further alter currents during special conditions (Isaksen et al.

2019), perhaps causing further migration delay. Nonetheless, simulations can be useful when getting at challenging ecological questions (DeAngelis and Grimm 2014), and Zabel and Anderson (1997) and Booker et al. (2008) both utilized individual-based simulations to reveal salmon trajectories. Similarly, Papastamatiou et al. (2013) simulated tiger shark movements using a random walk model to explore what factors might impact the observed partial migration in this species. By addressing ecological aspects of smolt migration that is usually hard to investigate, the mechanistic model used in this study can offer novel information in an efficient and biological sensible way.

The implications of smolts lacking the ability to efficiently navigate lakes are multifold. First, increased lake residency can increase the predation rate. Secondly, the energy expenditure for smolts in lakes would be high, as long distances are covered, possibly leading to reduced fitness (Strople et al. 2018). In this simulation, smolts travelled a mean 57 km through the lake, covering the length of the lake nine times, the same ratios as one of three smolts observed by Honkanen et al. (2018). Thirdly, delays of migration can lead to suboptimal timing of sea-entry (McCormick et al. 1998). Orciari and Leonard (2011) found that genetics can impact migration timing, and genetically distinct local populations within rivers adapted for their specific life-histories have been found in Atlantic salmon (Heggberget et al. 1986). A large lake may be a natural barrier for salmon that separates populations such that there might be distinct populations downstream and upstream of Lake Evangervatnet. Rearing of hatchery smolts has been utilized to save the Vosso population (Barlaup et al. 2018). Smolts are towed out of the river because of high rates of mortality among smolts released in the river, allowing them to bypass a potentially important selective bottleneck. A long-term consequence of this may be to degrade the population by breeding salmon from different populations in the river and letting smolts bypass the lake that might be an important cull of the population and might also explain the apparent random migration through the lake.

Migration out of Evanger is not necessarily predictive of smolt success. The Bolstadfjord downstream of Evanger is also a slow-moving area that may impede migration and expanded research should include receivers further downstream of Evangervatnet to improve our understanding of migration and survival. Further, by placing receivers in triangulated grids in the first basin of Lake Evangervatnet, the fine-scale movements of smolt and trout can be obtained (Leander et al. 2020), helping us understand the effect of currents, the Evanger Hydropower Station and predator-prey relations in Lake Evangervatnet. A more refined model can also benefit from the added triangulation information, by getting in situ estimates of smolt turning angles ( $\theta$ ) and/or turning angle SD ( $\sigma$ ) and mean swimming speeds

of smolts in the lake. Additionally, the model could be improved by implementing flow patterns, which probably impact smolt movement.

## 5.0 Conclusion

Despite limitations of the predation sensor based on laboratory validation, this study reveals the potential for added information granted from these novel tags (because of the small size and limited tag burden), retaining the possibility to separate live and predated smolts. The present study provides evidence that smolts are subject to heavy predation in lakes, and struggle to navigate through still waters. Further, the results from the field study have shown that Atlantic salmon smolts predominantly migrate nocturnally in lakes. The observations that smolts seemed to migrate nocturnally and at random was strengthened by simulating smolt movement through the lake via a mechanistic correlated random walk model, and this method can aid in mitigation efforts in Vosso, possibly also in other catchments containing lakes and offers a novel approach to investigating the lesser studied smolt migration through lakes. Further research in Lake Evangervatnet, utilizing a larger sample size and triangulation of movements to better understand mechanisms behind the high number of mortalities around the power station also observed by Haugen et al. (2017), can improve our knowledge of smolt migration through lakes and at the same time offer improved parameters for the mechanistic model.



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## 7.0 Appendices

### Appendix 1

*Appendix 1. Trout and smolt ID, length (cm), weight (g), operation time (s) and study output. Shifted signal (yes/no), retention time (days) and signal lag (h).*

<b>Predator Tag ID</b>	<b>Smolt length</b>	<b>Smolt weight</b>	<b>Trout length</b>	<b>Trout weight</b>	<b>External trout tag ID</b>	<b>Length of operation</b>	<b>Shifted signal</b>	<b>Retention time</b>	<b>Signal lag</b>
50188	14.2	19	40	501	LFI06241	406	yes	8	61
50190	15.6	28	45	769	LFI06238	230	yes	18	31
50194	12.9	17	39	460	LFI06234	260	yes	22	42
50198	13.2	15	48	1025	LFI06240	301	yes	3	13
50204	14.5	22	55	1560	LFI06237	255	yes	8	30
50192	14.2	22	37	448	LFI06235	190	no	10	N/A
50196	14.4	23	36	528	LFI06236	190	no	8	N/A
50200	13.4	19	54	1922	LFI06242	425	no	3	N/A
50202	14.5	23	37.5	470	LFI06233	214	no	10	N/A
50206	15.8	30	39.5	452	LFI06239	241	no	8	N/A

### Appendix 2

*Appendix 2. Overview of smolts utilized for the field study; ID nr is the tag id, Total length of operation is the whole procedure from start of sedation to return of tagged smolts in tank in seconds, Length of surgery is the part of the operation with surgical tagging intervention in seconds, Length(total length  $L_T$ ) in centimeters and Weight in grams.*

<b>ID nr</b>	<b>Total length of operation</b>	<b>Duration of surgery</b>	<b>Length</b>	<b>Weight</b>
50100	354	123	16.0	29
50120	320	88	15.4	26
50122	322	102	14.9	23
50124	382	182	17.0	33
50126	274	128	13.3	18
50128	276	94	14.6	22
50130	310	85	16.8	37

50132	294	88	14.1	20
50134	285	123	13.7	17
50136	305	109	13.2	16
50138	286	115	13.6	17
50140	269	82	14.6	23
50142	247	85	14.1	22
50144	211	70	13.0	16
50146	251	103	14.0	20
50148	238	88	13.2	17
50180	240	86	12.8	17
50182	265	131	14.4	22
50184	227	73	13.8	20
50186	274	92	13.4	18

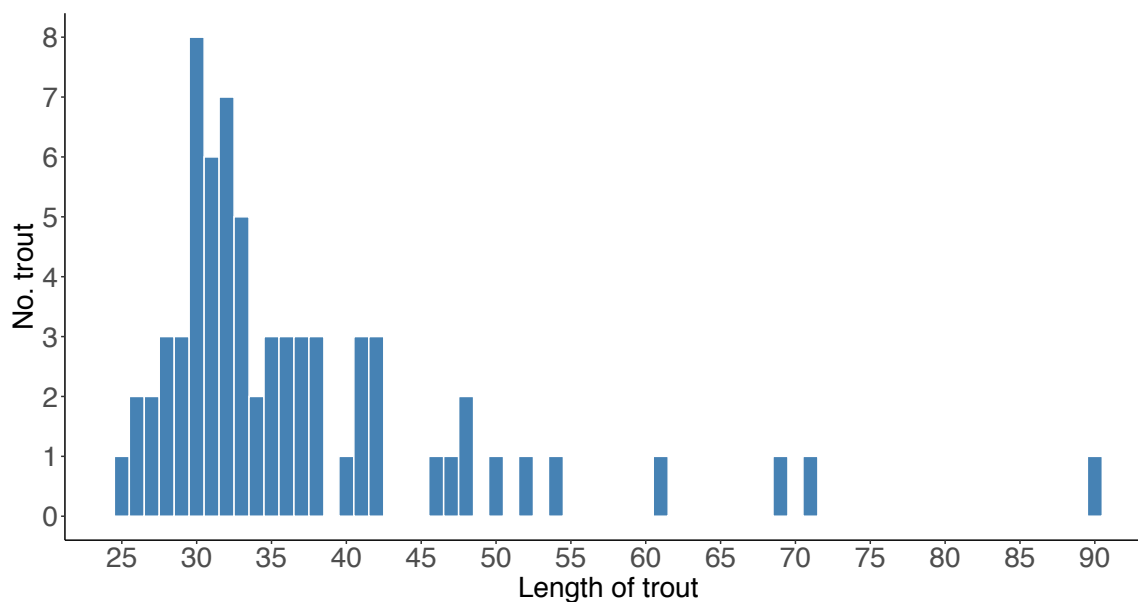
### Appendix 3

*Appendix 3. Capture site, depth (m) length (cm) of trout from sample fishing in Lake Evangervatnet from 07.05.2019 to 18.09.2019. Catch-per-unit-effort as number of fish/hour. Coordinates N/E in Decimal Degrees.*

<i>Catch date</i>	<i>Species</i>	<i>Length [cm]</i>	<i>Fishing depth</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Catch per unit effort (CPUE)</i>
<b>07.05.2019</b>	Trout	29	1	60.6484	6.0957	0.75
<b>07.05.2019</b>	Trout	47	1	60.6533	6.082	0.75
<b>07.05.2019</b>	Trout	31.5	3	60.6509	6.0937	0.75
<b>11.05.2019</b>	Trout	31.5	1	61.0897	6.1407	1
<b>15.05.2019</b>	Trout	31	3	60.648	6.0945	0.22
<b>15.05.2019</b>	Trout	31	3	61.0875	6.1524	0.22
<b>18.05.2019</b>	Trout	29	1	60.6507	6.0903	1
<b>18.05.2019</b>	Trout	30.5	3	61.0761	6.0899	1
<b>18.05.2019</b>	Trout	28	3	61.0737	6.0858	1
<b>18.05.2019</b>	Trout	46.5	3	61.0807	6.016	1

<b>24.05.2019</b>	Trout	34.5	3	61.0688	6.073	0.375
<b>24.05.2019</b>	Trout	30	1	61.0688	6.073	0.375
<b>24.05.2019</b>	Trout	90	3	61.0703	6.0664	0.375
<b>06.06.2019</b>	Trout	48	2	61.0915	6.1303	0.5
<b>05.07.2019</b>	Trout	30	2	61.0864	6.1496	1
<b>05.07.2019</b>	Trout	30	1	61.0856	6.1468	1
<b>05.07.2019</b>	Trout	26	2	61.0898	6.144	1
<b>05.07.2019</b>	Trout	33	1	61.0933	6.1264	1
<b>05.07.2019</b>	Trout	32	1	61.0812	6.0989	1
<b>13.09.2019</b>	Trout	31	2	61.0743	6.0674	2
<b>18.09.2019</b>	Trout	41	2.5	60.6514	6.0939	0.5
<b>18.09.2019</b>	Trout	31	2.5	60.6488	6.0546	0.5
<b>18.09.2019</b>	Trout	42	2.5	60.6524	6.0604	0.5

#### Appendix 4



*Appendix 4. Histogram of trout caught from research fishing in 2016 and 2019. Length of trout given in cm.*