

Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes

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Abstract

Smolt migration through lakes is hazardous, as the predation pressure can be extreme and the hydrology a great contrast to that of a riverine area. However, the mechanisms yielding these challenges have been scarcely investigated. We conducted an acoustic telemetry field study in Lake Evangervatnet, Voss, Norway, utilising Vemco V5 predation tags. Atlantic salmon (*Salmo salar*) smolts ($N = 20$) were tagged with the novel predation sensor tag to investigate mortality, the lacustrine migration behaviour of smolts, and the applicability of these tags for smolt studies. A total of 60% of tagged Atlantic salmon (*Salmo salar*) smolts perished in the lake. Half of the mortalities (30% of tagged fish) were directly attributed to predation by brown trout (*Salmo trutta*) based on predation sensors. The surviving smolts were slow to traverse the 6.5 km lake, with progression rate between lake inlet and outlet on average 0.016 m/s over a mean of 7.9 ± 6.2 (SD) days. Acoustic detections revealed a consistent pattern of nocturnal migration and multidirectional movements within the lake. By running a series of correlated random walks under varying parameters and comparing the simulated travel times to the observed travel time used by the tagged smolts, we emulated the observed behaviour of the smolts. These simulations suggested that smolts lacked the ability to efficiently navigate through the lake, instead swimming in random directions until they reached the lake outlet. Predation sensors can offer improved resolution when tracking the behaviour and fate of smolts and can facilitate better mitigation efforts by identifying survival bottlenecks and separating predation from non-predatory mortality.

KEYWORDS

biologging, conservation, migration, random walk, salmon, telemetry, trout

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1 | INTRODUCTION

Throughout their anadromous life cycle, Atlantic salmon (*Salmo salar*) encounter a variety of threats and survival bottlenecks, one of the most vital being the smolt and post-smolt migration phase (Thorstad, Whoriskey, et al., 2012). The downstream migration of smolts towards the sea generally occurs in springtime and is triggered by environmental cues such as water discharge and temperature (Bjerck et al., 2021; Jonsson & 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 (Fängstam, 1993). The riverine migration phase is well studied (Davidsen et al., 2009; Hansen & Jonsson, 1985; Ibbotson et al., 2006; Jonsson & Ruud-Hansen, 1985; Persson et al., 2019), but less focus has been put on migration through natural lakes, and knowledge about behaviour, migration patterns, predation, and other mechanisms of migration through lakes is limited (Lennox et al., 2020; Thorstad, Whoriskey, et al., 2012).

A third of Norwegian salmon rivers contain lacustrine areas. Studying these habitats is therefore vital for further conservation actions and to better manage Atlantic salmon populations (Thorstad, Whoriskey, et al., 2012). 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 lakes can make them especially demanding for actively migrating fish to navigate. Inefficient navigation through lakes can prolong exposure to predators, increase energetic expenditure, and desynchronise migration with optimal conditions at sea, negatively impacting smolt fitness (Rikardsen et al., 2004). Among the few studies on smolt migration through lakes and reservoirs, most report high mortality rates and attribute this mortality to predation (Honkanen et al., 2018; Jepsen et al., 1998; Kennedy et al., 2018).

Identification of predation events has long been a frontier in telemetry science (Gibson et al., 2015; Mech, 1967; 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 (Berejikian et al., 2016; Strøm et al., 2019; Thorstad, Uglem, et al., 2012). 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 (Daniels et al., 2019; Gibson et al., 2015). 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 the 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, Whoriskey, et al., 2012). 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 recent advance in telemetry science has led to the innovation of predation tags, sensors that can identify predation events.

There is a clear discrepancy between the number of river systems including lakes and the level of knowledge about smolt behaviour and mortality in this type of habitat (Lennox et al., 2020). The few studies that have observed smolts in lakes report deviant behaviour and high mortality rates (Honkanen et al., 2018; Kennedy et al., 2018). There is a need for research that focuses on migrating Atlantic salmon smolts in lakes. By utilising novel predation sensor technology, we aimed to improve the understanding of smolt migration 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 20 wild smolts with acoustic tags containing predation sensors. The study aimed to evaluate the role of predation and survival through a lake, subsequently gather information on smolt behaviour in lacustrine areas, and use a mechanistic simulation to explore spatial and temporal aspects of smolt migration in Lake Evangervatnet.

2 | METHODS

2.1 | Study site

The study was carried out during May–September 2019, with the smolt migration occurring in May and early June (henceforth defining study period as: May 7–June 14) in Lake Evangervatnet in the Vosso River system in Vestland County, Norway (Figure 1). During the 1980s, the Vosso salmon population collapsed, and it has not yet recovered. The salmon stock is now composed of wild spawned fish, fish originating from hatchery eggs planted in the substrate, and hatchery-reared fish that are towed out from Bolstadfjorden and released in the outer fjords.

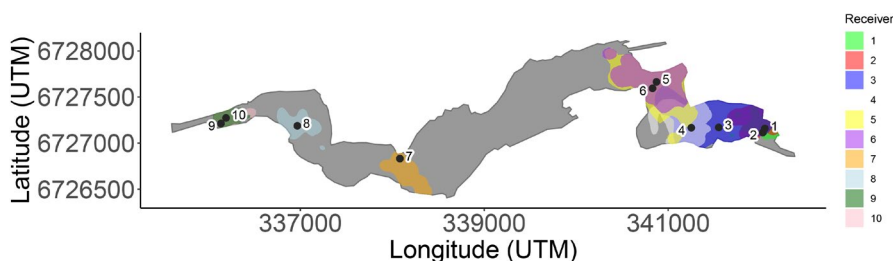


FIGURE 1 Range of the ten receivers in Lake Evangervatnet based on 95% kernel home range density estimates from range testing. The black point represents the receiver locations, the colours are coded for each receiver. The 95% estimated range is the size of coloured polygons

The Vosso catchment is the largest in western Norway (1497 km²) (Barlaup et al., 2018) with 18 km of the 35 km upstream migration limit consisting of the two lakes Lake Evangervatnet and Lake Vangsvatn. Lake Evangervatnet covers an area of approximately 3 km² (Figure 1) and has a maximum depth of 114 m. The lake stretches from Vassenden in the west upstream to Evanger in the east. At the narrowest part (around receiver 5 and 6), the width is 186 m, and the area between the river inlet and this narrow part is further referred to as “the first basin”. The river upstream of Lake Evangervatnet is called Vosso River, and the river downstream of the lake is called Bolstad River, which has a mean annual discharge of 71 m³/s (Barlaup et al., 2018). During the study period (May 7–June 14), the mean discharge flowing into Lake Evangervatnet was 117 m³/s (min–max: 25–244). River Teigdalselva also drains into Evangervatnet with a mean annual discharge of 1 m³/s (Gabrielsen et al., 2011). In the inner part of a small bay, Evanger Hydropower Station (EHS) discharges water abstracted from River Teigdalselva and the neighbouring catchment River Ekso through a tunnel at a mean rate of 23.6 m³/s (2009–2019), increasing annual discharge and contributing to a change in temperature regime in Lake Evangervatnet and the Bolstad River (Raddum & Gabrielsen, 1999). During the study period the station had a mean discharge of 16.9 m³/s (range: 0–50).

2.2 | Sampling and tagging

The Norwegian Food Safety Authority approved all experimental procedures (FOTS id: 19364). Twenty smolts originating gene bank planted eyed eggs were captured during their downstream migration on May 6 and 7 in the Vosso Wolf trap. 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 O₂ concentration of 106%. A minimum size limit for tagging was set to 12.0 cm total length. The smolts measured between 12.8 and 17 cm total length (mean 14.3 ± 1.2 SD), weighed in between 16 and 37 grams (mean 21.7 ± 5.7 SD) and had a mean tag burden (tag weight relative to smolt weight) of 3.1% ± 0.7 SD. Smolts were tagged and released on May 7.

The smolts were tagged with Vemco V5D 180-kHz Predation Tags (Vemco Ltd., Halifax, NS, Canada). The tags weighed 0.68 g in air and measured 12.7 × 5.6 × 4.3 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, flipping an internal switch that changes the signal communicated by the tag to the receiver, indicating predation (Halfyard et al., 2017).

The tagging procedure started by anaesthetising the smolts in 100 mg/L MS-222 Tricaine Methanesulfonate, buffered with 100 mg/L sodium bicarbonate. The smolts were held in 10-L containers with water and anaesthetics for 2–3 min. Weight and total length were recorded prior to surgery. Water with 50% of the anaesthetic

dose was continuously pumped over the gills during surgery. All the equipment was disinfected with chlorhexidine (1 mg/ml) and rinsed in distilled water between surgeries. 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 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 45 cm). After handling, fish were placed in a large container with fresh water. Equilibrium was regained after 3–4 min. After the procedure, the fish were monitored for some time to check for abnormal activity. No negative effects of tagging were observed.

Smolts were returned to the container (water: 7.2°C and 106% O₂) after tagging and kept for 5–7 h to recover prior to transportation. The smolts were transferred with a plastic colander (to minimise handling and damage to the fish) into plastic bags with oxygenated river water and transported by car for 30 min, 18 km downstream of the capture site (0.6 km upstream of the lake). The 20 smolts were released in two groups of ten individuals, a couple of meters apart, during dark (23:14), to maximise probability of survival (Vollset et al., 2017).

2.3 | Tracking

Ten passive acoustic receivers were positioned in Lake Evangervatnet (Figure 1) on May 5 and retrieved on September 13, 2019. Receivers were attached to a rebar with cable ties, and the rebar was embedded in a concrete weight (25–30 kg). 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. The receivers were deployed in depths ranging from 13.1 to 27.5 m. During and after the study, manual tracking was undertaken to search for lost tags.

To get an approximation of the range of each receiver, range tests were conducted at several times throughout the study period, during varying flow and temperature conditions. A range test tag (V5-1x-180k-3; Vemco, NS, Canada) was attached to a rope and towed 2 m behind a boat, 1 m below the surface. Transects across the whole lake were conducted, to identify the range as exact as possible. The range test tag emitted a signal every 3 s. In the boat, a GPS tracker was continuously recording position. The boat engine was running on idle speed to reduce noise, so range may have been slightly larger than we estimated due to engine interference. 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 & Fortmann-Roe, 2006) in (Rstudio-Team, 2016).

2.4 | Statistical analysis

All statistical analyses and visualisations of data were conducted in R-studio 1.1.456 (Rstudio-Team, 2016). False detections were

removed before data analysis by manually going through the raw data. False detections were defined as detections of the same individual with a time interval shorter than the emitted signal interval (i.e. under 60 s), single detections at receivers at obviously unrealistic timepoints, or ID-codes of fish other than those utilised in this study. Single detections were not necessarily removed.

2.4.1 | Survival

Smolts were assumed dead if the tag changed signal based on the predation sensor, if the tag disappeared within the lake, or if the tag was detected by a single receiver for the rest of the study period. Only smolts with tags that switched the predation sensor were counted as predated. If a tag disappeared or was detected by a single receiver for the remainder of the study period, the mortality was assumed to result from other mortality, although it may have been a false negative. Indeed, laboratory evaluation of these tags found that only 50% of the predation sensors recognised predation when euthanised smolts were force fed to trout (Lennox et al., 2021). The location of tag switch was defined as the site of mortality for predated fish, whereas the location of the last receiver to register a tag that was subsequently lost or stopped moving was designated as site of non-predator mortality. Because there was almost complete overlap in area covered 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 generalised linear model (*glm*; binomial family) was used.

To estimate survival per kilometre through the lake, the progression in kilometres for a given smolt was defined as distance between inlet and the farthest receiver it was detected at. If a fish was last detected at the outlet (Receiver 9 and 10), it was defined as a successful migrant. If a smolt was registered as predated, the most downstream receiver detection of the pre-predated signal was used.

To test the efficacy of predation tags, we compared conclusions on the survival of smolts by constructing two datasets using the detections gathered from the tagged fish ($N = 20$). The naïve dataset assumed that no predation-specific information was collected and thus included movements of both live and post-predated smolt. The sensor-enhanced dataset included the predation-specific information and therefore only contained movements of live smolts. Thus, a comparison between the information gathered using standard telemetry tags (naïve dataset) and predator tags (sensor-enhanced dataset) was made to reveal predation bias (Daniels et al., 2019).

To obtain an indication of the size range, spatial distribution, and species of predators, rod and reel fishing was employed during the study period, for a total of 40 rod hours. Artificial lures (Rapala, Finland) between 7 and 12 cm imitating smolts were utilised during fishing. Coordinates, fishing depth, and length of fish were recorded. Different areas of the lake were fished with approximately the same effort, with increased effort around the first basin and the outlet of the lake. All fish were released after registration.

2.4.2 | Smolt behaviour

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 m. 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 diel 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.

To estimate diel horizontal migration, the R-package *suncalc* (Agafonkin & 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; night-time (between sunrise and sunset), dim period (interval of 2 h after sunrise and before sunset), and daytime (between the dim period). Thus, a 24-h day was disproportionately split, where night-time represented a mean of 27.5%, dim period 16.7%, and daytime 55.8% of the day. Via Rayleigh test of uniformity, the diel movement of smolts into, within, and out of the lake was tested, by utilising the *r.test* within the *CircStats* package (Lund & Agostinelli, 2018). Time of day in hours was transformed into radians by multiplying hour by 12 divided by π .

Progression rate was defined as the speed between the first detection at the inlet receiver and a given downstream receiver in the lake. To test if progression rate had an effect on survival, a generalised linear model (*glm*; binomial family) was used.

2.4.3 | Mechanistic simulation modelling

To estimate total distance travelled by smolts and whether smolts could be moving randomly throughout the lake before they reach the outlet, we conducted several simulation experiments on 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 longer time intervals, this correlation decreases, meaning that the movement on a large scale is multidirectional, but locally occurs in a straight fashion (Codling et al., 2008). One simulation run yields a two-dimensional virtual track of a smolt through Lake Evangervatnet. We ran simulations under four different scenarios with varying parameters (step length and standard deviation of turning angle, see below)

and compared the simulated travel times to the observed travel time used by tagged smolts.

In our CRW simulations, we made several assumptions regarding the distributions of 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, θ , followed a Gaussian distribution with mean μ and standard deviation σ . 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). The initial direction of the first step was set West, because the water flow direction at this point is westerly. The end line was set vertical at the location of Receiver 10 (outlet receiver). If the simulation path crossed this line (i.e. was located more to the West than the end line), the smolt was defined as through the lake and simulation terminated. Step length was set to 50 m after 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 μ was set to 0 in all simulations. The strength of the correlation varied depending on σ , which took one of four values (1, 5, 10, and 20°), distributed in four respective simulation groups (see below).

For each σ value we simulated 5000 CRW. The total distance travelled for one simulated smolt track was calculated by multiplying the number of steps by the step length. Swimming speed was estimated assuming that the smolts had the mean length of smolts in our study (14.3 cm TL) and swam at a speed of 1.2 body lengths per second (Thorstad et al., 2004), equating to 0.17 m/s swimming in the lake. From this, and knowing that each step was 50 m in length, dividing distance by speed yielded an estimate of time spent in the lake.

Smolt movement mostly occurs at night (Thorstad, Whoriskey, et al., 2012). Based on the observations from Lake Evangervatnet, where smolts mainly migrated during night and dim periods (44.2% of a 24 h day), we divided the estimate by two, representing 50% of the day spent migrating (i.e. nocturnal migration).

Salmon trajectories in the lake were calculated for all 20,000 simulations, and thus, the output of the study was threefold: individual paths, total distance travelled, and time spent to traverse the lake. For comparison 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, giving the minimum estimate of time needed to navigate the lake.

The observed mean travel time was based on the time passed 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 ($N = 8$). Sum of squares (Equation 1) was used to find the CRW model that most closely resembled the observed data:

$$\sum_i (E_i - u_s)^2 \quad (1)$$

where i denotes individual fish, s the simulation number, u_s the mean travel time of simulated fish, and E_i the mean travel time for tagged fish.

All simulations ended when the fish crossed the horizontal end line, meaning that 100% of simulated fish reached the end of the lake. Multiple assumptions were made in the CRW simulation. First, we assumed that migrating individuals move independently of each other. Second, the smolts were assumed to move continuously at the same speed at a constant. The third assumption was that the smolts moved randomly through the lake, without flow, temperature, or other stimuli to guide them. Fourth, the smolts were assumed to swim forwards (head first).

3 | RESULTS

3.1 | Survival

Migration success through Lake Evangervatnet was low, with eight smolts (40%) successfully transiting the lake. The remaining twelve (60%) died in the lake, with six of these (i.e. 30% of total tagged fish) mortalities positively registered as predation. Mortality was highest in the river-lake confluence (first 2 km of the lake) with 45% (i.e. 22.5% km⁻¹) of smolts dying, but lower in the main body (9% or 3.6% km⁻¹) and the outlet (20% or 10% km⁻¹). 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, $z_{1,19} = 1.12$, $p = 0.23$).

Because the only fish caught during experimental fishing was brown trout (*Salmo trutta*), it was believed to be the only piscine predator in the lake, and the large size of trout indicates piscivory. The trout ranged from 25 to 90 cm (mean = 37 cm) ($N = 23$). Catch per unit effort (CPUE) was 0.6 trout/rod hour. 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 ($N = 3$). The mortality hotspot was located approximately 1.5 km downstream of the inlet, around the narrowest part (receiver 5 and 6) of Lake Evangervatnet (Figure 2b). This was also in the area where most trout were caught during experimental fishing. Of the six positive predation events, one was located in the first basin (receiver 1–4), two around the narrow sound (receiver 5 and 6), two approximately 4 km downstream (receiver 7), and one at the lake outlet (receiver 9 and 10).

The cumulative survival per kilometre through the lake showed that all smolts were detected at least once 1.5 km from the inlet (Receiver 5); however, only 55% ($N = 11$) made it further downstream. The comparison of the naïve and sensor-enhanced dataset showed minor differences between in-lake survival (between receiver 5 and 8) estimates, where ten (50%) of the smolts successfully migrated this distance based on the sensor-enhanced dataset, whereas 11 (55%) migrated the same distance based on the naïve dataset (Figure 2a). No difference between naïve and sensor-enhanced data was observed for the total survivorship through the lake.

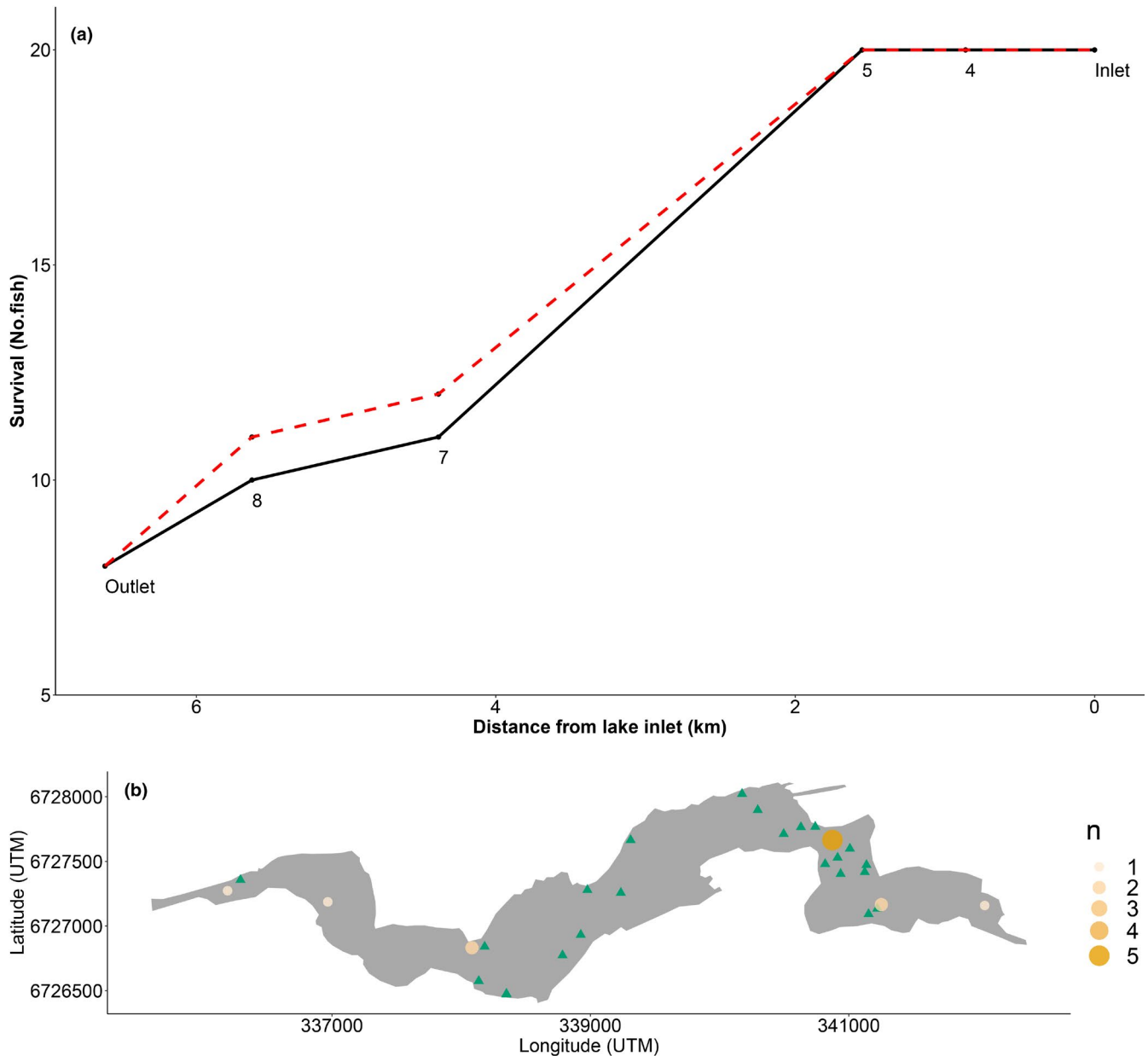


FIGURE 2 (a) Survival per km through Lake Evangervatnet for the 20 smolts. Black line representing sensor-enhanced dataset (i.e. information included from predator tags), and dotted red line representing naïve dataset (i.e. no information included from predator tags). Location of mortality is based on first post-predation detection for the predated individuals in the sensor-enhanced dataset, whereas the mortalities estimated without the predation sensor were attributed to the location of the last receiver a smolt was detected at. Line corresponding numbers indicate receiver ID. (b) 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 experimental fishing 2019 (green triangles)

3.2 | Behaviour

3.2.1 | Movement and progression rates

The Atlantic salmon smolts movement in the lake was not unidirectional, where smolts progressed consistently westwards to the lake outlet. Many smolts spent a long time in the first basin (between the lake inlet and the narrow sound where receiver 5 and 6 were placed) before dying or getting out into the main part of the lake. Among the smolts that made it past the first basin, ten (90%) exhibited

several periods of eastwards movement, opposite the lake outlet. Several smolts reached the outlet, only to turn east again, swimming back and forth between receivers up to 10 times before exiting the lake. Progression rates (calculated between inlet and 1.5 km downstream at receiver 5 and 6) for the 20 salmon smolts varied from 0.018 to 0.38 m/s (mean 0.15 ± 0.12) and had no effect on survival ($z_{1,19} = -0.7, p = 0.48$).

To reach the outlet (first registration at receiver 9 or 10), the eight surviving smolts spent between 3 and 17 days (mean 7.9 ± 6.2 SD). Progression rates between lake entry and outlet ranged from

0.004 to 0.028 m/s (mean 0.016 ± 0.001 m/s SD). Smolts did not exit the lake upon reaching the outlet, but spent a mean three days around the lake exit before last registration in the lake. Therefore, to navigate the entire lake (last detection in the lake at receiver 9 or 10), survivors spent between 3 and 22 days (mean 11.1 ± 6.4 SD), and progression rate from lake entry to lake exit varied from 0.0035 to 0.026 m/s (mean 0.01 ± 0.007 m/s SD).

3.2.2 | In-lake diel movement

The smolt migration into, within, and out of Lake Evangervatnet was not uniform ($r_{\text{bar}} = 35.4$, $p < 0.01$; Figure 3), with 68% of movements occurring at night, 23% during the dim period, and 9% during daytime. Most of the smolts entered the lake within 6 h after release, and 95% of them entered the lake during night-time. Lake exit was also primarily at night, with 75% of smolts leaving during dark.

3.3 | Mechanistic model simulations

The simulated mean time spent to progress through the lake varied among the four simulation scenarios. The smaller the value of σ , the faster they progressed through the lake. Assuming the simulated smolts moved constantly through a 24-h day, the simulation output was skewed to the left compared to the observed values for all σ (Figure 4a). By accounting for nocturnal migration the mean travel time was more similar to the observed data (Figure 4b).

The total distance travelled by the simulated smolts within the 6.5 km lake followed the same pattern, where total travel distance decreased with smaller σ . Three of the simulation outputs (σ : 1, 5,

10) estimated mean travel distances of around 50 km, whereas the $\sigma = 20$ output mean was 76 km.

The model that best fitted the observed data had a σ of 10 and nocturnal migration (Figure 5), giving a mean travel time through the lake of 7.5 ± 5.6 SD days. Assuming simulation 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 standstill at day.

Assuming smolts followed the most direct track, they would use 10.6 h to traverse the 6.5 km lake at a speed of 0.17 m/s. However, simulated smolts made extensive movements throughout the lake, concurring with what was observed from the field data (Figure 6).

4 | DISCUSSION

This is the first study to directly investigate predation on migrating Atlantic salmon smolts in a lake environment, a habitat that has previously been recognised as a bottleneck for smolt survival (Honkanen et al., 2018; Kennedy et al., 2018). The wild smolts in the 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. A mechanistic simulation model revealed potential spatiotemporal movement patterns of smolts in the lake, where simulated smolts travelled a total distance nine times (mean) the length of the lake and exhibited non-directional movement in concurrence with field data, resulting in similar travel time distributions for both simulated and observed smolts.

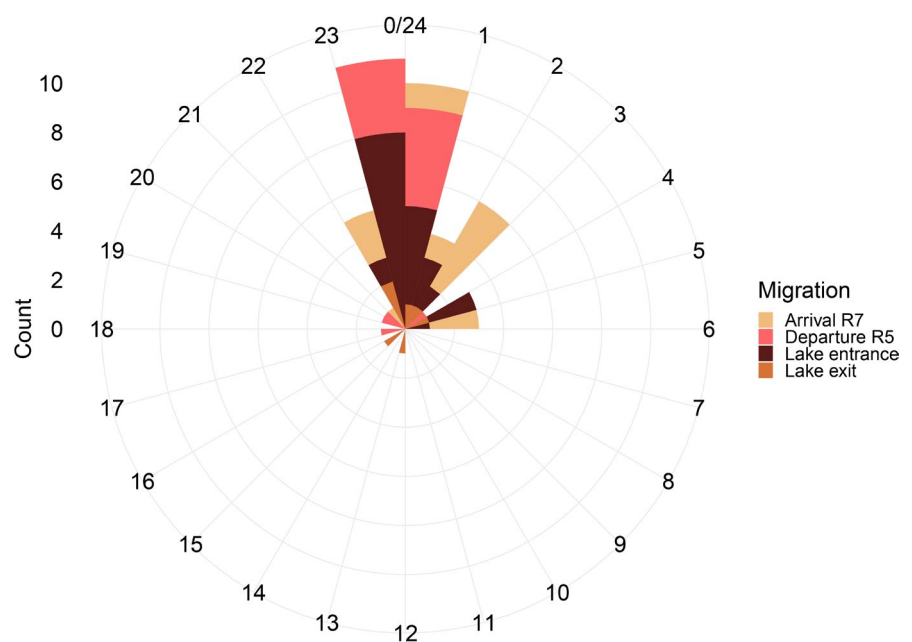


FIGURE 3 Polar histogram showing time of diel migration into, within and out of Lake Evangervatnet for Atlantic salmon smolts. Colours represent the different parts of the lake migration. In-lake migration is represented by records of last detection at receiver 5 (Departure R5) and corresponding first detection at receiver 7 (Arrival R7). Radial distance (count, y-axis) represents the number of movement events

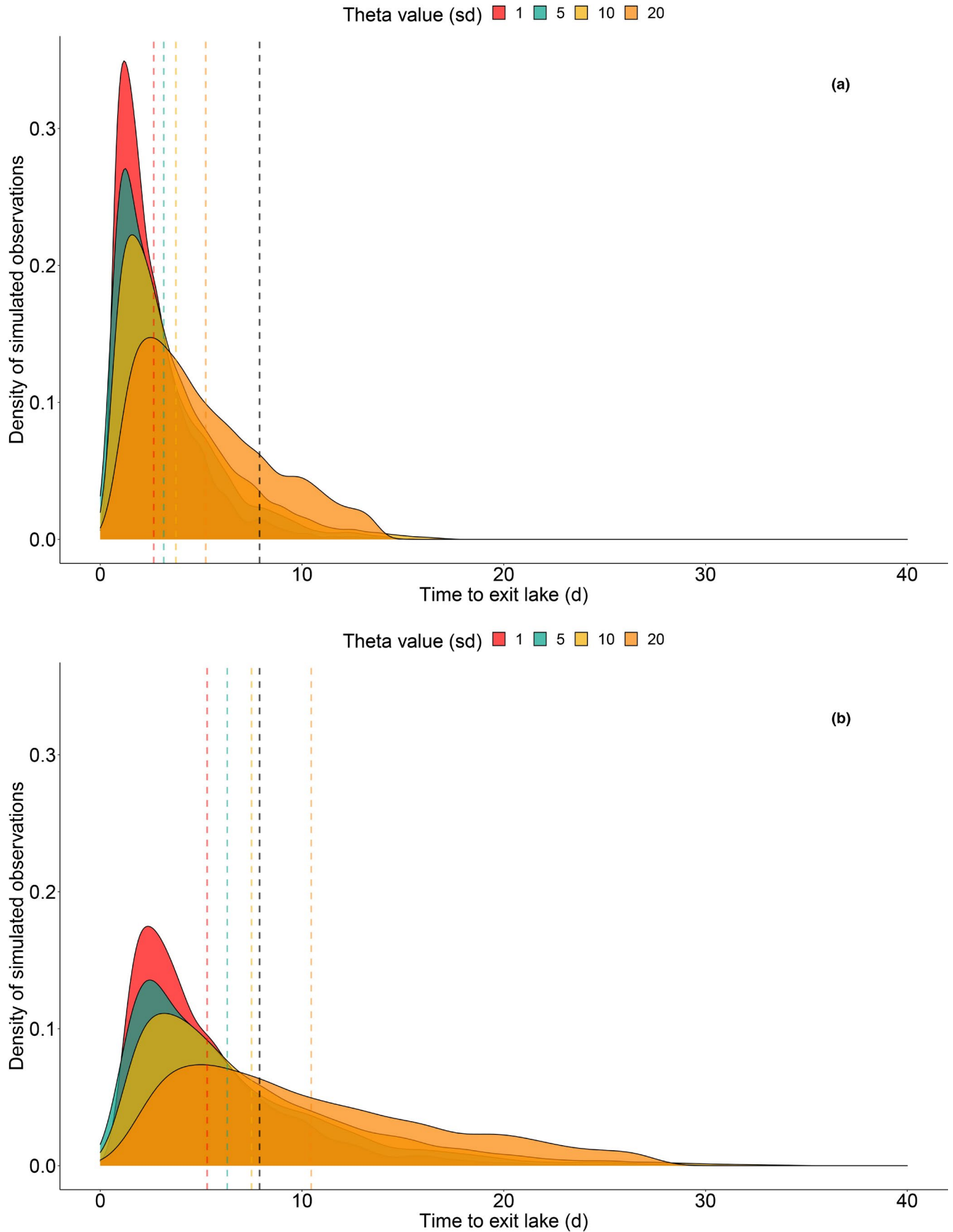


FIGURE 4 Density distribution of simulated travel time through Lake Evangervatnet in days for four scenarios of σ (SD of turning angle). (a) illustrates constant movement at day and night assuming 0.17 m/s speed. (b) illustrates constant movement at night (12 h of a 24-h day) and standstill at day, assuming speed of 0.17 m/s. Dashed lines indicate the mean number of days to traverse the lake for the four simulations with different σ (colours), and the black dashed line represents the mean of the observed data

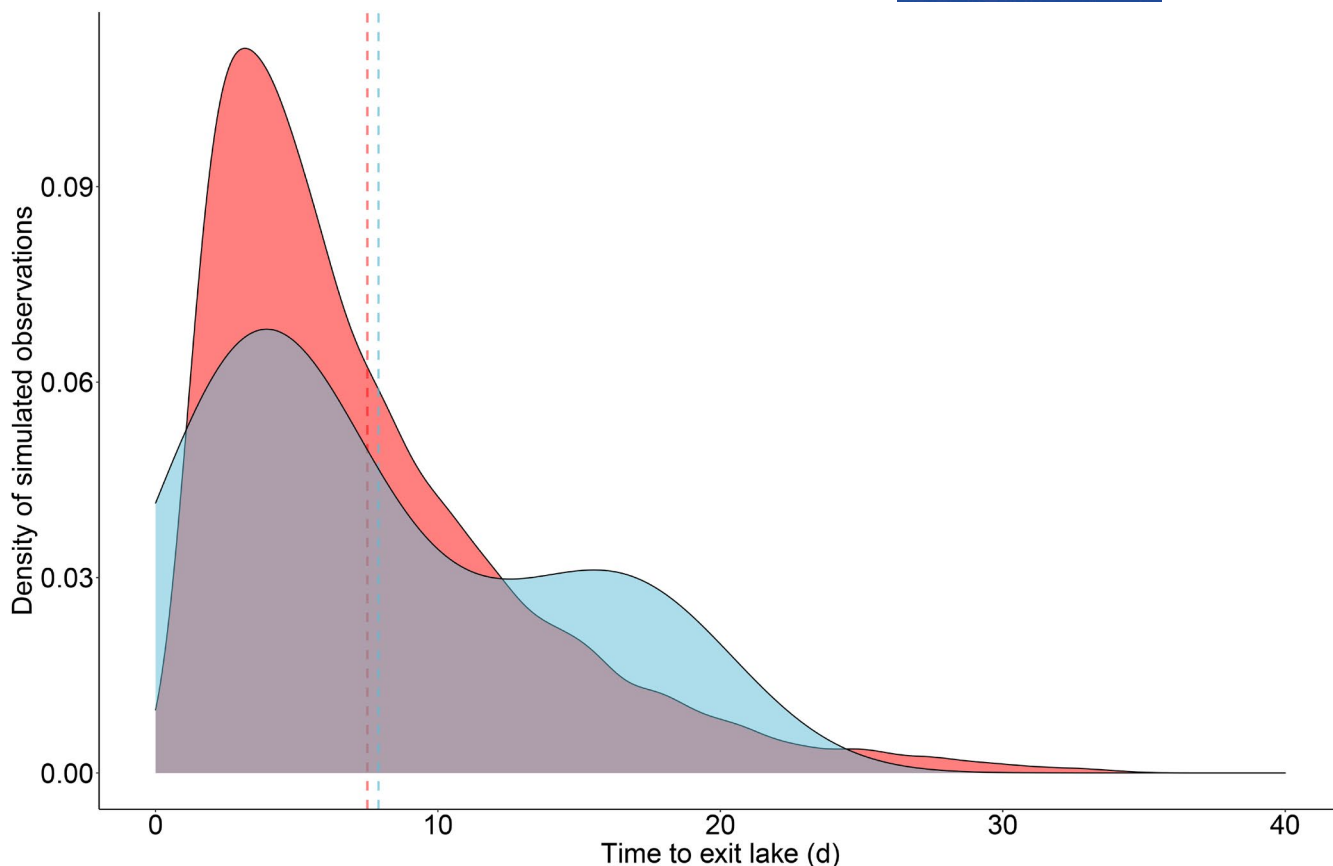


FIGURE 5 Plot showing the best fit model with $\sigma = 10$ and movement for 12 (night-time) hours a day (blue) and the observed values (red). Dashed lines indicate mean time spent navigating the lake

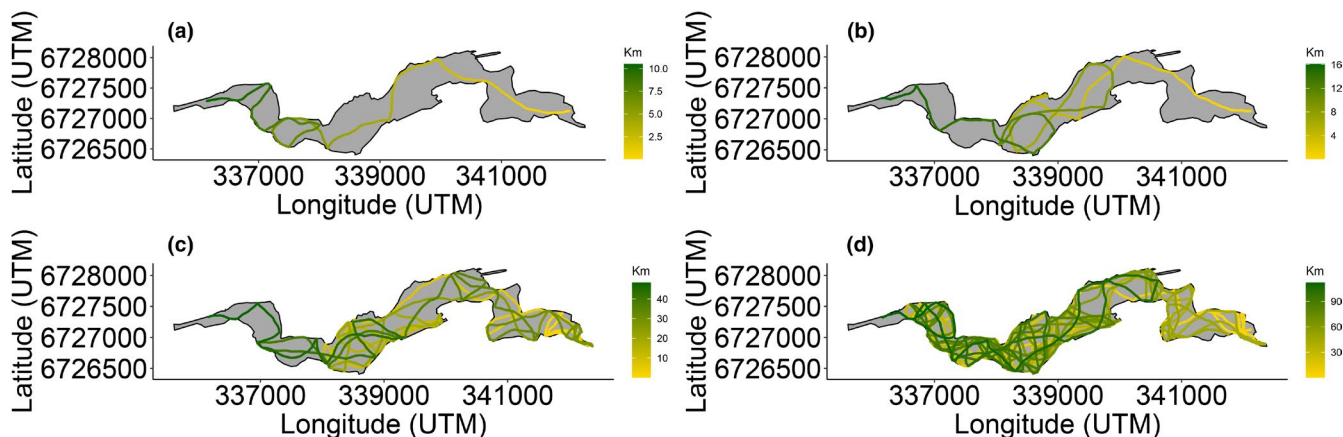


FIGURE 6 Example of simulated tracks for four smolts using the best fit model (for model explanation see section 2.8.3 and 3.3). Yellow indicating start of track, green indicating end and successful passage through the lake. (a): Simulated smolt travelled 11 km and used 1.6 days to exit the lake. (b): Simulated smolt travelled 16 km and used 2.7 days to exit the lake. (c): Simulated smolt travelled 48 km and used 6.5 days to exit the lake. (d): Simulated smolt travelled 115 km and used 15.6 days to exit the lake

4.1 | Field study – smolt survival and behaviour

Smolt mortality through Lake Evangervatnet was high compared to riverine mortality rates (2–3% km⁻¹ median) (Thorstad, Whoriskey, et al., 2012), with 60% (i.e. 9.2% km⁻¹ mortality through the whole lake on average) dying in the lake. Half of

mortalities were attributed to predation by trout. Both resident and anadromous trout are opportunistic predators (L'Abée-Lund et al., 1992) that primarily feed on fish after the trout reach a size of >31 cm (Keeley & Grant, 2001). Additionally, three smolts disappeared within the lake, possibly due to avian predation by mergansers (*Mergus serrator*) or cormorants (*Phalacrocorax carbo*;

Koed et al., 2006) observed in Lake Evangervatnet. Mortality was highest during the first two kilometres of the lake (22.5 km^{-1}), 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 and Honkanen et al. (2021), which reported 31% to 55% mortality in a series of lakes in Scotland. Kennedy et al. (2018) assumed predation by pike (*Esox lucius*) 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 mainly be caused by predation (Honkanen et al., 2018), without empirical evidence or *a priori* decision criteria for attributing mortality to predation. Haugen et al. (2017) also reported high mortality in Lake Evangervatnet, with mortality rates for wild smolts of 49% and 82% from two different tag types (Vemco V7D & V71D respectively). Haugen et al. (2017) concluded that predation by trout accounted for most of the mortality.

The light weight and small size of the V5 tags make the tags suitable for tagging of wild Atlantic salmon smolts. In general, the lower the tag weight ratio is, the more reduced tag effects are (Brown et al., 2010), and upper tag burden limits between 2% and 10% are recommended (Jepsen et al., 2002). This puts the observed tag burdens in this study of ~3% at an appropriate level and the tag effects can be assumed to be within reason. The process of surgery, however, can lower survival rates when smolts are released shortly after tagging (Daniels et al., 2021). In our study, six of the twelve smolts that died, died without the predation sensor indicating predation. This might be due to mortality caused by surgery, tag burden, or natural mortality, but during a parallel laboratory validation study of the sensor, a false-negative rate of 50% was observed (Lennox et al. 2021), corresponding to the 50% unknown mortalities in our field study. False positives (i.e. tag switch signal from pre- to post-predated without predation occurring) may overinflate the predation estimate. A paper by Klinard et al. (2021) revealed a 17% false positive rate, utilising the larger V9 tags, and this could impact our study as well. However, based on the movement (lack of movement) of predated smolts and the findings by Halfyard et al. (2017) showing that false positives first were observed after 47 days for the V5 tag, we argue this is not likely to be a substantial source of error in this study. Because quantifying predation from telemetry is inherently complicated (Hightower et al., 2001), and identifying predation occurrences both spatially and temporally by use of behavioural analysis of predator and prey might not be accurate enough (Gibson et al., 2015), the novel predation tag technology utilised in this study has the potential to offer more reliable predation estimates, yet refinement of the technology is still needed (Lennox et al., in press). Studying predation on yellow perch (*Perca flavescens*), Weinz et al. (2020) identified the predation tag as a useful tool for investigating predation, pending stronger validation of the technology. Indeed, we were able to attribute half of mortalities to predation utilising the new sensor technology.

The wild smolts exhibited mostly 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, the highest activity was also observed at night, with only 9% of smolt migration occurring during daytime. Nocturnal migration is well documented in riverine smolt migration (Ibbotson et al., 2006; Moore et al., 1998) and is thought to be a strategy for predator avoidance (Thorstad, Whoriskey, et al., 2012). Nocturnal migration in lakes was also observed in Loch Voil, Scotland (Thorpe et al., 1981). Most smolts migrated between the furthest receivers (nr. 5 and 7) during one night, though a fraction of smolts exhibited migration over consecutive days. These smolts could in theory migrate the distance also during the day with a slower progression rate but seeing as smolts entered the downstream gate at night, and not at random throughout a 24-h 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 study period. 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 higher temperature. In this study, increased activity during daytime was mainly observed after lake temperature reached 7°C on May 17, fitting well with the findings by Thorpe et al. (1994) who reported the same 7°C threshold for change in diurnal migration in rivers. This suggests that Atlantic salmon smolts follow the same environmental cues in both riverine and lacustrine environments.

The surviving smolts were slow to migrate through the 6.5 km lake, with a mean progression rate 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, Whoriskey, et al., 2012), 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. Lakes contain more complicated flow patterns and sections of still water, and among the scarce studies on wild smolt migration through natural lakes, only one reports progression rate, with a mean of 0.02 m/s (Hansen & Jonsson, 1985). Despite the old conceptions of passive smolt migration through lakes (Thorpe et al., 1981), several studies now suggest that active movement is the main mechanism of displacement (Bourgeois & O'Connell, 1988; Honkanen et al., 2018).

Our conclusions in this study are limited by some methodological shortcomings (Brownscombe et al., 2019), which offer potential for refinement in the future. The capacity to only instrument 20 smolts resulted in a small sample size of both survivors and mortalities, which complicates mortality estimates and models. Moreover, the smolts were taken from a stock of hatchery origin

salmon planted as eggs; hatchery rearing may affect behaviour compared to wild counterparts (Jonsson & Jonsson, 2006). Other studies have similarly been limited by sample size (e.g. Honkanen et al., 2018) but results consistently suggest high mortality in lakes; still, future studies must overcome this limitation for a clearer image of lake survival. Accounting for possible alternative causes of mortality will be important, although identifying avian predation requires further tag validation (i.e. for aquatic birds such as ducks and cormorants) and may be impossible for fully terrestrial species such as raptors and corvids (Lennox et al., 2021). Factors such as water temperature, conspecific density, predator density, and water flow will affect smolt migration patterns (Thorstad, Whoriskey, et al., 2012), contributing to interannual variation in survival that must be accounted for in a multi-year study. Nevertheless, our efforts represent an important advance in studying the lake ecology of Atlantic salmon smolts that has been largely overlooked (Lennox et al., 2020). Our findings are relevant considering the existing literature (Honkanen et al., 2018, 2021; Kennedy et al., 2018; Thorpe et al., 1981) and highlight novel applications in the field of acoustic telemetry methods and behavioural ecology of salmon.

4.2 | Revelations of smolt behaviour by mechanistic model

The mechanistic model simulating smolt movement through Lake Evangervatnet assuming nocturnal migration provided realistically timed tracks, suggesting that smolt movement could be close to a correlated random walk. The model parameters are biologically relevant (Zabel and Anderson 1997), derived from the literature on smolt movement (Honkanen et al., 2018; Thorpe et al., 1981; Thorstad et al., 2004), 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 & 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 <11 h. Instead, surviving smolts from our field study spent a mean of 7.9 days in the lake and did not swim directionally through. Similarly, the smolts from the simulations based on the best fit model exhibited travel times of 7.5 days, with extensive movements in all directions, covering a mean travel distance of 57 km (nine times the length of the lake). These results correspond with those of Honkanen et al. (2018), where non-directional movement of smolts through Loch Lomond was observed, with smolts migrating distances of up to nine times the length of the lake, as in our simulations. Honkanen et al. (2021) additionally reported that 49% of directional movements in a lake were in a direction opposite to

that of the lake outlet. 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 h, perhaps corresponding to the nocturnality observed in Lake Evangervatnet, although the timing of movements was not detailed in that study. Regardless, this supports the reasoning for nocturnal migration in this paper. Although the model does not prove that smolt migrate through lakes in a random fashion, it does provide a likely scenario to the pattern that we are seeing in this study and others.

The model simulations simplify reality, and even though it explains travel times and behaviour of smolts well, all models will have limitations. First, assuming individual movement of smolts might be inaccurate because smolts can form schools during downstream migration (Riley et al., 2014). Further, the simulation assumes the lake to be homogenous, whereas we know from observations 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 display negative rheotaxis (McCormick et al., 1998), currents moving in other directions than the downstream direction might confuse and delay the smolt migrations. Additionally, the Evanger Hydropower Station outlet can further alter currents during certain conditions (Isaksen et al., 2019) and may lead to additional migration delay. Nonetheless, simulations can be useful when addressing challenging ecological questions (DeAngelis & Grimm, 2014). For example, Zabel and Anderson (1997) and Booker et al. (2008) utilised 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 are usually hard to investigate, the mechanistic model used in this study can offer novel information in an efficient and biologically sensible way. A more refined model can also benefit from triangulation information, by getting in situ estimates of smolt turning angles (θ), turning angle σ , and mean swimming speeds of smolts in the lake. Additionally, the model could be improved by implementing flow patterns and temperature, which also may impact smolt movement.

The present study provides evidence that smolts are subject to high predation in lakes and that they struggle to navigate through still waters, not simply moving downstream in a linear direction. The observation that smolts seemed to migrate nocturnally and without clearly directed movement towards the outlet was strengthened by simulating smolt movement through the lake via a mechanistic correlated random walk model and offers a novel approach to investigating smolt migration through lakes.

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AUTHOR CONTRIBUTIONS

EMH designed the study, collected, and analysed data, tuned the mechanistic model, and wrote the paper. KWV designed the study, collected, and analysed data and wrote the text. AGVS designed the study and proof-read the text. BB designed the study and collected the data. KW did the statistical analysis in relation to the mechanistic model. TEI collected data. ESN tagged the fish and collected data. MH collected data and proof-read the text. RJL designed the study, collected, and analysed data and wrote the text.

CONFLICT OF INTEREST

The authors declares no conflict of interest for this publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in <https://members.oceantrack.org/OTN/projects> at <https://ocean-trackingnetwork.org/>.

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