

A tale of two fishes: The depth preference of migrating Atlantic salmon smolts, and their aquatic predator Brown trout, in a Norwegian freshwater lake

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Abstract

A growing area of interest in salmonid ecology is the survival bottleneck that lakes present to the successful migration of salmon smolts. With smolt mortality shown to be high in lakes, it is important to collect information on predator-prey interactions within these habitats. We tagged 45 Atlantic salmon smolts and 27 Brown trout and recorded their depth use in Lake Evanger, Norway with the use of acoustic telemetry during the spring migration of 2020. I then modelled the average depth of each species against solar azimuth, time of year and surface water temperature using generalised additive models (GAMs). Both species displayed diel vertical migrations to shallower depths at sunrise and sunset. Further, I revealed that salmon smolts responded to warming temperatures in the lake by changing depth preferences whereas trout did not appear to react to the changing temperature. Neither species showed a response to the changing length of daylight over the study period based on the solar azimuth. Mortality was high amongst the tagged salmon, with only an estimated 30% successfully navigating through the lake. This study provides insight into the temporal overlap of predator and prey suggesting both species make use of the antipredation window provided by low light levels during the crepuscular hours as a predator avoidance strategy. This study serves as a channel for future research into the predator-prey interactions that drive salmonid evolution.

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1 Introduction

Atlantic salmon (*Salmo salar*) is a species of significant historical, cultural, and economic importance in the North Atlantic. Their migrations are possibly one of the most well known aquatic migrations in the public sphere. However, during the late 20th century the population of Atlantic salmon declined dramatically on both sides of the Atlantic and, despite restoration efforts, populations remain at worrying levels (Parrish et al. 1998; Chaput 2012; ICES 2019). Attempts to support the wild populations are ongoing including efforts to increase access of through their migration pathways (NOAA 2021) and the release of hatchery reared fish to bolster the population (Vollset et al. 2014). Yet, the challenges facing salmon recovery are multifaceted and include anthropogenic factors such as changes in aquatic conditions, dams, intensive aquaculture and pollution (Parrish et al. 1998). In order to rise to the challenge of meeting salmon restoration an extensive understanding of the species ecology is required.

The seaward migration is a life history stage where salmon smolts are particularly vulnerable and suffer from a high mortality (Aarestrup and Koed 2003; Jepsen et al. 2010; Thorstad et al. 2012a; Honkanen et al. 2018; Flávio et al. 2019; Lennox et al. 2021a; Honkanen et al. 2021). Salmon parr go through a process known smoltification in preparation for their migration from freshwater systems to the sea (Thorstad et al. 2012). The smolt migration primarily occurs in springtime so as to synchronize arrival at sea when conditions are at their most favourable (Thorstad et al. 2012). The migration is believed to be triggered by abiotic factors such as warming temperatures and water discharge (Jonsson and Ruud-Hansen 1985; Whalen et al. 1999; Vollset et al. 2021). The Atlantic salmon smolt migrations represent a key movement of resources and energy from the freshwater environment into the marine environment (Lennox et al. 2019). During this time, the smolt are particularly vulnerable to predation and physical barriers that may slow down or impede their migration routes (Aarestrup and Koed 2003; Jepsen et al. 2010; Flávio et al. 2019). Predation in particular presents a problem for a species such as Atlantic salmon. Wherein, if predators do not possess, or cannot adapt, the dietary flexibility to the reduced numbers of a prey population then the already dire situation can be exacerbated beyond the threshold of recovery, possibly leading to extirpation or extinction (Gascoigne and Lipcius 2004).

Studying the interactions and obstacles within this migration has therefore become an area of interest. Within the freshwater stage of the migration, a greater focus of research has been directed towards the movements, survival and migratory behaviour of smolts through the river sections of their migration pathway (Svendsen et al. 2007; Davidsen et al. 2009; Flávio et al. 2019). Previous research has indicated that mortality can vary greatly from year to year in rivers (Flávio et al. 2019) and that the estuarine stage of the migration has the highest mortality (Thorstad et al. 2012). Evidence suggests that migration through rivers and streams is predominantly passive with some evidence of active swimming with speeds recorded greater than that of water velocity (Fångstam 1993). In contrast, comparatively little attention has been paid to migrations through standing water and lakes, which have been shown to be a greater obstacle to navigate with higher numbers of mortality (Honkanen et al. 2018, 2021; Lennox et al. 2021). Smolts have been shown to spend a significant amount of time in lakes, whether in physiological preparation for marine conditions or due to a greater difficulty in navigation, the reasons remain poorly understood (see review by Lennox et al. 2021). However, the lack of strong currents and presence of eddies have been

proposed as some of the reasons smolt navigation appears to be impaired by lakes (Lennox et al. 2021). In a study by Honkanen et al (2021), the difficulty salmon appear to have in navigating lakes was demonstrated by the fact that 49% of directional movements were in the opposite direction of the migration pathway. This prolonged residency can result in negative consequences to smolt survival such as exposure to predators, increased energy expenditure and the possibility of later arrival at sea (Rikardsen et al. 2004).

Recent studies have suggested that mortality in lakes is higher than previously assumed. In a study by Honkanen et al (2021) a higher rate of mortality was observed in migration pathways in lakes (16 to 53% km⁻¹) compared to that in rivers further downstream (3.9 to 10.8% km⁻¹), demonstrating how lakes can be a bottleneck with a mortality of 90%. Predation is thought to be the cause of a large proportion of the mortality observed in lakes (Jepsen et al. 1998; Honkanen et al. 2018; Kennedy et al. 2018). Various predators, such as northern pike and brown trout, have been observed aggregating in lakes to take advantage of the smolt migration (Jepsen et al. 2006; Furey et al. 2015; Kennedy et al. 2018; Hanssen 2020). Understanding the interspecific relations between predator and prey is therefore of intense interest to ecologists and conservationist in order to better inform management strategies.

A variety of factors influence the three dimensional location of freshwater fish such as salmon smolts including buoyancy requirements, food availability and predation risk (Clark and Levy 1988; Mehner 2012). For the purpose of this study, light was assumed to be the major influencer towards predation risk from aquatic, visual piscivores. As such, I investigated whether salmon smolts perform diel vertical migrations (DVM). DVM is a common phenomenon in a variety of freshwater fish and one believed to be associated with predator avoidance (Mehner 2012). The strategy is commonly referred as the antipredation window; an avoidance mechanism where fish occupy darker, deeper depths during the day before traveling to shallower depths in the crepuscular hours in order to avoid visual predators (Scheuerell and Schindler 2003; Mehner 2012). Several species of salmon have been observed performing DVM (Eggers 1978; Scheuerell and Schindler 2003; Richardson et al. 2017). With Brown trout (*Salmo trutta*) believed to be the main aquatic predator of salmon smolts in lake Evanger (Lennox et al. 2019) this study set out to see how the depth preferences of salmon smolts and Brown trout changed within the photoperiod. In order to investigate the depth use of salmon smolts and trout, we deployed the use of acoustic telemetry to monitor the movements of both species during the migration period. Acoustic transmitters work by emitting a sonic pulse that is then detected and logged by receivers positioned in fixed locations. Acoustic tags have provided management with critical information by providing spatio-temporal data of species and interspecific relations (Young et al. 2013; Hussey et al. 2015; Crossin et al. 2017). For example, in the Fraser river system, Canada, telemetry has provided information on the effects of climate changing and fishing activities on five species of Pacific salmon (Young et al. 2013). By surgically implanting depth tags into salmon and trout, we collected data on depth usage of both species from 27.04.2020 to 08.06.2020. I then created generalised additive models (GAMs) to simulate at which depths these species would most likely be found at, both on a daily scale and how these preferences changed as the migration period progressed. We monitored the movements of 45 Atlantic salmon smolts and 27 Brown trout, with depth sensor acoustic tags. The aim was to increase our understanding of how these animals use lakes and how that use may change over time. I hypothesised that: (1) salmon smolts will behave according to the antipredation window theory in order to minimise chances of contact with Brown trout; (2) due to the lengthening amount of daylight, salmon smolts will adapt

their behaviour later in the study period, spending less time in shallow depths. I also expected to record a high level of mortality amongst the salmon that entered the lake. In order to test these hypotheses I created generalised additive models (GAMs) to show how salmon and trout move in the water column.

2 Materials and Methods

2.1 Study site

The study was undertaken at lake Evangervanet (referred hereon as Evanger), a part of the Vosso River system in Vestland county, Norway. The river Vosso is the largest river in the Osterfjord complex, having a catchment area of 1,497 km². Lake Evanger has an area of approximately 3 km², is 114m deep at its maximum depth and is 186m wide at the narrowest point. At the most western point of the lake, the output flows into the Bolstad river with a mean discharge of 71 m³/s. There are two natural inputs into the lake. The first input is from the Vosso river on the eastern side of the lake. Secondly, the Teigdalselva tributary feeds into the lake from the north. A third input comes from the Evanger hydroelectric powerplant discharge, which transfers hypolimnetic water from Teigdalselva and Eksingdalen via a tunnel. The river has traditionally been well populated by salmonids, however in the late 20th century the population of Atlantic salmon faced a major decline from which it has yet to recover. The current wild population is being supplemented by hatchery-reared fish.

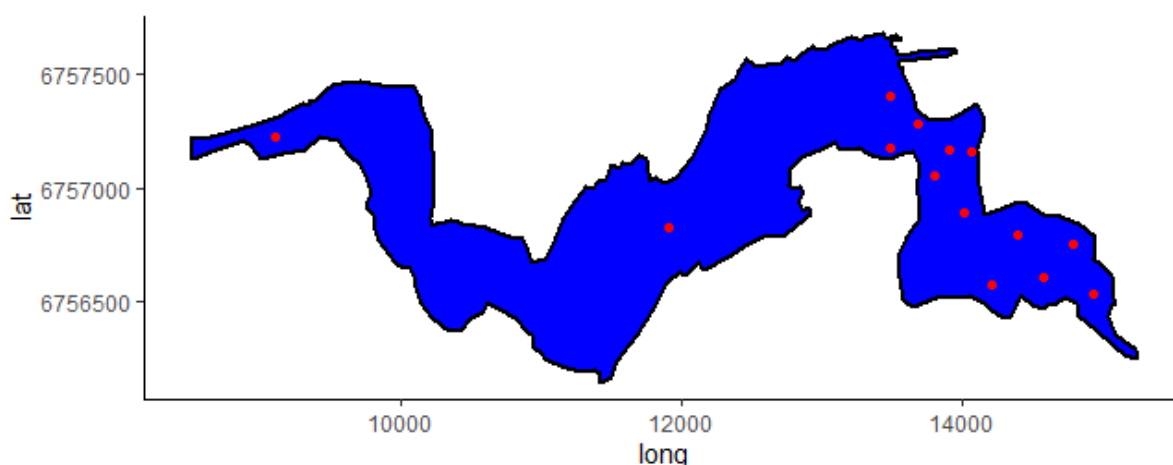


Figure 1. A map of lake Evanger and the locations of receivers.

2.2 Study Design

Data collection was timed to coincide with the smolts seaward migration, taking place between 17.04.2020 and 20.06.2020. Fourteen TBR 700 acoustic receivers were set up and deployed in lake Evanger, with detections recorded from 18.04.2020 to 20.06.2020. Twelve were placed in the eastern basin of the lake. This covered the entry point of the salmon and where the trout were most likely to congregate. This was due to a previous study by Haugen et al. (2017) that found this area had the highest rate of mortality. One receiver was placed in the centre of the lake and another at the entrance to the river Bolstad and only outlet of lake Evanger. Each receiver was secured to a rebar anchored in a concrete weight (10-20 kg), which was connected to a mooring rope and buoy to mark its location on the surface. The receivers recorded the tag ID, depth of the fish and date and time of detection. Surface temperatures were taken from a receiver in the eastern basin equipped

with electronic thermometers. Temperatures were recorded every 15 minutes from 15.04.2020 to 16.06.2020.

2.2.1 Fish capture and tagging

45 smolts (mean length 147.9 ± 7.93 mm, mean weight 26.96 ± 6.39 g) were captured via electrofishing, due to its reliability as a form of capturing fish with fork lengths varying from 10-20 cm (Chaput 2012), and fish were then retrieved from the water using hand nets. Salmon were captured between the 17.04.2020 and 21.04.2020. Individuals were identified as salmon smolts by their morphological characteristics. Capture sites were recorded for each individual. Smolts were transported from their capture sites to the Voss hatchery in aerated containers filled with fresh water sourced from the river Vosso. Holding time was limited to less than a day and the fish were kept in free-flowing water in order to minimise stress. A day after capture, the fish were individually anaesthetised in tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate (NaHCO_3). Acoustic tags were then surgically implanted into the peritoneum (mean surgery time 03:04 minutes). A 2-3mm incision was made to allow for the implantation into the peritoneal cavity and then the incision closed with interrupted Ethicon sutures (Ethicon suture EH7144H 4-0 polyglactin suture with FS-2 19 mm 3/8c swaged on needle). The tags selected for this study were 6 mm Thelma Biotel's, set to transmit at 69 kHz. These tags were smaller than the ones used for trout with a quieter decibel output and therefore smaller range, and an expected battery life of four months. Weight, fork length and surgery time were recorded for each individual as well as any visual observations concerning an individual's wellbeing (see appendix). Twenty seven brown trout (mean length 512.77 ± 75.96 mm, mean weight $1,200.89 \pm 759.26$ g) were captured by rod and reel from the 23.04.2020 to the 12.06.2020. Trout were held in a submerged cage in lake Evanger for a maximum of three days before surgery was undertaken on the shore (mean surgery time 03:51 minutes). The trout, being of a larger size than the smolts, enabled us to use larger tags with louder pings, LP13-D with an expected battery life of three years. Otherwise, surgery and measurements followed the same methodology for the salmon. To identify each species salmon tags were numbered 1 – 45 and trout tags 136 – 161. Releases were always carried out just before sunset due to the expected higher post-release survival rates at night (Vollset et al. 2020). All animal handling and experimental procedures were approved by the Norwegian Food Safety Authority FOTS application 22861.

2.3 Statistical analysis

Statistical analysis and data visualization were performed with R 4.04 (R Core Team, 2020. Version 4.0.3). Data were analysed with general additive models using the mgcv package in R (see overview by Wood, S.N 2017). Generalised additive models (GAM) use the sum of smooth functions of covariates which allows our dependent variable to not be a linear function of the explanatory. Due to the large size of the data set, the model was fitted using the bam function. Bam saves on memory and requires less computational power than a standard GAM. The R package suncalc (Thieurmél & Elmarhraoui, 2019) was used to find the solar azimuth during each day of the study. The suncalc package provides the solar position in radians from east to west with 0 being the midpoint for that day. By analysing the salmon and trout's responses to the solar azimuth, it excludes the changing length of the daylight over the year compared to using hour of day. Vertical movement was also tested against the time of the year to test how salmon and trout adapted their

depth usage as the days became longer. The final part of the GAM tested salmon and trout's responses to warming temperatures over the period, which excluded the effect of daily light duration. Smoothers were applied to azimuth, time of year and temperature variables in order to observe how these variables affected the salmon and trout's variation in depth throughout the study period.

2.3.1 Data Filtering

A total of 2,828,120 detections were recorded over the study period for the raw data from lake Evanger. An individual was marked as deceased if the tag disappeared having not passed the receiver at the outlet into the river Bolstad or if the tag descended to one depth and then remained at that depth from then on. This appeared to be improbable behaviour and assumed to be a sign that the tag had been expelled from a predator. Other false detections that were excluded were "random" detections at receivers after the fish had presumed to have previously died or left, if that detection was unsupported by detections from nearby receivers. These detections were most likely due to incomplete pings from another individual's tag. I excluded similar random detections recorded before the individual entered the lake i.e., if a singular ping was detected several hours or a days before a continuous run of pings were recorded. Once these false detections had been filtered out the number of detections were reduced to 2,686,412.

In order to practically run a model, the data set had to be reduced again for a time period when both smolts and trout were present in the lake. The dataset was reduced to 2,262,047 observations, recorded between 23.04.2020 and 08.06.2020. Of these detections 124,179 detections were salmon and 2,137,868 were trout.

2.3.2 Model selection

2.3.2.1 Autocorrelation testing

The first model tested included three variables (azimuth, time of year and temperature) with smooth term functions applied and two fixed effect variables (length and weight), and depth set as the response variable. Individuality (ID) was applied as a random effect.

Due to the nature of animal movements, the data was expected to be temporally correlated. As such, autocorrelation structure was tested in the second model. Autocorrelation testing informs the model that the previous n point influences current observation. The preferential model was chosen by comparing the AIC for each model. The Akaike Information Criterion (AIC) is useful for comparing models of the same data set in a time series. It measures how well each model best fits the data by scoring it with a numerical value, adding penalties for complexity as this can lead to overfitting.

2.3.2.2 Exclusion testing

The model with the lowest AIC was then used for further testing. Three more models were created, each one had one of the smoother variables excluded. AIC values were generated for each of these new models and then compared with the first stage.

3 Results

3.1 Summary of data

Out of the 45 salmon that were tagged, 18 were excluded in the filtering process as no continuous data was provided by their tags. This resulted in a total of 124,179 smolt detections. Of the remaining 27, eight were judged to have successfully traversed the lake equalling a 70.4% mortality rate. Mean depth of successful migrants was 4.61 ± 3.56 m. Mean depth of the unsuccessful migrants was 4.2 ± 1.88 m. The mean residency time of successful migrants in the lake (calculated to the nearest half an hour) was 189.5 ± 197 hours. The shortest amount of time a successful migrant resided in the lake was 19 hours (ID 14) and the longest was 576 hours (ID 25) (Table 1). The shortest duration an unsuccessful migrant was counted in the lake was seven hours (ID 8) and the longest was 655.5 hours (ID 17) (Table 1). On an individual scale (Figure 2), salmon displayed a selection of depth preferences throughout the study. Some individuals stolidly remained in the upper 5m of the water column while others made extended forays to greater depths.

Of the 27 trout tagged for this study, one was filtered out of the results as its capture, tagging and release into the lake occurred after the study period required to run the model. This resulted in a total of 2,137,868 detections. Mean depth of trout over the study period was 3.13 ± 1.4 m. Mean residency time for the trout was 649.5 ± 335.5 hours. However, as trout were being tagged up to 31.05.2020, when four additional trout were tagged, residency time for trout in the lake is not an accurate representation of trout preference for lake Evanger. Residency time varied greatly for trout. Some resided in the lake for the entire study period with the longest resident staying for approximately 1,066.5 hours (Table 2). Others spent relatively little time in the lake with the shortest residency being 54 hours (ID 158) (Table 2). The majority of detections of trout appear to occur in the upper 10m of the water column (Figure 3). Trout were not limited to this depth and detections occurred as deep as 25m. Of particular interest was trout 146 which spent most of its time at the surface. Due to the continuous nature of the data and that detections moved between receivers the decision was made to include this individual with the model. (Figure 3)

Table 1: Approximate residency time (to the nearest half hour), mean depth in metres, number of detections and successful navigation of lake Evanger. A 1 marks the salmon as a successful migrant and 0 indicates mortality.

Fish ID	Species	Residency (hours)	Mean depth (m)	Detections	Survived
1	salmon	532.5	3.11 ± 2.45	9,348	0
3	salmon	48.5	3.28 ± 0.87	662	0
5	salmon	449.5	2.77 ± 2.02	10,327	1
6	salmon	34	5 ± 3.11	1,277	1
7	salmon	18.5	2.71 ± 2.23	532	0
8	salmon	7	2.14 ± 1.18	4,729	0
9	salmon	12	5.55±1.53	3,054	0
10	salmon	25	2.46±1.01	4,410	0
12	salmon	65.5	2.24±0.92	1,884	0
14	salmon	19	1.95±0.65	2,974	1
16	salmon	201	11.76±3.83	5,692	1
17	salmon	622.5	5.91±2.63	8,451	0
18	salmon	5.5	3.52±1.91	106	0
19	salmon	101.5	5.47±3.22	129	1
22	salmon	261.5	6.51±2.29	5,123	0
23	salmon	410	2.6±1.28	26,486	0
24	salmon	12.5	2.35±2.51	4,148	0
25	salmon	576	7.07±3.61	935	1
28	salmon	421.5	3.39±3.09	21,329	0
29	salmon	13	4.28±3.22	369	0
30	salmon	75.5	1.48 ± 2.18	324	1
31	salmon	135.5	6.32±4.29	283	0
32	salmon	196.5	8.48±4.27	2,362	0
33	salmon	46	1.4±1.86	275	1
35	salmon	317	6.54±2.88	4,760	0
39	salmon	202.5	3.05±2.03	928	0
43	salmon	311	5.28±4.58	3,282	0

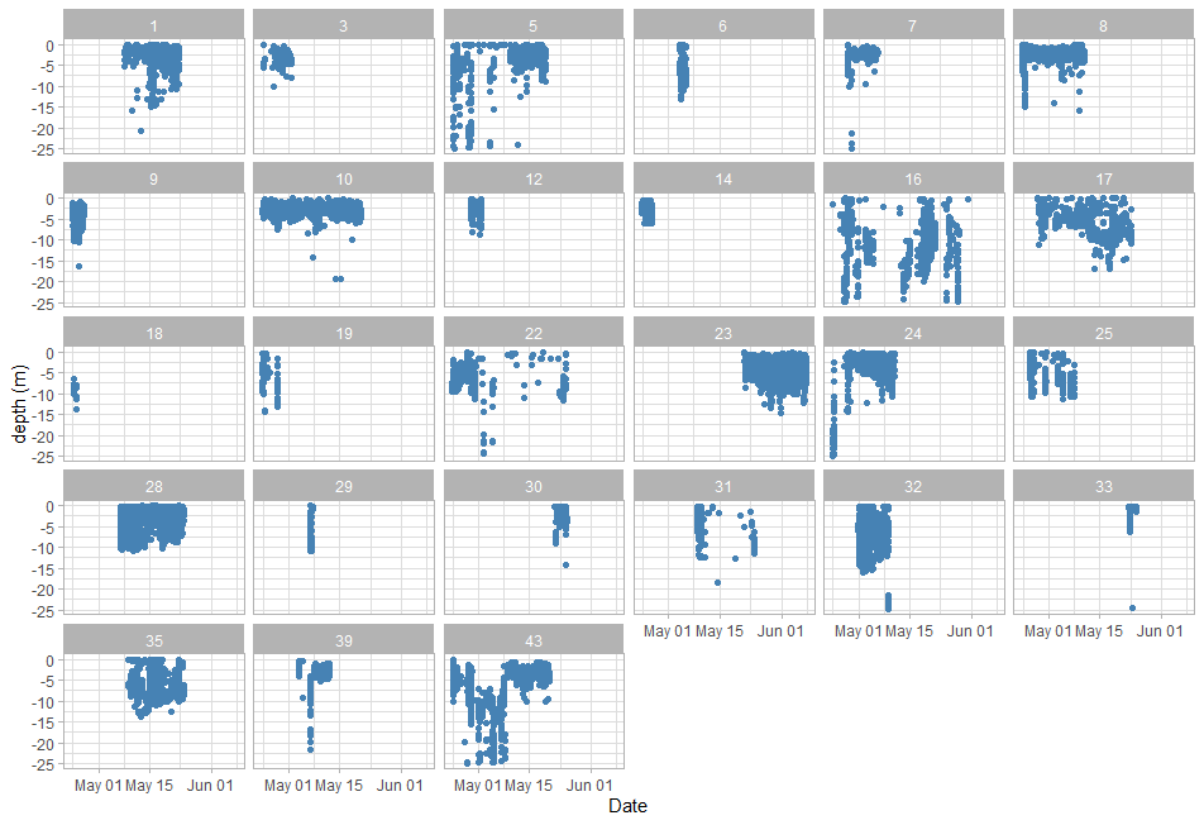


Figure 2: Individual detections of salmon showing their movement through the water column throughout the study period. Breaks in the detections are assumed to be caused by an individual moving out of receiver range. Depth is measured in metres from the surface.

Table 2: Approximate residency time (to the nearest half hour), mean depth in metres, number of detections and successful navigation of lake Evanger.

Fish ID	Species	Residency (hours)	Mean depth (m)	Detections
136	trout	245.5	4.84±1.36	72,580
137	trout	565	3.21±1.26	46,196
138	trout	887.5	2.05±1.5	16,717
139	trout	1,066.5	3.41 ± 1.670	146,645
140	trout	624.5	3.91±1.5	54,075
141	trout	235.5	6.12±3.82	57,156
142	trout	1,093	2.6±1.89	37,617
143	trout	459.5	2.31±1.05	136,790
144	trout	1,022	4.32±2.95	175,098
145	trout	1,022	2.19±1.1	316,574
146	trout	1,021.5	0±0.11	128,713
147	trout	730	2.65±1.22	12,829
148	trout	543.5	2.08±0.89	56,213
149	trout	1,021	3.02±1.57	104,130
150	trout	975	2.52±1.36	40,426
151	trout	975	2.81±1.29	107,687
152	trout	760	3.86±1.47	191,912
153	trout	286	5.51±3.17	8,251
154	trout	758.5	2.79±1.41	103,604
155	trout	758.5	2.48±0.79	35,996
156	trout	758.5	4.33±2.06	141,299
157	trout	481.5	2.02±0.98	73,223
158	trout	54	0.83±1.32	1,801
159	trout	181	2.67±1.54	27,674
160	trout	180.5	5.5±1.7	21,244
161	trout	180.5	3.31±2.32	23,418

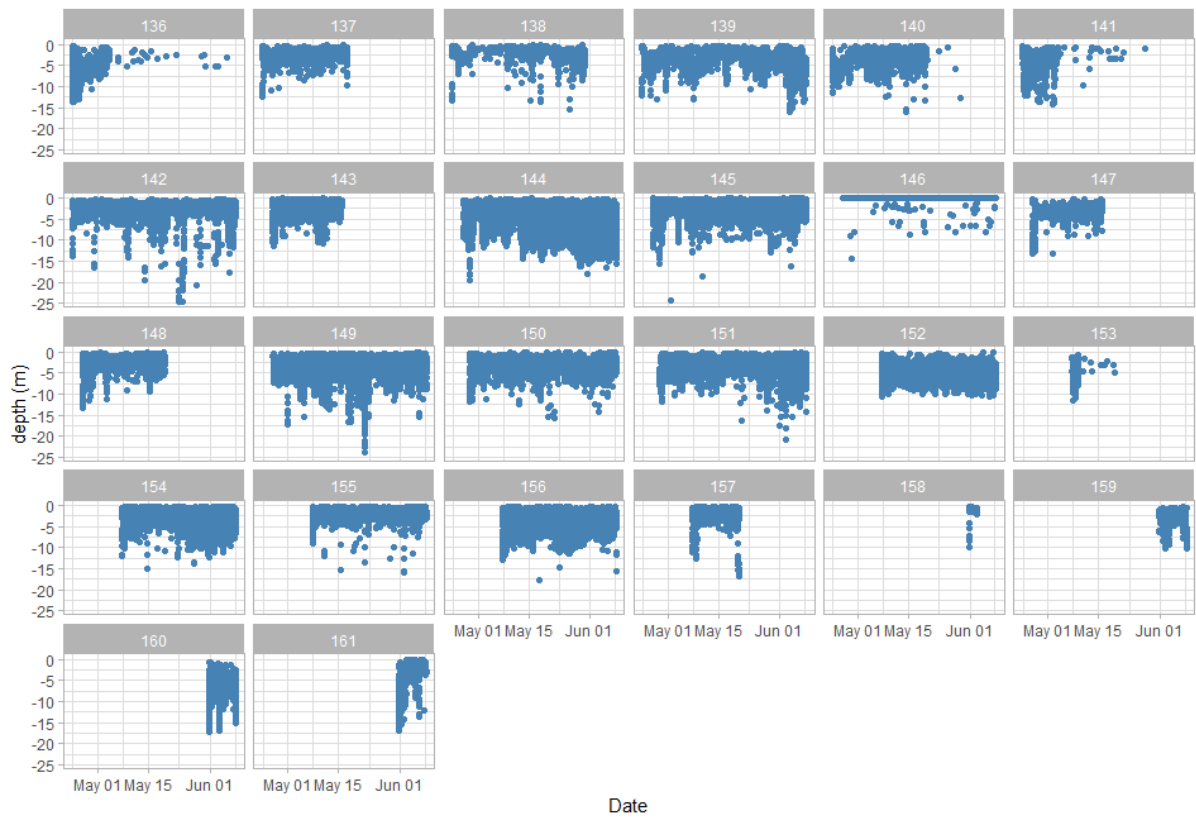


Figure 3: Individual detections of salmon showing their movement through the water column throughout the study period. Breaks in the detections are assumed to be caused by an individual moving out of receiver range. Depth is measured in metres from the surface.

3.2 Model summary

The AIC comparison between model 1 and 2 produced a lower AIC for model 2 (Table 3), showing that testing for autocorrelation structure was necessary. Checking model 2 revealed that the residuals for the smooth function for time of the year were not randomly distributed. Model 2 was refitted with a higher k to produce model 3. AIC comparisons showed model 3 to as the best fitted model (Table 3). Explanatory variables were removed to produce models 4 – 6, all of which produced a higher AIC than model 3, confirming model 3 as the best fit for the data (Table 3). The output for model 3 showed that all smooth terms were significant (Table 4). Both species showed a depth response to the progression of the solar day, demonstrating a preference for deeper waters when the sun was at its highest over the lake. Salmon showed a strong response to changing temperatures, opting to spend more time in shallower waters as the temperature increased but showed no clear response to time of year. Trout appeared unaffected by temperature and time of year, with time of year causing a depth variation of one metre and temperature causing no significant change to depth.

3.2.1 Model comparisons

Table 3: AIC comparison of the six fitted models. Model 3 produced the lowest AIC and was thus selected as the model with that best explains the data. Δ AIC shows the difference between the chosen, preferential model and the AIC of other models. The table is ordered by AIC instead of order of creation.

Δ AIC	AIC	Model	Fish ID	Species	Azimuth	Time of year	Temperature	Fork length (mm)	Weight (g)
0	1,993,660	3	X	X	X	X	X	X	X
314	1,993,974	6	X	X	X	X		X	X
1,731	1,995,391	2	X	X	X	X	X	X	X
3,763	1,997,423	5	X	X	X		X	X	X
9,062	2,002,423	4	X	X		X	X	X	X
6,694,011	8,687,671	1	X	X	X	X	X	X	X

3.2.2 Preferential model output

Table 4: Summary of model two, the model that produced the best fit for the data. ID and species were set as factors. Depth was tested against individual fish length and weight and the smooth terms azimuth, day of year and temperature. Individuals were set as a random effect.

R code: `model2 <- bam(d ~ ID + s(fID, bs="re") + s(azimuth, by=fsp, bs="cc") + s(yd, by=fsp, K=29) + s(temp, by=fsp) + Length.fork..mm. + Weight..g., rho=rho, AR.start = tev4$newtimeseries, data=tev4)`

Parametric coefficients	Estimates	Standard error	t-value	p-value
Intercept	3.784	0.856	4.421	<0.001
ID	-0.011	0.016	-0.657	0.511
Length (mm)	0.003	0.007	0.397	0.691
Weight (g)	-0.001	0.001	-0.544	0.586
Approximate significant smooth terms	edf	Ref.df	F-value	p-value
Smooth ID	47.46	49	293.741	<0.001
Smooth azimuth by species (salmon)	7.987	8.000	938.741	<0.001
Smooth azimuth by species (trout)	7.852	8.000	448.519	<0.001
Smooth date by species (salmon)	27.150	27.853	88.922	<0.001
Smooth date by species (trout)	25.932	27.654	48.851	<0.001
Smooth temperature by species (salmon)	8.503	8.937	30.565	<0.001
Smooth temperature by species (trout)	6.827	8.109	7.766	<0.001
Autocorrelation	Rho			
	0.97			

3.3 Hypothesis 1: Diel vertical migration

The diel vertical movement of smolt and trout changed. Salmon descend from depths at 2m to almost 5m at dawn before settling around 5m at sunrise. Interestingly, the salmon appear to ascend to 4m towards solar noon. Pre dusk, the salmon descend to post dawn depths of 4m before making their crepuscular ascent to shallower waters again (Figure 4; smolt: $F=979.0$, $P<0.001$, $df=8.0$). Trout displayed similar behaviour, though not as pronounced. At dawn, trout descended from 3m to 4m. Unlike the salmon, the trout remain at 4m throughout peak daylight before beginning their dusk ascent back to 3m. They remained at this depth before ascending again at dusk to 4 metres (Figure 4; trout: $F=610.5$, $p<0.001$, $df=7.9$). Ascent and descent seems to occur at approximately the same moment for both species, though the salmon display a more rapid ascent to shallower waters.

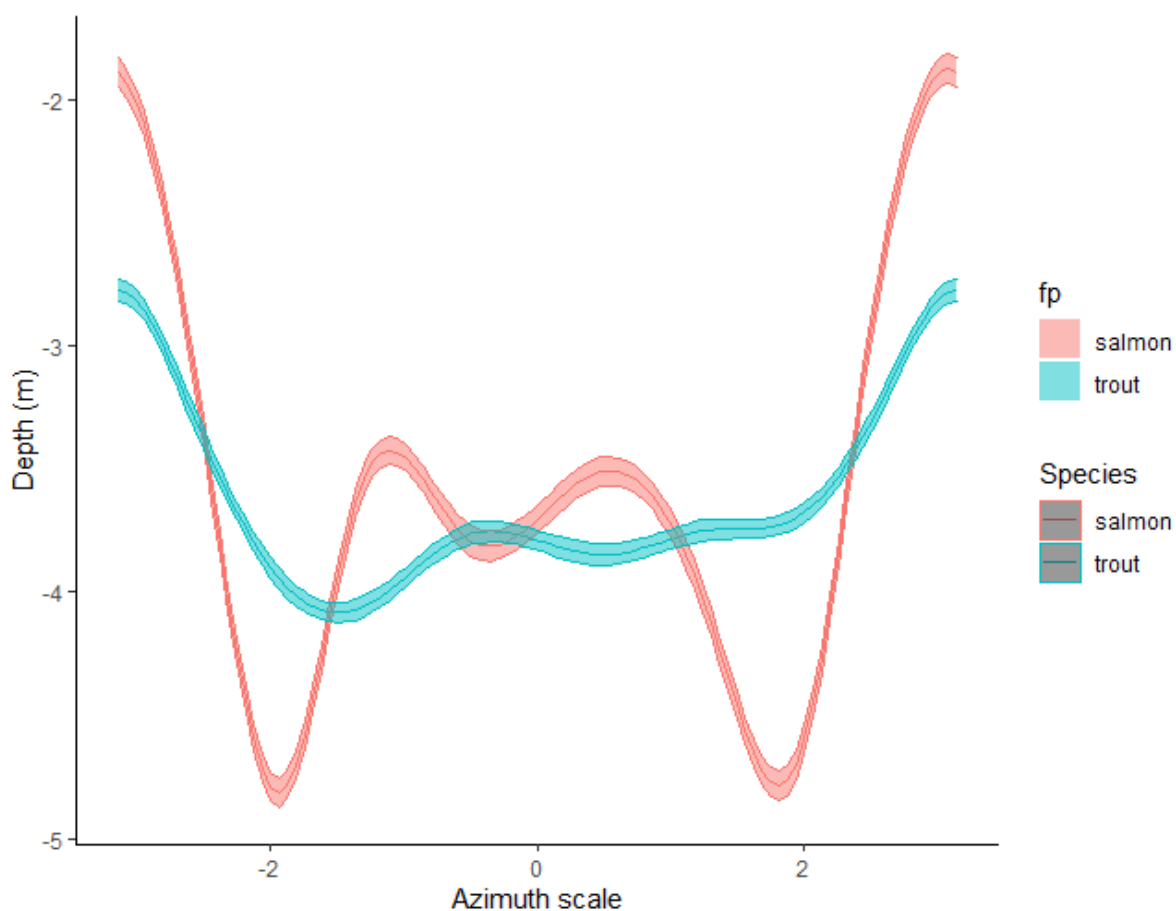


Figure 4: Model 2 (see table 4) produced significant smooth terms for the interaction between azimuth and depth. On the x axis, 0 represents solar noon in radians, negative values are before noon and positive values after noon. The y axis is the depth in the water column.

3.4 Hypothesis 2: The effect of time of year

Salmon appeared to modify their depths between 2m and 6m depths throughout the period (Figure 5; smolt: $F=88.9$, $p<0.001$, $df=27.9$). The wider confidence intervals for salmon towards the end of the study period is likely a result of there being fewer individuals in the lake as time goes on. By June only salmon 16 and 23 were still active in the lake. Trout maintained a more stable depth range between 3-4m throughout the study period (Figure 5; trout: $F=48.9$, $p<0.001$, $df=25.9$).

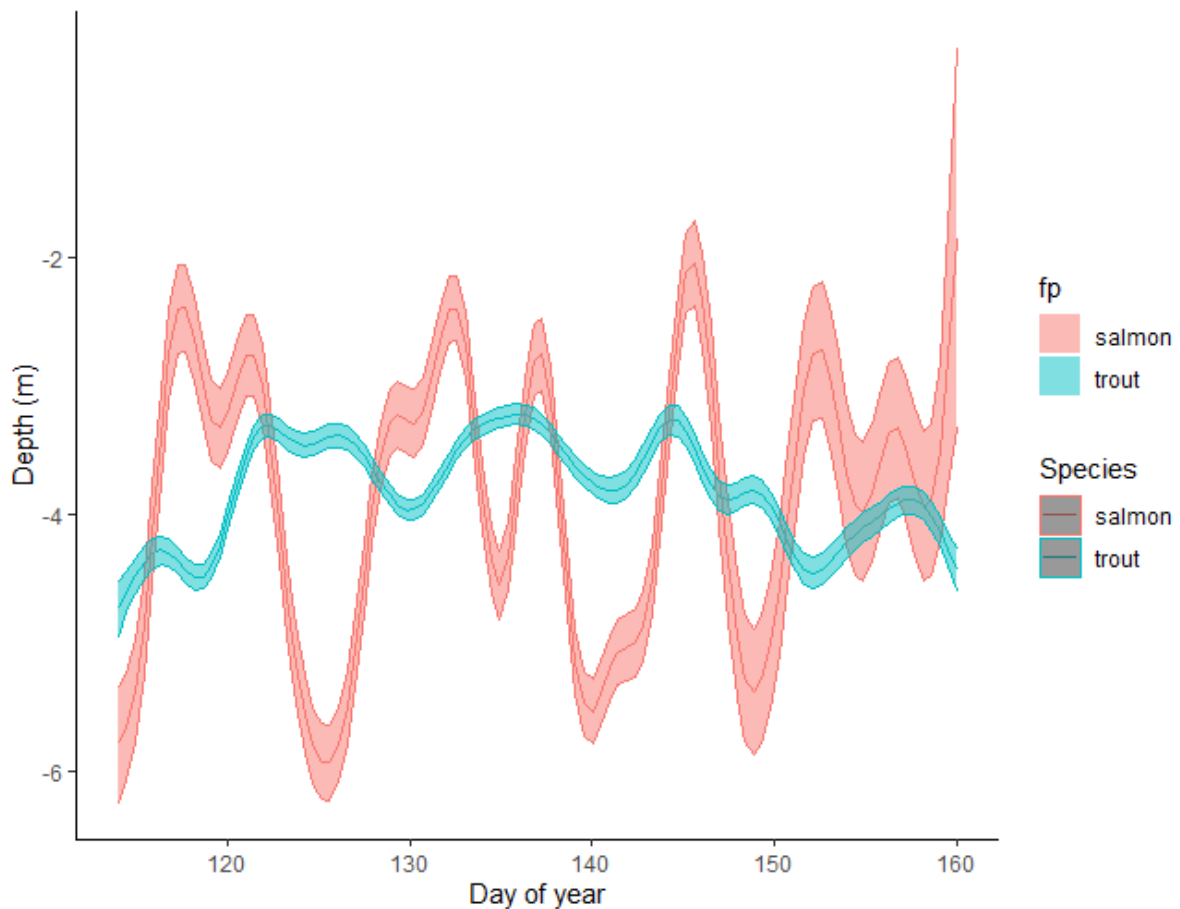


Figure 5: Shows the movement of salmon (pink) and trout (blue) through the water column from 23.04.2020 to 08.06.2020 with 95% confidence intervals, produced by model 3 (see table 4). X axis shows the day of the year as a numerical value while the y axis shows the depth from the surface.

3.4.1 The effect of temperature

Over the study period, the surface water temperature of lake Evanger ranged from a low of 4.35°C to a high of 7.92°C (Figure 6). At around 17.05.2020 temperature increased by over 1°C in just a few days (Figure 6). A second rapid increase, this time just under 1°C, occurred around 29.04.2020. Temperatures recorded at other depths during the study period showed very little variation, so the decision was made to use surface water temperature for ease of modelling. The average distribution of salmon moved to shallower depths in the water column, from 4m to 2.5m, as temperature increased from 5°C to 8°C (figure 7; smolt: $F=28.7$, $p<0.001$, $df= 8.9$). Trout appeared to be unphased by changing temperatures remaining around 3.5m deep throughout the temperature range (figure 7; trout: $F=5.9$, $p<0.001$, $df=7.8$).

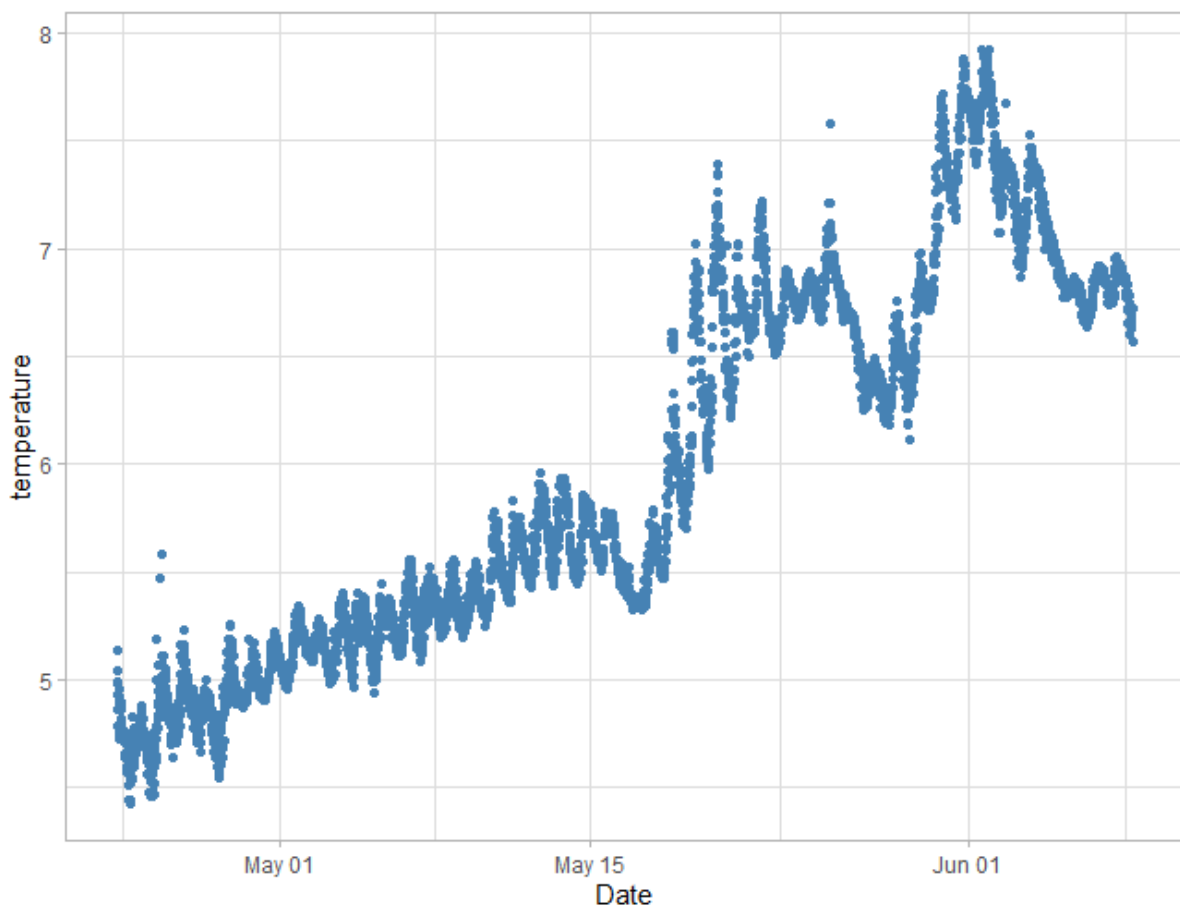


Figure 6: Shows the surface water temperature change from 23.04.2020 to 08.06.2020 created from the raw temperature data.

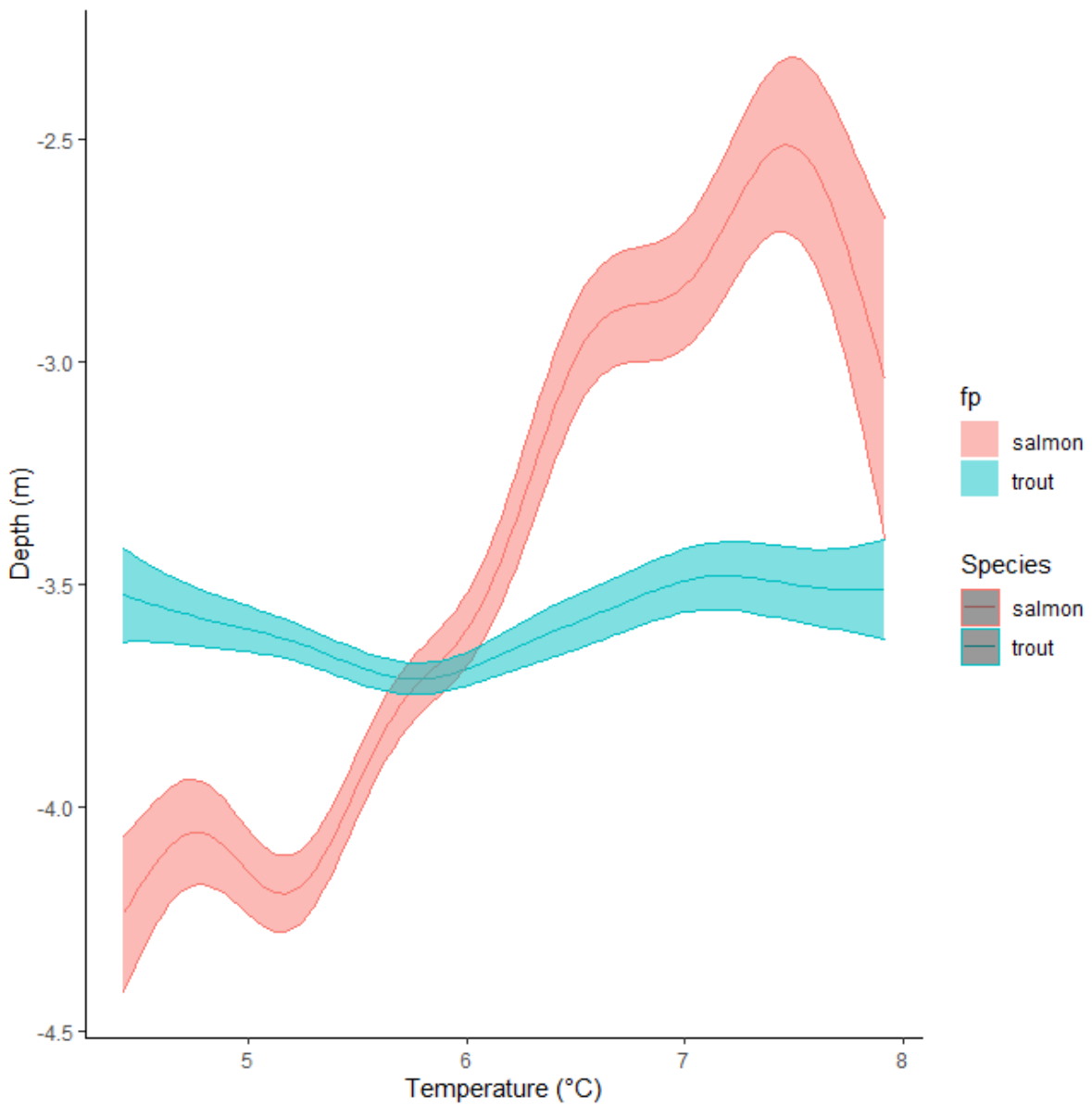


Figure 7: Shows the depth preference of salmon (pink) and trout (blue) as temperature changes with time of year data excluded and 95% confidence interval, produced by model 3 (see table 4).

4 Discussion

This study investigated how day light and temperature affected the distribution of salmon and trout throughout the water column. My study presented two hypotheses to investigate. The first, whether salmon made diel vertical movements during the crepuscular period, was supported by the GAM model. Both salmon smolts and their predator, Brown trout, showed diel movements that appeared to be induced by the angle of the sun over lake Evanger. This could be interpreted as the predator avoidance strategy in line with my hypothesis, being employed by both species. My second hypothesis was intended to test whether salmon would spend more time at deeper depths as the season progressed. This hypothesis was shown to be incorrect. Salmon moved through depths between 2-6m throughout the study period, indicating that time of year had no direct effect on depth preferences for salmon. However, as temperature warmed, salmon displayed a clear preference for shallower depths. Neither longer photoperiods nor warmer temperatures had an effect on the depth preferences of trout. Compared to mortality in other lake studies (Kennedy et al. 2018; Honkanen et al. 2021), salmon smolt mortality was high in lake Evanger with 70% of individuals failing to migrate through the lake.

4.1 Diel vertical migration

As the angle of the sun over the horizon changes relative to the lake, the salmon altered their depth supporting my first hypothesis. The diel illumination cycle acts as the proximate cause to the salmon's behaviour and is separated into three phases: daily, crepuscular, and nocturnal. During the day, when illumination is brightest, salmon were found deeper in the water column. Rapid changes in illumination during the crepuscular period then elicited a significant response in the salmon, which ascended to shallower depths. When the nocturnal period ended, the salmon descended once more to deeper waters. This diel vertical behaviour has been observed in many fish genera such as *Oncorhynchus*, *Corgonus*, *Lota* and *Osmerus* (Appenzeller and Leggett 1995; Scheuerell and Schindler 2003; Probst and Eckmann 2009; Busch and Mehner 2009).

Salmon have evolved phenotypic adaptations to help them avoid visual predators at dim light levels. A diel vertical migration (DVM) model was designed by Clark & Levy (1988), which examined the diel vertical behaviour of planktivorous juvenile Sockeye salmon. Clark & Levy asserted that juvenile sockeye salmon performed DVM as a trade-off between foraging and predator avoidance. The cryptic pattern (also referred to as countershading) provided juvenile Sockeye salmon with protection from its visual predators trying to locate them during the low light levels during crepuscular periods. Atlantic salmon smolt have also evolved a highly cryptic colouring pattern that helps the animal blend in with their environment; they are lighter on the ventral body and darker on the dorsal body (Clark and Levy 1988; Thorstad et al. 2012b). At the crepuscular periods, the camouflage is at its most effective, providing a defence against avian predators from above and piscivorous fish from below. The planktivorous salmon smolts would not be at a disadvantage themselves as zooplankton have not evolved countershading (Clark and Levy 1988). Hence, the diel movements are a response to the ultimate cause of predation, and we can see the idea of the antipredation window put in effect. This behaviour is most likely induced during smoltification as previously Atlantic salmon parr generally has a sit and wait feeding behaviour, and are territorial predators with patterns that camouflage them against the substrate of rivers and streams (Dill and Fraser 1984).

There is evidence that foraging plays an important role in the smolt migration in order to sustain growth rates that have the potential to increase later survival and fecundity. One study by Hulbak et al (2021) found that salmon smolts in the river Dale, Norway, had grown by a mean of $5 \pm 4\%$ in the course of their migration. In a study in the Bras d'Or lakes, Canada, Strople et al. (2018) asserted that 69% of their sample population of Atlantic salmon had enough energy reserves to survive their migration. Extrapolating from that study, foraging must be important for individuals starting the migration with low energy reserves, and even those with higher reserves would still have to engage in some foraging activities for growth (Strople et al. 2018; Hulbak et al. 2021). The antipredation window would also provide a safe time for the smolts to engage in migratory behaviour, which have been shown to predominantly occur during the nocturnal hours (Aarestrup et al. 1999; Hanssen 2020). The fact that both foraging and migratory behaviour occurs at these suggest predation must be a significant evolutionary driver for salmon.

The daily movements up and down within the water column can come at an energetic cost to the smolts which may have an impact on later survival. Both the energy required for swimming and buoyancy control may explain the limitation we observe in the average depth the salmon descended to. In the matter of buoyancy, salmon are generally forced to remain in shallower waters in order to achieve neutral buoyancy and maintain energy efficiency (Macaulay et al. 2020). As physostomous fish, salmon do not possess the rete mirabile, a specialised tissue used to refill the swimbladder, and must inhale air from the surface in order to fill their swimbladder (Clemens and Stevens 2007; Macaulay et al. 2020). While the debate surrounding the energetic costs of swimbladder regulation is still unresolved (Mehner 2012) compensatory behaviour has generally been agreed upon. At greater depths, salmon would have to generate lift by tilting their bodies and swimming with their fins (Alexander 1990; Strand et al. 2005), yet more energy diverted from potential growth. Testing the bioenergetic costs of DVM in lakes as behavioural strategy would be a logical next step after this study.

Trout follow a similar diel pattern to the salmon, supporting my first hypothesis, and the movements appear to occur almost simultaneously. Clark & Levy (1988) make the point that the Sockeye salmon sacrifice maximum foraging efficiency as the risk of predation prevents them from following their zooplankton prey, which perform reverse DVM. In the trout, we can observe a species that does not face this same risk. In fact, the trout would still benefit from the antipredation window by avoiding avian predators that pose a risk to the trout (Eldøy et al. 2017). Within the sampled population of trout, some individuals may spend their entire lives in fresh water, whilst others will spend summer in the marine environment before returning to overwinter in freshwater (Jonsson 1989; Jonsson and Jonsson 2002). As temperatures warm in the spring, the activity of the trout increases but their fat to body ratio is at its lowest (Klemetsen et al. 2003). All this would suggest that Brown trout and the Atlantic salmon smolt migration would be an example migration coupling. Migrant coupling is where consumers take advantage of the large scale migrations of their prey, for example Bull trout predate migrating Sockeye salmon (see review by Furey et al. 2018). The salmon smolt run in the Vosso river system would be an excellent source of nutrition for the trout, especially the trout preparing to return to the ocean. However, despite spatial overlap in the species, Lennox et al (2019) did not find evidence of a strong temporal overlap of the species. Though the hypothesis of migratory coupling could not be proved, observatory reports confirmed salmon smolts still formed a partial part of the trout's diet (Lennox et al. 2019). Following similar depth preferences and DVM patterns to a potential prey would help trout offset the bioenergetic costs of this behaviour. Unlike the salmon

smolts, the trout have the potential for prey encounters throughout their movement patterns making up for the energy lost to movement and buoyancy regulation.

4.2 Modification of depth over time

My second hypothesis predicted that salmon would spend less time at shallower depths due to the longer photoperiod. The prediction was based on the idea that if the salmon were simply following DVM behaviour they would be forced to spend more time at deeper depths because the nights were getting shorter. However, the data did not support my second hypothesis. Resident species of lakes may change their diel vertical behaviour with changing photoperiods. For example, coregonids in a polar lake in northern Norway abandoned DVM completely during the polar summer in June, sacrificing food availability under the predation pressure of local Brown trout, and then returned to their diel behaviour in September (Kahilainen et al. 2009). As day length is a stable abiotic factor it is a common indicator for organisms from a variety of taxa that a behavioural change is required (Bradshaw and Holzapfel 2009). From insects to mammals it can trigger the production of hormones, breeding seasons and migrations, its reliability as an indicator emanating in its stability as an abiotic for generations over the course of their evolutionary history (Bradshaw and Holzapfel 2009). For the salmon smolts, their ultimate goal is to navigate their way out of the lake and reach the sea when conditions are most favourable (Thorstad et al. 2012). If day length was an indicator for smolt migration one might expect a shift in depths from deeper to shallower as the salmon smolts spend more time searching for a way out of the lake. In my results, the smolts varied their depth throughout the study period suggesting that increasing day length is not an indicator to smolts that they are running out of time to complete their migrations.

Increasing temperature led to a shift in the average depth preferences of smolt from deeper to shallower. There is evidence that temperature and discharge act as abiotic indicators (Antonson 2011; Byrne 2003; Whalen 1999). In the studies by Byrne (2003) and Whalen (1999), investigating smolt migrations in Ireland and the USA respectively, both found that migrations began when surface temperatures were around 5°C. However, the results from lake Evanger show the migration beginning when temperatures were between 3-4°C in mid-April. Time series data of smolt migrations in eastern Canada have also suggested that populations have responded to the effects of climate changing, including higher temperatures of up to 10°C, by initiating their migrations earlier (Otero et al. 2014). This could indicate that temperature acts as a regional indicator for the optimum arrival time at sea (Thorstad et al. 2012). My results support the evidence that temperature acts as an abiotic indicator for smolt migration. Spending more time at shallower depths suggests that the smolts are increasing the amount of time searching for an exit to the lake to continue their migration. The warmer temperatures come with benefits and costs to the smolt. If temperatures are below optimum, warming can accelerate ectothermic fishes reaction time, helping them to avoid predators at the cost of a faster metabolism (Claireaux et al. 2006). Further, there is evidence that the higher temperatures decrease the time salmon can go without food which provide another stimulus to reach the richer foraging grounds of the marine environment (Strople et al. 2018). Due to the high mortality in lakes, those individuals that are able to navigate and leave the lakes earlier would gain higher chances of survival and eventual migration success (Honkanen et al. 2018, 2021). The warmer temperatures would also reduce the oxygen saturation in the lake, leading the smolts to spend more time closer to the surface waters (Jonsson and Jonsson 2009; Remen et al. 2013). Measuring the saturation levels of the lake would make a good addition for future studies.

In contrast to the salmon, the trout displayed very little variation in depth, both as the study period went on and as temperature changed. Variation in depth when tested against the changing photoperiod and temperature was between 3-4m. What is most likely being recorded is the natural variation of the trout's depth. Trout in rivers in western and Eastern Norway have been shown to occupy depths down to 50m but fish density decreases with depth (Jonsson 1989). My results showed that the tagged trout primarily remained near the surface in line with the distribution of tagged salmon smolts. Another study on the depth preferences of brown trout in Norwegian fjords found their depth presence to be between 1m and 3m below the surface (Eldøy et al. 2017), which closer reflects my results. This near surface depth preference is most likely a combination of balancing prey availability and bioenergetic costs of deeper water, such as buoyancy control. The fact that we observed no major change suggests that neither a temperature nor an oxygen saturation threshold had been reached for the trout, though further testing would be needed to support this. The trout may also be at a depth where they can navigate the lake and don't need to move shallower in order to find a way out of the lake. Many individuals appeared to leave the lake by the end of the study period, however they may have remained outside of the range of the receivers.

4.3 Mortality

Smolt mortality recorded in lake Evanger in this study was 70%. This level of mortality is high. Mortality in lakes have been recorded from lows of 30% at Loch Meig, Scotland (McLennan et al. 2018) and 55% in the lakes of the Conon river system, Scotland (Honkanen et al. 2021), to as much as 90% in lake Tange, Denmark (Jepsen et al. 1998). Previously, estuaries had been considered the major area of mortality due to the activities of predators which ranged from 0.6 – 36% (Thorstad et al. 2012). When we consider that predation in lakes can be as high as 90% it is clear that the lakes present a potentially more lethal hazard to salmon (Honkanen et al. 2021). Not only is the lake an area for predator aggregation but the difficulty of navigating these lakes can slow down the migration of salmon potentially leading to a mismatch between when the salmon leave the freshwater systems and when the most beneficial time of entering the marine systems. A late arrival may miss out on suitable prey and suffer from reduced growth rates greatly impacting their chances of survival (Thorstad et al. 2012). Diel vertical migration is an evolved response to high predation pressure. The evidence presented in this study showed that salmon have a behavioural response to diel patterns and other studies have shown that migratory movements occur predominantly at night with a greater increase in diurnal movements as water temperatures increase (Thorstad et al. 2012; Honkanen et al. 2018; Hanssen 2020). Salmon have evolved other strategies to combat predation. Salmon are believed to synchronise their movements and form shoals in order to swamp predators (Thorstad et al. 2012; Furey et al. 2020). Shoals may consist only of salmon, though there is evidence that brown trout smolt, on their own sea ward migration, bolster the numbers in these shoals (Armstrong et al. 2003). Predatory strategies must be well adapted to lakes.

Despite the antipredatory behaviour of salmon mortality remains high. Piscivorous fish have been observed to aggregate at the entrances to lakes and estuaries, especially in those where depths increase to 25m and deeper (Jepsen et al. 2006; Kennedy et al. 2018). This effective strategy could be countered by the salmon by timing migrations before the predators have a chance to gather in large numbers. Early migrants have shown a higher rate of survival (Thorstad et al. 2007) for example, in Lough Erne, Northern Ireland (Kennedy et al. 2018). If some salmon smolt populations

are migrating earlier due to higher temperatures as suggested by Otero et al (2014), studies into whether their predators which exhibit aggregative behaviour to take advantage of the migration are also changing would be an astute next step from this study. Examining their spatial and temporal overlaps during the migration period, for example Lennox et al. (2019), could provide evidence of the existence migratory coupling and whether predators are also adapting to the behavioural changes of their prey.

4.4 Limitations and areas for future study

Despite the high rates of mortality recorded, in this and other studies, it is generally accepted that these results should be considered as higher estimates. Telemetry studies come with some challenges. One cannot dismiss the effects that the tagging process and tags themselves have on individuals. The tagging process could lead to a change in behaviour, higher levels of stress and increased mortality compared to untagged fish (Jepsen et al. 2002; Berhe 2021). Overestimation of survival can occur in studies without predation sensors if predators mimic behaviour similar to that of their prey (Gibson et al. 2015; Flávio et al. 2019; Daniels et al. 2019). This can establish false conclusions and impair the quality of decisions based around this data. The complexities involved in predator-prey interactions makes it difficult to estimate which behavioural changes caused by the stress of tagging results in higher mortality to predators. Even so, telemetry remains a powerful tool in the field of aquatic ecology and an increased understanding of predator-prey interactions is a pathway to mitigating the risks of survival bias in studies where predation tags are unsuitable.

Another potential bias revolves around the capture methods. If the capture methods are biased towards capturing slower or larger individuals, then this can lead to over or under estimations of mortality. We used electrofishing for smolt which allowed us to capture a sample of fish of a variety size and conditions. However, electrofishing trout is a more difficult process and angling was considered to be the most fitting capture method. Tag failure can also play a part in overestimations. It is common to assume that sudden disappearances of tagged fish are a result of avian predation, as such the likelihood of tag failures should be accounted for in any study focusing on avian predators. Trout 148 showed unusual behaviour in that it remained at the surface for the majority of the study period. This could have suggested that it had died or was a tag malfunction. As there was no way of confirming either of these assumptions, and due to the longevity of the detections, I made the decision to leave it in the data set.

Current limitations in technology means we were unable to use tags that contained both predation and depth sensors as they are too large for salmon smolts. By excluding those individuals whose tags descended and then remained at the bottom, as well as detections unsupported by surrounding receivers after the individual was believed to have traversed the lake or died, I believe I have mitigated the majority of bias from dead individuals to the best of my ability. Unfortunately, it was still not possible to get an exact date and time of predation. In studies like these, where the subjects size limits the size of tags, deciding on the time of predation events is very subjective and hard to duplicate (Halfyard et al. 2017). Further behavioural studies done in tandem with individuals tagged with predation may help define predation events for studies where no predation sensors are involved. A larger sample size could have led to more support to the findings in this study but considering the number of detections I believe the data behind this study are sound. It would have been preferable to be able to include all 45 salmon initially tagged. The 18 salmon excluded were

assumed not to enter the lake and such events are not uncommon in field studies, for example in Hulbak et al. 2021 where an estimated 28% of tagged salmon did not migrate just 300m to a wolf trap downstream of the release site. Plenty of data was collected on the trout, however, the diversity of trout sampled could be increased by fishing at different depths or using multiple gear types. In a study by Jonsson (1989), trout were shown to inhabit different depths based on age and sex. It would be interesting to see how the ratio of anadromous to resident trout may be stratified by depth. Although it has been suggested that those trout that spend their time in deeper water feed at those depths, mapping which areas trout forage in could reveal behavioural characteristics among conspecifics. Further insight into hunting strategies, population dynamics and predator avoidance behaviour could be gained.

In order to take this study further, spectrometers could be placed alongside some receivers so that the light attenuation over the study period could be compared with depth choice of both species. Other studies have investigated the illumination threshold for successful foraging activities in Salmonids. In studies of Rainbow, Cutthroat and adult Lake trout, maximum reactive distances of 50-60cm have been estimated at 15-20 lux (Mazur and Beauchamp 2003; Vogel and Beauchamp 1999) but below 0.4 lux these visual piscivores appear severely disadvantaged. In a study on brown trout, feeding on shrimp was reduced but continued at levels as low as 0.001 lux (Elliott 2011). By recording the level of illumination in water one might be able to estimate the risk salmon face at different depths and times of their diel behaviour. The sensitivity of deep water lantern fish eyes was estimated in a review by Busserolles and Marshall (2017). If sensitivity could be calculated for the eyes of salmon and trout, and light attenuation recorded throughout the diel movements, new insight could be gained into the effectiveness of DVM as an antipredation behaviour in salmon smolts. Future studies would benefit from tracking wind speed and surface currents. Comparing them with salmon movements when they are close to the surface would support the assumption that salmon move into shallower depths at least partially to utilise the surface currents as a means for navigating their way through the lake. External works have provided evidence salmon use surface currents to navigate lakes (Aarestrup et al. 1999).

4.5 Conclusion

My results suggest that salmon make use of diel vertical movements which may be useful as a predator avoidance mechanism. As the temperature warms, salmon begin to move into shallower depths, perhaps to help navigate their way out of the lake. My results support previous studies suggesting that lakes pose hazards to migrating salmon smolts on their migration. They are areas of increased predator contact and difficult obstacles to navigate. The high mortality recorded in my study suggests that managers should take particular notice of lakes when devising strategies for the restoration of salmon populations. Riverine systems that contain lakes likely have higher mortalities than systems without and therefore different survival estimates should be accounted for in these systems in order to ensure the better accuracy of population estimates. It is clear that the interspecific interactions in lakes are complicated and further study is required. Predator culling as a reaction to these higher mortalities should not be undertaken without definitive conclusions on how this would affect local systems. All stakeholders should be included in consultations before any decisions are made that could have detrimental ecological, cultural or economic effects. To better assist managers, hypotheses should be tailored to fit management questions. Potential survival biases must be addressed in order to further the validity of results. Honest accounting of limitations

caused by such biases, as well as those that may occur from sample size or access to study sites, means that telemetry studies should work to support, not eclipse, other management methods. This study should serve as a basis for other studies to build on to further understand the ecological significance of lakes in salmon migrations.

5 References

- Aarestrup, K., Jepsen, N., Rasmussen, G., and Økland, F. 1999. Movements of two strains of radio tagged Atlantic salmon, *Salmo salar* L., smolts through a reservoir. *Fish. Manag. Ecol.* **6**(2): 97–107. doi:10.1046/j.1365-2400.1999.00132.x.
- Aarestrup, K., and Koed, A. 2003. Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecol. Freshw. Fish* **12**(3): 169–176. John Wiley & Sons, Ltd. doi:10.1034/J.1600-0633.2003.00027.X.
- ALEXANDER, R.M. 1990. Size, Speed and Buoyancy Adaptations in Aquatic Animals. *Am. Zool.* **30**(1): 189–196. Oxford Academic. doi:10.1093/ICB/30.1.189.
- Appenzeller, A.R., and Leggett, W.C. 1995. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). *Can. J. Fish. Aquat. Sci.* **52**(3): 504–511. NRC Research Press Ottawa, Canada. doi:10.1139/F95-051.
- Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fish. Res.* **62**(2): 143–170. Elsevier. doi:10.1016/S0165-7836(02)00160-1.
- Berhe, S. 2021. Effect of tag weight on vertical behavior of Atlantic salmon (*Salmo salar*), Master thesis, University of Bergen, Norway.
- Bradshaw, W.E., and Holzapfel, C.M. 2009. Light, Time, and the Physiology of Biotic Response to Rapid Climate Change in Animals. *Annu. Rev. Physiol.* **72**: 147–166. Annual Reviews. doi:10.1146/ANNUREV-PHYSIOL-021909-135837.
- Busch, S., and Mehner, T. 2009. Hydroacoustic Estimates of Fish Population Depths and Densities at Increasingly Longer Time Scales. *Int. Rev. Hydrobiol.* **94**(1): 91–102. John Wiley & Sons, Ltd. doi:10.1002/IROH.200811092.
- Busserolles, F. de, and Marshall, N.J. 2017. Seeing in the deep-sea: visual adaptations in lanternfishes. *Philos. Trans. R. Soc. B Biol. Sci.* **372**(1717). The Royal Society. doi:10.1098/RSTB.2016.0070.
- Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES J. Mar. Sci.* **69**(9): 1538–1548. Oxford Academic. doi:10.1093/icesjms/fss013.
- Claireaux, G., Couturier, C., and Groison, A.-L. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). *J. Exp. Biol.* **209**(17): 3420–3428. The Company of Biologists. doi:10.1242/JEB.02346.
- Clark, C.W., and Levy, D.A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* **131**(2): 271–289. University of Chicago Press. doi:10.1086/284789.
- Clemens, B.J., and Stevens, E.D. 2007. Comparative Gas Bladder Anatomy of a Deepwater Cisco and a Shallowwater Cisco: Implications for Buoyancy at Depth. *J. Great Lakes Res.* **33**(2): 505–511. Elsevier. doi:10.3394/0380-1330(2007)33[505:cgbaoa]2.0.co;2.
- Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby,

- G.D., and Cooke, S.J. 2017. Acoustic telemetry and fisheries management. *Ecol. Appl.* **27**(4): 1031–1049. Ecological Society of America. doi:10.1002/eap.1533.
- Daniels, J., Sutton, S., Webber, D., and Carr, J. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. *Anim. Biotelemetry* **7**(16). BioMed Central. doi:10.1186/S40317-019-0178-2.
- Davidson, J.G., Rikardsen, A.H., Halttunen, E., Thorstad, E.B., Økland, F., Letcher, B.H., Skarðhamar, J., and Næsje, T.F. 2009. Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. *J. Fish Biol.* **75**(7): 1700–1718. John Wiley & Sons, Ltd. doi:10.1111/j.1095-8649.2009.02423.x.
- Dill, L.M., and Fraser, A.H.G. 1984. Behavioral Ecology and Sociobiology Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *In* *Behavioural Ecology and Sociobiology*.
- Eggers, D.M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance 1. *Limnol. Oceanogr.* **23**(6): 1114–1125. John Wiley & Sons, Ltd. doi:10.4319/lo.1978.23.6.1114.
- Eldøy, S.H., Davidson, J.G., Thorstad, E.B., Whoriskey, F.G., Aarestrup, K., Næsje, T.F., Rønning, L., Sjørnsen, A.D., Rikardsen, A.H., and Arnekleiv, J. V. 2017. Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway. *J. Fish Biol.* **91**(5): 1268–1283. John Wiley & Sons, Ltd. doi:10.1111/JFB.13463.
- Elliott, J.M. 2011. A comparative study of the relationship between light intensity and feeding ability in brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). *Freshw. Biol.* **56**(10): 1962–1972. John Wiley & Sons, Ltd. doi:10.1111/J.1365-2427.2011.02627.X.
- Fängstam, H. 1993. Individual downstream swimming speed during the natural smolting period among young of Baltic salmon (*Salmo salar*). *Can. J. Zool.* **71**(9): 1782–1786. NRC Research Press Ottawa, Canada. doi:10.1139/Z93-253.
- Flávio, H., Kennedy, R., Ensing, D., Jepsen, N., and Aarestrup, K. 2019. Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fish. Manag. Ecol.* **27**(1): 92–101. Blackwell Publishing Ltd. doi:10.1111/fme.12405.
- Furey, N.B., Armstrong, J.B., Beauchamp, D.A., and Hinch, S.G. 2018. Migratory coupling between predators and prey. *Nat. Ecol. Evol.* **2**: 1846–1853. Nature Publishing Group. doi:10.1038/s41559-018-0711-3.
- Furey, N.B., Hinch, S.G., Lotto, A.G., and Beauchamp, D.A. 2015. Extensive feeding on sockeye salmon *Oncorhynchus nerka* smolts by bull trout *Salvelinus confluentus* during initial outmigration into a small, unregulated and inland British Columbia river. *J. Fish Biol.* **86**(1): 392–401. John Wiley & Sons, Ltd. doi:10.1111/JFB.12567.
- Furey, N.B., Martins, E.G., and Hinch, S.G. 2020. Migratory salmon smolts exhibit consistent interannual compensatory predator swamping: Effects on telemetry-based survival estimates. *Ecol. Freshw. Fish: eff.* 12556. John Wiley & Sons, Ltd. doi:10.1111/eff.12556.
- Gascoigne, J.C., and Lipcius, R.N. 2004. Allee effects driven by predation. *J. Appl. Ecol.* **41**(5): 801–810. John Wiley & Sons, Ltd. doi:10.1111/J.0021-8901.2004.00944.X.
- Gibson, A.J.F., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J.W., and Redden, A.M. 2015. Effects of

- predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. *Can. J. Fish. Aquat. Sci.* **72**(5): 728–741. NRC Research Press. doi:10.1139/CJFAS-2014-0245.
- Halfyard, E.A., Webber, D., Papa, J. Del, Leadley, T., Kessel, S.T., Colborne, S.F., and Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods Ecol. Evol.* **8**(9): 1063–1071. John Wiley & Sons, Ltd. doi:10.1111/2041-210X.12726.
- Hanssen, E.M. 2020. Novel telemetry predation sensors and mechanistic models reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes, Master thesis, University of Bergen, Norway.
- Honkanen, H.M., Orrell, D.L., Newton, M., McKelvey, S., Stephen, A., Duguid, R.A., and Adams, C.E. 2021. The downstream migration success of Atlantic salmon (*Salmo salar*) smolts through natural and impounded standing waters. *Ecol. Eng.* **161**: 106161. Elsevier B.V. doi:10.1016/j.ecoleng.2021.106161.
- Honkanen, H.M., Rodger, J.R., Stephen, A., Adams, K., Freeman, J., and Adams, C.E. 2018. Counterintuitive migration patterns by Atlantic salmon *Salmo salar* smolts in a large lake. *J. Fish Biol.* **93**(1): 159–162. Blackwell Publishing Ltd. doi:10.1111/jfb.13650.
- Hulbak, M., Hanssen, E.M., Lennox, R.J., Salvanes, A.G.V., Barlaup, B., Gharbi, N., Nilsen, T.O., and Vollset, K.W. 2021. Validating timing of salmon smolt runs obtained by telemetry studies. *Fish. Manag. Ecol.* **00**: 1–9. John Wiley & Sons, Ltd. doi:10.1111/FME.12495.
- Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Flemming, J.E.M., and Whoriskey, F.G. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. *Science* (80-). **348**(6240): 1255642. American Association for the Advancement of Science. doi:10.1126/science.1255642.
- ICES. 2019. Report of the Working Group on North Atlantic Salmon (WGNAS). Copenhagen, Denmark. doi:<https://doi.org/10.17895/ices.pub.4978>. Retrieved from: https://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/Fisheries%20Resources%20Steering%20Group/2019/WGNAS/WGNAS_2019.pdf
- Jepsen, N., Aarestrup, K., Økland, F., and Rasmussen, G. 1998. Survival of radiotagged Atlantic salmon (*Salmo salar* L.) – and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia* **371–372**(0): 347–353. Springer. doi:10.1023/A:1017047527478.
- Jepsen, N., Holthe, E., and Økland, F. 2006. Observations of predation on salmon and trout smolts in a river mouth. *Fish. Manag. Ecol.* **13**(5): 341–343. John Wiley & Sons, Ltd. doi:10.1111/J.1365-2400.2006.00509.X.
- Jepsen, N., Klenke, R., Sonnesen, P., and Bregnballe, T. 2010. The use of coded wire tags to estimate cormorant predation on fish stocks in an estuary. *Mar. Freshw. Res.* **61**(3): 320–329. CSIRO PUBLISHING. doi:10.1071/MF09038.
- Jepsen, N., Koed, A., Thorstad, E.B., and Baras, E. 2002. Surgical implantation of telemetry transmitters in fish: how much have we learned? *In* *Aquatic Telemetry*. Springer, Dordrecht. pp. 239–248. doi:10.1007/978-94-017-0771-8_28.
- Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshw. Biol.* **21**(1): 71–86. John Wiley & Sons, Ltd. doi:10.1111/j.1365-2427.1989.tb01349.x.
- Jonsson, B., and Jonsson, N. 2009. A review of the likely effects of climate change on anadromous

- Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *J. Fish Biol.* **75**(10): 2381–2447. John Wiley & Sons, Ltd. doi:10.1111/J.1095-8649.2009.02380.X.
- Jonsson, B., and Ruud-Hansen, J. 1985. Water Temperature as the Primary Influence on Timing of Seaward Migrations of Atlantic Salmon (*Salmo salar*) Smolts. *Can. J. Fish. Aquat. Sci.* **42**(3): 593–595. NRC Research Press Ottawa, Canada. doi:10.1139/F85-076.
- Jonsson, N., and Jonsson, B. 2002. Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshw. Biol.* **47**(8): 1391–1401. John Wiley & Sons, Ltd. doi:10.1046/J.1365-2427.2002.00873.X.
- Kahilainen, K.K., Malinen, T., and Lehtonen, H. 2009. Polar light regime and piscivory govern diel vertical migrations of planktivorous fish and zooplankton in a subarctic lake. *Ecol. Freshw. Fish* **18**(3): 481–490. John Wiley & Sons, Ltd. doi:10.1111/J.1600-0633.2009.00363.X.
- Kennedy, R.J., Rosell, R., Millane, M., Doherty, D., and Allen, M. 2018. Migration and survival of Atlantic salmon *Salmo salar* smolts in a large natural lake. *J. Fish Biol.* **93**(1): 134–137. John Wiley & Sons, Ltd. doi:10.1111/JFB.13676.
- Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O’Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecol. Freshw. Fish* **12**(1): 1–59. John Wiley & Sons, Ltd. doi:10.1034/j.1600-0633.2003.00010.x.
- Lennox, R.J., Olsen Espedal, E., Barlaup, B.T., Mahlum, S., and Vollset, K.W. 2019. A test of migratory coupling in the salmon-trout predator-prey complex of a subarctic fjord. *Boreal Environ. Res.* **24**: 189–199.
- Lennox, R.J., Pulg, U., Malley, B., Gabrielsen, S.E., Hanssen, E.M., Cooke, S.J., Birnie-Gauvin, K., Barlaup, B.T., and Vollset, K.W. 2021. The various ways that anadromous salmonids use lake habitats to complete their life history. *Can. J. Fish. Aquat. Sci.* **78**(1): 90–100. Canadian Science Publishing. doi:10.1139/cjfas-2020-0225.
- Macaulay, G., Wright, D., Oppedal, F., and Dempster, T. 2020. Buoyancy matters: Establishing the maximum neutral buoyancy depth of Atlantic salmon. *Aquaculture* **519**: 734925. Elsevier B.V. doi:10.1016/j.aquaculture.2020.734925.
- Mazur, M.M., and Beauchamp, D.A. 2003. A comparison of Visual Prey Detection Among Species of Piscivorous Salmonids: Effects of Light and Low Turbidities. *Environ. Biol. Fishes* **67**: 397–405. Springer. doi:10.1023/A:1025807711512.
- McLennan, D., Rush, E., McKelvey, S., and Metcalfe, N.B. 2018. Timing of Atlantic salmon *Salmo salar* smolt migration predicts successful passage through a reservoir. *J. Fish Biol.* **92**(5): 1651–1656. John Wiley & Sons, Ltd. doi:10.1111/JFB.13606.
- Mehner, T. 2012, July 1. Diel vertical migration of freshwater fishes - proximate triggers, ultimate causes and research perspectives. John Wiley & Sons, Ltd. doi:10.1111/j.1365-2427.2012.02811.x.
- NOAA. 2021. Species in the Spotlight—Atlantic Salmon. Prior. actions 2021-2025. Retrieved from: https://atlanticsalmonrestoration.org/news-announcements/atlantic-salmon-recovery-news-releases/species-in-the-spotlight-5-year-action-plan-for-atlantic-salmon/index_html

- Otero, J., L'Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B., Russell, I.C., Jensen, A.J., Baglinière, J.-L., Dionne, M., Armstrong, J.D., Romakkaniemi, A., Letcher, B.H., Kocik, J.F., Erkinaro, J., Poole, R., Rogan, G., Lundqvist, H., MacLean, J.C., Jokikokko, E., Arnekleiv, J.V., Kennedy, R.J., Niemelä, E., Caballero, P., Music, P.A., Antonsson, T., Gudjonsson, S., Veselov, A.E., Lamberg, A., Groom, S., Taylor, B.H., Taberner, M., Dillane, M., Arnason, F., Horton, G., Hvidsten, N.A., Jonsson, I.R., Jonsson, N., McKelvey, S., Næsje, T.F., Skaala, Ø., Smith, G.W., Sægrov, H., Stenseth, N.C., and Vøllestad, L.A. 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Glob. Chang. Biol.* **20**(1): 61–75. John Wiley & Sons, Ltd. doi:10.1111/GCB.12363.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **55**(SUPPL.1): 281–287. National Research Council of Canada. doi:10.1139/d98-012.
- Probst, W.N., and Eckmann, R. 2009. The influence of light on the diel vertical migration of young-of-the-year burbot *Lota lota* in Lake Constance. *J. Fish Biol.* **74**(1): 150–166. John Wiley & Sons, Ltd. doi:10.1111/J.1095-8649.2008.02120.X.
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Remen, M., Oppedal, F., Imsland, A.K., Olsen, R.E., and Torgersen, T. 2013. Hypoxia tolerance thresholds for post-smolt Atlantic salmon: Dependency of temperature and hypoxia acclimation. *Aquaculture* **416–417**: 41–47. Elsevier. doi:10.1016/J.AQUACULTURE.2013.08.024.
- Richardson, N., Beaudreau, A.H., Wipfli, M.S., and Finkle, H. 2017. Prey partitioning and use of insects by juvenile sockeye salmon and a potential competitor, threespine stickleback, in Afognak Lake, Alaska. *Ecol. Freshw. Fish* **26**(4): 586–601. Blackwell Munksgaard. doi:10.1111/eff.12302.
- Rikardsen, A.H., Haugland, M., Bjørn, P.A., Finstad, B., Knudsen, R., Dempson, J.B., Holst, J.C., Hvidsten, N.A., and Holm, M. 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *J. Fish Biol.* **64**(6): 1655–1679. John Wiley & Sons, Ltd. doi:10.1111/J.0022-1112.2004.00425.X.
- Scheuerell, M.D., and Schindler, D.E. 2003. Diel vertical migration by juvenile sockeye salmon: Empirical evidence for the antipredation window. *Ecology* **84**(7): 1713–1720. Ecological Society of America. doi:10.1890/0012-9658(2003)084[1713:DVMBJS]2.0.CO;2.
- Strand, E., Jørgensen, C., and Huse, G. 2005. Modelling buoyancy regulation in fishes with swimbladders: bioenergetics and behaviour. *Ecol. Modell.* **185**(2–4): 309–327. Elsevier. doi:10.1016/J.ECOLMODEL.2004.12.013.
- Strople, L.C., Filgueira, R., Hatcher, B.G., Denny, S., Bordeleau, X., Whoriskey, F.G., and Crossin, G.T. 2018. The effect of environmental conditions on Atlantic salmon smolts' (*Salmo salar*) bioenergetic requirements and migration through an inland sea. *Environ. Biol. Fishes* **101**: 1467–1482. Springer. doi:10.1007/S10641-018-0792-5.
- Svendsen, J.C., Eskesen, A.O., Aarestrup, K., Koed, A., and Jordan, A.D. 2007. Evidence for non-random spatial positioning of migrating smolts (*Salmonidae*) in a small lowland stream. *Freshw. Biol.* **52**(6): 1147–1158. Blackwell Publishing Ltd. doi:10.1111/j.1365-2427.2007.01743.x.
- Thieurmél, B and Elmarhraoui, A (2019). *suncalc: Compute Sun Position, Sunlight Phases, Moon*

Position and Lunar Phase. R package version 0.5.0. <https://CRAN.Rproject.org/package=suncalc>

- Thorstad, E.B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P.A., and McKinley, R.S. 2007. Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. *Dev. Fish Telem.* **195**: 99–107. Springer, Dordrecht. doi:10.1007/978-1-4020-6237-7_11.
- Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *J. Fish Biol.* **81**(2): 500–542. doi:10.1111/j.1095-8649.2012.03370.x.
- Vogel, J.L., and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Can. J. Fish. Aquat. Sci.* **56**(7): 1293–1297. NRC Research Press Ottawa, Canada. doi:10.1139/F99-071.
- Vollset, K.W., Barlaup, B.T., Mahlum, S., Skår, B., Skoglund, H., Normann, E.S., Holst, J.C., Wennevik, V., Skaet, G., and Davidsen, J.G. 2014. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *In* *Laboratorium for ferskvannøkologi og innlandsfiske*.
- Vollset, K.W., Lennox, R.J., Lamberg, A., Skaala, Ø., Sandvik, A.D., Sægrov, H., Kvingedal, E., Kristensen, T., Jensen, A.J., Haraldstad, T., Barlaup, B.T., and Ugedal, O. 2021. Predicting the nationwide outmigration timing of Atlantic salmon (*Salmo salar*) smolts along 12 degrees of latitude in Norway. *Divers. Distrib.* **27**(8): 1383–1392. John Wiley & Sons, Ltd. doi:10.1111/DDI.13285.
- Vollset, K.W., Lennox, R.J., Thorstad, E.B., Auer, S., Bär, K., Larsen, M.H., Mahlum, S., Näslund, J., Stryhn, H., and Dohoo, I. 2020. Systematic review and meta-analysis of PIT tagging effects on mortality and growth of juvenile salmonids. *Rev. Fish Biol. Fish.* **30**: 553–568. Springer Science and Business Media Deutschland GmbH. doi:10.1007/s11160-020-09611-1.
- Whalen, K.G., Parrish, D.L., and McCormick, S.D. 1999. Migration Timing of Atlantic Salmon Smolts Relative to Environmental and Physiological Factors. *Trans. Am. Fish. Soc.* **128**(2): 289–301. doi:10.1577/1548-8659.
- Wood, S.N. (2017) *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman and Hall/CRC.
- Young, N., Gingras, I., Nguyen, V.M., Cooke, S.J., and Hinch, S.G. 2013. Mobilizing New Science into Management Practice: The Challenge of Biotelemetry for Fisheries Management, a Case Study of Canada's Fraser River. *J. Int. Law Policy* **16**(4): 331–351. Taylor & Francis Group. doi:10.1080/13880292.2013.805074.

6 Appendices

Appendix 1

Overview of all salmon tagged for this study. ID is the tag number, fork length in mm, weight in gram and time is the surgery time, including measurements.

Date	Tag no.	Length-fork (mm)	Weight (g)	Time (min:sec)
17.04.2020	1	141	27	03:22
17.04.2020	2	132	22	02:45
17.04.2020	3	133	25	03:36
17.04.2020	4	142	26	02:10
17.04.2020	5	136	23	02:20
17.04.2020	6	133	22	03:32
17.04.2020	7	136	23	02:57
17.04.2020	8	131	22	03:00
17.04.2020	9	131	21	02:37
17.04.2020	10	130	22	02:27
17.04.2020	11	133	23	NA
17.04.2020	12	137	25	NA
17.04.2020	13	144	19	02:30
21.04.2020	14	129	21	NA
17.04.2020	15	140	27	NA
21.04.2020	16	172	55	02:47
21.04.2020	17	133	24	03:57
21.04.2020	18	144	28	02:29
21.04.2020	19	137	29	02:29
21.04.2020	20	147	31	03:19
21.04.2020	21	134	26	03:51
21.04.2020	22	137	22	02:47
21.04.2020	23	138	29	02:22
21.04.2020	24	144	31	04:32
21.04.2020	25	136	25	04:30
21.04.2020	26	145	38	02:54
21.04.2020	27	128	24	02:31
21.04.2020	28	127	20	03:09
21.04.2020	29	137	27	02:15
21.04.2020	30	148	27	02:33
21.04.2020	31	128	21	03:34
21.04.2020	32	145	33	04:18
21.04.2020	33	133	26	02:10
21.04.2020	34	134	33	02:12
21.04.2020	35	135	31	02:05
21.04.2020	36	145	39	03:38
21.04.2020	37	149	34	02:42
21.04.2020	38	134	26	02:07
21.04.2020	39	141	30	05:12
21.04.2020	40	135	28	02:37
21.04.2020	41	130	24	04:08

21.04.2020	42	136	28	02:58
21.04.2020	43	129	22	04:52
17.04.2020	44	133	20	02:52
21.04.2020	45	145	34	02:48
		Mean Length (mm)	Mean weight (g)	Mean surgery time (min:sec)
		137.49±7.93	26.96±6.39	03:04

Appendix 2

Overview of all trout tagged for this study. ID is the tag number, fork length in mm, weight in gram and time is the surgery time, including measurements.

Date	Tag no.	Length-fork (mm)	Weight (g)	Time (min:sec)
23.04.2020	136	610	1618	05:00
23.04.2020	137	560	1312	04:00
23.04.2020	138	500	1030	03:00
23.04.2020	139	590	1811	04:35
23.04.2020	140	630	1823	03:45
23.04.2020	141	530	1020	04:21
23.04.2020	142	420	580	04:21
26.04.2020	143	460	790	04:00
26.04.2020	144	500	1034	03:00
26.04.2020	145	440	655	05:00
26.04.2020	146	420	806	03:32
26.04.2020	147	430	553	03:10
26.04.2020	148	560	1289	03:00
26.04.2020	149	390	480	NA
28.04.2020	150	460	587	03:17
28.04.2020	151	440	519	NA
07.05.2020	152	630	2130	NA
07.05.2020	153	430	683	NA
07.05.2020	154	500	845	NA
07.05.2020	155	540	1017	NA
07.05.2020	156	470	568	NA
07.05.2020	157	530	964	NA
31.05.2020	158	650	3900	NA
31.05.2020	159	490	1131	NA
31.05.2020	160	600	2440	NA
31.05.2020	161	465	913	NA
12.06.2020	162	600	1907	NA
		Mean Length (mm)	Mean weight (g)	Mean surgery time
		512.78±75.96	1,200.19±759.26	03:51

