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Spatiotemporal use of freshwater habitats in Atlantic salmon (*Salmo salar*) smolts from the Stryn and Hornindal watercourses

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Preface

This thesis has been a subject of the project “Kunnskaplsøft for sjøaure og laks I Strynevassdraget- kunnskapbasert lokal forvaltning 2017–2021» with the acronym KLAFF (KunnskapLaksAureForvaltningFiske). KLAFF is, or has been, funded by Fylkesmannen i Sogn og Fjordane, Noregs forskningsråd, Blom Fiskeoppdrett AS, Nordfjord Laks AS, K. Strømmen Lakseoppdrett AS, Mowi AS, Coast Seafood AS, Nordfjord Forsøksstasjon AS, Eid and Stryn river owner organiztations, and Marine Harvest Norway AS. Selstad AS provided the project with floats and ropes. INAQ and NMBU provided with acoustic receivers.

I would like to thank my main adviser, professor Thrond O. Haugen for all the good help, and for the opportunity to have this topic for my thesis. Along with help from Henning A. Urke and Torstein Kristensen, my external advisers, this went fine. They both need to be thanked for all the help, feedback and advising they provided for me. I would also like to thank Aksel Fiske and his Polo for good company and rides around the west coast, and everyone that helped in any way.

Thanks for letting me be part of this project, I learned a lot!

Ås, June 2020

Sigurd Domaas

Abstract

The Atlantic salmon (*Salmo salar*) is a species with a lot of variation in portraited life-history-strategies – the most common one, includes a migration from its natal river to the Atlantic Ocean at a vulnerable stage in life. The smolt migration through rivers and lakes is usually studied in combination with manmade reservoirs and hydropower dams, and many studies have demonstrated substantial smolt mortality through such lakes.

In this study, multiple transects of acoustic receivers were placed throughout the migration course, and in April 2019 a total of 199 salmon presmolts were caught (electrofishing) and tagged with acoustic transmitters. The purpose was to identify how environmental drivers like water discharge and water temperature affect the smolt migration, and how two large natural lakes affect the smolt migration in two non-hydropower affected watercourses in Western Norway: The Hornindal watercourse with the river Horndøla that runs into lake Hornindalsvatnet which empties into the river Eidselva, and Stryn watercourse with the river Hjelledøla that runs into lake Strynevatnet which empties into the river Stryneelva.

Initiation of migration for the tagged smolts was found to be correlated differently to water discharge and day of year in the four rivers. In Eidselva, initiation was correlated to date, water discharge and the relative change in water discharge from the previous day. In Stryneelva, initiation was correlated to date and the relative change in water discharge, whilst in Horndøla it also correlated to the interaction between the mentioned drivers. In Horndøla it correlated to the water discharge. The tagged smolts from all four rivers were showing clear signs of multiple migration peaks arriving in the estuaries (Eidselva and Stryneelva) and river mouths (Horndøla and Hjelledøla) almost a month apart. In Eidselva, Stryneelva and Hjelledøla the first migration peak coincided with increased water discharge during the days around April 23, and a second peak during the days around May 20. In Horndøla the first migration peak took place during the days around May 19, and a second peak in the days around June 1. The Horndøla smolts were found to be late migrators, both due to a later start and the delay caused by traversing the Hornindalsvatnet, where the median progression rate was 0.16 body lengths per second, bringing the migration duration up to almost thirteen weeks in the Hornindal watercourse. None of the Hjelledøla tagged smolts were observed downstream of Strynevatnet.

Apparent survival through the watercourses was estimated using a sequential approach to Cormack-Jolly-Seber models on the detection data. The apparent survival (95% CI) was estimated to be as low as 2% (0%–12%) through Strynevatnet and 19% (3%–46%) through Hornindalsvatnet. The apparent survival (95% CI) from release to the fjord was estimated to 4% (0%–28%) and 47% (29%–63%) for the Horndøla and Eidselva smolts, respectively, and 0% and 33% (25%–51%) for the Hjelledøla and Stryneelva smolts, respectively. Survival was found to be size related in Hornindalsvatnet and the Eidselva estuary, and predation avoidance behavior was seen in the tagged smolts. Depth use in Strynevatnet was correlated to smolt weight, were depth decreased with weight, to date, where individuals lighter than ~27 grams went deeper whilst heavier individuals went shallower as the year progressed, and to night and daytime, where the tagged smolt went shallower during night. The night and daytime difference was the strongest in late April and evened out by mid-June. In Hornindalsvatnet, one individual was responsible for more than 95% of the data, and no analyses were done on depth use.

This study has increased the knowledge on the smolt migration of the Atlantic salmon stocks in the Hornindal and Stryn watercourses. It has shown that very few, or none, of the tagged smolts from the rivers Hjelledøla and Horndøla made it to the fjord during the spring run in 2019.

1 Introduction

Migration is a behavior seen in many species, both on land and in water. Some species migrate to habitats better suited for reproduction, whilst some migrates to areas where the food is more abundant (Dingle & Drake, 2007). The Atlantic salmon (*Salmo salar*) is an anadromous species where pre-mature individuals undergoes long migrations from freshwater to sea at vulnerable stage in life to exploit its resources and increase growth (Klemetsen et al., 2003; Thorstad et al., 2012). For the salmon smolts, the migration can be a perilous journey, faced with new habitats and novel predators, and is often characterized by high mortality (Thorstad et al., 2012).

Migration and timing is specific to individual watercourses and year, but it generally takes place over a three to seven-week period in April to July and is significantly influenced by environmental factors like water temperature and discharge in the rivers (Harvey et al., 2020; Thorstad et al., 2012). It is believed that populations have adapted to their specific river's conditions to time the migration to ideal sea temperatures (Hvidsten et al., 1998), and there are evidence for a genetic component influencing the migration timing (Aarestrup et al., 1999). The timing of migration, has been linked to survival of downstream migration where early and late migrating groups have had different survival probabilities (McLennan et al., 2017; McLennan et al., 2018). High mortalities in downriver migration is often linked to the estuaries, where mortality rates can be more than double of that in the rivers (Thorstad et al., 2012), probably due to predation from piscivore fish (Hvidsten & Møkkelgjerd, 1987). The number of manmade weirs and dams in the system has also been correlated to decreased survival probabilities (Aarestrup & Koed, 2003; Stich et al., 2015), where predation from resident piscivore fish is one of the threats for the migrating smolts (Schwinn et al., 2018). However, little is known about migration through natural lakes, and the migration patterns and mechanisms associated with such habitats (Thorstad et al., 2012).

Kennedy et al. (2018) found in their study on smolt migration through lake Lough Erne that entry was heavily biased to after dark and that more than 50% of the tagged salmon smolts were lost shortly after entering the lake, suggesting that predation plays a big role on smolt survival and migration timing in natural lakes. Honkanen et al. (2018) found that after entering lake Loch Lomond, and making it past the river mouth, salmon smolts showed clear signs of multidirectional movement, more than doubling the necessary migration distance, as well as extended periods of residency in the lake adding up to a total varying from eight hours to two days. Haugen et al. (2017) found tendencies for the smolt to do deep dives down to 30 meters as they entered Vangsvatnet and Evangervatnet, and found support for diurnal migration through the lakes, where the smolts go deeper during daytime than night, possibly as a predator avoidance behavior.

In addition to natural threats and challenges faced by the salmon smolts, they now must face anthropogenic threats and habitat degradations in many of their native systems. The Norwegian Scientific council for salmon management (Vitenskapelige råd for lakseforvaltning – VRL) (Anon, 2018a) identified that escaped farmed salmon, Salmon lice (*Lepeophtheirus salmonis*) and Infections tied to salmon farming pose the biggest threats to wild salmon populations in Norway. Alongside the salmon farming problematics, there are also challenges tied to hydropower regulation accompanied with altered water discharges and water temperatures (Anon, 2018a; Haugen et al., 2017).

To understand how the mentioned threats affect the smolts and the smolt migration, information is important. The introduction of acoustic telemetry, where individual fish are tagged with an acoustic transmitter that can be detected at passive acoustic receivers throughout the watercourse, and novel tags that provides depth data, has made it possible to monitor salmonid smolt and post-smolt movement through watercourses, lakes and fjords with great precision (e.g., Schwinn et al. (2018), Haugen et al. (2017) and Urke et al. (2013)).

The Hornindal and Stryn watercourses are two non-hydropower affected watercourses consisting of large natural lakes running into the fjord Nordfjord in Vestland region, Norway. The two watercourses, with the nearby fjord areas are protected from aquaculture as a part of the National Atlantic Salmon Watercourses and Fjords (NASW) management scheme (Vøllestad et al., 2013), however, outside the protected area in the fjord there is a substantial amount of aquaculture activity (Urke et al., 2018). In the Hornindal watercourse, smolts from the river Horndøla must migrate through lake Hornindalsvatnet and river Eidselva before entering Nordfjord in Nordfjordeid. In the Stryn watercourse, smolts from the river Hjelledøla must migrate through lake Strynevatnet and river Stryneelva before entering the Nordfjord in Stryn.

Migration timing and survival for salmon smolts in Eidselva and Stryneelva has been investigated in previous studies (Haugen et al., 2019; Urke et al., 2018), but new to this study will be the in-depth analysis of the freshwater migration phase, and the novel addition of lake migration through Strynevatnet and Hornindalsvatnet by smolt groups from the Hjelledøla and Horndøla.

By using acoustic telemetry on tagged presmolts from the Hornindal and Stryn watercourses, I aim to identify the migration patterns and mechanisms associated with lake migration in the two watercourses, and to create a more fact-based and complete picture of the smolt migration in the two watercourses.

My problem statement is defined as:

Is the salmon migration from freshwater to saltwater in the Hornindal and Stryn watercourses affected differently by environmental drivers like water level and temperature, and how do the two lakes affect the smolt migration?

My study aim is divided into these hypotheses:

i. The tagged salmon smolts from the Horndøla and Hjelledøla will start their migration earlier than the Eidselva and Stryneelva smolts, respectively, to reach the fjord at the same time.

ii. The tagged salmon smolts will start their migration with increased water discharge and water temperature.

iii. The survival rates will be lower in Hornindalsvatnet and Strynevatnet, and in the Eidselva and Stryneelva estuaries, compared to the rest of the systems.

iv. In Hornindalsvatnet and Strynevatnet the tagged smolt will display a diurnal vertical migration pattern. During night, the study-individuals will be closer to the surface than during the daytime.

Lastly, I will discuss what implications these results have for future management of the Hornindal and Stryn salmon populations.

2 Methods and materials

2.1 Study Area

The capture, tagging and release was done in the Stryn and Hornindal watercourses (Figure 1), they consist of the rivers Hjelledøla and Horndøla upstream of respectively lakes Strynevatnet and Hornindalsvatnet, which are drained by the rivers Stryneelva and Eidselva into the fjord Nordfjord in the Vestland region, western Norway at 61°54'N and 5°41'E. The Nordfjord is the northernmost fjord in Vestland and stretches 106 km from Husevågøy in the west to Loen in the east (Thorsnæs & Askheim, 2017).

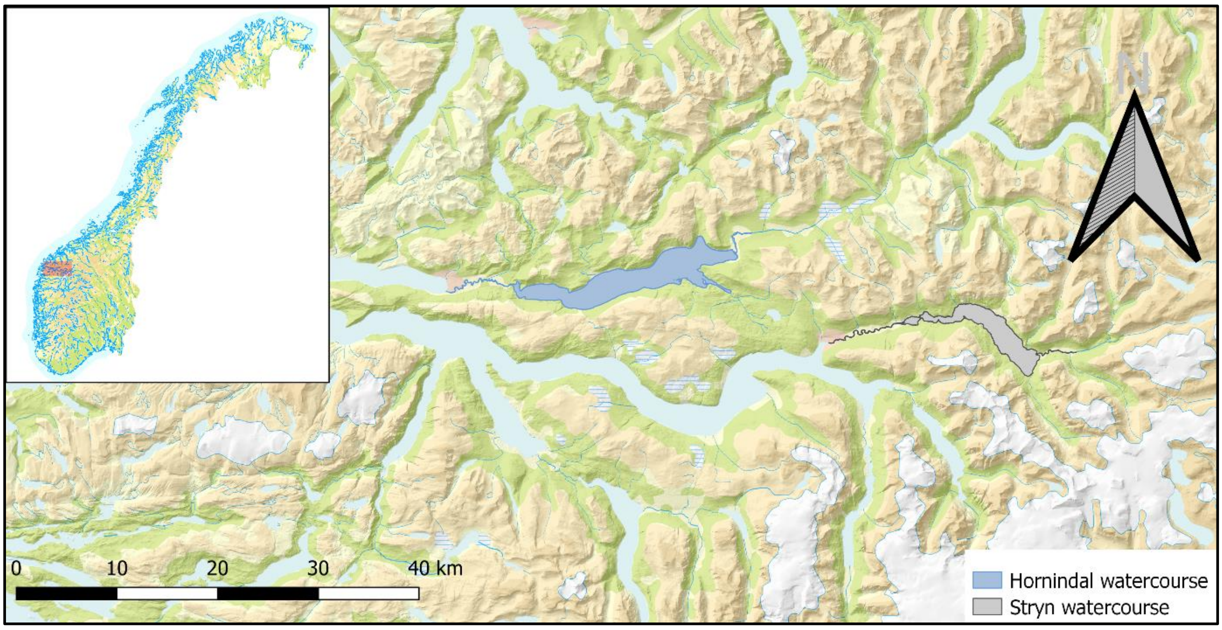

Figure 1: Location of the two study systems, Hornindal watercourse and Stryn watercourse, marked by different colors. The adjacent fjord is the Nordfjord.

2.1.1 Description of the Hornindal watercourse

The Hornindal watercourse is the westernmost watercourse of the two study areas and enters the Nordfjord in Nordfjordeid and has a catchment area of 428 km^2 (atlas.nve.no). The study system consists of Horndøla, Hornindalsvatnet and Eidselva. Horndøla is the biggest of multiple influent tributaries (Samdal & Enevold, 2009b) with an average water discharge of 10.6 m^3/s (nevina.nve.no), entering Hornindalsvatnet at its east end in Grodås. Twenty square kilometers of Horndøla's catchment is regulated into a neighboring catchment (Urdal et al., 2003). This has an effect on summer discharge and temperatures in Horndøla, but due to Hornindalsvatnet's equalizing effect, this has a low effect on temperature in Eidselva, but the water discharge during the summer months has decreased due to the diverted area is a higher lying snow and glacier field (Urdal et al., 2003).

Hornindalsvatnet, the main lake of the catchment, is a long and narrow fjord lake surrounded by tall mountains reaching up to more than 1100 meters above sea level (i.e. Snøtuva and Glitregga). It has an area of 50.4 km^2, length of 22 km, a surface elevation of 53 meters above sea level and a maximum depth of 514 meters, making it the largest lake in western Norway and the deepest lake in Europe (Askheim, 2019; Samdal & Enevold, 2009b; Urdal et al., 2003). Eidselva, exiting the lake at its west end at Kviafossen, is the only effluent channel, entering the fjord in Nordfjordeid. Kviafossen has a dam with a pool and weir fishway, but fish have been observed climbing the adjacent waterfall (Pers. com. Urke, H.A). Eidselva is about 6 km long and meanders through farmed land before reaching the Nordfjord in Nordfjordeid. Eidselva had an average water discharge of 18.5 m^3/s in 2019.

2.1.2 Description of the Stryn watercourse

The Stryn watercourse is the easternmost watercourse of the two study systems. It enters the Nordfjord in Stryn and has a catchment area of 537 km^2 (atlas.nve.no). The study system consists of Hjelledøla, Strynevatnet and Stryneelva. Hjelledøla is one of multiple influent tributaries to the Strynevatnet and is affected by glacier runoff from Videdøla river (upstream of Hjelledøla) and Sunndøla river, entering Hjelledøla in Grov. Hjelledøla has an average water discharge of 15.6 m^3/s (nevina.nve.no) and is characterized by a high summer discharge, a low winter discharge and large sediment transportation (Samdal & Enevold, 2009a). Strynevatnet, the main lake of the catchment, is a long and narrow fjord lake surrounded by tall mountains reaching up to more than 1300 meters above sea level (i.e. Hjellehyrna). It has an area of 22.9 km^2, length of 16 km, maximum depth of 198 meters and surface elevation of 29 meters above sea level (Askheim, 2017; Samdal & Enevold, 2009a). Strynevatnet has one effluent channel reaching the fjord, the Stryneelva, exiting the lake at its west end. Stryneelva is 8 km long and meanders through farmed land before reaching the Nordfjord in Stryn. Stryneelva had an average water discharge of 29.7 m^3/s in 2019.

2.1.3 NASW and status after the quality norm.

Together with the inner parts of the Nordfjord, the Stryneelva and Eidselva are parts of a Norwegian management scheme called National Atlantic Salmon Watercourses and Fjords (NASW), which serves as a management tool to help conserve selected populations of Atlantic salmon in Norway (Vøllestad et al., 2013).

The VLR (Anon, 2018b) described the Stryneelva and Eidselva, in the period from 2010 to 2014, to be “very bad” and “very good/good”, respectively, after the quality norm. Which is a norm using a population’s reproduction, harvesting potential and genetic integrity to calculate a status (Kvalitetsnorm for ville bestander av atlantisk laks, 2013).

2.2 Study species – Atlantic salmon

The Atlantic salmon is an important species of anadromous fish in Norway. The salmon’s native range is in the northern Atlantic Sea and has been present along the Norwegian coast since the last ice-age. Salmon is found in more than 400 watercourses from the Swedish-Norwegian border in the south to the Russian-Norwegian border in the north, which are spawning grounds to a large proportion of the world’s wild salmon populations. Salmon is easy to catch, making it a popular target for both commercial and recreational anglers in Norwegian rivers, lakes, and the sea, and are of economic and cultural importance. (Forseth et al., 2017; Thorstad et al., 2011).

The salmon can portray an array of life histories, but with the exception of the “Byglandsbleke” and “Småblanken” which are relict populations in lake Byglandsfjord and the Namsen watercourse, most populations are anadromous (Barlaup, 2011; Jonsson & Jonsson, 2011; Thorstad et al., 2011). To be anadromous means that the life cycle starts with a juvenile phase in freshwater followed by a phase of feeding and growth in the ocean before returning to their natal rivers for spawning.

2.2.1 The salmon’s life cycle

The salmon’s life starts in freshwater where the eggs are laid in gravel on the riverbed, before hatching in spring or early summer. The newly hatched larvae are called alevins or sac fry. The alevins stay in the gravel for a few weeks feeding on a yolk they carry with them in a sac underneath their belly. When the alevins reach a length of about 20 mm or the yolk is almost completely absorbed, they emerge from the gravel and start feeding in the near area. At this stage they are called fry. As the fry grow bigger, they turn into juveniles called parr, which are identified by a fingerlike pattern on the sides. Now they typically disperse to other parts of the river and side streams. The parr will undergo a morphological and physiological transformation, called smoltification, to be able to cope in saltwater. The result is a smolt with a length ranging from 7 to 30 cm (Thorstad et al., 2011), looking like an adult salmon with a silvery coloration. From the salmon egg hatches, until the juvenile undergoes the transformation to a smolt can take from one to eight years (Thorstad et al., 2011). The salmon then typically spends one to four years at sea before returning to their natal watercourses in

May-August to spawn in autumn. (Jonsson & Jonsson, 2011; Klemetsen et al., 2003; Thorstad et al., 2011).

2.3 Capture and tagging of presmolts with acoustic transmitters

Presmolts of salmon were captured using electrofishing (Bohlin et al., 1989) and tagged with acoustic transmitters. Approval was granted by the Norwegian Animal Research Authority (FOTS ID 12002) and Atlantic salmon presmolts considered to smoltify the same spring with a minimum total length (TL) of 12 cm were tagged. The tagging was done by surgically inserting the acoustic transmitter into the body cavity of the presmolts using the surgical method described in Urke et al. (2013): After being caught, the presmolts were handled with utmost care and grouped and stored in holding tanks with fresh and flowing water in accordance to where and when they were caught. Individuals were then netted from the holding tank into an anesthetic bath containing 60 mg/L MS 222 (tricaine methane sulphonate) anesthetic where they reached surgical anesthesia after about 2 minutes. The presmolt was then weighed and placed ventral up on a V-shaped surgical table where length (TL) was recorded and a tube constantly pumping aerated water with a concentration of 40 mg/L MS 222 was placed in its mouth, pumping the water over its gills. By using a scalpel, a midline ventral incision of 9-10 mm was made just behind the pelvic fins, allowing the acoustic transmitter to be placed in the coelom. The incision was then closed with three stitches using monofilament material (Suture 4/0) and sealed using tissue adhesive (Histoacryl) (Figure 2). The process takes around one to two minutes per fish. The presmolts were then put into a recovery tub where they were closely monitored and made sure to recover as fast as possibly by actively stirring the water and constantly refilling the tub with fresh aerated water. Recovery was considered as regained balance and active swimming, which was usually seen within two minutes. After an observation time ranging from minutes to hours in bigger holding tanks, the presmolt was released back into the river at locations close to the capture sites.

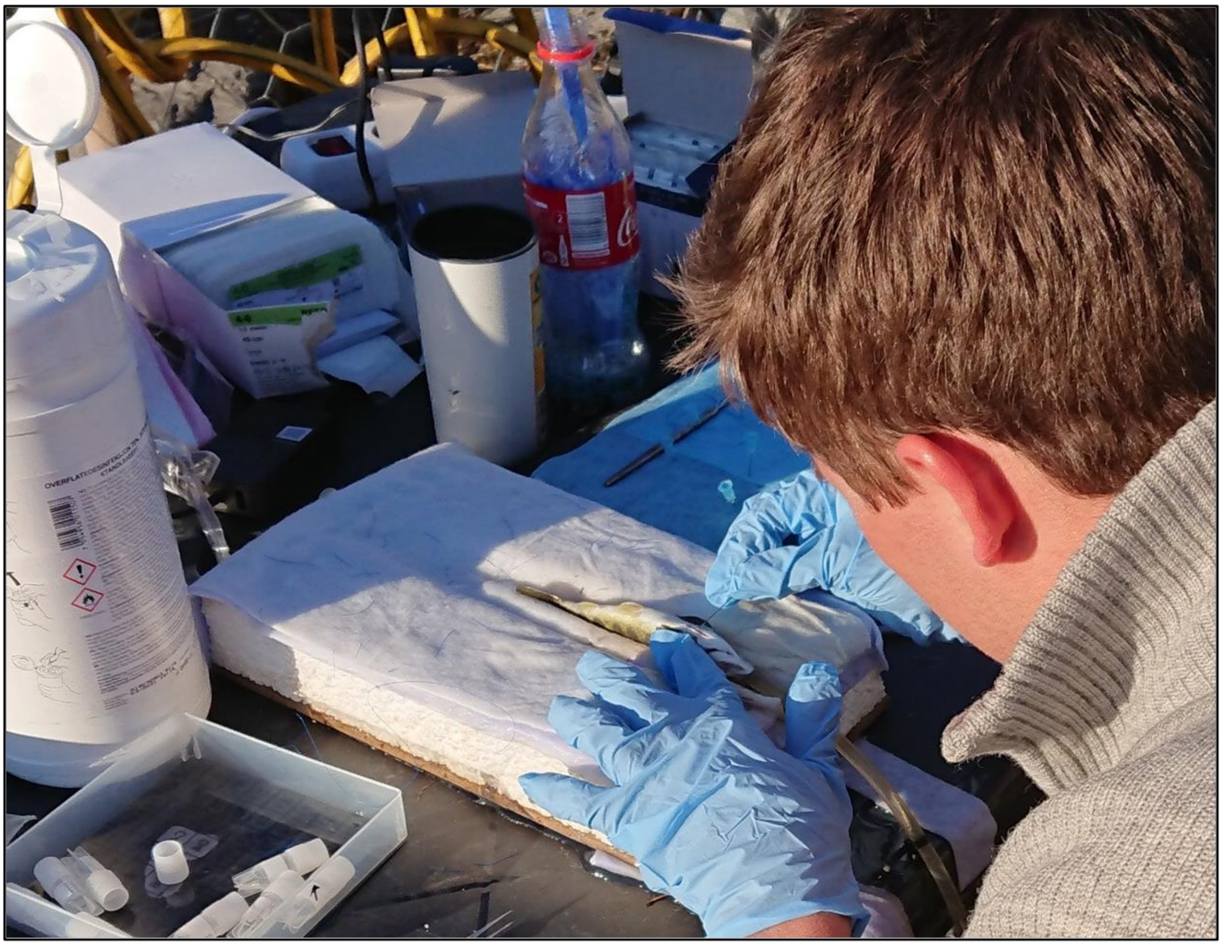

Figure 2: Here we see Msc. student Aksel Fiske closing an incision on a presmolt after he surgically inserted an acoustic transmitter into its coelom, or body cavity. We also see the use of the V-shaped surgical table and the tube pumping the aerated anesthetic solution in the presmolt's mouth. Photo: Sigurd Domaas.

Two different types of acoustic transmitters, a total of four different tags, produced by Thelma Biotel AS (www.biotel.no) were used for tagging the presmolts: A 2018 and 2019 model of an ID-tag that transmits an ID (ID-LP7) and a 2018 and 2019 model of a depth-tag that in addition to transmit an ID also transmits depth information with a 0.2 m resolution (D-LP7) (Table 1). Which tag a presmolt got was length specific, a TL of at least 12 cm was required for the ID-tags whilst a TL of 14 cm was required for the depth-tag.

Table 1: Physical specifications of the five types of acoustic transmitters (tags) that were used for the study and a count of how many of each tag that was used. 2018 means the tag is a 2018 model. The D-LP9L tag was used on trout tagged in 2018.

Tag specifications	ID-LP7	D-LP7	ID-LP7(2018)	D-LP7 (2018)	D-LP9L
Diameter	7.3mm	7.3mm	7.3mm	7.3mm	9.0mm
Length	17mm	21.5mm	18mm	22,5mm	27.5mm
Weight air	1.8g	2g	1.9g	2.1g	4.3g
Weight water	1.1g	1.2g	1.2g	1.2g	2.5g
Power output	139	139	139	139	142
Code repeat rate (s)	30-90	30-90	30-90	30-90	40-100
Battery time (month)	5.7	5.5	5	5	18
Count	100	81	16	2	23

2.3.1 Stryn tagging

From the 12th to the 13th of April 2019, a total of 104 salmon presmolts were tagged in the Stryn watercourse. From the Hjelledøla, 25 presmolts of adequate length were captured between the river mouth and the intersection with state highway 15 in Hjelle, a stretch of river approximately 2 km long. The smolts were released back into the river approximately 800 meters downstream of the mentioned intersection. This is the "upper" group in Stryn watercourse. From the Stryneelva, 79 presmolts of adequate length were captured in the stretch of river from Stauri bridge to Soget, approximately 2 km long. The presmolts were released upstream Gjørvenfossen waterfall. This is the "lower" group in Stryn watercourse.

2.3.2 Hornindal tagging

From the 13th to the 14th of April 2019, a total of 95 salmon presmolts were tagged in the Hornindal watercourse. From the Horndøla, 31 presmolts of adequate length were captured between the river mouth and Kvivsbrua, the bridge on the European route E39. The smolts were released back into the river about 100 meters downstream the Kvivsbrua. This is the "upper" group in Hornindal watercourse. In the Eidselva, 64 presmolts of adequate length were captured in the upper parts in the area of Bjørlo–Hjelle, a stretch of river about 1.5 km long. The presmolts were released at Hildenes, in the middle of the mentioned stretch, approximately 5.5 km up the river. This is the "lower" group in Hornindal watercourse.

2.4 Acoustic tracking

The movement of the tagged smolts were monitored by a network of 71 submersible hydroacoustic receivers (VR2W, Vemco, Canada) positioned in both watercourses and in the fjord. Most of the receivers have been in operation since April 2017, since the start of the

KLAFF project (Urke et al., 2018). In April 2018, the KLAFF project expanded the network to include the inner parts of the fjord, Eidselva and Hornindalsvatnet (Haugen et al., 2019), and in 2019 the network now also includes Hjelledøla, Horndøla and Strynevatnet.

In the rivers and part of the lakes, the receivers were strapped to a heavy metal cross or parabola and moored to land by a wire as to not being swept away by the current (Figure 3). In the fjord and rest of the lakes, the receivers were strapped on a rope at about five meters depth with a floating buoy on the surface and an anchor resting on the bottom to prevent the receivers from drifting out of position.

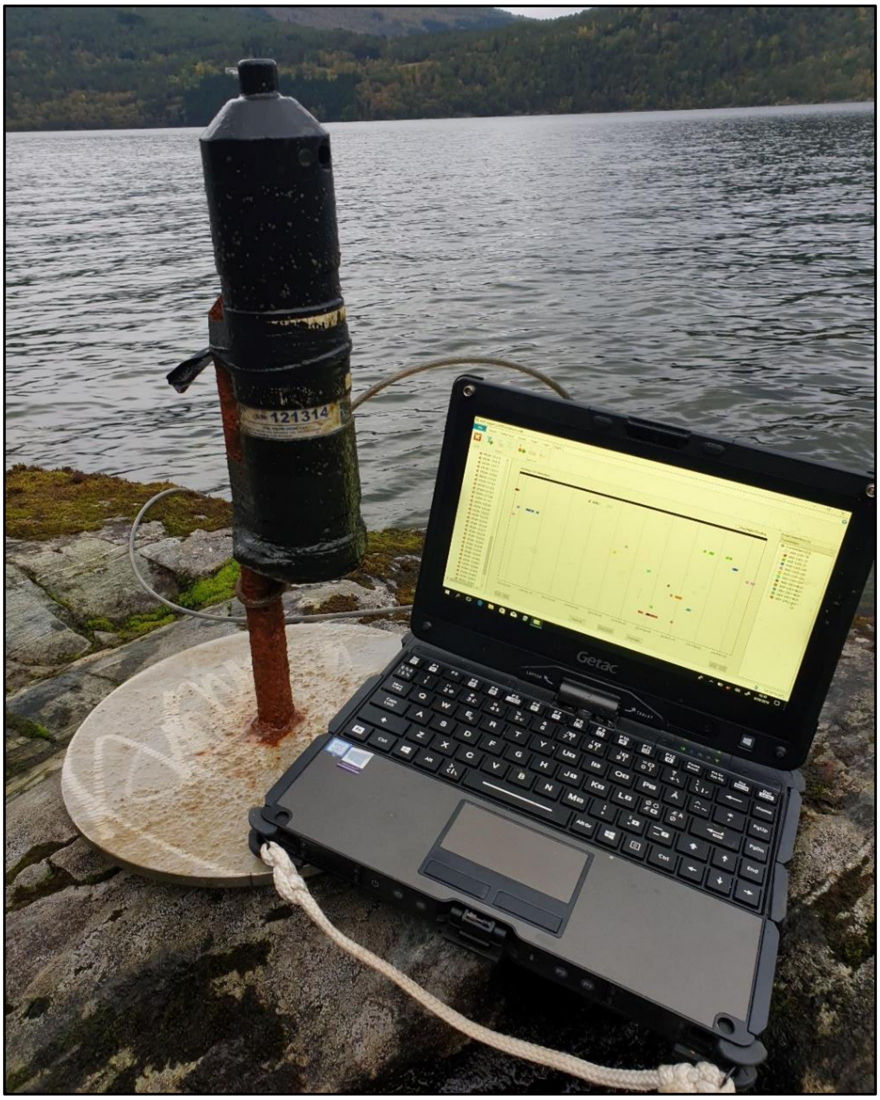

Figure 3: Here we see a picture of an acoustic receiver (VR2W, Vemco, Canada) strapped to a metal parabola that keeps the receiver in place in Hornindalsvatnet. We can also see the mooring wire attached to the metal parabola, and the transferring of observations stored on the receiver via Bluetooth to a laptop. When the transferring was complete, the receiver was put back in the lake. Photo: Aksel Fiske.

The acoustic transmitters, from now on called tags, transmit a unique acoustic signal at 69 kHz. The receivers register these signals, and store information about tag ID, time, date, and sensor value (depth if it is a depth tag). The observation range of a tag is dependent on the physical conditions in the water around the receivers. Reubens et al. (2019) found that offshore receivers have good observation probabilities up to 200 meters before decreasing rapidly beyond this. Similar observation range can be expected in lakes, whilst in rivers inference from noise and turbulent water can decrease the range (Cooke et al., 2013).

Observations were offloaded from the receivers for the last time the 30th of September 2019 in the rivers and lakes, and the 6th of October 2019 in the fjord.

2.5 Telemetry station network

Of the 71 receivers, 61 had observations from the tagged presmolts, and the receiver networks for the analyses were made with those 61 receivers. Two separate receiver networks were made, one in the Stryn watercourse and one in the Hornindal watercourse (Figure 4). One fjord station was made by aggregating the fjord receivers which was shared by both station networks. Both networks consisted of twelve receivers placed throughout the watercourses. In the Hornindal watercourse the receivers were divided into five stations, and with the addition of the release location in Horndøla and the fjord station, the Hornindal study system had seven stations. In the Stryn watercourse the receivers were divided into eight stations, and with the addition of the release location in Hjelledøla and the Fjord station, the Stryn study system had a total of ten stations.

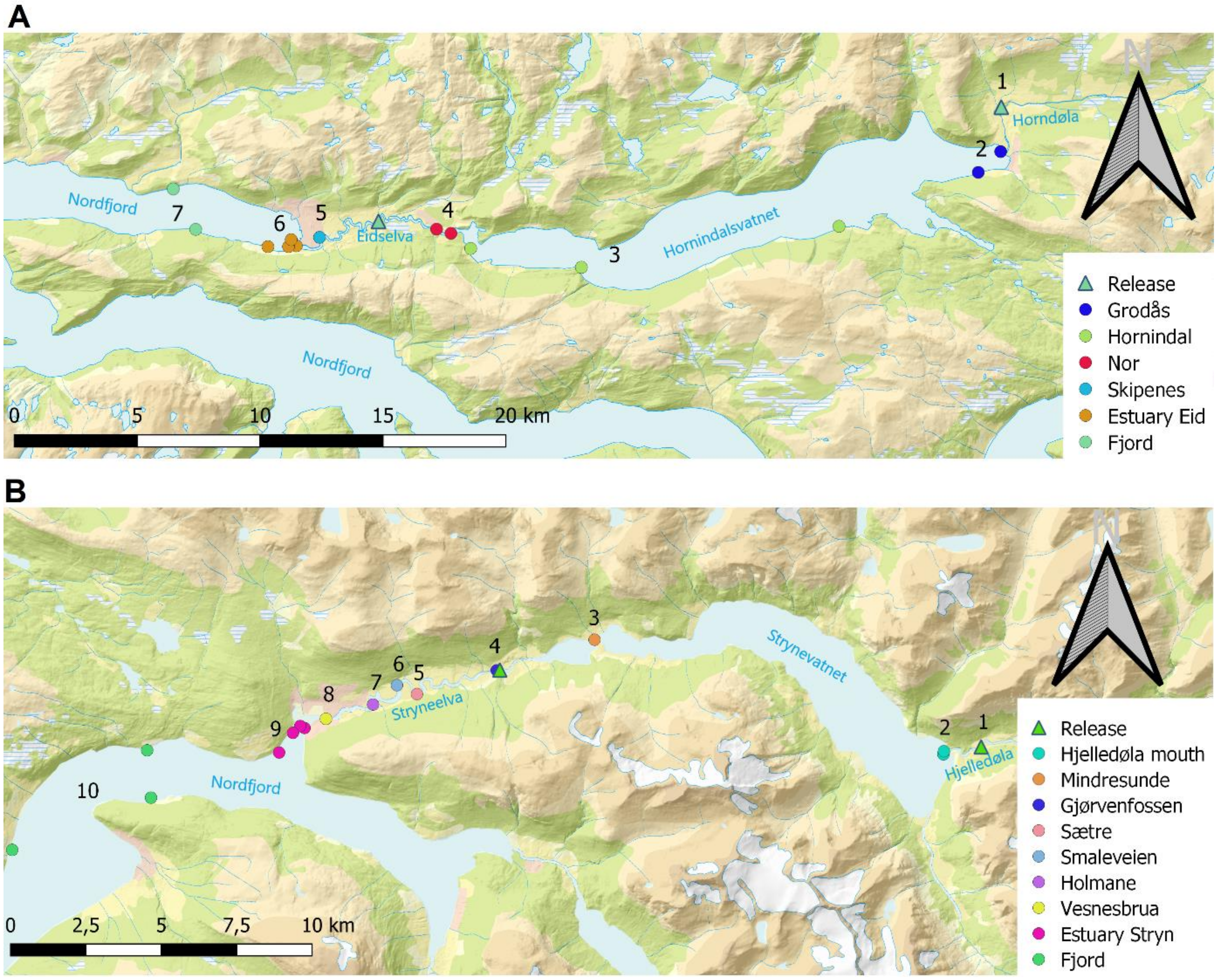

*Figure 4: The station networks in: **A**. Hornindal watercourse and **B**. Stryn watercourse. Numbers on map corresponds to station number and colored points represent the receivers and name of station. Locations of release is marked by triangles. Rightmost triangle marks release for upper group and is also station number 1. Leftmost triangle marks release for lower group and is not a station on its own.*

The stretches between the stations are zones, and the distances of the zones are shown in Table 2. The zone distances were measured following the watercourse to and from the center of the stations. In Hornindalsvatnet this roughly corresponds to the placement of the numbers in Figure 4. The zones into the fjord were measured from the estuary stations to a little past the first fjord receivers to account for that some individuals might not be observed at the receivers closest to the estuary.

Table 2: The zone number, stations and distance (km) of the zone in the Hornindal and Stryn study systems. 4 LG is the distance from the Eidselva release site to Station 5.

		Distance	
Zone	**Note**	**Hornindal**	**Stryn**
1	From station 1 to 2	2.7	1.7
2	From station 2 to 3	15.2	13
3	From station 3 to 4	8.1	3.6
4	From station 4 to 5	7.4	3.8
4 LG	From release to station 5	4.4	-
5	From station 5 to 6	1.9	1
6	From station 6 to 7	10	1.5
7	From station 7 to 8		1.9
8	From station 8 to 9		1.5
9	From station 9 to 10		8

2.6 Water Temperature and discharge

Water temperature and discharge data was obtained from The Norwegian Water Resources and Energy Directorate (NVE) from the stations in Figure 5. Water temperature and discharge for the Eidselva and Stryneelva was collected from the Hornindalsvatn and Strynsvatn measuring stations, respectively.

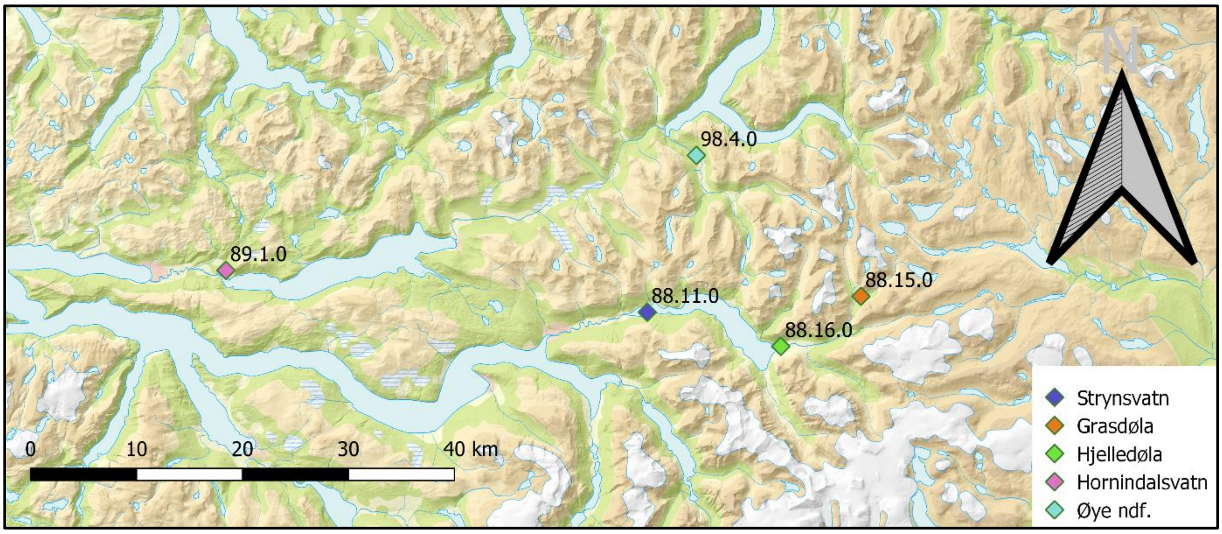

Figure 5: Water discharge and water temperature measuring stations from The Norwegian Water Resources and Energy Directorate (NVE) used in the study. Numbers correspond to the station number whilst the color correspond to the station's name.

The Hjelledøla measuring station had its last measuring in 2017 and the water discharge in the Hjelledøla from April to July in the 2019 season was predicted using a least square linear regression with data from Grasdøla and Hjelledøla measuring stations. Grasdøla is an upstream tributary to Hjelledøla. Water discharge data from 2525 days (one reading a day) in the period of 14th of April to the 23rd of July from various years from 1982 until 2017 was used. Regression results are shown in Table 3.

Table 3: Parameter estimates and model statistics for water discharge in Hjelledøla. Grasdøla is the water discharge in the river Grasdøla, DoY is day of year.

Predictors	Estimates	CI	p	df
(Intercept)	-1.84	-3.65 – -0.02	**0.047**	2521.00
Grasdøla	3.72	3.24 – 4.21	**<0.001**	2521.00
DoY	0.03	0.02 – 0.05	**<0.001**	2521.00
Grasdøla * DoY	0.01	0.00 – 0.01	**<0.001**	2521.00
Observations	2525			
R^2 / R^2 adjusted	0.895 / 0.895			

The Horndøla river does not have a measuring station, and the method applied for the Hjelledøla was not an option. The Horndøla water discharge was estimated by scaling the water discharge at Øye ndf. measuring station in the Korsbrekke river, using the formula below:

$$Q\ Horndøla = \frac{Q\ average\ Horndøla}{Q\ average\ \mathrm{Korsbrekke}}\ x\ Q\ Øye$$

Q: water discharge in m^3/s.

Q average was calculated by multiplying the catchment size and specific average runoff of the catchment. Data was collected from NVE’s map service, NEVINA (nevina.nve.no). The Horndøla water discharge was estimated to be 1.2178 times the water discharge in Korsbrekke the same day.

Temperature in Hjelledøla and Horndøla was not estimated, and no temperature data from these rivers were obtained.

2.7 Biotic conditions

2.7.1 Hornindalsvatnet

An extensive mapping of Hornindalsvatnet's fish fauna was conducted from the 17th to the 19th of August 2017 by The Norwegian Institute for Nature Research (Gjelland et al., 2018): The fish community in Hornindalsvatnet consists of brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*), Three-spined stickleback (*Gasterosteus aculeatus*) and European eel (*Anguilla anguilla*). Of these, the trout and charr are considered potential predators on migrating smolts. Trout was found to dominate (on average 9 individuals per 100 m^2 fishing nets, per night (CPUE)) in the top ten meters of the lake with a rapidly decreasing abundance with increased depth. Charr was found in the top 10 meters (~1/5 the amount of trout) and increased linearly up to ca. 8.5 CPUE at 30-40 meters depth. A peak in biomass, using echo sounding, was found at 18 meters depth, which coincided with twice the secchi depth and a water temperature of 8°C. The general density of fish was estimated to be 1.34 kg per hectare. The majority of the captured charr were shorter than 30 cm, whilst 25 % of the trout specimen were longer than 25 cm, suggesting that parts of the trout population are piscivores.

2.7.2 Strynevatnet

In Strynevatnet a gillnet survey of the fish community was conducted from the 13th to the 15th of September 1999 by Rådgivende Biologer AS (Sægrov, 2000). The fish community consisted of brown trout, Arctic charr, European eel and [Three-spined] stickleback. They found the brown trout and Arctic charr to have a 20/80 distribution, respectively, with most of the biomass at two times the secchi depth at 5 to 8 meters. The general density of fish was estimated to be 1.6 kg per hectare, and partly consisting of piscivore trout.

2.7.3 Echosounding

To estimate fish size distribution and biomass in the two lakes in 2019, echosounding was conducted (Bjerkeng et al., 1991), using similar echosounder and settings as in (Gjelland et al., 2018). The echosounding was done from boat, after sunset, the 14th of October in the Hornindalsvatnet and the 28th of September in the Strynevatnet (Figure 6). The thermocline was found to be at 25 meters in Strynevatnet, and this value was used in both lakes. The estimated biomass in kg per hectare, above and beneath the thermocline is shown in Table 4. And the target-strength (TS)-derived length distribution is shown in Figure 7. The TS-length-relationship was estimated from TS = 22.5 log(L) – 68.6 (Gjelland et al., 2018).

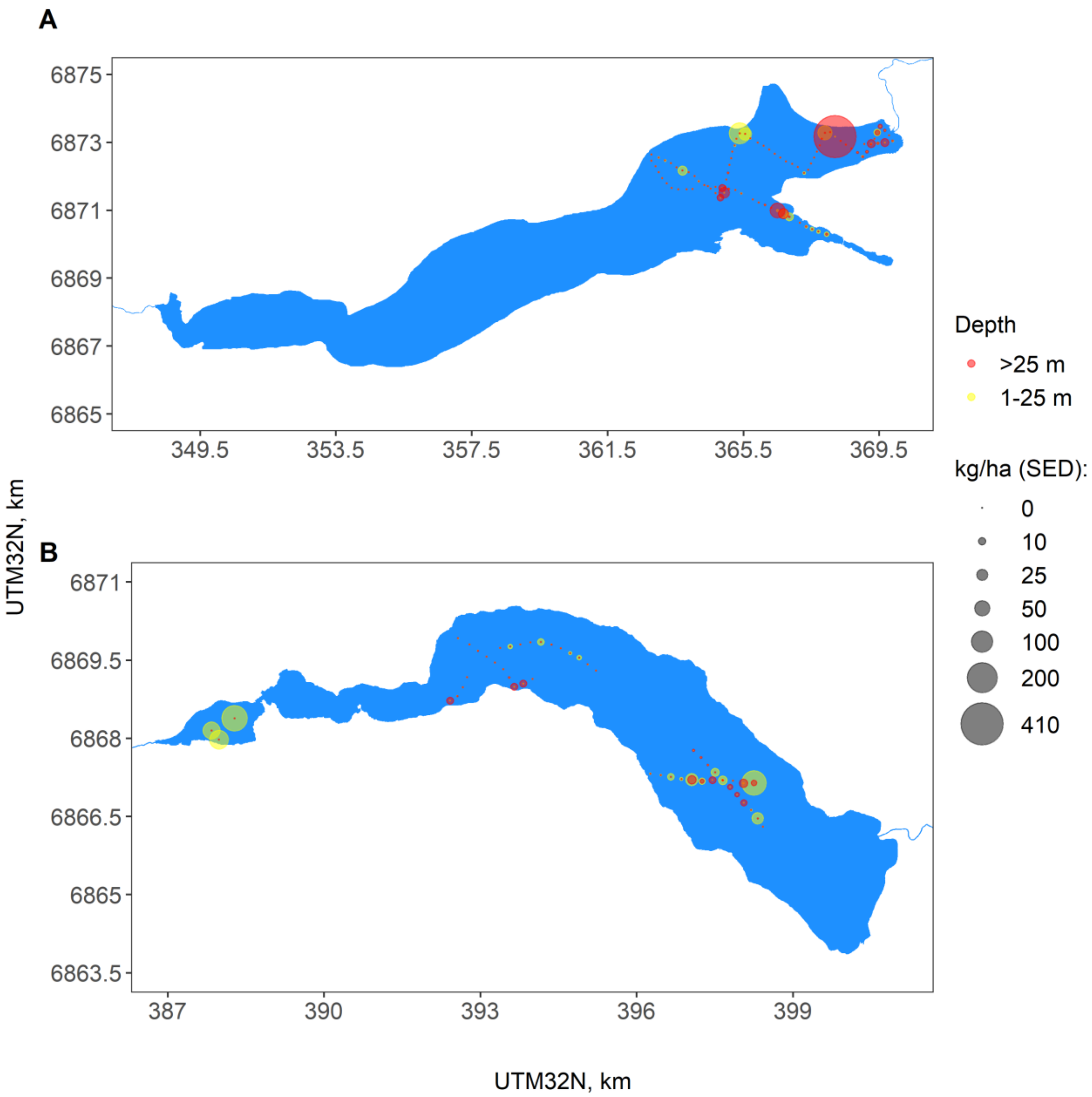

Figure 6: Map showing biomass density (kg per hectare (kg/ha (single-echo detections, SED))) distribution in ***A****. Hornindalsvatnet (14.10.2019), and* ***B****. Strynevatnet (28.09.2019). Size of point represents biomass density, and color at what depth layer (above or beneath the Strynevatnet thermocline value), in meters.*

Table 4: Distribution of estimated biomass in Hornindalsvatnet and Strynevatnet, in the depth layer 1 to 25 meters, and 25 meters and down. Biomass density ± SD is given in kg per hectare (kg/ha).

Lake	Depth layer	kg/ha
Hornindalsvatnet	1-25 m	2.6±11.9
Hornindalsvatnet	>25 m	6.3±43.7
Strynevatnet	1-25 m	10.6±30.2
Strynevatnet	>25 m	1.6±3.4

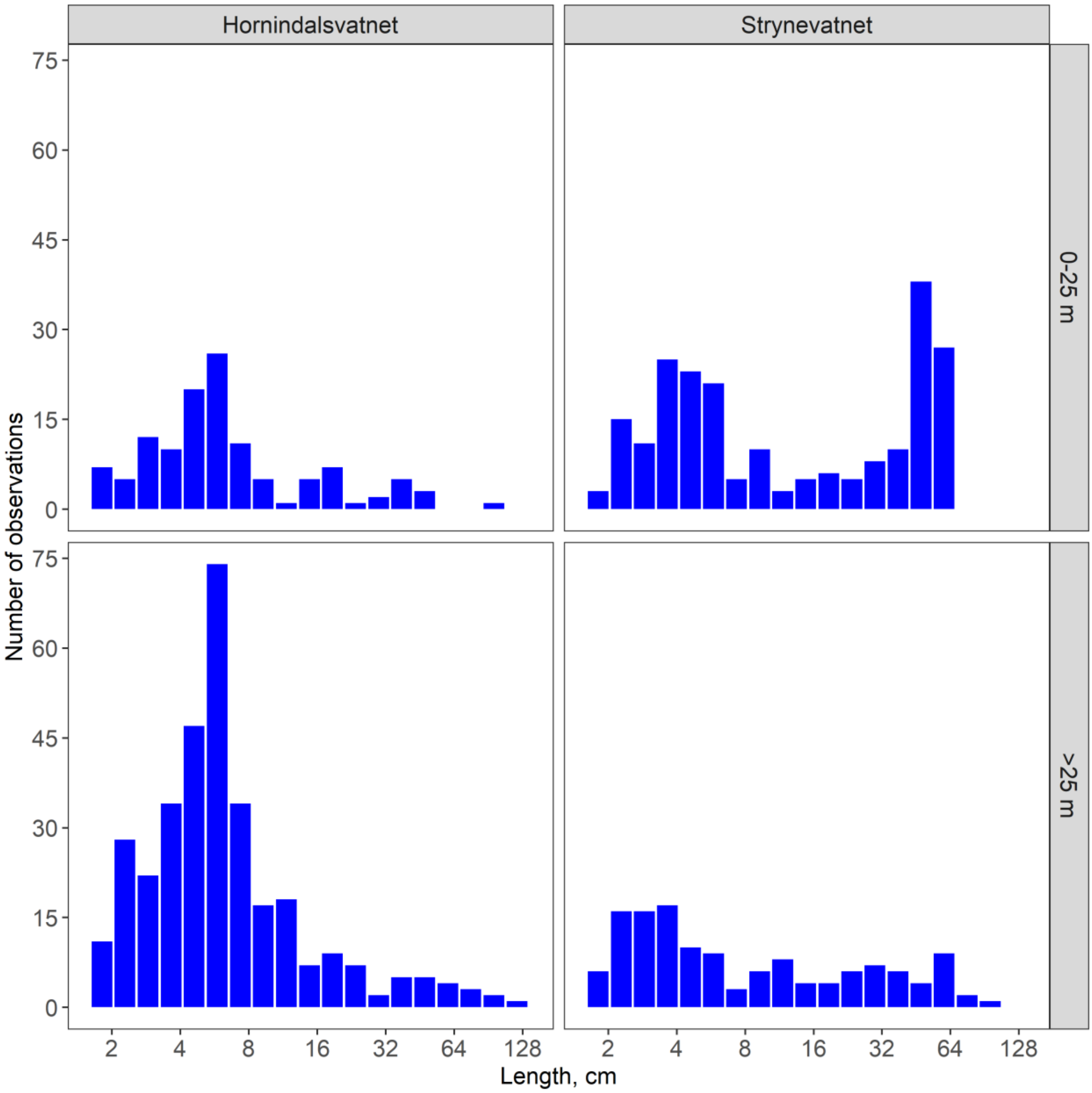

Figure 7: Target-strength-derived length distribution of the fish community in the Hornindalsvatnet and Strynevatnet as estimated from echosounding data, above and beneath the Strynevatnet thermocline value. The TS-length-relationship was estimated from TS = 22.5 log(L) – 68.6 (Gjelland et al., 2018). The x-axis is given on a base-10 log scale.

2.7.4 Tagged trout

A sample of trout considered to be anadromous, tagged in 2018 by the KLAFF project, was available for tracking during this study (Figure 8). After limiting the observations between the 1st of April and 1st of August and excluding observations from the fjord station, 23 individuals tagged with D-LP9L transmitters (Table 1) were observed. Average length (± SD, range) was 39.13 cm (±15.8 cm, 22 cm–84 cm) at tagging in April (n=1), September (n=7) and November (n=15).

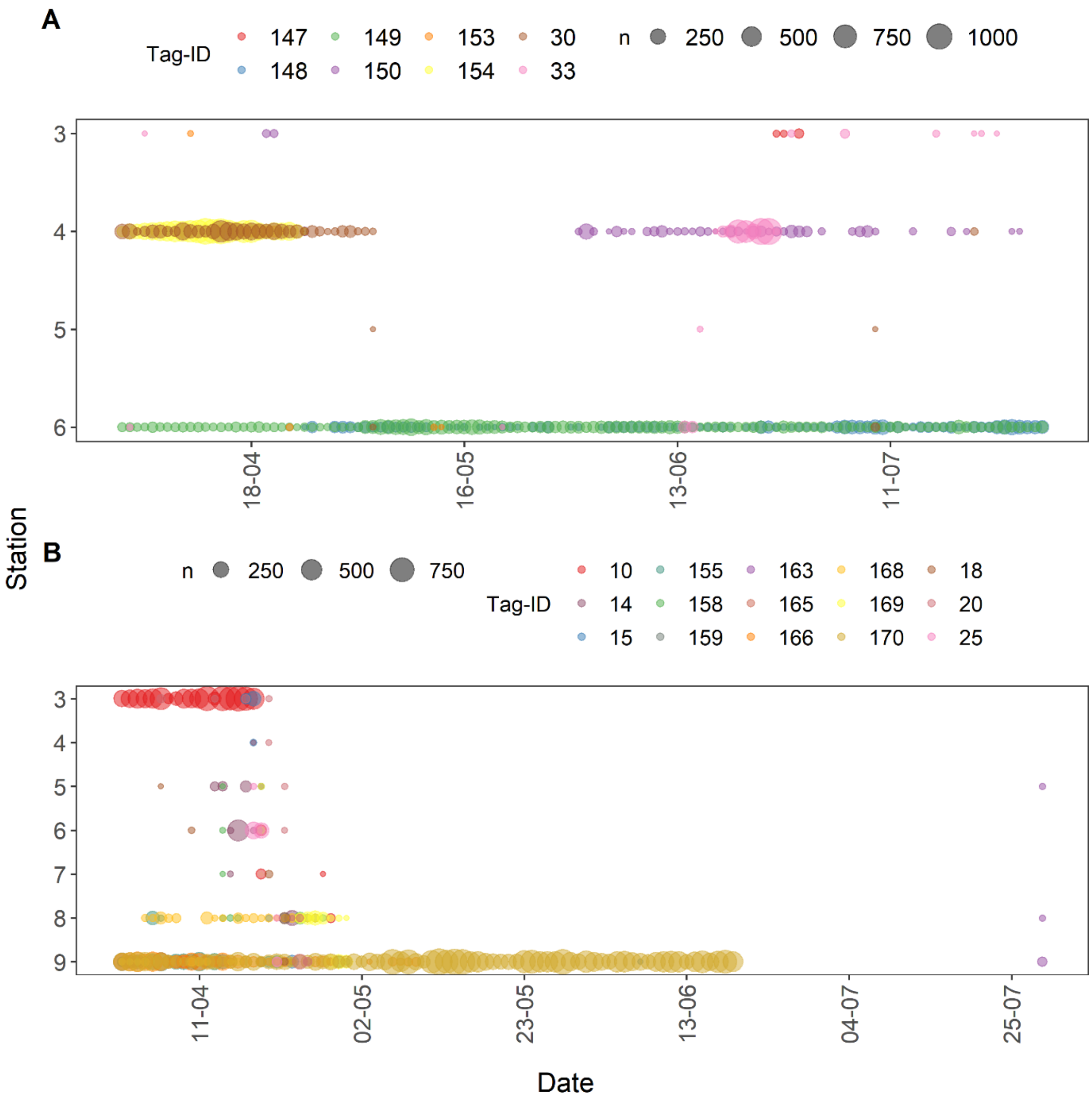

*Figure 8: Brown trout observations in **A**. Hornindal watercourse, and **B**. Stryn watercourse. X-axis shows the date and the y-axis shows at what station the observation was made. Station 3 in both figures is in the lakes, stations 6 (A) and 9 (B) are in the estuaries. Size of the point represents number of observations per day. Length at tagging in fall 2018 was 39.13 ±15.82cm, range= 22.00cm–84.00cm, n=23.*

2.8 Data handling and quantitative analyses

Acoustic telemetry provides a lot of information in the form of observations every time a signal sent from a tag is received at a receiver. Acoustic telemetry is prone to "catching" false observations in disturbing conditions: That can be during rough waters, noise from passing boats and colliding signals from multiple tags (Reubens et al., 2019; Simpfendorfer et al., 2015). An extensive cleaning of the raw data was done, removing spatially and temporally displaced observations.

The program VUE (Vemco, Canada) was used to offload the observations data from the receivers. The program R, version 3.5.2 and version 3.6.2 (R Core Team, 2020) with RStudio (RStudio Team, 2015) and the packages “ggplot2” (Wickham, 2016), “AICcmodavg” (Mazerolle, 2019), ”directlabels” (Hocking, 2020), “lattice” (Sarkar, 2008),”ggpubr” (Kassambara, 2020), “sjPlot” (Lüdecke, 2020) and “lmer4” (Bates et al., 2015) were used for handling, cleaning, analyzing and visualizing the data. Microsoft Office Excel 2016 and MARK version 9.0 (White & Burnham, 1999) were used for the mark recapture analysis, and QGIS version 3.10.0 and newer (QGIS Development Team, 2020) with layers from Kartverket (kartverket.no) were used in the making of the maps.

To assess and quantify effects of different groups (e.g., release location and migration faction) and environmental or individual variables (e.g., water discharge and smolt size) on different performance and migration related responses (e.g., survival) for the smolts, a generalized linear model (GLM) was fitted. For binominal responses (e.g., migrate/not migrate) a logit-link was used in the GLMs. For the logit-link GLMs, the coefficient of discrimination, R^2 Tjur (Tjur, 2009) was calculated.

To account for skewed and biased representation from the small sample size, a restricted maximum likelihood (REML) (Corbeil & Searle, 1976; Harville, 1977) approach, with smolt ID as the random effect was made when fitting models for predicted depth use and arrival at the different stations along the watercourse. The model selections were based on the maximum likelihood method, as REMLs are not suited for model selection with mixed models (Zuur et al., 2009), and then fitted with REML after the model selection to give the most unbiased estimates. For the REMLs a marginal and conditional R^2 is given. The marginal R^2 is the proportion of the total variance explained by the fixed effects, whilst the conditional R^2 is the proportion of variance explained by both the fixed and random effects (Nakagawa et al., 2017). The random effect intercept represents the difference (variance) between the intercept for each individual (smolt) and the overall intercept.

Multiple candidate models were fitted with combinations of predictor variables under influence of variables in my study objectives. But before fitting, between-variables correlations were estimated, where pairs of predictor variables with correlation levels above 0.3 were avoided in the same candidate model.

For each candidate model an Akaike Information Criterion (AIC) was estimated. The AIC is an information-theoretic approach that let you compare models based on information loss (Burnham et al., 2011). The AIC of a model is the deviance plus a penalty of two times the number of parameters, and in this way deals with the risk of over- or underfitting. An AIC value by itself does not tell much and needs to be compared with the AIC of other models fit to the same data. The most supported model by the data is the candidate model with the lowest AIC, (Burnham & Anderson, 2002). The larger the difference, or ΔAIC from the best model, the less plausible it is that the fitted model is the best, given the data (Burnham & Anderson, 2002). A ΔAIC of two or less means the model still have substantial empirical support, however, models with a ΔAIC less than seven still have some support and should not necessarily be dismissed (Burnham & Anderson, 2002; Burnham et al., 2011). The ΔAIC of the second-most supported model is therefore mentioned as being higher or lower than two when talking about model selection. For models explaining behaviors from data with low sample sizes, a corrected version of the AIC (AICc) was estimated. The AICc is the AIC plus a "small sample correction" and works in the same way to compare models.

2.9 Definitions and technicalities

Daily migration probability was calculated as the number of tagged smolts that migrated a given day, compared to the number of tagged smolts that have yet not migrated.

Arrival at a station was defined as the earliest observation an individual had at that station. Migration time between stations was calculated as the time difference between the last observation at a given station and the earliest observation at a succeeding station. As stated in Daniels et al. (2019), the migration timing between successive stations cannot be summed to give a cumulative migration time if residency or directional changes is present in the observation data, as that will lead to periods of time being unaccounted for or double counted.

The average day of migration start for the upper and lower groups in both watercourses was calculated based on the first observations, disregarding the release, from each individual smolt in the given group. Based on when the individual tagged smolts started migrating, they were split into early and late factions.

In Hornindalsvatnet , the progression rates were measured as time used since the last observation at the first receiver at station 2 (in sequential order from release to the fjord) to the first observation at the last station 3 receiver a smolt was observed at. In Strynevatnet it was measured as time used since the last observation at station 2 to the first observation at station 3. Progression rates were standardized as body lengths per second.

To account for the skewed representation from individual smolts, the median depth use during daytime and night for each smolt was used for the average depth analysis.

Time spent at station 2 was calculated on data from individuals that portrayed signs of being alive, that includes depth-tagged presmolts that had active vertical migrations, and ID-tagged presmolts observed downstream of station 2.

2.10 Depth data

The depth tag has a depth sensor range from 0 to 255 and each step is 0.2 meters. Maximum sensor value is equal to 51 meters. The depth tags have a known issue where the depth sensors can "lock out" at maximum value. The tag can of course also show max value if that is the experienced depth. Observations at continuous maximum sensor value were removed from the data during analysis on depth use.

2.11 Survival analysis

An apparent survival for the factions was calculated as the percentage of smolts from each faction observed in the fjord. And a tag-type apparent survival was calculated as the percentage of tags used, observed in the fjord. This apparent survival is not to be mixed with the survival estimates mentioned below.

To account for a less than 100% observation efficiency for the receivers, a sequential approach to Cormack-Jolly-Seber (CJS) mark-recapture models (Lebreton et al., 1992) was used to estimate survival for the migrating smolts. This model has two types of parameters: Observation probability (p) at the stations and survival probability (φ) between the stations. The φs and ps are calculated based on the smolts' capture histories. For each tagged smolt a capture history is made. If a tagged smolt is observed at a station it will get the value "1" and if it is not, it will get the value "0", regardless of it being alive or dead (Figure 9).

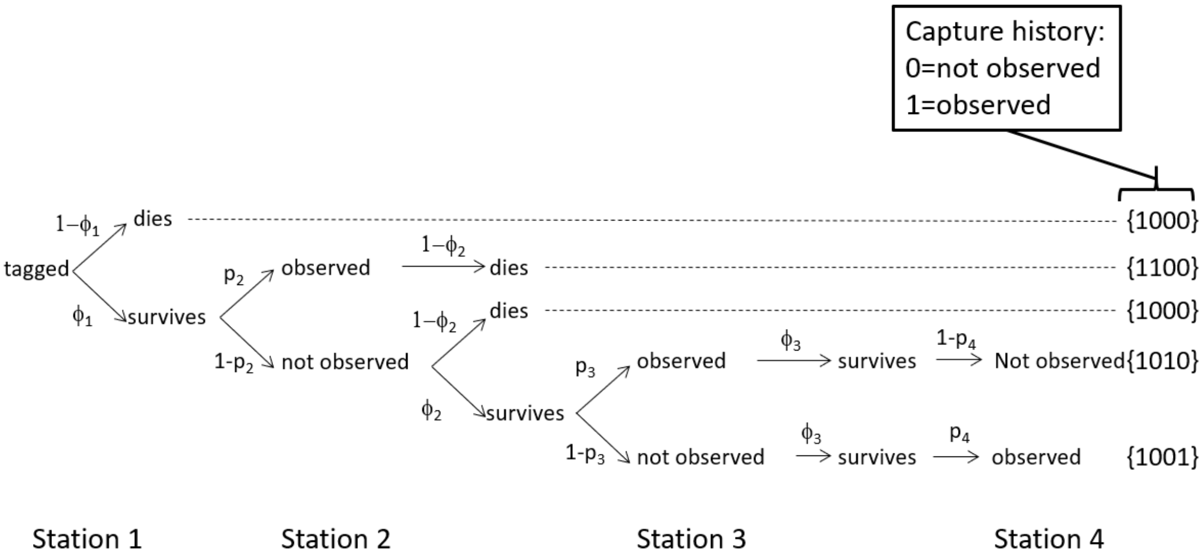

Figure 9: Fate diagram for tagged smolts with five examples of capture histories with given parameters for a Cormack-Jolly-Seber model structure. φ_i represents the survival probability between station i and i+1, and p_i represents the detection probability at station i.

With a capture history for every tagged individual, MARK was used to estimate the apparent survival and detection probabilities in the two study systems. The model parameters can be estimated to be constant or zone dependent (Figure 10), e.g. same in the lakes, but different in the rivers. Without any further information past the last zone and station the *p* and φ are inseparable. This means that these parameters will not be estimated and rather a product of the two are used. If you know the value of the last *p* it is possible to also estimate the last φ.

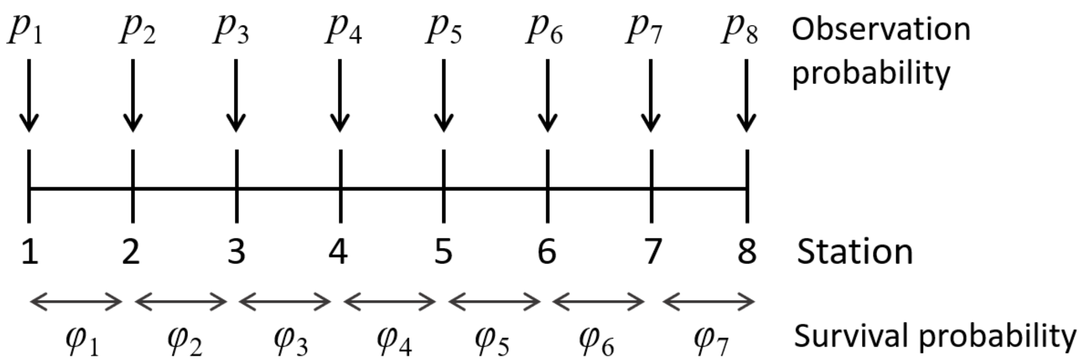

Figure 10: CJS-parameters of the model [φ(zone), p(zone)]. In this model, each zone and station will have its own estimates for survival and detection probability. In the last zone, the φ and p cannot be estimated separately, just the product of them.

To facilitate comparison between the survival in the different zones and to other studies, the estimates were standardized to survival per km. In this study, the smolts were divided into two groups: Upper and lower, according to river. There was also information about length and weight, which were made into three individual covariates (individual characteristics): length, weight, and k-factor (weight/length^3*100). The groups can be used to estimate separate φs and ps for the two groups at the same stations and zones. The covariates can be used to estimate the parameters as a function of the covariate, this can be helpful to see if survival is related to the individual characteristics mentioned above.

2.11.1 Mark modelling

A prerequisite of a good model is that all parameters are estimated. An extensive pre-analysis was therefore done in MARK to establish what parameters were estimable with the data at hand, and a base model was proposed. What this means in practical terms is that separate φs and ps could not be estimated for every zone and station, rather they were estimated for sections of the watercourses ([φ(section), p(section)]). Candidate models including covariates were added to the proposed base model.

Parameters were fixed to 1 or 0, either due to parameters being estimated to be close to 1 or 0 and MARK could not count it, or the parameter did not make sense. The latter applies to the survival and observation probabilities for the lower groups at zones and stations upstream of their release site.

3 Results

Of the 199 tagged salmon presmolts, 147 were observed by the receivers after release. Of the 31 tagged presmolts released in Horndøla, 24 were observed in the Horndøla mouth, thirteen were observed in Hornindalsvatnet (station 3), five were observed at station 4, and two were observed in the fjord (station 7). Of the 64 tagged presmolts released in Eidselva, 54 were observed in the river and 28 were observed in the fjord (station 7). Of the 25 tagged presmolts released in Hjelledøla, 20 individuals were observed in the Hjelledøla mouth (station 2), one was observed at station 3 and none was observed further downstream in the system. Of the 79 tagged presmolts released in Stryneelva, 49 was observed in the river and 28 were observed in the fjord (station 10) (Table 5).

Table 5: Number of unique ID observations on each station in Hornindal and Stryn watercourses from the upper and lower groups. Number of tagged smolts are the number of salmon presmolts tagged in given group. Number of unique observations is the number of unique ID's observed from the respective group through the whole study system, % is the share of the tagged smolts that were observed.

	Unique (%) observations in Hornindal		Unique (%) observations in Stryn	
Station	**Upper**	**Lower**	**Upper**	**Lower**
1	31 (100)	-	25 (100)	-
2	24 (77)	-	20 (80)	-
3	13 (42)	-	1 (4)	-
4	5 (16)	-	0 (0)	29 (37)
5	2 (6)	41 (64)	0 (0)	43 (54)
6	2 (6)	54 (84)	0 (0)	41 (52)
7	2 (6)	28 (44)	0 (0)	33 (42)
8			0 (0)	35 (44)
9			0 (0)	35 (44)
10			0 (0)	28 (35)
n tagged smolts	31	64	25	79
n unique smolt obs. (%)	24 (77)	54 (84)	20 (80)	49 (62)
Total unique smolt obs. (%)	147 (74%)			

3.1 Timing of migration

The tagged smolts from the Hornindal watercourse were detected in the estuary for the first time in the period from the 22nd of April to the 15th of July (range = 85 days). The same dates for the Stryn watercourse tagged smolts were from the 21st of April to the 6th of June (range = 47 days). First observations in the river mouths in Horndøla and Hjelledøla was respectively in the period from the 21st of April to the 20th of June and from the 15th of April to the 24th of May. Common for all rivers, except for Horndøla, is that they all were showing clear migration peaks in late April/very early May (up until 2nd of May) and another one in mid-late May about two weeks after the first one. In Horndøla the migration was postponed by almost a month compared to the other rivers (Figure 11).

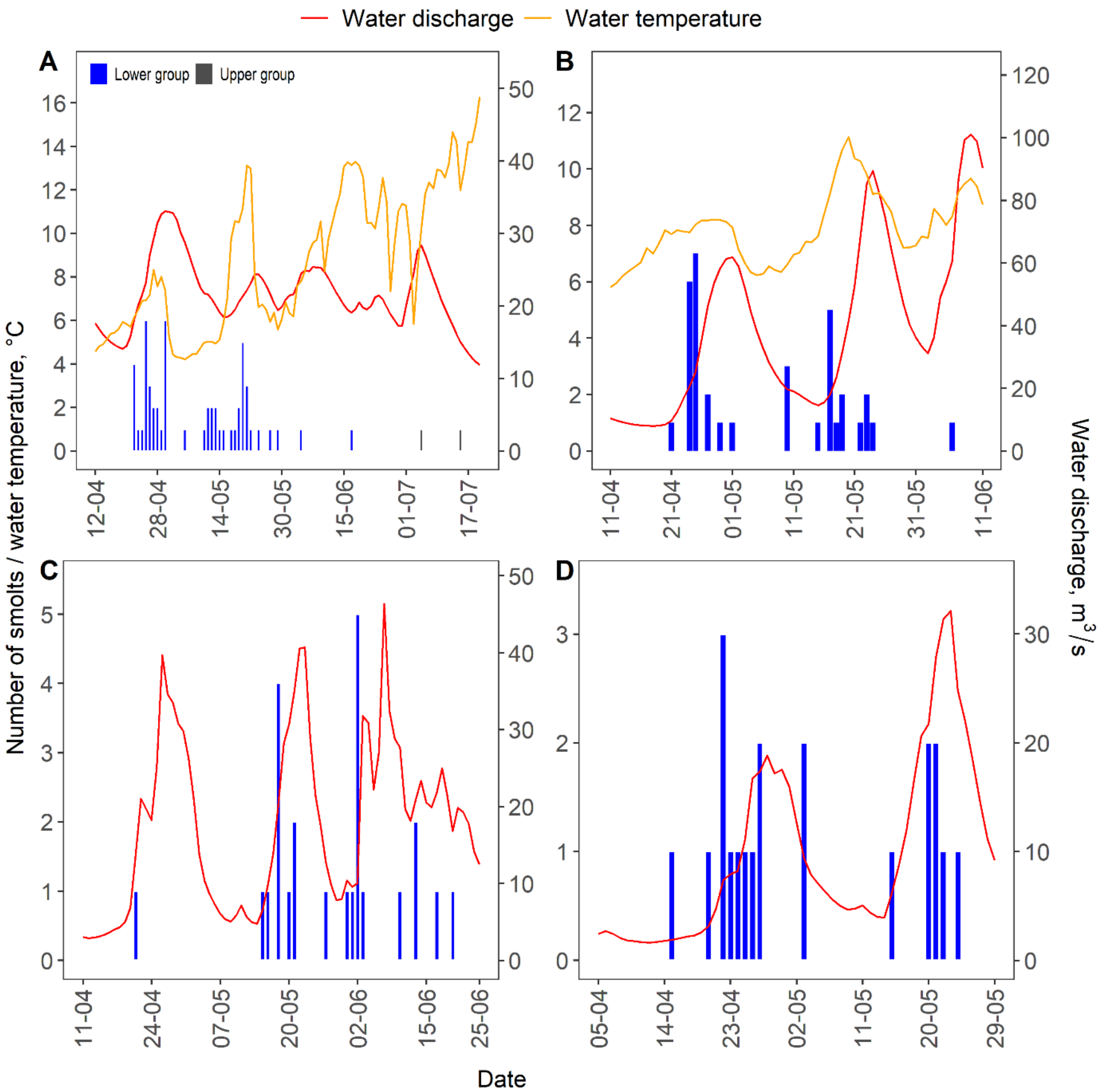

Figure 11: Count of first observations at river mouth with temperature and water discharge in respective rivers in 2019. ***A****. Eidselva estuary, water discharge and temperature from measuring station Hornindalsvatn, blue bars are observed individuals from the smolts tagged and released in Eidselva, grey bars are observations from the smolts tagged and released in Horndøla.* ***B****. Stryneelva estuary, water discharge and temperature from measuring station Strynsvatn* ***C****. Horndøla, lake entry, upscaled water discharge as described in chapter 2.7.* ***D****. Hjelledøla, lake entry, predicted water discharge as described in chapter 2.7.*

The tagged smolts from Eidselva showed most support for a migration driven by day of year (DoY), water discharge (Q), and the relative change in water discharge from the previous day (t-1) to the next (t) ($\Delta Q/Q$, $\Delta Q_t = Q_t - Q_{t-1}$) ($\Delta AICc < 2$, Table B-1). The tagged smolts from Stryneelva showed most support for a migration driven by DoY and $\Delta Q/Q$ ($\Delta AICc < 2$, Table B-1). The tagged smolts from Horndøla showed the most support for a migration driven by

DoY, ΔQ/Q and the interaction between them (ΔAICc < 2, Table B-1), whilst Hjelledøla showed the most support for a migration driven by Q (ΔAICc < 2, Table B-1). The selected candidate models' parameters can be found in Table 6.

The Eidselva model predicts an increase in migration probability with an increase in DoY and to less extent with an increased ΔQ/Q, it also predicts that the effects from DoY and ΔQ/Q is stronger with increased Q (Figure A-1). The Stryneelva model predicts an almost equal increase in migration probability with increased DoY and ΔQ/Q. The Horndøla model estimates an increased migration probability with an increase in DoY and ΔQ/Q until the ~19th of June, where the probability decreases with increased ΔQ/Q. The Hjelledøla model estimates an exponential increase in migration probability with an increase in Q. The selected candidate models are illustrated in Figure 12.

Table 6: Coefficient estimates and test statistics for the selected canditae models estimating migration probability in ***A.*** *Eidselva,* ***B.*** *Stryneelva,* ***C.*** *Horndøla, and* ***D.*** *Hjelledøla. Q = water discharge (m^3/s), ΔQ = change in waterdischarge from the previous day (m^3/s), reldeltaQ = ΔQ/Q, DoY = day of year, SE = standard error, p = significance, df = degrees of freedom.*

	A	**Eidselva**			**B**	**Stryneelva**		
Predictors	Estimate	SE	p	df	Estimate	SE	p	df
(Intercept)	-15.28	1.99	**<0.001**	50	-10.47	1.67	**<0.001**	52
ΔQ/Q	13.12	2.74	**<0.001**	50	5.98	1.39	**<0.001**	52
DoY	0.09	0.01	**<0.001**	50	0.06	0.01	**<0.001**	52
Q	0.05	0.03	0.058	50				
Observations				54				55
R^2 Tjur				0.099				0.029

	B	**Horndøla**			**C**	**Hjelledøla**		
Predictors	Estimate	SE	p	df	Estimate	SE	p	df
(Intercept)	-19.07	3.06	**<0.001**	66	-4.25	0.44	**<0.001**	40
reldeltaQ	21.93	9.37	**0.019**	66				
DoY	0.11	0.02	**<0.001**	66				
DoY * ΔQ/Q	-0.13	0.06	**0.038**	66				
Q					0.06	0.02	**<0.001**	40
Observations				70				42
R^2 Tjur				0.037				0.029

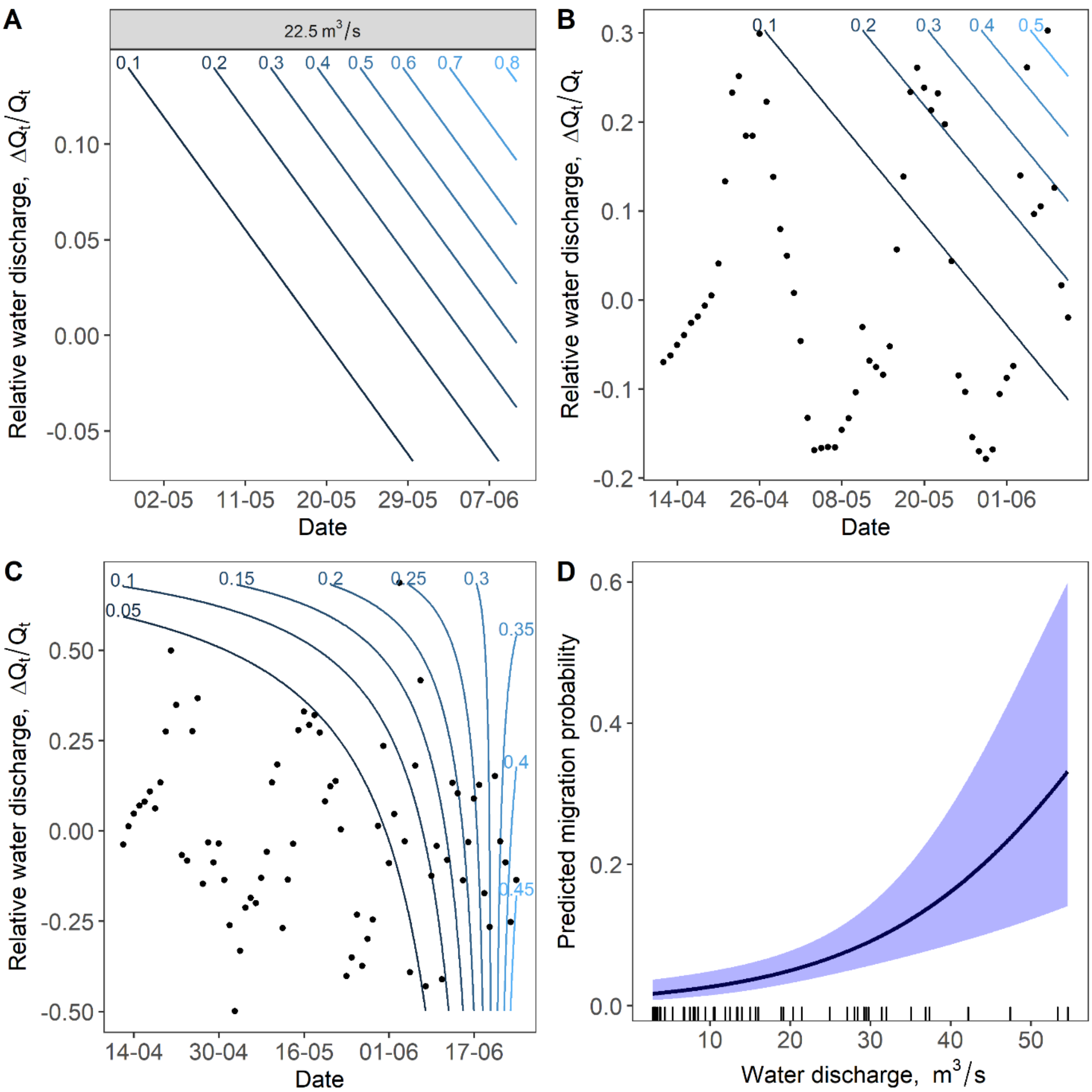

*Figure 12. Plots of selected model predictions for daily migration probability for salmon smolts in 2019. Model parameters are shown in Table 6. **A**. Contour plot of the model predictions for daily migration probability in Eidselva as a function of Date and relative change in water discharge from the previous day with a water discharge of 22.5 m^3/s. A figure with more levels of water discharge is found in the Appendix (Figure A-1). **B**. Contour plot of the model predictions for daily migration probability in Stryneelva as a function of the relative change in water discharge from the previous day and date. **C**. Contour plot of the model predictions for daily migration probability in Horndøla as function of relative change in water discharge from the previous day and date. **D**. A linear model of the model predictions for daily migration probability and a 95% confidence interval (blue ribbon) in Hjelledøla as a function of water discharge (m^3/s). The points in **A**., **B**. and **C**., and the rug in **D**. represents the predictor data the model was based on.*

The majority of the tagged smolts was observed entering the estuaries during night (time between sunset and sunrise), especially in the early hours after sunset. Of the tagged smolts in Hornindal watercourse, 73.2% entered the estuary during night. Of those, 75.6% were first detected before midnight. The same numbers for the Stryn watercourse smolts, entering the estuary, were 88.6% and 71%. (Figure 13 A & B). A less distinct preference for night-migration was seen for the smolts entering Hornindalsvatnet and Strynevatnet. Of the Horndøla smolts, 62.5% was first detected at station 2 during night. Of those, 46.7% were first detected before midnight. The same numbers for the Hjelledøla smolt, at station 2 were 60% and 50%. (Figure 13 C & D).

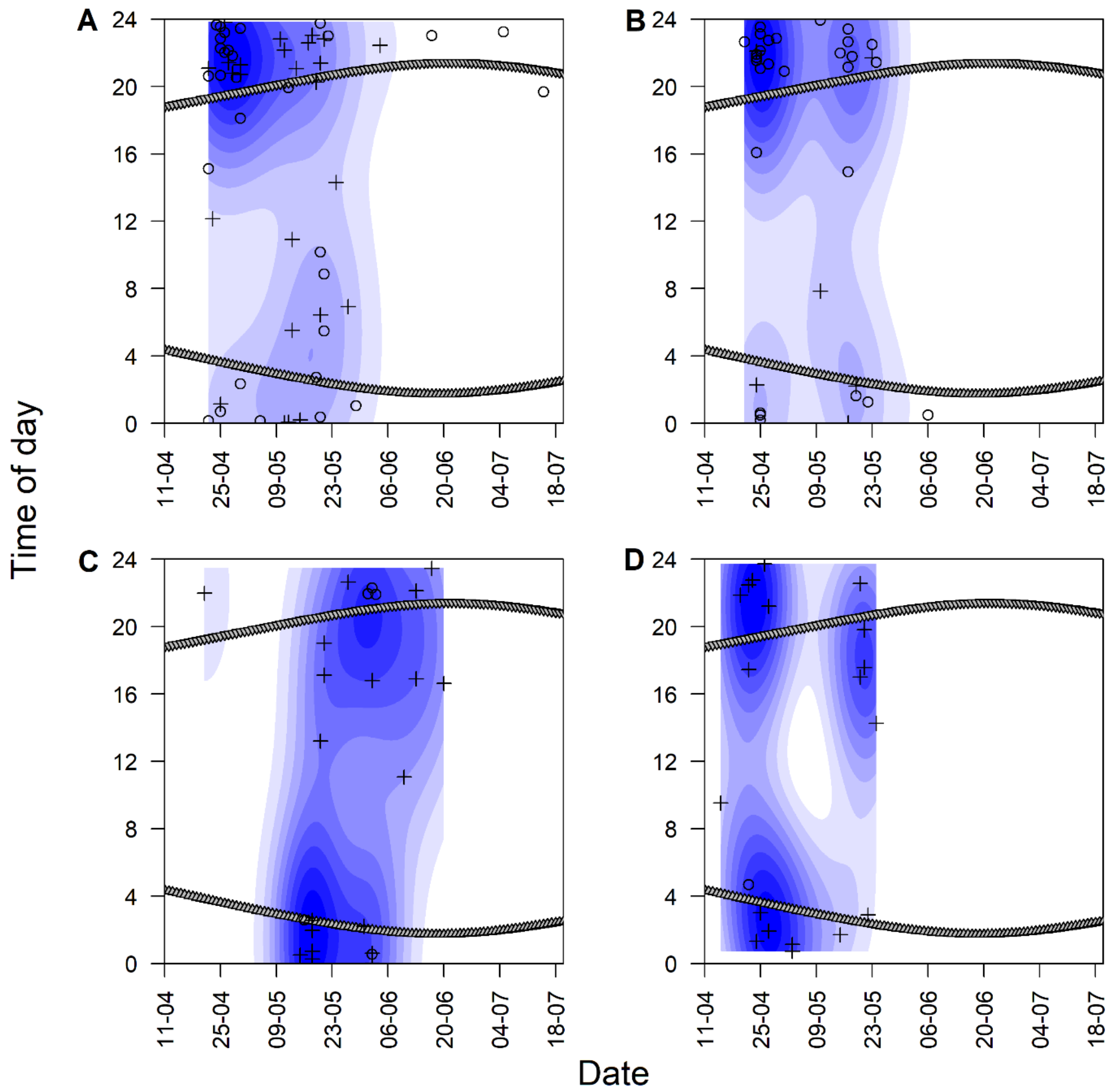

Figure 13: Date and time of day for the first observations from the tagged smolts from: ***A.*** *Hornindal watercourse entering the Eidselva estuary,* ***B.*** *Stryn watercourse entering the Stryneelva estuary,* ***C.*** *Horndøla entering Hornindalsvatnet, and* ***D.*** *Hjelledøla entering Strynevatnet in 2019. Triangles pointing up represents time of sunset and triangles pointing down represents sunset. The darker the colors are on the probability kernels, the higher the probability is of migrating into the estuaries and river mouths. Circles represent individuals observed at a downstream station, crosses represent individuals not observed at a downstream station.*

3.1.1 Time used to migrate through the watercourses

Average day of migration start for the lower group in Hornindal watercourse was the 7th of May, whilst for the upper group it was the 28th of May. The same dates for the Stryn watercourse groups were the 30th of April and the 4th of May. The upper group from the Stryn watercourse was not observed downstream of station 3. The course of migration, when the smolts were observed for the first time at the stations, is illustrated in Figure 14.

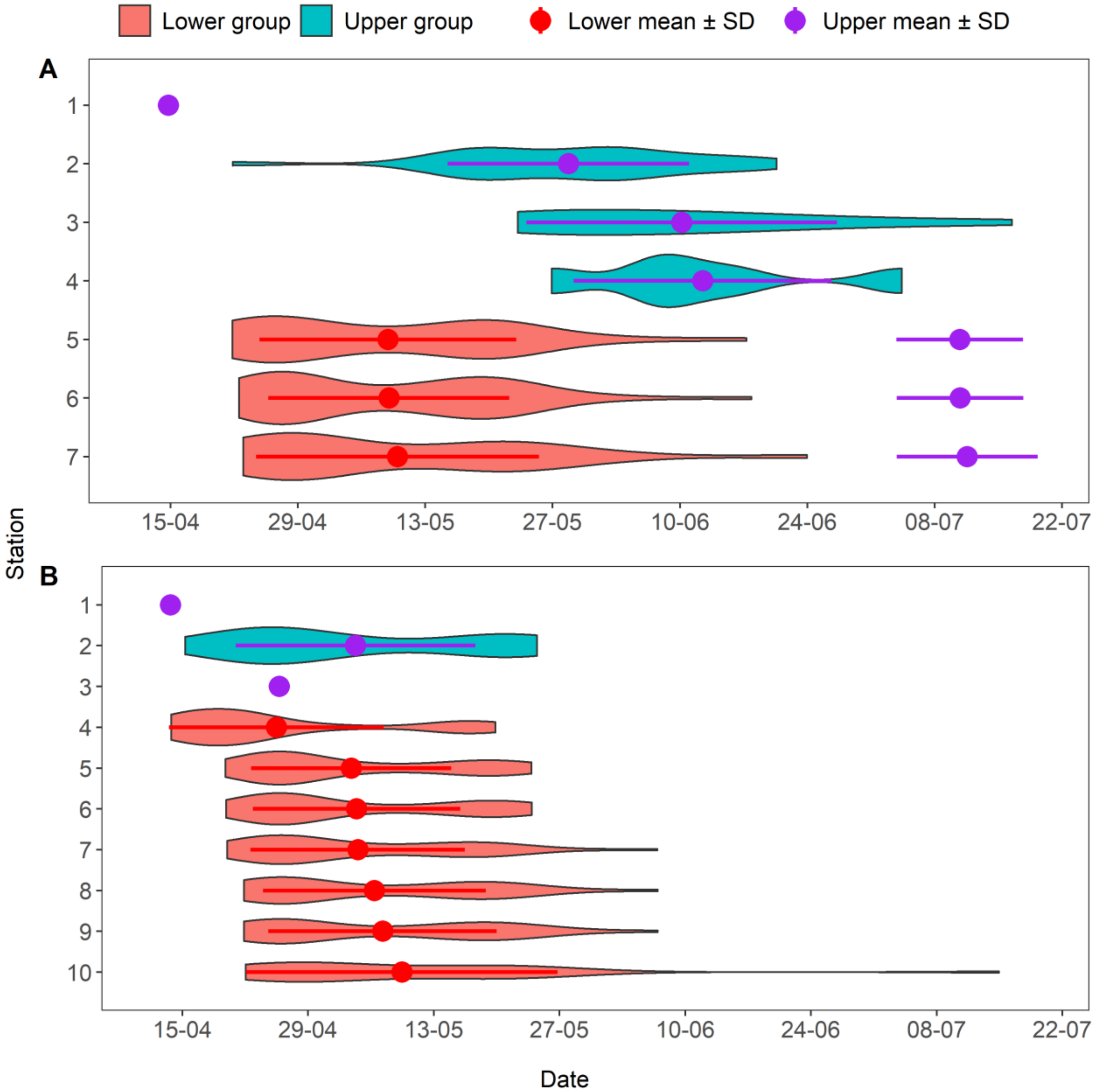

Figure 14: Violin plots of dates when tagged salmon smolts from ***A.*** *Hornindal watercourse and* ***B****. Stryn watercourse was first observed at the given station in 2019. Width of violin shows relative distribution of observations. Points represent the mean date whilst tails represent the standard deviation of first observations at the given station. The points at station 1 is the release and therefore the same date for all individuals in the group, and no violin. For the other stations, the lack of violins means the station had observations from two or fewer individuals from given group.*

The upper group from Hornindal watercourse spent on average (±SD) 24.55 (±12.16) days (n=2) from station 2 to station 7 was. For the lower group in Hornindal watercourse the average time from station 5 to station 7 was 3.29 (±3.65) days (n=23). The lower group in Stryn watercourse used an average (±SD) of 10.65 (±9.91) days from station 4 to station 10 (n=16). Longer residence times were seen in the release zones, e.g. zones 1 in both watercourses and zone 4 in Stryneelva (Table 7).

Table 7: Days spent by n smolts in the given zones with a 10, 50 and 90 percentile ([10%;50%;90%]) and average ± SD, for the Hornindal and Stryn watercourses. Zone 1 shows time spent in the zone from time of release to first observation at station 2.

	Days spent through zones, Hornindal watercourse			Days Spent through zones, Stryn watercourse		
Zone	**[10%;50%;90%]**	**Average ± SD**	**n**	**[10%;50%;90%]**	**Average ± SD**	**n**
1	[31.85;47.15;60.00]	43.96 ± 13.3	24	[8.32;14.23;39.10]	20.61 ± 13.3	20
2	[2.58;4.30;10.42]	5.50 ± 3.42	14	[2.82;2.82;2.82]	2.82 ± 0	1
3	[0.06;0.09;0.33]	0.17 ± 0.18	4	NA	NA	0
4	[5.23;7.86;10.5]	7.86 ± 4.64	2	[0.93;2.87;11.9]	5.31 ± 5.55	24
5	[0.02;0.18;2.82]	1.02 ± 2.45	43	[0.03;0.04;0.46]	0.19 ± 0.42	40
6	[0.18;0.67;3.75]	1.66 ± 2.65	30	[0.02;0.06;1.90]	1.55 ± 4.43	38
7				[0.02;0.33;1.05]	0.60 ± 0.79	31
8				[0.01;0.02;0.22]	0.09 ±0.21	34
9				[0.19;0.75:3.50]	2.73 ± 6.88	28

In the Hornindal watercourse, a slower progression rate was found for the Horndøla tagged smolts compared to the Eidselva tagged smolts, whilst no difference in progression rates were found between the early and late factions. In the Stryn watercourse, there was a lot of insecurity around the progression rate for the Hjelledøla tagged smolts, but it was estimated to be quicker than for the Stryneelva tagged smolts. No difference in progression rates were found between the early and late Stryneelva smolt factions. The model parameters can be found in Table 8 and is illustrated in Figure 15 (ΔAICc < 2 in Hornindal watercourse, and ΔAICc > 2 in Stryn watercourse, Table B-2).

Table 8: Fixed effects parameter estimates for the selected linear mixed effects models fitted to predicted arrival dates along the migration routes. The two group effects are based on whether the smolts were released in Horndøla or Hjelledøla (Upper) or in Eidselva or Stryneelva (Lower), and if the individual smolts migrated before (Early) or after (Late) the respective average migration start date for their Upper or Lower group. Intercept is the lower, late group. The model was fitted using smolt ID as a random effect, ID (intercept) is the variance in the random effect, and N_{ID} is the number of unique smolts in the analysis.

	Hornindal watercourse			**Stryn watercourse**		
Predictors	Estimates	SE	df	Estimates	SE	df
Intercept	140.17	1.34	164	138.67	1.57	258
Distance	0.32	0.08	164	0.58	0.07	258
UpperLower [Upper]	41.39	2.35	164	16.53	3.64	258
EarlyLate [Early]	-23.09	1.66	164	-20.32	1.94	258
Distance* UpperLower [Upper]	0.41	0.1	164			
UpperLower [Upper]* EarlyLate [Early]				-5.73	4.08	258
Random Effects						
ID (intercept)	45.20 ± 6.72			35.76 ± 5.98		
N_{ID}	78			69		
Observations	171			265		
Marginal R2 / Conditional R2	0.853 / 0.964			0.639 / 0.858		

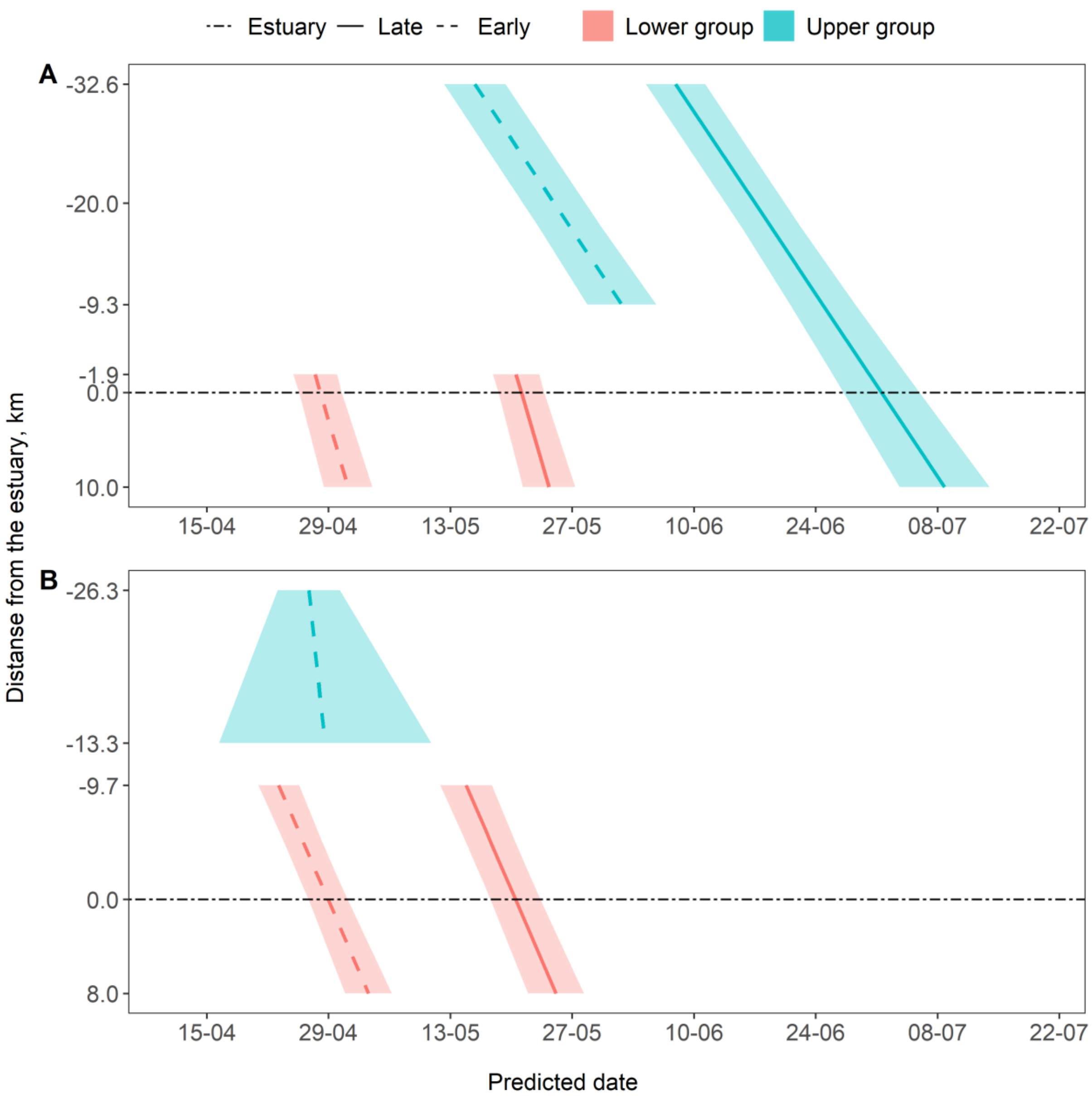

Figure 15: Predicted dates when smolts will be at a certain point along the migration course in 2019. Model parameters in Table 8. Confidence intervals are given in ribbons along the model predictions. The x- and y-axes are swapped to make the figure more intuitive to read, and the y axis represent the distance from the estuary, in km. Negative y-value is in the watercourse, positive is in the fjord. The horizontal line represents the estuary. ***A****. Hornindal watercourse, early and late migration factions from Horndøla (Upper group), and early and late migration factions from Eidselva (Lower group). -32.6 on the y-axis marks station 2, -9.3 marks station 4, -1.9 marks station 5, and 10 marks the fjord station.* ***B****. Stryn watercourse, early and late migration factions from Hjelledøla (Upper group), and early and late migration factions from Stryneelva (Lower group). -26.3 on the y-axis marks station 2, -13.3 marks station 3, -9.7 marks station 4, and 8 marks the fjord station.*

3.2 Lake and diurnal depth migrations

3.2.1 Progression rates

The progression rate through Hornindalsvatnet was estimated to be 0.26 ± 0.18 body lengths per second, and 0.37 body length per second through Strynevatnet (Figure 16). These estimates came from twelve individuals from the Horndøla, and one from Hjelledøla.

*Figure 16: Boxplot of progression rates in the Hornindalsvatnet lake. Black vertical line is the median progression rate, the box represents the 25th and 75th percentiles, the whiskers extend to 1.5 * the length of the box, or if there are no cases within this range, to the minimum and maximum values. Points are progression rates for individuals (n = 12), from the river mouth to the 1st (closest to the river mouth), 2nd or 3rd (furthest from the river mouth) station 3 receiver.*

3.2.2 Depth use

Average depth use (± SD) in Hornindalsvatnet was 8.92 (± 12.98) meters during daytime and 3.60 (± 4.83) meters during night. The same numbers for Strynevatnet was 4.67 (± 2.34, n=11) and 4.11 (± 2.07). Daytime and night depth use in both watercourses is illustrated in Figure 17. These estimates came from five individuals in Hornindalsvatnet and from twelve individuals in Strynevatnet.

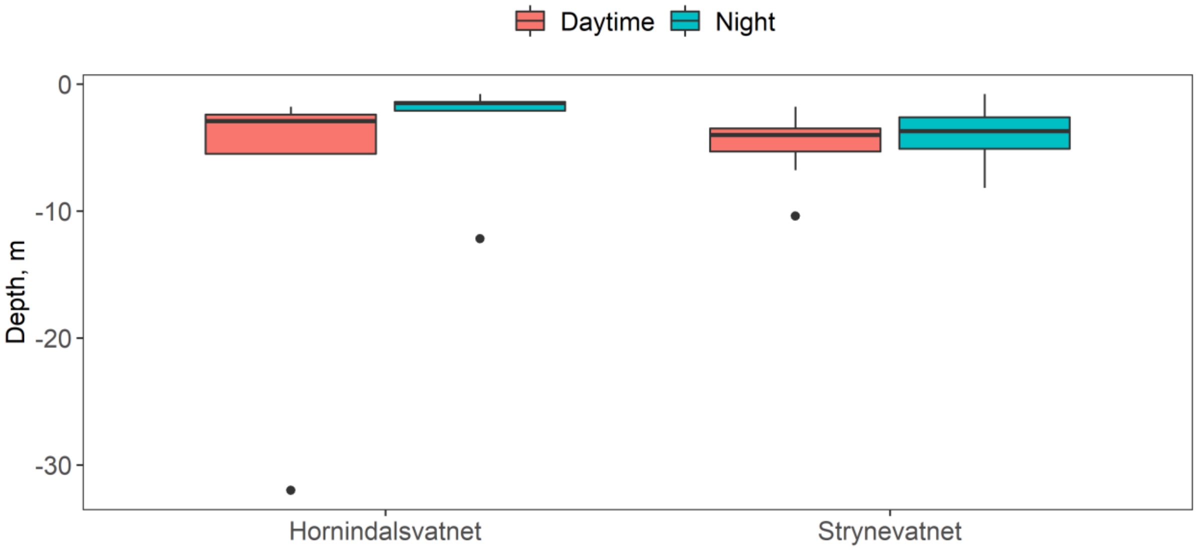

*Figure 17: Boxplot of daytime and night depth use at station 2 and 3 in Hornindalsvatnet and Strynevatnet. Values were made from median depth use during daytime and night provided by five individuals in Hornindalsvatnet. In Strynevatnet, it was provided by eleven individuals during daytime and twelve individuals during night. Black horizontal lines are the median depth use, the boxes represent the 25th and 75th percentiles, the whiskers extend to 1.5 * the height of the box, or if there are no cases within this range, to the minimum and maximum values. Points are outliers.*

Whilst there was no clear difference in depth use during daytime and night, the time spent near station 2 and depth use varied between individuals. Time spent at station 2 in the Hornindal watercourse varied from zero to 46 days, whilst in the Stryn watercourse it varied from zero to 93 days. Certain individuals had multiple migrations down to depths deeper than 50 meters over the course of their stay in the lake. The Horndøla individuals showed fewer signs of stationarity and vertical migrations, and one individual accounted for more than 95% of the observations (Table 9 and Figure 18).

Table 9: Days spent by n tagged individuals near the river mouth (Station 2) in lake Hornindalsvatnet and lake Strynevatnet, with a 10, 50 and 90 percentile ([10%;50%;90%]).

Days spent near river mouth, Hornindalsvatnet		Days spent near river mouth, Strynevatnet	
[10%;50%;90%]	**n**	**[10%;50%;90%]**	**n**
[0.01;0.05;25.55]	15	[1.78;30.67;58.05]	12

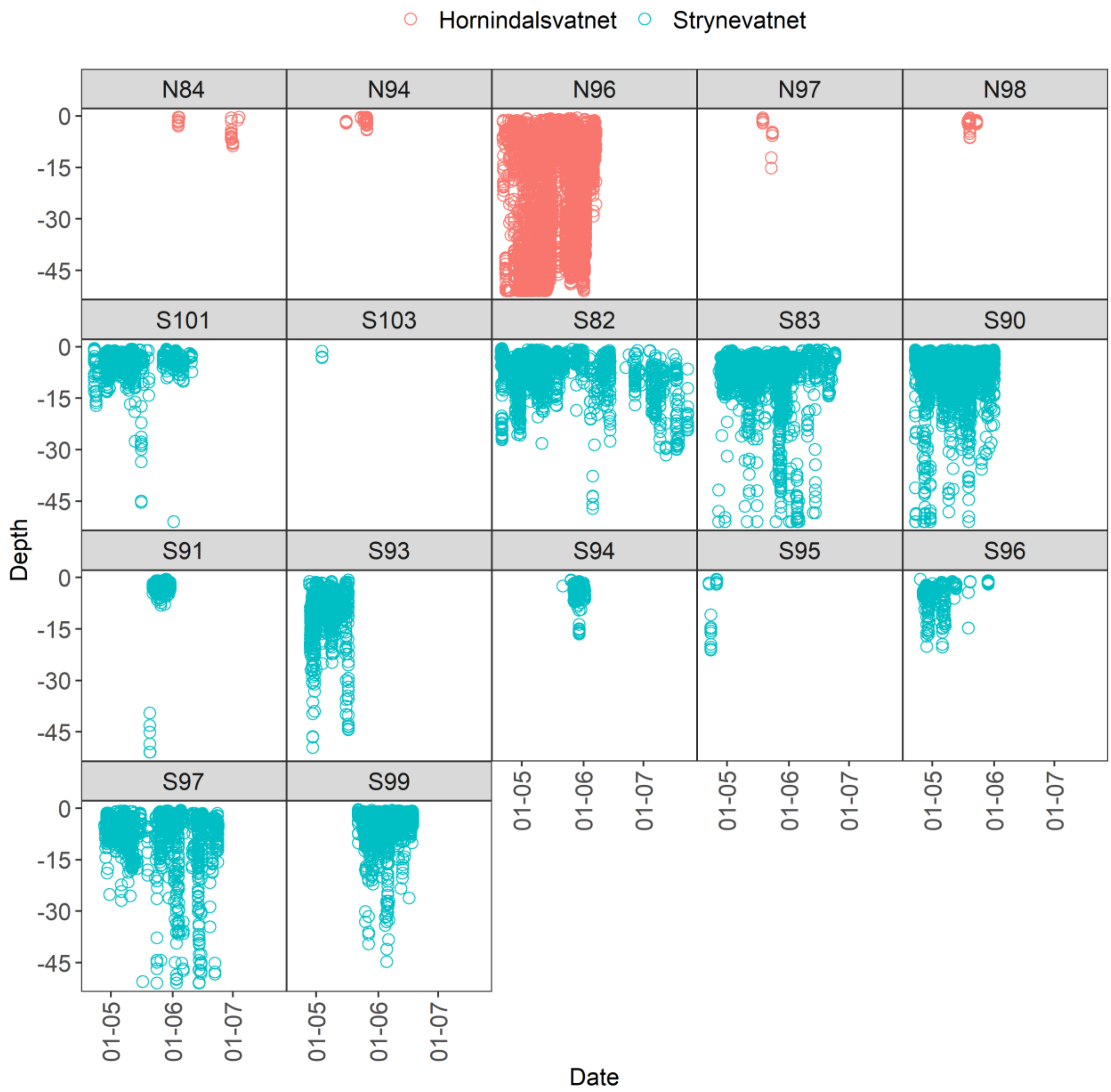

Figure 18: Individual observations of depth use at station 2 and 3 in Hornindalsvatnet and station 2 in Strynevatnet. Tag-ID is given in the panel header, date on the x-axis and depth in meters below surface on the y-axis.

Depth use in the Strynevatnet was most efficiently explained by daytime or night, weight, date (Julian), and the interactions between them (ΔAICc > 2, Table B-3). The model predicts heavier individuals to go shallower in the lake, and that the weight effect increases with increased Julian. For individuals heavier than ~27 grams the model predicts a shallower depth use with an increase in Julian, whilst for individuals lighter than ~27 grams the depth is predicted to increase (deeper) with an increase in Julian. The model also predicts a slightly shallower depth use during night. As Julian increase, the predicted depth is less dependent on daytime and night (Table 10 and Figure 19).

Table 10: Fixed effects parameter estimates for the selected linear mixed effects model fitted to depth use in Strynevatnet. Depth is given with positive numbers, meaning that a negative value means shallower. Intercept is the predicted daytime depth. The model was fitted using smolt ID as a random effect, ID (intercept) is the variance in the random effect, and N_{ID} is the number of unique smolts in the analysis.

Predictors	Estimates	SE	df
Intercept	29.02	5.33	29713
DayNight [Night]	30.08	4.85	29713
Weight	-1.26	0.20	29713
Julian	-0.32	0.02	29713
DayNight [Night] * Weight	-0.98	0.18	29713
DayNight [Night] * Julian	-0.19	0.04	29713
Weight * Julian	0.01	0.00	29713
(DayNight [Night] * Weight) * Julian	0.01	0.00	29713
Random Effects			
ID (intercept)	4.42 ± 2.10		
N_{ID}	12		
Marginal R^2 / Conditional R^2	0.044 / 0.142		
Observations	29723		

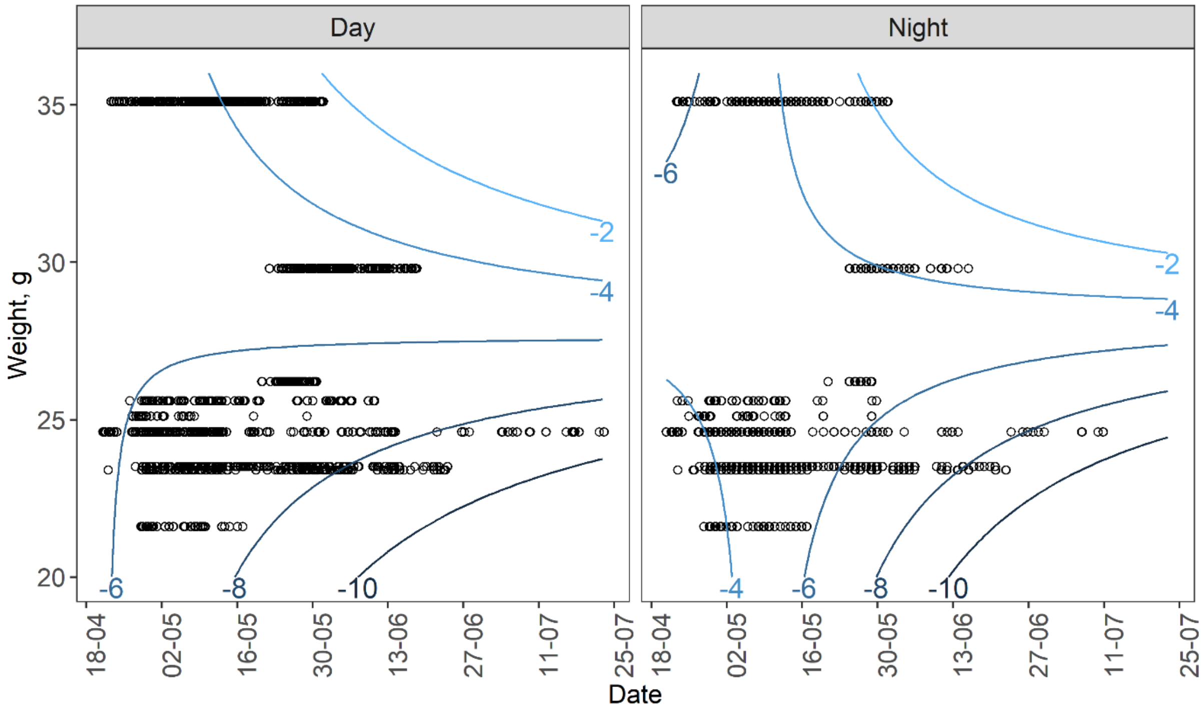

Figure 19: Contour plot of predicted depth use in Strynevatnet as a function of Daytime and night (panel headers), weight (y-axes), and day of year (x-axes). Model parameters in Table 10. The points represent the predictor data the model was based on.

3.3 CJS analyses in Hornindal and Stryn watercourses

The estimated apparent survival rates from the CJS-models shows bottlenecks in both lakes and part of the rivers were release took place (ΔAICc < 2, Table B-4). In Horndøla, Hornindalsvatnet and in the Eidselva estuary, the estimated apparent survival probability increased with increased weight. In Stryneelva, the estimated apparent survival decreased with increased k-factor in zones 4 to 6. (Table 11 and Figure 21).

*Table 11: Parameter estimates for apparent survival rates per kilometer in given zones and observation probability at given stations in given watercourse. UG = upper group, LG = lower group, and 95% CI = 95% confidence interval. Notes: Weight means the parameter was estimated for an average weight of 22.66 grams, Combined means the zones or stations are combined with a common estimate, Fixed means that the parameter is fixed to set value, and k-factor means the parameter was estimated for an average k-factor of 0.82. [1,2] Two separate weight effects were estimated with different slopes (Figure 21 A & B), annotation shows which is used where. * Weight[2] was only applied to zone 6. ** The k-factor effect was not applied to survival rate in zone 7.*

Parameter	Estimate	95% CI	Note
Hornindal watercourse			
UG survival probability through:			
zone 1	0. 92	0. 84–0. 96	Weight[1]
zone 2	0. 97	0. 93–0. 99	Weight[1]
zone 3	0. 86	0. 74–0. 93	Weight[1]
zones 4, 5 and 6	0. 93	0. 81–0. 98	Combined/Weight[2]*
LG survival probability through:			
zone 4 LG and 5	0. 97	0. 95–0. 99	Combined
zone 6	0. 94	0. 91–0. 96	Weight[2]
Observation probability			
UG, stations 2 and 4	1		Fixed/Combined
UG, station 3	0.83	0.38–0.98	
UG and LG, stations 5 and 6	0.87	0.79–0.93	Combined
UG and LG, station 7	1		Fixed
Stryn watercourse			
UG survival probability through:			
zone 1	0. 88	0. 74–0. 95	
zone 2 and 3	0. 78	0. 64–0. 88	Combined
zones 4, 5, 6, 7, 8 and 9	0		Fixed and combined
LG survival probability through:			
Zone 4	0. 84	0. 78–0. 88	K-factor
Zones 5, 6 and 7	0. 95	0. 90–0. 97	Combined and k-factor**
Zones 8 and 9	0. 98	0. 95–0. 99	Combined
Observation probability:			
UG, stations 2, 3 and 4, and LG station 4	1		Fixed and combined
UG and LG, station 5 and 6	0.99	0.91–1.00	Combined
UG and LG, station 7	0.85	0.70–0.94	
UG and LG, stations 8, 9 and 10	0.98	0.89–1.00	Combined

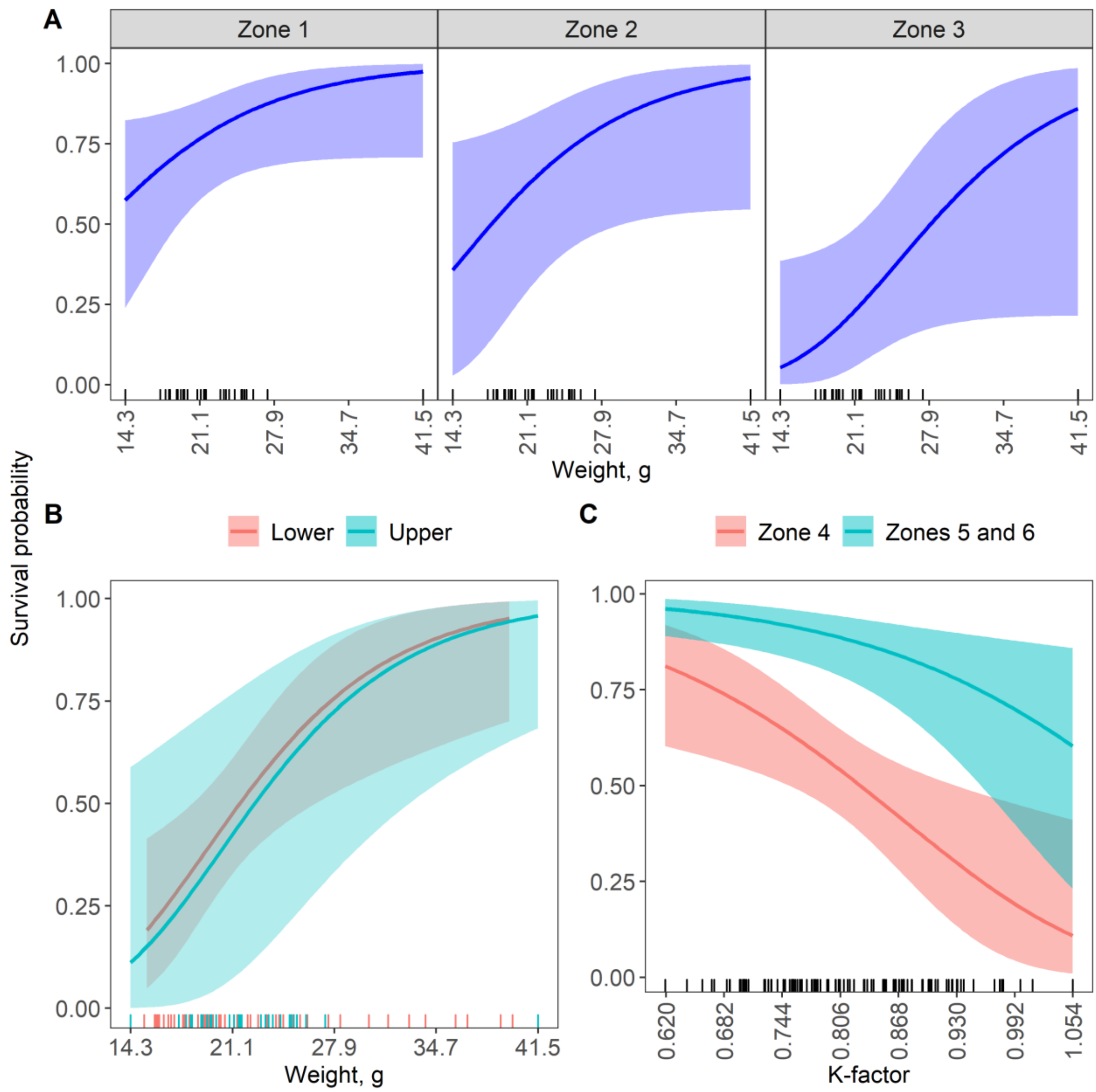

*Figure 20: **A**. CJS-estimated survival probabilities during migration in Hornindal zones one to three as function of weight for the tagged smolts. The probability is given for the whole distance of the zones and the 95% confidence interval is shown as blue ribbons. **B**. CJS-estimated survival probabilities during migration in Hornindal zone six for the upper and lower group as a function of weight for the tagged smolts. The probability is given for the whole zone and the 95% confidence interval is shown as ribbons. **C**. CJS-estimated survival probabilities during migration in Stryn watercourse zones four, and five and six, as a function of k-factor for the tagged smolts. The probability is given for the whole distance of zone four and the combined distance of zone five and six, the 95% confidence interval is shown as blue and red ribbons. The rug along the x-axis represents the weights and k-factors of the tagged presmolts from respective rivers and watercourses.*

3.4 Release-to-fjord survival

Except for the Horndøla tagged smolts, the early factions had the higher apparent survival of 44% vs. 33% for the late group. And the depth-tagged smolts had a higher apparent survival of 53% vs 29% for the ID-tagged smolts. The tagged smolts from Eidselva and Stryneelva had a higher apparent survival than the tagged smolts from Horndøla and Hjelledøla, respectively (Table 12).

Table 12: Percentage of individual tagged smolts from early and late migrating factions observed in the fjord. As well as the percentage of individuals tagged with ID- and depth tags observed in the fjord. The percentages are given for each river and overall.

	Horndøla	Hjelledøla	Eidselva	Stryneelva	Overall
Early	0%	0%	62.07%	61.29%	44.05%
Late	15.38%	0%	40%	50%	33.33%
ID-tag (ID-LP7)	5.26%	0%	36.67%	42.86%	28.92%
Depth-tag (D-LP7)	20.00%	0%	70.83%	76.19%	53.12%

4 Discussion

This study found that the Eidselva and Stryneelva tagged smolts arrived in the fjord in two peaks. The average fjord entry dates for the Eidselva and Stryneelva smolts were respectively the 8th of May (±13 days) and the 6th of May (±12 days). Two migration peaks were also seen in the Horndøla and Hjelledøla tagged smolts, however, only two individuals from Horndøla were observed in the fjord, both from the second peak, respectively the 5th and 15th of July. For all four smolt groups, the migration probability was most supported by unique combinations of the variables at hand. Common for three of the models was an increased migration probability with DoY and $\Delta Q/Q$. The only exception was in the selected model for the Horndøla smolt migration where the migration probability increased with Q alone. Q was also a variable in the selected model for the Eidselva smolt migration. The environmental factors and DoY did however have low explanatory values on the smolt migration probability in the two watercourses, respectively 9.9%, 2.9%, 3.7% and 2.9% for the Eidselva, Stryneelva, Horndøla and Hjelledøla smolts.

As for how the lakes affected the migration, they were associated with low apparent survival probabilities (95% CI) of 19.21% (3.13–46.14%) through Hornindalsvatnet and 1.68% (0.00–11.95%) through Strynevatnet, and slow progression rates of 0.26 ± 0.18 body lengths per second trough Hornindalsvatnet, and 0.37 body lengths per second through Strynevatnet. Long periods of residencies of more than 25 days were also observed in both lakes, and depth use correlating to night or daytime, weight, and date was found in Strynevatnet. Depth use was predicted to be deeper during daytime and to decrease with weight. Over time, lighter individuals were predicted to go deeper, whilst heavier individuals were predicted to go shallower.

Survival bottlenecks, compared to the typical downriver migration apparent survival rates found by Thorstad et al. (2012) of 0.3-7% per kilometer, were found in the Horndøla, Hjelledøla, zones 4 and 5 in Eidselva, and zone 4 in Stryneelva. In zones 1 to 3, and the estuary in the Hornindal watercourse, the apparent survival probability increased with weight, whilst in zone 4 in Stryneelva, an increased k-factor correlated to a lower survival probability. This added up to that about 32% of the Hornindal watercourse tagged smolts, and about 27% of the Stryn watercourse tagged smolts were observed in the fjord.

4.1 Migration timing

If smolt migration is timed to optimal conditions in the sea (Hvidsten et al., 1998), a synchronous arrival in the ocean from the four rivers should be expected, and I hypothesized that the Horndøla and Hjelledøla tagged smolts would migrate earlier than the Eidselva and Stryneelva tagged smolts respectively, to reach the fjord at the same time. From the witnessed and predicted fjord entry dates (Figure 14 and Figure 15), we see that the fjord entry dates for the Eidselva and Stryneelva smolts were quite similar, with the first peak entering the fjord around the 28th of April and the second peak around the 21st of May. However, the fjord entry dates for the Horndøla smolts are much later, and the Hjelledøla tagged smolts never reached the fjord.

The Horndøla smolts were observed for the first time in the Horndøla river mouth from the 21st of April to the 20th of June. The earliest observed lake entry date was one day earlier than the first observed marine entry date for the Eidselva smolt, but the second earliest entry was 25 days later, the 16th of May. Two individuals from the Horndøla late faction were observed entering the fjord the 5th of July and the 15th of July. These entry dates are well outside the range observed from the Eidselva smolts, and the predicted marine entry date for the Horndøla late faction is more than nine weeks later than the predicted entry date for the Eidselva early faction, and six weeks later than the Eidselva late faction.

The Hjelledøla smolts were observed for the first time in the Hjelledøla river mouth from the 15th of April to the 24th of May, which is on average slightly earlier than what the first observed marine entry was for the Stryneelva smolts. This suggesting a synchronized fjord entrance with the Stryneelva smolts. However, none of the tagged Hjelledøla smolts were observed downstream station 3, and a predication of arrival time in the estuary was not possible. But taking into consideration the slow progression rates associated with lake migration (Figure 16) (Haugen et al., 2017) and the longer migration route, it all points to that the mean date for when the Hjelledøla smolts enter the fjord is later than the mean fjord entry date for the Stryneelva smolts.

4.2 Migration cues

I hypothesized that the tagged presmolts would start their migration with increased water discharge and water temperature as such environmental factors are found to correlate to migration timing (Harvey et al., 2020; Hvidsten et al., 1995; Whalen et al., 1999). Whilst the migration probability in this study was correlated to environmental factors, water temperature was not preferred in any of the selected candidate models. Rather, day of year was found to be preferred where temperature and date had an estimated correlation too high to be used in the same candidate model (Table A-1 and Figure B-1). Water discharge on its own was only present in the selected candidate model for Hjelledøla. In the selected candidate model for

Eidselva, water discharge was in a combination with the relative change in water discharge from the previous day and day of year, which otherwise seemed to be the most preferred factors; however, the migration probability was poorly explained by environmental factors, and day of year in this study.

In the most explanatory model of the four selected candidate models, only 9.9% of the variation in migration probability was explained by the input factors. Considering how migration timing has been found to be significantly influenced by environmental factors (Harvey et al., 2020) and compared to what has been found in the Eidselva and Stryneelva in previous years, these were low numbers. In 2017, 97% of the variation in migration probability for salmon smolt in the Stryneelva was accounted for by the relative daily change in water discharge alone (Urke et al., 2018). Whilst in 2018, 67% of the variation in Eidselva and Stryneelva was explained by water discharge, change in water discharge, water temperature, and the interactions between them (Haugen et al., 2019). This goes to show that whilst water discharge and water temperature can give good explanatory models some years, the same migration model will not necessarily be as explanatory, or be given the same support other years, as the influence of a parameter is found to vary based on year and the interaction between the factors (Harvey et al., 2020).

This study did however provide novel information about smolt migration from the Horndøla and Hjelledøla. In the two rivers, predicted water discharge was the only environmental factor available in addition to day of year to predict the migration probability. Whilst the Horndøla migration probability was found to be best explained by the relative daily change in discharge and day of year, the Hjelledøla migration probability was best explained by the water discharge alone. In higher lying catchments characterized by snow and glacier fields, like the Horndøla and Hjelledøla catchments, air temperature can affect the water discharge in associated streams and rivers by increased runoff with increased snow melting. Whilst increased snow melting leads to higher runoff and water discharge, the runoff is cold. Therefore, the water temperature increase will have a low slope as long as there is significant amounts of snow and ice in the catchment (Kvambekk & Melvold, 2010), and water temperature might be correlated to day of year in these two rivers, as it was in the Eidselva and Stryneelva (Table A-1). In Horndøla, the majority of the tagged smolts migrated on the second or third water discharge peak (Figure 11), suggesting that water discharge alone is not enough, and that water temperature might be a considerable cue for migration in this river. In the glacier fed Hjelledøla however, the majority of the tagged smolts were observed to migrate on the first discharge peak (Figure 11), suggesting that water temperature is not a considerable factor for the Hjelledøla smolts. Whalen et al. (1999) compared migration timing in three tributaries and found a tendency for Atlantic salmon smolts to migrate earlier in the warmest tributary compared to the coolest one, suggesting that temperature might explain why migration started almost a month earlier in the Hjelledøla compared to Horndøla.

Genetic differences have been found between populations in different rivers, and even between tributaries (King et al., 2005; Wennevik et al., 2019), and genetics have been linked to behavior and migration timing (Aarestrup et al., 1999). It is therefore imaginable that the 20 km^2 of Horndøla's catchment, which water is diverted into a neighboring catchment, has altered the conditions in Horndøla to such an extent that are causing a discrepancy in the genetic adaptations made in the Horndøla salmon population.

4.3 Downstream survival

I hypothesized lower survival rates in the Hornindalsvatnet and Strynevatnet, as well as in the Eidselva and Stryneelva estuaries compared to the rest of the watercourse. The estimated apparent survival rates in the selected CJS-models support this hypothesis when it comes to lake survival, whilst it is more nuanced in the estuaries.

In zone 2 in Hornindalsvatnet the apparent survival rate (95% CI) was estimated to be 97.4% (93.4%–99.0%) per km, whilst in zone 3 it was estimated to be 85.7% (74.2%–92.6%) per km. In zone 2 and 3 in Strynevatnet, the apparent survival rate was estimated to be 78.1% (63.6%–88.0%) per km. The Hornindal zone 3 and Stryn zone 2 and 3 survival rates are significantly lower than what was estimated for the Eidselva and Stryneelva tagged smolts, respectively, in the lower parts of the watercourses.

For the Horndøla smolts, the estimated apparent survival rate in the estuary was combined with the survival rates in zones 4 and 5, and estimated to be 93.3% (81.2%–97.9%) per km. This survival rate is on the lower end of the typical survival rates of 93.0%–99.7% per km (Thorstad et al., 2012) during downriver migration, which suggests that the low survival rate might come from a low estuarine survival rate, which has been found to typically be between 64.0% and 99.4% per km (Thorstad et al., 2012). However, an apparent estuarine survival rate of ~95% (~89%–97%) per km has been found in Eidselva previously (Haugen et al., 2019), and the estimated estuarine apparent survival for the Eidselva smolts in this study was 94.2% (91.0%–96.3%), suggesting that the survival through the Eidselva estuary is not any lower than the survival rates found through the rest of the watercourse.

In the Stryn estuary, the apparent survival rate was combined with zone 8 and estimated to be 97.8% (95.2%–99.0%) per km, which was the highest estimated apparent survival rate in the whole watercourse. This estimate is similar to the estimated estuarine apparent survival of ~98.1% (~96.5%–%99.1%) per km in Stryneelva in 2017 (Urke et al., 2018), and higher than the estuarine apparent survival rate of ~91.0% (~85.0%–%94.0%) per km estimated in 2018 (Haugen et al., 2019).

The selected CJS-candidate models supported a k-factor dependent survival in zones 4 to 6, and a weight dependent apparent survival through Hornindalsvatnet and the Estuary (Figure 21). The k-factor effect, where a higher k-factor is linked to a lower survival seen in Stryneelva might be linked to the low recapture numbers (62%) for the tagged Stryneelva smolts after release, which might again be related to the number of individuals that smoltified, or rather did not. When a juvenile salmon undergoes smoltification, large physiological and hormonal changes happen with the fish, which in return lead to morphological changes: The fish takes on a slimmer and longer body, or in other words, a lower condition factor (Folmar & Dickhoff, 1980; Gorbman et al., 1982). Therefore, I suspect that the effects illustrated in Figure 21 C and the low recapture numbers in the lower group in the Stryneelva is partially due to a tag effect and a high number of tagged individuals that did not smoltify this year.

Individuals with a high k-factor are fatter fish, a theory could therefore be that a fat fish has less room for a tag in its coelom, and as such be more at risk of the effects from having a tag, leading to an increased mortality with increased k-factor. Tag expulsion due to pressure necrosis of the body wall (Lucas, 1989) could also be an explanatory factor, as pressure on the body wall from the tag might be greater in fatter individuals.

Size dependent survival is also expected to be present taking tag effects into consideration. The smaller an individual is, the more the relative weight of the tag is. This must be believed to influence swimming performance, and therefore predator avoidance capabilities. The survival difference between smolts tagged with ID-tags and depth-tags (Table 12), points to that the tag or the tagging procedure affects the smolts. Bigger presmolts were selected for the depth-tags to compensate for the larger tags. As a result, the ID-tagged smolts had a higher average (± SD) relative tag weight compared to the depth-tagged smolts, respectively 10.9% (± 1.7%) and 8% (± 1.5%) of their bodyweight (air weight). Because the depth-tagged smolt had a higher (non-CJS-estimated) apparent survival and a lower average relative tag weight than the ID-tagged smolts, it is reasonable to believe that the survival and migration behavior for the depth tagged smolt is closest to the non-tagged smolts.

Previous studies on surgical implantations in salmonids have found the preferred tag–bodyweight ratios to be within 2.2% and 5.6% for a minimal effect on swimming performance and predator avoidance ability (Adams et al., 1998). However, transmitter weight ratios between 6% and 12% have been found to not alter swimming performance (Brown et al., 1999) and is also a more realistic and feasible weight ratio in acoustic telemetry studies on salmonid smolts (Welch et al., 2007). It is still reasonable to believe that the survival from the depth–tagged group is also lower than for the non–tagged smolts, and that the survival estimates from this study makes a minimum–estimate. And due to the smolts stationarity observed in both lakes (discussed in sub-chapter 4.4 Lake use), the apparent survival estimates through the lakes from the CJS-models are likely under-estimated, as the resident smolts are counted as deceased in the CJS-analyses if they are not observed at a station further down in the system.

A difference in the percentage of smolts observed in the fjord was seen between early and late migrating factions. From the Horndøla tagged smolts, only individuals from the late migrating faction were observed in the fjord, whilst from Eidselva and Stryneelva the early factions had the highest apparent survival probability. Due to the same tagging procedures for all groups and rivers, the different apparent survival is probably due to that the tagged smolts migrated under different environmental circumstances, and maybe mostly due to different predation circumstances. The observations from trout tagged in 2018 shows that potential predators were present in both systems during the migration period in 2019, overlapping both in time and space with the migrating smolts, particularly in the estuaries (Figure A-6).

4.4 Spatiotemporal lake use

I hypothesized that the tagged smolts would display a diurnal vertical migration pattern where the tagged smolts would be closer to the surface during night compared to daytime. In Hornindalsvatnet, an effect of night and daytime was seen in portrayed depth use (Figure 17). Whilst it was not necessarily clear from the portrayed depth use, a night and daytime effect was supported by the selected candidate model for estimated depth use in Strynevatnet (Table 10). However, the depth use in Strynevatnet was also correlated to smolt weight and date, suggesting that predation is a factor that effects depth use in lakes.

Smolt size was a repeating factor in this study. The selected CJS-candidate model for the Hornindal watercourse showed signs of a weight dependent apparent survival through Hornindalsvatnet (Figure 21 A), and the selected candidate model for estimated depth use in Strynevatnet estimated weight to be a significant factor for depth use in the Strynevatnet

(Table 10). The lakes are habitats where predation is believed to play a big role on survival for migrating smolts (e.g., Kennedy et al. (2018) and Haugen et al. (2017)). And if predation from piscivore fish is a real threat for the migrating smolts in these areas, an increased survival probability with increased size should be expected, as predator avoidance ability might increase with size (Lundvall et al., 1999). Though the size of some of the potential predators in the lakes (Figure 7) suggest that not even the biggest of the smolts are too big of a prey (Keeley & Grant, 2001), it is an expected response to see if dives are a predation avoidance response. The tagged smolts were also estimated to go deeper as the year progressed, which is strongly correlated with increased day length and visibility. These are also predator avoidance responses expected to see as predation risk is found to decrease with decreased visibility (Barrett et al., 1992), and the smolts therefore seek these darker habitats.

Other examples of what is believed to be typical predation avoidance behaviors for migrating smolts are migration during high water levels, to synchronize their migration and to enter lakes after nightfall (Haugen et al., 2017; Thorstad et al., 2011). The mentioned behaviors were seen in both the Horndøla and Hjelledøla smolts. In both rivers, peaks in migration were seen in relation to increased water discharge (Figure 11), and the highest probabilities for entering the lakes were found to be in the hours around sunset and before sunrise (Figure 13). What was also seen in the smolts tagged with depth-tags were deep dives down to more than 50 meters just after entering the lake (Figure A-2). The same behavior, with deep dives just after lake entry, was also found in smolts tagged with depth tags in the Vosso watercourse (Haugen et al., 2017).

For the migrating smolts, the slow progression rates found in the Hornindalsvatnet and Strynevatnet are comparable to what has been found before. Haugen et al. (2017) found progression rates of less than 0.6 body lengths per second for first time lake migrating smolts, and multiple studies have found lakes to delay migration for migrating smolts (e.g., Cooke et al. (2013), Hansen et al. (1984), and Honkanen et al. (2018)).

A big portion of the depth–tagged smolts from both the Horndøla and Hjelledøla had periods of residencies near the river mouths. The river mouth residency tendency was more prominent in the Strynevatnet, where the 90% quantile for residency was 58 days compared to 26 days in the Hornindalsvatnet (Table 9). Some of the ID-tagged smolts were observed in the river mouth throughout the whole study–period, but separating live smolt from lost tags is impossible without an additional dimension (e.g., depth). The residency data is therefore based on a low number of individuals, where the ID-tagged smolts that were used in the calculation are smolts observed downstream in the systems, and might not represent the rest of the population.

What happened to these smolts after their last observation is hard to say. Six of the depth tags were observed laying on the bottom (Figure A-3) and four of these were showing signs of changed behavior a few days before the tag was stationary at the bottom of the lake, which might imply that the smolt was eaten before the tag was defecated (Figure A-4). That is not to say that other tagged smolts were not eaten or died outside of the observation range of the receivers, or if they migrated to other parts of the lake either as their destination or to migrate to the ocean at a later point.

Autumn migrating salmon smolts have been observed in multiple populations (Cunjak et al., 1989; Pinder et al., 2007; Youngson et al., 1994), but is something we know little about and could be a more widespread strategy than previously believed (Thorstad et al., 2011; Youngson et al., 1994), and might an explanation for the smolt residencies seen in the lakes.

The smolts that were observed making it through the Hornindalsvatnet were mainly late migrators entering the lake during night, with short residence (< 72 minutes) at the river mouth. However, the two individuals that were observed making it into the fjord sticks out: Individual N74 spent the most time through the lake, almost 13 days, and individual N84 spent 27 days near the river mouth.

The one individual (S95) from Hjelledøla that made it to station 3 in Strynevatnet returned to the river mouth shortly after. It initially spent less than one day at station 2 and was detected at station 3 three days later, where it spent six hours. Six days later it was observed at station 2 again, where it was for the remainder of the study period, explicitly at a sub 48 meters depth (Figure A-5).

4.5 Methodology and data quality

A low number of the tagged individuals from Horndøla and Hjelledøla were observed in or downstream of the lakes, and a lot of insecurity was tied to the ID-tagged smolts of whether they were dead or alive near the river mouths. Therefore, a lot of the analyses done on behavioral and spatiotemporal predictions were done on low Ns.

The Norwegian Animal Research Authority put constraints on the minimum required length (12 cm, TL) the pre-smolts must be to be allowed to be tagged. This gives results that we should be careful to extrapolate to smolts smaller than 12cm, which is just under the average smolt lengths of 12.7 ± 0.2 cm found in the Stryneelva (Jensen & Johnsen, 1986).

Caution should also be made when generalizing results from studies done on an individual level, up to a population level. Same goes for generalizing the results from a one-year study, when the conditions experienced in 2019 could be atypical of the more general conditions experienced in the Stryn and Hornindal watercourses. The 100% tagged smolt survival rate found by Urke et al. (2018) in the calm part of the Stryneelva (zones 4 to 7 in this study) in 2017, compared to the lower apparent survival rates found in this study demonstrates the issue with generalizing results from a one year study.

For multiple reasons there is also an amount of insecurities associated to the tagging of presmolts, and it must be expected that not all individuals are observed after release. When capturing and choosing what individuals to tag, signs pointing to smoltification, like size, form, and coloration are important. There is however a possibility that individuals not smoltifying this year were tagged, which might therefore not migrate. The capture and tagging procedure itself could also have a negative effect on the recapture results, or the presmolts might have expelled the tag via the body wall (Lucas, 1989). The estimated survival probabilities for the tagged smolts are therefore probably lower than what it is for non–tagged smolts.

4.5.1 Capture of smolts using electrofishing

There is no doubt that being incapacitated by an electric current can yield permanent effects, like mortality, but the use of electrofishing as a capture method has shown to be effective and safe when done properly to capture salmon smolts in rivers and streams, e.g.: Urke et al. (2013), Haugen et al. (2016), Haugen et al. (2017), Urke et al. (2018) and Haugen et al. (2019). The size range of the tagged smolts from close to the minimum 12 cm required length and up (Table C-1), and the high observation numbers of the tagged smolts after release during this study, suggest that the method used was valid.

4.5.2 Surgical procedures

The method and materials used in this study has been used by the same team as in, among other studies, Urke et al. (2018) and Haugen et al. (2019), following the same surgery protocol described in (Urke et al., 2013) which has been followed in a number of other studies (e.g., Kristensen et al. (2011) and Urke et al. (2011)). In Urke et al. (2018) and Haugen et al. (2019) the post-release observations of up to 90% of the tagged smolts suggests that the surgical procedures used are valid, and there is no reason to believe that the survival rates or behaviors seen in this study are more influenced by the tagging than in other telemetry studies.

4.5.3 Acoustic telemetry

The strength of acoustic telemetry, and studies based on this methodology, is bound to the large amount of data per individual. Whilst there could lay an inherent weakness in the low number of individuals and the challenges associated with the statistical methods of handling such large amount of information (Cooke et al., 2013; Haugen et al., 2019), the method is reliable, cost effective, and therefore suitable to use over longer time periods. Acoustic telemetry as a method is also in a large degree independent of water levels and takes place 24 hours of the day, giving actual and reliable data on individuals. (Cooke et al., 2013; McMichael et al., 2010; Urke et al., 2018). Due to a river's natural containment, acoustic telemetry arrays in rivers have proven to give high returns for investment compared to in open water bodies related to the range of acoustic receivers (Cooke et al., 2013), which is recognized in the > 85% CJS–estimated in–river observation probabilities in this study.

4.5.4 Improvement suggestions

To improve the data quality in future studies a higher number of presmolts should be tagged and the receiver network should be expanded, especially around the river mouths and throughout the lakes. The addition of tags that can detect whether it has been predated or not would be very beneficial in identifying if a tagged individual has been predated.

We don't know what the tagged smolts did after this study ended, and because the battery life of the tags is coming to an end, we will not find out. A suggestion is therefore to use passive integrated transponder (PIT) tags and PIT tag reader antennas. PIT tags are relatively inexpensive which allows tagging of more individuals, and have unlimited life expectancy (Castro-Santos et al., 1996), which allow tracking of the Horndøla and Hjelledøla smolts over multiple seasons. The use of PIT tags and an antenna network can therefore be beneficial to increase the understanding of the Horndøla and Hjelledøla salmon populations.

4.6 Management implications

Nilsen et al. (2017) have made it clear that the timing of when smolts migrates from the river is an essential input to define whether a river population is defined to have a high or low salmon lice induced mortality, and that further research is needed in key watercourses. Whilst this study was done on data from one year, I argue that it did provide important results that should be taken into consideration in future management of the two study systems.

The smolts from all four rivers were found to migrate in multiple peaks reaching the fjord at different points in time, and that smolts from the Horndøla and the Hjelledøla are likely to reach the fjord later than the Eidselva and the Stryneelva smolts. Implications from these results are that the use of a mean watercourse entry date as a salmon lice induced mortality input, will take little consideration to the earlier and later migration groups.

5 Conclusion

The Hjelledøla tagged smolts started their migration in accordance with the Stryneelva smolts, but were never observed entering the fjord. The Horndøla tagged smolts started their migration as the late migrating faction from Eidselva entered the fjord, resulting in a nine–week difference between the first and last observed tagged smolt from the Hornindal watercourse. Whether this is natural behavior observed from the Horndøla smolts, or if it is a result of anthropogenic changes in the watershed is hard to say. My hypothesis stating that the smolts from the upper rivers would start their migration earlier than the smolt from the lower rivers, was supported in the Stryn watercourse, but proven wrong in the Hornindal watercourse.

At first glance, the migration in the four rivers looked to be timed well with increase in water discharge and temperature, but migration timing was found to be poorly explained by environmental factors in 2019. My second hypothesis was supported by the fact that functions of water discharge was present in all the selected candidate models predicting migration probability, however it was proven wrong by the fact that temperature was not present in any of the said models.

Significantly lower apparent survival rates in both lakes compared to the lower rivers were estimated in both watercourses. As for the survival rates in the estuaries, the estimated apparent survival rate in the Stryn estuary was the highest in the whole water course, and the estimated apparent survival rate in the Eid estuary was inseparable from the rest of Eidselva. My hypothesis stating that there would be lower survival rates in the lakes was supported, but my statement saying that there would also be lower survival rates in the estuaries was proven wrong.

The tagged smolt from Horndøla and Hjelledøla did show diurnal vertical migrations, where the study-individuals were closer to the surface during night compared to daytime. And in Strynevatnet, smolt weight and date correlated with depth use in the tagged smolts. My hypothesis stating that there would be diurnal vertical migrations in the two lakes was supported

A lot of interesting behaviors were seen in the two lakes and further research is needed to say anything for sure as a lot of the analyses were done on low Ns and therefore associated with high insecurities. This was also a one-year study, and the results should therefore be interpreted as explanatory for the 2019 migration. However, as the number of studies done on lake migration in natural lakes are few, the results from this study could be of interest and of value to both biologists and natural resource managers.

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Appendix A – Extra tables and figures

Table A-1: Table showing correlation between parameters used for the migration probability models for given river. DoY = Day of year, Q = water discharge (m^3/s), T = water temperature (°C), ΔQ= change in water discharge from the previous day (t-1) ($\Delta Q_t = Q_t - Q_{t-1}$), ΔT = change in water temperature from the previous day (t-1) ($\Delta T_t = T_t - T_{t-1}$), reldeltaQ = ΔQ/Q.

Eidselva	DoY	Q	T	ΔQ	ΔT	reldeltaQ
DoY	1					
Q	0.21	1				
T	0.48	0.09	1			
ΔQ	-0	0.1	0.5	1		
ΔT	-0	-0.25	0.22	0.07	1	
reldeltaQ	-0	0.1	0.49	0.98	0.08	1
Stryneelva	DoY	Q	T	ΔQ	ΔT	reldeltaQ
DoY	1					
Q	0.65	1				
T	0.5	0.55	1			
ΔQ	0.13	0.26	0.61	1		
ΔT	-0	-0.36	0.14	0.28	1	
reldeltaQ	0	0.11	0.67	0.88	0.3	1
Horndøla	DoY	Q	ΔQ	reldeltaQ		
DoY	1					
Q	0.31	1				
ΔQ	-0.1	0.23	1			
reldeltaQ	-0.2	0.14	0.89	1		
Hjelledøla	DoY	Q	ΔQ	reldeltaQ		
DoY	1					
Q	0.57	1				
ΔQ	-0.2	0.11	1			
reldeltaQ	-0.3	-0.02	0.88	1		

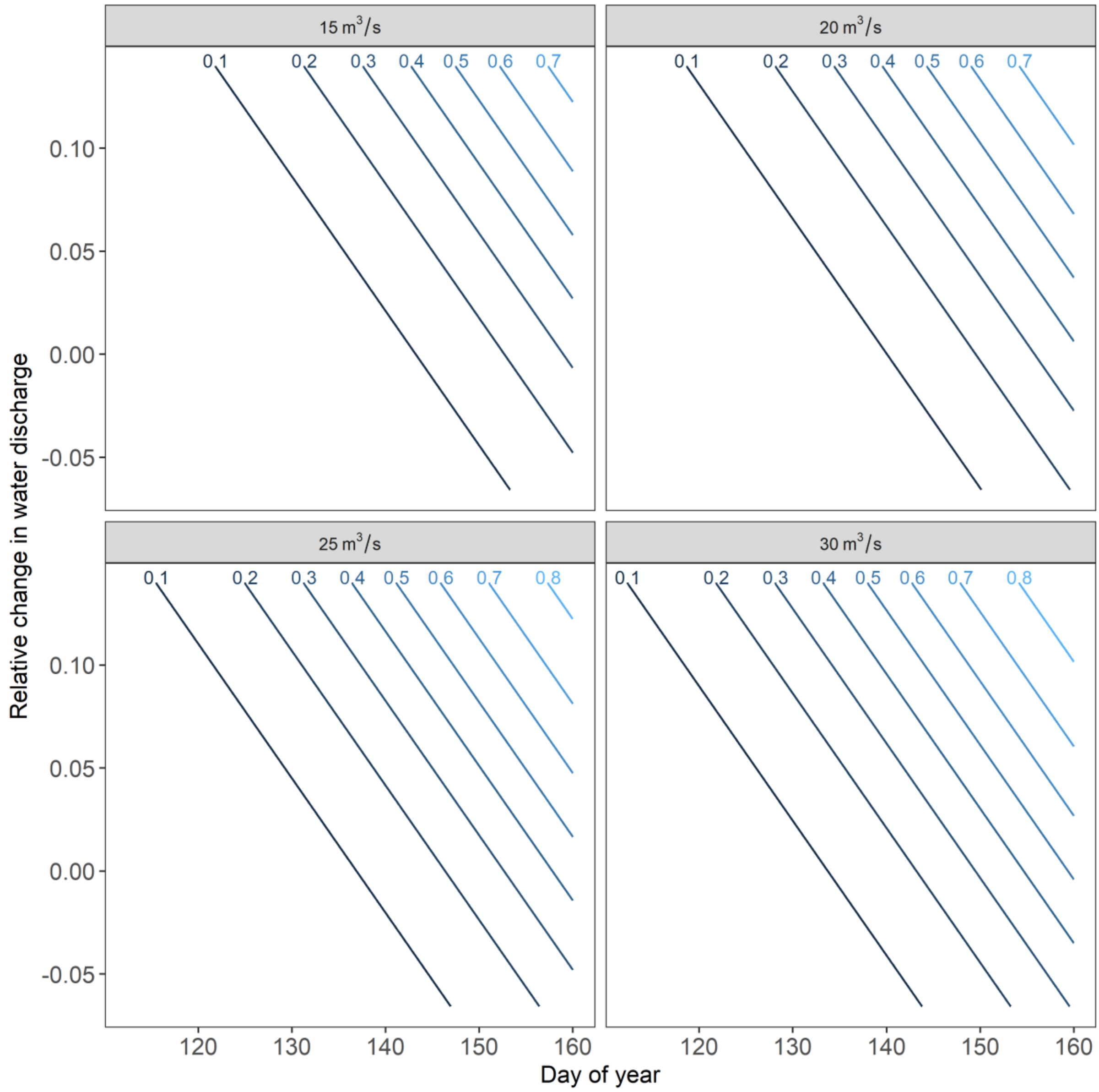

Figure A-1: Contour plot of the model predictions for daily migration probability in Eidselva as a function of Day of year, relative change in water discharge from the previous day, and water discharge (Table 6 A). This figure contains countour plots of the mentioned migration probability under four different levels of water discharge: 15 m^3/s, 20 m^3/s, 25 m^3/s, 30 m^3/s, as stated in plot header.

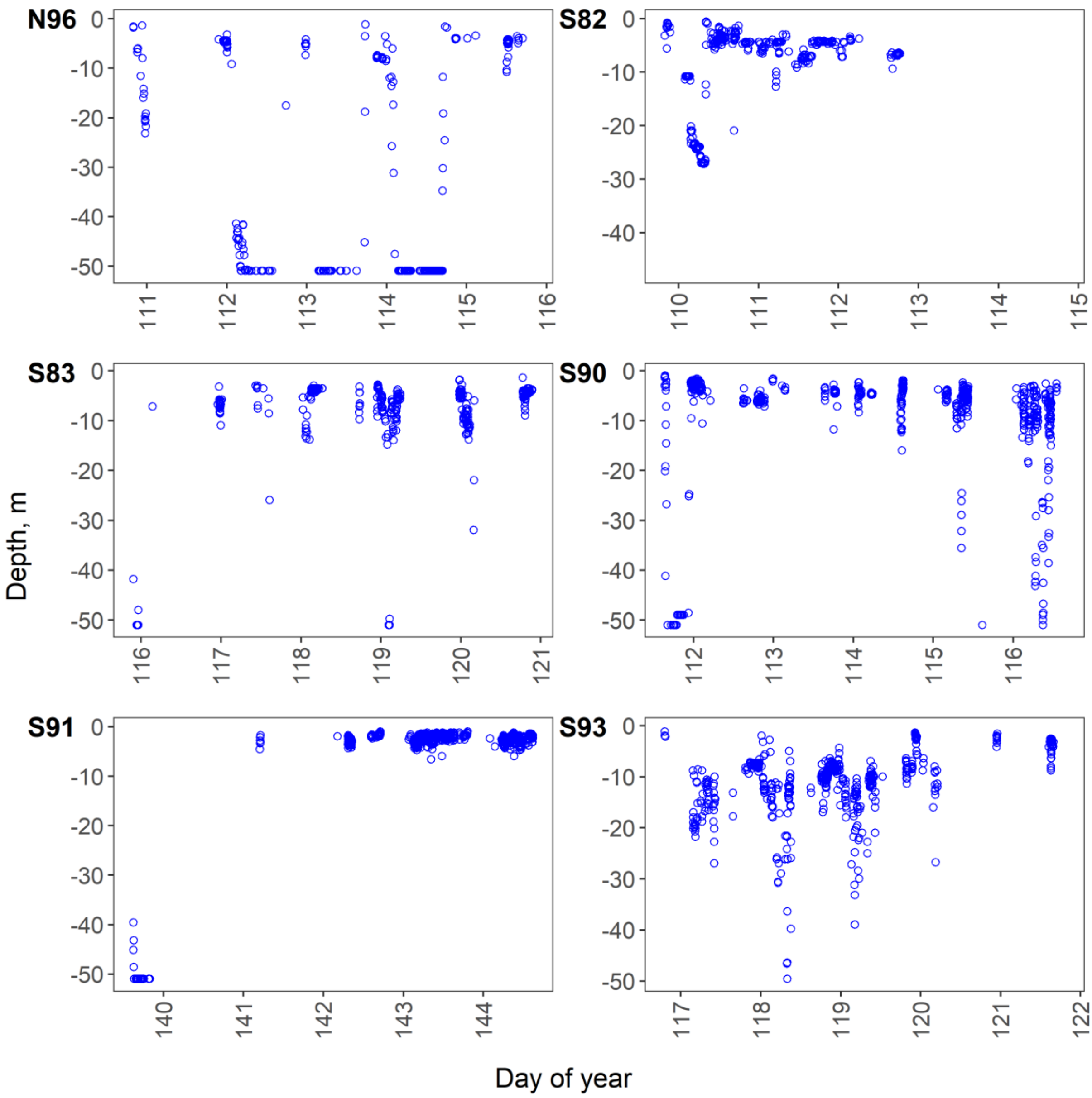

Figure A-2: Depth use for six tagged smolts the five first days after entering the lakes. N96 is from Hornindalsvatnet, the rest are from Strynevatnet. X-axis shows day of year, 110 = April 19, 120 = April 29, 140 = May 19. Y-axis shows depth in meters below surface.

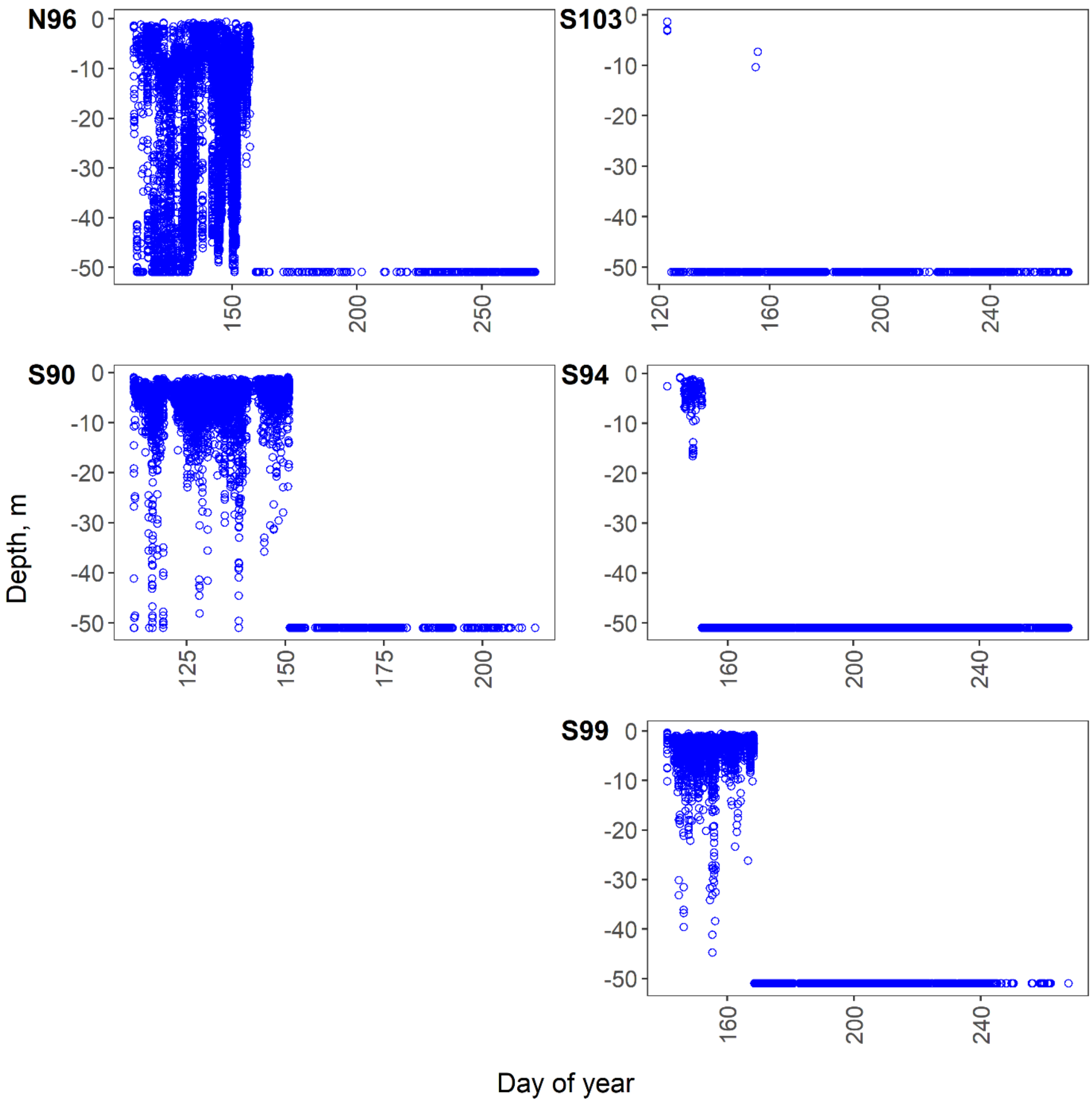

Figure A-3: Depth plot of lost tags. X-axis shows day of year, 120 = April 29, 150 = May 29, 200 = July 18, 250 = September 6. Y-axis shows depth in meters below surface.

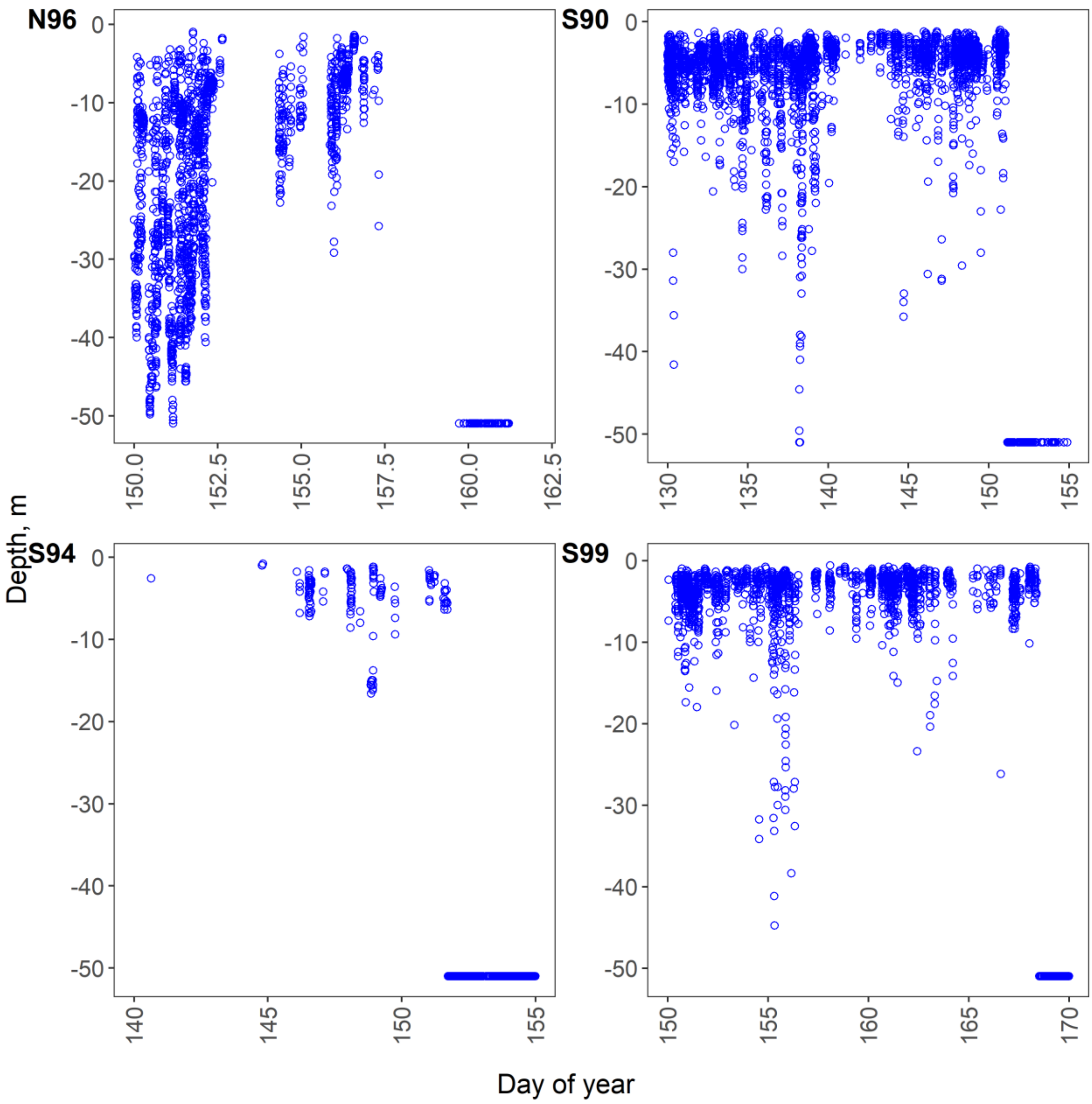

Figure A-4: Depth use of individuals showing sign of changed behavior a few days before lost. X-axis shows day of year, 150 = May 29, 170 = June 18. Y-axis shows depth in meters below surface.

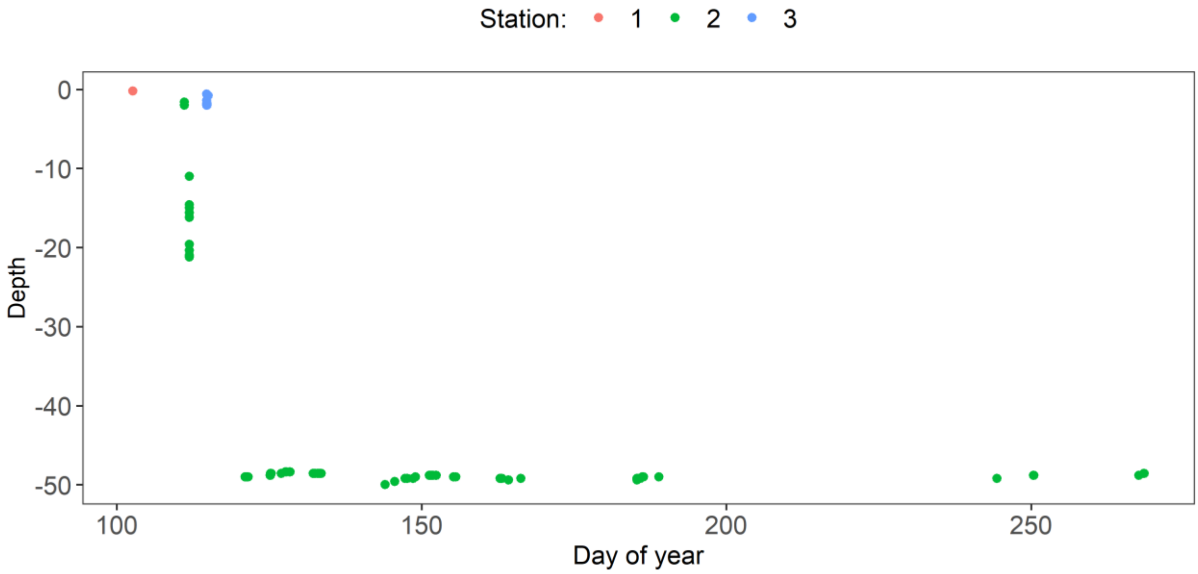

Figure A-5: Smolt S95 depth use at station 2 and 3. Observed doing a deep dive as it enters the lake, staying shallow at station 3 at the outlet-end of the lake, before returning to the Hjelledøla river mouth staying deep. X-axis shows day of year, 100 = April 9, 150 = May 29, 200 = July 18, 250 = September 6. Y-axis shows depth in meters below surface.

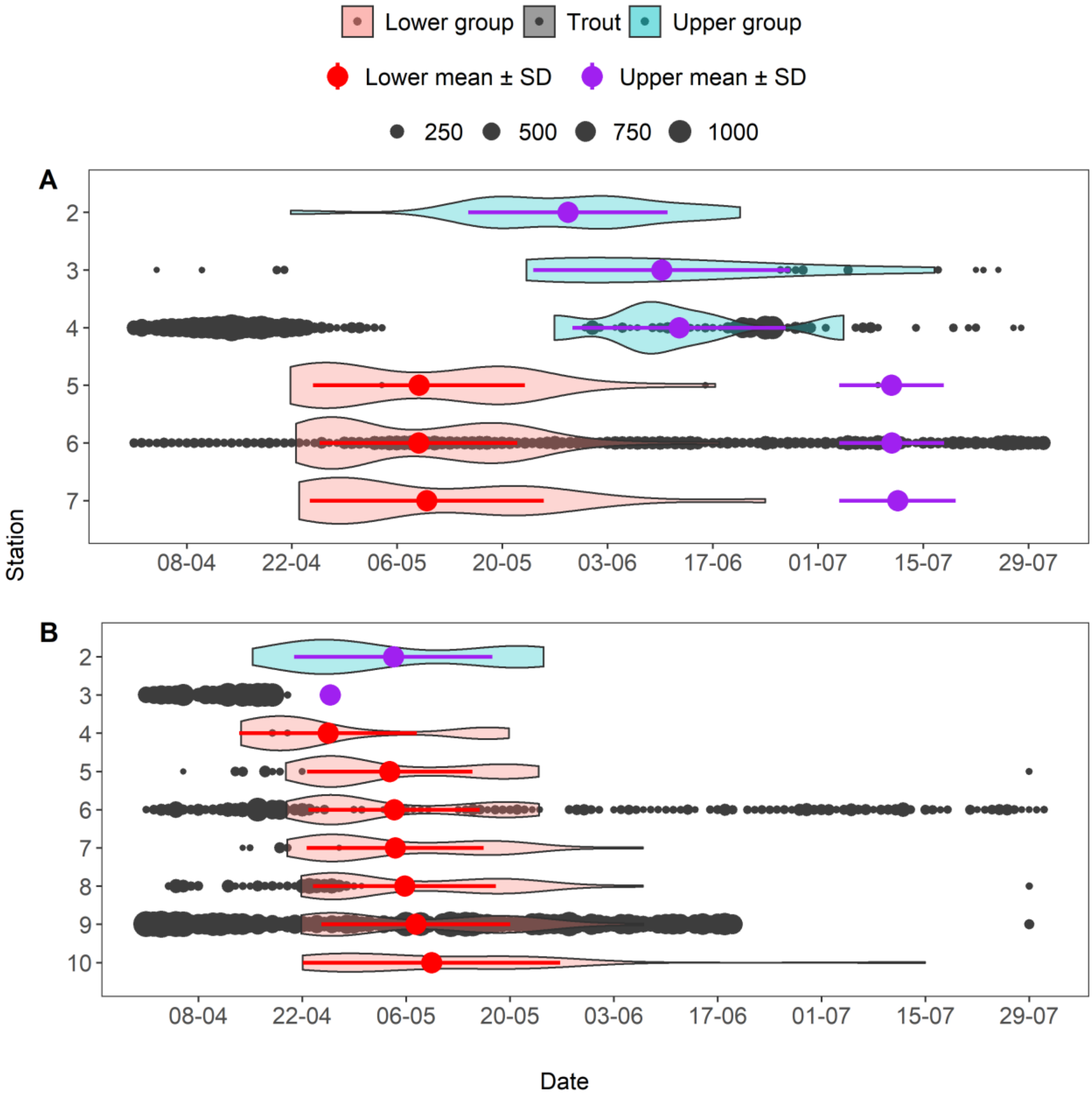

Figure A-6: earliest arrival in zones with trout overlay (Figure 2 and 9) Trout observations (points, size represent number of detections) at given station over the course of the smolt migration, with violin plots of dates when tagged salmon smolts from ***A.*** *Hornindal watercourse and* ***B****. Stryn watercourse was first observed at the given station in 2019. Width of violin shows relative distribution of observations, points represent the mean date whilst tails represent the standard deviation of first observations at the given station. The points at station 1 is the release and therefore the same date for all individuals in the group, and no violin. For the other stations, the lack of violins means the station had observations from two or fewer individuals.*

Appendix B – AICc tables

Table B-1: Model selection table for candidate models that predicts migration probability for smolts in given river. DoY = Day of year, Q = water discharge (m^3/s), T = water temperature (°C), Δ = change from the previous day (e.g., $\Delta Q_t = Q_t - Q_{t-1}$), reldeltaQ = $\Delta Q/Q$, K = number of parameters in the model, AICc = corrected Akaike information criterion, AICcWt = AICc weight (relative support), Cum.Wt = cumulative AICc weights, and LL = log likelihood.

Models	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Horndøla						
DoY*reldeltaQ	4	84.93	0	0.7	0.7	-38.18
DoY+reldeltaQ	3	86.75	1.81	0.28	0.98	-40.2
DoY*ΔQ	4	91.96	7.03	0.02	1	-41.69
DoY	2	95.56	10.63	0	1	-45.7
reldeltaQ	2	126.39	41.46	0	1	-61.11
Hjelledøla						
Q	2	68.68	0	0.55	0.55	-32.2
reldeltaQ+Q	3	70.49	1.81	0.22	0.77	-31.97
reldeltaQ*Q	4	71.27	2.59	0.15	0.92	-31.16
ΔQ*Q	4	72.77	4.09	0.07	0.99	-31.91
DoY	2	77.96	9.28	0.01	0.99	-36.84
DoY*reldeltaQ	4	78.76	10.08	0	1	-34.91
Eidselva						
reldeltaQ+DoY+Q	4	120.86	0	0.41	0.41	-56.07
reldeltaQ+DoY	3	122.12	1.26	0.22	0.63	-57.85
DoY*ΔQ	4	122.68	1.81	0.17	0.8	-56.98
reldeltaQ*DoY	4	123.34	2.48	0.12	0.92	-57.31
eldeltaQ*DoY*Q	8	124.32	3.45	0.07	0.99	-52.75
DoY*ΔQ*ΔT	8	128.91	8.05	0.01	1	-55.04
Stryneelva						
DoY+reldeltaQ	3	109.9	0	0.63	0.63	-51.73
DoY*reldeltaQ	4	111.32	1.42	0.31	0.94	-51.29
DoY*ΔQ	4	116.92	7.02	0.02	0.96	-54.09
DoY+ΔQ	3	117.08	7.18	0.02	0.98	-55.32
T	2	117.85	7.96	0.01	0.99	-56.82
T+ΔT	3	119.88	9.98	0	1	-56.72

Table B-2: Model selection table for candidate models that predicts day of arrival in the river for smolts given watercourse. Distance = Distance from the estuary (km), UpperLower = whether the smolt is from Horndøla or Hjelledøla (Upper) or from Eidselva or Stryneelva (Lower), EarlyLate= whether an individual starts migrating before or after the average date in their respective Upper or lower group, K = number of parameters in the model, AICc = corrected Akaike information criterium, AICcWt = AICc weight (relative support), Cum.Wt = cumulative AICc weights, and LL = log likelihood.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Hornindal watercourse						
Distance*UpperLower+EarlyLate	7	1115.28	0.00	0.50	0.50	-550.30
Distance*UpperLower*EarlyLate	10	1116.14	0.86	0.33	0.83	-547.38
$Distance^2$*UpperLower+EarlyLate	9	1117.46	2.19	0.17	1.00	-549.17
Distance+UpperLower*EarlyLate	7	1130.50	15.22	0.00	1.00	-557.91
Distance*UpperLower	6	1210.01	94.73	0.00	1.00	-598.75
Stryn watercourse						
Distance*UpperLower+EarlyLate	7	1719.13	0.00	0.47	0.47	-852.35
Distance+UpperLower*EarlyLate	7	1720.24	1.11	0.27	0.73	-852.90
Distance*EarlyLate+UpperLower	7	1720.25	1.12	0.27	1.00	-852.91
Distance*UpperLower	6	1803.18	84.04	0.00	1.00	-895.43
Distance	4	1810.58	91.44	0.00	1.00	-901.21

Table B-3: Model selection table for candidate models that predicts depth use for smolts in the lake Strynevatnet. DayNight = whether it is daytime or night, Weight = presmolt weight (grams), Length = presmolt fork length (cm), k-factor = presmolt k-factor, Julian = day of year, K = number of parameters in the model, AICc = corrected Akaike information criterium, AICcWt = AICc weight (relative support), Cum.Wt = cumulative AICc weights, and LL = log likelihood.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
DayNight*Weight*Julian	10	193070.14	0	1	1	-96525.07
DayNight*Length*Julian	10	193138.37	68.23	0	1	-96559.18
Weight*Julian	6	193376.67	306.53	0	1	-96682.33
DayNight*k-factor*Julian	10	193472.56	402.42	0	1	-96726.28
DayNight*Weight	6	193540.14	470	0	1	-96764.07

Table B-4: Cormack-Jolly-Seber model selection table for candidate models estimating survival probability and detection probability in the Hornindal and Stryn watercourses. Because of the complexity of the models, this table is to show what individual covariates (ind.cov) were shown the most support, none = no covariate.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Hornindal watercourse						
1, ind.cov(weight)	10	317.98	0	0.29	0.29	-297.00
2, ind.cov(weight)	10	318.38	0.41	0.24	0.53	-297.41
3, ind.cov(weight)	10	318.72	0.74	0.2	0.74	-297.74
4, ind.cov(weight)	11	319.92	1.94	0.11	0.85	-296.74
5, ind.cov(weight)	11	320.17	2.19	0.1	0.95	-296.99
6, ind.cov(weight)	12	321.73	3.75	0.05	0.99	-296.33
7, ind.cov(length)	10	326.25	8.27	0	1	-305.27
8, ind.cov(none)	8	330.15	12.18	0	1	-313.52
Stryn watercourse						
1, ind.cov(k-factor)	9	303.268	0	0.2	0.2	-284.67
2, ind.cov(k-factor)	9	303.309	0.04	0.19	0.39	-284.71
3, ind.cov(k-factor)	9	303.577	0.31	0.17	0.56	-284.97
4, ind.cov(k-factor)	9	303.962	0.69	0.14	0.7	-285.36
5, ind.cov(k-factor)	9	304.076	0.81	0.13	0.83	-285.47
6, ind.cov(k-factor)	10	305.61	2.34	0.06	0.89	-284.87
7, ind.cov(length)	9	306.991	3.72	0.03	0.92	-288.39
8, ind.cov(length)	11	307.816	4.55	0.02	0.94	-284.93
9, ind.cov(length)	9	308.515	5.25	0.01	0.95	-289.91
10, ind.cov(length)	9	308.569	5.3	0.01	0.97	-289.97
11, ind.cov(length)	9	309.082	5.81	0.01	0.98	-290.48
12, ind.cov(none)	8	309.226	5.96	0.01	0.99	-292.75
13, ind.cov(weight)	10	310.791	7.52	0	0.99	-290.05
14, ind.cov(weight)	9	311.117	7.85	0	1	-292.51

Appendix C – Tag-ID lists

Table C-1: All tagged presmolts with date of tagging, watercourse and river it belongs to, transmitter type, ID, total length (TL) in cm and weight in grams at tagging, k-factor, tag to body weight ratio, and whether it migrated early or late (NA = not detected after release).

ID	Date	River	Transmitter type	TL	Weight	k-factor	Tag ratio	Early/ Late
N1	14.04.2019	Eidselva	ID-LP7	12.2	17.8	0.98	11.20 %	Early
N2	14.04.2019	Eidselva	D-LP7	14.1	24.2	0.86	8.30 %	Late
N3	14.04.2019	Eidselva	D-LP7	14	19.3	0.7	10.40 %	Early
N4	14.04.2019	Eidselva	ID-LP7	12.3	16.5	0.89	12.10 %	NA
N5	14.04.2019	Eidselva	D-LP7	15.7	34	0.88	5.90 %	Early
N6	14.04.2019	Eidselva	ID-LP7	15	16.2	0.48	12.30 %	Late
N7	14.04.2019	Eidselva	ID-LP7	12.6	15.2	0.76	13.20 %	Early
N8	14.04.2019	Eidselva	D-LP7	14.9	25.6	0.77	7.80 %	Early
N9	14.04.2019	Eidselva	ID-LP7	13.2	20.2	0.88	9.90 %	Early
N10	14.04.2019	Eidselva	D-LP7	14.4	27.5	0.92	7.30 %	Early
N11	14.04.2019	Eidselva	ID-LP7	13.4	27.5	1.14	7.30 %	Early
N12	14.04.2019	Eidselva	ID-LP7	12.8	19.8	0.94	10.10 %	NA
N14	14.04.2019	Eidselva	D-LP7	13.7	19.4	0.75	10.30 %	Early
N15	14.04.2019	Eidselva	ID-LP7	13.8	20.6	0.78	9.70 %	Late
N16	14.04.2019	Eidselva	ID-LP7	12.5	17.9	0.92	11.20 %	NA
N17	14.04.2019	Eidselva	ID-LP7	12.9	16	0.75	12.50 %	Early
N18	14.04.2019	Eidselva	ID-LP7	12.5	19.6	1	10.20 %	Early
N19	14.04.2019	Eidselva	ID-LP7	12.6	20.3	1.01	9.90 %	Late
N20	14.04.2019	Eidselva	ID-LP7	13.1	19.7	0.88	10.20 %	Late
N21	14.04.2019	Eidselva	ID-LP7	13.1	22.8	1.01	8.80 %	Early
N22	14.04.2019	Eidselva	ID-LP7	12.8	17.8	0.85	11.20 %	Late
N23	14.04.2019	Eidselva	D-LP7	14.2	25.1	0.88	8.00 %	Early
N24	14.04.2019	Eidselva	D-LP7	15.1	23.5	0.68	8.50 %	Early
N25	14.04.2019	Eidselva	ID-LP7	12.9	16.8	0.78	11.90 %	NA
N26	14.04.2019	Eidselva	ID-LP7	12.5	17	0.87	11.80 %	Early
N27	14.04.2019	Eidselva	D-LP7	16	32.9	0.8	6.10 %	Early
N28	14.04.2019	Eidselva	D-LP7	15.7	30.2	0.78	6.60 %	Early
N29	14.04.2019	Eidselva	ID-LP7	12.9	15.9	0.74	12.60 %	Late
N30	14.04.2019	Eidselva	ID-LP7	14.2	19.2	0.67	10.40 %	Late
N31	14.04.2019	Eidselva	D-LP7	14	21.4	0.78	9.30 %	Early
N32	14.04.2019	Eidselva	ID-LP7	12.8	16.1	0.77	12.40 %	Late
N33	14.04.2019	Eidselva	ID-LP7	12.9	18.2	0.85	11.00 %	Late
N34	14.04.2019	Eidselva	ID-LP7	12.9	20.6	0.96	9.70 %	Early
N35	14.04.2019	Eidselva	ID-LP7	13.2	19.3	0.84	10.40 %	Early
N36	14.04.2019	Eidselva	D-LP7	16.2	36	0.85	5.60 %	NA
N37	14.04.2019	Eidselva	ID-LP7	13.7	22.3	0.87	9.00 %	Late
N38	14.04.2019	Eidselva	D-LP7	15.1	26	0.76	7.70 %	NA

N39	14.04.2019	Eidselva	ID-LP7	13.2	18.2	0.79	11.00 %	Early
N40	14.04.2019	Eidselva	D-LP7	16.7	39.8	0.85	5.00 %	Early
N41	14.04.2019	Eidselva	ID-LP7	12.7	17	0.83	11.80 %	Late
N42	14.04.2019	Eidselva	D-LP7	14.4	24	0.8	8.30 %	Early
N43	14.04.2019	Eidselva	D-LP7(2018)	15.9	39	0.97	5.40 %	NA
N44	14.04.2019	Eidselva	D-LP7	15.1	26.1	0.76	7.70 %	Early
N45	14.04.2019	Eidselva	ID-LP7	12.7	18.8	0.92	10.60 %	Late
N46	14.04.2019	Eidselva	D-LP7	14.3	23.8	0.81	8.40 %	Late
N47	14.04.2019	Eidselva	D-LP7	14.7	26	0.82	7.70 %	Late
N48	14.04.2019	Eidselva	D-LP7(2018)	15.7	32.9	0.85	6.40 %	Late
N49	14.04.2019	Eidselva	ID-LP7	13.9	21.7	0.81	9.20 %	Late
N50	14.04.2019	Eidselva	D-LP7	16.7	34	0.73	5.90 %	Late
N51	14.04.2019	Eidselva	D-LP7	16.1	36.8	0.88	5.40 %	Early
N52	14.04.2019	Eidselva	ID-LP7	13.7	17.5	0.68	11.40 %	Early
N53	14.04.2019	Eidselva	D-LP7	14.2	19.8	0.69	10.10 %	Late
N54	14.04.2019	Eidselva	ID-LP7	12.6	19.3	0.96	10.40 %	Early
N55	14.04.2019	Eidselva	ID-LP7	13.7	22.1	0.86	9.00 %	Early
N56	14.04.2019	Eidselva	ID-LP7	13.9	23.4	0.87	8.50 %	Late
N57	14.04.2019	Eidselva	D-LP7	15.9	31.5	0.78	6.30 %	Late
N58	14.04.2019	Eidselva	ID-LP7	13.1	17.2	0.77	11.60 %	Early
N59	14.04.2019	Eidselva	ID-LP7	13.3	19.5	0.83	10.30 %	NA
N60	14.04.2019	Eidselva	D-LP7	14.6	25	0.8	8.00 %	Late
N61	14.04.2019	Eidselva	D-LP7	14.3	24.5	0.84	8.20 %	Late
N62	14.04.2019	Eidselva	ID-LP7	13.7	17.5	0.68	11.40 %	NA
N63	14.04.2019	Eidselva	ID-LP7	13.5	23.5	0.96	8.50 %	NA
N64	14.04.2019	Eidselva	ID-LP7	13	15.9	0.72	12.60 %	Late
N65	14.04.2019	Eidselva	D-LP7	15.5	28.3	0.76	7.10 %	Late
N67	14.04.2019	Horndøla	ID-LP7	13.2	18	0.78	11.10 %	Late
N68	14.04.2019	Horndøla	ID-LP7	12.6	14.3	0.71	14.00 %	Late
N69	14.04.2019	Horndøla	ID-LP7	13	20	0.91	10.00 %	Late
N70	14.04.2019	Horndøla	ID-LP7	14.9	27.3	0.83	7.30 %	Early
N71	14.04.2019	Horndøla	ID-LP7	13.1	21.6	0.96	9.30 %	Late
N72	14.04.2019	Horndøla	ID-LP7	13	19.1	0.87	10.50 %	Early
N73	14.04.2019	Horndøla	ID-LP7	13.6	21.7	0.86	9.20 %	Early
N74	14.04.2019	Horndøla	ID-LP7	14.1	24.3	0.87	8.20 %	Late
N75	14.04.2019	Horndøla	ID-LP7	13.87	23	0.86	8.70 %	Early
N76	14.04.2019	Horndøla	ID-LP7	13.3	18.4	0.78	10.90 %	Late
N77	14.04.2019	Horndøla	ID-LP7(2018)	14.2	24.3	0.85	7.80 %	Early
N78	14.04.2019	Horndøla	ID-LP7(2018)	13	19.4	0.88	9.80 %	NA
N79	14.04.2019	Horndøla	ID-LP7(2018)	13.1	19	0.85	10.00 %	Late
N80	14.04.2019	Horndøla	ID-LP7(2018)	13	20.9	0.95	9.10 %	NA
N81	14.04.2019	Horndøla	ID-LP7(2018)	13.1	19	0.85	10.00 %	Early
N82	14.04.2019	Horndøla	ID-LP7(2018)	13.1	17.5	0.78	10.90 %	Early
N84	14.04.2019	Horndøla	D-LP7	14.2	26	0.91	7.70 %	Late
N85	14.04.2019	Horndøla	ID-LP7(2018)	13.2	18.3	0.8	10.40 %	Late
N86	14.04.2019	Horndøla	ID-LP7(2018)	13.6	21.5	0.85	8.80 %	NA

N87	14.04.2019	Horndøla	ID-LP7(2018)	13.7	25.2	0.98	7.50 %	Late
N88	14.04.2019	Horndøla	ID-LP7(2018)	13.5	23.3	0.95	8.20 %	NA
N89	14.04.2019	Horndøla	ID-LP7(2018)	13.2	25.4	1.1	7.50 %	Late
N90	14.04.2019	Horndøla	ID-LP7(2018)	13.7	25	0.97	7.60 %	NA
N91	14.04.2019	Horndøla	ID-LP7(2018)	14.2	19.7	0.69	9.60 %	NA
N92	14.04.2019	Horndøla	ID-LP7(2018)	13.7	23.8	0.93	8.00 %	Late
N93	14.04.2019	Horndøla	ID-LP7(2018)	13.3	19.6	0.83	9.70 %	Late
N94	14.04.2019	Horndøla	D-LP7	17.2	41.5	0.82	4.80 %	Early
N95	14.04.2019	Horndøla	ID-LP7(2018)	13.7	21.2	0.82	9.00 %	NA
N96	14.04.2019	Horndøla	D-LP7	14.3	24.3	0.83	8.20 %	Early
N97	14.04.2019	Horndøla	D-LP7	14.2	24.9	0.87	8.00 %	Early
N98	14.04.2019	Horndøla	D-LP7	14.6	23.5	0.76	8.50 %	Early
S1	13.04.2019	Stryneelva	ID-LP7	14.6	25.4	0.82	7.90 %	Late
S2	13.04.2019	Stryneelva	ID-LP7	12.8	16.9	0.81	11.80 %	Early
S3	13.04.2019	Stryneelva	D-LP7	13.3	22.3	0.95	9.00 %	NA
S4	13.04.2019	Stryneelva	D-LP7	17	34.5	0.7	5.80 %	Early
S5	13.04.2019	Stryneelva	ID-LP7	12.8	21.2	1.01	9.40 %	NA
S6	13.04.2019	Stryneelva	D-LP7	13.9	22.9	0.85	8.70 %	Late
S7	13.04.2019	Stryneelva	D-LP7	14.3	25.3	0.87	7.90 %	NA
S8	13.04.2019	Stryneelva	ID-LP7	13.6	23.4	0.93	8.50 %	NA
S9	13.04.2019	Stryneelva	ID-LP7	13.2	20.1	0.87	10.00 %	Late
S10	13.04.2019	Stryneelva	D-LP7	17.1	45.1	0.9	4.40 %	Early
S11	13.04.2019	Stryneelva	D-LP7	16.2	36.2	0.85	5.50 %	NA
S12	13.04.2019	Stryneelva	ID-LP7	13.1	18.7	0.83	10.70 %	NA
S13	13.04.2019	Stryneelva	ID-LP7	12.6	19.6	0.98	10.20 %	NA
S14	13.04.2019	Stryneelva	D-LP7	14.1	23.3	0.83	8.60 %	NA
S15	13.04.2019	Stryneelva	D-LP7	14.1	23.3	0.83	8.60 %	NA
S16	13.04.2019	Stryneelva	D-LP7	14.3	20.7	0.71	9.70 %	Early
S17	13.04.2019	Stryneelva	D-LP7	14.3	21.8	0.75	9.20 %	Late
S18	13.04.2019	Stryneelva	D-LP7	13.7	23.8	0.93	8.40 %	NA
S19	13.04.2019	Stryneelva	ID-LP7	12.5	18	0.92	11.10 %	NA
S20	13.04.2019	Stryneelva	ID-LP7	13	19.8	0.9	10.10 %	Late
S21	13.04.2019	Stryneelva	ID-LP7	12.6	18	0.9	11.10 %	Late
S22	13.04.2019	Stryneelva	ID-LP7	12.8	18.5	0.88	10.80 %	Late
S23	13.04.2019	Stryneelva	D-LP7	14.1	22.2	0.79	9.00 %	Late
S24	13.04.2019	Stryneelva	ID-LP7	12.7	18.3	0.89	10.90 %	NA
S25	13.04.2019	Stryneelva	D-LP7	13.9	23.7	0.88	8.40 %	Late
S26	13.04.2019	Stryneelva	ID-LP7	12.8	17.6	0.84	11.40 %	NA
S27	13.04.2019	Stryneelva	D-LP7	14.3	23.8	0.81	8.40 %	Early
S28	13.04.2019	Stryneelva	D-LP7	13.3	20.3	0.86	9.90 %	Late
S29	13.04.2019	Stryneelva	ID-LP7	12.8	17.9	0.85	11.20 %	Late
S30	13.04.2019	Stryneelva	D-LP7	15.7	31	0.8	6.50 %	NA
S31	13.04.2019	Stryneelva	D-LP7	13.4	22.4	0.93	8.90 %	NA
S32	13.04.2019	Stryneelva	D-LP7	14.7	28.7	0.9	7.00 %	Late
S33	13.04.2019	Stryneelva	ID-LP7	12.4	18.5	0.97	10.80 %	NA
S34	13.04.2019	Stryneelva	ID-LP7	12.8	16.4	0.78	12.20 %	Early

S35	13.04.2019	Stryneelva	D-LP7	14.1	23.9	0.85	8.40 %	NA
S36	13.04.2019	Stryneelva	ID-LP7	13.2	17.3	0.75	11.60 %	Early
S37	13.04.2019	Stryneelva	ID-LP7	13.1	18.3	0.81	10.90 %	Early
S38	13.04.2019	Stryneelva	D-LP7	14.6	21.9	0.7	9.10 %	Early
S39	13.04.2019	Stryneelva	ID-LP7	12.6	18.5	0.92	10.80 %	Late
S40	13.04.2019	Stryneelva	ID-LP7	12.5	14.3	0.73	14.00 %	Early
S41	13.04.2019	Stryneelva	D-LP7	13.7	20	0.78	10.00 %	Early
S42	13.04.2019	Stryneelva	ID-LP7	12.8	16	0.76	12.50 %	Late
S43	13.04.2019	Stryneelva	D-LP7	17	33	0.67	6.10 %	Late
S44	13.04.2019	Stryneelva	D-LP7	13.5	20.7	0.84	9.70 %	NA
S45	13.04.2019	Stryneelva	ID-LP7	13.2	17.6	0.77	11.40 %	Early
S46	13.04.2019	Stryneelva	ID-LP7	13.2	17.6	0.77	11.40 %	NA
S47	13.04.2019	Stryneelva	ID-LP7	13.2	17.9	0.78	11.20 %	Early
S48	13.04.2019	Stryneelva	ID-LP7	12.9	15	0.7	13.30 %	NA
S49	13.04.2019	Stryneelva	D-LP7	14.2	22.2	0.78	9.00 %	Early
S50	13.04.2019	Stryneelva	ID-LP7	12.6	15.6	0.78	12.80 %	NA
S51	13.04.2019	Stryneelva	ID-LP7	12.3	14.9	0.8	13.40 %	NA
S52	13.04.2019	Stryneelva	ID-LP7	13.1	16.8	0.75	11.90 %	Early
S53	13.04.2019	Stryneelva	D-LP7	14.1	22	0.78	9.10 %	NA
S54	13.04.2019	Stryneelva	ID-LP7	12.9	13.3	0.62	15.00 %	Early
S55	13.04.2019	Stryneelva	D-LP7	15.6	26.8	0.71	7.50 %	Early
S56	13.04.2019	Stryneelva	ID-LP7	12.6	15.3	0.76	13.10 %	NA
S57	13.04.2019	Stryneelva	D-LP7	14.2	19.7	0.69	10.20 %	NA
S58	13.04.2019	Stryneelva	ID-LP7	13.1	15.4	0.69	13.00 %	Early
S59	13.04.2019	Stryneelva	ID-LP7	13	16.1	0.73	12.40 %	Early
S60	13.04.2019	Stryneelva	ID-LP7	12.8	15.9	0.76	12.60 %	NA
S61	13.04.2019	Stryneelva	ID-LP7	13.1	17.5	0.78	11.40 %	Early
S62	13.04.2019	Stryneelva	ID-LP7	12.7	17.1	0.83	11.70 %	Late
S63	13.04.2019	Stryneelva	D-LP7	14.2	21.6	0.75	9.30 %	NA
S64	13.04.2019	Stryneelva	ID-LP7	13	16.7	0.76	12.00 %	Early
S65	13.04.2019	Stryneelva	ID-LP7	12.7	14.1	0.69	14.20 %	NA
S66	13.04.2019	Stryneelva	D-LP7	14.6	26.9	0.86	7.40 %	Early
S67	13.04.2019	Stryneelva	D-LP7	13.9	18.8	0.7	10.60 %	Early
S68	13.04.2019	Stryneelva	ID-LP7	12.7	13.7	0.67	14.60 %	NA
S69	13.04.2019	Stryneelva	ID-LP7	13.9	19.5	0.73	10.30 %	Late
S70	13.04.2019	Stryneelva	ID-LP7	13.6	19	0.76	10.50 %	Early
S71	13.04.2019	Stryneelva	D-LP7	14.6	25.2	0.81	7.90 %	Early
S72	13.04.2019	Stryneelva	D-LP7	14.6	20	0.64	10.00 %	Early
S73	13.04.2019	Stryneelva	D-LP7	14.4	23	0.77	8.70 %	Early
S74	13.04.2019	Stryneelva	D-LP7	14.6	22.7	0.73	8.80 %	Early
S75	13.04.2019	Stryneelva	ID-LP7	13.2	16.2	0.7	12.30 %	Late
S76	13.04.2019	Stryneelva	D-LP7	14.3	21.2	0.72	9.40 %	NA
S77	13.04.2019	Stryneelva	ID-LP7	14.6	20.5	0.66	9.80 %	Early
S78	13.04.2019	Stryneelva	ID-LP7	14.6	23	0.74	8.70 %	Early
S79	13.04.2019	Stryneelva	ID-LP7	13.1	17	0.76	11.80 %	Early
S80	13.04.2019	Hjelledøla	ID-LP7	13.1	20.4	0.91	9.80 %	NA

S81	13.04.2019	Hjelledøla	D-LP7	13.2	18.5	0.8	10.80 %	Early
S82	13.04.2019	Hjelledøla	D-LP7	14.1	24.6	0.88	8.10 %	Early
S83	13.04.2019	Hjelledøla	D-LP7	14.2	23.5	0.82	8.50 %	Early
S84	13.04.2019	Hjelledøla	ID-LP7	13	20.6	0.94	9.70 %	Late
S85	13.04.2019	Hjelledøla	ID-LP7	13.3	21.2	0.9	9.40 %	Early
S86	13.04.2019	Hjelledøla	D-LP7	16.6	39.1	0.85	5.10 %	NA
S87	13.04.2019	Hjelledøla	ID-LP7	13.3	21.2	0.9	9.40 %	NA
S88	13.04.2019	Hjelledøla	ID-LP7	14.1	26.2	0.93	7.60 %	Late
S89	13.04.2019	Hjelledøla	ID-LP7	12.8	22.1	1.05	9.00 %	NA
S90	13.04.2019	Hjelledøla	D-LP7	15.9	35.1	0.87	5.70 %	Early
S91	13.04.2019	Hjelledøla	D-LP7	14.1	26.2	0.93	7.60 %	Late
S92	13.04.2019	Hjelledøla	D-LP7	15.2	30.5	0.87	6.60 %	NA
S93	13.04.2019	Hjelledøla	D-LP7	13.9	21.6	0.8	9.30 %	Early
S94	13.04.2019	Hjelledøla	D-LP7	13.9	23.4	0.87	8.50 %	Late
S95	13.04.2019	Hjelledøla	D-LP7	13.9	23.4	0.87	8.50 %	Early
S96	13.04.2019	Hjelledøla	D-LP7	13.6	25.1	1	8.00 %	Early
S97	13.04.2019	Hjelledøla	D-LP7	13.7	23.4	0.91	8.50 %	Early
S98	13.04.2019	Hjelledøla	ID-LP7	13.2	22.5	0.98	8.90 %	Late
S99	13.04.2019	Hjelledøla	D-LP7	14.8	29.8	0.92	6.70 %	Late
S100	13.04.2019	Hjelledøla	D-LP7	14.4	21	0.7	9.50 %	Early
S101	13.04.2019	Hjelledøla	D-LP7	14.2	25.6	0.89	7.80 %	Early
S102	13.04.2019	Hjelledøla	ID-LP7	13.7	20.4	0.79	9.80 %	Early
S103	13.04.2019	Hjelledøla	D-LP7	13.7	25.1	0.98	8.00 %	Early
S104	13.04.2019	Hjelledøla	ID-LP7	12.9	18.3	0.85	10.90 %	Late

Table C-2: Observed tagged anadromous trout in the study period. Date of tagging, river, ID, tag type and length in cm at tagging.

Date	River	AT.ID	Tag type	Length
02.09.2018	Stryneelva	10	D-LP9L	35
21.04.2018	Stryneelva	14	D-LP9L	22
02.09.2018	Stryneelva	15	D-LP9L	39
02.09.2018	Stryneelva	18	D-LP9L	39
02.09.2018	Stryneelva	20	D-LP9L	38
02.09.2018	Stryneelva	25	D-LP9L	39
02.09.2018	Eidselva	30	D-LP9L	84
02.09.2018	Eidselva	33	D-LP9L	84
01.11.2018	Eidselva	147	D-LP9L	33
01.11.2018	Eidselva	148	D-LP9L	32
01.11.2018	Eidselva	149	D-LP9L	46
01.11.2018	Eidselva	150	D-LP9L	31
01.11.2018	Eidselva	153	D-LP9L	32
01.11.2018	Eidselva	154	D-LP9L	38
02.11.2018	Stryneelva	155	D-LP9L	35
02.11.2018	Stryneelva	158	D-LP9L	29
02.11.2018	Stryneelva	159	D-LP9L	28
02.11.2018	Stryneelva	163	D-LP9L	30
02.11.2018	Stryneelva	165	D-LP9L	31
02.11.2018	Stryneelva	166	D-LP9L	30
02.11.2018	Stryneelva	168	D-LP9L	27
02.11.2018	Stryneelva	169	D-LP9L	42
02.11.2018	Stryneelva	170	D-LP9L	56

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