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Migration pattern and fjord use of Atlantic salmon (*Salmo salar*) smolt from two watercourses in the Nordfjord system: effects from environmental drivers

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Preface

This thesis completes my MSc in Nature Resource Management, and my time at the Norwegian University of Life Science. It has been two good and comprehensive years, and I have gained a lot of knowledge and new friends.

First and foremost I would like to thank my main advisor professor Thrond Oddvar Haugen at the Norwegian University of Life Science for good help, discussions and guidance during this thesis. Your supreme knowledge and enthusiasm have been very motivating. I am also very grateful for the help, constructive comments and academic input from co- advisors Henning Urke at INAQ AS and Thorstein Kristensen at Nord university.

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The present study is a part of the project “Kunnskaplsøft for sjøaure og laks I Strynevassdraget- kunnskapbasert lokal forvaltning 2017–2021» with the acronym KLAFF. The project is founded by several interests, being; The county governor in Vestland, The research council of Norway, Blom Fiskeoppdrett AS, Nordfjord Laks AS, K. Strømmen Lakseoppdrett AS, Marine Harvest Norway AS, Mowi AS, Coast Seafood AS, Nordfjord Forsøksstasjon AS and Eid & Stryn river owner organization. Selstad AS provided the project with ropes and buoys. INAQ AS and NMBU provided the acoustic receivers used.

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Abstract

As a part of its complex life cycle, wild Atlantic salmon (*Salmo salar*) smolts must migrate from its natal river into marine residency for feeding and maturing, for then to return as adult salmon after 1-4 years. This capricious migration, characterized by high mortality rates, has possibly become even more grueling as the burden of human engagements increases in various ways such as increased infestation pressure from salmon lice (Lepeophtheirus salmonis) due to farmed Atlantic salmon. It is therefore important to map the timing of migration and the mortality rates along the migration course, to understand the effects inflicted by these human engagements. The purpose of this study was to explore effects from migration triggers- and patterns, fjord progression speed and survival of smolt from Eidselva and Stryneelva watercourses, both emptying into the Nordfjord system by use of acoustic telemetry. Smolts were captured and tagged at two sites from both watercourses, and in both of these watercourses the capture-sites were separated by a large lake. In Hornindal watercourse, smolts were caught upstream and downstream of Hornindalvannet in the rivers Horndøla and Eidselva respectively. In Stryneelva watercourse, smolts were caught upstream and downstream of Oppstrynvannet in Hjelledøla and Stryneelva respectively. In total,147 out of 199 (73.9 %) of the tagged smolts were later detected at one or more receivers throughout the study system. As the smolts tagged with acoustic transmitters migrated through the study system, from river to outer part of Nordfjord, they were detected at fixed receiver stations all along the migration course. I hypothesized that increasing water discharge- and temperature are the most important environmental cues for triggering smolt migration, and that migration will occur at multiple migration-peaks. The smolts will display a uniform, continuous migration pattern out of the fjord, and to little extent display vertical depth migrations. That smolt mortality will vary through the entire study system and that the mortality rates will be higher for smaller smolt.

The initiation of seaward migration for tagged smolts was found to correlate with combined effects of increased water discharge and day of year. In Eidselva, initiation of migration was correlated with day of year, water discharge and the relative change in water discharge from the previous day to the next. Migration initiation in Stryneelva was correlated with day of year and relative change in water discharge from the previous day. For both watercourses the smolts migrated at two major migrations peaks separated by 3.5 weeks, with one minor migration-peak in between. The median migration date for when the smolts entered the estuary from both watercourses was separated by 10 days, with median migration date 11th of May for Hornindal watercourse and 1st of May for Stryneelva.

For smolts migrating from Stryneelva, apparent survival bottlenecks were related to the estuary of Stryneelva (33.6 % estimated survival) and the outermost part of the fjord system (25.5 % estimated survival). In Eidselva, however, there only seems to be a slight decrease of apparent survival in the estuary (93 % estimated survival) compared to the rest of the fjord. For the entire study system, the estimated survival rates from river to outer parts of the fjord varied from 19.6 % confirmed survival (Eidselva) to 24.2 % confirmed survival (Stryneelva). For comparison, the previous studies in the same study system found no bottlenecks and estimated survival rates were found to be higher than 98 % in 2018. The survival rates were found to positively correlate with body length, as longer smolts migrating from Stryneelva had better predicted survival rates through their entire migration course. The same correlation was found in the estuary of Eidselva exclusively, for smolts migrating from the Hornindal watercourse. Most of the smolts entered marine residency after sunset but before midnight, and migrated out of the fjord at various progression speeds, depending on time of migration and river of origin. Both migration groups from Eidselva migrated with the same progression speed, being 0.86±0.09 BL/s. The first smolt group that migrated from Stryneelva displayed progression speeds of 0.92±0.10 BL/s, whereas the last group migrated at 2.42±1.07 BL/s. Migrating at these speeds, the Eidselva-smolt reached the outer part of Nordfjord after an average of 4.43±4.13 days, and the respective number of days for the Stryneelva-smolt was 9.48±3.85 days. The migration rate appeared to be quite linear throughout the fjord for smolts from both watercourses, indicating a uniform, continuous migration pattern, utilizing almost exclusively depths shallower than 2 meters. Diurnal depth migrations did not appear to occur extensively, as there was only a slight tendency of depth migrations in the estuary of both rivers.

This study has helped increase the knowledge about migration patterns and triggers, and survival rates for salmon smolts migrating from Hornindal and Stryn watercourse in Nordfjord, and highlights the variety in survival rates from year-to-year in such dynamic systems.

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1. Introduction

The Atlantic salmon (*Salmo salar*) in the genus Salmonidae is thought to be one of the most important fish species in the world due to it's recreational, ecological and economical value (Aas et al., 2010; Forseth et al., 2017). For centuries, Atlantic salmon has been an important resource for us humans and we have gradually acquired more knowledge about the species' biology throughout its entire geographical distribution (Thorstad et al., 2010).

Most Atlantic salmon individuals express an anadromous life history as they spend their juvenile phase in freshwater, followed by oceanic migration after entering marine residency for feeding, and then migrating back to fresh water for spawning. The migration from freshwater to marine habitats is characterized by high mortality rates as the smolts are very exposed to both natural and anthropogenic threats, both contributors to the decline of Atlantic salmon stocks during the past decades (Forseth et al., 2017; Harvey et al., 2020). Aquatic biotopes like rivers, streams and fjords are particularly vulnerable to human engagements, as altering and degradation of hydromorphology and surrounding habitats are likely to affect the aquatic fauna and flora (Pulg et al., 2019). In Norway, hydro morphological changes are considered to be the most common interference in watercourses, and it is here most measures are implemented to restore and secure good habitat quality for Atlantic salmon (Halleraker et al., 2016). As the Atlantic salmon is an anadromous, migrating species, it is affected by environmental changes over a broad geographical area. Assuring suitable conditions while being present in freshwater is of course important, as this is a crucial phase of the salmon's life cycle. The conditions as the salmon smolts migrates from their rearing rivers and enter marine habitats is however less focused on, even though this phase is just as important.

When conducting migrations from freshwater to marine habitats, the Atlantic salmon exploits the major food resources found at sea. Such life history strategies enables rapidly increase in body size, which strongly correlates with reproductive success (Gross et al., 1988). For the anadromous migrating salmon to achieve best fitness possible, it is essential that the smolts migrate into marine residence at a time when the nutrient access is ideal. As a result of homing, every Atlantic salmon population is native to the given watercourse where they are hatched. Due to reproductive isolation, the given population therefore has unique adaptations to their specific natal river and the constituting fjord system. There is evidence supporting a genetic component being linked to the migration timing, potentially reflecting the local adaptations to native environmental conditions (Aarestrup et al., 1999; Garcia de Leaniz et al., 2007; Jonsson & Jonsson, 2011; Harvey et al., 2020). The genetic differences among populations in smolt migration timing is thought to be a result of selection on ideal growth and survival opportunities in marine residency (Hvidsten et al., 1998; Stewart et al., 2006; McLennan et al., 2018; Harvey et al., 2020). The timing of migration often varies within a population, and it is thought that the genetic differences in this trait between populations are mitigated by environmental cues, which also helps initiate migration (Harvey et al., 2020). As smoltification is a prerequisite of migrating, smolts will often migrate in several groups based on time of smoltification, resulting in several migration-peaks, depending on the individual smolts and current environmental conditions (Jensen et al., 2012; Urke et al., 2018; Haugen et al., 2019). Diverse environmental cues have been found to be most important for triggering smolt migration, as this varies between studies. Temperature, light intensity and water discharge is however the most studied environmental migration triggers (Jonsson & Ruud-Hansen, 1985; Zydlewski et al., 2005; Jensen et al., 2012; Otero et al., 2014; Haraldstad et al., 2017). Previous studies has also showed that the smolts appears to enter coastal waters as the sea surface temperature is 8 °C or warmer (Hvidsten et al., 1998; Whalen et al., 1999). When interfering with rivers and fjord systems, one risk altering the benefits of these built-in adaptations. Vanishing of local adaptations may be expressed in several ways, and may be a result of various reasons. For anadromous species, one crucial change may be the shift of migratory behaviour, as the timing of migration is likely to be critical for survival (Antonsson et al., 2010; Thorstad et al., 2012). Understanding the environmental drivers governing the differences in migration patterns and timing of migration among anadromous species and rivers is essential for ensuring optimal management strategies.

When the smolts enters marine residency and migrates out of the fjord, they start schooling as an anti-predator strategy. This phase is thought to be a "bottleneck" as the post-smolts faces high mortality rates when struggling to cope with the presence of new predators and parasites, and adjusting to forage new food sources (Klemetsen et al., 2003). As they enter marine residency, the mortality rates are linked to increased presence of predators, especially in the rivers estuary (Fleming, 1996; Klemetsen et al., 2003; Thorstad et al., 2010; Forseth et al., 2017). The presence of predators is likely to vary in time and space, and due to this the survival rates are also expected to vary within the migration route. Many factors is known to impact the survival rates of migrating smolt, and several studies has previously suggested smolt length to be an important factor for survival (Salminen et al., 1994; Salminen et al., 1995; Kallio-Nyberg et al., 1999; Saloniemi et al., 2004). As a response to these threats the post-smolts migrate out of their natal river during dark hours in early spring, while the water is cold and the nights are dark. Later, as the water temperatures rises, a shift occurs and the smolts starts migrating during daytime (Moore et al., 1995; Koed et al., 2006; Davidsen et al., 2009; Haraldstad et al., 2017). Mainly utilizing depths shallower than 3 meters, they migrate fast through the estuaries and fjord system and enter open ocean areas, reaching progression speed up to 2-3 body lengths per second (Thorstad et al., 2012; Haugen et al., 2016).

In addition to the persistent natural threats to migrating Atlantic salmon smolts, the increasing anthropogenic threats are numerous (Hvidsten & Møkkelgjerd, 1987; Aas et al., 2010; Harvey et al., 2020). Some being hydropower regulation, freshwater acidification, over exploitation and habitat degradation, whereas escaped farmed salmon and salmon lice (*Lepeophtheirus salmonis*) from fish farms are identified as most crucial and expanding threats (Forseth et al., 2017; Urke et al., 2018; Bøhn et al., 2020). Norway is home to the world's largest populations of wild Atlantic salmon (est. 0.5 million individuals), while paradoxically supporting the world's largest Atlantic salmon-farming industry (est. 380 million individuals, January 2017) (Heuch et al., 2005; Kristoffersen et al., 2018; Bøhn et al., 2020). Even though salmon lice is naturally present in Norwegian fjords, the increased supply of hosts due to salmon farming aggregates artificial amounts of salmon lice in many fjord systems (Torrissen et al., 2013). In Nordfjord there are 13 aquaculture sites with open net-pen salmon farms. As the salmon smolts migrate into marine residency they may be met with large amounts of salmon lice, numbers depending on the production intensity of farmed salmon, environmental conditions etc. in the given area. The ectoparasite has great pathogenic impacts on the Atlantic salmon, as they feed on their blood and tissue. Depending on number of lice, salmon smolts risks dying directly because of the lice-infections, skin lesions, osmoregulatory impairment or indirectly due to fungal infections (Bøhn et al., 2020). It is imperative that the number of lice infection per fish must be kept to a minimum. One way to achieve minimum lice infection is to map the smolts migration pattern and timing in detail, so that measures in the fjord may be conducted. Knowing where, and at what time, the salmon smolts is present at different locations during their migration route, and how long they stay in the potential lice-infection area would be a powerful tool when managing the different salmon populations.

To protect some of Norway's most important salmon rivers and fjords, "The National Action Plan Against Salmon Lice on Salmonids" (NA) was implemented in 1997. Some of the main measures of the NA was the legal limits for maximum mean number of salmon lice per farmed fish, mandatory reporting of lice in the farms, and monitoring the infection of salmon lice in wild Atlantic salmon (Heuch et al., 2005). An important aspect for good estimates is knowing when the smolts migrates through Nordfjord, resulting in more studied fish and more representative estimates of mean lice per fish.

Knowing which natural and anthropogenic challenges the fish experiences, is crucial for securing good and correct management of this vulnerable species. After the development of acoustic telemetry more than 60 years ago, the research of aquatic animal behaviour was revolutionized. Acoustic telemetry has proven to be a powerful and flexible tool when studying aquatic species, allowing researchers to quantify previously unobserved important processes within a broad range of taxa (Hockersmith & Beeman, 2012; Crossin et al., 2017). By tagging fish with acoustic transmitters, and creating an array of deployed receivers, one may recognize and map each tagged fish in time and space. Being a relatively affordable study method along with the quality of the data provided, and the systems applicability in both fresh and saltwater, acoustic telemetry has become the most preferred method for studying aquatic animal behaviour (Crossin et al., 2017).

The landowners in Eidselva and Stryneelva, and the aquaculture industry in Nordfjord, seek more knowledge about the salmon smolts migration, to secure fact-based management of the respective salmon stocks. Based on the background described, the main aim of the present study is to investigate the following hypothesis;

i) Smolt migration is triggered by increase in water discharge and temperature.

ii) The smolts will migrate in multiple groups, resulting in several migration-peaks.

iii) The smolts will display a uniform, continuous migration pattern out of the fjord, with little vertical depth migrations after marine entry.

iv) Smolt mortality will vary through the entire study system and will be higher for smaller smolt.

1.1 Study species

The Atlantic salmon is found at sea and in watercourses, and is native to the temperate and subarctic regions of the North Atlantic Ocean (Thorstad et al., 2010). In the North-east Atlantic Ocean, the Atlantic salmon has historically been found from the northern parts of Portugal in south, to the North sea, Baltic sea and all along the Norwegian coast to the Barents and white sea areas of Russia in east. In west the salmon is found in sea areas surrounding Iceland and up north to Svalbard. In the North-western parts of the Atlantic Ocean the distribution of salmon ranges from northern parts of America to the northwest end of Canada and further to the sea area in south-Greenland (MacCrimmon & Gots, 1979; Verspoor et al., 2007; Chittenden et al., 2013).

A typical salmon lifecycle begins in a river during spring when salmon eggs are hatched, buried down in the gravel. Here the alevin stays hidden for about three to eight weeks while feeding on their nutrient-rich yolk sac (Thorstad et al., 2010). When the yolk sac is completely absorbed the alevin emerges through the gravel of the redd and starts to feed as fry. Timing of the alevin emergence is adjusted to the time period when there is most food present for the fry, and is therefore individual for all rivers (Thorstad et al., 2012). At this stage the fry develops into parr, and their distinctive "parr mark" becomes more appearing along the side of their body. They may remain in this fresh water phase, feeding, from one to eight years, all depending on the environmental conditions of their river and their genetics (Thorstad et al., 2010; Harvey et al., 2020).

At some point when the parr is ready to leave their rearing tributaries, several physiological, behavioural and biochemical changes takes place, known as smoltification (Hoar, 1988). The parr enters smolt phase, preparing them for downstream migration and marine residency. They lose their evident countershading and parr marks as they become more silvery and streamlined (Heggberget et al., 1992). Previous territoriality ceases and the smolt loses their positive reothaxis, enabling downstream movement (McCormick et al., 1998). This entire process is triggered by environmental conditions such as water discharge, water temperature and photoperiod (McCormick et al., 1998; Harvey et al., 2020).

2. Materials and methods

2.1 Study area

The Nordfjord fjord system is located in Vestlant county in western Norway (figure 1). Ranging 106 kilometers makes Nordfjord the 6th longest fjord in Norway. Eidselva and Stryneelva watercourses both empty into the fjord system, Eidsfjorden and Innvikfjorden respectively, and are listed as national salmon rivers. The inner parts of Eidsfjord and Nordfjord are national salmon fjords. The purpose of these national salmon rivers and fjords is to preserve a selection of important wild Atlantic salmon stocks and to ensure their full salmon production potential (Vøllestad et al., 2014).

The seawater in Nordfjord is affected by the supply of cold freshwater, as the main rivers Eidselva, Stryneelva, Loen and Oldenvassdraget are characterized by catchments from high mountain areas and glaciers. As the saltwater has higher density than freshwater, it leads to a stratum in the water column, where the water closest surface often consists of brackish water. In Nordfjord, this supply of freshwater results in distinct changes in salinity in the water column from spring to mid-summer, as the supply of freshwater increases as snow in the catchment areas melts. During spring, until early May, the entire water column may consist of almost only saltwater. From the middle of May, the supply of freshwater increases, and a distinct surface layer of freshwater is present, increasing in size as it cover almost the entire fjord out to Isane-Ytre by the beginning of July (figure 1, figure 2). This consistent supply of cold water also effects the water temperature in the fjord, and the entire water column close to the estuary of Eidselva and Stryneelva watercourses was less than 9 °C at least until the end of April, 2019 (figure 3).

The middle and outer part of Nordfjord is affected by intense aquaculture, as Atlantic salmon farming occurs from the innermost facilities at Lote, increasing in numbers further out of the fjord towards Måløy (figure 1). During April-July, 2019, there was 13 aquaculture facilities in the fjord system, and 6 of these had active production of farmed Atlantic salmon (Barentswatch.no).

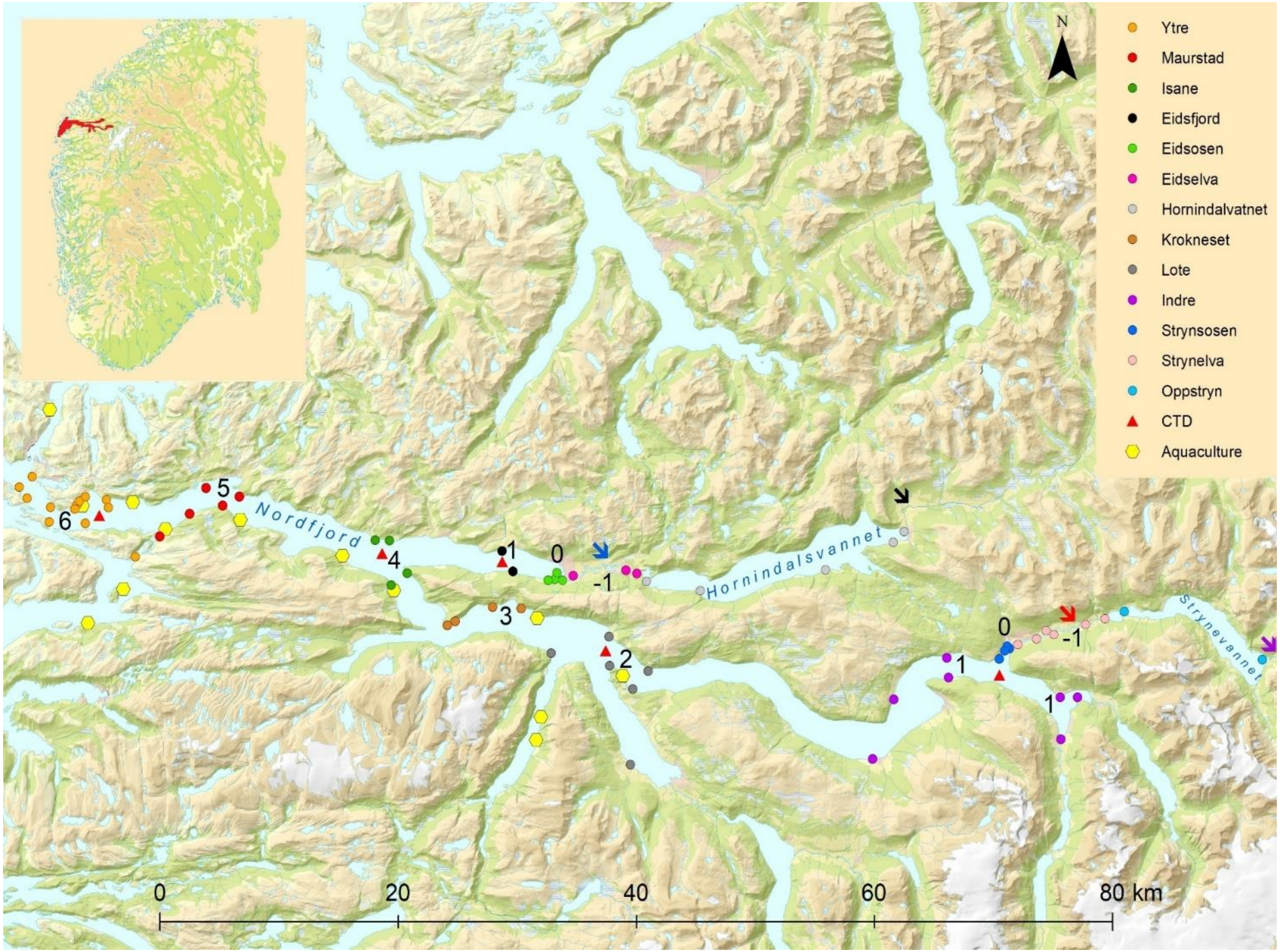
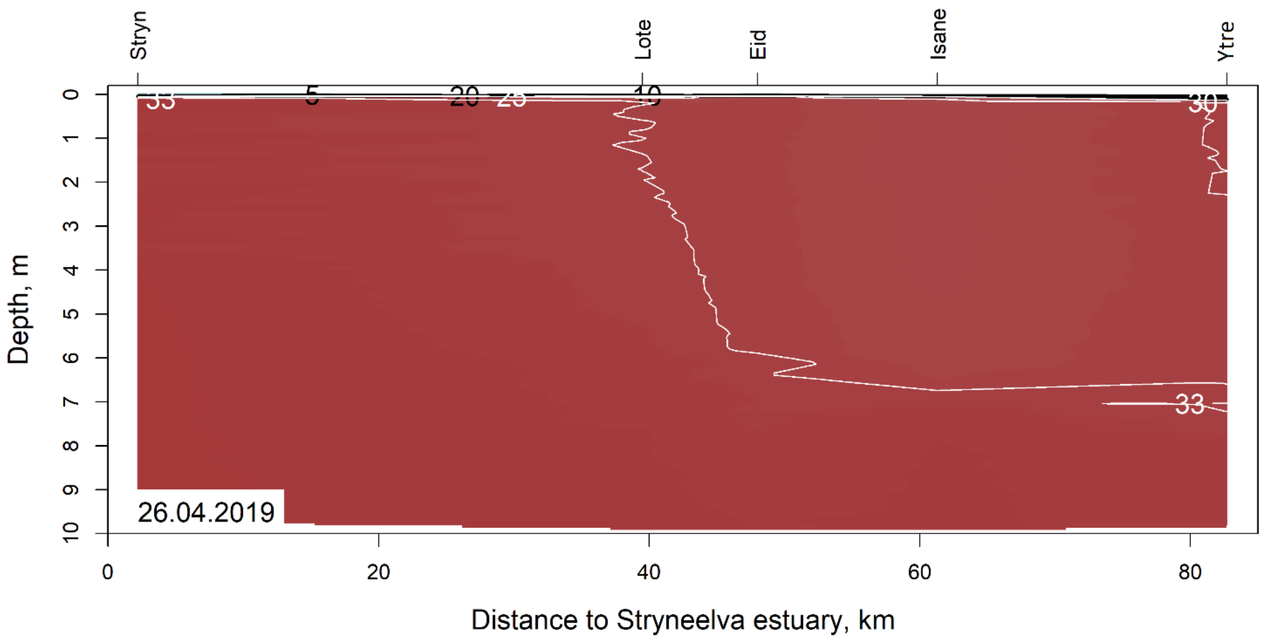
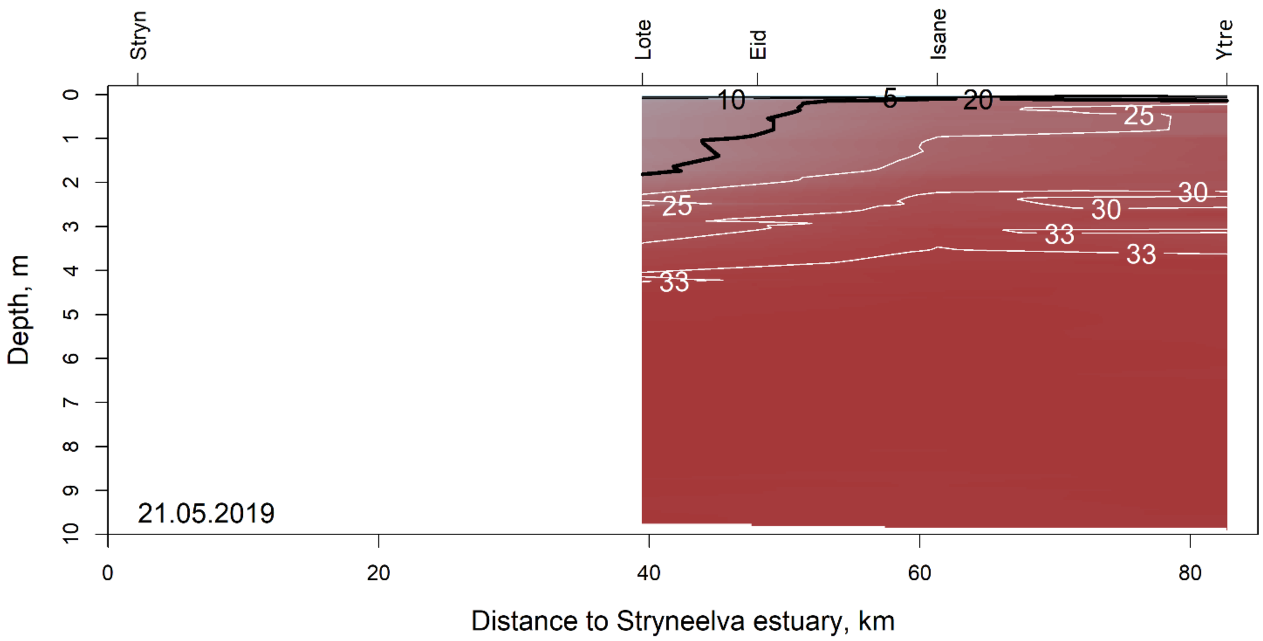


Figure 1. Receiver network and station numbering. Also CTD-stations, aquaculture facilities and point of release for AT-tagged smolts indicated by arrows in Stryneelva and Eidselva (see legend in top right corner of the map). Map in top left corner shows Nordfjords location.


Stryn
Lote
Eid
Isane
Ytre
Depth, m
26.04.2019
Distance to Stryneelva estuary, km


Stryn
Lote
Eid
Isane
Ytre
Depth, m
21.05.2019
Distance to Stryneelva estuary, km

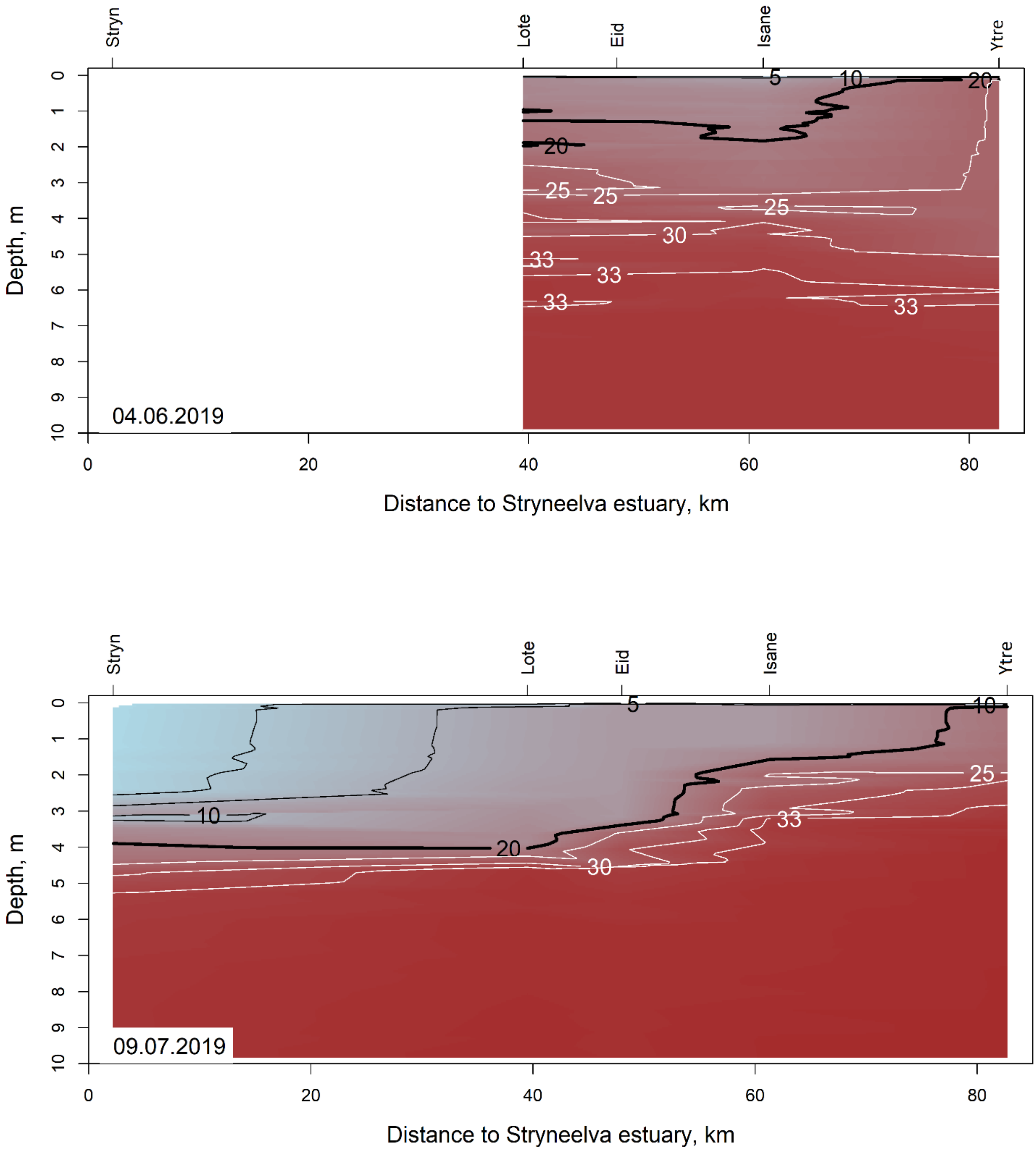


Figure 2: Interpolated longitudinal sections for CTD-derived vertical profiles of salinity from Stryn outward towards Ytre, down to 10 meters of depth at four different occasions from April-July 2019. Interpolations were made in R using the interp-function embedded in the akima library (Akima & Gebhardt, 2020). Thick black line illustrates 20 ppt salinity, as this is a threshold the salmon lice tends to avoid as they prefer salinities above 20. White areas illustrate areas without data coverage. The entire figure covers two pages.

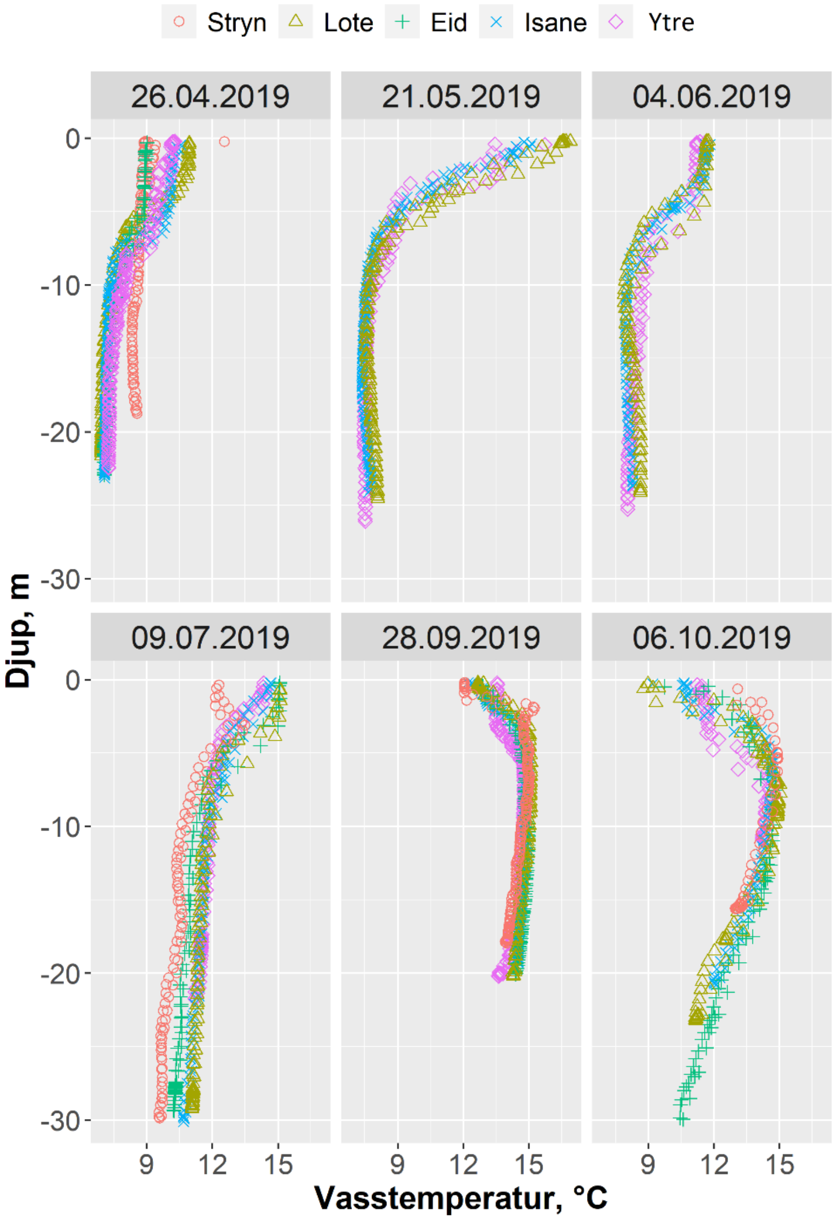


Figure 3: CTD-derived temperature depth-profiles at Stryn, Lote, Eid, Isane and Ytre from six different occasions during 2019 (figure 1).

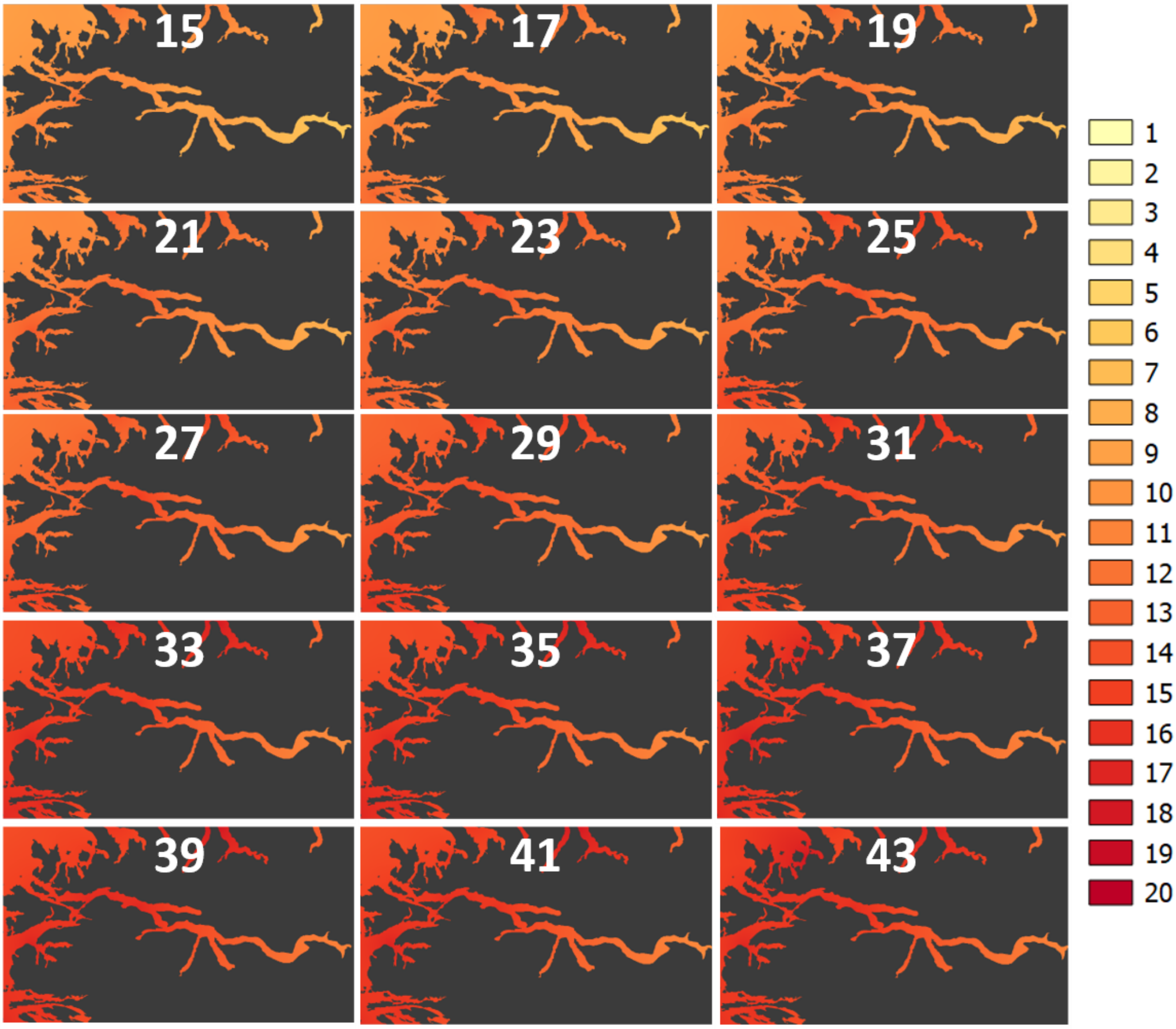


Figure 4: Bi-weekly heatmaps of infestation pressure (IP) indices of salmon lice in Nordfjord, 2019. The scale from 1-20 indicates the expected infestation of salmon louse per smolt after seven or fourteen days exposed to the given IP. If a smolt is exposed to infestation pressure 10 for seven days, it is expected to be infested with 0.01 louse, and 0.03 louse after fourteen days. After 7 days of exposure to IP 20, the smolt is expected to be infested with 66.9 louse, and 133.8 louce after fourteen days (Kristoffersen et al., 2018). The infestation pressure is color-graded, where light color indicates low infestation pressure, and the darker red color indicates high infestation pressure.

2.1.2 Eidselva

Eidselva river in the Hornindal watercourse is located in Eid municipality in Vestland county (61°54`22"N, 6°0`26"E). The upper reaches of the watercourse comprise of the river Horndøla, which empties into the 50.4 km^2 big lake Hornindalsvannet (52 m a.s.l), with a maximum depth of 514 meters. This part of the river is affected by watercourse regulations, as 20 km^2 of the river is transferred into another watercourse (Urdal, 2003). From Hornindalsvannet flows the river Eidselva which drains from a catchment of 428 km^2 (atlas.nve.no). With an average waterflow of 18.5 m^3/s (2019) it flows approximately 10 km from Hornindalsvannet to its estuary in Eidsfjord, making the total river catchment area 46.79 km^2 (atlas.nve.no). The species dominating the watercourse is arctic char (*Salvelinus alpinus*) and trout (*Salmo trutta),* but salmon, three-spined stickleback (*Gasterosteus aculeatus*) and eel (*Anguilla anguilla*) is also present (Solheim et al., 2018).

2.1.3 Stryneelva

The Stryneelva river is located in Stryn watercourse which runs through the municipalities Stryn in Vestland, and Skjåk in Oppland (61°54`33"N, 6°45`31"E). The rivers that drain the catchment origin from glaciers in surrounding mountains, creating high water discharge during summer, low water discharge during winter and high transportation of sediments. Several rivers commence in the lake Strynevannet, creating a catchment of 537 km^2 (NVE atlas). From there, Stryneelva flows with an average water level of 29.7 m^3/s (2019) through agricultural areas into its estuary in Innvikfjorden, in the inner part of Nordfjord. In the watercourse you mainly find fish species such as salmon, trout and arctic char, but eel and three-spined stickleback is also present (Sægrov, 2000).

2.2 Network of passive receivers

In 2017 and 2018, a total of 71 receivers (VR2W, Vemco) were deployed in the Nordfjord system and six in Stryneelva, to study migration timing and marine behaviour of Atlantic salmon smolt. As an extension of this project, receivers were deployed in Hornindalsvannet in Stryn watercourse and in Eidselva at the inner part of Eidsfjorden, in April 2018 (Urke et al., 2018).

In 2019, a total of 48 receivers were active in the fjord system and 17 in the study lakes and rivers. In the fjord, receivers were mounted on ropes at 3-5 meters, connected to mooring at the bottom and a buoy at the top. In freshwater the receivers were mounted on an anchor subsurface.
To make sure the entire migration period was covered, the receivers were left active in the fjord until 6th of October 2019. To prevent possible loss of important data, the entire network of receivers was retrieved at five occasions (April, May, July, August and October).

2.2.1 Eidfjord and Eidselva

From Eidselva to the outer part of Nordfjord the receivers were placed in a network consisting of 6 stations and 5 zones. Zone 1 is the area upstream of the estuary between station -1 to 0. Zone 2 is the area between station 0 and 1, zone 3 is the area between station 1 and 4, and further the zones are numbered successively throughout the fjord to station 6 (table 1, figure 1). Station 2 and three are not included for Eidselva, as detections there would be from smolts migrating inwards to Stryneelva instead of out of the fjord.

Table 1: Overview of the different zones and their length in kilometers, and stations from Eidselva (station -1) to Ytre (station 6).

Zone	Range	Distance(km)
1	from station -1 to 0	7.3
2	from station 0 to 1	4.8
3	from station 1 to 4	10.2
4	from station 4 to 5	15.6
5	from station 5 to 6	13.2

2.2.2 Innvikfjorden & Stryneelva

The receivers were placed in a network of 8 stations and 7 zones. The zones consist of the area between the individual receiver stations. Zone 1 is the area upstream of the estuary and covers all freshwater (station -1 to 0). Zone 2 is from station 0 to 1, Zone 3 from station 1 to 2, and further the zones are numbered successively all the way out of the fjord to station 6 (table 2, figure 1).

Table 2: Overview of the different zones and their length in kilometres, and stations from Stryneelva (station -1) to Ytre (station 6).

Zone	Range	Distance (km)
1	from station -1 to 0	6
2	from station 0 to 1	4.3
3	from station 1 to 2	35.2
4	from station 2 to 3	12.5
5	from station 3 to 4	11
6	from station 4 to 5	16
7	from station 5 to 6	11

2.3 Acoustic telemetry

Acoustic telemetry is based on diffusion of sound waves through waterbodies and works both in fresh and saltwater. By implanting an acoustic transmitter (AT-tag) into a fish, one may remotely track the study objects location in time and space. The small sound-emitting tag transmits acoustic signals that a receiver, being either fixed or mobile, detects and stores, provided the tag is within detection range. The receiver's detection range may vary from just a few meters in bad conditions up to more than 400 meters in good conditions (Reubens et al., 2019). This depends on environmental factors such as water conductivity, salinity, weather conditions, turbulence due to rapids, wind and waves etc.(Kessel et al., 2014; Reubens et al., 2019).

2.4 Fish capture and AT-tagging

During the period from 12th to 14th of April, a total of 199 salmon presmolts were captured, AT-tagged and released at capture site in Eidselva/Horndøla and Stryn/Hjelledøla. The fish were captured by electrofishing in the respective rivers, following standard procedures described in Bohlin et al. (1989) and Urke et al. (2013). All smolts tagged were showing morphological signs of smoltification such as their lean and clear silvery appearance and had a minimum fork length of 12 cm. Overview of the tagged smolts are given in the appendix, table C-1.

The 64 salmon presmolts gathered in Eidselva were caught in the upper part of the river, in the area from Bjørlo to Hjelle, and released by the cabin “Måløyhytta” at Bjørlo (red arrow figure 1). 31 presmolts were caught in Horndøla river, in the river stretch from Kvivsbrua bridge downstream to the estuary. All fish were released 100 meters downstream of Kvivsbrua (purple arrow figure 1).

The 79 salmon presmolts gathered in Stryneelva was caught in the upper part of the river, from Stauri bridge up to Soget, and released upstream of Gjørvenfossen by the pool Petter (blue arrow figure 1). 25 salmon presmolts were caught upstream of Strynevatnet in Hjelledøla river, from the estuary to the intersection into state highway 15 (RV15). The smolt were released in the middle of the sampled river stretch, approximately 800 meters downstream of the intersection (black arrow figure 1).

Two types of transmitters were used during this study, both manufactured by Thelma Biotel AS (Thelmabiotel.com/transmitter). The smallest type (ID-LP7) transmits ID information, and the other, slightly larger tag (D-LP7) transmits ID and depth values (resolution 0.2 m). The specifications of the tags are described in table 3. What type of tag the smolts were implanted, depended on the size of the smolt. Smolt longer than fork length 14 cm were implanted D-LP7- tags. The smaller smolt, i.e.

fork length 12 to 14 cm, were implanted ID tags. In order to avoid signal collisions, both tag types were programmed to transmit codes at random intervals between 30 to 90 seconds.

Table 3: Overview of specifications for the tags implanted into smolts during 2019. The ID- and D-LP7(2018) tags are leftover-tags from the tagging in 2018 and were used in 2019.

Tags specs:	ID-LP7	D-LP7	ID-LP7(2018)	D-LP7 (2018)
Diameter	7.3 mm	7.3 mm	7.3 mm	7.3 mm
Length	17 mm	21.5 mm	18 mm	22.5 mm
Weight air	1.8 g	2 g	1.9 g	2.1 g
Weight water	1.1 g	1.2 g	1.2 g	1.2 g
Power output (dB re 1μPa@1m)	139	139	139	139
Code repeat rate (s)	30-90	30-90	30-90	30-90
Battery time (month)	5.7	5.5	5	5
Number of tags used	100	81	16	2

Prior to the implantation, all surgical equipment was sterilized to secure aseptic conditions. The general recommendations for surgical implantation of tags into fish by Mulcahy (2003) and Cooke et al. (2004) were used during tagging. The well-documented procedure and protocol for anaesthesia, analgesia and surgery of fish previously described by Urke et al. (2013) was applied. By using a net, the smolt were moved from a holding tank, into a pre-anaesthetic sedation tank containing 60 mg L^{-1} metomidate for at least 1.5 minutes. The smolt were then moved to an anaesthetic tank containing 60 mg L^{-1} MS 222 (tricaine methane sulphonate). To sustain adequate water circulation, an aquarium pump with a silicone hose was added to the tank. Here the smolt were kept until it was unresponsive to tail pinching and no longer able to remain upright. Surgical anaesthesia was reached within four minutes, and the smolt were then transferred to a v-shaped surgical table covered in wet cloths. To prevent the smolt from oxygen deprivation, it was constantly aerated with water holding 40 mg L^{-1} MS222, using a small water pump with a silicone hose that was inserted into the fish's mouth (figure 5). A midline ventral incision of approximately 9-12 mm was executed before the transmitter was carefully inserted into the coelom. The incision was then closed by three stitches of single-layer, simple interrupted suture pattern using monofilament material (Resolon, 4/0 usp: www.resorba.com) (Mulcahy, 2003; Urke et al., 2013). Tissue adhesive was then applied to seal the incision area (Histoacryl; www.tissueseal.com). All surgery was done by trained personnel to lower handling time. After a total handling time of about one minute for each fish, they were immediately moved into a recovery tank and then closely monitored. Most fish regained balance and showed normal swimming behaviour within 0.5-2 minutes, and was after 36 hours of observation released at catch site. License to sample fish was given by the county governor in Vestland, and license to practice animal experiments were given by the Norwegian Food Safety Authority (FOTS-ID:12002).

Figure 5: Salmon smolt post-operation with a silicon hose inserted into the mouth and three stitches in the abdomen.

2.5 Water discharge and water temperature

Water discharge values was collected from measuring stations in Hornindalsvannet (NVE.89.1.0) and Strynevatnet (NVE88.11.0). The water temperature was registered using a submersible temperature data logger (Vemco Mini-Log II), placed upstream of the Gjørvenfossen waterfall in Stryneelva, and at Skipnes in Eidselva.

2.6 Vertical profile of salinity and temperature in the fjord.

To measure water temperature and salinity subsurface throughout the fjord, vertical profiles of the water column was sampled (figure 2). The samples were taken using the measure instrument SAIV SD204 (http://www.saivas.no), by lowering it from the surface down to 20 meters of depth, at approximately 1 meter each second. These samples were gathered in five different zones in Nordfjord from Stryn, Lote, Isane, Eidsfjord and Ytre (figure 1). The samples were taken every 2nd week from the middle of April to mid-June, and later once in July and October.

2.7 Data processing and statistical analysis

Vemco User Software (VUE), software version 2.6.1 was used to collect raw data from the receivers in the fjord system and watercourses. In VUE data from 1st of January 2019,00:00:00, to 26.10.2019 was extracted, resulting in 161 393 2 detections. The data was then merged with tag- ID and receiver-ID using R (R development Core Team 2018). This discarded all detected AT-tags and ID-numbers not used in this study. The data collected from the receivers contained a lot of “noise” as acoustic telemetry is prone creating false observations as a result of disturbances in the environment surrounding the receivers from e.g. bad weather, boats and other physical factors. These disturbances would be expressed as single or multiple detections. When knowing the realistic swimming speed for smolts, each case of doubt was assessed and discarded if not plausible, leaving approximately 1.2 million detections for further analysis.

The programs R version 3.5.2 (R development Core Team 2018), Microsoft Office Excel 2016 and MARK version 9.0 (White & Burnham, 1999) was used for the statistical analysis and for making the various tables and models. All maps were made using ArcMap version 10.7.1 and all cartographic data was collected from Geonorge.no. The packages “ggplot2” (Wickham, 2016), ”ggpubr” (Kassambara, 2020), “sjPlot” (Lüdecke, 2020), “lmer4” (Bates et al., 2014), “AICcmodavg” (Mazerolle, 2019) and “lattice” (Sarkar, 2008) were used for handling, analysing and visualizing the data.

2.7.1 Quantitative analyses

Candidate models were fitted with combinations of various predictor variables included in the studied objectives. Before fitting, correlations between pairs of predictor variables were estimated where correlations higher than 0.3 (r_p) were avoided included in the same candidate model (e.g. (Dormann et al., 2013).

A generalized linear model (GLM) was fitted to estimate and quantify effects of the different groups (e.g. migration faction or release location) and individual variables or environmental (e.g. smolt size and water discharge) on the different performance and migration related responses (e.g. migration timing and estimated survival) for the smolts. For the binominal responses (e.g. migrate/ not migrate), a logit-link was used in the GLM analysis.

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

For all candidate models, an Akaike Information Criterion (AIC) was estimated. The AIC is aninformation-theoretic approach that let you compare different candidate models based on the information loss (Burnham et al., 2011). The AIC of a given model represents the deviance plus a penalty of two times the number of parameters estimated, thus dealing with the risk of over- or underfitting. The model with most support in the dataset is the best candidate model, as it is given the lowest AIC. A single AIC value itself, does not give much information, and must therefore be compared with other models fit to the same dataset (Burnham & Anderson, 2002). The larger the difference (ΔAIC) is from the most supported model, the less support does the given model have in the dataset. If the ΔAIC is two or less, this means that the model still has substantial empirical support. Models with ΔAIC lower than seven still have some support in the dataset, and must not automatically be discarded (Burnham & Anderson, 2002; Burnham et al., 2011).
For the models explaining behaviour from dataset with low sample size, a corrected version of AIC (AICc) was estimated.

R^2 Tjur is a pseudo R2 value, and is an alternative to often used values like Nagelkerk’s R^2. It may be read as any other pseudo r2 values (Tjur, 2009).

2.7.2 Salinity profiles and estimated salmon lice infestation pressure

The model estimating infestation pressure of salmon lice on Atlantic salmon smolts between the given weeks in Nordfjord, are based on the salmon lice model provided by the Norwegian Veterinary Institute (figure 4) (Kristoffersen et al., 2018). This is a deterministic model based on weekly reports of the number of reproductive salmon lice, water temperature and amount of fish at aquaculture facilities, indicating the estimated production of salmon lice eggs. As the eggs hatch, they are transported away from the aquaculture facilities by tide and currents. This way the estimated infestation pressure decreases further away from the given aquaculture facility. When knowing these different variables, at every active aquaculture facility, one may estimate the expected infestation pressure along the entire coast.

2.7.3 Migration timing and zone use

Time of migration was defined as the first observation of a smolt in the estuary (station 0), of the given river. Arrival at the individual stations was defined as the earliest observation of a smolt at the given station. Migration time between stations was calculated as the difference between the last observation of a smolt at a given station, and the earliest detection at the following station (exit zone x → enter zone x). E.g. zone use in zone 2 may be calculated as the time a fish uses from its last detection at station 0 to its first detection in station 1

All fish that migrated from Eidselva and then started swimming inward the fjord towards Stryneelva was automatically placed in zone 4 if they did not later reach zone 5. The reason for this is that these individuals are not interesting in this analysis as migration out of the fjord is being studied.

2.7.4 Analysis of depth use and diurnal migrations

The depth tag (D-LP7) sends signals with a resolution of 0.2 meters, with a maximum depth value of 51 meters. A known issue for this tag is that the depth sensor sometimes locks at maximum depth, transmitting invalid signals of maximum depth values. Even though the depth values are correct, and the tag is in fact at maximum depth or deeper, these stationary signals were cut form the dataset before further analysis.

2.7.5 Estimating probability of survival and detection

Capture- recapture methodology was used to assess the survival rate of migrating smolts based on a sequential approach of Cormac-Jolly-Seber modelling, with the two parameter types survival probability (φ) between the stations and detection probability (p) at the stations (Lebreton et al., 1992). These two parameters types may be estimated to be zone dependent (zone) or constant (.) with all constituent combinations. E.g. the zones may be estimated as equal between the different zones throughout the fjord, different between every zone or different between some selected zones. This way every zone throughout the fjord is given individual estimates for both detection and survival probability (figure 6B). As the dataset contains smolt from both upper and lower reaches of Eidselva and Stryneelva, the smolts were divided into groups (upper/lower) as they origin from either the upper (Horndøla/ Hjelledøla) or lower (Eidselva/Stryneelva) part of the given watercourse

A detection- history for all the tagged smolts may then be plotted. If a fish is detected by one or more receivers in a zone, it is given the value “1”, if not detected it is given value “0” (figure 6A). This will result in a “detection history” which may look something like this: 10011000, for a smolt migrating from Stryneelva. This means that the smolt has been detected in the watercourse (-1) and midways throughout the fjord at Lote & Krokneset (station 2 & 3), but not in the estuary (0), inner part of the fjord (1) or at any of the outermost stations (5 & 6). Every fish is given value "1" in the watercourse (-1) as this is where the smolts were released and without doubt has been present. It is not possible to assess probability of detection or survival for the last zone or station (6), since there is no further information available. Therefore, in this last zone- interval the value P is stated to 1, so that the estimated survival is the product of the two parameter types. These detection histories are used in the program MARK to calculate the parameter estimates for the model structures using a log-likelihood method (White & Burnham, 1999).

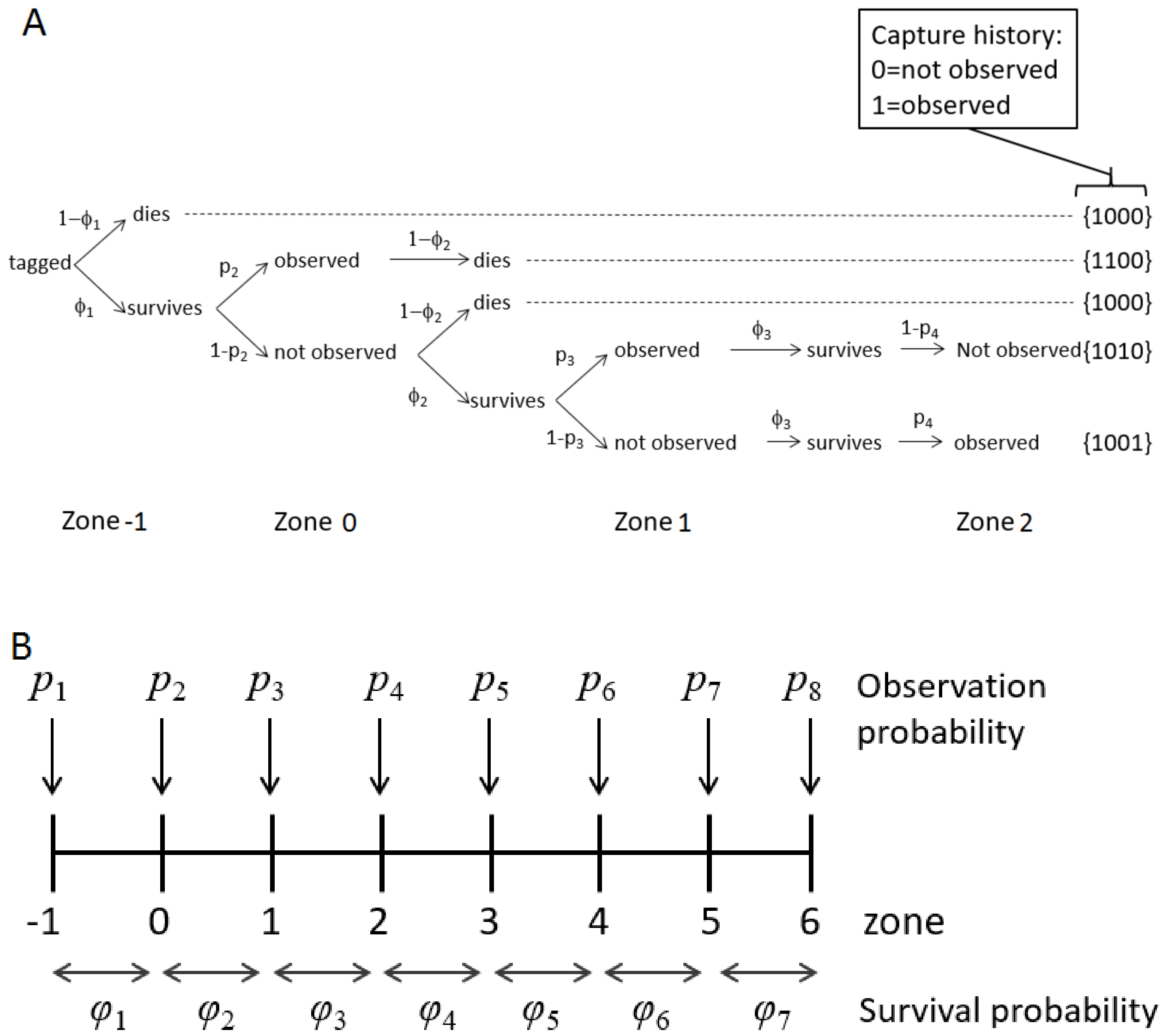


*Figure 6: **A**. An example of five detection histories for migrating smolt, with given parameters for the "Cormack-Jolly-seber (CJS) model structure. Φ_i indicates the survival probability between zone i and zone i+1, and p_i is the detection probability for zone i. **B**. CJS- parameterization of the model [Φ(sone), p(zone)]. Every zone will have their own estimates for both parameter types. As for the last sone, Φ and p cannot be estimated separately, only the product of them may be estimated. Figures are based on those given by (Haugen et al., 2019) page 17.*

2.7.6 Mark-recapture modelling

To create a good model, it is essential that all parameters available are estimated. Therefore, an extensive pre-analysis was done in MARK and several candidate models were made. As separate φs and ps could not be individually estimated for every station and zone, they were merged, and sections of the study system was estimated instead. Candidate models containing covariates was added to the proposed base model. For several stations, parameters were fixed to either 1 or 0. This is due to MARK not being able to estimate the parameter, or the estimates being very close to 1 or 0.

3. Results

3.1 Migration timing

Tagged smolts from Hornindal watercourse was first detected in the estuary in the period from 22nd of April to 15th of July (range: 85 days). There were two apparent major migration-peaks, and a smaller one. The first major peak in late April, around 25th, and the second major peak about 3.5 weeks later in the middle of May at approximately the 20th. A minor peak occurs from 10th to 15th of May. Two smolts from the upper group survived the migration from Hjelledøla and arrived the estuary at 5th and 15th of July (figure 7A). Due to the low numbers of smolts from the upper reaches of the Hornindal watercourse included in this dataset, they will be referred to as Eidselva smolt. The median date of arrival in estuary for all smolts was 11th of May.

The first detections of migrating smolts in Stryneelva was during the period from 21st of April to 6th of June (range: 47 days). In Stryn none of the smolts from the upper group was detected in the estuary. Also here there were two apparent major migration-peaks, and a smaller one. The first major peak in late April around the 25th and the other one about 3.5 weeks later in the middle of May at approximately the 17th. The smaller migration peak occured at 10th of May (figure 7B). Median date of arrival in the estuary for all smolts was 1st of May.

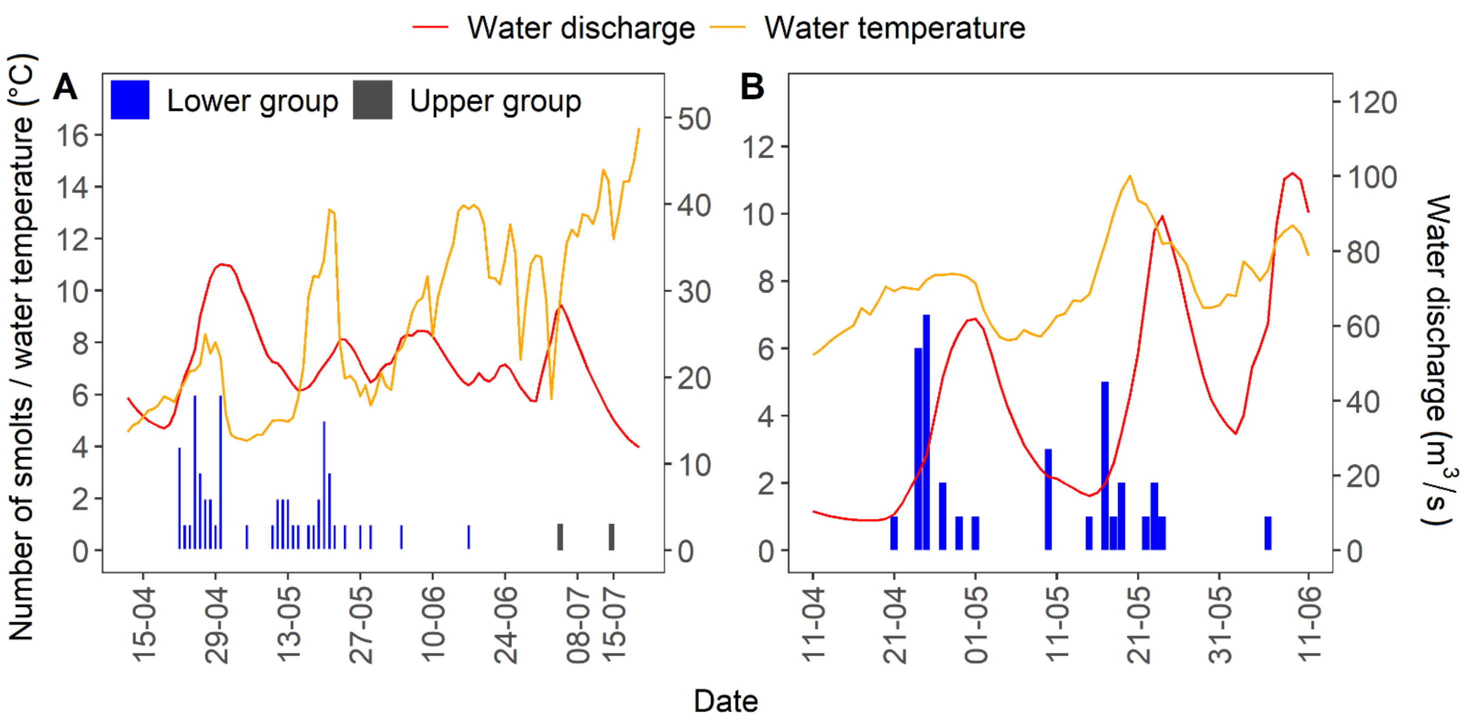


*Figure 7: Time of migration for salmon smolts tagged in Eidselva (**7A**) and Stryn (**7B**) watercourse in 2019, with numbers of smolt detected, water discharge- and temperature for the same time period. Numbers of observed smolts are illustrated as blue bars, while the grey bars in figure 7A are smolts detected from the upper group of the Hornindal watercourse.*

Migration from both watercourses mainly occurred at late evening after sunset but before midnight (20:00-24:00). For the first migrating smolt-group, the migration seems to be highly synchronous, as there were few anomalies. For the second group of smolts from Eidselva, the migration was more random and less synchronous. The migration is spread more widely over time and time of day, as several smolts migrated in the morning before noon (figure 8).

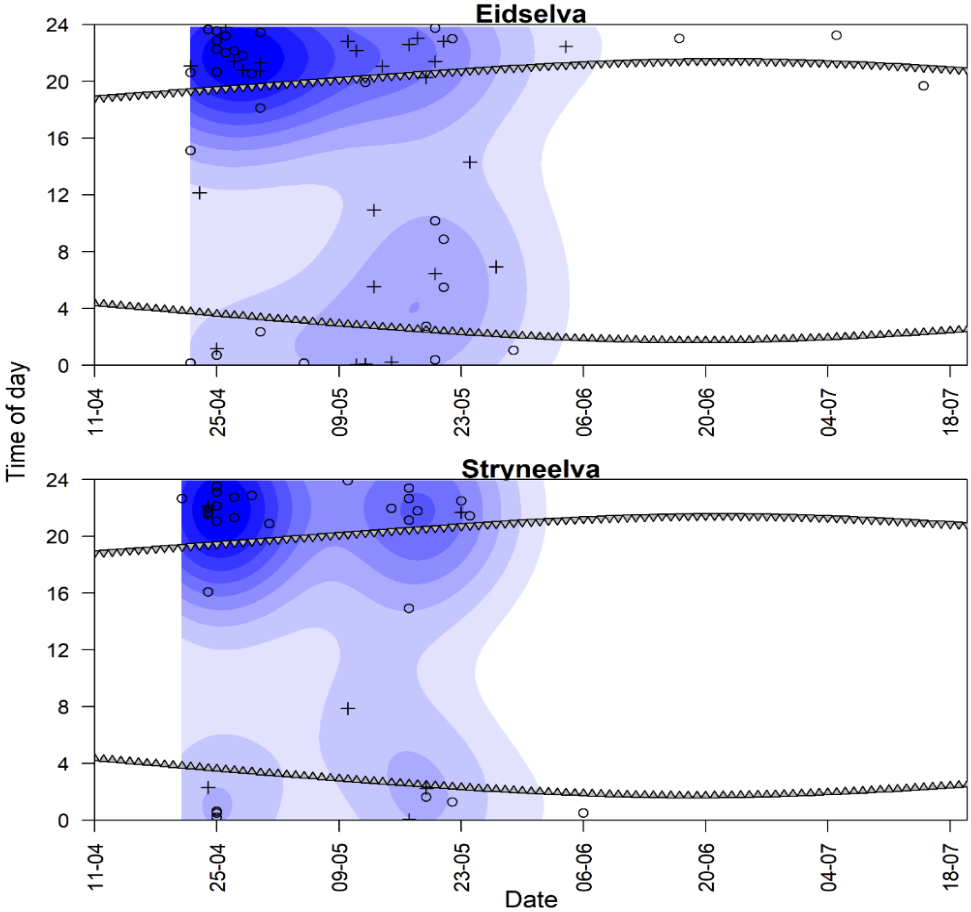


Figure 8: Time of day for smolt-migration from Eidselva and Stryneelva. Darker color indicates higher probability of migrating. Dots illustrates exact time of migration from river to fjord for smolt that was later detected in the fjord. Cross indicates smolt that was detected in the estuary but not further out the fjord. Lines of triangles pointing downwards illustrates sunset, and line of triangles pointing upwards illustrates sunrise.

3.2 Environmental migration triggers

Through model selection, the factors initiating smolt migration in 2019 was identified for both Eidselva and Stryneelva (table 4). The Eidselva model predicts increased migration probability as a function of water discharge (ΔQ), day of year (DoY) and relative change in water discharge from the previous day to the next ($\Delta Q_t = Q_t - Q_{t-1}$) (ΔAICc < 2, appendix table B-1). Increase of DoY seems to be a more controlling cue than the increase of ΔQ/Q. The model also predicts that the effects from DoY and ΔQ/Q is enforced with increased Q (figure A-1).

For Stryneelva, the chosen model predicts increased migration probability driven by DoY and ΔQ/Q (ΔAICc < 2, appendix table B-1). The migration probability increases almost in parallel with increased DoY and ΔQ/Q (appendix figure A-1).

The selected models had better AICc support, and parameter correlation was controlled and avoided for both models. Model selection table is provided in the appendix, table B-1, and model parameters are displayed in table 4. The migration probability is illustrated in figure 9.

Table 4: Logit-coefficient estimates for the selected migration models. Variables: ΔQ/Q -relative change in water discharge from one day to the next (m^3/s), DoY = day of year after 1.st of January, Q = water discharge (m^3/s).R^2 Tjur = calculations based on the method described by Tjur (2009). ***A****: Most supported model for Eidselva.* ***B****: Most supported model for Stryneelva.*

	A	**Eidselva**			**B**	**Stryneelva**		
Predictors	*Coeff*	*SE*	*p*	*df*	*Coeff*	*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

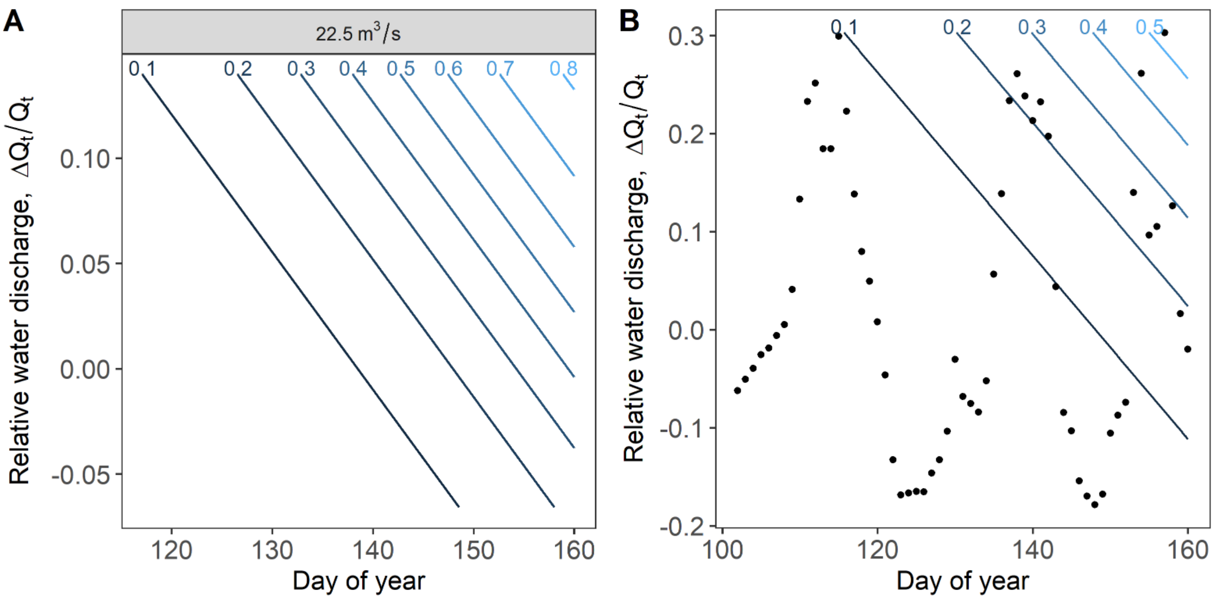


Figure 9: Model prediction for daily migration probability for salmon smolts in 2019. The dots represent the values the model is based on. Higher concentration of dots indicates more accurate estimates. Model parameters are given in table 4 ***A****: contour plot of the predicted daily probability of migrating for salmon smolts in Eidselva, as a function of day of year (DoY 120 = 120 days after1st of January),relative changes in water discharge from the previous day to the next with mean water discharge 22.5 m^3/s (see appendix A-1 for more figures)* ***B****: contour plot of the predicted daily probability of migrating for salmon smolts in Stryneelva, as a function of relative changes in relative water discharge from one day to the next, and day of year.*

3.3 Estimated survival- and detection probability during fjord migration.

In total, 199 salmon presmolts were tagged in 2019 and 147 (73,9 %) of these were later detected at one or more receivers throughout the study system, from receiver station -1 to 7 (table 1 & 2). In Eidselva a total of 95 smolts were tagged, and 56 (59 %) of these were confirmed migrating as they were later detected at station 0 in the estuary of Eidselva. From these, 30 smolts were detected after leaving the estuary and 11 smolts were confirmed survived as they were detected at station 6 (19.6 % confirmed survival from estuary to station 6) (table 5).

In Stryn watercourse a total of 104 smolts were tagged, and 33 (31.7 %) of these were confirmed migrating as they were later detected at station 0 in the estuary of Stryneelva. From these, 28 smolts were detected after leaving the estuary and eight smolts were confirmed survived as they were detected at station 6 (24.2 % confirmed survival from estuary to station 6)(table 5).

Table 5: Numbers of migrating smolts from Eidselva and Stryneelva detected at the different stations in Nordfjord.

Station	Eidselva	Stryneelva
0	56	33
1	16	16
2	0	15
3	0	9
4	13	10
5	10	4
6	11	8

Based on the plotted detection histories in figure 10, it appears that several of the tagged smolts dies. After normal migration behaviour, many of the tags ends up at the ocean bottom, and the estuary and “ytre” appears to be hotspots of mortality (figure 10, figure A-3, appendix figure A-4).

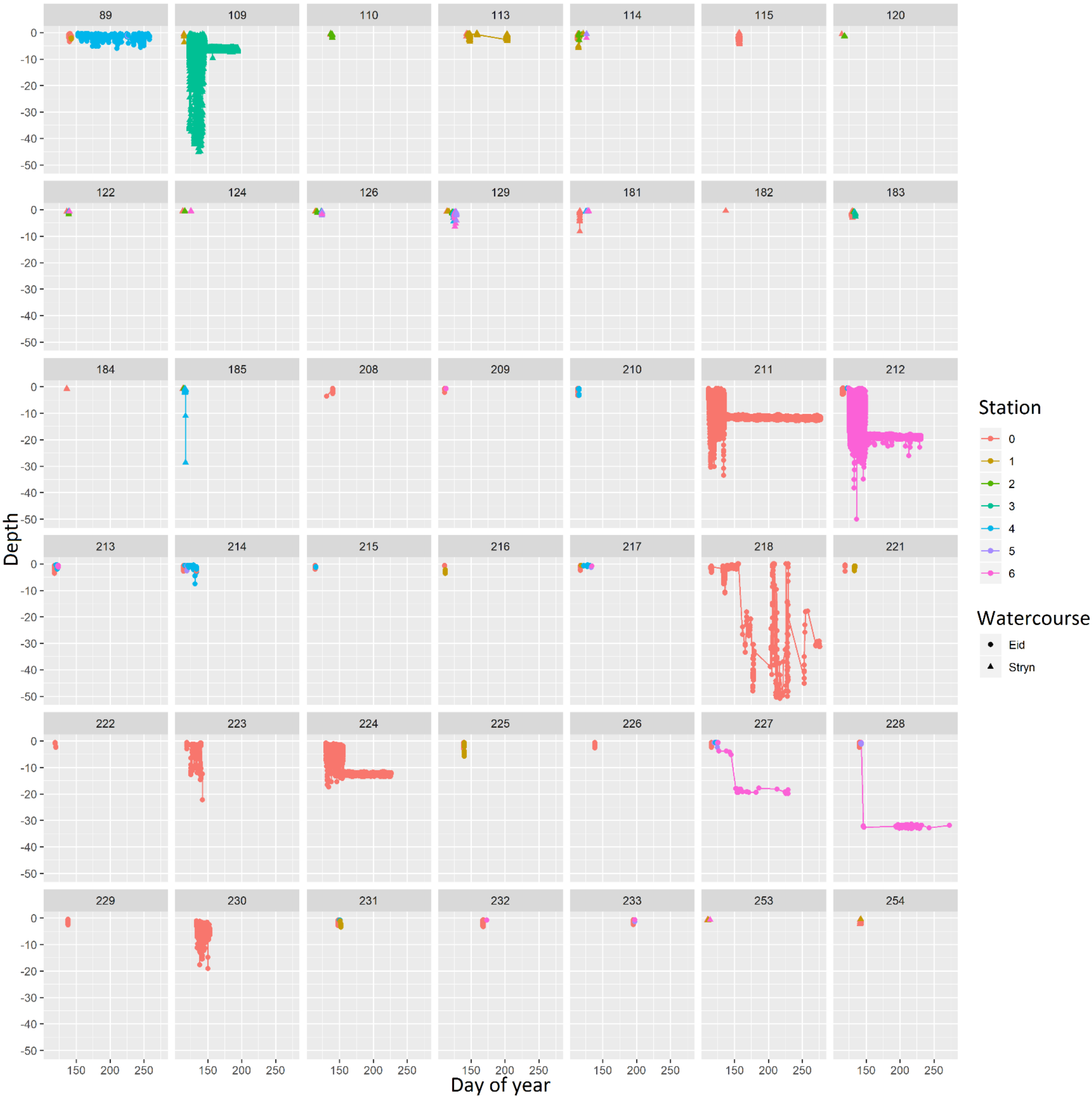


Figure 10: Detection histories of individual smolts from both Eidselva and Stryneelva, during their migration, illustrating location in time and space, containing depth, DoY and location values. Individual ID's shown in heading. Watercourse origin given as ●/▲. Enlarged plot given in appendix figure A3 and A4.

The estimated survival rates provided by the CJS-models, indicated bottlenecks associated to the estuary and outer part of Nordfjord, for smolts migrating from Eidselva (ΔAICc > 2, appendix table B-2). For the estimated survival rates in Eidselva, there was a length effect in the estuary (zone 2) for both smolt groups (table 6A). For Stryneelva the model contains a length effect for zone three to seven for the lower smolt group (ΔAICc < 2, appendix table B-2)(table 6B).

In Eidselva, the estimated survival rates for each zone indicates little difference in survival between the individual zones. The model also indicates length-dependent survival rates for the estuary, showing slightly lower estimated survival here than for the rest of the fjord (93 % survival). The longer the smolt was, the greater is its chances of surviving migration through the estuary (table 6A, figure 11A).

For smolts tagged in Stryneelva, the estimated survival rates for each zone through Nordfjord, points to a bottleneck in the river (33.6 % survival), as well as in zone 6 (25.5 % survival), showing significantly lower estimated survival rates here, than for the rest of the fjord. For fish migrating from Stryneelva, the model indicates a length effect all the way through Nordfjord, showing higher apparent survival rates for longer fish (table 6B, figure 11B).

Table 6: Estimated survival rates per kilometer and detection probability for each receiver station in Nordfjord, for fish tagged in Eidselva (table ***A****) and Stryneelva (table* ***B****). The model parameters belong to the selected models provided in table appendix table B-2. SR = estimated survival rate, DP = estimated detection probability, SE = standard error, LCI = lower confidence interval , UCI = upper confidence interval. "Fixed"= parameters are fixed to set value, "combined" = station is combined with a common estimate. "Length" = parameter is estimated for an average length: Eidselva-smolt = 13.87 cm, Stryneelva-smolt =13.75 cm . Raised numbers indicates which zone "length" is applied to for combined stations NA = not available*

Table A						
Parameter	**Group Upper/lower**	**Estimate**	**SE**	**LCI**	**UCI**	**Comment**
SR zone 1 & 2	both	0.93	0.01	0.91	0.95	Combined * length^2
SR zone 3 & 4	both	0.98	0.01	0.95	0.99	combined
SR zone 5	both	0.97	0.02	0.92	0.99	
DP zone 1	both	1				Fixed
DP zone 2	both	0.42	0.08	0.27	0.59	
DP zone 3	both	0.51	0.10	0.32	0.70	
DP zone 4	both	0.55	0.13	0.29	0.78	
DP zone 5	both	1				Fixed

Table B						
Parameter	**Group upper/lower**	**Estimate**	**SE**	**LCI**	**UCI**	**Comment**
SR zone 1	both	0.34	0.05	0.25	0.43	
SR zone 2	lower	1	NA	NA	NA	Fixed
SR zone 3	lower	0.71	0.09	0.49	0.86	Length
SR zone 4 & 7	lower	1				Fixed & length
SR zone 5	lower	0.86	0.18	0.24	0.99	length
SR zone 6	lower	0.26	0.12	0.09	0.54	length
DP zone 1 & 7	both	1				Fixed & combined
DP zone 2	both	0.51	0.08	0.35	0.67	
DP zone 3	both	0.65	0.10	0.43	0.82	
DP zone 4 & 5	both	0.52	0.08	0.35	0.69	Combined
DP zone 6	both	0.63	0.17	0.28	0.87	

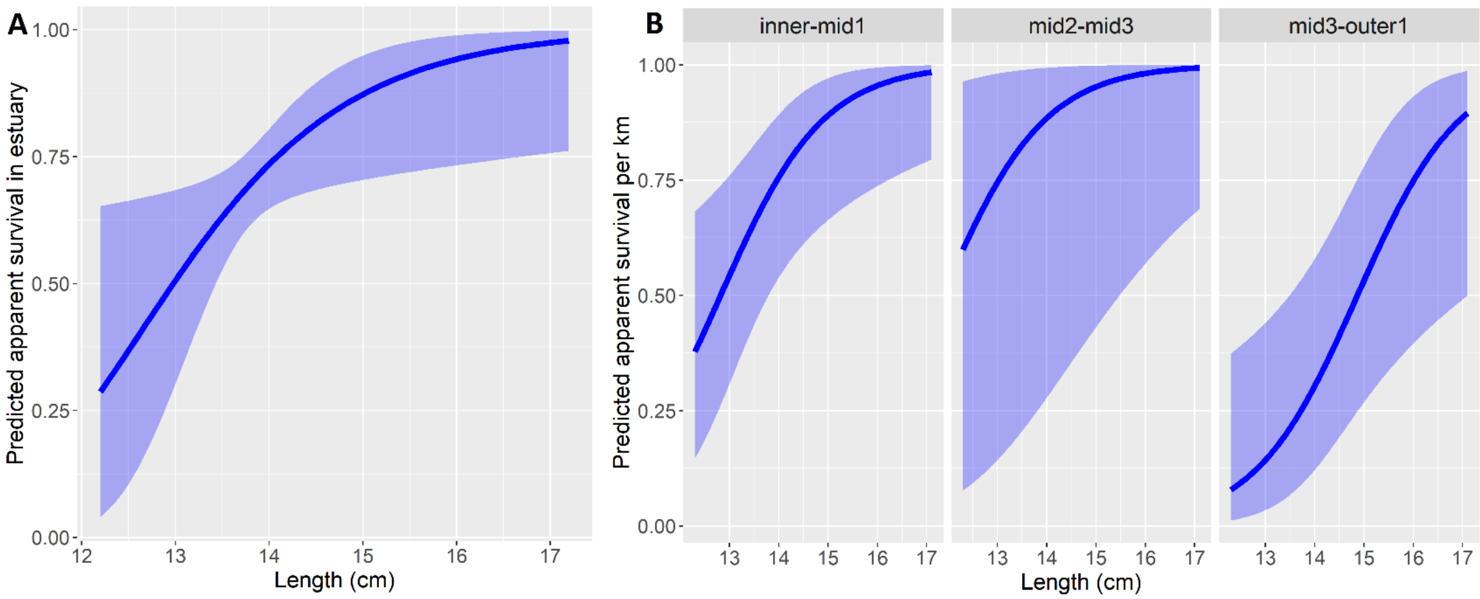


Figure 11: Estimated survival probability during migration through the estuary of Eidselva for smolts tagged in Eidselva, and migration through Nordfjord for smolts tagged in Stryneelva, as a function of length. The 95% confidence interval is shown as blue ribbons.

By adapting an GLM-candidate model, comparing the probability of surviving the entire fjord migration between the two populations and the four migration groups, the difference in survival rates between the groups is evident. The model predicts minimum survival rates for early and late-migrating groups of salmon smolts from both watercourses. The survival probability for the late-migrating group from Stryneelva, was lowest (approx. 0.14 = 14 % predicted survival), where only one smolt was confirmed survived (table 7, figure 12). The early-migrating group in Eidselva had best survival rates (approx. 0.37 = 37 % predicted survival) indicating significantly better survival rates than for the late group in Stryneelva (figure 12).

Table 7: Fates for early and late migrating smolt groups from Eidselva and Stryneelva. "Dies" indicates that the fish was not detected at station 5 or 6. "Survives" indicates that the smolt were detected at station 5 or 6.

Watercourse	Group	Fate	number
Eid	Early	Dies	18
Eid	Early	Survives	9
Eid	Late	Dies	23
Eid	Late	Survives	6
Stryn	Early	Dies	10
Stryn	Early	Survives	7
Stryn	Late	Dies	15
Stryn	Late	Survives	1

Table 8: Logit parameter estimates for the GLM-model predicting estimated minimum survival rates for early and late- migrating groups of salmon smolts from Eidselva and Stryneelva, migrating from estuary to the outermost zone in Nordfjord, 2019.

Predictors	*Estimates*	*std. Error*	*p*	*df*
(Intercept)	0.61	0.37	0.184	5
vassdrag [Stryn]	0.84	0.52	0.73	5
EarlyLate [Late]	0.32	0.52	0.028	5
Observations				8

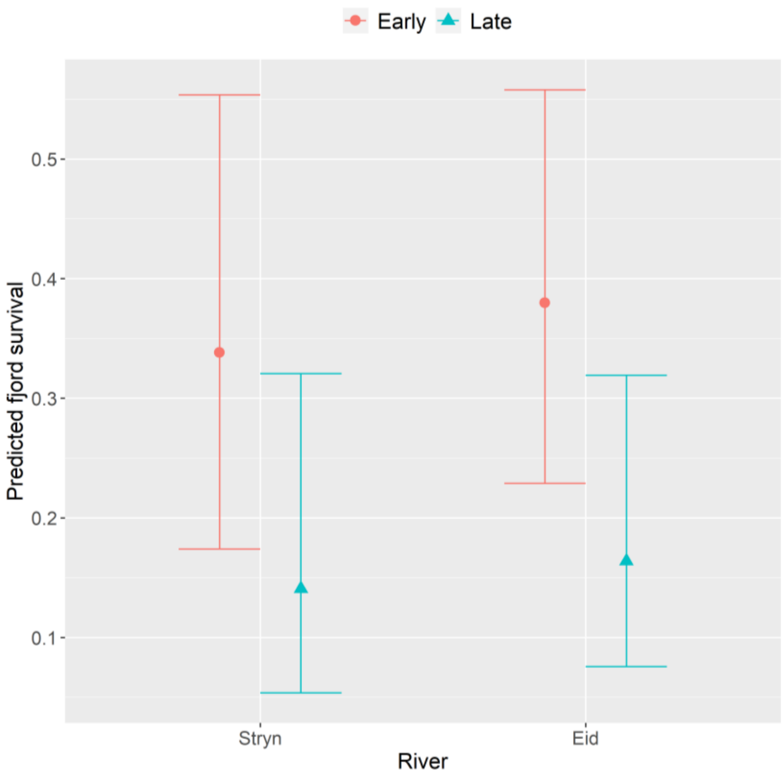


Figure 12: Estimated minimum survival rates for early and late- migrating groups of salmon smolts from Eidselva and Stryneelva, migrating from estuary to the outermost zone in Nordfjord. The vertical lines indicate the 95% confidence interval.

3.4 Fjord migration

3.4.1 Progression speed- and pattern through Nordfjord

The migration course appeared to be linear for smolts migrating from both Eidselva and Stryneelva, showing similar forward movement where only a few individuals used longer time migrating through some zones. Time of arrival at the different stations throughout Nordfjord for migrating smolts is illustrated in figure 13, and forward movement is illustrated in figure 14. The mean number of days it took for smolts to migrate from the estuary to zone 6 in the outer part of Nordfjord, for smolts from Eidselva was 4.43± 4.13 (n = 11) days. The respective number of days for Stryneelva-smolt was 9.48 ± 3.85 (n = 8) days. The Mean date of arrival at station 6 for smolts migrating from Eidselva was 22nd of May, and the respective dates for Stryneelva was 6th of May.

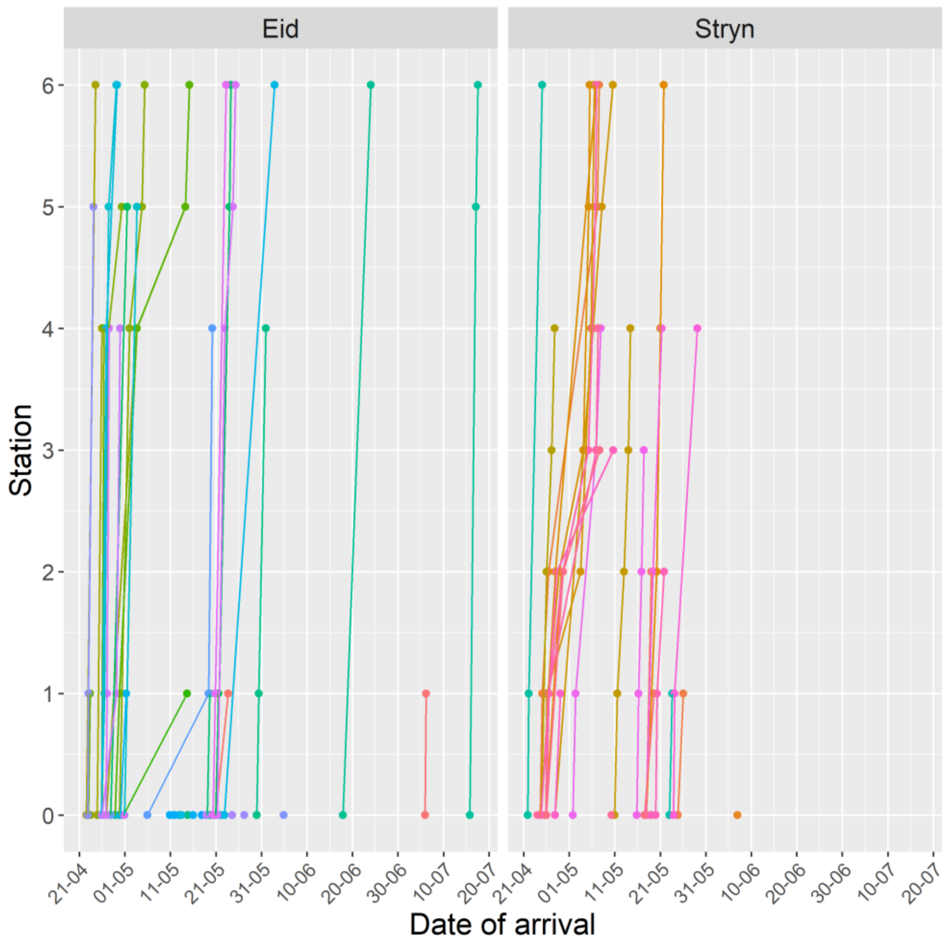


Figure 13: Arrival times at the different fjord stations for smolt migrating from Eidselva and Stryneelva. The dots illustrate detections at the given receiver station throughout Nordfjord, being 5 receiver stations from Eidselva and 7 for Stryneelva.

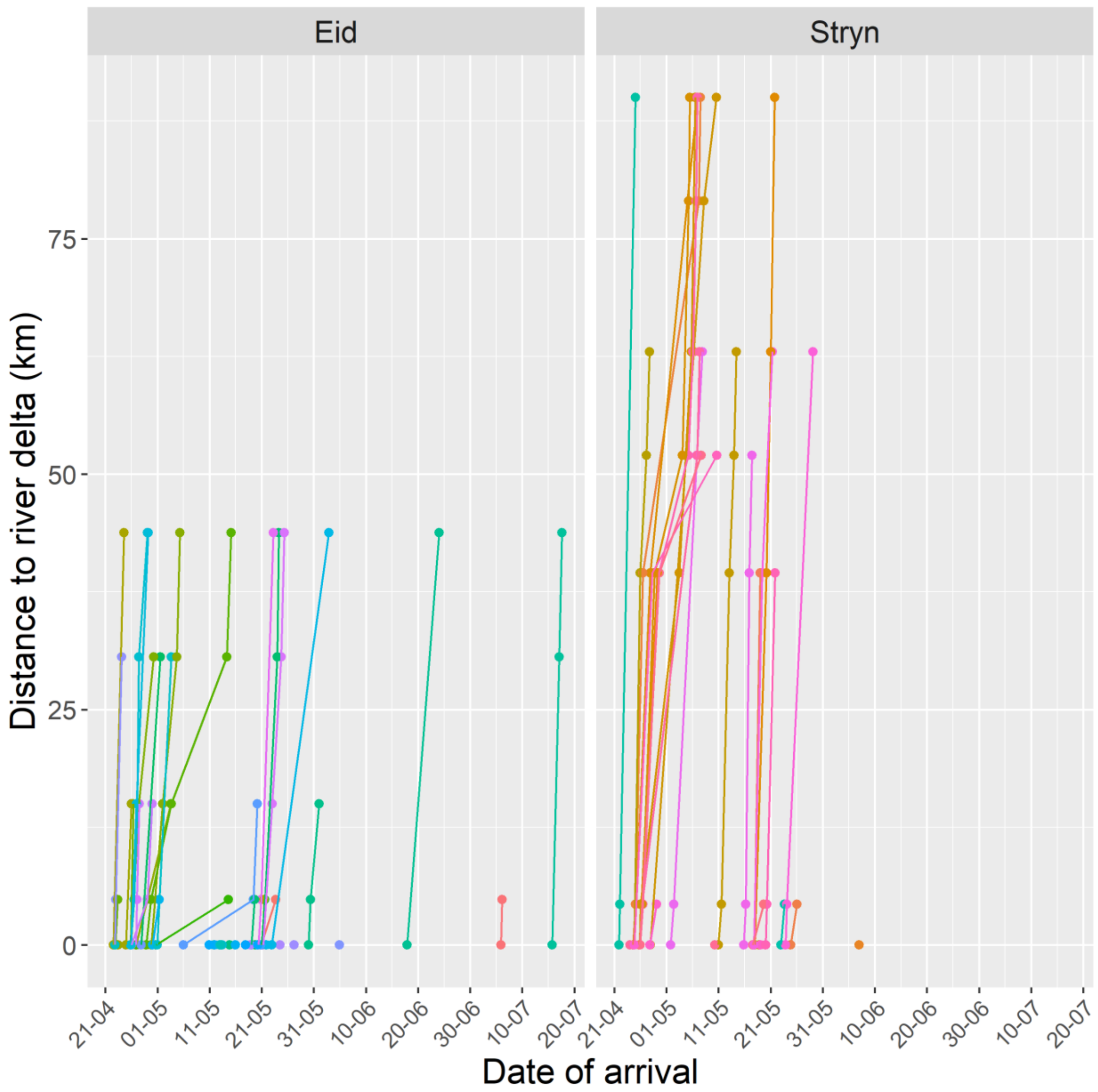


Figure 14: Progression pattern of smolts migrating from Eidselva and Stryneelva, illustrated as distance from the river estuary. The dots illustrate detections at the given receiver station throughout Nordfjord, being 5 receiver stations from Eidselva and 7 for Stryneelva.

Adaption of various GAM-candidate models for migration histories for smolts from both watercourses, favored simple linear- models for the migration, indicating constant migration progress. The parameter estimates and the constituting prediction-plots indicates that there was significant difference in progression speed between some of the smolt migration groups. Both migration groups from Eidselva migrated with the same progression speed, being 0.86±0.09 BL/s. The first smolt group that migrated from Stryneelva displayed progression speeds of 0.92±0.10 BL/s, whereas the last group migrated at 2.42±1.07 BL/s. All progression speeds are estimated assuming that the smolt length is 13.8 cm, as this is the mean length of all smolts included in this study (table 6). By use of figure 15, one may estimate where the smolts are at a given time during migration.

Table 9: parameter estimates for the selected linear mixed effects smolt-migration model, predicting time of arrival (day of year) as a function of distance from the river estuary for both watercourses.

	Eidselva				Stryneelva			
Predictors	*Estimates*	*CI*	*p*	*df*	*Estimates*	*CI*	*p*	*df*
(Intercept)	123.84	120.26 – 127.41	**<0.001**	100	122.42	119.13 – 125.72	**<0.001**	89
Distanse estuary	0.10	0.07 – 0.12	**<0.001**	100	0.09	0.07 – 0.11	**<0.001**	89
EarlyLate [Late]	12.71	11.04 – 14.38	**<0.001**	100	8.54	6.60 – 10.48	**<0.001**	89
dist.os * EarlyLate [Late]	0.00	-0.04 – 0.04	0.841	100	-0.06	-0.09 – -0.03	**<0.001**	89
Random Effects								
Residual				1.54±1.24				2.57±1.6
ID (intercept)				173.71±13.18				84.00±9.17
Observations				106				95
Marginal R^2 / Conditional R^2				0.197 /0.993				0.179 /0.976

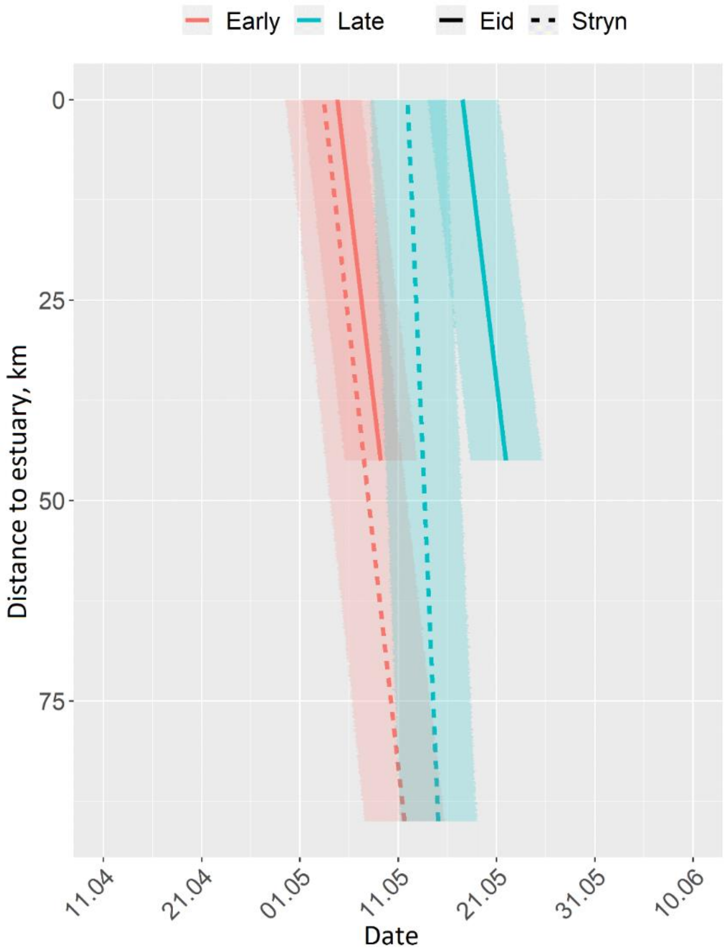


Figure 15: Estimated date of arrival at different locations during the migration route of early migrating (migrates before 5th of May) and late migrating (after 5th of May) salmon smolts from Eidselva and Stryneelva. The location is given as distance (km) from estuary for the respective rivers. Estimates used are from table 9. 95% confidence intervals are shown as shaded ribbons.

3.4.2 Depth use and diurnal migration

The depth-data indicates that salmon smolts from both Eidselva and Stryneelva migrated at almost exclusively depths shallower than 2 meters, with median values 1.4 meters depth during daytime and 1.2 meters of depth at night. There seems to be a slight tendency of diurnal migrations in the estuary, as the smolt that passed there appears to have migrated deeper during night versus daytime (figure 19).

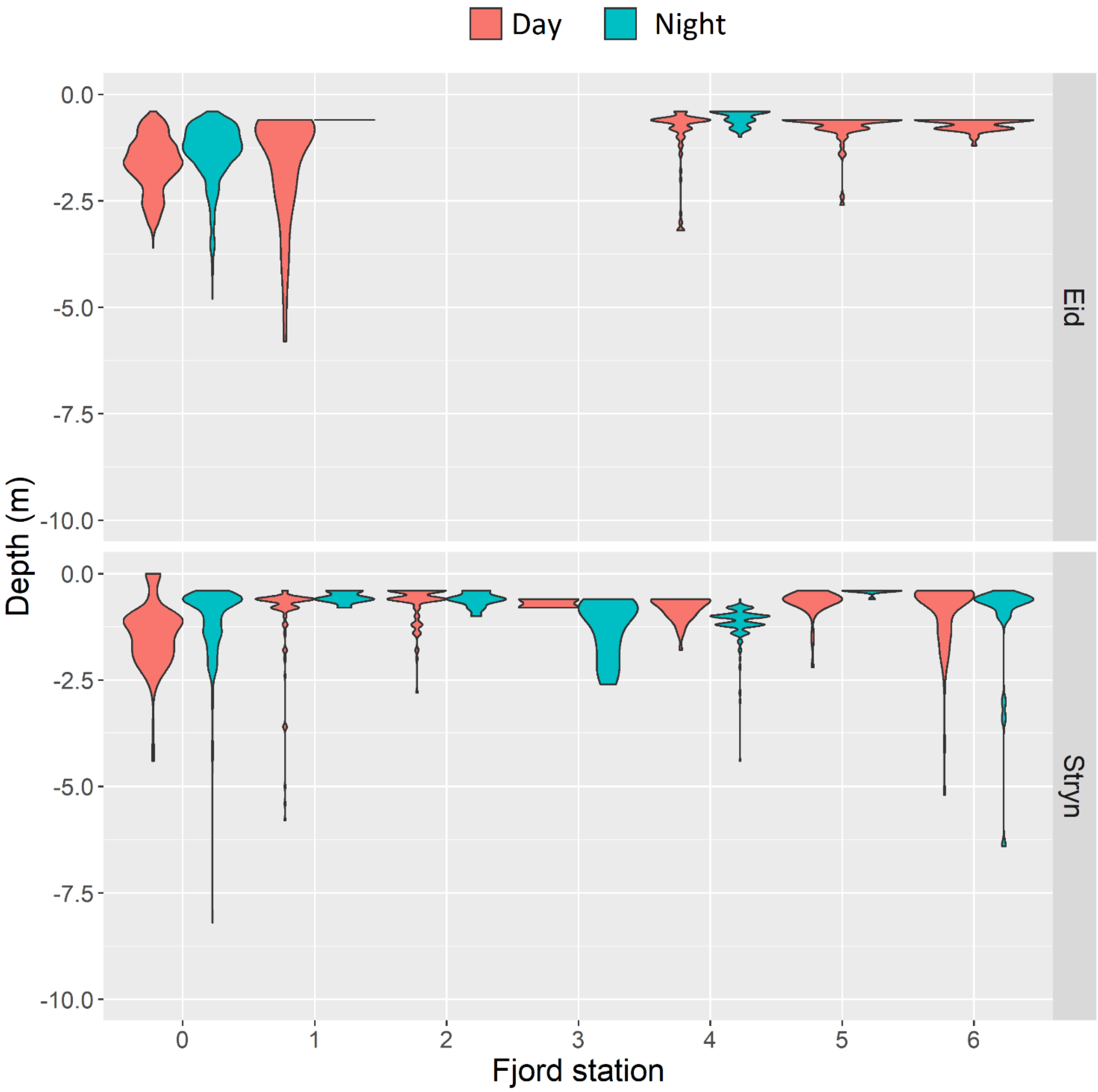


Figure 19: Violin plot of depth use and diurnal migration through Nordfjord, for smolt migrating from Eidselva and Stryneelva. The wider the "violin" is, the more detections are present for each group.

4. Discussion

This study has found that the smolt migration for both Eidselva and Stryn watercourse, spring 2019, was initiated by a mixture of increase in water discharge, relative change in water discharge from the previous day to the next and day of year. The smolts mainly migrated from the rivers in the hours after sunset, and they expressed linear migration patterns with little signs of diurnal depth migrations except when they passed the estuary. The timing of migration was very synchronous for both Eidselva and Stryneelva-smolts, whereas the survival rates were lower for the smolts that migrated from Stryneelva compared to Eidselva. The mortality rates also varied between the migration groups and fjord zones. No significant survival bottleneck was found for the smolts that migrated from Eidselva, but for the smolts from Stryneelva, significant bottlenecks were associated with the river estuary and the outermost zone of Nordfjord.

4.1 Environmental migration triggers

I hypothesized that smolt migration was triggered by increase in water discharge and temperature, based on results from previous studies (Jonsson & Ruud-Hansen, 1985; Zydlewski et al., 2005; Jensen et al., 2012; Otero et al., 2014; Haraldstad et al., 2017; Harvey et al., 2020). This was, however, not the case during spring 2019. The migration probability was correlated to environmental factors, but water temperature was not included in any of the selected candidate models. Rather, day of year was found included where date and temperature values had an estimated correlation which was too high to be used in the same model (appendix table A-1, table A-2). The models predicting probability of migration for both watercourses, indicates that the smolts were more likely to start migrating as an effect of the combination between increase in water discharge, day of year and relative change in water discharge from the previous day to the next.

For both study rivers, the catchment is characterized by high altitude, glaziers and snow, resulting in runoff with very low water temperatures. Therefor the increase in water temperature will have a rather low slope as long as the water discharge is continuously fed with cold water, and water temperature may this way be correlated to day of year in these two rivers (appendix table A-1). In comparison, Haraldstad et al. (2017) conducted a study in a river without high mountain catchments in southern parts of Norway. This study, along with several others, found water temperature to be an important environmental cue for triggering smolt migration (Whalen et al., 1999; Thorstad et al., 2012; Harvey et al., 2020). The spring temperature varies among rivers, even at the same latitudes. As stated by Haraldstad et al. (2017), it is thought that the migration initiating cues may be population-specific, which may explain the variability in conclusion between similar studies.

Studies previously conducted in Nordfjord, found that for Stryneelva in 2017, 97% of the variation in smolt migration probability was accounted for by the relative changes in water discharge (Urke et al., 2018). In 2018, 67% of the variation in migration probability in Eidselva and Stryneelva was explained by the combination of water discharge, changes in water discharge and water temperature (Haugen et al., 2019). For the 2019 dataset, the migration timing was however poorly explained by the environmental cues and day of year. Despite this being the most supported model, it had little explanatory power, as 2.9 % at lowest to 9.9 % at best of the variety of migration was explained by the input factors (table 4). This indicates that the probability of migration is not necessarily affected by one or two environmental factors alone, but rather the combination of them and their interactions in the given year. That each environmental factors cuing downstream migration may vary in importance between years is also found from other studies (Thorstad et al., 2012; Harvey et al., 2020).

4.2 Migration- groups and peaks

Tagged salmon smolts from Eidselva was first detected in the estuary during the period from 22nd of April to 17th of July, and the respective dates for Stryneelva was from 21st of April to 6th of June. In both rivers there were two major migration-peaks separated by about 3.5 weeks, with one smaller peak in between (figure 7). That the smolt migration in 2019 displayed several migration-peaks is as hypothesized and correlates to several previous studies (Jensen et al., 2012; Urke et al., 2018; Haugen et al., 2019).

By interpreting the figures, the major migration-peaks occurs at rising water discharge. The minor migration-peak in between, by the looks of figure 7, seems to occur in fading water discharge for both rivers. Local weather data reveals significant rainfall (28.5 mm) from 9th to 11th of May in Eidselva, resulting in the water discharge curve slightly flattening out for both rivers (figure 7, figure A-2). It is conceivable that this local rainfall triggered both minor migration peaks.

The smolts that migrated at the latest migration peak in Eidselva, appears to be more random and less synchronous in relation to what time of day they migrated (figure 8). This may simply be because these migrants reached smoltification at a later date than individuals from the first smolt-group. At this point the smolt had to start migrating and could not wait for perfect environmental conditions. Eidselva is also locally known to be quite turbid, resulting in browner water at rising water levels, allowing the smolts to safely migrate during daytime (Pers.comm. Urke, 2020). Studies conducted by Gregory and Levings (1998), also found turbid water to be beneficial for migrating fish, as it reduced predation. Previous studies have found the degree of night migrations to decrease as water temperatures in the river rises. Haraldstad et al. (2017) found that a shift occurred as the rivers water temperature rose above 12-13 °C and that the smolts started migrating during daylight. This may also be a reason to why the migration of the last smolt group in Eidselva was not so concentrated during night (figure 8). From figure 7, it is clear that the last smolt migration peak in Eidselva occurred around the 20th of April, correlating to a distinct spike in water temperature at the same time.

In 2017, tagged salmon smolts from Stryneelva had two apparent migration peaks; at 6-7th and 17-18th of May. In 2018, tagged smolts from Stryneelva and Eidselva also had two migration-peaks; one in the beginning of May until 15th of May, and the other peak 2.5- 3 weeks later (Urke et al., 2018). In 2019 the migration peaks occurred around 25th of April and 20th of May in Eidselva and 25th of April to 17th of May in Stryneelva. From these three consecutive years of study, it is evident that the time of migration-peaks varies between years, depending on local environmental conditions. Empiric data is needed to determine when to conduct sample fishing for migrating smolts, so that the monitoring of salmon lice infection on smolts are representative. In 2019, the Institute for Marine Research (IMR) conducted sample fishing of salmon smolts by trawling and use of trapnets at Måløy in Nordfjord, during week 21 and 22 (20th of May to 2nd of June) (Nilsen et al., 2019). This resulted in a total of 71 smolts caught during week 21, and 11 in week 22. Knowing that the last migration-peak occurred at 20th of May 2019, and that the median time of smolt migration through the system is 6-11 days, the sample fishing seems to be well timed and a representative amount of smolts was caught.

The tagged smolts from Eidselva was first detected in the estuary in the period from 22nd of April to 15th of July, within a range of 85 days. The respective range for Stryneelva was 47 days. The reason for this big variation of migration time is that the two smolts from the upper reaches of the Hornindal watercourse migrated very late, and none of the upper group smolts in Stryneelva was included in the figure as they did not survive to enter the estuary. By removing the two respective smolts from the dataset, the date-range of migration timing would me more similar.

4.4 Progression pattern and diel vertical migration

4.4.1 Progression pattern

The smolts that migrated from both Eidselva and Stryneelva during spring 2019, displayed as hypothesized, a uniform migration pattern when migrating outwards Nordfjord, where only a few smolts used longer time passing some zones. Both early and late migration groups from Eidselva migrated with an average progression speed of 0.86±0.09 BL/s. The early smolt group from Stryneelva migrated with an average progression speed of 0.92±0.10 BL/s, whereas the late migration group from Stryneelva migrated with an average progression speed of 2.42±1.07 BL/s. These numbers correspond to findings from similar studies, where the progression speeds was found to be between 0.4 to 3.0 BL/s (Thorstad et al., 2012; Urke et al., 2018; Haugen et al., 2019).

The mean number of days it took for smolts to migrate from the estuary to the outer part of Nordfjord for smolts from Eidselva was 4.43±4.13 days. The respective number of days for Stryneelva-smolt was 9.48 ±3.85 days. The smolt migrating from Stryneelva has a significantly longer migration course than those from Eidselva, and were therefore expected to use longer time migrating. The standard deviation is larger for the calculation of the Eidselva-smolt. This is likely a result of the few smolts migrating from Horndøla in the upper part of the Hornindal watercourse, as the few individuals included in this year's dataset migrated approximately six weeks later than the last smolt that migrated from Eidselva. The purpose of this study was however to include migration data from the entire watercourses, and therefore these individuals were still included.

Due to increased swimming capacity with increased water temperature, smolt that migrated in the end of July versus end of April, were able to migrate faster out of the fjord system, spending less time in the lice-infectious area (Beamish, 1978; Martin et al., 2012). This may be the reason why the latest smolt group migrating from Stryneelva is significantly faster than the other groups (figure 15). Another possible reason to this difference in migration speed may be the fact that the smolts migrating from Eidselva must migrate significantly shorter from estuary to the outer part of the fjord system compared to the Stryneelva-smolts (figure 1). Thus, the smolts from Stryneelva must migrate faster to reach the ocean at ideal point of time.

Even though figure 13 and 14 may give the impression that the smolts migrated in a perfectly straight line between the zones, this is most likely not the case. The figures are based on modelling of first detections at the given stations, not detections between the stations. It is likely that the smolts has a slightly more irregular migration pattern than illustrated by these figures, and swim longer between the stations than expressed by these figures. Still, these figures are suitable for illustrating the greater lines of the migration pattern, as they are highly compatible with previous studies conducted in the same and other study areas (Urke et al., 2018; Haugen et al., 2019)

An uncertainty in this dataset when studying the migration pattern is determining what fish was actually tagged, as the risk of tagging both brown trout and hybrids of Atlantic salmon and trout is present. Salmon smolts was the study subject, so to avoid analyzing wrong fish, a thorough filtering of the data was conducted. Smolt that apparently died, of predation or other natural causes, was cut so that only detections before death/predation was included. This is essential for getting precise and representative data when analyzing depth- and zone use, and progression speed throughout Nordfjord. E.g. fish ID; 109, 211, 212, 218, 224, 230 appears to have been predated, the tag was carried inside the predator's stomach and after up to 143 days (ID 218), freed from the predators body (figure 10, appendix figure A-5). For smolts like these, the movement after apparent predation is of no interest for further analysis, and was cut from the dataset which migration speed, zone- and depth use was based on. Smolt with migration histories like ID; 227 & 228 was removed, as the tag dropped to the bottom of the sea and continued to send signals (appendix figure A-6). It may look like the fish conducted horizontal movements after dropping to the ocean floor, but these apparent vertical movements are the tidal movements as each dot represents the depth values (figure 10). Several of the tagged smolts migrated outwards Nordfjord, but performed excessive migrations back towards the estuary (e.g. ID; 89, 214 and 231, appendix figure A-7). Smolts that performed long inwards migrations was removed from the dataset, even if they at a later point turned outwards. Salmon smolts often turns and migrates towards the estuary, before turning back outwards, but the smolts migrating several zones inwards was excluded as a precaution so that trout or hybrids would not be included in the analysis.

4.4.2 Depth use and diel vertical migrations.

I hypothesized that the migrating smolts would not conduct great vertical depth migrations, and found that the smolts migrated at depths almost exclusively shallower than 2 meters, with median values 1.4 meters depth during daytime and 1.2 meters of depth at night. As the average migration values was 20 cm shallower during night versus daytime, there are little indications that diurnal vertical migration occurs to large extent as the smolts migrated through the fjord. In the estuary for both rivers however, there seems to be a slight tendency of diurnal vertical migrations, as the smolt that passed here appeared to migrate deeper during night versus daytime (figure 19). These migration depths correlates with similar studies, and in fjords like Nordfjord, these depths will often equal salinity levels lower than 20 ppt (brackish water), meaning little to none infectious salmon lice (figure 2) (Heuch, 1995; Bricknell et al., 2006; Plantalech Manel-La et al., 2009; Heuch et al., 2009; Andreas Heuch, 2009).

In order to study depth use and diurnal vertical migrations for salmon smolt, it is conditioned that the study subject is in fact salmon. Knowing this may seem like a matter of course, but this year's data presented several problems when interpreting the migration patterns. Apparent deviating migration behaviour was common for many of the smolts migrating from both Eidselva and Stryneelva (figure

10). Depth migrations often occurs for migrating smolts, but for the 2019 data many of the tagged fish seems to have conducted migrations down to 30 to 50 meters depth frequently while staying in the same zone over a long time period (figure 10, appendix A-5). This is highly unlikely as previous studies, partly based on hatchery reared Atlantic salmon smolts, has found little evidence of diurnal vertical migrations for smolts, down to these depths (Davidsen et al., 2008; Plantalech Manel-La et al., 2009; Haugen et al., 2016). Several of the tags are likely to have been eaten by predators, characterized by excessive diurnal migrations followed by stationary signals as the tags presumably has been freed from the predator's body (ID: 227 & 228). When interpreting these data, it is important to be aware of these possible sources of error and misguidance, so that they are taken into account.

Several of the IDs was removed from the data due to assumed predation or other deviating Atlantic salmon behaviour, transmitted signals in the estuary area for long periods of time. When analysing these IDs, it was apparent that these fish conducting diurnal vertical migrations, where presumably migrating close to surface for feeding at night, and then migrating to the bottom at day (appendix figure A-5). Avoiding predators may be one reason to why the smolts conducts vertical migrations when passing through the estuary, as this has previously been found in other studies (Bremset et al., 2009; Gibson et al., 2015; Haugen et al., 2016).

4.4.3 Experienced environmental conditions during migration

The salmon smolts from Eidselva migrated in the time period from 22nd of April to 17th of July (week 17- 29), and the smolts from Stryneelva migrated from 21st of April to 6th of June (week 17-23). The median migration date was 11th of May and 22nd of May for the respective rivers. As the smolts migrated through the fjord system at different times, they encountered variable environmental conditions. By having measures of salinity, water temperature and estimated numbers of infectious salmon lice on aquaculture facilities in the study system, one may assess which environmental conditions and lice-infestation pressure the smolts experienced through their migration course (figure 2, figure 3, figure 4). These are all factors effecting smolt survival in the early migration phase, but may also affect mortality rates post-fjord migration. Even if the smolt did not necessarily die immediately from the salmon lice infections, they are likely to die at a later point if they migrated through areas with high lice-infection pressure. Mortality rates have been recorded to more than 50 times higher for smolt migrating through areas with high densities of salmon lice (Bøhn et al., 2020).

From the salmon lice infestation pressure model, it is clear that zone 6 and 7, from Isane and out of the fjord, is the area with highest infestation pressure (figure 4). This correlates with the bottleneck associated to this area for the Stryneelva-smolt. If the infestation pressure and environmental conditions were the only variables contributing to the high mortality rates in this area, equivalent mortality rates for the Eidselva-smolt would be expected. This was not the case in 2019, further supporting the possibility of local predation affecting the mortality rates.

Timing of sea-entry for migrating smolts is thought to be a local adaptation, as they must enter marine residency at a time with sufficient nutrient-access. This will affect the available food access which in turn affects the smolts anti-predator capacity (Salminen et al., 1995). When interpreting the vertical temperature-profiles, the temperature varies greatly and the variation within the study period, e.g. April versus July, is considerable (figure 3). Time of sea-entry in 2019 correlates with many other studies, as the smolts entered marine residency at a time where the sea water temperature were more than 8 °C (figure 3, figure 7) (Hvidsten et al., 1998; Whalen et al., 1999). The salinity in the fjord system and the experienced salinity for the migrating smolts also varied greatly within the study period. One might expect that the smolts that migrated by the end of April experienced high amounts of infectious salmon lice, since the entire water column was of high salinity concentration without noticeable freshwater. This was however probably not the case as the water temperature during this period was low (figure 3).

As the supply of freshwater continued during the summer months, the stratum grew and the smolts that migrated at e.g. 9th of July, experienced low levels of salinity if they migrated shallower than 2 meters. As the salmon lice is not infectious under 20-22 ppt, this was not an issue for the migrators until they reached the outer area of zone 6 (Heuch et al., 2009; Andreas Heuch, 2009). Some of the plots from figure 2 lacks measures from the inner part of Nordfjord. These measures are however not crucial as the innermost aquaculture facilities is located at Lote, and the inner part of the fjord contains much brackish water. Having measurements like these are important when studying smolt migration, as it is essential for seeing the dynamics within the water column and the migration course.

The survival probability for the late-migrating group from Stryn, seems to be lowest with 14 % predicted survival, where only one smolt was confirmed survived at outer part of Nordfjord (table 7, figure 12). The early-migrating group in Eidselva had best survival rates with approximately 37 % predicted survival through the study system, indicating significantly better survival rates than the late group in Stryneelva (figure 12). Previous studies has found early smolt-migration to be beneficial, as lower water temperatures are likely to result in less infestation from salmon lice (Kristoffersen et al., 2018). This is due to the seasonal dynamics of the louse, as it has temperature-dependent population booms late spring/ early summer (Samsing et al., 2016). As the mortality rates found in this year's study in many ways deviate from recent studies conducted in the same study system, it is hard to know if these mortality rates are result of the environmental conditions or just stochastic predation. Predation has previously shown to be the major contributor to the total smolt mortality rates (Vollset et al., 2014).

Many of this study's findings in relation to the environmental conditions correlates with previous studies. The overall mortality rates are however very different from the results found by Haugen et al. (2019) and Urke et al. (2018). This enhances the plausibility of predation being an important additional factor, contributing to some of the mortality rates in 2019. Having data on expected predators in the fjord system, could prove beneficial when studying these bottlenecks and mortality rates. It is very important being aware of all these factors and their combined interactions, and knowing that the salmon lice alone is not necessarily the only parameter affecting smolt mortality rates as fjords like this are very complex systems.

4.5 Apparent survival through the study system

4.5.1 Bottlenecks and survival between migration groups

In the previous study years, 2017 and 2018, there were found no apparent survival bottleneck along the migration route for the smolts migrating from Eidselva or Stryneelva (Urke et al., 2018; Haugen et al., 2019). The data presented in this study, showed a severe bottleneck in Stryneelva and zone 6 from Maurstad to Ytre, for smolts migrating from Stryneelva (table 6B). Only eight (24.2 %) of the confirmed migrating smolts from Stryneelva were detected in the outermost zone after leaving the estuary (table 5). For Eidselva there was no apparent bottleneck, and 11 (19.6 %) of the confirmed migrating smolts were detected at zone 6 after leaving the estuary (table 5 & 6A).

What causes this difference between years is up for discussion, and one plausible reasons is the variety of predation-pressure at site throughout the migration route, as this may vary among years (Vollset et al., 2016). Previous, comparable studies has shown similar variation in mortality-rates from year-to-year, site-to-site and high mortality-rates in river estuaries where predation was the common cause, further supporting my findings (Thorstad et al., 2012; Soares et al., 2013; Haugen et al., 2016; Chaput et al., 2018). The apparent high smolt death-rate (33.6 % survival) in Stryneelva may be explained by the river section called "Stilleelva", as this is a reach of approximately 5 kilometers where the river flows slowly, and higher predation pressure is expected. For comparison, the smolts passing the same section in 2018 had 100 % survival rates, emphasizing the year-to year dynamics (Urke et al., 2018).

There is uncertainty associated with the tagging of pre-smolts and when interpreting these data, it is important to know that disruption of signals does not necessarily signify the death of a fish. It is expected that some of the tagged smolts are never registered at the receiver stations for several reasons; one being the risk of tagging juvenile fish that is not smoltifying the current season. This is a direct result of difficulties when selecting pre-smolts for tagging, which most likely will be smoltifying the current year. As the smolts migrates fast, it is possible that they are never even registered at the receiver station as well, because they are not present long enough to be detected. In bad conditions this possible situation is enhanced, as the detection range is altered.

The estimated minimum survival rates of early and late-migrating smolt groups are only rough estimates of fjord-survival, as it is exclusively based on smolt with complete migration-histories. This requires that the smolts are detected in both estuary and zone 6 (figure 12). Therefore, the estimated survival rates are likely to be slightly underestimated. This was done for both groups in both rivers, and is therefore credible and suitable for estimating the differences in survival between the populations and groups.

4.5.2 Tag retention and size-dependent survival

The tagging-procedure has been identical between study years, using same personnel and equipment. Therefor the year-to-year difference in mortality rates is most likely a result of varied environmental conditions and presence of predators at the time of migration. It is conceivable that the mortality-rates are slightly underestimated for the tagged smolts versus smolts with no tags, as a direct result of capture, tagging and handling of the smolts. Despite this, the result is trustworthy and credible, and is highly suitable to uncover bottlenecks and environmental conditions which effects migration and smolt survival.

As the models for predicted survival rates for both Stryneelva and Eidselva, indicates higher survival rates the longer the fish was, it is debatable if this result reflects natural biological processes or is a result of poor tag retention (figure 11). Implanting of a tag into the abdomen of a smolt must be considered a liability. It is conceivable that the weight of the tag is so significant, that the burden of carrying the weight becomes to excessive for the smaller smolts, and the liability increases with decreasing smolt length. To “compensate” for the increased liability of a heavier depth-tag, larger presmolts (>14 cm) were selected for these tags. Previous studies have however shown high survival rates for tagged smolts, and positive size dependent survival rates for migrating Atlantic salmon smolts, further supporting these findings (Chaput et al., 2018; Urke et al., 2018; Haugen et al., 2019). Smolts dying of natural causes like predation is also highly plausible, and the death rates may be a combination of natural causes and increased liability related to tagging. Mortality rates and death to predators are both expected to be size-dependent, and therefore higher for smaller smolts compared to large smolts. For that reason, it is hard to assess weather death was a result of tagging-related increased liability or predation. When assessing the ideal smolt-size, these are factors that must be taken into account.

4.6 Methods and data quality

4.6.1 Acoustic telemetry

Acoustic telemetry has proven to be a relevant study method when investigating migration pattern and underlying migration triggers for salmon smolt in Nordfjord, as results with good explanatory factors were provided during this study. The data from the smolts detected at stationary receivers (>70%) after tagging, and the details of migration-triggers, vertical migrations, migration progress, zone use and survival appears to be of high quality compared with similar telemetry studies done within the same study area (Urke et al., 2018; Haugen et al., 2019).

Acoustic telemetry has shown several advantages compared to more traditional methods such as rotary screw wheel traps, and is known to be an effective method for studying tagged salmonids, and is over time economically suitable (Thorstad et al., 2000; Hedger et al., 2009). When having sufficient amount of receivers in a geographically narrow study area, the chances are good of getting high quality data of the study subject’s migration patterns, time of migration, and for some subjects, information about depth use (Hedger et al., 2009). Nordfjord is a highly suitable study system for use of acoustic telemetry, as none of the study watercourses are notably affected by hydropower, and the fjord is not to wide.

When using acoustic telemetry, one is independent of water discharge at the point of migration, as detections and data will be generated continuously at both high and low water levels. There are few technical difficulties which may potentially result in system downtime, and fish are detected both in turbid water, and at day and night. One of the biggest advantages with acoustic telemetry is the large amount of data generated from each study object, whereas an immanent uncertainty is present when having low numbers of individuals in the dataset. However, the use of acoustic telemetry does have its disadvantages. Due to the high costs of each tag, the number of smolts studied will of course be reduced compared to studies using PIT-tags. Receiver performance and detection range has in previous studies been found altered as a direct result of biofouling (Heupel et al., 2008; Davidsen et al., 2009). To prevent this from happening every single receiver throughout Nordfjord was scraped to remove fouling ahead of expected migration. When interpreting the data, it is important to be careful when generalizing, as the results may not be transferable from few individuals to the entire population. One must also be aware of the possibility that the given study year might not represent the general situation in the study area, as these river and fjord systems are highly dynamic.

Unlike the studies previously conducted in the same study area, the 2019 dataset contained tagged salmon smolts from the anadromous reaches above the lakes in the respective study watercourses. The details of the migration patterns of these fish are studied by a fellow student, and is not a part of this thesis, although the detections of the two smolts in the upper reaches of the Hornindal watercourse who survived all the way to the estuary are included.

4.6.2 Detection probability

As there are many factors influencing range of detection, the detection rate is not stable and will vary from day to day, and from station to station. There were no range-test conducted for the tags and receivers during this study. It was the zones, being the area between the different stations which was focused on. It is not possible to get a generalized receiver range for these zones, as the number of receivers and the distance between them varies from zone to zone. This was circumvented by a statistical approach, using mark-recapture analysis, where zone-specific detection probabilities were estimated under the assumption that that the smolt had a river-to-ocean directional migration pattern. Hence, individuals that were detected in both inner and outer parts of the fjord, but not in mid parts of the fjord would contribute to estimating detection probabilities to mid-fjord zones being estimated lower than 1.

When interpreting the estimated survival rates provided by the CJS-model, one must be aware of zones with low detection probabilities, e.g. zone 2, as these estimated survival rates are less reliable than for those from zones with high detection probabilities (table 6A).

4.6.3 Improvement suggestions

Even though one of the strengths of acoustic telemetry studies is the amount of data collected from every individual, this may be misguiding if only a few individuals are studied. When studying general effects for many individuals, e.g. salmon stocks in a river, it is important to have sufficient amount of study subjects. As this study has provided survival rates for salmon smolts to be, in some zones, as low as 26 % (table 6B), it is conceivable that more tagged smolts would have provided even more accurate migration data.

The tags used in this system does not directly indicate whether a fish has been eaten or died in any other way, or if the tagged smolt has just migrated outside of the receiver's detection range. One way to affirm death to predation would be the use of acoustic predation-tags. These tags detect stomach acid, and by utilizing such tags, one would be able to confirm if a smolt has been eaten or not (Gallien et al., 2014). Having supplementary real-time date on predators (e.g. big trout, cod etc.) known for feeding on migrating smolts would be beneficial, as this information could be compared and possibly related to the present bottlenecks in the study system (Hvidsten & Møkkelgjerd, 1987; Vollset et al., 2014). Supplementing with data from marine echo-sounding equipment/ sonar in areas with much predation could also help indicate predator size.

As one of the main goals of this study is to investigate the migration pattern and survival throughout the fjord system, having enough receivers in the study system is essential. Having more receivers between the receiver stations could prove beneficial, to eliminate the time period where the smolt is not counted for. This would open the possibilities of triangulating between the receivers, so that the position of the migrating smolt is always known throughout the migration course. Another possibility for getting complete, detailed migration histories is the use of an autonomous vessel. These boats are self-governing, and will pursuit tagged salmon smolts when transmitted signals are detected, and follow the smolts during their migration course, continuously receiving and storing the acoustic signals. Utilizing such autonomous vessels will allow the possibilities of performing adaptive sampling. This can in turn result in more detections and more accurate position measurements of the migrating smolts. It would also make it possible to study the migration pattern after the smolt has migrated out of the fjord and entered open ocean waters.

Having even smaller acoustic tags for implanting into the study objects would be ideal as the expected liability of carrying the tag would be smaller. This would give more reliable data, as the expected liability would be almost eliminated. The liability of carrying a tag could also be reduced by the use of PIT-tags. By using PIT-tags the amount of smolts tagged could also be increased as this is not as size-dependent as acoustic telemetry tags, given the small size of the PIT-tags. This would however only be ideal for supplementary data related to migration timing, as PIT would not be applicable when studying fjord migration due to the low detection probability. For supplementary data, use of video could also be an alternative as it is not size-selective. This method is however highly dependent on finding a good spot, and is not very applicable in larger watercourses as the smolts must ideally pass the video camera as close as possible.

4.8 Management implications

By increasing the knowledge about environmental migration triggers, time of migration, zone use and survival, and migration pattern at sea, this study may be compared to studies previously conducted in the study area, enforcing the knowledge about changes from year to year in such dynamic systems.

Knowing the exact time of migration is essential if the implementation of the National Action Plan Against Salmon Lice on Salmonids is to work as intended, which finally decides what traffic light “color” and production restrictions the given salmon production areas gets. Based on the studies conducted in Eidselva and Stryneelva from 2017-2019, the managing authorities and local aquaculture farmers may now conduct actions to reduce the amount of salmon lice, based on real, empiric data. Previously the predicted time of smolt migration in production area 4 (Nordhordaland-Stadt) has been based on the reference watercourse Vosso, which is highly affected by hydropower regulation. This as a reference system for both Eidselva and Stryneelva is not sufficient, as the respective rivers are not greatly affected by hydropower regulation (Urke et al., 2018; Haugen et al., 2019). Now, representative and accurate date are available, providing basis for precise management of the salmon stocks in these national watercourses.

5. Conclusion

This study has improved knowledge about migration patterns and survival rates for salmon smolts migrating from Eidselva and Stryneelva watercourse in Nordfjord.

- The smolt migrated at multiple migration-peaks in both rivers, trigged by a combination of several environmental variables. However, the migration timing was found poorly explained by environmental factors during spring 2019. One of the environmental cues found to initiate smolt migration in Eidselva and Stryneelva watercourse was water discharge, but not water temperature. Thus, my hypothesis that migration would be triggered by changes in water-discharge and temperature was partially proved wrong, as none of the models favored water temperature to affect migration.
- The median date of arrival in the estuary for smolts migrating from Eidselva was 11th of May, and date of arrival at the outer part of Nordfjord was 22nd of May. The migrating smolts from Stryneelva entered the estuary at median date 1st of May, and the outer part of Nordfjord at 6th of May. The mean number of days it took for smolts to migrate from the estuary to zone 6 in the outer part of Nordfjord, for smolts from Eidselva was 4.43± 4.13 days. The respective number of days for Stryneelva-smolt was 9.48 ± 3.85 (n = 8) days.
- The migrating smolts from both Eidselva and Stryneelva displayed a uniform, continuous migration pattern out of the fjord, as they migrated at speeds between 0.92±0.10 to 2.42±1.07 body lengths per second. The smolt migrated at almost exclusively depths shallower than 2 meters, with median values 1.4 meters depth during daytime and 1.2 meters of depth at night. Diurnal migration occurred to little extent, but there seemed to be a slight tendency of diurnal migrations in the estuary, as the smolt passing here appeared to migrate deeper during night versus daytime.
- The mortality rates for migrating smolts varied greatly between some of the locations during the migration route. The survival rates also appeared to vary between the earliest migrating group from Eidselva versus the last migrating group from Stryneelva. Generally, the survival rates appeared to be linked to body length, as longer smolts had higher predicted survival rates.

6. References

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6. Appendix

Appendix A- Figures and tables:

Figure A-1: Model prediction for daily migration probability for salmon smolts in Eidselva as a function of day of year, water discharge and relative change in water discharge from the previous day to the next. The contour plots illustrates the predicted migration probability at four different water discharges; 15 m3/s, 20 m3/s, 25 m3/s, 30 m3/s.

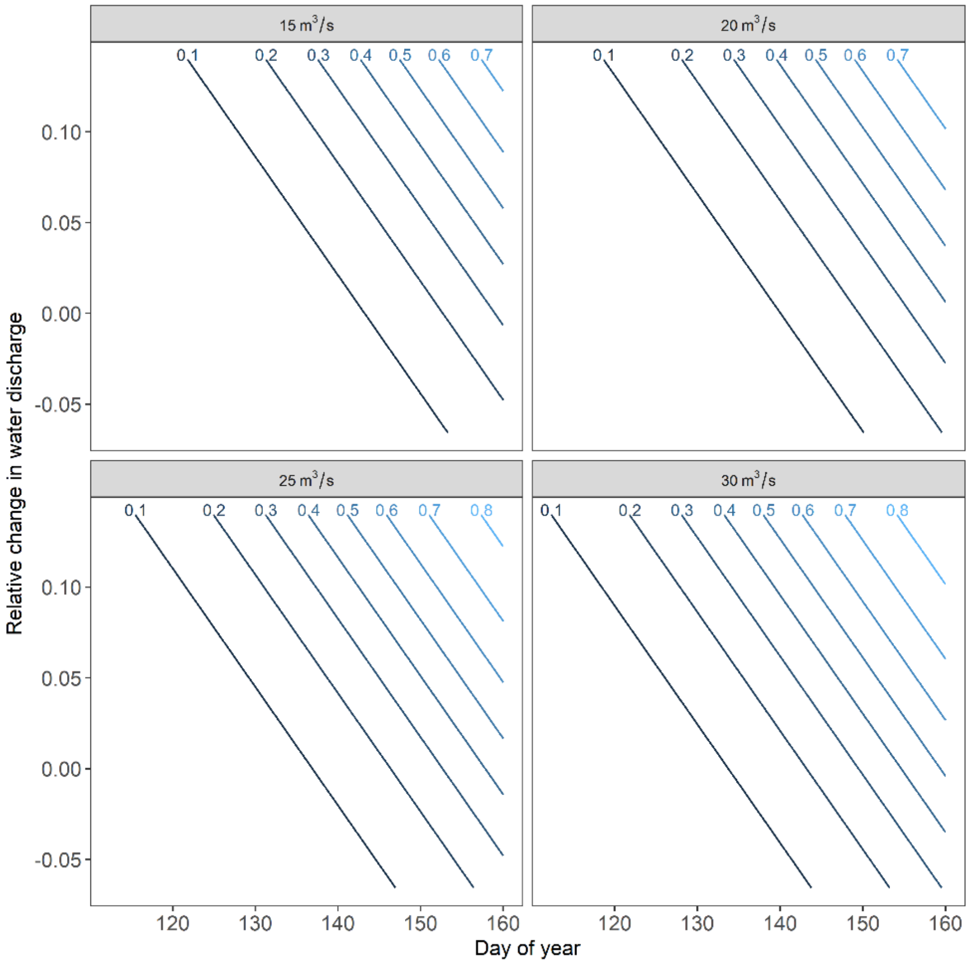

Figure A-2: Rainfall data from the weather station Nymark, in Nordfjordeid.

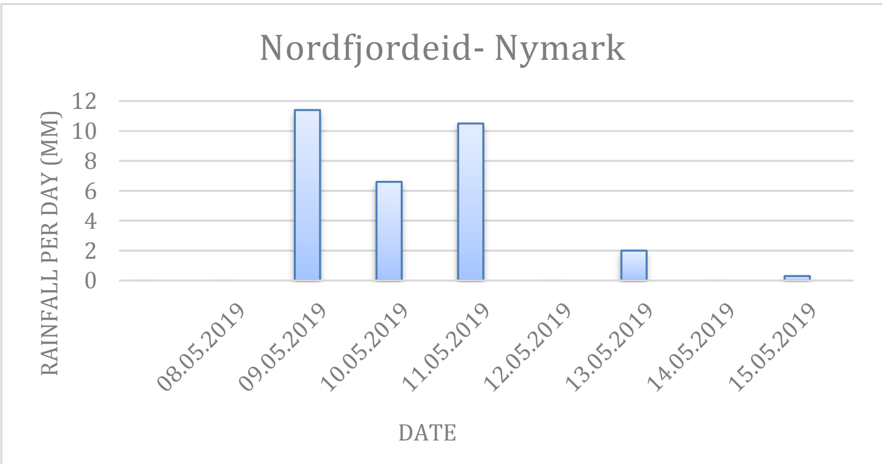

Figure A-3: Detections of migrating smolts through their migration route, illustrating location in time and space, containing depth, day of year and location values. Individual ID's shown in heading

Figure A-4: Detections of migrating smolts through their migration route, illustrating detection location, containing depth and day of year values. Individual ID's shown in heading.

Figure A-5: Vertical diurnal migrations from AT-tags presumed inside of predator, containing location, depth and day of year values.

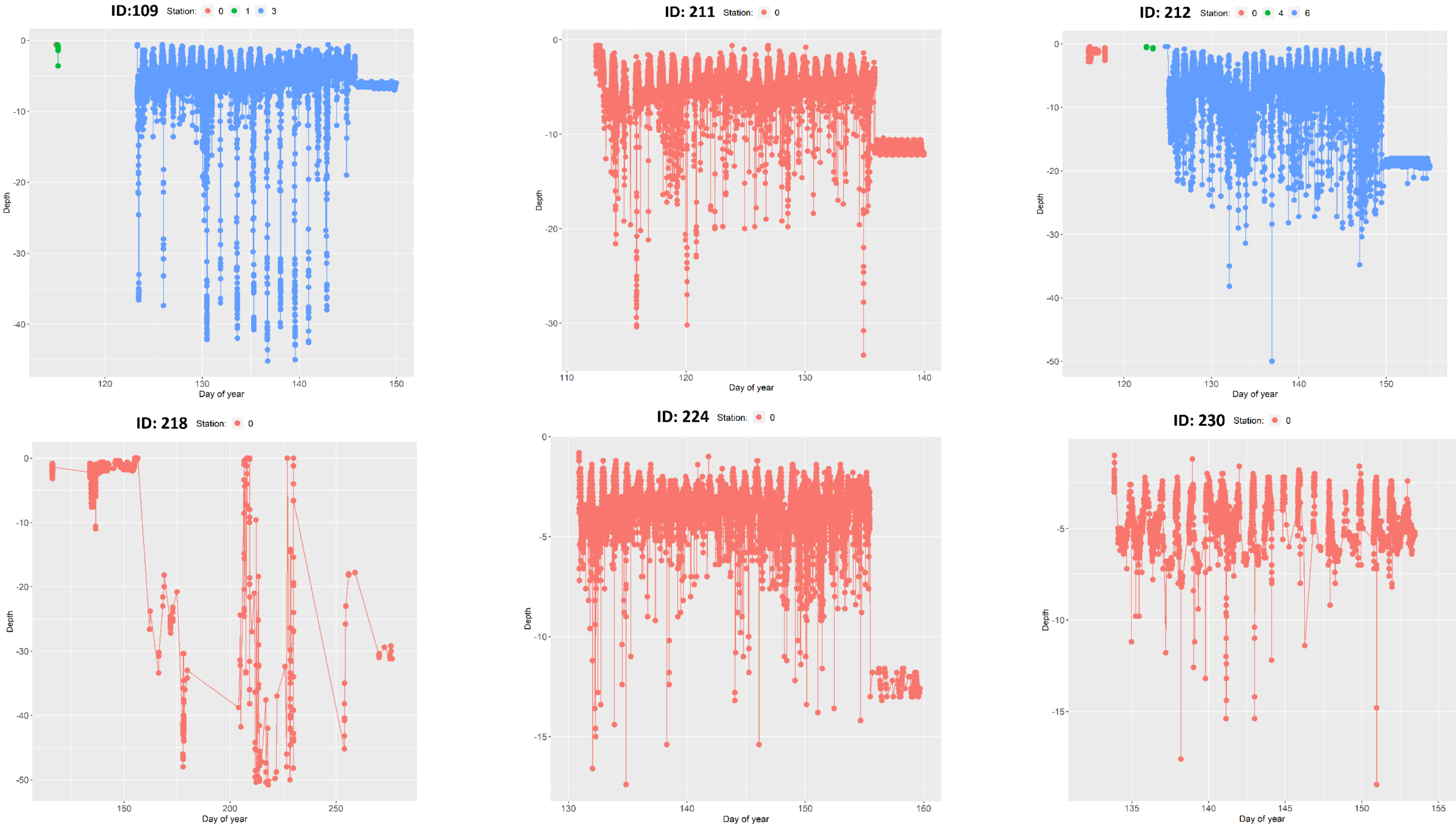

Figure A-6: Tags sending stationary signals after presumably being freed from predators body, containing location, depth and day of year values.

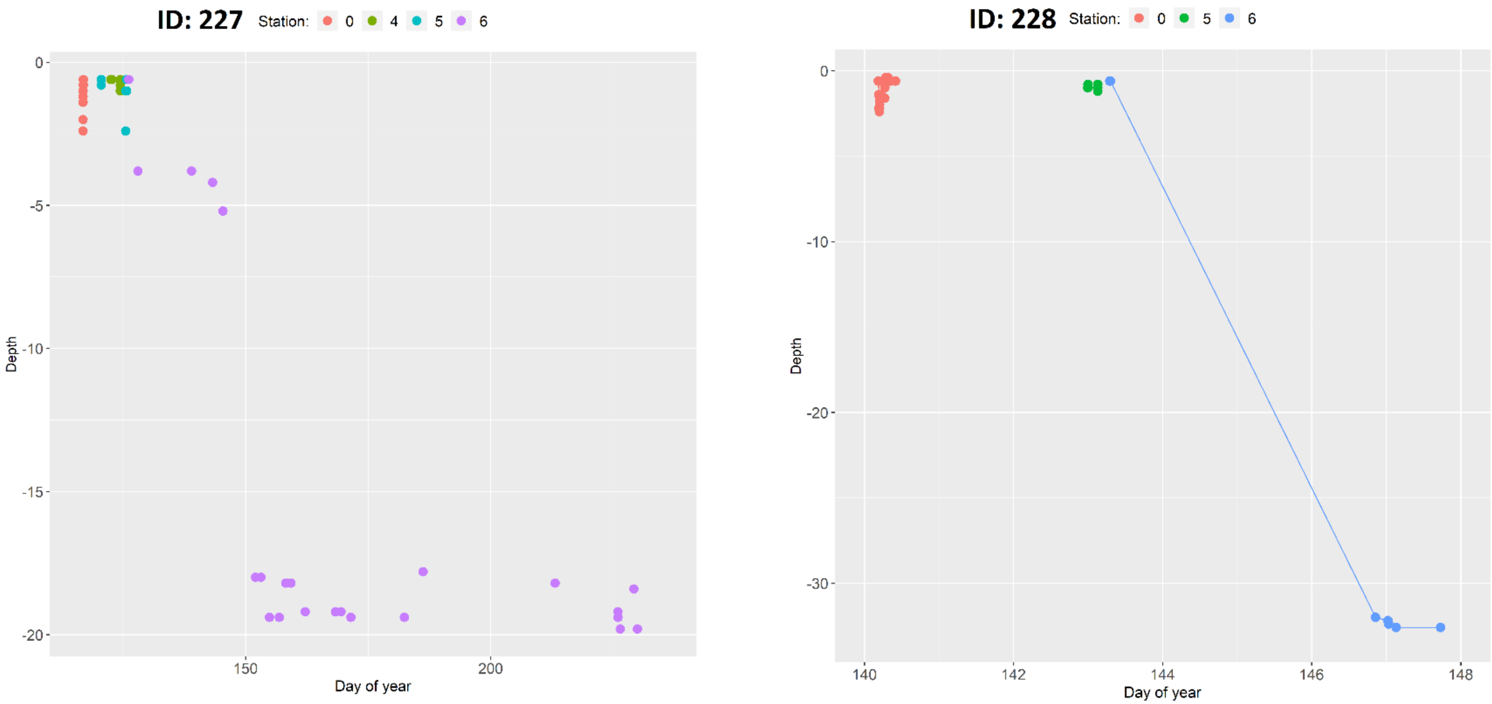

Figure A-7: Migration between zones, containing location, depth and day of year values.

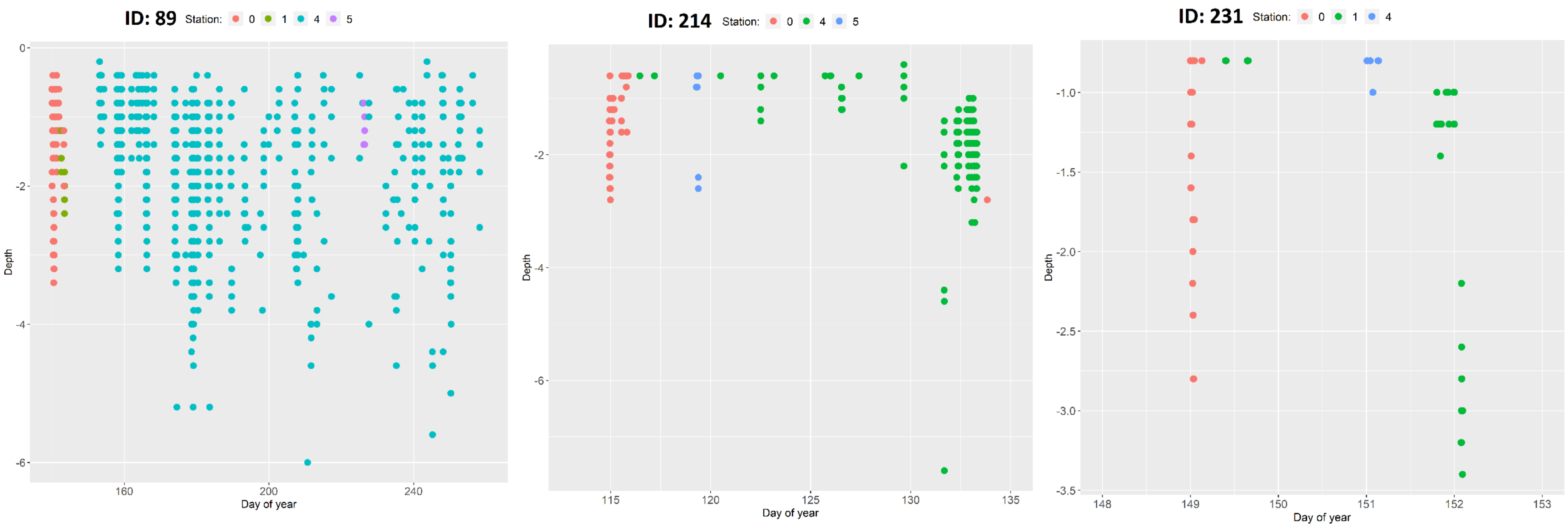

Table A-1: Correlation between parameters used for the migration probability models for Eidselva and Stryneelva. DoY = day of year, Q = water discharge (m3/s), T = water temperature, ΔQ = change in water discharge from the previous day to the next (ΔQt = Qt-Qt-1), ΔT = change in water temperature from the previous day to the next (ΔTt = Tt-Tt-1), reldeltaQ = ΔQ/Q.

Eidselva	*DoY*	*Q*	*T*	*deltaQ*	*deltaT*	*reldeltaQ*
DoY	*1*					
Q	*0.21*	*1*				
T	*0.48*	*0.09*	*1*			
deltaQ	*-0.04*	*0.1*	*0.5*	*1*		
deltaT	*-0.02*	*-0.25*	*0.22*	*0.07*	*1*	
reldeltaQ	*-0.02*	*0.1*	*0.49*	*0.98*	*0.08*	*1*
Stryneelva	*DoY*	*Q*	*T*	*deltaQ*	*deltaT*	*reldeltaQ*
DoY	*1*					
Q	*0.65*	*1*				
T	*0.5*	*0.55*	*1*			
deltaQ	*0.13*	*0.26*	*0.61*	*1*		
deltaT	*-0.04*	*-0.36*	*0.14*	*0.28*	*1*	
reldeltaQ	*0*	*0.11*	*0.67*	*0.88*	*0.3*	*1*

Table A-2: Model selection table for the candidate models predicting migration probability for smolts in Eidselva and Stryneelva. DoY = day of year, Q = water discharge (m3/s), T = water temperature (°C), Δ = change from the previous day (e.g. ΔQt = Qt-Qt-1), reldeltaQ = ΔQ/Q, K = number of parameters in the model, AICc = corrected Akaike information criterion, AICcWt = AICc weight (relative support), and LL = log likelihood.

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*deltaQ*	*4*	*122.68*	*1.81*	*0.17*	*0.8*	*-56.98*
*reldeltaQ*DoY*	*4*	*123.34*	*2.48*	*0.12*	*0.92*	*-57.31*
*reldeltaQ*DoY*Q*	*8*	*124.32*	*3.45*	*0.07*	*0.99*	*-52.75*
*DoY*deltaQ*deltaT*	*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*deltaQ*	*4*	*116.92*	*7.02*	*0.02*	*0.96*	*-54.09*
DoY+deltaQ	*3*	*117.08*	*7.18*	*0.02*	*0.98*	*-55.32*
T	*2*	*117.85*	*7.96*	*0.01*	*0.99*	*-56.82*
T+deltaT	*3*	*119.88*	*9.98*	*0*	*1*	*-56.72*

Appendix B- AIC tables:

Table B-1: Model selection table for factors initiating smolt migration in Eidselva and Stryneelva watercourses, 2019. DoY = Day of year, Q = water discharge (m^3/s), T = water temperature (°C), Δ = change from the previous day to the enxt (e.g., ΔQt = Qt-Qt-1), reldeltaQ = ΔQ/Q, AICc = corrected Akaike information criterion, K = number of parameters in the model, AICcWt = AICc weight (relative support), Cum.Wt = cumulative AICc weights, and LL = log likelihood.

Models	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
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 Cormack-Jolly-Seber candidate models, estimating the survival- and detection probability of smolts migrating from both Eidselva and Stryneelva. This table shows the support of the individual covariates.

Stryneelva watercourse						
Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
1, ind.cov(weight)	9	364.17	0.00	0.42	0.42	-345.24
2, ind.cov(weight)	10	365.41	1.24	0.23	0.65	-344.26
3, ind.cov(weight)	10	367.12	2.94	0.96	1.61	-345.97
4, ind.cov(weight)	11	367.49	3.31	0.08	1.69	-344.01
5, ind.cov(weight)	10	367.52	3.34	0.08	1.77	-346.36
6, ind.cov(weight)	9	369.96	5.78	0.02	1.79	-351.02
7, ind.cov(weight)	9	369.97	5.80	0.02	1.81	-351.03
8, ind.cov(weight)	10	370.04	5.87	0.02	2.01	-348.90
9, ind.cov(weight)	9	370.68	6.50	0.02	2.21	-351.74
Eidselva watercourse						
Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
1, ind.cov(weight)	9	365.38	0.00	0.60	0.60	-350.77
2, ind.cov(weight)	10	367.46	2.08	0.21	0.81	-350.68
3, ind.cov(weight)	10	368.43	3.05	0.13	1.94	-355.97
4, ind.cov(weight)	11	370.41	5.03	0.05	1.99	-355.80

Appendix C- Tag-ID list:

Table C-1: Overview of all presmolts tagged in 2019, with date of tagging, watercourse and river affiliation, type of transmitter, ID, total presmolts length in cm (TL), Weight (grams), K-factor ($K = 100 \frac{W}{L^3}$), tag to bodyweight ratio and migration group (early/late), NA= not detected after release.

Date	Watercourse	River	Transmitter Type	ID	**TL**	Weight	k-factor	Tag ratio	Early/Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N1	**12.2**	17.8	0.98	11.2 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N2	**14.1**	24.2	0.86	8.3 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N3	**14**	19.3	0.70	10.4 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N4	**12.3**	16.5	0.89	12.1 %	NA
14.04.2019	Hornindal	Eidselva	D-LP7	N5	**15.7**	34	0.88	5.9 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N6	**15**	16.2	0.48	12.3 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N7	**12.6**	15.2	0.76	13.2 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N8	**14.9**	25.6	0.77	7.8 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N9	**13.2**	20.2	0.88	9.9 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N10	**14.4**	27.5	0.92	7.3 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N11	**13.4**	27.5	1.14	7.3 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N12	**12.8**	19.8	0.94	10.1 %	NA
14.04.2019	Hornindal	Eidselva	D-LP7	N14	**13.7**	19.4	0.75	10.3 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N15	**13.8**	20.6	0.78	9.7 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N16	**12.5**	17.9	0.92	11.2 %	NA
14.04.2019	Hornindal	Eidselva	ID-LP7	N17	**12.9**	16	0.75	12.5 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N18	**12.5**	19.6	1.00	10.2 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N19	**12.6**	20.3	1.01	9.9 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N20	**13.1**	19.7	0.88	10.2 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N21	**13.1**	22.8	1.01	8.8 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N22	**12.8**	17.8	0.85	11.2 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N23	**14.2**	25.1	0.88	8.0 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N24	**15.1**	23.5	0.68	8.5 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N25	**12.9**	16.8	0.78	11.9 %	NA
14.04.2019	Hornindal	Eidselva	ID-LP7	N26	**12.5**	17	0.87	11.8 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N27	**16**	32.9	0.80	6.1 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N28	**15.7**	30.2	0.78	6.6 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N29	**12.9**	15.9	0.74	12.6 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N30	**14.2**	19.2	0.67	10.4 %	Late

14.04.2019	Hornindal	Eidselva	D-LP7	N31	**14**	21.4	0.78	9.3 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N32	**12.8**	16.1	0.77	12.4 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N33	**12.9**	18.2	0.85	11.0 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N34	**12.9**	20.6	0.96	9.7 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N35	**13.2**	19.3	0.84	10.4 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N36	**16.2**	36	0.85	5.6 %	NA
14.04.2019	Hornindal	Eidselva	ID-LP7	N37	**13.7**	22.3	0.87	9.0 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N38	**15.1**	26	0.76	7.7 %	NA
14.04.2019	Hornindal	Eidselva	ID-LP7	N39	**13.2**	18.2	0.79	11.0 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N40	**16.7**	39.8	0.85	5.0 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N41	**12.7**	17	0.83	11.8 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N42	**14.4**	24	0.80	8.3 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7(2018)	N43	**15.9**	39	0.97	5.4 %	NA
14.04.2019	Hornindal	Eidselva	D-LP7	N44	**15.1**	26.1	0.76	7.7 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N45	**12.7**	18.8	0.92	10.6 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N46	**14.3**	23.8	0.81	8.4 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N47	**14.7**	26	0.82	7.7 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7(2018)	N48	**15.7**	32.9	0.85	6.4 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N49	**13.9**	21.7	0.81	9.2 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N50	**16.7**	34	0.73	5.9 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N51	**16.1**	36.8	0.88	5.4 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N52	**13.7**	17.5	0.68	11.4 %	Early
14.04.2019	Hornindal	Eidselva	D-LP7	N53	**14.2**	19.8	0.69	10.1 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N54	**12.6**	19.3	0.96	10.4 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N55	**13.7**	22.1	0.86	9.0 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N56	**13.9**	23.4	0.87	8.5 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N57	**15.9**	31.5	0.78	6.3 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N58	**13.1**	17.2	0.77	11.6 %	Early
14.04.2019	Hornindal	Eidselva	ID-LP7	N59	**13.3**	19.5	0.83	10.3 %	NA
14.04.2019	Hornindal	Eidselva	D-LP7	N60	**14.6**	25	0.80	8.0 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N61	**14.3**	24.5	0.84	8.2 %	Late
14.04.2019	Hornindal	Eidselva	ID-LP7	N62	**13.7**	17.5	0.68	11.4 %	NA
14.04.2019	Hornindal	Eidselva	ID-LP7	N63	**13.5**	23.5	0.96	8.5 %	NA
14.04.2019	Hornindal	Eidselva	ID-LP7	N64	**13**	15.9	0.72	12.6 %	Late
14.04.2019	Hornindal	Eidselva	D-LP7	N65	**15.5**	28.3	0.76	7.1 %	Late

14.04.2019	Hornindal	Horndøla	ID-LP7	N67	**13.2**	18	0.78	11.1 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7	N68	**12.6**	14.3	0.71	14.0 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7	N69	**13**	20	0.91	10.0 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7	N70	**14.9**	27.3	0.83	7.3 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7	N71	**13.1**	21.6	0.96	9.3 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7	N72	**13**	19.1	0.87	10.5 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7	N73	**13.6**	21.7	0.86	9.2 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7	N74	**14.1**	24.3	0.87	8.2 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7	N75	**13.87**	23	0.86	8.7 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7	N76	**13.3**	18.4	0.78	10.9 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N77	**14.2**	24.3	0.85	7.8 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N78	**13**	19.4	0.88	9.8 %	NA
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N79	**13.1**	19	0.85	10.0 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N80	**13**	20.9	0.95	9.1 %	NA
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N81	**13.1**	19	0.85	10.0 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N82	**13.1**	17.5	0.78	10.9 %	Early
14.04.2019	Hornindal	Horndøla	D-LP7	N84	**14.2**	26	0.91	7.7 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N85	**13.2**	18.3	0.80	10.4 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N86	**13.6**	21.5	0.85	8.8 %	NA
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N87	**13.7**	25.2	0.98	7.5 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N88	**13.5**	23.3	0.95	8.2 %	NA
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N89	**13.2**	25.4	1.10	7.5 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N90	**13.7**	25	0.97	7.6 %	NA
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N91	**14.2**	19.7	0.69	9.6 %	NA
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N92	**13.7**	23.8	0.93	8.0 %	Late
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N93	**13.3**	19.6	0.83	9.7 %	Late
14.04.2019	Hornindal	Horndøla	D-LP7	N94	**17.2**	41.5	0.82	4.8 %	Early
14.04.2019	Hornindal	Horndøla	ID-LP7(2018)	N95	**13.7**	21.2	0.82	9.0 %	NA
14.04.2019	Hornindal	Horndøla	D-LP7	N96	**14.3**	24.3	0.83	8.2 %	Early
14.04.2019	Hornindal	Horndøla	D-LP7	N97	**14.2**	24.9	0.87	8.0 %	Early
14.04.2019	Hornindal	Horndøla	D-LP7	N98	**14.6**	23.5	0.76	8.5 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S1	**14.6**	25.4	0.82	7.9 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S2	**12.8**	16.9	0.81	11.8 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S3	**13.3**	22.3	0.95	9.0 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S4	**17**	34.5	0.70	5.8 %	Early

13.04.2019	Stryn	Stryneelva	ID-LP7	S5	**12.8**	21.2	1.01	9.4 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S6	**13.9**	22.9	0.85	8.7 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S7	**14.3**	25.3	0.87	7.9 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S8	**13.6**	23.4	0.93	8.5 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S9	**13.2**	20.1	0.87	10.0 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S10	**17.1**	45.1	0.90	4.4 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S11	**16.2**	36.2	0.85	5.5 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S12	**13.1**	18.7	0.83	10.7 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S13	**12.6**	19.6	0.98	10.2 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S14	**14.1**	23.3	0.83	8.6 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S15	**14.1**	23.3	0.83	8.6 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S16	**14.3**	20.7	0.71	9.7 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S17	**14.3**	21.8	0.75	9.2 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S18	**13.7**	23.8	0.93	8.4 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S19	**12.5**	18	0.92	11.1 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S20	**13**	19.8	0.90	10.1 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S21	**12.6**	18	0.90	11.1 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S22	**12.8**	18.5	0.88	10.8 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S23	**14.1**	22.2	0.79	9.0 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S24	**12.7**	18.3	0.89	10.9 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S25	**13.9**	23.7	0.88	8.4 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S26	**12.8**	17.6	0.84	11.4 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S27	**14.3**	23.8	0.81	8.4 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S28	**13.3**	20.3	0.86	9.9 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S29	**12.8**	17.9	0.85	11.2 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S30	**15.7**	31	0.80	6.5 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S31	**13.4**	22.4	0.93	8.9 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S32	**14.7**	28.7	0.90	7.0 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S33	**12.4**	18.5	0.97	10.8 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S34	**12.8**	16.4	0.78	12.2 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S35	**14.1**	23.9	0.85	8.4 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S36	**13.2**	17.3	0.75	11.6 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S37	**13.1**	18.3	0.81	10.9 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S38	**14.6**	21.9	0.70	9.1 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S39	**12.6**	18.5	0.92	10.8 %	Late

13.04.2019	Stryn	Stryneelva	ID-LP7	S40	**12.5**	14.3	0.73	14.0 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S41	**13.7**	20	0.78	10.0 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S42	**12.8**	16	0.76	12.5 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S43	**17**	33	0.67	6.1 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S44	**13.5**	20.7	0.84	9.7 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S45	**13.2**	17.6	0.77	11.4 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S46	**13.2**	17.6	0.77	11.4 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S47	**13.2**	17.9	0.78	11.2 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S48	**12.9**	15	0.70	13.3 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S49	**14.2**	22.2	0.78	9.0 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S50	**12.6**	15.6	0.78	12.8 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S51	**12.3**	14.9	0.80	13.4 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S52	**13.1**	16.8	0.75	11.9 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S53	**14.1**	22	0.78	9.1 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S54	**12.9**	13.3	0.62	15.0 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S55	**15.6**	26.8	0.71	7.5 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S56	**12.6**	15.3	0.76	13.1 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S57	**14.2**	19.7	0.69	10.2 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S58	**13.1**	15.4	0.69	13.0 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S59	**13**	16.1	0.73	12.4 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S60	**12.8**	15.9	0.76	12.6 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S61	**13.1**	17.5	0.78	11.4 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S62	**12.7**	17.1	0.83	11.7 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S63	**14.2**	21.6	0.75	9.3 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S64	**13**	16.7	0.76	12.0 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S65	**12.7**	14.1	0.69	14.2 %	NA
13.04.2019	Stryn	Stryneelva	D-LP7	S66	**14.6**	26.9	0.86	7.4 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S67	**13.9**	18.8	0.70	10.6 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S68	**12.7**	13.7	0.67	14.6 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S69	**13.9**	19.5	0.73	10.3 %	Late
13.04.2019	Stryn	Stryneelva	ID-LP7	S70	**13.6**	19	0.76	10.5 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S71	**14.6**	25.2	0.81	7.9 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S72	**14.6**	20	0.64	10.0 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S73	**14.4**	23	0.77	8.7 %	Early
13.04.2019	Stryn	Stryneelva	D-LP7	S74	**14.6**	22.7	0.73	8.8 %	Early

13.04.2019	Stryn	Stryneelva	ID-LP7	S75	**13.2**	16.2	0.70	12.3 %	Late
13.04.2019	Stryn	Stryneelva	D-LP7	S76	**14.3**	21.2	0.72	9.4 %	NA
13.04.2019	Stryn	Stryneelva	ID-LP7	S77	**14.6**	20.5	0.66	9.8 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S78	**14.6**	23	0.74	8.7 %	Early
13.04.2019	Stryn	Stryneelva	ID-LP7	S79	**13.1**	17	0.76	11.8 %	Early
13.04.2019	Stryn	Hjelledøla	ID-LP7	S80	**13.1**	20.4	0.91	9.8 %	NA
13.04.2019	Stryn	Hjelledøla	D-LP7	S81	**13.2**	18.5	0.80	10.8 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S82	**14.1**	24.6	0.88	8.1 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S83	**14.2**	23.5	0.82	8.5 %	Early
13.04.2019	Stryn	Hjelledøla	ID-LP7	S84	**13**	20.6	0.94	9.7 %	Late
13.04.2019	Stryn	Hjelledøla	ID-LP7	S85	**13.3**	21.2	0.90	9.4 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S86	**16.6**	39.1	0.85	5.1 %	NA
13.04.2019	Stryn	Hjelledøla	ID-LP7	S87	**13.3**	21.2	0.90	9.4 %	NA
13.04.2019	Stryn	Hjelledøla	ID-LP7	S88	**14.1**	26.2	0.93	7.6 %	Late
13.04.2019	Stryn	Hjelledøla	ID-LP7	S89	**12.8**	22.1	1.05	9.0 %	NA
13.04.2019	Stryn	Hjelledøla	D-LP7	S90	**15.9**	35.1	0.87	5.7 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S91	**14.1**	26.2	0.93	7.6 %	Late
13.04.2019	Stryn	Hjelledøla	D-LP7	S92	**15.2**	30.5	0.87	6.6 %	NA
13.04.2019	Stryn	Hjelledøla	D-LP7	S93	**13.9**	21.6	0.80	9.3 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S94	**13.9**	23.4	0.87	8.5 %	Late
13.04.2019	Stryn	Hjelledøla	D-LP7	S95	**13.9**	23.4	0.87	8.5 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S96	**13.6**	25.1	1.00	8.0 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S97	**13.7**	23.4	0.91	8.5 %	Early
13.04.2019	Stryn	Hjelledøla	ID-LP7	S98	**13.2**	22.5	0.98	8.9 %	Late
13.04.2019	Stryn	Hjelledøla	D-LP7	S99	**14.8**	29.8	0.92	6.7 %	Late
13.04.2019	Stryn	Hjelledøla	D-LP7	S100	**14.4**	21	0.70	9.5 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S101	**14.2**	25.6	0.89	7.8 %	Early
13.04.2019	Stryn	Hjelledøla	ID-LP7	S102	**13.7**	20.4	0.79	9.8 %	Early
13.04.2019	Stryn	Hjelledøla	D-LP7	S103	**13.7**	25.1	0.98	8.0 %	Early
13.04.2019	Stryn	Hjelledøla	ID-LP7	S104	**12.9**	18.3	0.85	10.9 %	Late

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