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Effect of Salmon lice (*Lepeophtheirus salmonis*) Infestations on the Behaviour of Prematurely Returned Sea Trout (*Salmo trutta*) in the Hardangerfjord

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Biology

Preface

This thesis completes my MSc in Biology and my time as a student at the Norwegian University of Life Science (NMBU). I have truly loved being a student and treasure the knowledge I have gained during my time here.

First, I want to give a huge thanks to my main supervisor professor Thronn Oddvar Haugen for all the good help and guidance during the making of this thesis. Your good mood and enthusiasm for the field have been very inspiring and motivating. I will also thank my co-supervisor Henning Andre Urke at INAQ for sharing your knowledge and guiding me through the fieldwork.

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Abstract

The expansion of the salmon farming industry along the Northern coasts has caused a higher concentration of salmon lice (*Lepeophtheirus salmonis*) in the coastal waters and fjords. There has been observed that Sea trout (*Salmo trutta*) have adapted their behaviour as a response to the increased amount of salmon lice in the fjords. Sea trout infested with salmon lice from three rivers in the Hardangerfjord were captured and tagged with acoustic transmitters before being released back into the river again. The data that were retrieved and analysed were recordings from between mid-June to December 2021, from a total of 48 sea trout, where 40 were observed in the fjord. Results showed that the river most exposed to high salmon lice concentrations had the lowest proportion of migrants and that the probability of seaward migration decreased significantly with higher levels of salmon lice infestations. The time of river exit was found to be influenced by the water discharge in two of three study rivers, and the maximum distance travelled and the time they spent in the fjord after they had deloused was mainly influenced by individual characteristics such as length and weight. The depth use in the fjord was generally shallow with a mean depth of 1.16 meters across all rivers. The depth analysis showed several significant interaction effects, where the post-smolt performed small diel vertical migrations and that the depth increased slightly with higher chlorophyll density in two of the rivers.

When comparing the trout tagged with acoustic transmitters (AT) to trout tagged with passive integrated transponders (PIT), of PIT-tagged trout that were tagged at the same time as AT-tagged trout, 0 was identified as migratory individuals, while 63 % of the AT-tagged trout was observed in the fjord. Of all PIT-tagged trout, only 8 of 104 fulfilled the criteria for being defined as migratory.

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1. Introduction

The anadromous form of Brown trout (*Salmo trutta*), called sea trout, exploits habitats in both fresh- and seawater. While the stationary Brown trout utilizes freshwater only, sea trout spawn in freshwater and usually migrate out to sea in spring to feed and grow before heading back to freshwater again to spawn or stay over winter (Jonsson & Jonsson, 2011; Klemetsen et al., 2003). The eggs hatch in spring and the alevins consume the yolk before emerging from the gravel as fry to feed on insect nymphs and larvae. This is a crucial time for the trout as the mortality is high during the trout's first year of living (Jonsson & Jonsson, 2011).

Before seaward migration, juvenile trout must go through a transition called smoltification, which is initiated by environmental factors such as day length and temperature (Jonsson & Jonsson, 2011) and involves morphological and physiological changes crucial for survival at sea. During this process, the trout change its appearance beneficial to a more pelagic lifestyle and develop a tolerance to salty seawater. The age at which juveniles become smolt varies between and within populations, depending on temperature and growth (Klemetsen et al., 2003). After smoltification, the smolt starts the migration downstream. The migratory behaviour is mainly influenced by water temperature and discharge (Thorstad et al., 2016). In the marine phase, the trout have been observed mainly in the upper part of the water column, with sometimes deeper dives by larger trout (Lyse et al., 1998; Rikardsen et al., 2007; Thorstad et al., 2016). The duration of their sea journey depends on water temperature and decreases with higher latitude (Klemetsen et al., 2003). Some individuals may also choose to remain in the fjords and estuaries during the winter.

If a brown trout becomes migratory or not, depends on genetics, phenotypic plasticity, and to some degree growth rate (Jonsson & Jonsson, 1993).

The benefits of seaward migration include more feeding opportunities which allow them to grow more compared to stationary brown trout. Increased growth benefits the individual trout as bigger fish often has better fitness. In female fish, an increased body size leads to bigger eggs and thus bigger offspring (Einum & Fleming, 1999), and bigger offspring will have an advantage when it comes to intracohort competition and the risk of predation. In males, a larger body size may increase competitiveness on the spawning site, hence reproductive success. But sea migration does also come with a cost, as the migratory journey requires much energy and increases the chance of predation, especially during the trout's first sea-run. If the costs start to exceed the benefits of marine migration, sea trout may adapt their behaviour and change to a more stationary lifestyle.

The sea trout's wide habitat utilization creates opportunities, but it also makes them vulnerable to many different disturbances. In 2017, almost half of 430 sea trout populations in Norway were classified as in poor or very poor status due to human activities such as agriculture, road crossings, hydropower regulations, and salmon lice (Anon., 2019). Salmon lice (*Lepeophtheirus salmonis*) were found to have the biggest impact in terms of the portion of populations affected and reduction in population size.

Salmon lice is a naturally occurring ectoparasite in the northern hemisphere, but its numbers have increased greatly as a consequence of an expanding salmon farming industry. The parasite is dispersed in the fjords by the currents, and the sea trout are therefore especially vulnerable to infestations as they utilize the fjords where the farms are located. Salmon lice infestations cause several problems for the infected salmonid. It lives off the fish's skin, mucus, and blood, creating wounds and further problems such as stress responses, osmoregulatory failure, and secondary infections (Bjørn et al., 2001) and can result in death. Salmon lice have for instance caused higher mortality in sea trout smolt in the Hardangerfjord (Skaala et al., 2014).

The salmon louse's life cycle consists of eight stages (Hamre et al., 2013) where the mobile stages cause the most damage to the fish (Wells et al., 2007). Salmon lice have a low tolerance to freshwater, and lower salinities have been found to decrease concentrations of salmon lice copepodids (Crosbie et al., 2019), which is the stage in which salmon lice attach themselves to the fish.

The threat salmon lice constitute makes it less beneficial for trout to migrate to sea and impacts the trout's migratory behaviour. In the last three decades, more sea trout have been observed returning to rivers and estuaries earlier than normal, called premature return. High salmon lice pressure in the fjord increase the risk of salmon lice infections, and sea trout have found a way to exploit salmon lice's low tolerance to freshwater by returning to the streams and estuaries where the waters are more influenced by freshwater runoff from the river (Birkeland & Jakobsen, 1997; Gjelland et al., 2014; Halttunen et al., 2018; Serra-Llinares et al., 2020; Sægrov et al., 2020). The inner part of the fjord will also be more influenced by freshwater runoff from the rivers and will have lower salinities than the middle- and outer parts of the fjord, where the prematurely returned sea trout are observed. Halttunen et al. (2018) studied the effect of salmon lice infestations on sea trout's behaviour and survival in Etnefjorden, a sidearm in the Hardangerfjord, using acoustic telemetry. Over three years they captured fish and grouped them into treated and non-treated fish (control), where the former

group was given treatments against salmon lice infestations. They found no difference in survival neither between groups nor between years, but their results did show that the trout spent more time in delousing areas and stayed closer to the river outlets for longer periods in years with high lice pressure compared to fallowed years, and that smaller trout in worse condition had a smaller average distance than bigger trout in better condition (Halttunen et al., 2018).

Another acoustic telemetry study carried out by Serra-Llinares et al. (2020) captured and tagged post-smolt trout in Sandnesfjorden, Southern Norway, an area with low lice pressure. The tagged fish were divided into two groups, one artificially infested with salmon lice before sea-run, and one control group. Their results showed that the infested group returned to freshwater significantly earlier and stayed closer to estuaries when at sea than the control group. Infested trout were also observed at slightly shallower depths during the day than trout in the control group (Serra-Llinares et al., 2020).

The main purpose of this study is to investigate how the sea trout post-smolts utilize the streams and fjord after prematurely returning to freshwater, and their response to different environmental- and individual characteristics, using acoustic telemetry in three study rivers in the Hardangerfjord. In addition, data from PIT-tagged trout from one of the same study rivers will be compared to see if there is a difference between post-smolt tagged with acoustic telemetry tags and PIT tags.

Based on the background information from former studies, the following hypotheses were investigated:

- i) H1: Post-smolt with higher amounts of salmon lice attached will be more likely to not perform seaward migration.
- ii) H2: The timing of seaward migration will mainly take place with higher discharge in the river.
H3: Trout more infected by salmon lice will migrate after a longer period of time in the river than trout less infected.
- iii) H4: Trout more infested with salmon lice will remain closer to the estuary.
- iv) H5: Trout less infested by salmon lice will spend longer time at sea compared to trout that are more infested.
- v) H6: Infested trout remain closer to the surface than less infested trout.

2. Materials and method

2.1 Study area

The study was conducted in three relatively small rivers located in the middle part of the Hardangerfjord in Vestland county. The Hardangerfjord is a complex fjord with multiple inlets, sidearms, and islands. It's the second-longest fjord in Norway and is approximately 180 km long and has a maximum depth of 830 m. The middle and outer part of the Hardangerfjord are the locations of many aquaculture facilities, and in 2019 multiple sea trout populations in the fjord were found to be in moderate to bad shape and salmon lice were the biggest threat (Anon., 2019). Prematurely returned sea trout have been observed in all of the three study rivers. In 2020 most of the sea trout returned in week 24 (Sægrov et al., 2020).

None of the study rivers are connected to lakes and they are mainly drainage from precipitation and runoff from mountains and forests in the catchments. Water discharge is therefore influenced by precipitation.

2.1.1 Mundheimselva

Mundheimelva is a river that runs through the valley of Mundheimsdalen in Kvam municipality. It has a catchment area of 9.04 km² and an average discharge of 0.8 m³/s and is mainly runoff from forests. The riverbed consists of rocks in a variety of different sizes, and rocks, bedrock, and vegetation such as trees, bushes, and grass constitute the riverbanks. The watercourse consists of multiple small tributaries, but many of these are most likely not used by smolts because of steep slopes. The river meets the fjord in Mundheimsvika.

The sea trout population in this river was considered endangered in 2013, where salmon lice were the main threat (www.lakseregisteret.no), but in 2017, Lamberg and Kvitvær (2018) found through video monitoring that the number of spawning individuals was at least 118, one of the highest densities of spawners found of 44 rivers in the western Norway that year.

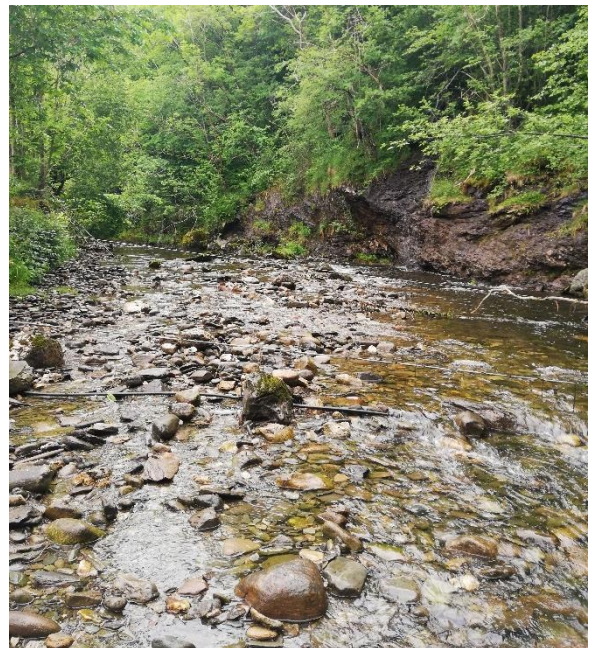


Figure 2.1.1: Picture of parts of Mundheimselva with the upstream PIT antennas.

2.1.2 Daleelva

The river Daleelva is in Kvinnherad municipality with a catchment of 5.79 km² and an average discharge of 0.33 m³/s. It has multiple tributaries and is mainly run-off from mountains and forests. The river was partially channelized from the river mouth to approximately 100 m upstream.



Figure 2.1.2: Picture of the river Daleelva with the estuary and fjord in the background.

2.1.3 River in Herøysund

The river in Herøysund is located on the southern side of the fjord, in Kvinnherad municipality. The river has a catchment of 3.33 km² and an average discharge of 0.3 m³/s. It starts in the mountain and runs through the forest and cultural landscape before it reaches the fjord.

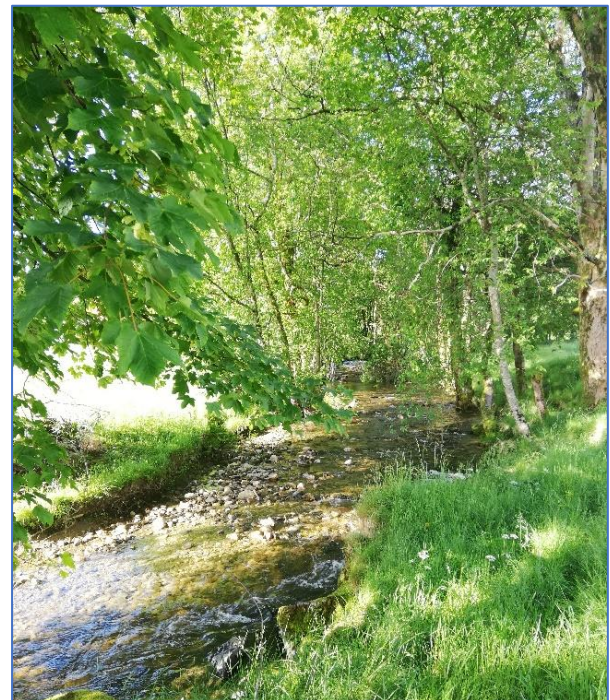


Figure 2.1.3: Picture of the river in Herøysund.

2.1.4 Water discharge

The water discharge in the three rivers was estimated by Rådgivende Biologer AS. Station 55.4 Røykenes is a reference to Dale- and Munheimselva and station 42.2 Djupevad is a reference to the river in Herøysund. Discharge simulations are based on catchment and run-off per km² retrieved from The Norwegian Water Resources and Energy Directorate (NVE).

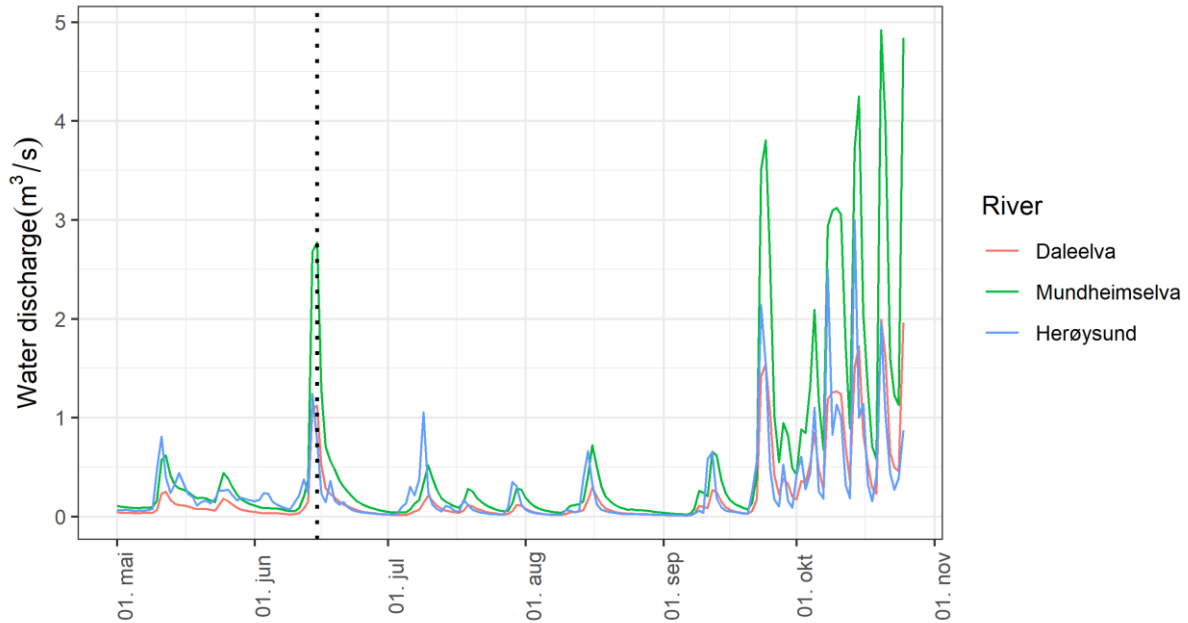
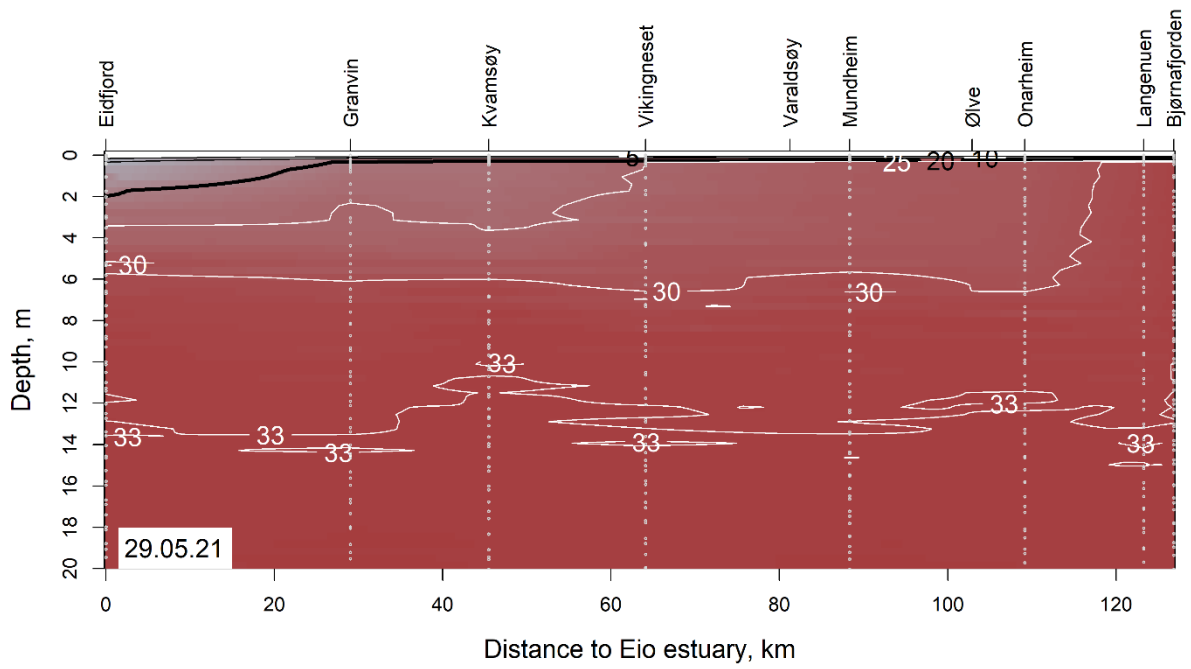
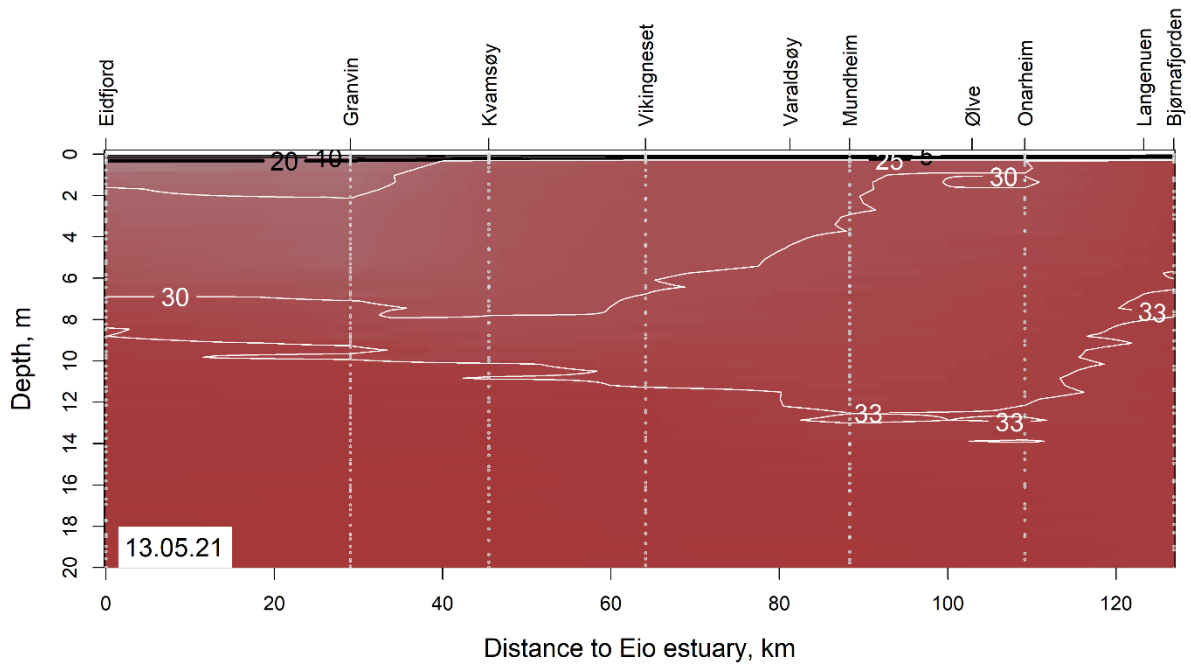
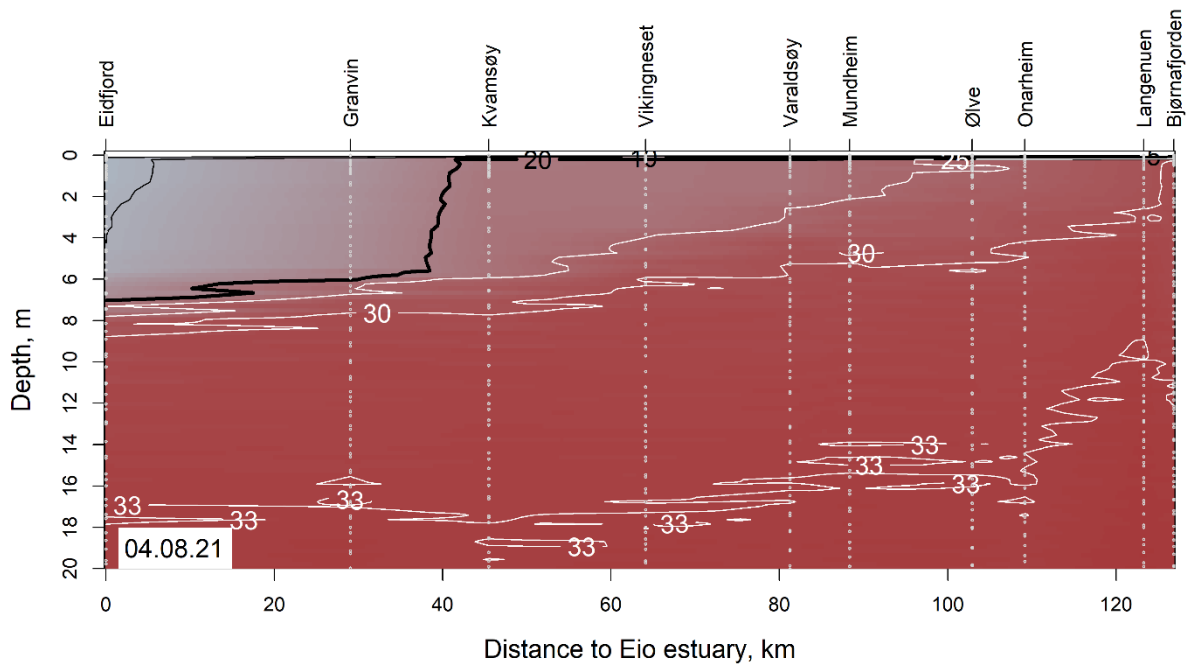
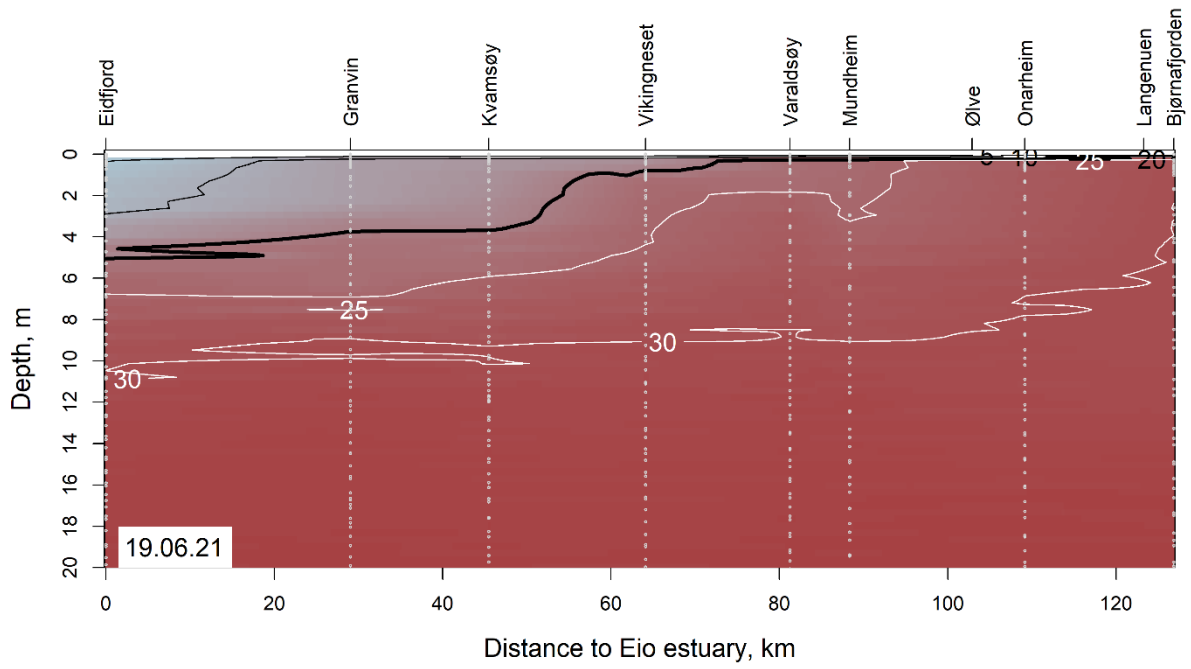


Figure 2.1.4: Estimated water discharge (m^3/s) in the rivers Daleelva, Munheimselva, and the river in Herøysund, from 1st of May to 25th of October 2021. The vertical dotted line represents the first day of tagging (15th June 2021).

2.1.5 CTD vertical profiles

Temperature and salinity measurements (CTD) used to create the vertical profiles were performed on 14 occasions at 10 locations during 2021. Five occasions of relevance for this study. SAIV SD204 probe (<https://saiv.no/sd204-ctd-profiler>). The probe was turned on by a magnet, then led down the water column 1 meter per second down to approximately 25 meters depth, then slowly taken upwards towards the surface.





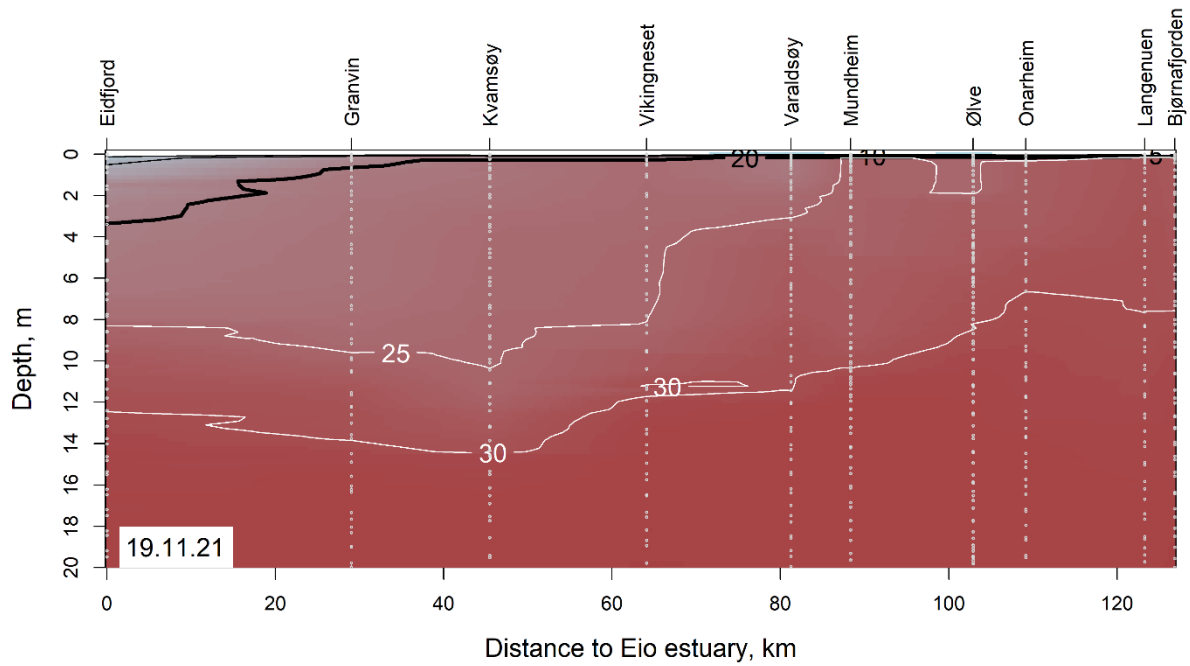


Figure 2.1.5: CTD-derived vertical profiles showing the salinity (ppt) at depths down to 20 meters from inner to the outer fjord, respectively from Eidfjord to Bjørnafjorden, at five different times between the 13th of Mai and 19th of September 2021. The 20 ppt salinity threshold is represented by the black line, and the white vertical dotted lines represent the CTD stations.

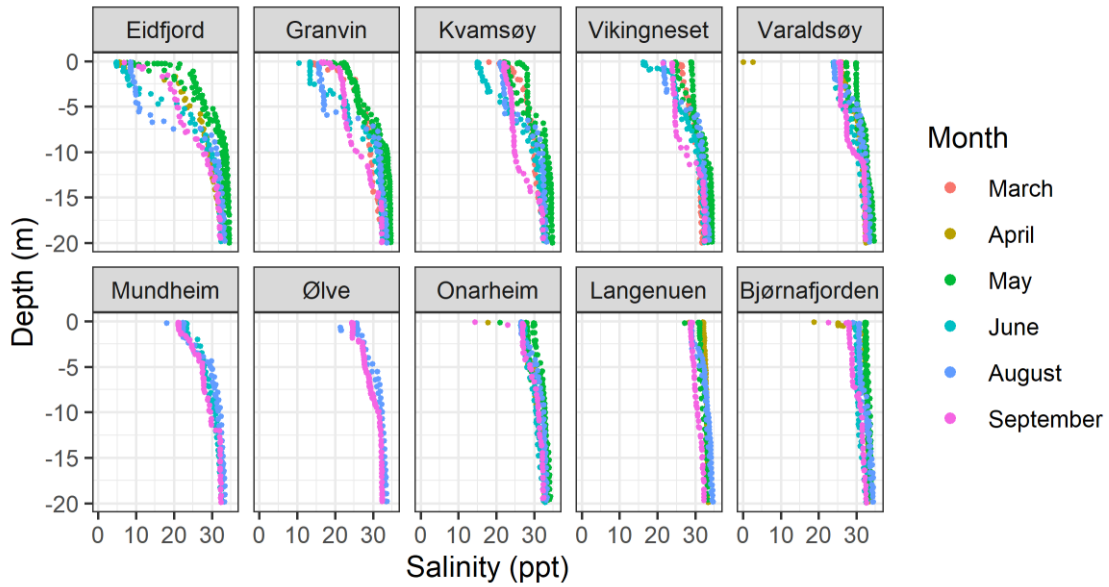


Figure 2.1.6: Vertical salinity profiles derived by CTD. Figures show salinity at depths at 10 different CTD stations in the Hardangerfjord. Colors represent the month measuring took place.

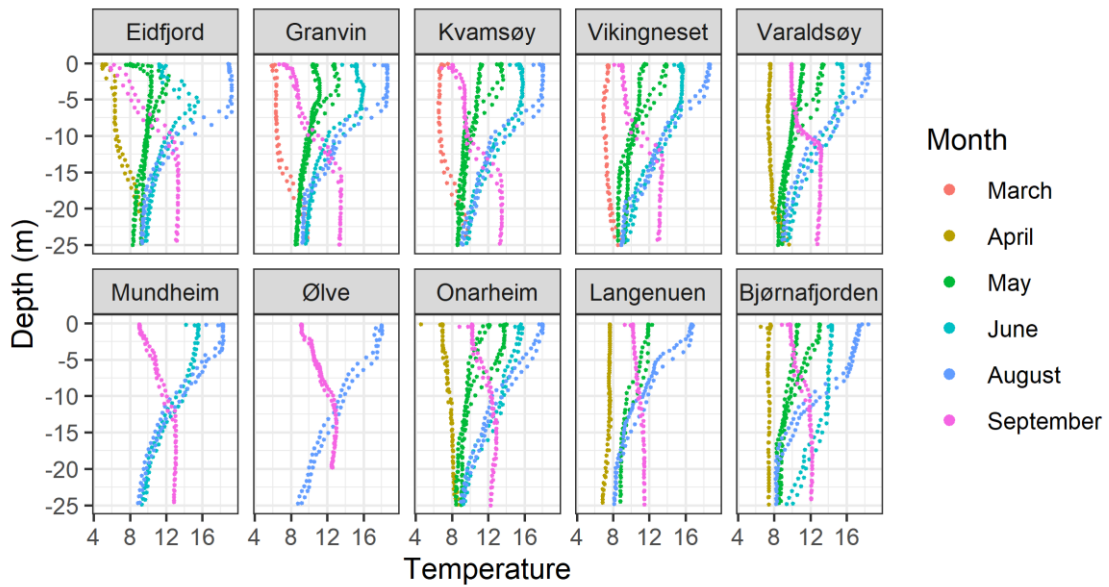
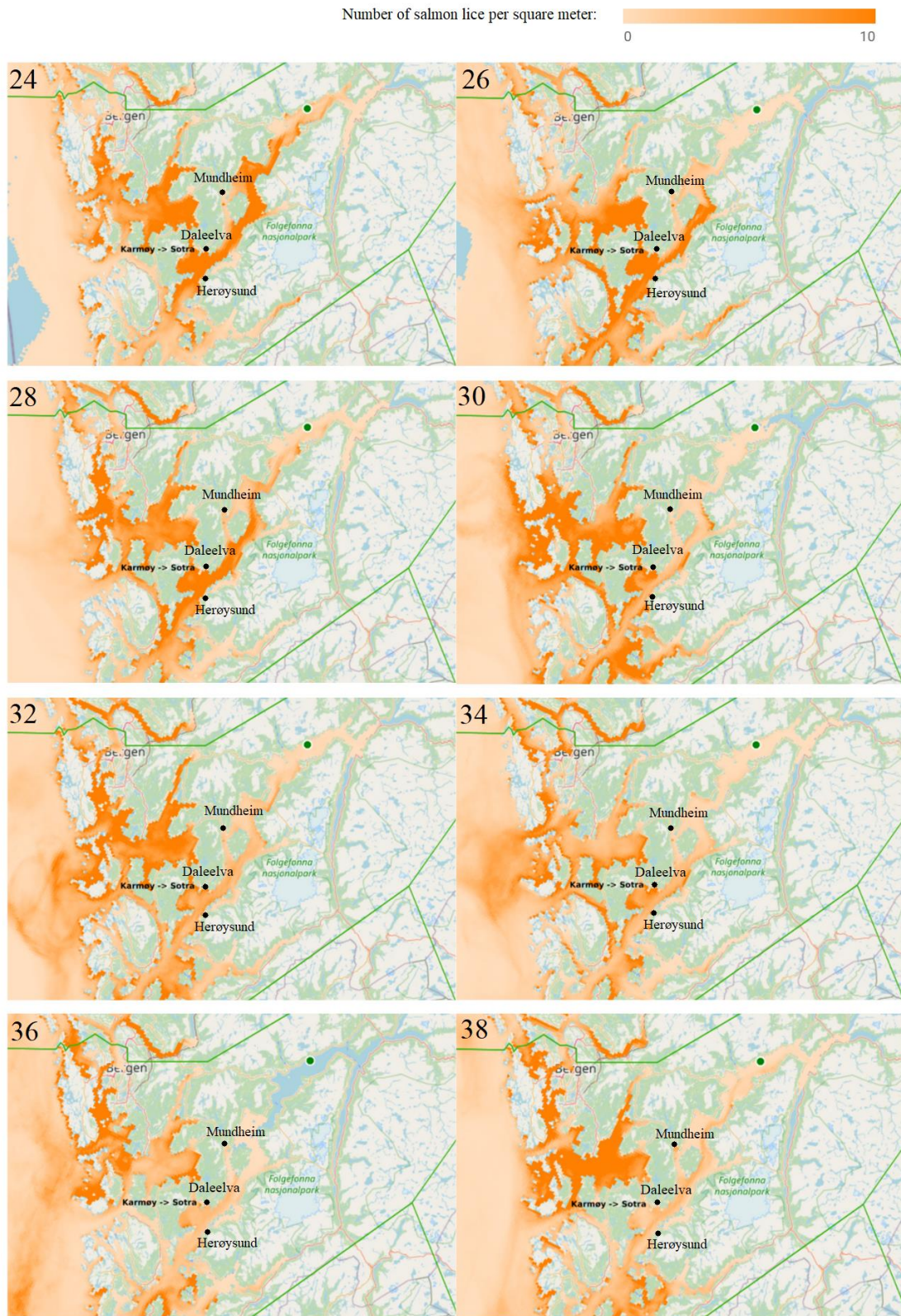


Figure 2.1.7: Vertical temperature (°C) profiles derived by CTD. Figures show temperatures at depths at 10 different CTD stations in the Hardangerfjord. Colors represent the month measuring took place.

2.1.6 Infestation pressure of salmon lice in the fjord



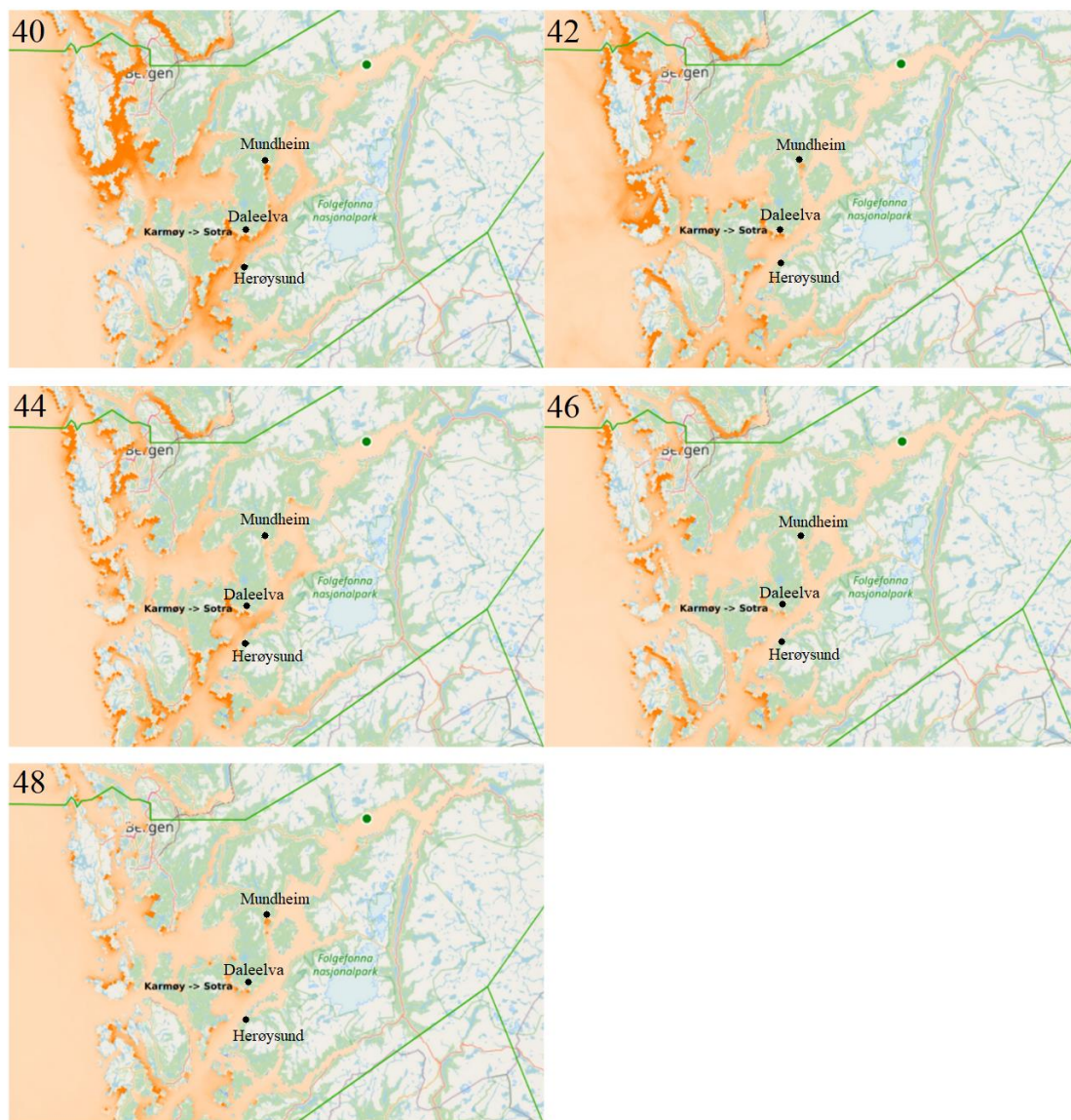


Figure 2.1.8: Biweekly infestation pressure by salmon lice in the Hardangerfjord. The given week is represented by a number in the upper left corner. The number of contagious salmon lice larvae per m^2 increases with darker red color, shown by the color scale in the upper left corner. Retrieved from Havforskningsinstituttet (<https://www.hi.no/forskning/marine-data-forskningsdata/lakseluskart/html/lakseluskart.html>) and the infestations pressure are based on their hydrodynamic dispersal model.

2.2 Acoustic telemetry

Acoustic telemetry consists of acoustic transmitters (AT-tags) and acoustic receivers. When the receiver is inside the tags detection range, the AT-tag transmits a coded acoustic signal that is recorded by the receiver and stored in its internal memory. The detection range depends on the receiver size and the noise levels in the surrounding environment. The information that is received is tag ID and other selected variables such as depth. Which depth the tag is located in is determined by a pressure sensor in the tag. To avoid code collisions the tags transmit repeated codes in random time intervals and the receivers support several frequency channels.

Acoustic telemetry is beneficial to use when studying salmonids as it can be used in both fresh- and seawater. Thelma Biotel AS (www.thelmabiotel.com) was the supplier of tags and receivers used in this study.

Data were retrieved from a total of 191 active TBR 700 receivers located in the Hardangerfjord (Figure 2.2.1). Collected data were transferred from receivers by Bluetooth and the software ComPort V.3.1.2. Of all the receivers, 29 were located in freshwater while 162 receivers were located in the fjord during this study. Of the receivers located in freshwater, only one was placed in a river relevant to this study, which was the river Mundheimselva.

Table 2.2.1: Specification for implanted tags.

Tags specs	D-LP6	ID-LP6	ID-LP7	D-2LP7	D-LP9L
Diameter	6.3 mm	6.3 mm	7.3 mm	7.3 mm	9 mm
Length	22 mm	14.5 mm	17 mm	27.7 mm	27.5 mm
Weight air	1.9 g	1.2 g	1.8 g	2.9 g	4.3 g
Weight water	1.2 g	0.7 g	1.1 g	1.8 g	2.6 g
Power output	137 dB	137 dB	139 dB	139 dB	142 dB
Number of tags used	30	27	2	2	2

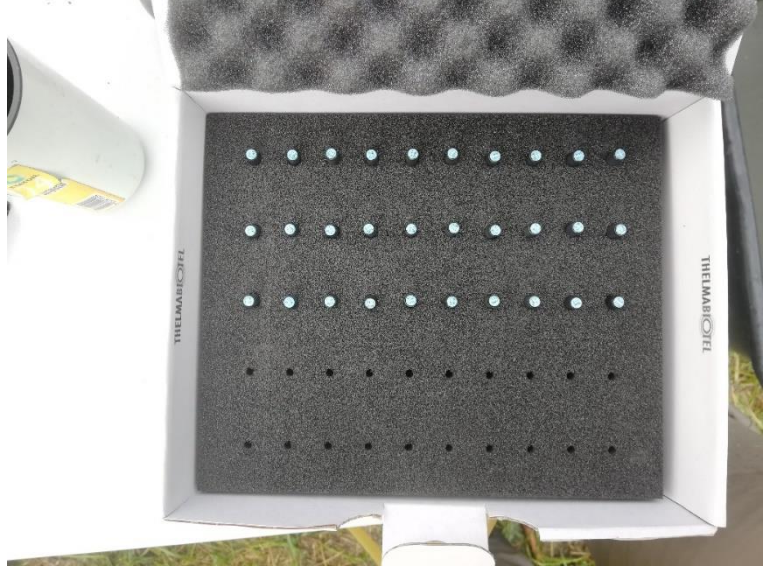


Figure 2.2.1: Transfer of data from receiver to the software ComPort.6 mm (left) and AT-tags with depth sensors from Thelma Biotel (right).

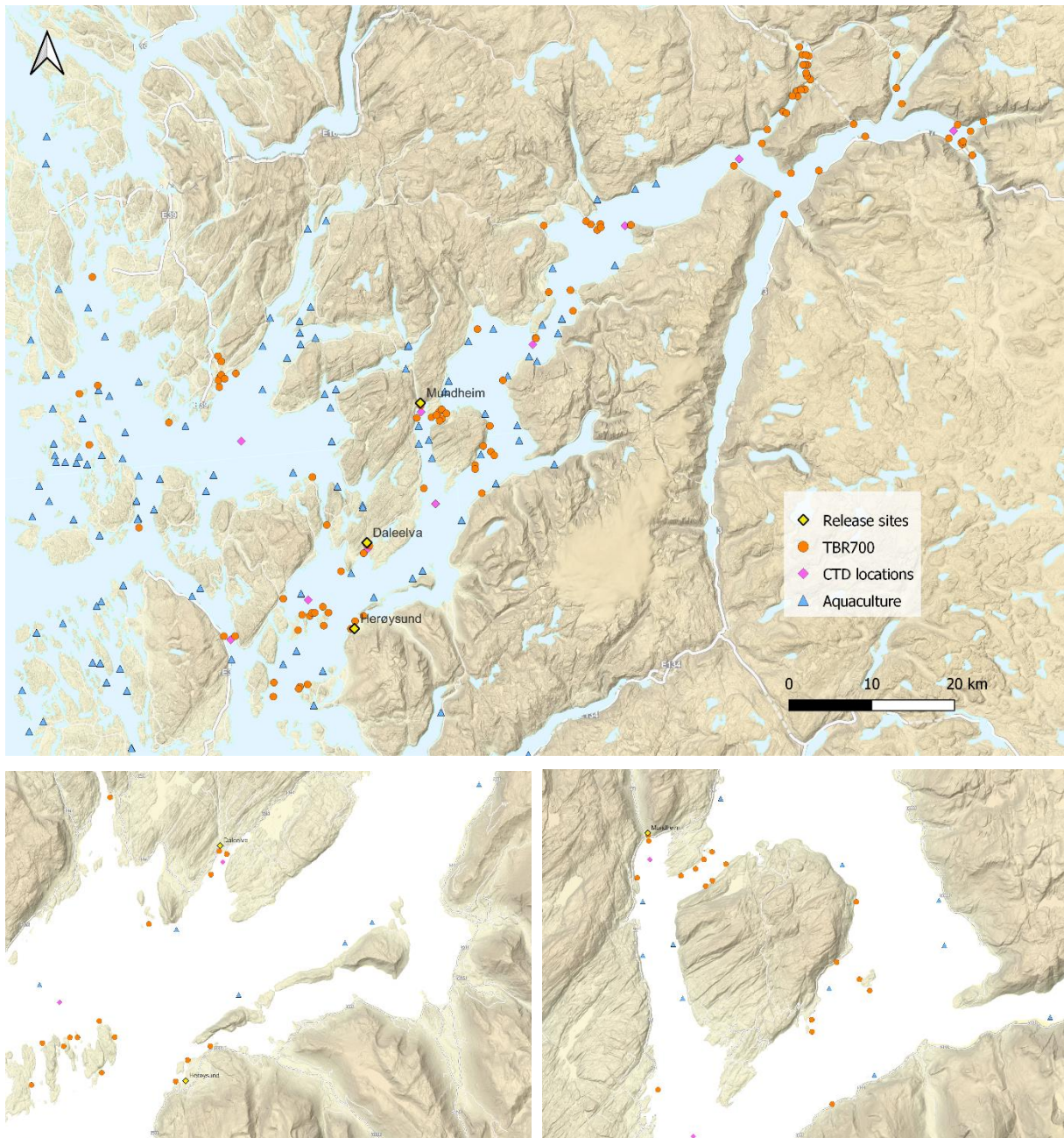


Figure 2.2.2: Map of the Hardangerfjord, with release sites (yellow), TBR locations (orange circles), CTD stations (green circles) and active aquaculture sites (blue triangles). The maps on the bottom are zoomed in on Daleelva and Herøysund to the right, and Mundheims to the left.

2.3 PIT (Passive Integrated Transponder)

PIT (Passive Integrated Transponder) tags are passive tags that are activated when the tag is within the range of a magnetic field created by an antenna. The PIT-tag is inserted into the fish's abdomen with a single incision. Each tag has a unique code which make it possible to identify each fish, and the fish can be detected throughout its lifetime. This method is cheap compared to acoustic telemetry, and it is also possible to tag smaller fish.

Captured post-smolts less than 12.5 cm were tagged with PIT tags in all three study sites, in this study. Mundheimselva was the only river of the three that had antennas placed in the river, and results from PIT are all based on observations from Mundheimselva.

2.4 Capture and tagging

A total of 63 post-smolt trout from the river Mundheimselva ($n=40$, length $\bar{x}=15.3$ cm, $s=1.9$ cm, weight $\bar{x}=34.0$ g, $s=15.3$ g), Daleelva ($n=16$, length $\bar{x}=15.8$ cm, $s=3.6$ cm, weight $\bar{x}=41.6$ g, $s=40.7$ g), and the river in Herøysund ($n=6$, length $\bar{x}=16.3$ cm, $s=2.2$ cm, weight $\bar{x}=42.1$ g, $s=18$ g), were captured and tagged with acoustic telemetry transmitters (AT-tags) on the 15th and 16th of June 2021 (Week 24). The size of tags was adjusted to the size and condition of the post-smolt by trained personnel. The smallest individuals (min. 12.5 cm) were tagged with the smallest transmitters (diameter 6.3 mm; $n=57$) while bigger trout were tagged with 7 mm or 9 mm transmitters (Table 2.2.1).

Both capturing and tagging were conducted with the required permits (Animal welfare authorities, permit No FOTS: 23256) and by trained personnel.

The fish was captured by electro-fishing from the river outlet and approximately 100 m upstream of each river. This was repeated until no more fish were observed. Only trout that showed signs of smoltification were captured. The fish were then held in plastic tubs with a continuous flow of river water before the tagging procedure began. Captured trout was measured, weighed, and photographed. The number of salmon lice, at which stage they had reached, and the amount of damage caused by salmon lice were determined by an employee at Rådgivende Biologer AS. Amount of skin damage was classified as little, medium, or much damage. All trout were weighted after the insertion of tags.

Before the incision, the fish were moved to a separate tank and sedated by the use of Tricaine Pharmaq 1000 mg/g (100 mg/L). When the fish was on its side and nonresponsive to stimuli, after approximately two to five minutes, it was moved to the operation table. The trout was then laid on its back in a shaped Styrofoam so it would lay steady during the surgery. A tube with a continuous supply of oxygen-rich river water was inserted into the trout's mouth to avoid hypoxemia. An incision was then made through the ventral midline and a tag was inserted into the coelom. After insertion of the tag, the incision was closed by three stitches using the suture resolon resorba 4/0 and further sealed with the tissue adhesive histoacryl, n-butyl-2-cyanoacrylate. After transplant of transmitters, the transmitter signal and tag-id were checked using a TBR700 receiver. Then, 4-5 scales from each fish were sampled from above the lateral line, between the tail and dorsal fin. Tagged trout were then monitored and stimulated for faster recovery before they were released in the same river from where they were captured. In Herøysund there was few fish captured, and therefore we went to the river Hellvikelva, adjacent to the river in Herøysund and where they were released. Only one fish from Hellvikelva was captured and tagged before being released together with the other fish.



Figure 2.4.1: Sea trout post-smolt from Daleelva after tagging, with salmon lice attached to its body and operculum.

Captured post-smolt smaller than 12.5 cm were tagged with PIT instead of AT tags. PIT-tagging was done by an employee in Rådgivende Biologer AS. This procedure is less intrusive than the AT-tagging procedure, as the PIT tags are smaller and its not necessary to close the incision with stitches.

2.5 Age and growth

The different growth rates during summer and winter make it possible to estimate age and back-calculate the annual growth. Age determination by scale-reading for brown trout is an accepted method and the average percentage of error is found to be low for smaller individuals and increases with age (Rifflart et al., 2006). Brown trout start to grow its scales on a particular place on its body, more precisely just above the ventral line, between the tail and dorsal fin. It's therefore important that all scales are collected from this part of the body. Several samples in this study contained only non-original scales and were not included in further analysis (n=5).

Leica S9i magnifier and the software Leica Application Suite X (LAS X) was used to capture images and determine age and measure the radius of each winter zone (n=48). The rest was read using an old magnifier and radiuses were measured by hand (n=9). The back-calculation of fish lengths was calculated using the Lea-Dahls formula: $L_n = \frac{S_n}{S} L$, where L_n is the length at age n, S_n is the scale radius at age n, S is the total scale radius, and L is the fish length when the scale was sampled.

When applying this formula, the assumption of a proportional linear relationship between fish length and relative scale radius should be satisfied to get correct results, which was later found to not be the case in this study (Intercept=15.52).

Several scales were considered as difficult to read as they did show a considerable increase in growth before they stagnated but did not look like a typical winter zone. This was seen in several individuals and may be explained by the that they have had a short trip out to the estuary/fjord before quickly returning to freshwater again. These growth patterns were not considered as a winter zone in the analysis. Damage to the scales did also contribute to the difficulty to read some of the samples. Scales from three trout clearly showed sea growth the previous year.



Figure 2.5.1: Scale from tagged post-smolt trout. White lines and numbers represent the length from the center to the end of each winter zone. The center of the scale and ends of winter zones are marked with a transverse line. Picture captured by Leica S9i magnifier and the software Leica Application Suite X (LAS X).

2.6 Fultons condition factor

Fulton's condition factor (k-factor), a measure of the fish's condition (Froese, 2006), was included as a predictor variable in several models explaining the post-smolts response. The k-factor was calculated by the following formula:

$$K\text{-factor} = 100 \times \frac{\text{weight}}{\text{length}^3}$$

Because the post-smolt was weighted after the incision of the tag, the tag weight was subtracted from the weight before calculating the k-factor.

2.7 Data handling and statistical analyses, AT

The software ComPort V.3.1.2. from Thelma Biotel AS was used to upload and filter the raw data by year, frequencies, and protocols, before it was downloaded as CSV-file.

Further data processing and statistical analyses were done in R version 4.1.2. R packages used included “sf”, “ggplot2”, “lme4”, “AICcmodavg”, “car”, and “StreamMetabolism”.

Maps were made in QGIS 3.18.3 and layers retrieved from Kartverkets kartolog (GeoNorge) and NVE (www.NVE.no).

The dataset consisted of 408 131 detections of premature sea trout 15 premature trout were not detected by any of the receivers.

Before the analyses, detections with different protocols than the protocol to a given tag and detections outside the interval in which a given tag was active, were removed from the dataset. Detections of one premature sea trout were also removed due to overlapping with another tagged fish that were not relevant to this study.

Only one trout was observed in two different zones in the fjord, and analyses regarding zone use were therefore not feasible.

2.7.1 Statistical analysis

Generalized linear models (GLM) were fitted to predict seaward migration (river exit), with different individual characteristics such as length, weight, number, salmon lice density, and k-factor as predictors. The link function was used for the binomial response exit/no exit. The timing of migration was estimated by fitting a generalized linear mixed-effects model with ID as the random effect, and discharge and other individual characteristics as effects. Linear models (LM) were fitted to estimate the maximum distance from the river mouth in which the trout was released, and the maximum time spent in the fjord as a logarithmic response, with characteristics as predictors. Predicted depth use in the fjord was estimated by fitting linear mixed-effects models, with trout ID as a random effect, and individual characteristics as effects.

Akaike's Information Criterion was used for model selection (Akaike, 1974). Akaike's information criterion is a tool used to compare candidate models that explain a specific response. The model with the lowest AIC score is the model with the better fit and is more likely to minimize the information loss.

An own model selection for estimations with growth variables as predictors were performed as some of the AT-tagged trout lacked back-calculated growth data due to unreadable scale samples.

Salmon lice were categorized into three stages: chalimus, preadult, and adult lice. Lice density was calculated by the total amount of lice (the number of chalimus + number of preadult + number of the adult) divided by the fish length.

PIT data was not statistically analysed because the number of migrants that remained after data filtering was low (n=8).

Estimating the probability of migration:

Trout was defined as a migratory individual if it was detected by a receiver located in the fjord. Individuals that were never detected by receivers in the fjord were defined as non-migratory.

Two individuals were only detected in the fjord at locations far from their release site, more precisely one from Daleelva and one from Mundheimselva. The one from Daleelva was only detected twice by a receiver located in Os, Bjørnafjorden (approximately 27 km direct line from Daleelva), and the one from Mundheim was sporadically detected four times by a receiver located near Onarheim (approximately 29 km direct line from Mundheim). Both Os and Mundheim had several receivers located in the area and if the trout were alive and swimming, it would most likely be detected by other receivers nearby. Therefore, these individuals were not included in the analysis.

Timing of migration

The time at which a smolt left the river was defined as the first time it was detected in the fjord by the receiver closest to the estuary of the river it was released in.

When estimating the timing of migration as a function of the environmental variables such as discharge, tag ID was estimated as a random effect, while the predictor variables discharge and the number of chalimus were estimated as fixed effects.

Before the amount of discharge could be compared between the study rivers, the discharge was standardized in the three rivers by the following calculation:

Standardized discharge = $\frac{X-\bar{X}}{SD}$, where X is the discharge at a given day the river, \bar{X} is the mean discharge in the river, and SD is the standard error in the given river, where Daleleva discharge parameters were: 0.24 ± 0.39 ; Mundheim: 0.60 ± 0.96 ; Herøysund: 0.26 ± 0.46

Individuals that migrated to the fjord in October or later (n=4) were removed from the data before estimating the timing of migration, as the rest of the smolt migrated between the 16th of June and the 16th of August.

Depth

Detections recorded at depths larger than 10 meters were excluded from the analysis, which was only detections from one individual presumed dead due to a sudden change from a regular depth use between 0.6 to 5.4 meters to 50 meters as its last detections (Appendix Figure A-6).

The time of day was grouped into three: night, day, and twilight. Twilight was defined as half an hour before and after sunrise and half an hour before and after sunset.

Distance from estuary

The maximum distance migrated was defined as the observation of the maximum distance from the river mouth of the release site.

Both the number and density of copepodids and mobile stages (preadults and adults) were also tested as variables together with the variable length. Many different combinations of these got a high AICc score, but after the removal of objects with high leverage, that was not the case anymore, and the model with length as a variable was the model of best fit.

Return date and time in fjord

The time of return was defined as the last detection by the receiver located near the estuary. Two individuals from the river in Herøysund had an exit time equal to the time of return and several individuals were observed further away from the fjord after the time of return to their respective estuary (Appendix Figure A-9)

The approximate distance between the river mouth and the nearest receiver in Mundheim, Daleelva, and Herøysund was respectively 150 m, 150 m, and 420 m. Detection data recorded by the nearest located receiver to the river in Herøysund was not extracted during this study, and the second nearest receiver was used instead. Because this receiver was located further away from the river mouth, the water experienced by the sea trout here would be less affected by the freshwater runoff from the rivers. Due to this and the small sample size (n=6), responses in trout from Herøysund were emphasized.

Maximum time spent in the fjord was found by subtracting the time of which the trout migrated from the time of return. Note that the calculated time spent in the fjord excludes the time a trout spent in the fjord after the defined time of return.

Survival

Survival and mortality were not estimated in this study because of how the study was conducted. The rivers were all relatively small streams, and therefore difficult to place receivers here. Only Mundheim had a receiver placed in freshwater, near the river mouth. Therefore, survival was not estimated as we do not know if the trout were alive or dead in the river. Only three individuals were believed to have died because of sudden movement across large distances and a sudden, extreme increase in depth use.

2.8 Data handling, PIT

The PIT-data used in this study was received from Rådgivende Biologer AS. The dataset contained tag data of 156 PIT-tagged premature returned sea trout from Mundheim (n=104, length \bar{x} =14.6 cm, s=2.4 cm, weight \bar{x} =29.2 g, s=16.5 g), Daleelva (n=27), and Herøysund (n=25), on seven different occasions during a period between 31st of May 2021 and 12th of July 2021, including trout that were captured during the same time and space as the AT-tagged trout. Mundheimselva was the only river of the study rivers that had installed PIT-antennas. Three stationary PIT antennas were located in the river, one top antenna and two bottom antennas (one standing and one laying down). The top antenna was placed 1-2 meters upstream of the standing bottom antenna, and these were approximately 20 meters upstream from the laid down bottom antenna.

A total of 26 562 detections in Mundheimselva. One post-smolt tagged in Daleelva was detected by the PIT-antennas in Mundheim. PIT detections were further filtered by location and arranged after the time of detection with information on which type of antenna it was detected by. The time difference between two detections of the same ID was calculated by taking the time of one detection and subtracting the time of the detection before. Trout was defined as a migrating individual when detections formed a pattern where they first were detected by minimum one of the two antennas upstream (top- and standing bottom antenna), then by the antenna downstream, and then by a downstream antenna again. Because a migratory trout would be in the fjord for some time, a time gap between the two detections by the bottom antenna had to be chosen. A too small of a gap could result in an overestimation of migratory trout as we cannot know for sure if the trout are in the river or fjord. On the other hand, if the limit is too big, fish that have been in the fjord for a short time would be excluded. Therefore, a time gap of two days was chosen as the threshold between migratory and non-migratory trout. Individuals with detection patterns different than the one shown above were defined as non-migratory/uncertain. This was to avoid overestimating the number of individuals that migrated. If an individual was detected upstream, then downstream, and never to be detected again, we cannot know if it has migrated and/or has died. If an individual is detected upstream, then downstream, and then upstream again with a two days time gap, we cannot know if it has been in the fjord and not detected by the downstream antenna, or if it's been in the river the whole time.

After finding detection patterns that fulfilled the preconditions, the minimum date of river exits, and the maximum return date were filtered out per individual. Time spent in the fjord was calculated by subtracting the date of exit from the return date.

3. Results

3.1 Salmon lice infestations

Signs of salmon lice infections were found on all captured sea trout. Eight trout from Mundheim did not have any alive salmon lice on them, but they all had remnants of dead lice. All tagged trout from Herøysund and Daleelva had salmon lice on them. The number of chalimus ranged between 0 and 60 with a mean number of 15, while the mean chalimus density among the rivers was 0.95 and ranged between 0 and 3.9. The mean number of mobile salmon lice varied between 0 and 39 lice per fish, with a mean of 2.26, and the densities of the mobile stages ranged between 0 and 2.4 with a mean of 0.14 lice per cm fish.

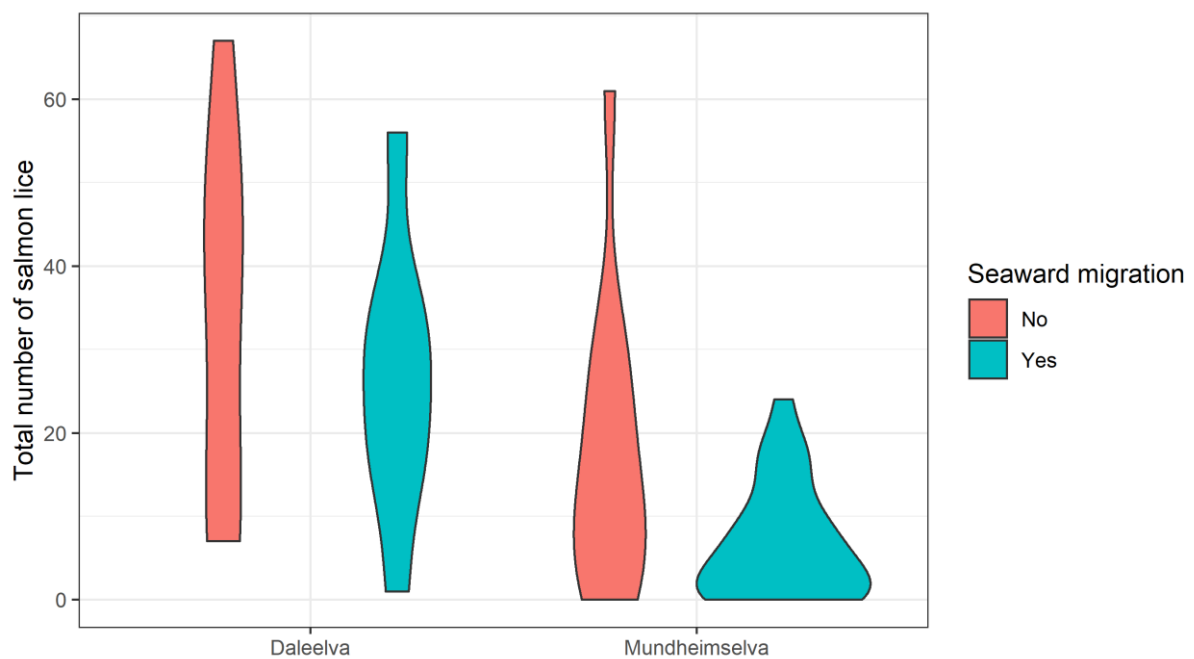


Figure 3.1.1: The distribution of the number of salmon lice found per trout in each river. Color indicates if the trout migrated to the fjord or not.

3.2 Migration probability

Of a total of 62 trout tagged with acoustic tags, 40 individuals were detected in the fjord. The proportion of trout detected in the fjord was highest in Herøysund (83%), then Mundheimselva (67.5%), while Daleelva had the lowest proportion of trout detected in the fjord (50 %; Figure 3.2.1).

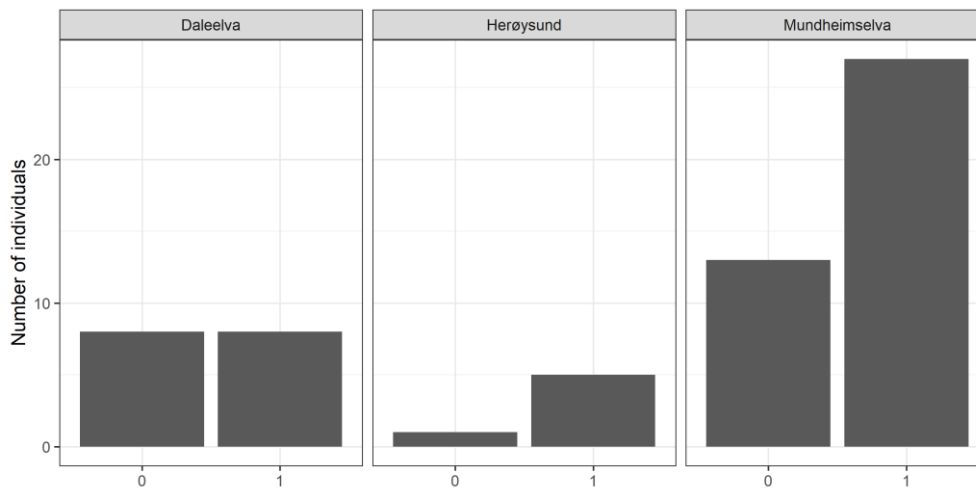


Figure 3.2.1: The number of trout that were observed exiting/not exiting their respective river. 1= exit, 0= no exit.

Of the candidate models, the model containing an interaction between the total amount of salmon lice and the study river had the best AICc score, followed by 12 models with a delta AICc less than two, all containing a lice variable (Appendix Table A-1).

The model with the most support showed that the river effect was non-significant, but that the total sum of salmon lice had a significant negative effect on migration and that the negative interaction effect was almost significant (Table 3.2.1 and 3.2.2; Figure 3.2.2).

The second-most supported model with lice density as a predictor also had a significant negative effect on migration ($p=0.01$).

The model with chalimus got a better AICc score than models with preadult and adult, all with a negative effect on migration, but only chalimus ($p=0.012$) and preadult ($p=0.021$) had a significant effect.

Table 3.2.1: Parameter estimates (GLM) for the most supported model (Appendix Table A-1) with river exit as response to river and the total sum of salmon lice (sumLice). Parameter estimates are on logit-scale.

	Estimate	Std. Error	z-value	Pr(> z)
Intercept	5.70E-01	9.632E-01	0.592	0.554
River[Herøysund]	2.02E+02	2.01E+04	0.01	0.992
River[Mundheim]	1.10E+00	1.05E+00	0.892	0.372
sumLice	-1.94E-02	2.79E-02	-0.694	0.488
River[Herøysund]*sumLice	-2.98E+00	3.02E+02	-0.010	0.992
River[Mundheim]*sumLice	-7.17E-02	4.97E-02	-1.442	0.149

Table 3.2.2: ANOVA table for the most supported model (Appendix Table A-1, Table 3.2.1) with river exit as response to river and the total sum of salmon lice (sumLice).

	Df	Deviance	Redid. Df	Resid. Dev	Pr(>Chi)
River	2	2.6145	59	78.034	0.271
sumLice	1	7.742	58	70.292	0.005
River:sumLice	2	5.309	56	64.983	0.080

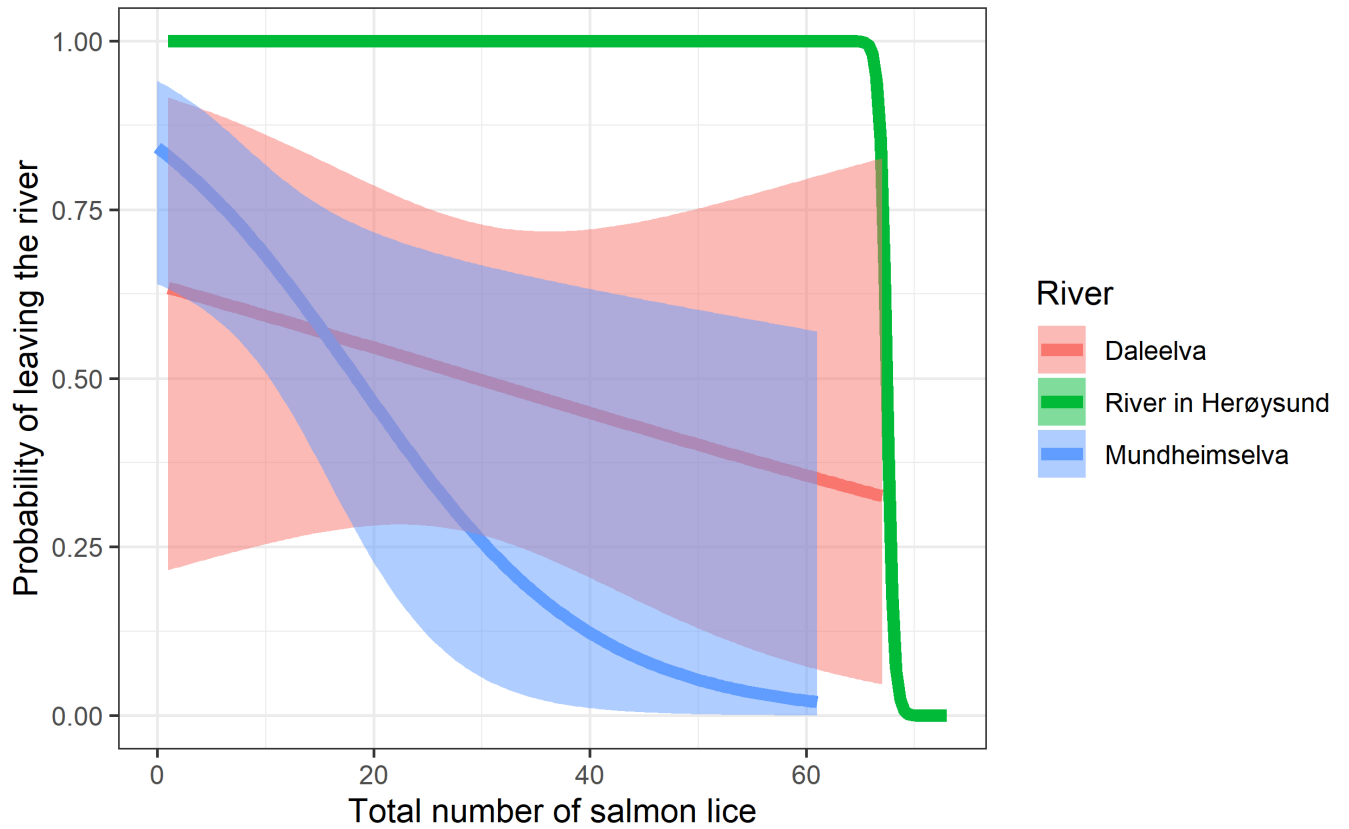


Figure 3.2.2: The predicted probability of river exit as a function of the total amount of lice attached at each study site. Predictions were made from the selected model in Appendix Table A-1 & Table 3.2.1. Release sites are represented by different colored lines, with 95% confidence intervals represented by the shaded area. Confidence intervals were excluded from the river in Herøysund.

3.3 Migration probability with growth predictors

When running a model selection for GLM-models estimating the probability of migration with growth predictors, the model with estimated length at their first year of living was the most supported GLM-model (Appendix Table A-2). The growth during their first year had a positive effect on migration (Table 3.3.1; Figure 3.3.1), but was not significant (Table 3.3.2).

Table 3.3.1: Parameter estimates) for the most supported GLM-model (Appendix Table A-2) with river exit as response to length in year 1 (L1). Parameter estimates are on logit-scale.

	Estimates	Std. Error	z value	Pr(> z)
Intercept	-0.687	1.214	-0.566	0.571
L1	0.028	0.024	1.154	0.249

Table 3.3.2: ANOVA table for the most supported GLM-model (Appendix Table A-2, Table 3.3.1) with river exit as response to length at year 1 (L1). Parameter estimates are on logit-scale.

	Df	Chisq	Resid. Df	Resid. Dev	Pr(>Chi)
L1	1	1.372	55	71.191	0.242

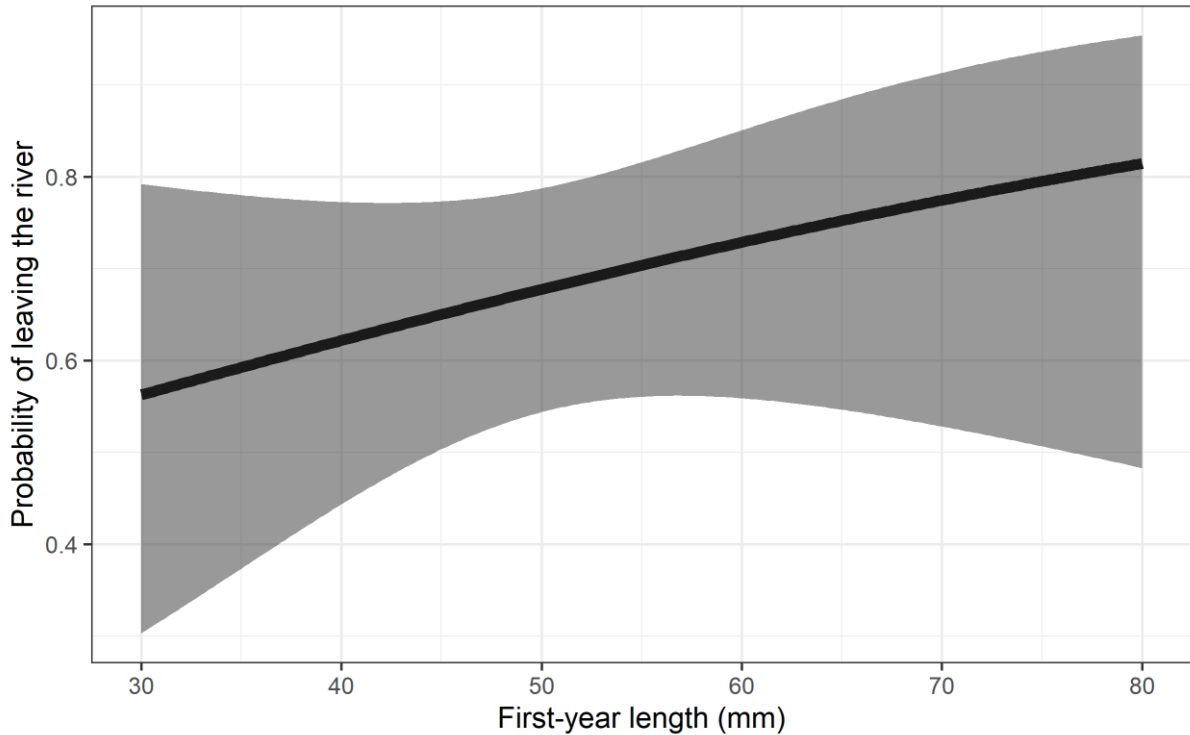


Figure 3.3.1: The predicted probability of river exit against the trout's first-year length (mm; p-value=0.242). The shaded area represents the 95% confidence interval. Made from the selected model from Appendix Table A-2 & Table 3.3.1.

3.4 Time of migration

The timing of migration differed among the three rivers. In Daleelva, all trout detected in the fjord migrated out of the river before July, while most trout in Herøysund and Mundheim migrated between late June and mid-July (Figure 3.4.1). The latest migrating individual was trout released in Mundheim. Four individuals were first detected in the fjord in October and November.

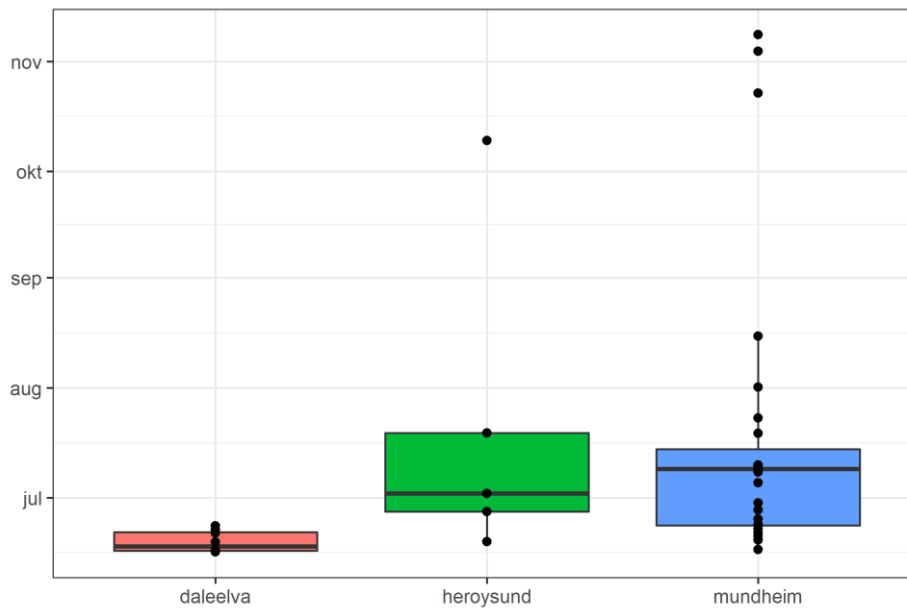


Figure 3.4.1: The time of river exit in each study river. The boxes represent the 25th and 75th interquartile, and whiskers represent the minimum and maximum values within 1.5 times the interquartile range. Points outside the whisker range are outliers.

Based on the AIC model selection, the model that explained most of the variation in the dataset when assessing the timing of migration was the model with the interaction between river and standardized discharge (stDsischarge; Appendix Table A-3). The following two models included, in addition to relative discharge, the number of chalimus and chalimus density as additive effects, but were not significant effects.

The model with the timing of migration as a function of river and relative discharge showed a highly significant interaction effect (Table 3; $p=2.66E-07$). The time of migration in context to discharge for trout in Daleelva deviated from trout in Mundheimselva and the river in Herøysund, where trout in Daleelva had a negative response to the relative discharge, while they in Mundheimselva and Herøysund had a positive response (Table 3.4.1; Figure 3.4.1). The response to discharge in Mundheim and in Daleelva differed significantly from a relative discharge that ranged from -0.6 to 1.2 (Figure 3.4.2).

Table 3.4.1: Parameter estimates for the most supported general linear mixed-effects model (Appendix A-3) with time of migration as response to river and standardized discharge (stDischarge). ID as a random effect (var= 0.8853). Intercept represents Daleelva.

	Estimate	Std. Error	z value	Pr(> z)
Intercept	4.198	0.421	9.985	< 2e-16
River[Herøysund]	-1.939	0.651	-2.979	0.003
River[Mundheim]	-2.136	0.465	-4.599	4.25E-06
stDischarge	-0.314	0.129	-2.440	0.015
River[Herøysund]*stDischarge	0.742	0.249	2.977	0.003
River[Mundheim]*stDischarge	0.696	0.145	4.790	1.67E-06

Table 3.4.2: ANOVA table for the most supported general linear mixed-effects model Appendix Table A-3, Table 3.4.1) with time of exit as response to river and standardized discharge (stDischarge). ID as random effect (var=0.8853).

	Chisq	Df	Pr(>Chisq)
River	16.065	2	0.0003
stDischarge	18.251	1	1.94E-05
River*stDischarge	23.732	2	7.03E-06

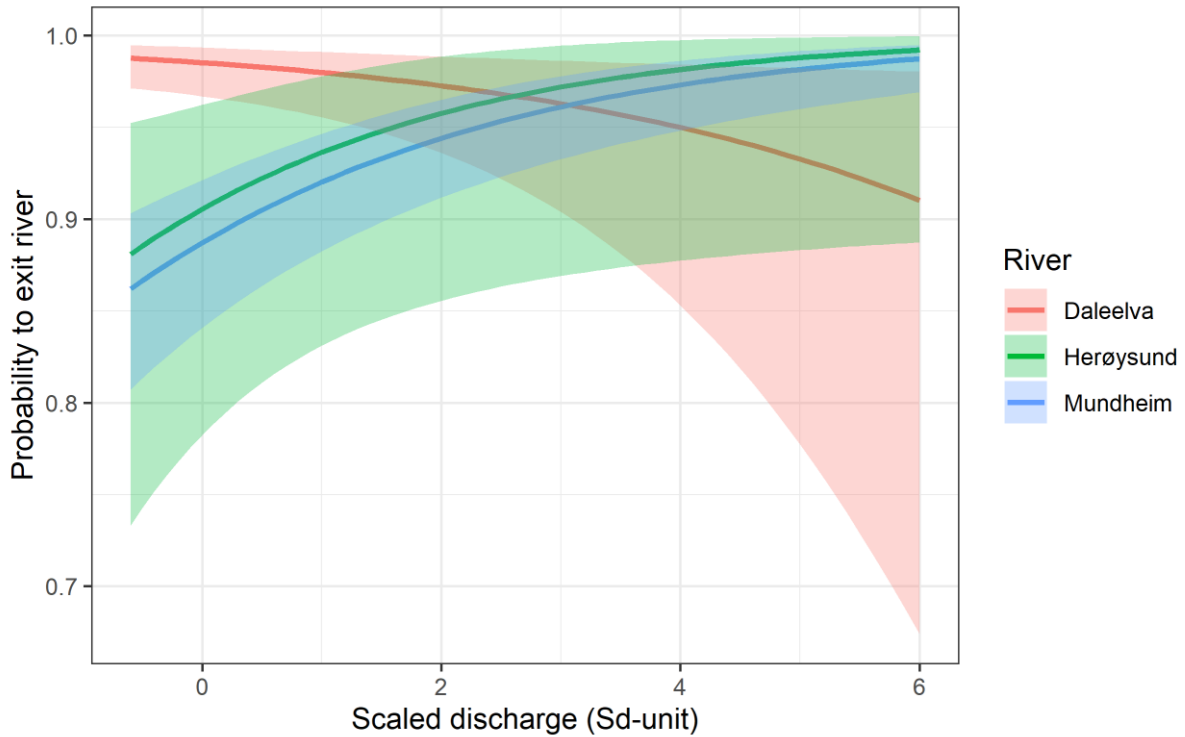


Figure 3.4.2: The predicted time of migration as a function of standardized discharge in the three study rivers, with a 95% confidence interval. Made from the selected model in Appendix Table A-3 & Table 3.4.1.

Of the candidate models explaining the time of migration as a function of different individual characteristics, the model with river as a predictor was highest ranked in the model selection, followed by a model with condition factor and river as additive effects (Appendix Table A-4), where river group was the only predictor that had a significant effect ($p=0.0016$).

In Daleelva the trout migrated significantly earlier than the trout from Mundheimselva, while trout from Herøysund did not migrate at a significantly different time than trout in Daleelva or Mundheim (Figure 3.4.3).

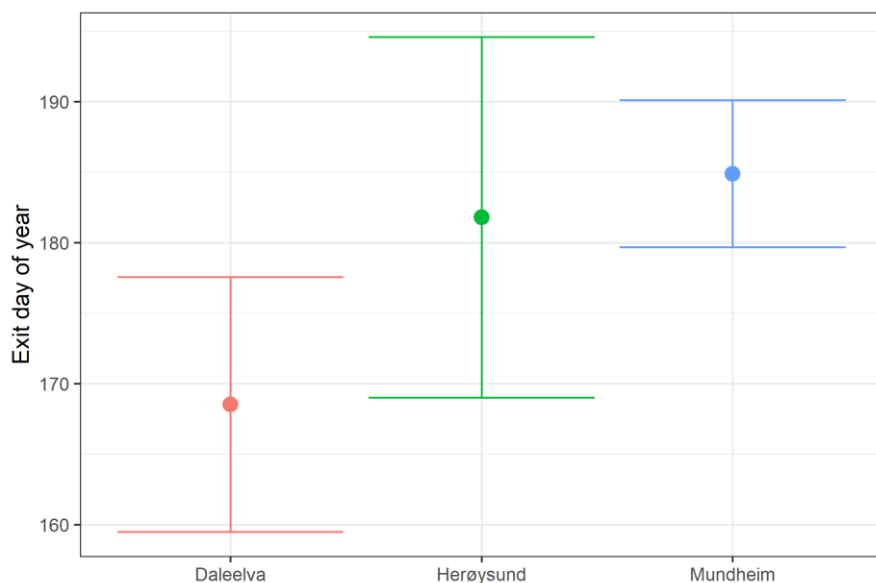


Figure 3.4.3: The predicted exit day (days since 01.01.2021) in the three study rivers. Exit day 165 equals the date 15.06.2021. Bars represent means, and whiskers a 95 % confidence interval. Made from the selected model in Appendix Table A-4.

3.5 Depth use in the marine environment

Tendencies to observations at deeper water during the day compared to night (Figure 3.5.1). The mean water depth across all rivers was 1.16 meters, while the mean depth used for trout from each river was 1.12 m for Mundheimselva, 1.00 m for Daleelva, and 1.56 m for the river in Herøysund.

Candidate models with river, time of day, and density of chalimus attached at capture dominated with an AICc weight at 1 at the AIC model selection (Appendix Tabel A-5). The single effect of both river and chalimus density on depth use was not significant nor was the interaction effect between river and chalimus density (Table 3.5.2).

The interaction between river and time of day, chalimus density and diel migration, and river, chalimus density, and time of day were all significant (Table. 3.5.2).

Trout from Mundheim showed a positive response to night and twilight, while the interaction effect chalimus density had a negative effect on depth use during both night and twilight (Table 3.5.1).

Trout from Daleelva had a negative response in depth use during the night, twilight, and to chalimus density. The interaction effect between chalimus density and time of day differed with a slightly negative response to chalimus density at twilight and a slightly positive response to chalimus density at night.

Trout from Herøysund showed a negative response in depth use during night and twilight, while chalimus density had a positive effect on the trout's depth use. Chalimus density had a negative effect on depth use at night (Table 3.5.1).

Trout from Mundheimselva swam significantly shallower than trout from the other rivers at night and twilight when chalimus densities were higher than approximately 0.75 (Figure 3.5.2).

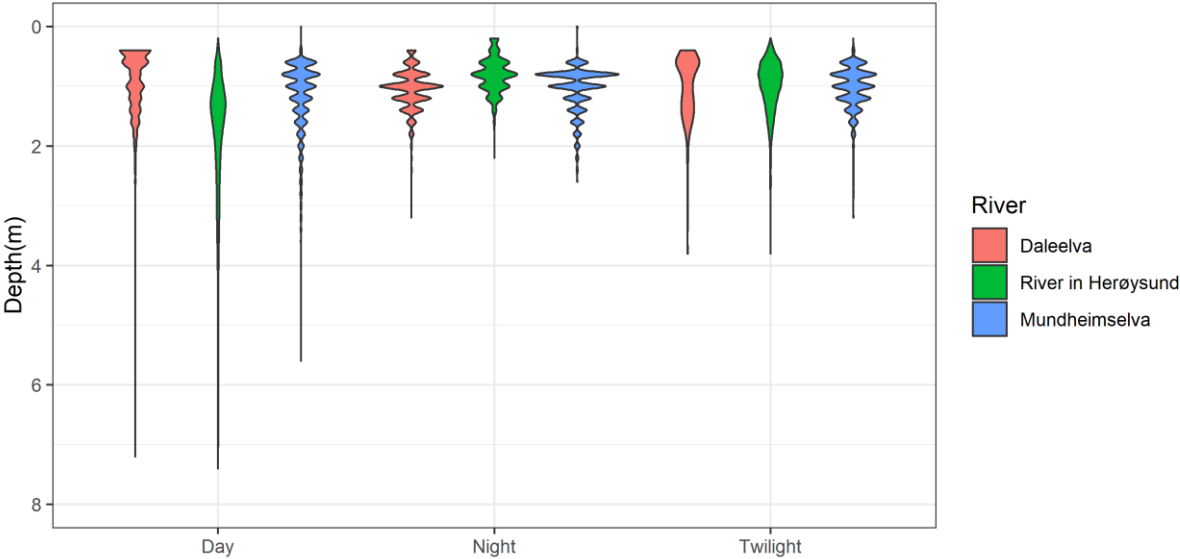


Figure 3.5.1: Depth use (m) by post-smolt from each study river (color) during the day, night, and twilight.

Table 3.5.2: Parameter estimates for the most supported linear mixed-effect model (Table Appendix A-5) with the logarithmic depth as response to river, time of day (ToD), and chalimus density, ID. as a random effect (var= 0.2993).

	Estimate	Std. Error	t-value
Intercept	0.257	0.542	0.474
River[Herøysund]	0.156	0.798	0.195
River[Mundheim]	-0.275	0.582	-0.472
ToD[Night]	-0.357	0.014	-25.999
ToD[Twilight]	-0.124	0.023	-5.302
chaliDens	-0.281	0.295	-0.955
River[Herøysund]*ToD[Night]	-0.344	0.058	-5.920
River[Mundheim]*ToD[Night]	0.380	0.015	26.006
River[Herøysund]*ToD[Twilight]	-0.376	0.025	-14.982
River[Mundheim]*ToD[Twilight]	0.126	0.025	5.128
River[Herøysund]*chaliDens	0.341	0.432	0.790
River[Mundheim]*chaliDens	-0.273	0.526	-0.519
ToD[Night]*chaliDens	0.048	0.007	6.649
ToD[Twilight]*chaliDens	-0.004	0.011	-0.364
River[Herøysund]*ToD[Night]*chaliDens	-0.153	0.301	-0.508
River[Mundheim]*ToD[Night]*chaliDens	-1.986	0.035	-56.444
River[Mundheim]*ToD[Twilight]*chaliDens	-1.168	0.057	-20.375

Table 3.5.3: ANOVA table for the most supported linear mixed-effects model (Appendix Table A-5, Table 3.5.2) with the logarithmic depth as response to Time of day (ToD), chaimus density (chaliDens) and river. ID as random effect (var=0.2993).

	Chisq	Df	Pr(>Chisq)
river	3.521	2	0.172
ToD	5593.831	2	<0.0001
chaliDens	1.585	1	0.208
river*ToD	2701.219	4	<0.0001
river:chaliDens	2.724	2	0.256
DayNight:chaliDens	37.155	2	<0.0001
river:DayNight:chaliDens	3215.016	3	<0.0001

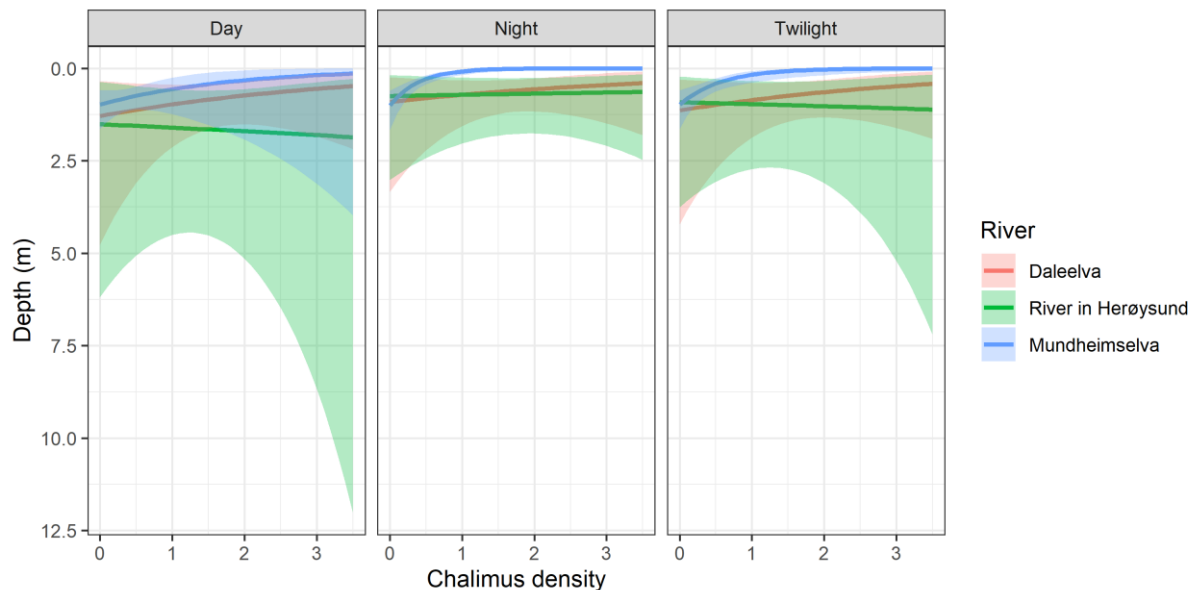


Figure 3.5.2: The predicted depth use (m) against chalimus density during the day, night, and twilight. Color represents the release site, and the shaded area is the 95% confidence interval. The figure was made from the selected model in Appendix Table A-5 & Table 3.5.2.

3.6 Maximum distance from the river mouth

78.6 % of all detection in the fjord was by the receiver closest to the river mouth. The proportion of detection made by trout from Daleelva, Mundheimselva, and the river in Herøysund was respectively 99.9%, 73.6%, and 99.7 %.

The maximum distance from the river mouth ranged between 0.5 to 35.6 km, with a mean distance of 3.4 km. Most of the trout did not travel further than 10 km from the river mouth (Figure 3.6.1). Four individuals were observed with a maximum distance greater than 10 km.

The candidate model that got the most support when running an AIC model selection, was the model with length as a predictor variable, followed by the model with length and condition as additive effects (Appendix Table A-6). The most supported models showed that length had a significant positive effect on the maximum distance travelled by sea trout (Table 3.6.1 and 3.6.2; Figure 3.6.2). The second most supported model showed a negative response to the condition factor but was far from significant ($p=0.6$).

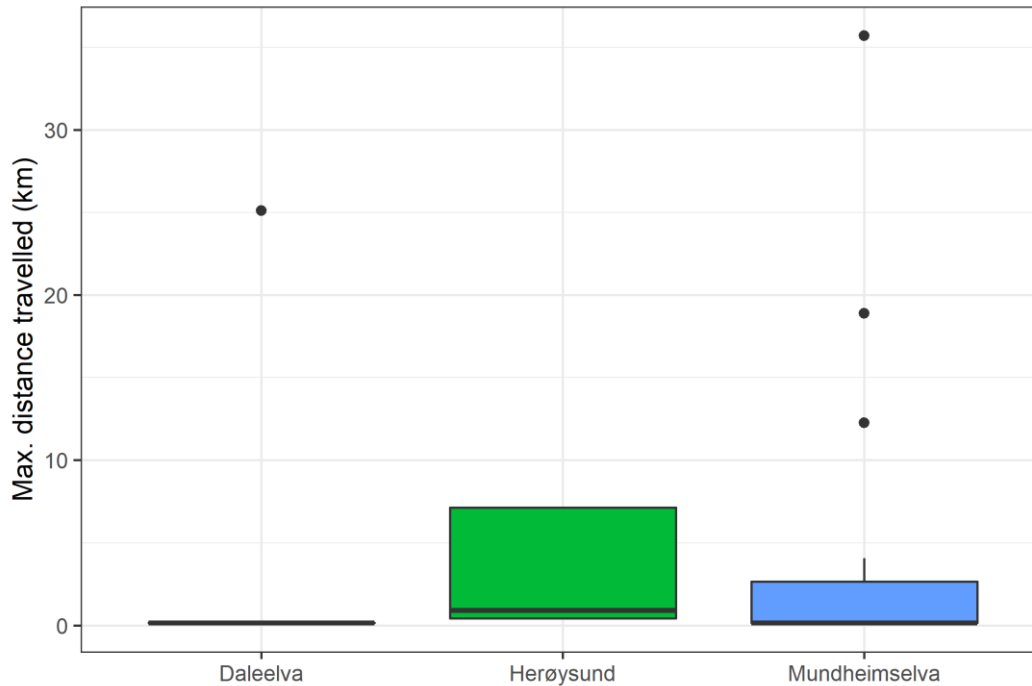


Figure 3.6.1: Maximum migration distance (km) from the river mouth by sea trout from the respective river.

Table 3.6.1: Parameter estimates for the most supported linear model (Appendix Table A-6) with maximum distance as response to fish length.

	Estimate	Std. Error	t value	Pr(> t)
Intercept	-24.459	8.732	-2.801	0.008
length	1.830	0.569	3.219	0.003

Multiple R-squared: 0.2188, Adjusted R-squared: 0.1976

Table 3.6.2 ANOVA table for the most supported linear model (Appendix Table A-6, Table 3.6.1) with maximum distance as response to fish length.

	Df	Sum sq	Mean Sq	F value	Pr(>F)
length	1	465.88	465.88	1.36	0.003
Residuals	37	1663.80	44.97		

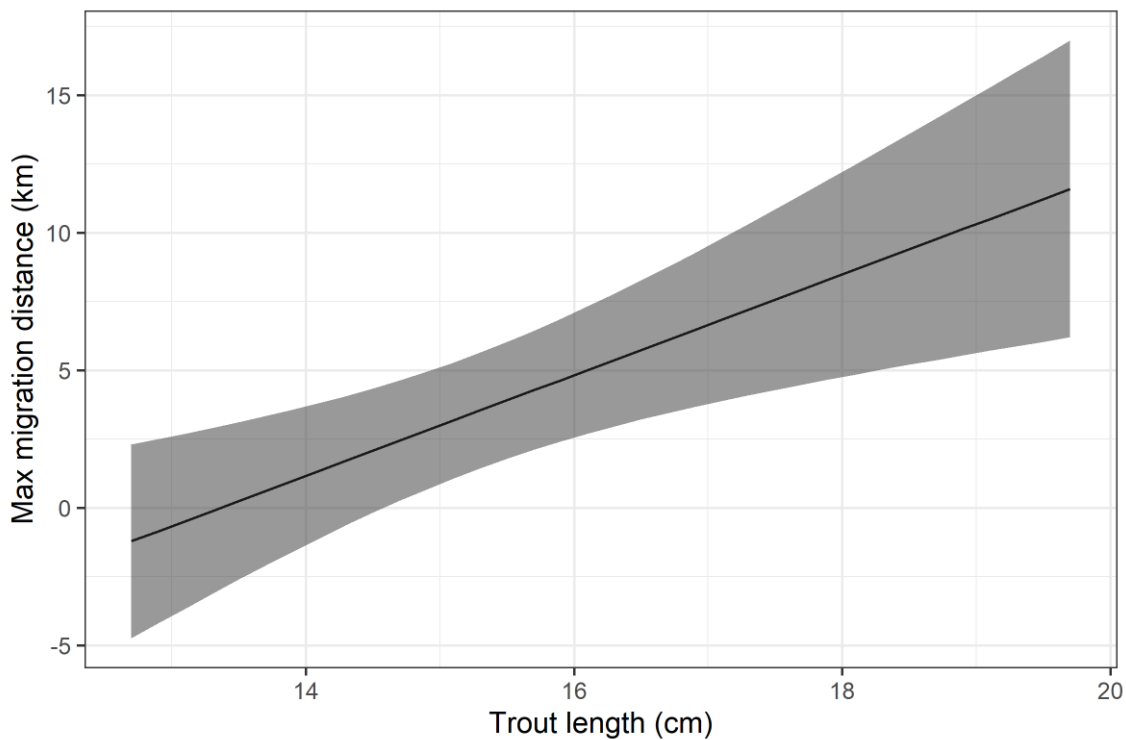


Figure 3.6.2: The predicted maximum distance travelled (km) from the estuary as a function of trout length (cm), the shaded area represents the 95% confidence interval. The figure was made from the selected model in Appendix Table A-6 & Table 3.6.1.

3.7 Return date and time spent in the fjord

A total of 36 trout returned to the estuary where they were released, including the two individuals that first migrated in November. The mean return date was the 14th of August for trout from both Daleelva and the river in Herøysund, and the 28th of August for trout from Mundheimselva. One sea trout from Daleelva had its last observation in the fjord by the estuary of Mundheimselva. The minimum time spent at sea was 0.007 days, while the maximum time was 168.5 days. For trout from Daleelva, Mundheimselva, and the river in Herøysund, the mean time period of which the post-smolt spent in the fjord was respectively 58.8 days, 41.8 days, and 43.7 days. Eight individuals had a sea time of fewer than two days (Figure 3.7.1). Three individuals had an exit date equal to the return date.

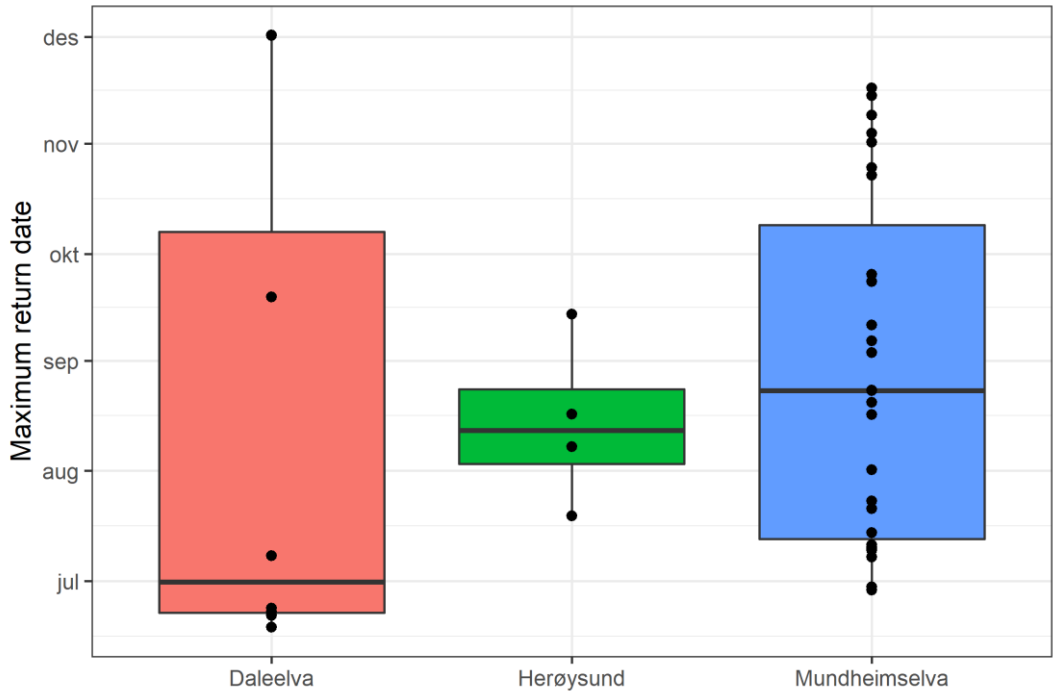


Figure 3.7.1: The maximum date of return to freshwater. All trout, except one, had a return date by the river they were released in.

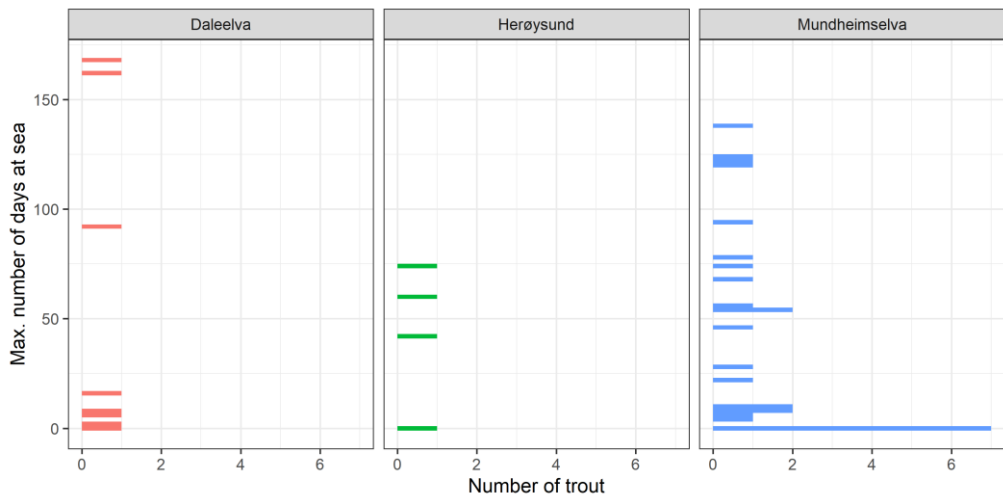


Figure 3.7.2: Number of sea trout and their respective maximum number of days spent in the fjord. Each bar on the y-axis represents one day.

The model with weight as a predictor variable got the best AICc score, closely followed by two models with length and k-factor (Appendix Table A-7). Weight had a slightly positive effect on time spent in the fjord, but not significant and with high uncertainty for heavier trout (Table 3.7.1 and 3.7.2; Figure 3.7.3). The models with length and k-factor had both positive, but not significant effects.

Table 3.7.1: Parameter estimates for the most supported linear model (Appendix Table A-7) estimating the period of time spent at sea, with fish weight as the predictor.

	Estimate	Std. Error	t-value	Pr(> t)
Intercept	1.80595	0.683	2.645	0.012
weigh	0.018	0.014	1.223	0.23
Multiple R-squared: 0.04095, Adjusted R-squared: 0.01355				

Table 3.7.2: ANOVA table for the most supported linear model (Appendix Table A-7, Table 3.7.1) estimating the period of time spent at sea, with fish weight as the predictor.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
weight	1	9.524	9.524	1.495	0.23
Residuals	35	223.032	6.3723		

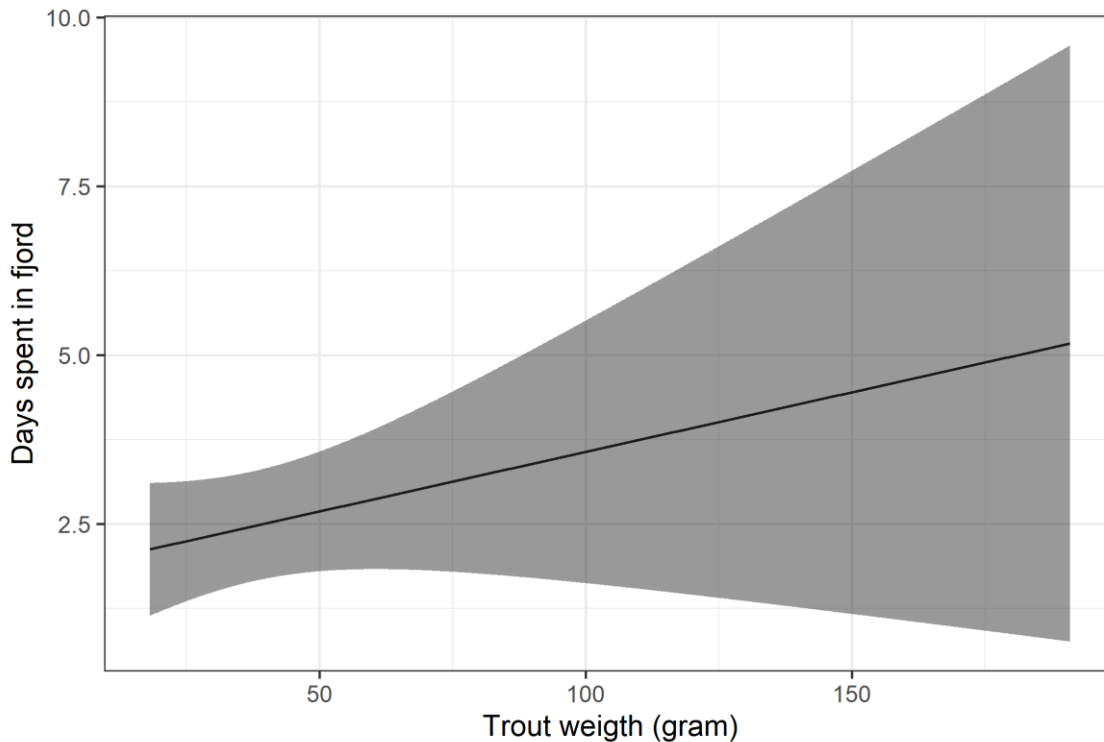


Figure 3.7.2: The predicted time spent in the fjord as a response to trout weight (g). The shaded grey area represents the 95 % confidence interval. The figure was made from the selected model in Appendix Table A-7 & Table 3.7.1.

3.8 Comparison between AT- and PIT-tagged sea trout

Of the PIT-tagged trout (n=104), a total of 19 observations were defined as seaward migrations, by eight individuals where five had travelled to the fjord more than once. One individual had up to eight seaward migrations. Of the eight migrating individuals, three were tagged 31st of May and five 29th of June. Trout tagged in May spent respectively 4, 9, and 128 days maximum at sea.

The timing of seaward migration in PIT-tagged sea trout was more spread throughout the study period compared to AT-tagged (Figure 3.8.1), and figure 3.8.2 shows that there was more variation between rivers for AT-tagged trout than between PIT-tagged and AT-tagged trout in Mundheim, regarding the timing of return. Compared to AT-tagged trout in all rivers, PIT-tagged sea trout spent a shorter period of time in the fjord (Figure 3.8.3).

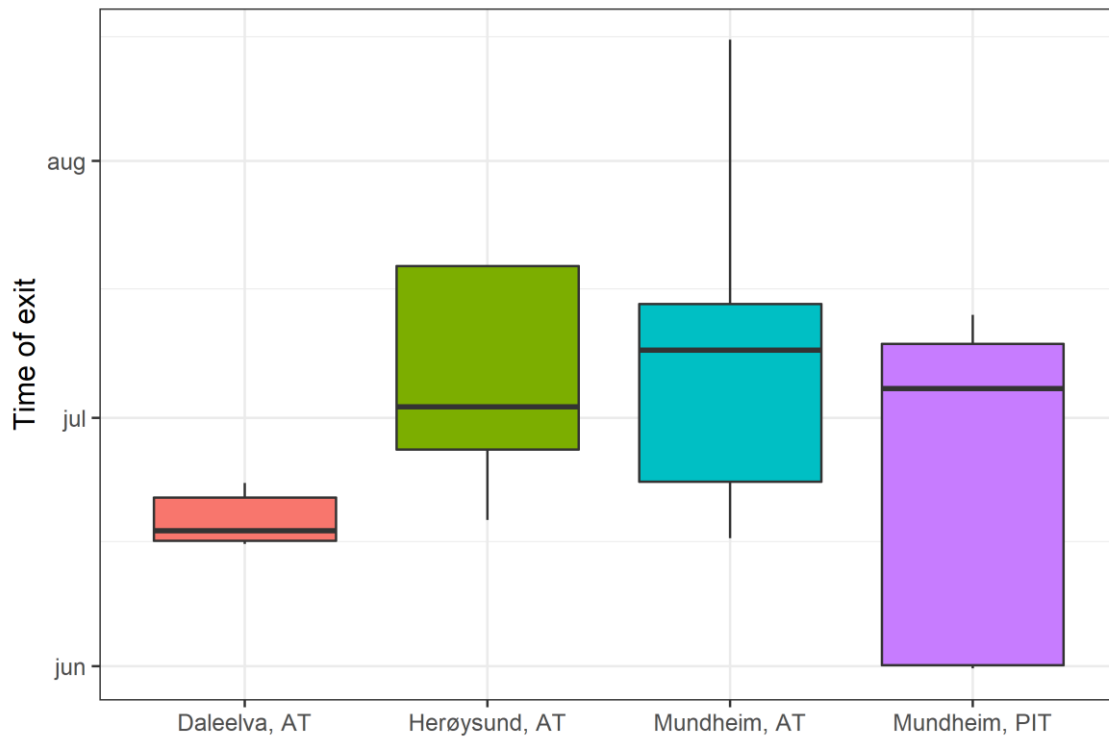


Figure 3.8.1: Timing of first seaward migration per individual trout, by AT- and PIT-tagged sea trout. AT-tagged trout from the three study rivers, and PIT-tagged trout from Mundheim. Trout PIT-tagged in Mundheim as of 31st of May, while all trout with AT-tag tagged the 15th and 16th of June.

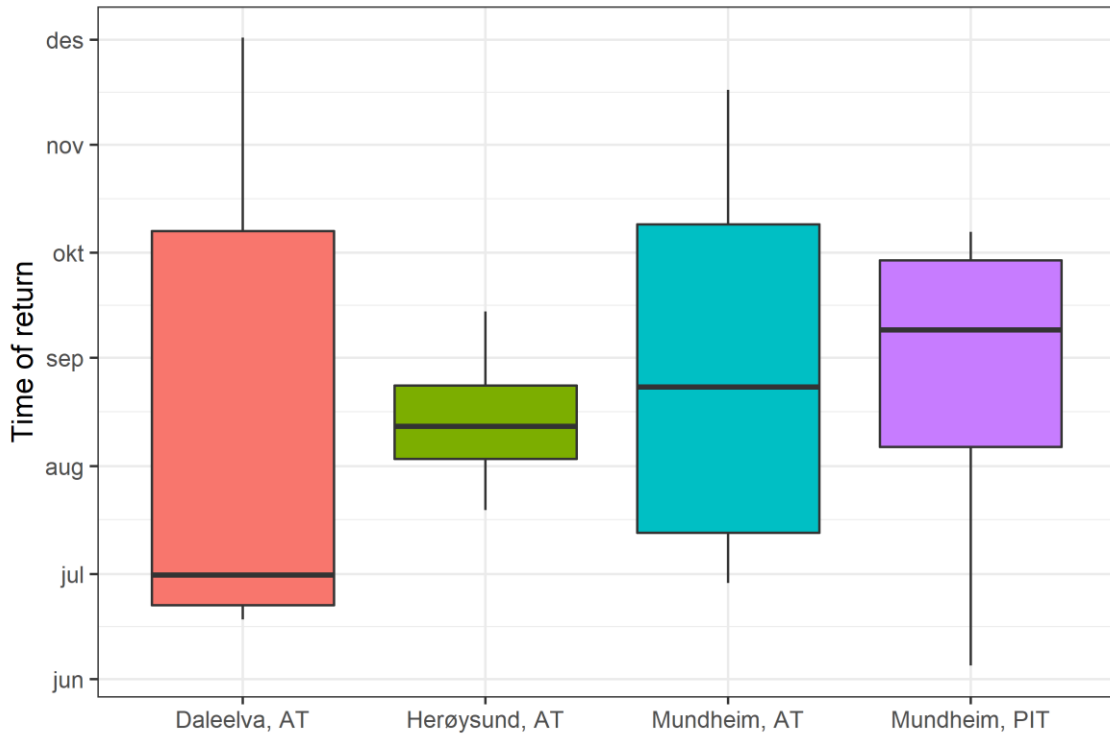


Figure 3.8.2: Time of latest return from the fjord per individual trout, by AT-tagged trout from the three study rivers and PIT-tagged trout from Mundheim.

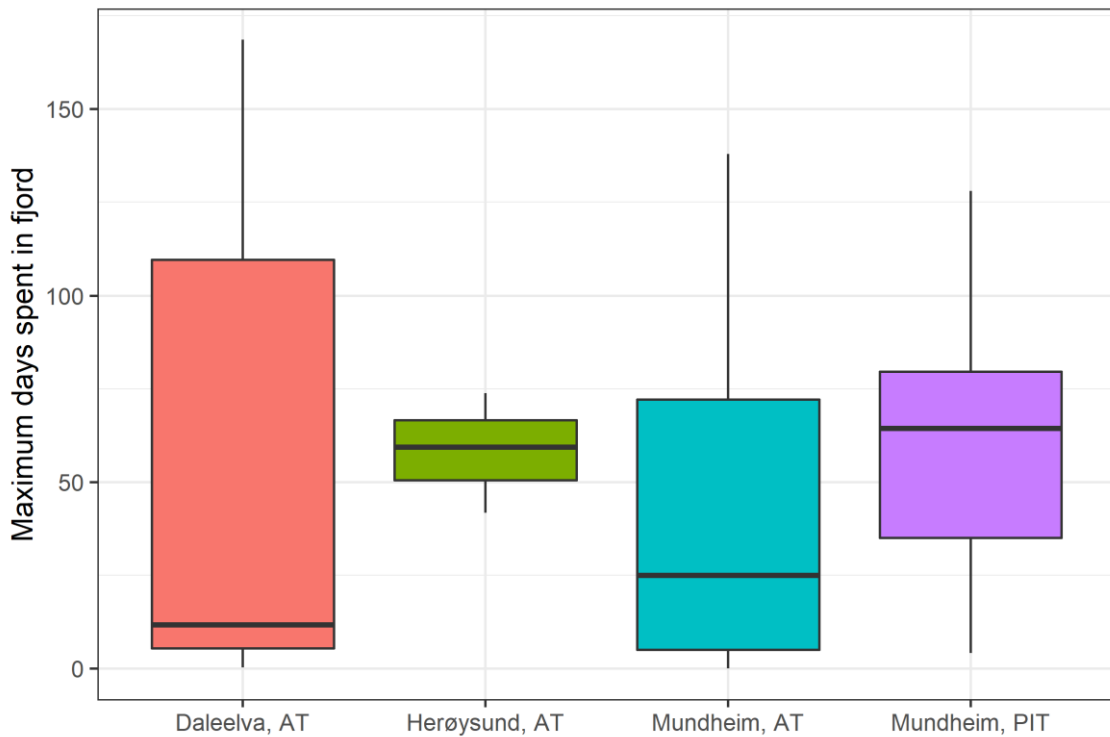


Figure 3.8.3: The maximum time period which sea trout spent in the fjord before returning to their respective estuaries, by AT-tagged trout from the respective rivers, and PIT-tagged trout from Mundheim.

4. Discussion

4.1 Migration

4.1.2 The effect of salmon lice on migration probability

Migration after premature return occurred in all three study rivers. Of the three study rivers, Daleelva was the river that was most exposed to salmon lice in the fjord (Figure 2.1.8), and trout in this river had also the highest amount of salmon lice attached (Figure 3.1.1).

Mundheimselva, on the other hand, was the river least exposed to salmon lice in the fjord, and trout here had also the lowest amount of salmon lice attached. This coincides with Daleelva having a lower proportion of migratory trout compared to Mundheim. The migration analysis strongly suggests that salmon lice infestations influence the probability to migrate after delousing in the river as several models showed a significant negative effect of salmon lice variables, and therefore agree with the hypothesis. This further agrees with the suggestion made by Halttunen et al. (2018), that high infestation pressure may reduce anadromy in trout. However, it's uncertain if the individuals that did not migrate were because of mortalities or other problems caused by the salmon lice. It's also possible that the post-smolt was predated on by other animals or due to other explanations.

There was also an almost significant effect of the interaction between rivers and the total number of salmon lice, meaning that there could be a difference in response to the number of salmon lice attached. The probability of river exit decreased more rapidly with a higher number of salmon lice in Mundheimselva than in Daleelva. This is most likely due to a generally higher number of salmon lice and higher variation in the salmon lice number on the trout in Daleelva. While there was less variation in the salmon lice number in Mundheimselva, one trout deviated from the other trout with a difference of minimum 28 salmon lice from the rest of the trout.

There was also a tendency towards a higher probability to migrate with a higher growth rate as 0+. However, these results should be considered with scepticism as the growth data did not fulfil the assumption of the Lea-Dahls formula for back-calculated growth. This could be corrected, but there was also a large variation in the scale radius among fish of approximately the same size, which indicates flaws in the sampling method, for instance, that the scales were not sampled from the same part on the trout's body. Correcting the formula wouldn't

necessarily give the correct back-calculated fish lengths. But, despite all this, the model still showed a positive trend.

4.1.2 Time of migration and environmental cues

I hypothesized that discharge would be the main factor influencing the time of migration, and the analysis of migration timing showed a significant response to discharge. However, the effect of discharge differed between rivers, and sea trout in Daleelva responded to discharge opposite of sea trout in Mundheimselva and Herøysund. The trout from Mundheimselva and Herøysund had a higher probability to migrate with increased discharge and thereby supporting the hypothesis. But, in Daleelva, the trout responded with a higher probability to migrate with less discharge. The trout here also performed the seaward migrations within a much smaller window of time than trout from the other rivers. All migrating trout from Daleelva had left the river within 8 days after release and had the narrowest time period for seaward migration, while trout from Mundheim had the broadest time period for when they performed seaward migration, where all had migrated within 61 days after release, and 75 % of them within 8 days after release. All trout from the river in Herøysund had left the river within 31 days, also 75 % within 8 days (n=3). The seaward migrations by trout in Daleelva did also occur right after a peak in discharge, as the discharge was decreasing (Appendix Figure A-10), meaning that the actual discharge at which they responded to could be smaller than the mean discharge in the river. For instance, in Mundheimselva the trout had a higher probability to migrate when the discharge was higher than the mean discharge in the river. Trout here also migrated in a broader time span, and they responded to several peaks of discharge happening in the river. In addition, the river Daleelva did also have fewer and shorter peaks and lower discharge in general (mean=0.24, SE=0.39) than Mundheimselva (mean=0.60, SE=0.96; Figure 2.1.4). Other studies have suggested that both discharge and river temperature can influence downstream migration (Aldvén et al., 2015; Jonsson & Jonsson, 2011). Trout and salmon studied by Aldvén et al. (2015) in the river Himleån on the west coast of Sweden, performed downstream migration that coincided with both increased discharge and temperature. However, the most influencing factor differed between years. In the year 2011, the downstream migration peaked with increased temperatures in 2011, while in 2012 it peaked with higher discharge in the river. In addition, in 2012 they found that smolt showed a preference towards turbid water when migrating downstream, but this was not found in 2011. They suggested that these observations were a result of less precipitation in

2011, hence low discharge, which forced the smolt to migrate even at low discharge and in more clear waters than in 2012 (Aldvén et al., 2015). The differences among years in this study show that as the variation in temperature and discharge between years differ, the response in smolts also shifts, indicating a complex relationship between different migration cues and downstream migration. Low discharge can for instance cause higher temperatures in the river. Also, in Daleelva, where the trout was captured, had very little riparian vegetation compared to the two other rivers, which allows more sunlight to reach the water surface. Depending on the weather, this could in theory cause the trout in Daleelva to experience higher temperatures.

Another explanation could be that the water discharge used in the analysis was roughly estimations of the discharge and not actual measurements from the rivers. This means that other local conditions could be excluded from the estimation of discharge, such as local precipitation. It is therefore plausible that the different behaviour observed in Daleelva was because the response was more complex and influenced by several variables, or that they did respond to a higher discharge that was not included in the estimation and therefore also not in the analysis of migration timing.

I also hypothesized that trout more infected by salmon lice would migrate later than trout less infected, but the results did not support this hypothesis. Models that included salmon lice as a predictor showed a slightly negative response to higher numbers of salmon lice infections but were far from significant (chalmus number: $p=0.52$). The river effect was the only significant effect found when investigating the time of migration with individual characteristics as potential effects. This result indicates that the seaward migration mainly is influenced by environmental factors, such as discharge seen in the former analysis.

But, the hypothesis should not be discarded completely. The time of migration was estimated based on the trout that was observed in the fjord, and because the analyses of whether the trout migrated to the fjord or not strongly suggested that trout with higher salmon lice count had a higher chance of remaining in the river, it's possible that the response to salmon lice on the timing of migration is "covered over" by that the migrating trout was less infected by salmon lice.

4.2 Effects on behavioural responses in the fjord

4.2.1 Vertical diel migrations and salmon lice infections

The post-smolt was in general observed at shallow depths. 97.8 % of all recorded depths were within 3 meters and 91 % within 2 meters from the water surface. None of the observations was recorded deeper than 7.5 meters, which is in agreement with other studies describing the sea trout depth preferences in the marine phase (Lyse et al., 1998; Rikardsen et al., 2007; Serra-Llinares et al., 2020). Figure 3.5.1 shows that trout from Daleelva had more detections closer to the surface than trout from Mundheim, even though 70% of the detections by fish with depth sensors were of trout from Mundheimselva. This coincides with Daleelva being in an area with higher salmon lice pressure (Figur 2.1.8), and therefore being more exposed to salmon lice and would benefit from the less saline water in the upper part of the water column (Figure 2.1.6).

I hypothesized that trout with higher levels of salmon lice infections would use shallower depths compared to trout less infected, and the result was ambiguous. The effect of salmon lice on depth use was not directly significant, but there was a trend to use shallower depths with higher densities of chalimus infections at capture. The response to chalimus densities did however differ significantly among the time of day and rivers. Of the trout from Mundheimselva, individuals with higher chalimus densities were predicted to swim significantly shallower during night and twilight than the trout from the other rivers. However, these vertical movements were on a small scale, and with a maximum of 7.4 meters which was recordings from only two individuals. Also, the proportion of detection with depth data was highly skewed. Over 70% of all the data was detections from fish captured in Mundheimselva, while data from Daleelva constituted only 16.5%, and Herøysund 12.6%. Because Mundheimselva had so much more data, it also got more power in the analysis, which can explain the significance in depth use between Mundheimselva and the other two rivers (Figure 3.5.2). It's also not necessarily of biological relevance as the movements were so small. The results did however show that there was a significant effect of chalimus density on the diel vertical movements, where the predicted depth use was shallower with increased chalimus density.

Several studies suggest that trout more infested with salmon lice prefer shallower depths, which often are less saline due to river runoff than trout less infested, to counteract osmoregulatory failure caused by infestations of salmon lice (Gjelland et al., 2014; Serra-

Llinares et al., 2020). But, in the depth analysis, it was the chalimus stage that was found to influence depth use. The attachment of chalimus to the fish has been observed to cause a stress response in the trout's behaviour shortly after the trout has been infested (Wells et al., 2006), but it's not the stage that causes the most harm (Wells et al., 2007), such as osmoregulatory failure. It is, however, possible that trout with higher chalimus density generally used deeper water, and therefore got exposed to higher salmon lice concentrations and thereby got higher chalimus density as presented in the analysis. The difference in depth between high and low chalimus density and day and night was however on a small scale, and it's uncertain if the difference in depth would have made a difference in the exposure of salmon lice as the water is continuously moving. Also, the seawater by the estuaries of the study rivers was not very influenced by freshwater from the rivers (Figure 2.1.5), as the mean salinity in the upper two meters of the water column was 22.38 ppt by Mundheimselva and 25.03 ppt by Daleelva, Ølve, which is within the threshold value found to be preferred by salmon lice. But even though the shallow depth uses are not as beneficial as they could be in the inner part of the fjord where the water is more influenced by river runoff, it can still be the best bad choice in terms of salmon lice concentrations and osmoregulation.

An explanation to the differences in depths between night and day can however be explained as an antipredator behaviour as the use of deeper depths during the day can increase the chance of not being predated on by airborne predators which is a risk especially for post-smolt after sea entry (Dieperink et al., 2001; Dieperink et al., 2002), or it could be due to feeding purposes. The difference in response to chalimus density between day and night could then be explained by a trade-off. The trout from Mundheim, especially, showed a slightly shallower depth use during the night with increased chalimus density but did not show the same pronounced response to chalimus during the night. This could be a trade-off between avoiding predation or finding food, and the impact of salmon lice, either if it's due to post-infection issues or the salmon lice concentration in the fjord.

Other variables, such as temperature could also affect the depth use in post-smolt. A study has shown that dives performed by sea trout kelts from a Danish river increase with higher temperatures (Kristensen et al., 2018). The temperatures measured by Daleelva and Mundheimselva show a difference in temperature by the surface from approximately 18 °C to 9 °C (Figure 2.1.7). This could affect the depth use depending on the depth preferences for the post-smolt. But kelts are larger trout that have newly spawned, and possibly with a diet that differs from smaller post-smolt, and therefore also have different preferences. Temperatures

could also have an effect on the distribution of salmon lice, which further could have affected the post-smolts depth use. The dept utilization by the trout become generally shallower around September (Appendix Figure A-4) when the temperatures were lower (Figure 2.1.7) and the concentration of salmon lice in the fjord decreased (Figure 2.1.8, week 34-36). It is however uncertain if temperatures in the fjord influenced the post-smolts depth use, as it was not included in the analysis.

4.2.2 Maximum distance travelled from the river mouth

The salmon lice infestations experienced by the trout in the fjord were unknown in this study, and it was therefore believed that post-smolt with higher levels of salmon lice infestations at capture would be more negatively affected later, and thereby remain closer to the river mouth. But the results did not support this hypothesis. The results showed that the maximum distance travelled by the sea trout was mostly explained by the fish length, with smaller fish staying closer to the estuary than bigger fish. This partly coincides with the results presented by Halttunen et al. (2018) which showed that bigger fish in better conditions travelled further away than smaller fish in worse conditions. The model with length and condition factor as potential effects tested in this study show a negative, but not significant, interaction effect ($s=7.159$, $p=0.15$). But this present study had a much smaller sample size compared to Halttunen et al. (2018), and with a size distribution shifted towards smaller individuals (min=12.7cm, mean=15.54 cm, max=28.4 cm), creating more uncertainty in the response among bigger individuals (Appendix Figure A-1). A larger sample size could potentially change the response in larger-sized fish. But, it could also potentially result in bigger fish staying closer to the estuary as seen in the study conducted by Serra-Llinares et al. (2020). They found that trout artificially infested with salmon lice stayed closer to the estuary, with bigger trout closer than smaller trout. They also found that infested fish stayed closer to the estuary (Serra-Llinares et al., 2020), meaning that bigger fish would be more infested than smaller fish. However, figure A-7 (Appendix) shows tendencies toward a higher salmon lice count on larger individuals, which could be the result of bigger trout swimming further away from the estuary, thereby also longer residence time, and being more exposed to salmon lice. Larger fish would require more energy, hence more food. Results in this study show that a high proportion of the detections in the fjord were mainly by the estuary, meaning that most of the fish stayed at a close distance to the river. This could cause higher competition for food here, and larger trout may therefore take bigger risks and travel further away in the search for food.

Also, smaller trout remaining closer to shore could be an antipredator behaviour, as suggested by Lyse et al. (1998), and have more problems regarding osmoregulation than bigger individuals (Handeland et al., 1998).

Even though the analysis of the distance travelled did not show an effect of salmon lice infestations, the high percentage of detections in the estuary of Daleelva did coincide with the fact that trout from Daleelva had the highest levels of salmon lice infections and therefore possibly experience more negative consequences caused by salmon lice. But the analysis did not show any relationship between the amount of salmon lice infestations, the condition factor, and distance travelled. This can be explained by the that the trout already has deloused and that the response we see is an indirect result of Daleelva being in an area with extremely high salmon lice pressure. Because Daleelva is the river that is most exposed to salmon lice in the fjord among the three rivers, which can explain why trout from Daleelva stay so close to the river compared to trout from the other rivers in areas with lower salmon lice pressure. This indicates that it's the experienced salmon lice pressure in the fjord that influences the distance travelled, and not late effects from salmon lice infections in trout of this study.

4.2.3 Time spent in the fjord

I hypothesized that trout less infested by salmon lice would stay in the fjord for a longer period of time but was not supported by the results. The analysis showed that the predicted time period at sea increased with the fish weight. It was however not significant. Although, in the analysis of maximum distance travelled, larger trout were predicted to travel further away from the river and estuary than smaller trout. It's therefore logical that larger fish, which most likely also is heavier, spend more time at sea as they also swim larger distances. This is further supported by the fact that the second-best model explaining the time period which the trout spent in the fjord, was the model with length as a predictor which also showed a positive trend with longer periods of time.

The time period which the trout spent in the fjord was however not the actual time they spent in seawater. Detections of the trout from Mundheimselva, which also had a receiver located in freshwater, show that several trout performed multiple trips in and out of the river (Appendix Figure A-9). This means that even though the trout spent a long period of time in the fjord, it could have gone back to the freshwater to delouse many times, and therefore overestimate the

time which the trout spent in the fjord. On the other hand, some trout were observed in the fjord even after the defined return date, which means that the period of time at sea could be underestimated.

4.3 Differences between trout tagged with AT-tag vs PIT-tags

Many of the PIT-tagged trout migrated out to the fjord earlier than most of the AT-tagged trout in Mundheim, but later than the AT-tagged trout in Daleelva and most of the trout from Herøysund. Even though many of the trout were tagged as early as the 31st of May, most of the seaward migrations happened in Juli.

Before comparing the fish tagged with PIT and fish tagged with AT-tag, there are two things to consider. The first and most important problem to consider is that the presentation of PIT-tagged trout and their migration timing and time spent at sea, include individuals tagged up to 16 days before the AT-tagged trout was tagged, meaning that many of the PIT-tagged trout had the possibility to migrate earlier and several times more than the AT-tagged trout.

Second, the PIT-tagged trout is defined as migrants based on when they are assumed to leave and enter the river, while the AT-tagged trout is defined as migrating based on observations in the fjord. This can result in a time delay between the two groups. For instance, if two sea trout with a different type of tags left the river at approximately the same time, the PIT-tagged trout would be observed leaving the river earlier and entering the river later, than the AT-tagged trout.

When considering the information given above, we can see that even though most of the trout PIT-tagged in Mundheim were tagged before the trout with AT-tags, most of the PIT-tagged trout exited the river close to the time of exit by AT-tagged trout from Mundheim (Figure 3.8.1). PIT-tagged trout did also return later and had a longer period of time spent at sea (Figure 3.8.2 and 3.8.3). In earlier analyses of AT-tagged trout, fish size was shown to be the most influencing variable on the time spent in the fjord, with larger fish spending a longer period of time than smaller ones. But this does not agree with the fact that PIT-tagged trout had a mean fish length and mean fish weight shorter and lighter than the AT-tagged trout.

Of the PIT-tagged trout that were tagged on the same day as the AT-tagged trout from Mundheim, none of them were categorized as migrants. All of these were also smaller than the AT-tagged trout, as the trout smaller than 12.5 cm were PIT-tagged. This could indicate that the seaward migration after premature return to freshwater is size-dependent, as suggested by Birkeland (1996).

Suggestions for improvement and further studies

Of the trout that migrated, almost all returned to the estuary of the river they deloused in, which can indicate that they delouse in the river they hatched in. The return date in this study was the last time they were observed by the estuary. This routine does not consider that sea trout may travel back into the fjord after that last detection in the estuary of one of the study rivers. Several sea trout were observed in the fjord after the defined return date. This means that the river they deloused in not necessarily was the place they spent the upcoming spawning season and winter. Another take on this could therefore be to find trout that had their last detection in the fjord by the estuaries, and define these detections as the actual return date, which further would give a more accurate time which they spent at sea. Also, these individuals would most likely have migrated upstream the respective river. Individuals that had their last detection recorded by receivers other than the ones that were placed by the estuaries would be individuals without a return date and could be considered as trout that migrated upstream another river or stream, or that overwintered in the fjord. Genetical analysis could also give further insight into if the post-smolt return prematurely to their local rivers. Tissue samples were collected from the trout in this study and it's therefore possible in the future to examine and assess if these trout are from the same populations or not.

Due to the flaw in the routine to find the return date, the time at sea could have been underestimated. But the time at sea could also have been underestimated as post-smolt could perform several trips between fresh- and sea water, meaning that they could remain in the river for an unknown time before they were detected in the fjord again. Further investigation of the actual time they are in the fjord, and if it is influenced by the salmon lice infestations and concentration, could be of importance as lost time at sea could further affect growth and if the trout will benefit from seaward migration or not.

When analysing the time of migration, one potential important effect variable was not included. The temperature in the river has previously been found to influence the time of river exit in sea trout. The temperatures in the study rivers were, however, not measured during the study period, and could therefore not be included in the analysis. If river temperatures had been included, in addition to real measures of the river discharge, it could give a further insight into the trout's behaviour, and perhaps give a further explanation to the response seen in Daleelva. To implement measure of the river temperatures and discharge in future studies is

essential to understand the complexity of when the prematurely returned sea trout initiate their seaward migrations.

In the analysis of the post-smolts depth use, the temperatures in the fjord were not included as a potential variable. It is possible that the trout responded to temperatures directly or indirectly by the concentration of salmon lice in the fjord, as the vertical distribution of salmon lice in the water column has been found to respond to temperatures (Crosbie et al., 2020).

The survival of post-smolt that has returned prematurely to the river is still unknown. Further studies of the survival in post-smolt, and if it differs between individuals that return to the river to delouse and those that do not, could give much insight and knowledge about the effect of premature return. This could further be used in the management of salmon farms and the protection of wild sea trout stocks.

Implications to management

The results in this study strongly suggest that post-smolt use the rivers as refugee where they can get rid of and recover from the infestations of salmon lice. The post-smolt was also observed remaining close to the estuaries after entering the fjord, and protection of these areas is therefore crucial for the survival of sea trout post-smolt.

Further management of the salmon farm industry are also of importance. It's important to take into account that the salmon lice concentrations caused by salmon farms not only can increase sea trout mortality, but also impact other aspects of the sea trout's life.

Conclusion

This study show that salmon lice infestations do have an effect on whether the sea trout post-smolt do enter the fjord again after delousing in the river. By prematurely returning to freshwater, the trout get rid of already attached parasites and prevents further damage and possible mortalities. But it may also reduce the trout's time at sea, hence reducing the feeding opportunities, which can further reduce growth (Birkeland, 1996), which again can reduce the migratory behaviour in sea trout. Body size was found to be the variable that influenced how

far from the river mouth they travelled and how long they utilized the fjord. But it was not established how many times they migrated back and forth between fresh- and seawater, or how long time they spent in the river for each time they went back. The time of exit and how they used the vertical depths was shown to be more complex. The river exit was mainly initiated by higher discharge in the rivers, but the lack of important measures such as river temperatures and real measures of the water discharge leaves the results more open for interpretation. The post-smolts depth use was even more complex as they were shown to be influenced by several interactions, and most likely has to find a compromise.

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Appendix

Table A-1: Model selection for estimating the probability of migration. sumLice = total sum of salmon lice attached at capture, liceDens = salmon lice density, chali = chalimus, chaliDens = chalimus density.

	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
river*sumLice	6	78.510	0.000	0.096	0.096	-32.491
liceDens	2	78.687	0.177	0.088	0.184	-37.242
river*chalimus	6	78.862	0.352	0.081	0.265	-32.668
river+sumLice	4	78.994	0.484	0.075	0.340	-35.146
sumLice	2	78.998	0.488	0.075	0.416	-37.397
river*liceDens	6	79.079	0.569	0.072	0.488	-32.776
river+liceDens	4	79.389	0.879	0.062	0.550	-35.344
river*chaliDens	6	79.536	1.026	0.058	0.607	-33.004
chaliDens	2	79.809	1.299	0.050	0.658	-37.803
river+chalimus	4	79.820	1.310	0.050	0.708	-35.559
chalimus	2	80.031	1.521	0.045	0.752	-37.914
river+chaliDens	4	80.399	1.889	0.037	0.790	-35.848
sumLice*river+tagBurden	7	80.406	1.896	0.037	0.827	-32.166
river*chalimus+tagburden	7	80.936	2.426	0.029	0.856	-32.431
chalimus+tagBurden	3	81.401	2.891	0.023	0.878	-37.493
preadult	2	81.576	3.066	0.021	0.899	-38.686
chalimus*tagburden	4	82.357	3.847	0.014	0.913	-36.828
k-factor	2	82.376	3.866	0.014	0.941	-39.086
1	1	82.715	4.205	0.012	0.953	-40.324
adult	2	83.496	4.986	0.008	0.961	-39.646
river+k-factor	4	83.770	5.260	0.007	0.968	-37.534
chalimus*tagBurden+river	6	83.810	5.300	0.007	0.974	-35.141
weight	2	84.383	5.873	0.005	0.979	-40.090
river	3	84.448	5.938	0.005	0.984	-39.017
tagburden	2	84.608	6.098	0.005	0.989	-40.202
length	2	84.833	6.323	0.004	0.993	-40.315
river+chaliDens*tagburden	6	84.850	6.340	0.004	0.997	-35.661
river+length	4	86.718	8.208	0.002	0.999	-39.008

Table A-2: Model selection for GLM-models estimating the probability of migrating with growth variables as predictors.

	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
L1	2	75.41	0.00	0.38	0.38	-35.60
L2	2	77.42	2.01	0.14	0.51	-36.60
L1+river	4	77.78	2.37	0.11	0.63	-34.51
L1*river	6	78.12	2.70	0.10	0.73	-32.22
growth.2021*river	6	78.15	2.73	0.10	0.82	-32.25
growth.2021	2	78.55	3.14	0.08	0.90	-37.17
L2*river	6	79.93	4.52	0.04	0.94	-33.14
L2+river	4	79.98	4.57	0.04	0.98	-35.61
growth.2021+river	4	80.97	5.56	0.02	1.00	-36.11

Table A-3: Model selection for general linear mixed-effect models when estimating the timing of migration, with ID as a random effect.

	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
river*stDischarge	7	3027.597	0	0.276	0.276	-1506.787
river*stDischarge+chali	8	3028.887	1.290	0.145	0.421	-1506.429
river*stDischarge+chaliDens	8	3028.928	1.330	0.142	0.564	-1506.449
river*stDischarge+liceDens	8	3029.056	1.459	0.133	0.697	-1506.513
river*stDischarge+kf	8	3029.384	1.787	0.113	0.810	-1506.677
river*stDischarge+length	8	3029.386	1.789	0.113	0.923	-1506.678
river*stDischarge*liceDens	13	3032.561	4.964	0.023	0.946	-1503.242
river*stDischarge*sumLice	13	3033.348	5.750	0.016	0.962	-1503.636
river*stDischarge*kf	13	3033.756	6.158	0.013	0.974	-1503.840
river*stDischarge*length	13	3034.257	6.659	0.010	0.984	-1504.090
river*stDischarge*chaliDens	13	3034.517	6.920	0.009	0.993	-1504.221
river*stDischarge*chali	13	3035.061	7.463	0.007	1.000	-1504.492

Table A-4: Model selection for linear models with the time of migration as response to individual characteristics.

	K	AICc	$\Delta AICc$	AICcWt	Cum.Wt	LL
river	4	293.28	0.00	0.50	0.50	-142.00
kf+river	5	295.22	1.94	0.19	0.70	-141.61
chali+river	5	295.53	2.24	0.16	0.86	-141.76
kf+chali+river	6	297.78	4.50	0.05	0.91	-141.44
chali*river	7	298.40	5.11	0.04	0.95	-140.20
chali	3	299.10	5.81	0.03	0.98	-146.17
kf*river	7	300.00	6.72	0.02	1.00	-141.00
kf*chali	5	303.56	10.27	0.00	1.00	-145.78
kf+chali+river	13	312.70	19.41	0.00	1.00	-135.08

Table A-5: AIC table with the candidate linear fixed-effects models estimating depth use. ID as a random effect.

	K	AICc	$\Delta AICc$	AICcWt	Cum.Wt	LL
river*DayNight*chaliDens	19	98983.57	0	1	1.00	-49472.78
river*DayNight*chali	19	99302.42	318.85	0.00	1.00	-49632.20

Table A-6: AIC table model selection for candidate models with the maximum distance travelled from the river mouth as a response.

	K	AICc	$\Delta AICc$	AICcWt	Cum.Wt	LL
length	3	263.74	0.00	0.44	0.44	-128.53
kf+length	4	266.03	2.29	0.14	0.58	-128.43
weight	3	266.19	2.45	0.13	0.70	-129.75
kf*length	5	266.36	2.61	0.12	0.82	-127.27
river+length	5	268.02	4.28	0.05	0.87	-128.10
river+kf*weight	7	268.21	4.47	0.05	0.92	-125.30
river+kf+length	6	270.38	6.64	0.02	0.94	-127.88
river+weight	5	270.82	7.08	0.01	0.95	-129.50
river+kf*length	7	271.23	7.49	0.01	0.96	-126.81
river*length	7	271.27	7.53	0.01	0.97	-126.83

Table A-7: Model selection for candidate models with the logarithmic maximum time spent in the fjord as a response.

	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
weighth	3	178.195	0	0.211	0.211	-85.734
length	3	178.344	0.148	0.196	0.408	-85.808
kf	3	178.846	0.650	0.153	0.560	-86.059
length+kf	4	179.483	1.288	0.111	0.671	-85.117
length*kf	5	180.104	1.908	0.081	0.753	-84.084
length+weighth	4	180.717	2.521	0.060	0.812	-170.850
river	4	180.841	2.646	0.056	0.869	-85.796
river+weighth	5	181.817	3.622	0.035	0.903	-84.941
river+length	5	181.985	3.790	0.032	0.935	-85.025
length+weighth+kf	5	182.158	3.963	0.029	0.964	-85.111
river+kf	5	182.717	4.521	0.022	0.986	-85.391
river+length+weighth	6	184.677	6.482	0.008	0.994	-84.939
river*weighth	7	187.584	9.388	0.002	0.996	-84.861

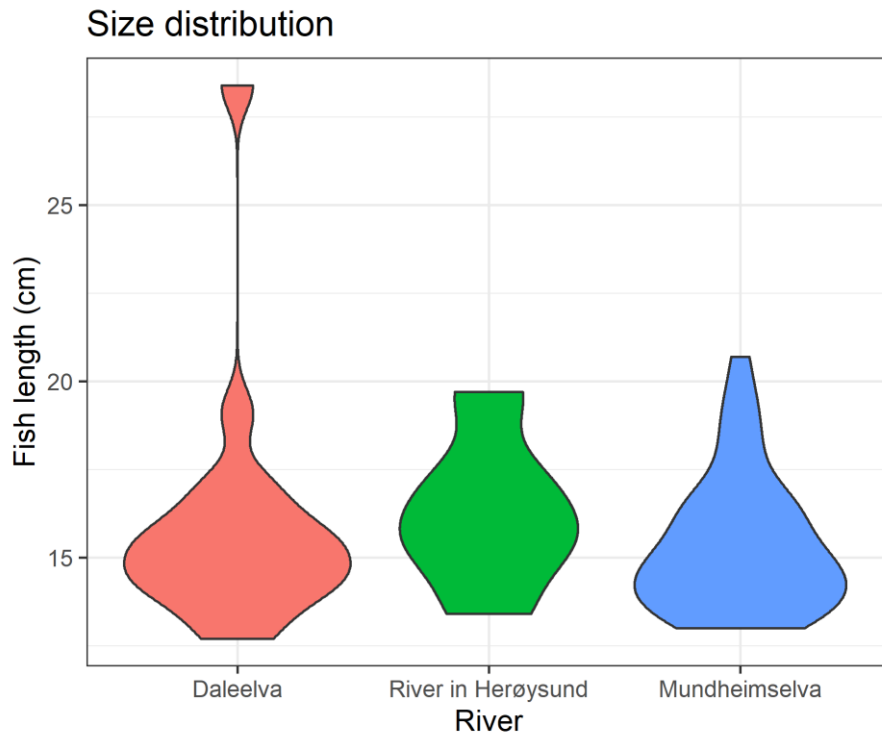


Figure A-1: Length distribution of tagged sea trout in each river.

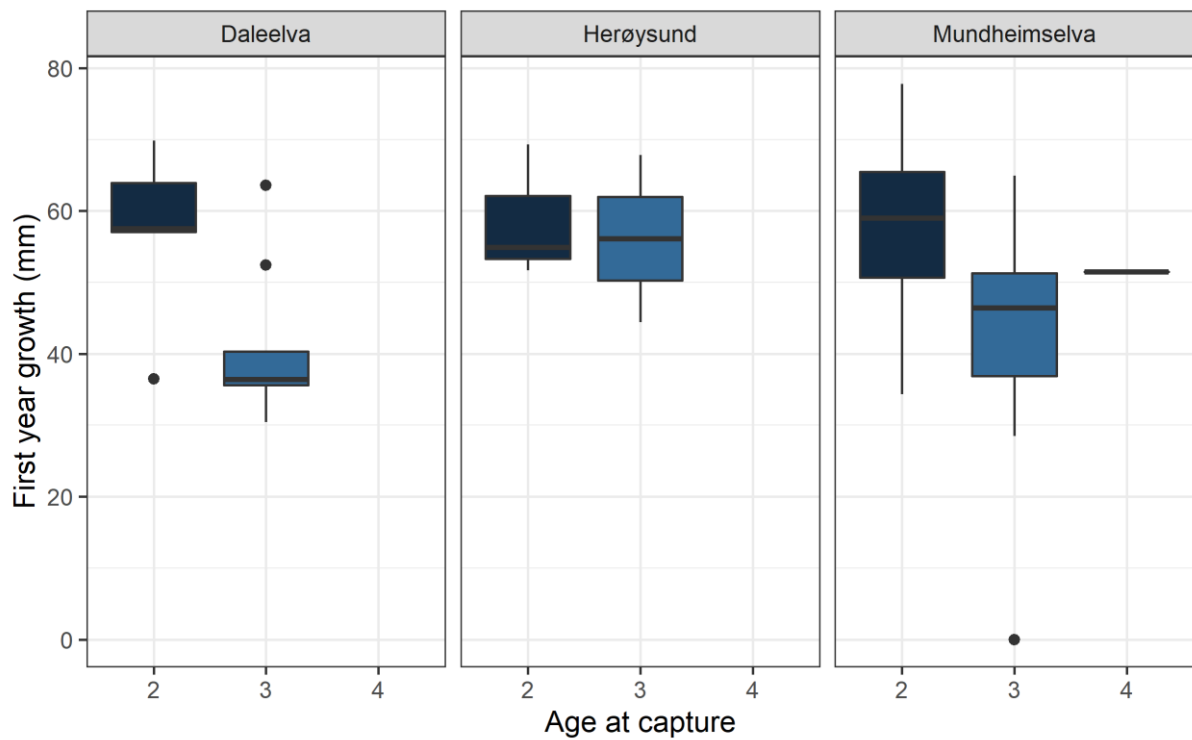


Figure A-2: Boxplot of back-calculated growth (mm) in the trout's first year. Colours indicate the age at which they were tagged, together with the age presented on the x-axis.

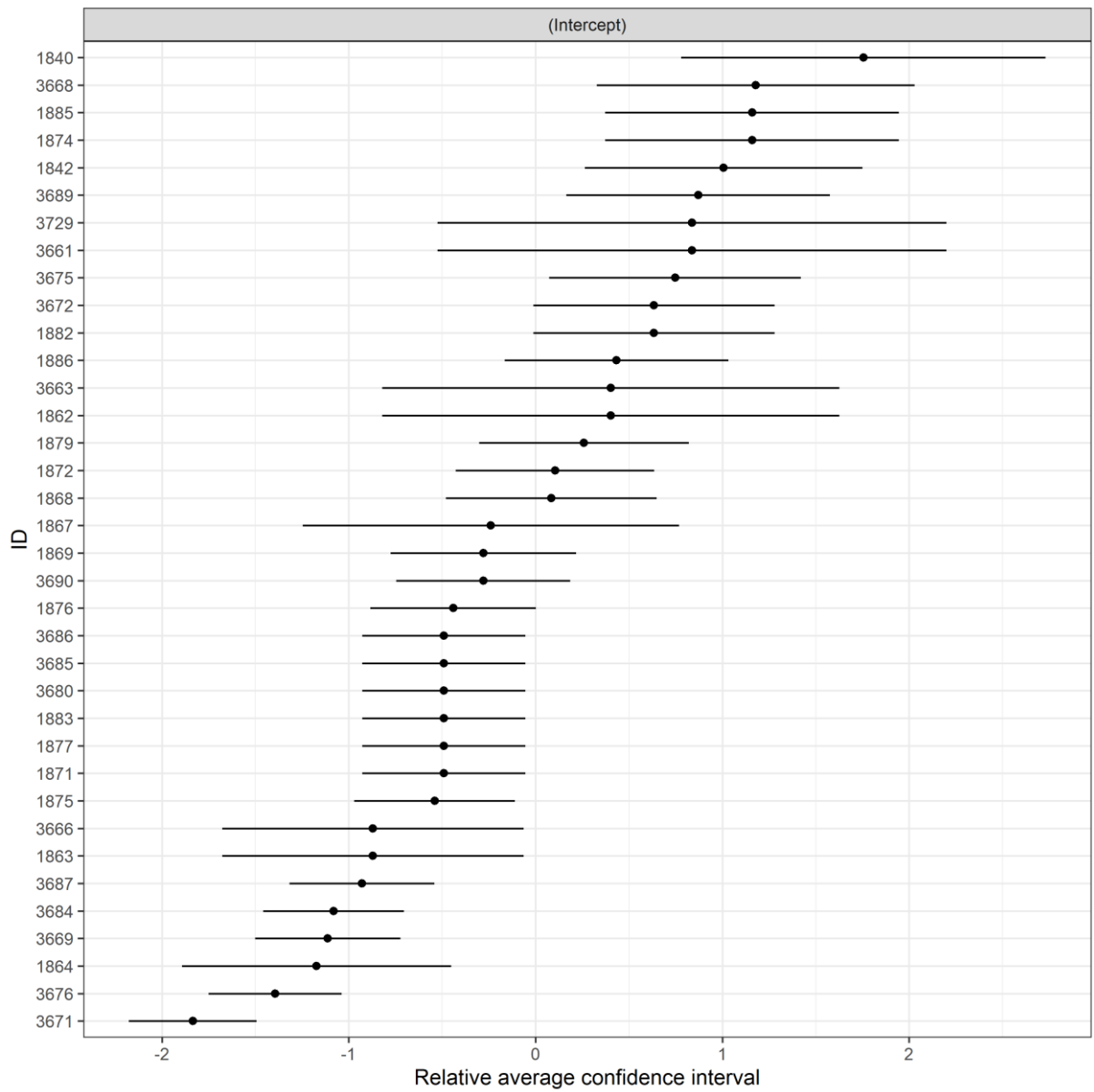


Figure A-3: The random effects from the generalized linear mixed-effects model estimating the time of river exit. Bars represent 95 % confidence interval.

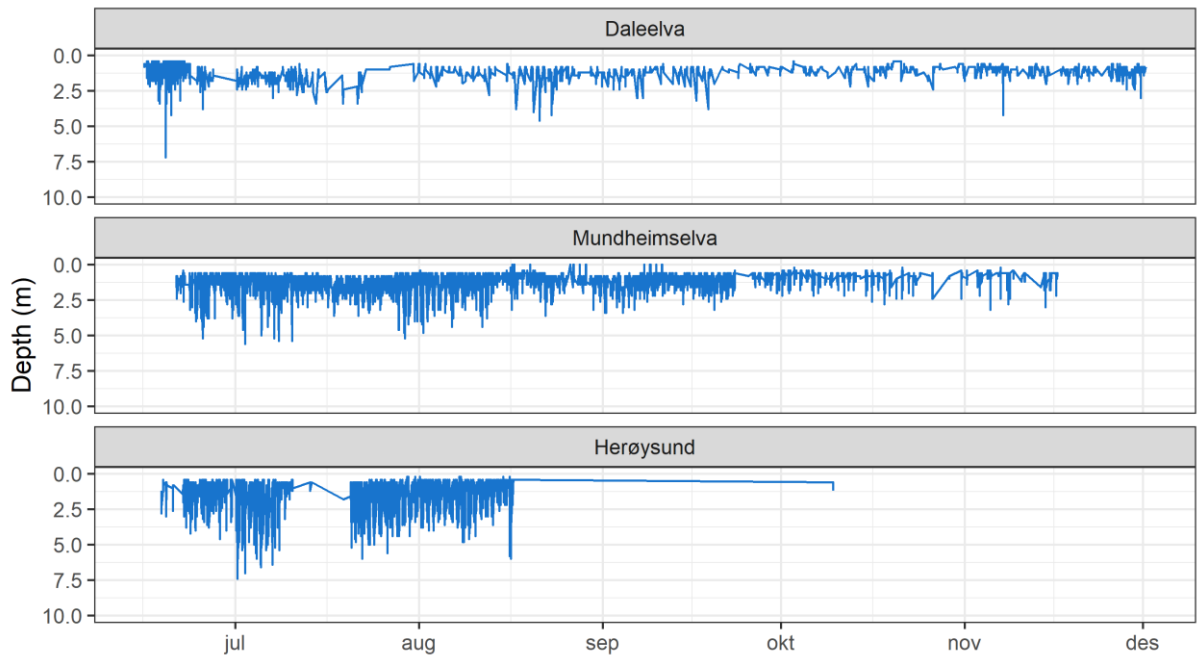


Figure A-4: Temporal depth use in the fjord by AT-tagged sea trout with depth sensors in the three study rivers.

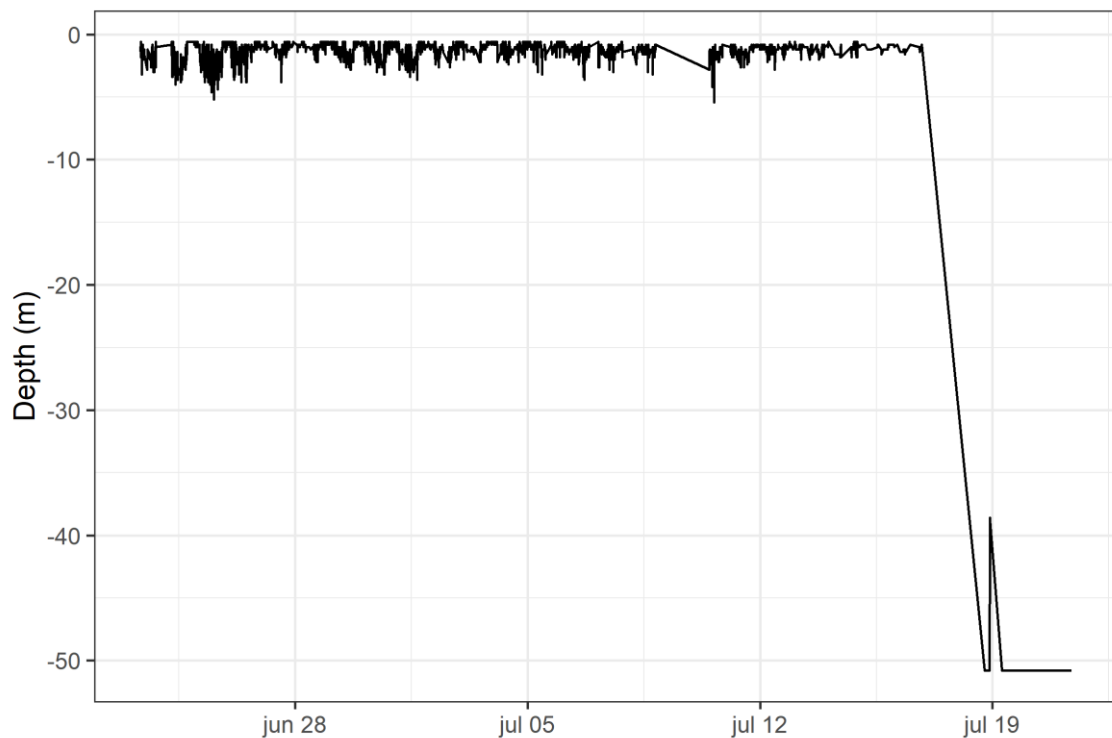


Figure A-6: Depth use in the fjord by a single sea trout (ID 3672) that is presumed dead. The only individual that was observed deeper than 7.5 meters.

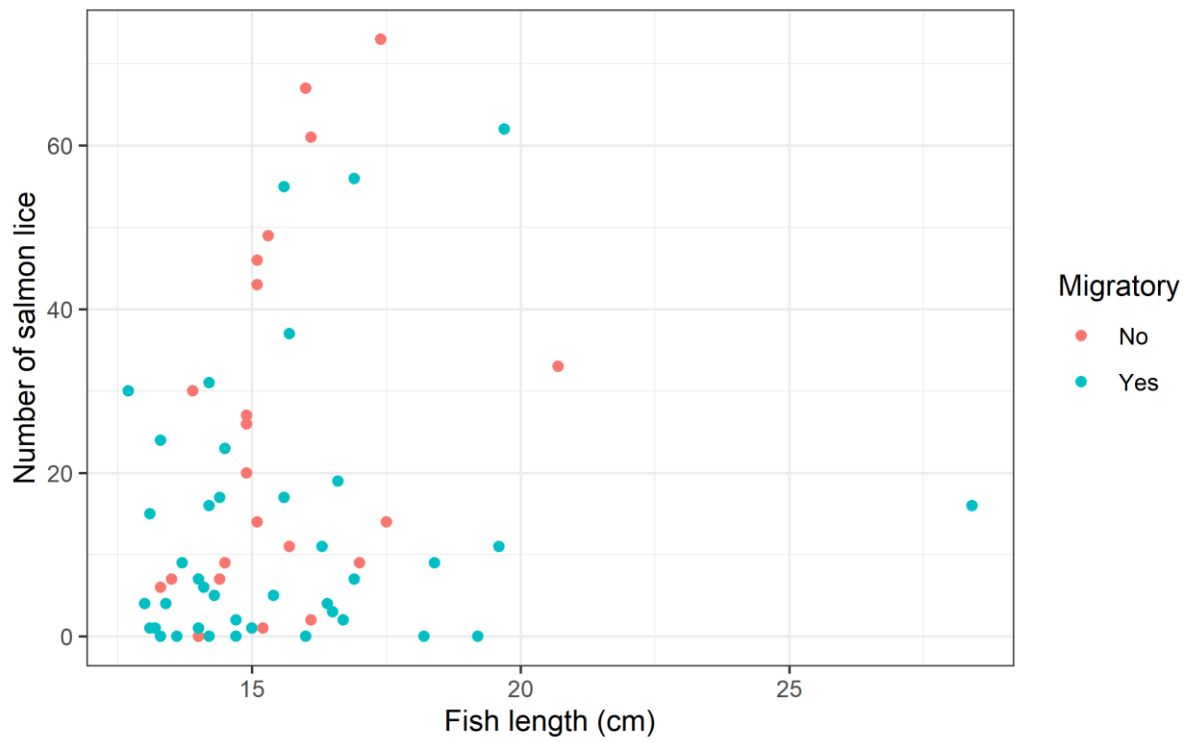


Figure A-7: The total number of salmon lice on sea trout of different sizes. Colors indicate if the trout was observed in the fjord or not.

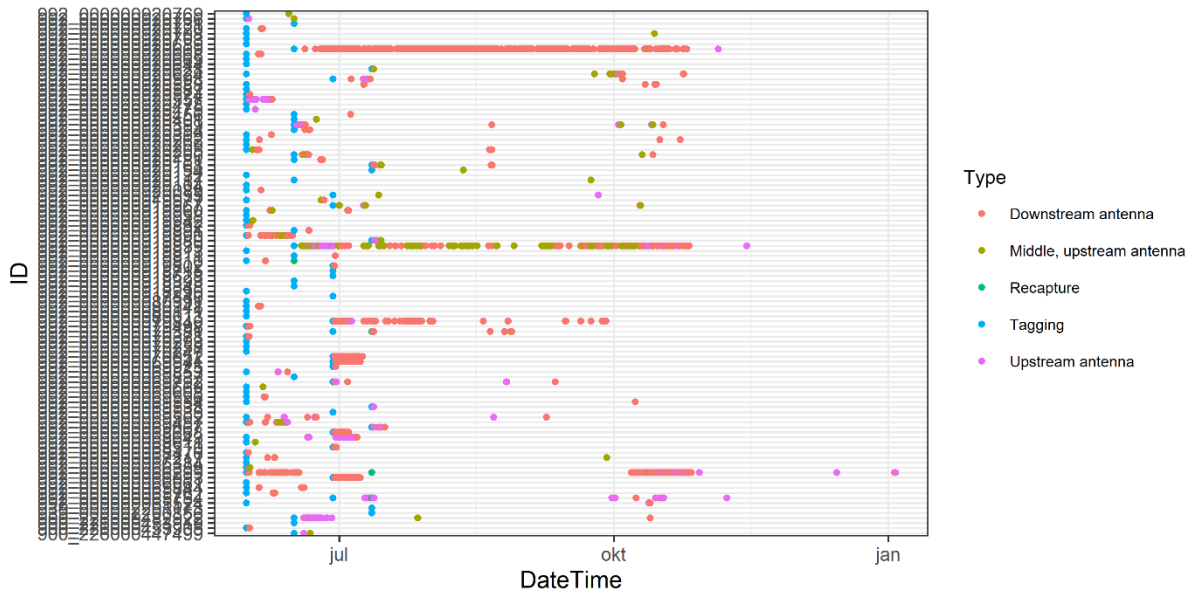


Figure A-8: PIT-detections of sea trout in Mundheim. Colors represent tagging and the different types of detections.



Figure A-9: Detections of AT-tagged trout from all study rivers. Colors show where the trout is detected (fjord or river) and shape shows the respective release site. Note that only Mundheims had a receiver placed in freshwater.

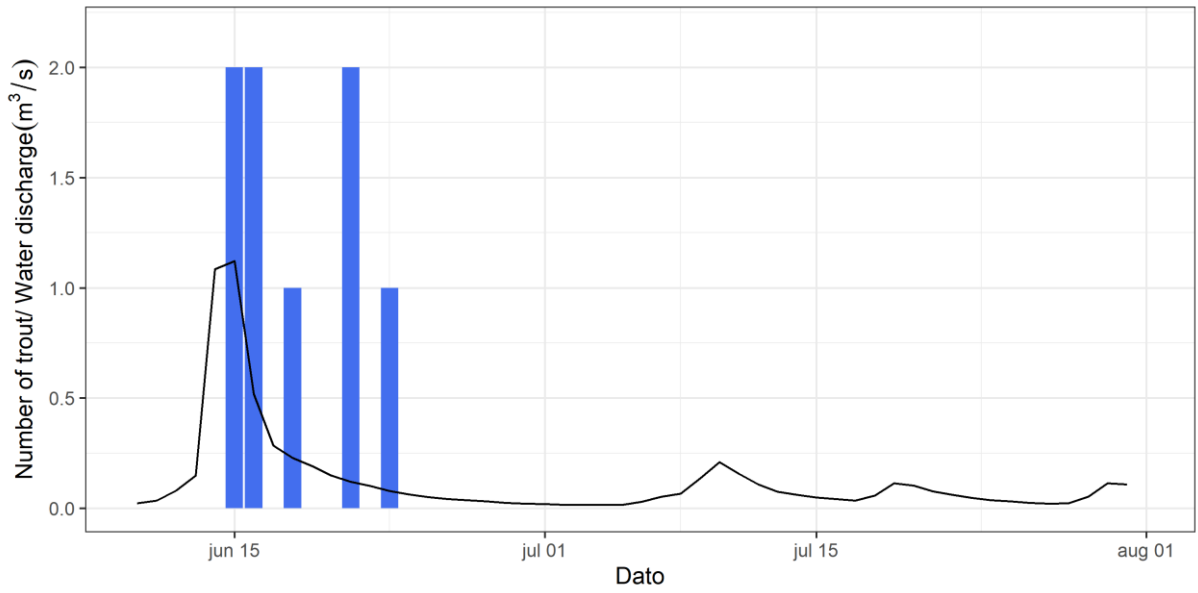


Figure A-10: Time of migration for trout tagged in Daleelva (bars) and the water discharge (m^3/s) at the corresponding time (line).

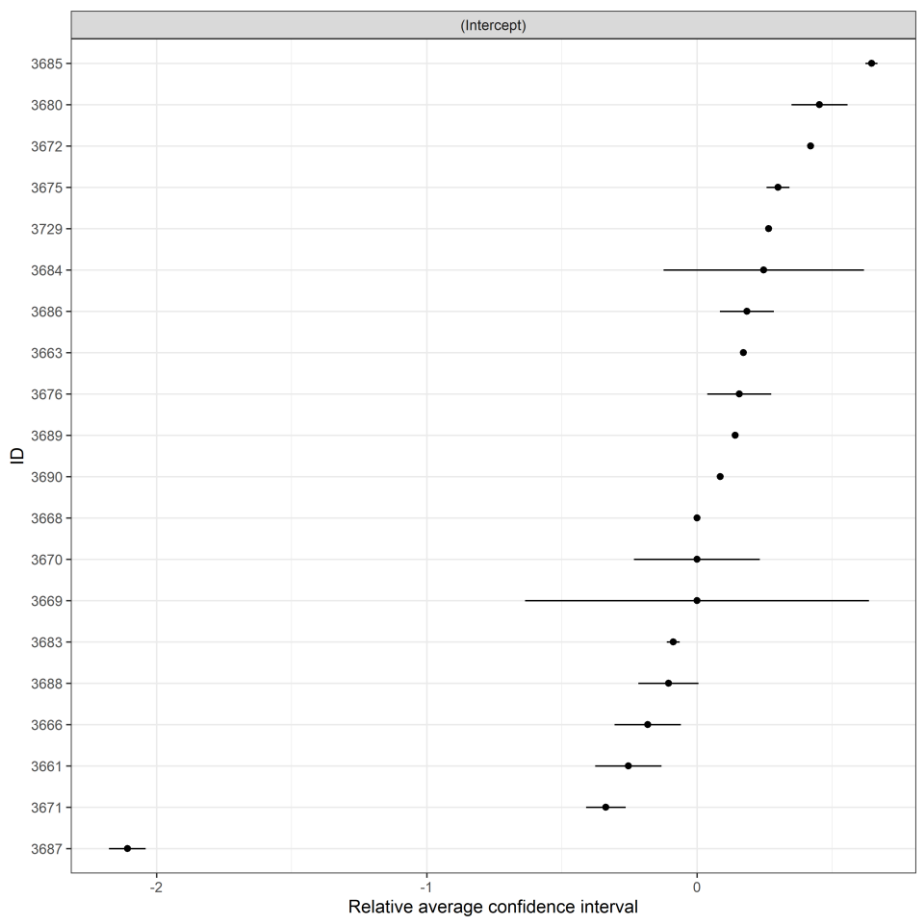


Figure: The random effects from the linear mixed-effects model estimating the depth used by post-smolts in the fjord. Bars represent 95 % confidence interval



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