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What affects migration and large-scale area use of brown trout (*Salmo trutta*) smolt?

– an acoustic telemetry study from four Oslofjord populations

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Preface

This thesis completes my MSc in Nature Resource Management, and my time at the Norwegian University of Life Sciences (NMBU).

First and foremost, I would like to thank my main advisor professor Thrond Oddvar Haugen for his unparalleled enthusiasm, inspiration and knowledge in the work of this thesis. Statistics and R has gone from Greek to fun in a few months, and when my motivation was at its lowest a chat with you always brought back the eager to do my best. Thank you so very much.

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Guttorm Christensen, Jenny Jensen and Jonathan Colman also deserve great thanks for the field work, regarding placing and retrieving receivers, and fishing and tagging smolt.

Without the help, guidance and excellent equipment of Hilde Raanaas Kolstad and Lene Cecilie Hermansen at the Imaging Centre, I would still be trying to read my own dandruff instead of scales at the fish lab. Thank you for helping me get off that struggle bus.

I would also like to thank:
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A special thanks to PhD Candiate Solrun Karlsen Lie for moral support, all sorts of help with the thesis and the wonders of the academic world, and a jolly good time letting me be your office mate for a month. Without you I probably would have gone mad.

Lastly, I want to dedicate this thesis to my dad, who passed away during my master's degree. I think you would be very glad to know that your favorite hobby fishing, would also be the theme of my thesis and future work.

Ås, June 2018

Karina Gjerde

Abstract

The brown trout (*Salmo trutta*) is one of the most studied fish species, due to its recreational and economic value. The smolt life stage, is however less studied. In this thesis, I used acoustic telemetry to increase understanding of what affects migration and large-scale area use of four brown trout smolt populations from the rivers Årung, Lier, Sande and Selvik, all draining into the Oslofjord.

I hypothesized that increasing water discharge and temperature causes the brown trout smolt to migrate into the river mouth, which were supported by my findings. For large-scale area use, maximum distance travelled away from the river mouth were used as a measure. Previous studies have shown a positive correlation between body length and distance travelled away from river mouth. This was not the case for my study, where back-calculated length of 1st winter and condition factor and had a negative correlation with the maximum distance travelled.

Gyrodactylus salaris is a freshwater parasite on Atlantic salmon (*Salmo salar*), causing an 86% reduction of salmon parr in infected rivers in Norway. In laboratory experiments *G. salaris* have survived on brown trout for up to 100 days, hence brown trout can be a vector organism spreading the parasite. In my study, smolt individuals from *G. salaris*-infected rivers utilized river mouths of non-infected rivers, like the Aulivassdrag. Increasing flooding events of the Oslofjord can cause lower salinity and this might lead to a higher survival of the parasite when attached to seaward-migrating sea trout smolt, and thus increased risk of spreading to new river systems.

My findings show that what happens during the first years of the brown trout's life in fresh water, does have an impact on how it later in life utilizes the marine system. This is of relevance to managers, who should have the entire life span of the brown trout in mind when making decisions affecting brown trout stocks. This study also shows that the large-scale area use of the smolt should be taken into consideration when determining methods for the potential elimination of *G. salaris* from Norwegian watercourses.

1 Introduction

Brown trout, *Salmo trutta,* is a very popular species for recreational fisheries. It is found all over Europe, northern Africa and western Asia, but has also been introduced to areas all over the world due to its recreational value (Jonsson & Jonsson 2011a; Klemetsen et al. 2003; Thorstad et al. 2016). Brown trout can colonize and thrive in many habitats due to variation and flexibility in the life-history strategies expressed. These include ability to utilize different habitats, from small streams to big fjords, with great variation in size and dietary plasticity exhibited (Klemetsen et al. 2003). Seaward migration of brown trout, known as anadromy, can occur across northern Europe (Klemetsen et al. 2003). Anadromy is a life history trait that all brown trout genetically can do, and it means moving or migrating from marine to freshwater for spawning. This trait is considered an adaption, resulting from a selection tug-of-war between the pros of greater food availability and quality and the cons associated with the energetic costs of migrating large distances, adapting to salt water and higher risk of predation (Thorstad et al. 2016). There is a greater tendency of anadromy the higher the latitude, which is believed to be due to marine waters exceeding fresh water in productivity at higher latitudes (Gross et al. 1988; Thorstad et al. 2016).

Mature sea trout normally return to their natal river for spawning. Newly hatched sea trout are called alevins and feed of a yolk sac attached to their body for the first weeks of their life in the spring (Jonsson & Jonsson 2011a). During summer, alevins start external feeding and turn into parr, recognized by dark long spots on their side, and from this stage they can develop as smolts already after one year (Jonsson & Jonsson 2011a; Thorstad et al. 2016). Smoltification is the process of adapting from fresh to sea water and includes several physiological and behavioral changes (Hoar 1988). The timing of this transformation, depends on factors such as day length, body size (Finstad & Ugedal 1998), discharge and water temperature, but in Norway this generally occurs between spring and early summer (Bohlin et al. 1993; Finstad & Ugedal 1998; Hembrel et al. 2001; Jonsson & Jonsson 2002; Thorstad et al. 2016). The age at which smoltification occurs increases with increasing latitude (Jonsson & L'Abée-Lund 1993). However, Jonsson and L'Abée-Lund (1993) did not find any correlation between smolt size and latitude. The environmental cues that initiate seaward migration are not that well studied in brown trout (Thorstad et al. 2016), but environmental factors such as temperature and water discharge are known triggers in other salmonids (Haraldstad et al. 2017; Hembrel et al. 2001; Jonsson & Ruud-Hansen 1985; Jonsson et al. 2001; Klemetsen et al. 2003). In a study from Stryneelva, Norway, migration in both brown trout and salmon (*Salmo salar*) smolt was influenced by the relative difference in daily water discharge (Urke et al. 2018). Flaten et al. (2016) found that larger individuals were more likely to migrate to sea than smaller smolt individuals who were more likely to remain in freshwater as residents. However, in a smaller stream it might be advantageous to migrate into sea at a small body size to avoid periods of drought in the river (Borgstrøm & Heggenes 1988; Jonsson et al. 2001; Klemetsen et al. 2003).

There are several studies on sea trout behavior at sea, but studies on behavior after the smolt has left freshwater are few (Haraldstad et al. 2017; Thorstad et al. 2016). A study in Denmark showed that there were two types of smolt, one that stayed in the inner parts of the fjord system throughout the summer, and one that left for the sea (del Villar-Guerra et al. 2014). Physical features can be a driver for what areas the smolt use in the fjord, e.g. narrow channels and tidal flats were not of preference (del Villar-Guerra et al. 2014), but staying close to land, in shallow water away from steep cliffs were most common (Flaten et al. 2016). Water temperature in the fjord can also influence habitat usage of sea trout smolt in areas where cold sea water is generally a stress factor, but the brown trout can also tolerate sea temperatures down to 1-2 °C (Jensen & Rikardsen 2012; Jensen et al. 2014; Thorstad et al. 2016). Most sea trout smolt are found within 100 km of their natal rivers, but have also been found to cross seas or disperse large distances along the coastline (Berg & Berg 1987; Klemetsen et al. 2003). A study by Hawley et al. (in press) found that larger, later migrating smolts with low condition factor, were more likely to migrate further relative to the rest of the river population. Flaten et al. (2016) also found that larger individuals had larger maximum distances away from their natal river. A recent report from Stryn stated that large individuals with a low condition factor migrated the furthest (Urke et al. 2018). Sea trout smolts mainly prefer shallower waters, often meaning they reside closer to land (Klemetsen et al. 2003; Knutsen et al. 2001) and mainly close to their natal rivers (Davidsen et al. 2014a; Flaten et al. 2016). A study from Aurland Fjord in the Sognefjord region of Norway, monitored seven smolt and their spatial use, showing that all individuals stayed close to land and their natal river mouth (Lyse et al. 1998). There seem to be no studies on smolt use of non-natal river mouths and this should therefore be more explored.

The use of telemetry was a revolution for aquatic life research when it was first applied 60 years ago, and the further development of acoustic telemetry has been a great help for fisheries researchers in improving their understanding of fish behavior (Crossin et al. 2017). The method has been used to monitor habitat use in fjord systems from north to south in Norway (Davidsen et al. 2014b; Dzadey 2014; Jensen & Rikardsen 2012). Acoustic telemetry is a preferred method because it is cost-effective and applicable in both fresh and marine environments (Crossin et al. 2017).

This thesis' research is part of the project Gyrofri. The objective of Gyrofri is to prevent further spreading of the salmon parasite *Gyrodactylus salaris*, from the infected Drammenfjord watercourse to other watercourses in the Oslofjord region. *G. salaris* have caused a mean of 86% reduction of salmon parr in infected rivers (Johnsen et al. 1999). The Norwegian fish management authorities (Miljødirektoratet) has requested more knowledge on the potential risk for spreading *G. salaris* with both salmon and brown trout as vector organisms under now changing salinity conditions, driven by more powerful and frequent flood conditions. The Gyrofri project was initiated to elucidate this knowledge gap. Studies have shown that brown trout is immune to disease of this parasite, however the parasite might survive on brown trout for up to 100 days (Paladini et al. 2014). Hybridizations also occur between brown trout and salmon, and therefore brown trout is also being monitored because they might be a source of spreading *G. salaris* to other watercourses (Bakke et al. 1999; Urke et al. 2013). This study includes brown trout individuals from the infected Lier and Sande rivers and the uninfected Selvik River. In addition, I included the Årung River brown trout population to explore if individuals from inner parts of the Oslofjord system overlap with outer populations and if the seaward migration and area use of anadromous brown trout is driven by the same factors.

My study aim can be divided into three hypotheses;

i. Brown trout smolts migrate from freshwater and enter the river mouth with increasing water temperature and discharge.
ii. Increasing body length of brown trout smolts increases migration distance from natal river.
iii. Brown trout smolt use shallow near-shore areas, remaining in river mouth areas close to their natal river.

Lastly, I will discuss what implications these results have for management and possible spreading of *G. salaris*.

2. Methods

2.1 Study area

The Årung River is located in Akershus county, the Lier River in Buskerud county, and the Sande and Selvik rivers in Vestfold county (Figure 1). The rivers are located within agricultural land and are therefore subjective to runoffs and eutrophication. The Årung watercourse drains an area of about 50 km^2 (figure 2) and has a high variation in water discharge, with periods of drought leaving the river bed completely dry, expect minor groundwater supplies in the lower reach (Borgstrøm & Heggenes 1988). The Lier watercourse has a drainage area of approximately 300 km^2 (figure 2) and is has a quick response to precipitation leading to a great variation in water discharge levels (Hindar et al. 2018). Mean discharge levels at the river mouth are at around 5.2 m^3/s (figure 2) and normally the discharge peaks occur in April and May due to snow melt (Hindar et al. 2018). The Sande watercourse drains approximately 200 km^2, and has a mean water discharge level at river mouth at around 3.8 m^3/s (Hindar et al. 2018). The catchment area of the Selvik watercourse is about 30 km^2 (figure 2).

The rivers in this study all drain into the Oslofjord. The Oslofjord parts into the Drammensfjord with a depth to about 123 m and Inner Oslofjord which consists of two basins, Bunnefjorden and Vestfjorden with a depth to about 160 m (Baalsrud & Magnusson 2002). However most of the Inner Oslofjord is no deeper than 100 m (Thaulow & Faafeng 2014) and most of the Drammenfjord is around 60 m (Hindar et al. 2018). The salinity, normally between 20-35, of the Oslofjord is fluctuating, between seasons and year, depending on weather, mixing of water layers and freshwater inflow from the bigger rivers, like the Drammen River and Glomma (Baalsrud & Magnusson 2002). Because of the topography of the fjord and the moraine in Svelvik the Drammenfjord can be perceived as a fresh water lake, due to the low levels of salinity in the top layer, but the Inner Oslofjord can also reach salinity levels down to 10(Baalsrud & Magnusson 2002; Hindar et al. 2018). The Oslofjord, especially the Inner Oslofjord, is the fjord system in Norway with the most use, both recreational and industrial transportation and fisheries (Thaulow & Faafeng 2014). The Oslofjord has during the last decades faced several challenges regarding eutrophication leading to parts and periods with severely low levels of oxygen causing areas of the fjord to have little to no benthic fauna (Baalsrud & Magnusson 2002).

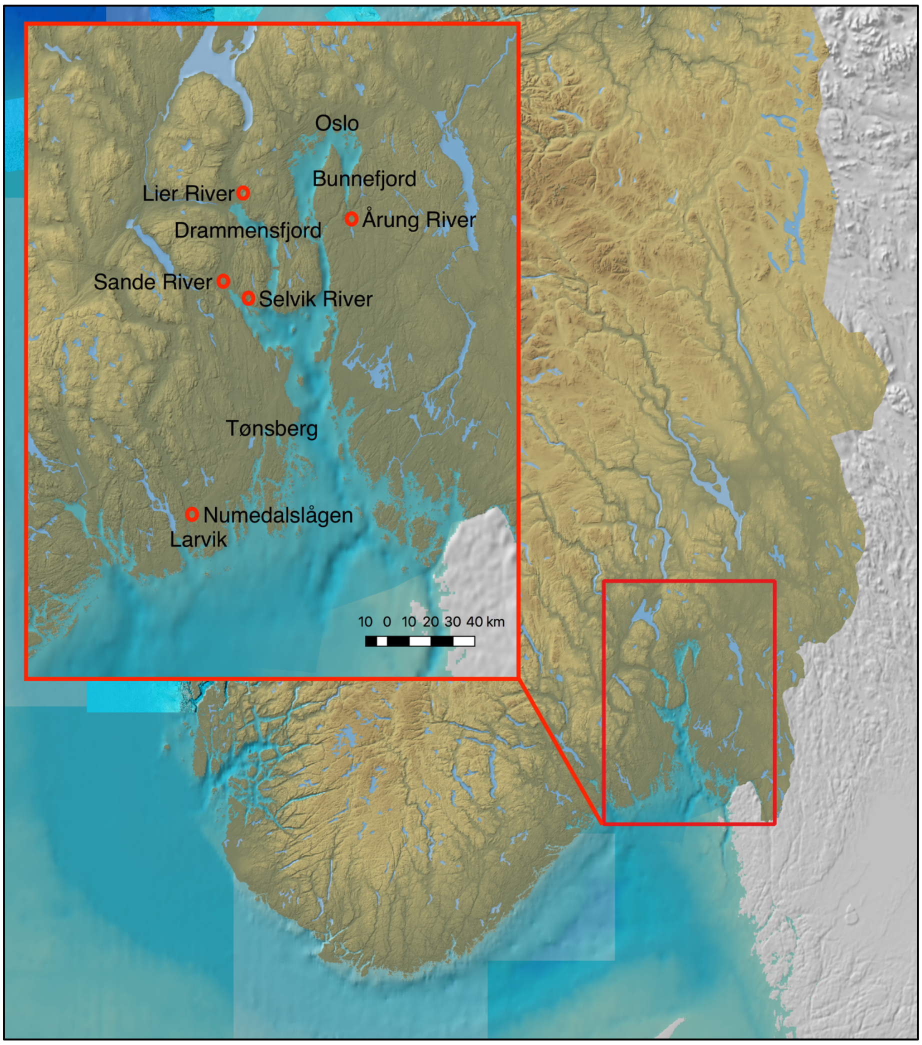

Figure 1 Map of the study area.

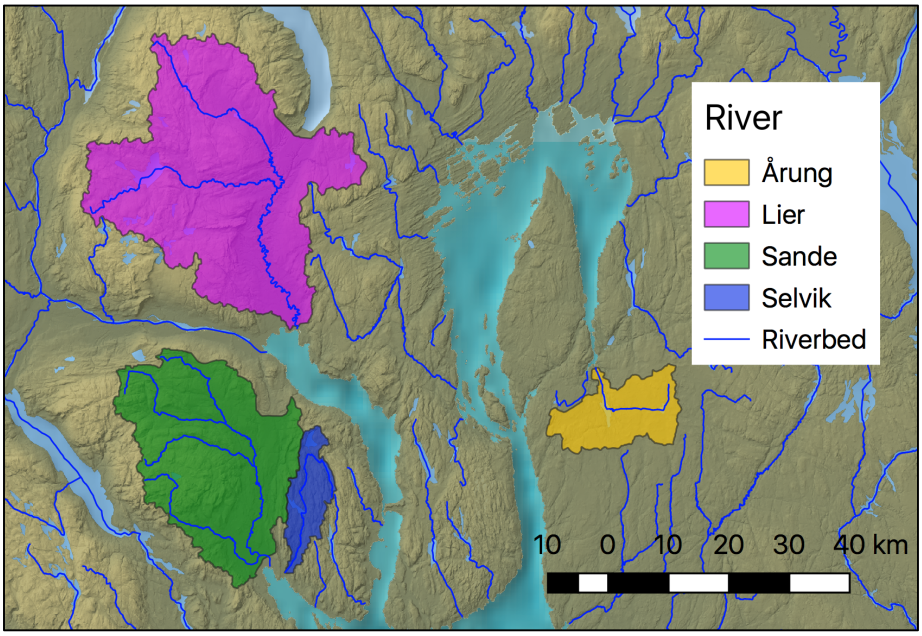

Figure 2 Catchment area of the Årung, Lier, Sande and Selvik rivers.

2.2 Acoustic telemetry

All transmitters, hereby called tags, transmit an acoustic signal that a receiver (TBR), that is either fixed or mobile, can detect and store. The date and time of each tag detection is also stored. Some tags might also give extra information, such as temperature, depth or even physiological data (Crossin et al. 2017). In this study, I used tags with a unique ID, so we could separate individuals and 55 of the tags also gave depth data. In addition, the receivers I used logged temperature readings every two hours. The detection range of a receiver is about 400 m, depending on weather, water conductivity and other physical factors. Due to this the receivers were placed in transects to maximize detection probability, and these transects were placed in narrower parts of the fjord system (Figure 3). A total of 84 receivers were used. Seven of the 14 receivers in the Bunnefjord were lost, while 26 of the 70 in the Oslofjord were lost. 11 receivers were found someplace else than where they were deployed and returned via members of the public.

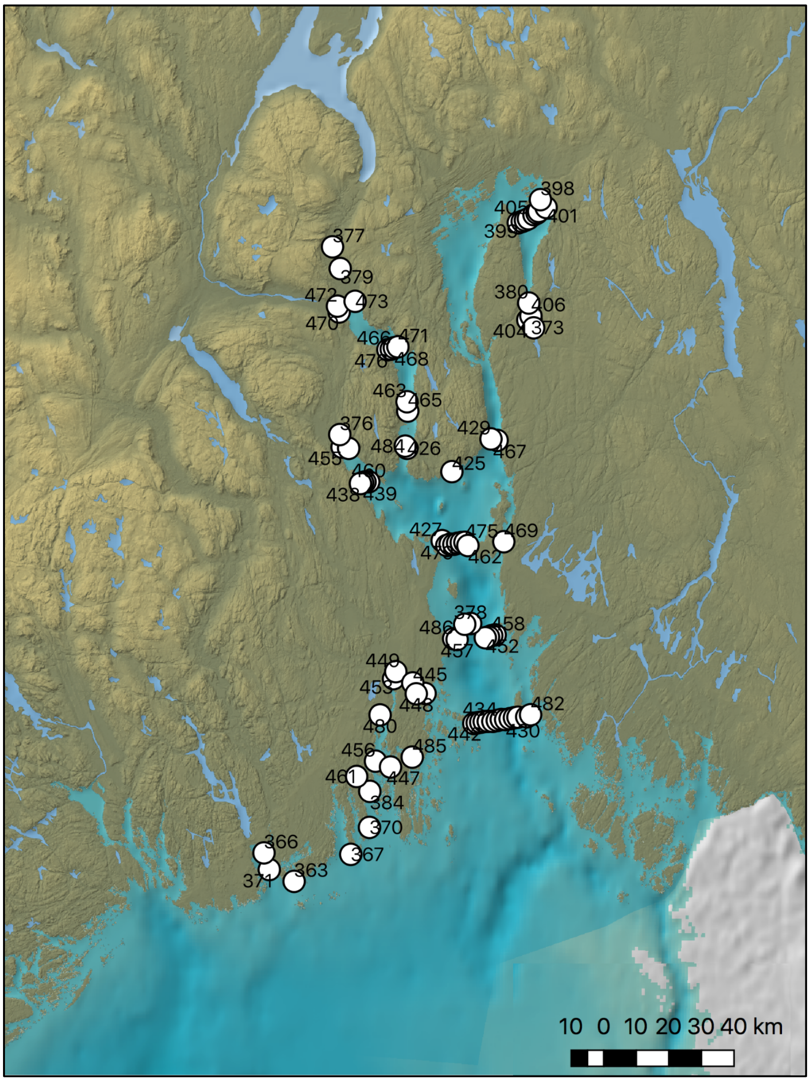

Figure 3 Receivers' placement in the Oslofjord 2017.

Previous studies have stated that surgical implantations into the body cavity have close to no effect on survival or behavior on salmonids, provided tags are less than 2.2-5.6% of total weight, and is recommended over gastric implantation. (Adams et al. 1998a; Adams et al. 1998b; Bridger & Booth 2003; Lucas 1989; McCleave & Stred 1975). However, there have been no studies on this directly in brown trout, but experiences from previous field studies show that brown trout cope well with the tagging procedure (Flaten et al. 2016). Behavior is another aspect that might be affected by tagging, but comparative behavioral studies are hard to execute due to the challenging nature of studying species under water (Mulcahy 2003).

2.3 Fish capture and tagging

The fish were captured using electro-fishing in the rivers. The fishing was carried out in the period between 10.04.2017 to 03.05.2017. It was important to wait until the water level in the rivers were low enough to make the electro-fishing as effective as possible, but at the same time crucial to execute before the smolt migrated out of the rivers, to maximize our sample size, as well as determine potential cues instigating migration onset.

Electro-fishing in the Sande River.

Top left: a tag halfway in the abdomen of a smolt. Top right: The equipment used in field for measuring and tagging the smolt. Bottom left: Tagging of a smolt. Bottom right: smolt with scale envelope.

All fish were tagged with Thelma Biotel tags (Thelma Biotel AS, Norway, www.thelmabiotel.com). Fish that were larger than 14 cm (FL) got depth tags and the rest got ID tags (Table 2, Table 1). The tagging was done by skilled professionals with certification allowing them to execute the procedures and approved by the Norwegian Food Safety Authority (FOTS ID 10112). The fish was sedated using benzocaine (30 mg L^{-1}) until it was unresponsive when clenching the caudal peduncle. The abdomen was opened with a small incision anterior to the pelvic fin before the tag was inserted. The incision was closed with a single-layer, simple interrupted suture pattern. After, scale samples were taken and measurements of weight (0.1 g resolution, mean±SD: 44.3±26.8 g), fork length and/or total length was done (total length; mean±SD: 158±51 mm). The tagged fish were kept for observation until it became responsive and capable of remaining upright before released into the environment again. It is advantageous to release the fish back into the environment as soon as possible, as long as the fish is fully recovered (Mulcahy 2003). In the Lier River, fish from the DOFA-hatchery (DOFA-Sjåstad,) were also tagged to increase the total number of marked fish and include them in analysis with wild fish as stocking is a common practice in these river systems (Table 1).

Table 1 Overview of specs for the tags used.

	Depth tag (ADT-LP 7.3)	ID tag (AT-LP-7.3)
Length (mm)	22	18
Diameter (mm)	7,3	7,3
Weight (air, g)	2,0	1,9
Weight (water, g)	1,1	1,2
Effect (dB re 1µPa@1m)	139	139
Duration (month)	6	7
Code repeat rate (s)	30-90	30-90

2.4 Fish tracking and detection data

Out of a total of 74 marked fish, 51 gave detections on the receivers (Table 2).

Table 2 Overview of the number of individuals (N) tagged from each river, N ID tags, N Depth tags, mean of Total length (TL) at capture in mm., N weighed within a river, the mean weight in g, % of the total individuals detected from each river and N hatchery fish from each river.

River	ID tags (N)	Depth tags (N)	TL (mean)	Weight (N)	Weight (mean)	% of total detection	Hatchery (N)
Lier (N= 20)	4	16	165	10	72.2	27	7
Sande (N=10)	6	4	111	10	38.9	10	0
Selvik (N=25)	9	16	128	25	35.24	35	0
Årung (N=19)	0	19	213	0	-	27	0

2.5 Scale readings

To explore eventual effects of early-life performance on smolt migration, I read scales to back-calculate juvenile growth. Firstly, the scales were cleaned by putting them for two days into a microtiter plate with soap water. After, they were placed on a glass plate until dry, before photos were taken. A LEICA DCF 425 CCD camera (Leica Microsystems GmbH) in a Leitz Aristoplan microscope (Ernst Leitz Wetzlar GmbH) was used for taking the photos. “Image Pro Express” (Media Cybernetics Inc.) was the software used for the measurements of the scale. The scale reading principle is that if you mark the edge (Y, Figure 4) and the different annulus (V, Figure 4), you can back-calculate the actual fish lengths with using the relation between the number of pixels between the marked points (Lea 1910).

$$LF = Lt\ \frac{SF}{St}$$

LF= back-calculated fish length at annulus f,
Lt=fish length at capture (Ltot),
Sf= scale length to annulus f and
St= total scale length.

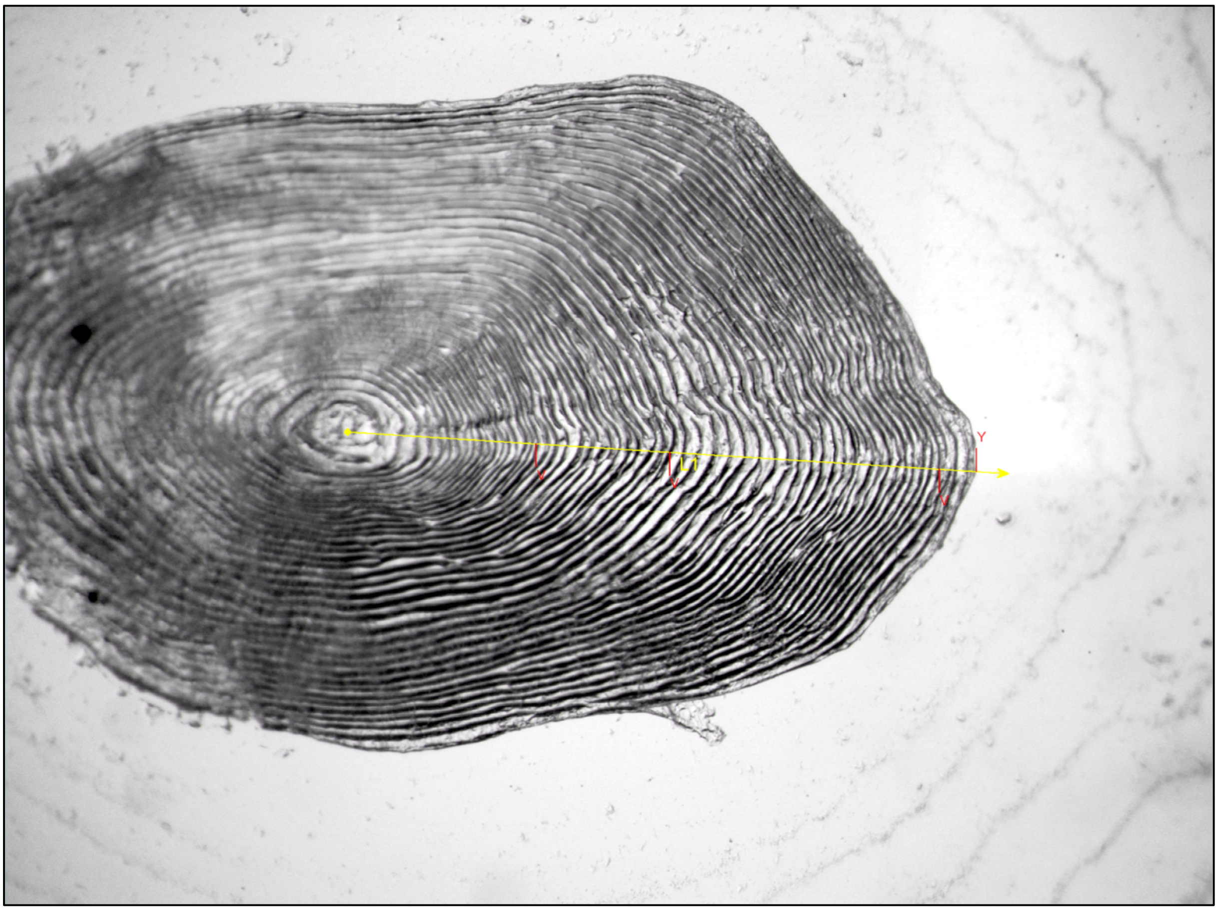

Figure 4 Example of a read scale. The Y marks the end of the scale and the V's mark the end of annulus.

For 19 individuals, the scales were hard or not possible to read and were determined as replacement scales. Scale samples were not taken of the hatchery fish. The reading error was 7%.

2.6 Data handling and analysis

No water temperature or discharge data was available for the Sande and Selvik rivers. The discharge data for the Lier River were obtained from the Norwegian Water Resources and Energy Directorate (NVE). The fish from the Årung River were captured at different reaches of the river, and classified in upper, middle and lower reach for the analysis.

The maps were made using QGIS (QGIS Development Team 2018) with layers from the Norwegian Water Resources and Energy Directorate (NVE), the Norwegian Mapping Authority (Kartverket) and the Norwegian Directorate of Fisheries (Fiskeridirektoratet).

The data from the receivers contained a lot of noise due to acoustic disturbances from e.g. boats, physical conditions and other activities. The cleaning of the data was conducted in ComPort V2.0.1 (Thelma Biotel AS), removing all false AT-types and ID numbers not used in our study. In JMP (SAS Institute Inc. 2016) it was possible to remove other false detections by comparing detections and removing ones that were too close in time and space, based on known swimming speeds for juvenile brown trout (Ojanguren & Brana 2003).

Because only seven of a total of 74 tagged individuals were hatchery fish, and only four of these were detected, I chose not to compare hatchery with wild fish in the analysis, because there were too few individuals.

The receivers were also categorized into zones in the outer Oslofjord to make the results for the Lier, Sande and Selvik rivers easier to present (Figure 5).

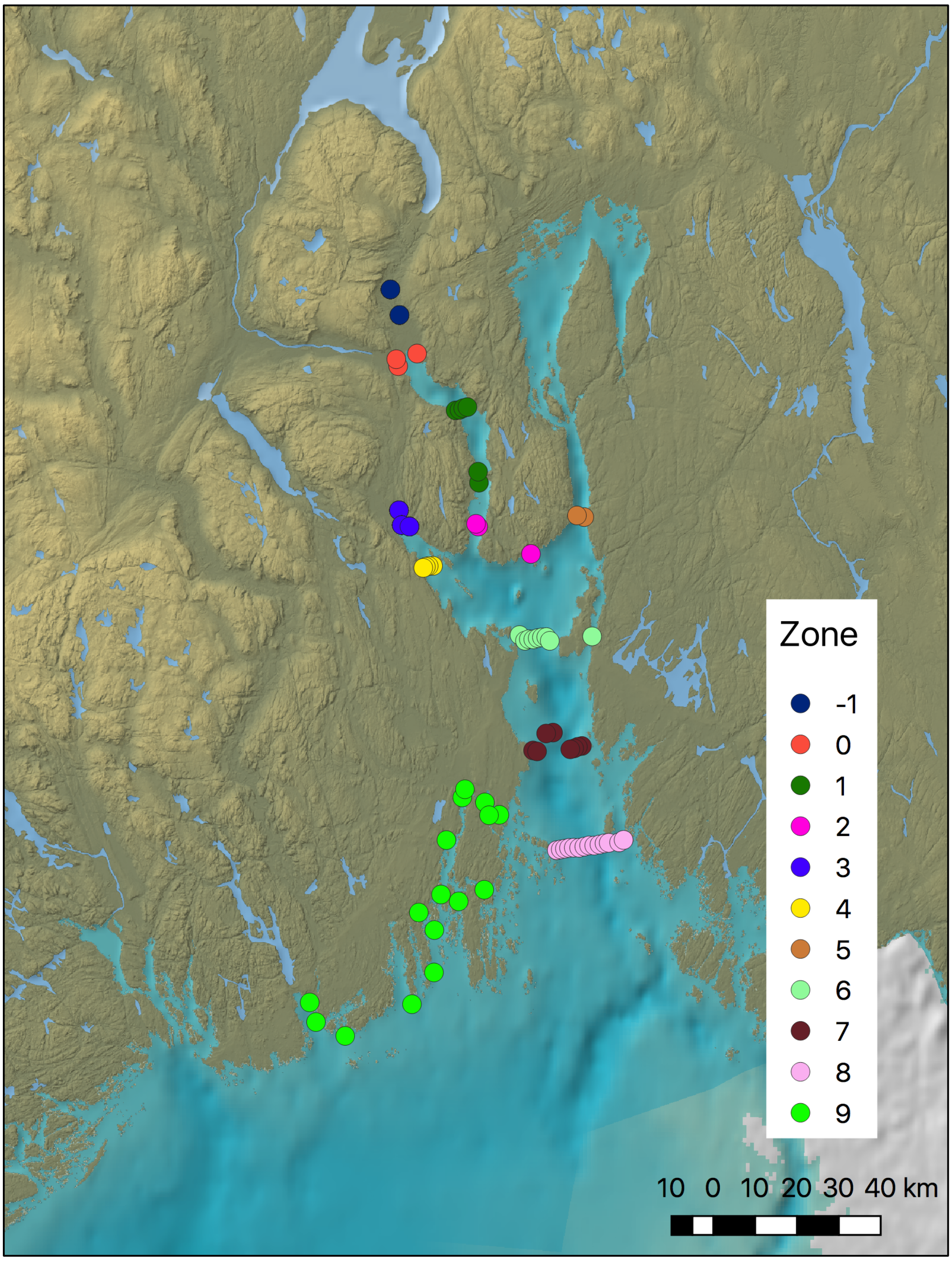

Figure 5 The zones for the different receivers in the Drammenfjord and outer Oslofjord. Each color marks a zone.

For further data handling and analyses, we used R (R Development Core Team 2018) and scripted in RStudio (RStudio Team 2016). The packages "Lattice", "LatticeExtra", "ggplot2" and "Hmisc" were installed for handling the data and creating the plots used in this study.

To explore the hypotheses, I fitted candidate linear models (or generalized linear models in the case of migration probability) with combinations of predictor factors and covariates pertinent to the hypothesis in question (Searle 1971; McCullagh & Nelder 1989). For each candidate model a corrected version of the Akaike Information Criterion (AIC) was estimated. AIC is an information-theoretic (I-T) approach that can be used to compare which hypothesis/models that receives most support in the data (Burnham et al. 2011). The AIC constitute the sum between unexplained variance and the number of parameters where the number of parameters is multiplied with a penalty factor of two. Hence, the principle is to minimize AIC as this will constitute the best balance between model complexity and explained variance. AIC_c is the AIC adjusted for a small sample sizes (Burnham et al. 2011; Hurvich & Tsai 1989). AIC_c is therefore better suited to ecological behavior studies and was therefore used to compare between the models in this study. The models used in this study estimated probability of migration to river mouth and maximum distance. The R package "AICcmodavg" was used to calculate the AIC_c and to construct a ranked list of candidate models.

Some of the predictor variables fitted to the candidate models were calculated using the following formulas;

K-factor, or condition factor, is a measure of quality of the fish and was calculated using The Fulton formula (Froese 2006);

$$K = 100\frac{W}{L^3}$$

K: condition factor,
W: weight in gram,
L: total length in cm.

The difference between two days in temperature and water discharge (Urke et al. 2018);

$$\Delta T = T_t - T_{t-1}$$
$$\Delta P = P_t - P_{t-1}$$

$\Delta T/\Delta P$: Difference in temperature (diffT)/water discharge (diffP)
T_t/ P_t: Temperature/ water discharge of the actual day
T_{t-1}/ P_{t-1}: Temperature/ water discharge of the day before the actual day

The relative difference in temperature and water discharge (Urke et al. 2018);

$$\text{rel}\Delta T = \frac{\Delta T}{\text{Tt}}$$
$$\text{rel}\Delta P = \frac{\Delta P}{\text{Pt}}$$

relΔT/relΔP: Relative difference in temperature (diffT)/water discharge (diffP)
$\Delta T/\Delta P$: Difference in temperature (diffT)/water discharge (diffP)
T_t/ P_t: Temperature/ water discharge of the actual day

When AICc was calculated for the candidate models of maximum distance for the Lier, Sande and Selvik rivers there were two different models that got the lowest AICc-value depending on if individuals with or without replacement scales were included. When including individuals with replacement scales L1 + K were the model with the highest model structure. Because of this I removed individuals with replacement scales from the data tested, and then the model structure with only K gave the lowest AICc-value. Therefore, I chose to use the estimates with individuals without replacement scales in the analysis and results, because the back-calculated length values were not correct because they were calculated on replacement scales.

3. Results

3.1 Arrival times

3.1.1 The Årung River

The first fish from the lower reach, closest to the mouth of the Årung River enter the river mouth and inner parts of the Bunnefjord in late April, whereas individuals from the middle and upper reach enter mostly in mid and late May (Figure 6). Only one individual, tagged from the middle reach of the river migrated to the outer part (<10km) of the Bunnefjord. All individuals that reached the outer are of the Bunnefjord do this before the end of June.

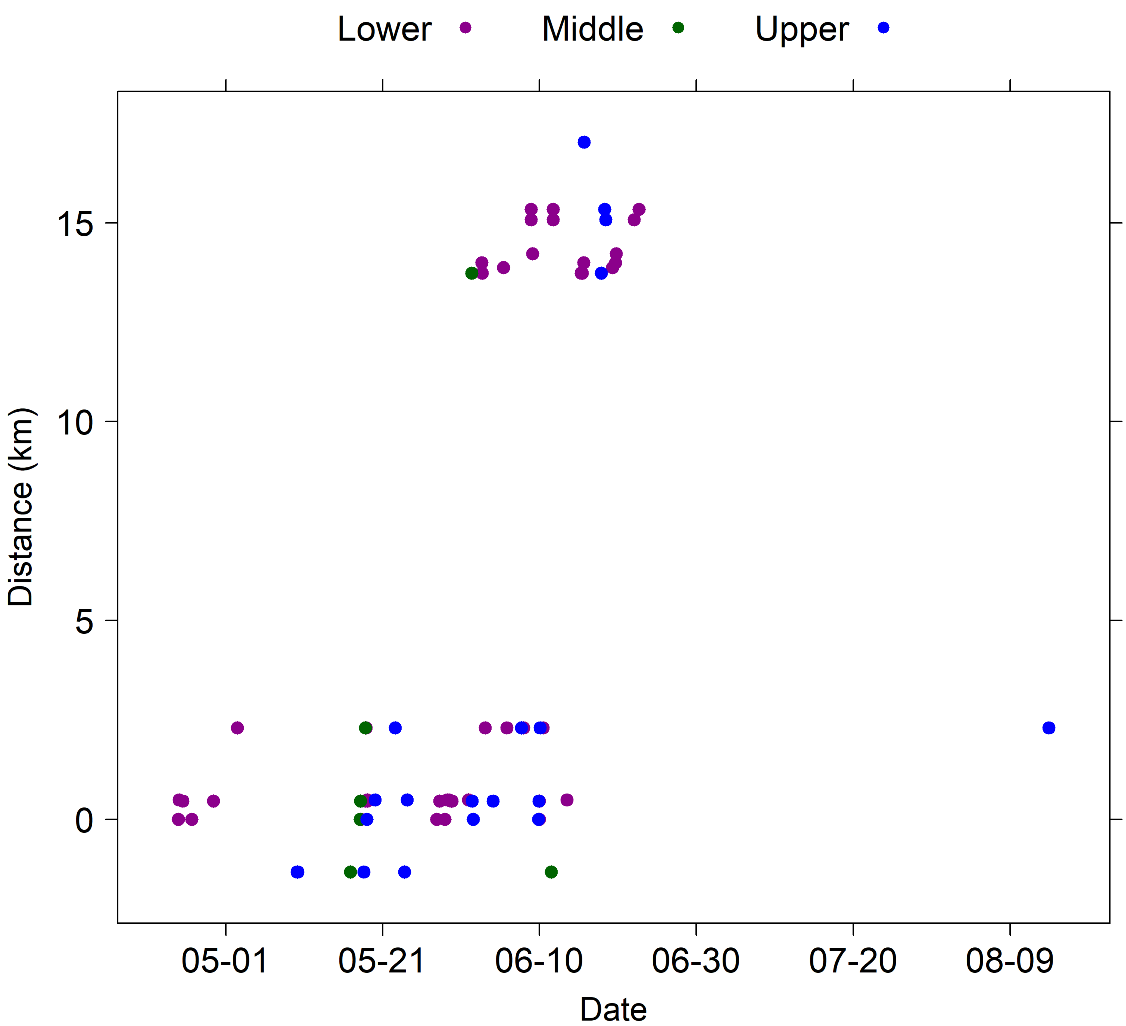

Figure 6 Brown trout smolt arrival time at different distances relative to the river mouth of the Årung River 2017. Maximum possible distance is 17 km. Y-axis gives length in km away from river mouth and the different colored dots mark if the fish were from the lower (purple), middle (green) or the upper (blue) reach of the Årung River. The date (mm-dd, x-axis) is the date for when each individual first arrived at the different distances.

3.1.2 The Lier, Sande and Selvik rivers

The fish from the Lier River travel throughout the zones quickly (Figure 7). None of the fish from the Sande or Selvik rivers arrived in zone 1 or 2 first, this is because these zones are located within the Drammenfjord (Figure 5).

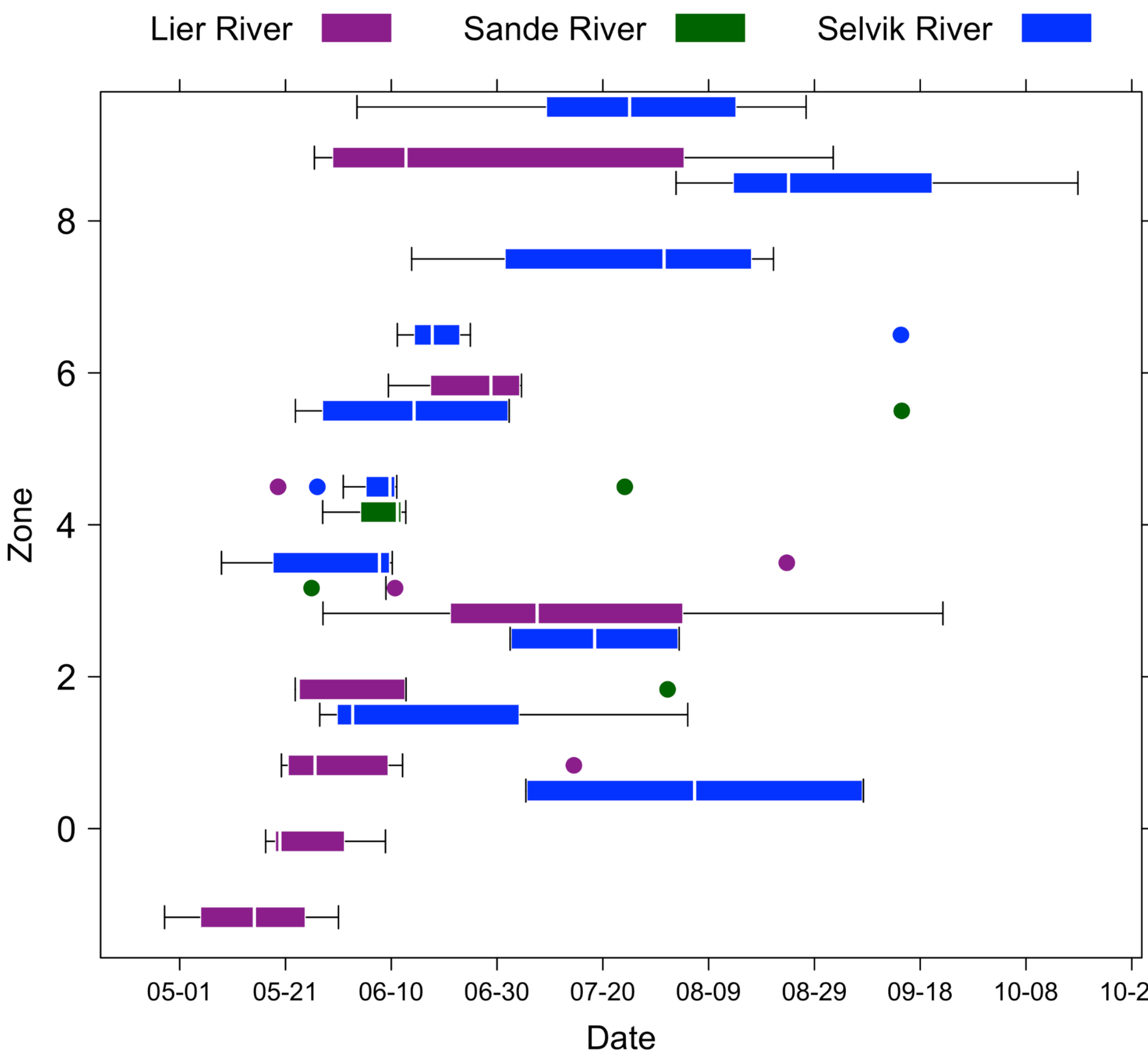

Figure 7 Brown trout smolt arrival in different zones in the Oslofjord 2017. X-axis marks the date (mm-dd) for arrival and y-axis marks the different zones as seen on map (Figure 5). Quantile boxplots (0.25/0.75) show the distribution of arrival for each river in different color. The median is marked as a white line in the middle of the boxplot. The black line out from the boxplot marks the 0.1 and 0.9 quantile, and outliers are plotted as dot circles.

3.2 Arrival time in river mouth

3.2.1 The Årung River

The first fish entered the river mouth on the 24th of April, shortly after an increase in water temperature (Figure 8). These fish were from the upper reach of the river. Most of the fish in the Årung River entered the river mouth in the middle to the end of May. The discharge, measured in pressure, peaked the day before four individuals migrated. The last two individuals that migrated did so on the 9th of June, around the same time as the pressure had a peak. One individual did not leave the river. The temperature in the river steadily increased during the study period.

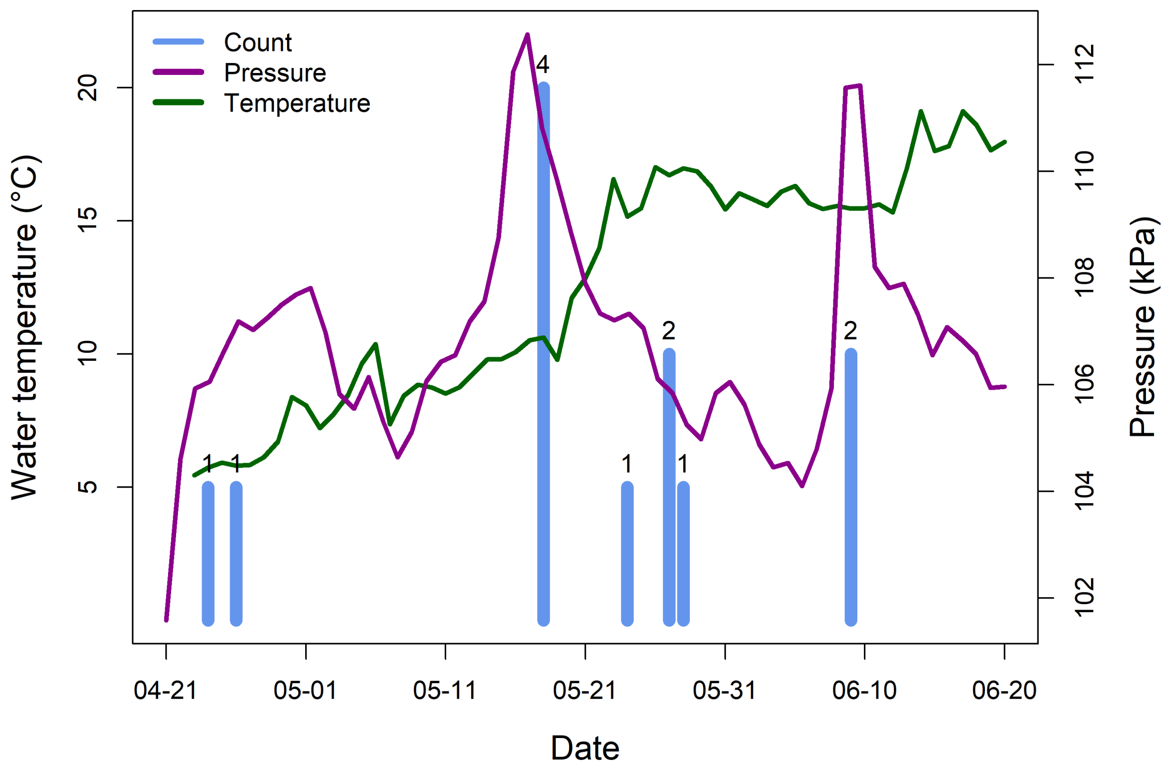

Figure 8 Number of brown trout smolts migrating into the river mouth of the Årung River during spring and early summer of 2017. The blue columns, with a number on top, represent the number of smolts entering the river mouth on a given date. The green line marks water temperature (left y-axis) on a given date (mm-dd) and the purple line marks discharge measured in pressure (right y-axis) on a given date.

The model with the lowest AICc-value (Table 3) for when smolts migrate into the river mouth from the Årung River (Figure 9) accounted for almost 90% of the AICc-weight. Higher value of temperature and water discharge measured in pressure leads to a higher probability of migrating into the river mouth.

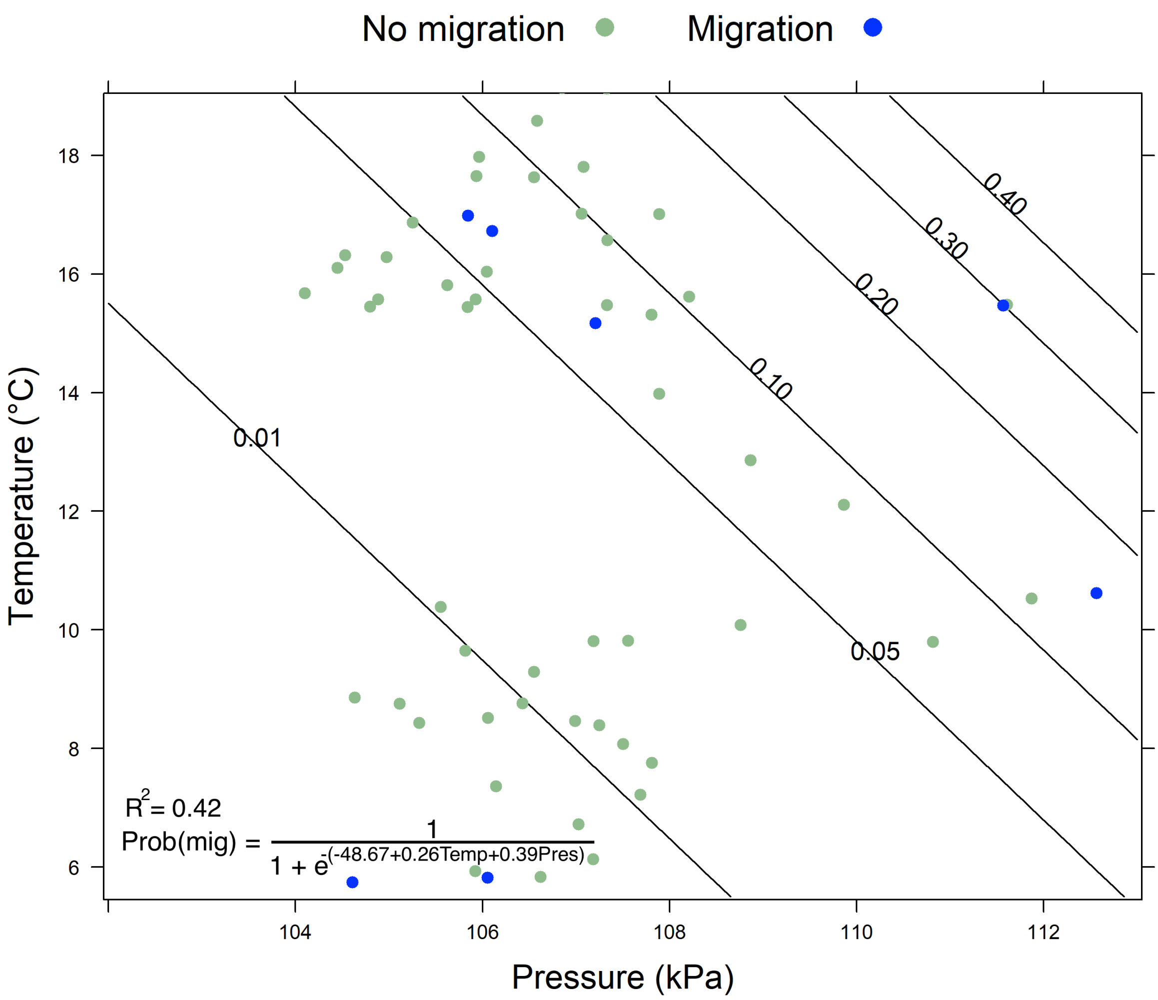

Figure 9 Probability of migration (Prob(mig)) into the river mouth based on temperature and water discharge (pressure) for the Årung River 2017. X-axis displays values of pressure, measured in kPa and the y-axis are temperature in °C. The contour lines represent the probability of migrating into the river mouth. The dot circles represent actual days from the study period where migration occurred (blue dots) or did not occur (green dots).

3.2.2 The Lier, Sande and Selvik rivers

The first fish enter the river mouth of the Selvik River the 7th of May, with the median the 7th of June (Figure 10). The last fish from the Selvik River arrive at 22nd of August, making the Selvik River the river with the first and last to arrive in the river mouth. The first fish from the Lier River arrive at 16th of May, with median 19th of May, and last 8th of June. In the Sande River the first fish arrive 24th of May, median 7th of June and last at the 10th of June.

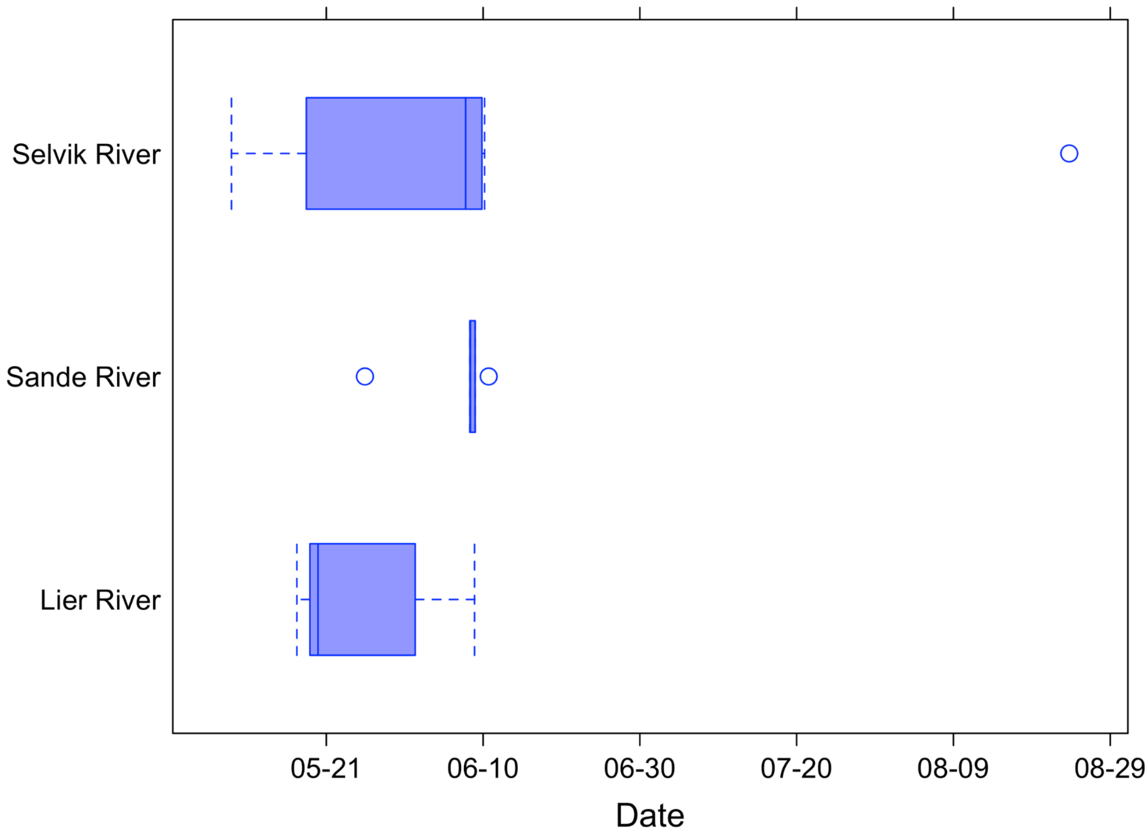

Figure 10 Arrival in respective river mouth for brown trout smolts from the Lier, Sande and Selvik rivers in the Oslofjord 2017. X-axis gives the dates for first arrival, and y-axis is for the different rivers. The boxplot marks the 0.25 to 0.75 quantile, with median as a continuous line in the boxplot. The dashed line are the 0.1 and 0.9 quantile and outliers are marked as dot circles.

Maximum discharge in the Lier River during the study period were 54 m^3/s and the maximum temperature was 16 °C (Figure 11). The discharge had two peaks, during early/mid May, followed by the main migration, and early/mid June, while temperature steadily increased. The first discharge peak was followed by most of the smolts migrating into the river mouth.

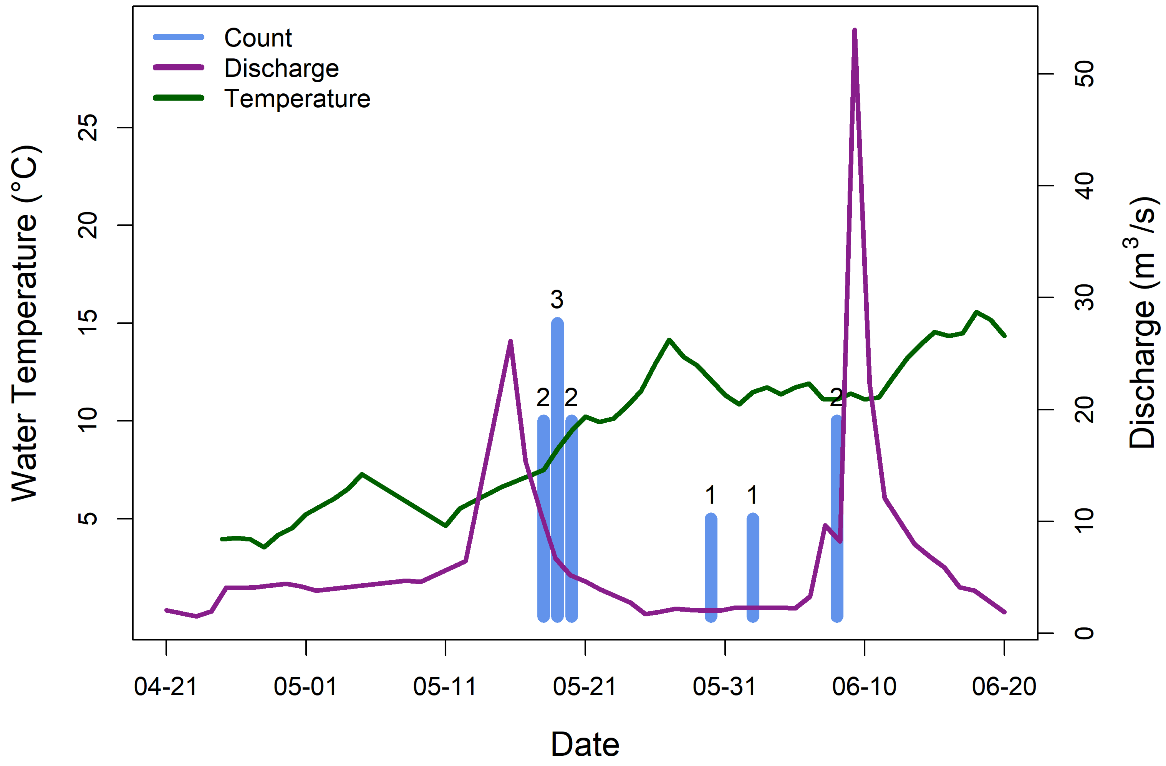

Figure 11 Number of individuals migrating into the Lier river mouth in spring and early summer of 2017. The blue columns, with a number on top, represent the number of smolts entering the river mouth on a given date. The green line marks temperature (left y-axis) on a given date (mm-dd) and the purple line marks discharge (right y-axis) on a given date.

Based on the AICc-value the model with the relative difference of temperature and discharge (rel.diffT*rel.diffP) had the highest support, and had 36% of the AICc-weight compared to the other models (Table 3). The probability of migrating in to the river mouth increases with increasing levels of rel.diffP and rel.diffT up to a certain level (Figure 12). If the rel.diffP increases over about 0.45 and rel.diffT over about 0.8 the probability of migration decreases again.

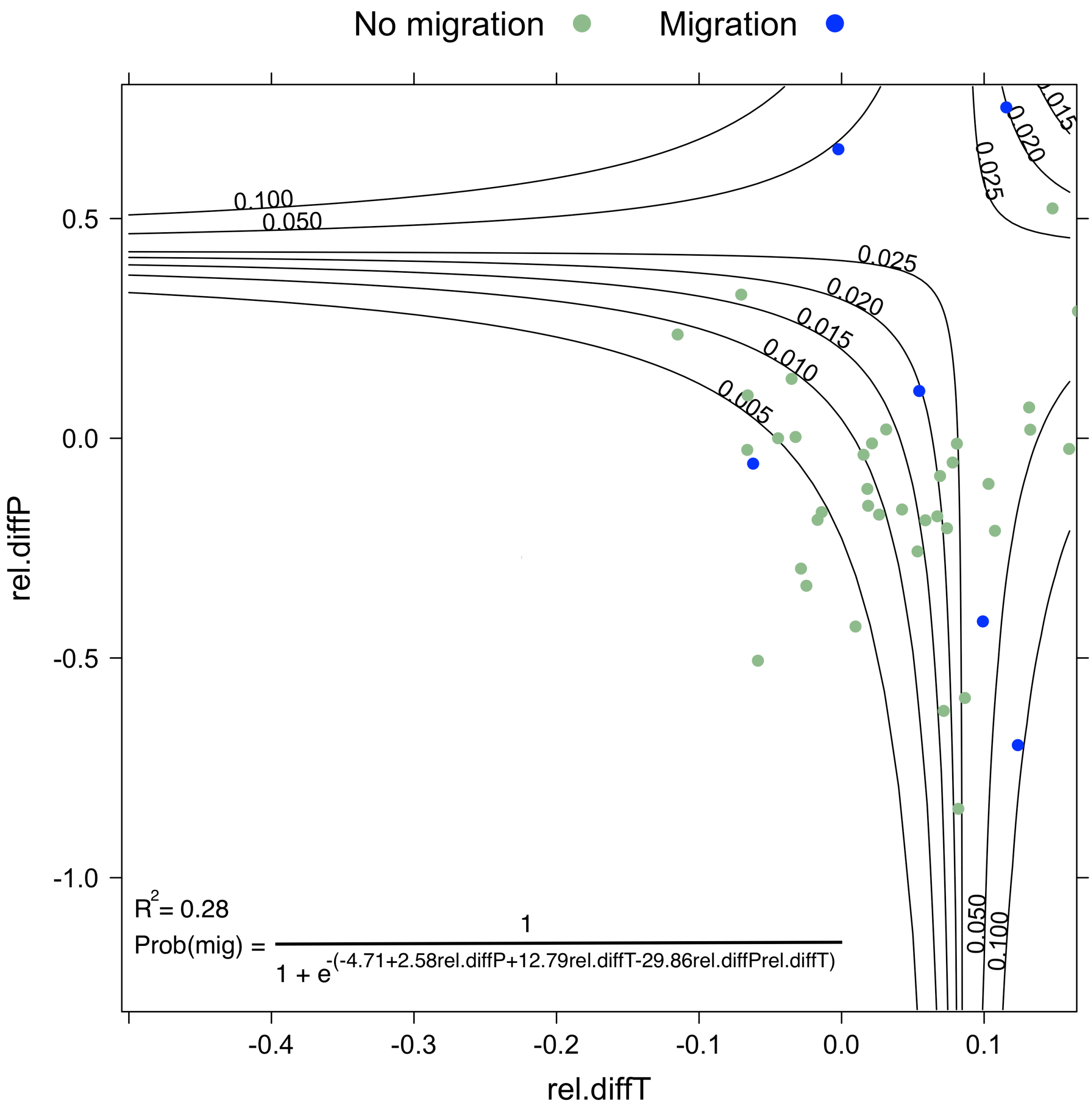

Figure 12 Probability of smolt migration (Prop(mig)) into the river mouth of the Lier River 2017. X-axis (rel.diffT) is the difference between water temperature between two days divided by water temperature for the actual day. Y-axis (rel.diffP) is the difference between water discharge between two days divided by water discharge for the actual day. The contour lines mark the probability of migration into the river mouth. The dot circles represent actual days from the study period where migration occurred (blue dots) or did not occur (green dots).

3.3 Maximum distance

3.3.1 The Årung River

The maximum distance reached for the population, in the Årung River was 17 km away from the river mouth (Figure 13). This was by an individual caught in the upper river reach. Maximum distance travelled by fish captured in the middle reach was 14 km and 15 km by fish caught in the lower reach. Mean±SD was 10±7 km for lower, 13±0 km for middle and 9±8 km for upper reach.

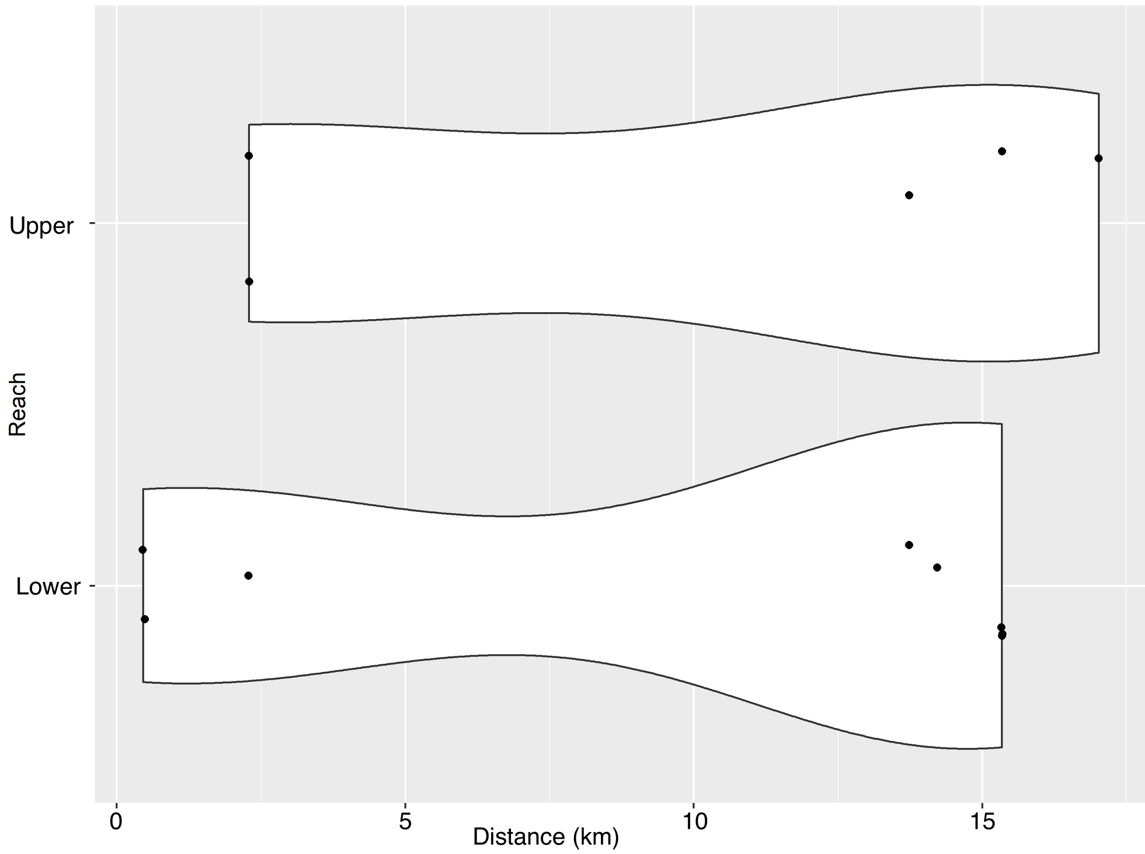

Figure 13 Maximum distance in km away from river mouth reached by wild brown trout smolt individuals from the Årung River in 2017. X-axis is distance from river mouth measured in km, and y-axis is what part (reach) of the Årung River the individuals are from. Each dot marks one individual, but thicker width of the white area means more individuals on given distance.

The candidate model that included just a linear effect of first-year length on maximum migration distance attained the highest AICc support in the data (Table 3). This model got more than 50% of the AICc-weight compared to all the other candidate models. The selected model estimated maximum distance away from river mouth to decrease as a function of the back-calculated length at 1st winter (Figure 14).

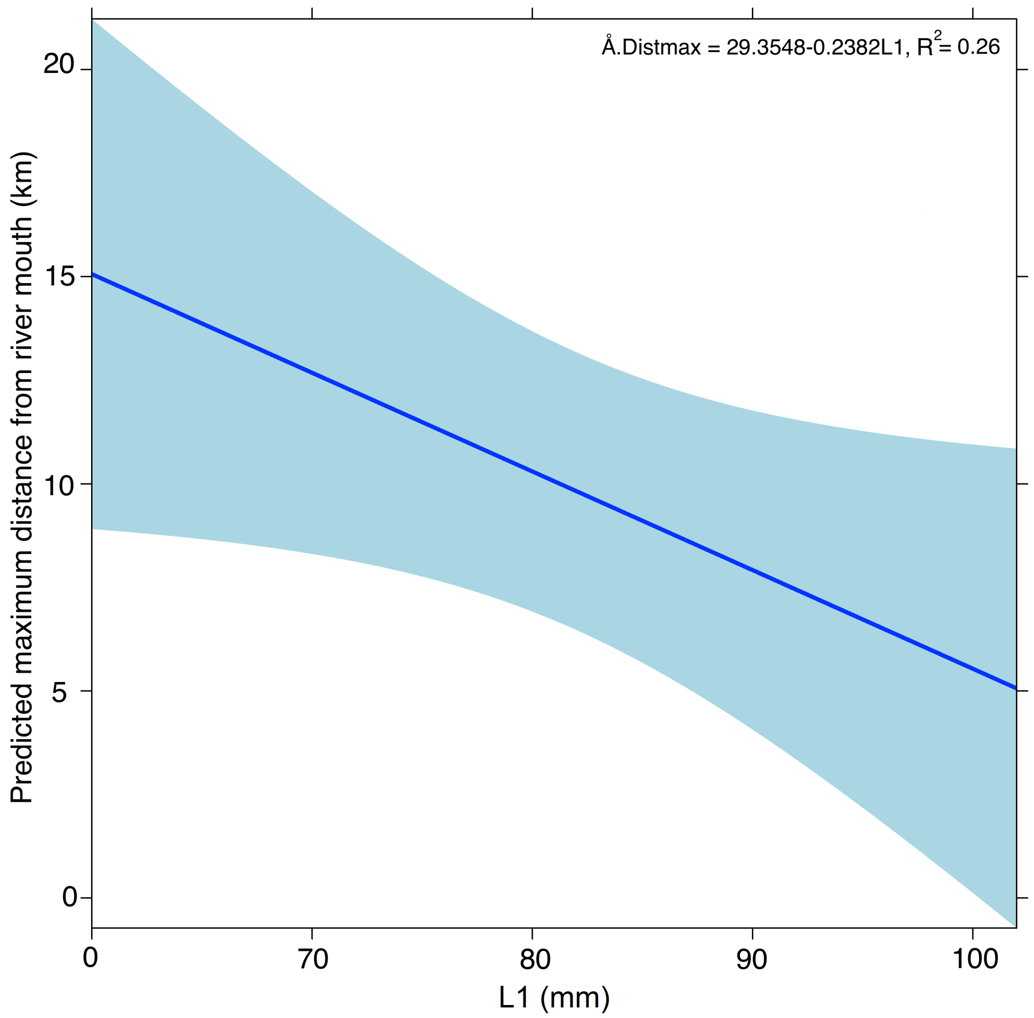

Figure 14 Predicted maximum distance from river mouth for the individuals from the Årung River in 2017. X-axis is the smolt length at 1st winter in mm, and y-axis is the distance from river mouth in km. The light blue is the 95% confidence interval.

3.3.2 The Lier, Sande and Selvik rivers

The furthest distance reached is 104 km by an individual from the Lier River (Figure 15). Mean±SD distances travelled from the rivers are; The Lier River; 47±30 km, The Sande River; 13±10 km and Selvik River, 28±23 km.

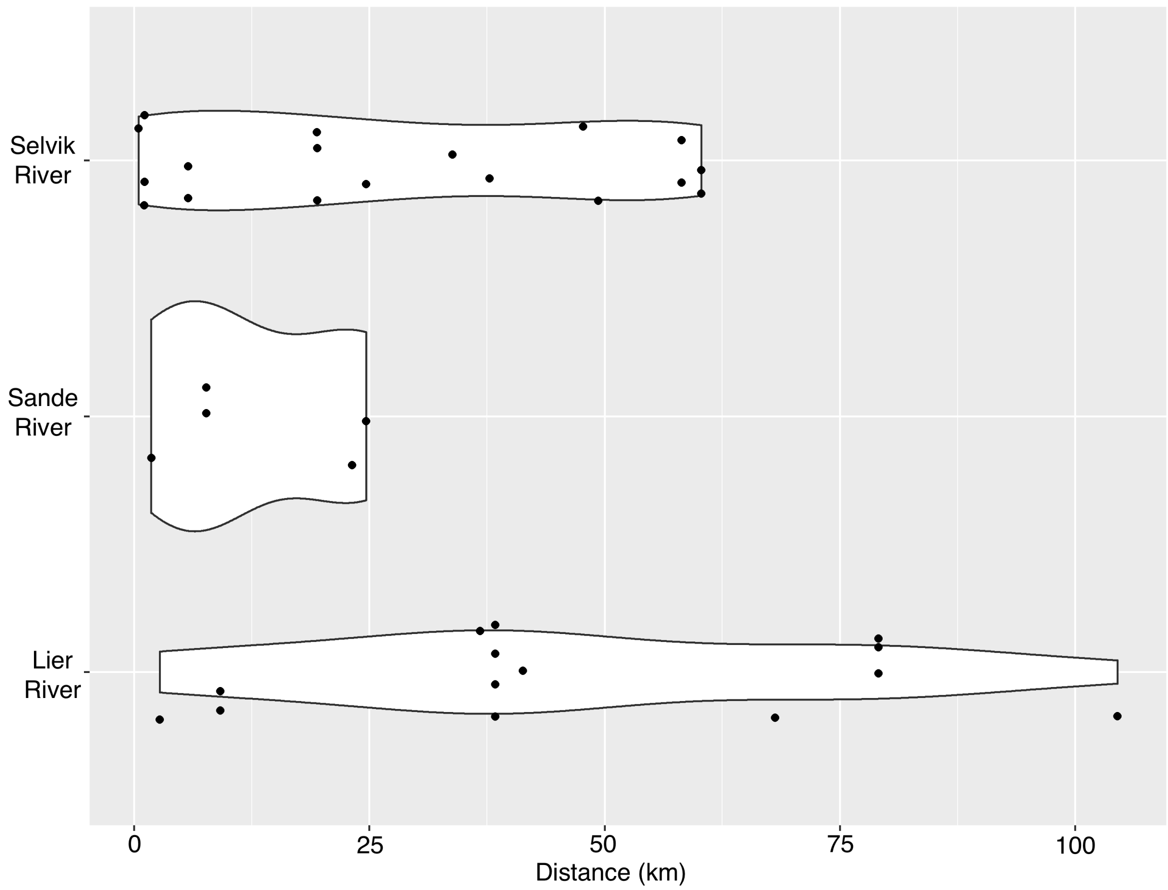

Figure 15 Maximum distance away from river mouth reached by brown trout individuals in The Oslofjord 2017. X-axis is distance away from river mouth in km and y-axis is which river the individual was caught and tagged. Each dot mark one individual's maximum distance and the width of the white area is relative to number of individuals on given maximum distance.

The candidate model with the highest AICc support in the data (Table 3) had K-factor as the explaining parameter. This model got 42% of the AICc-weight compared to the rest (Figure 16). AIC_c-test gave this the lowest AIC_c when tested with individuals without replacement scales.

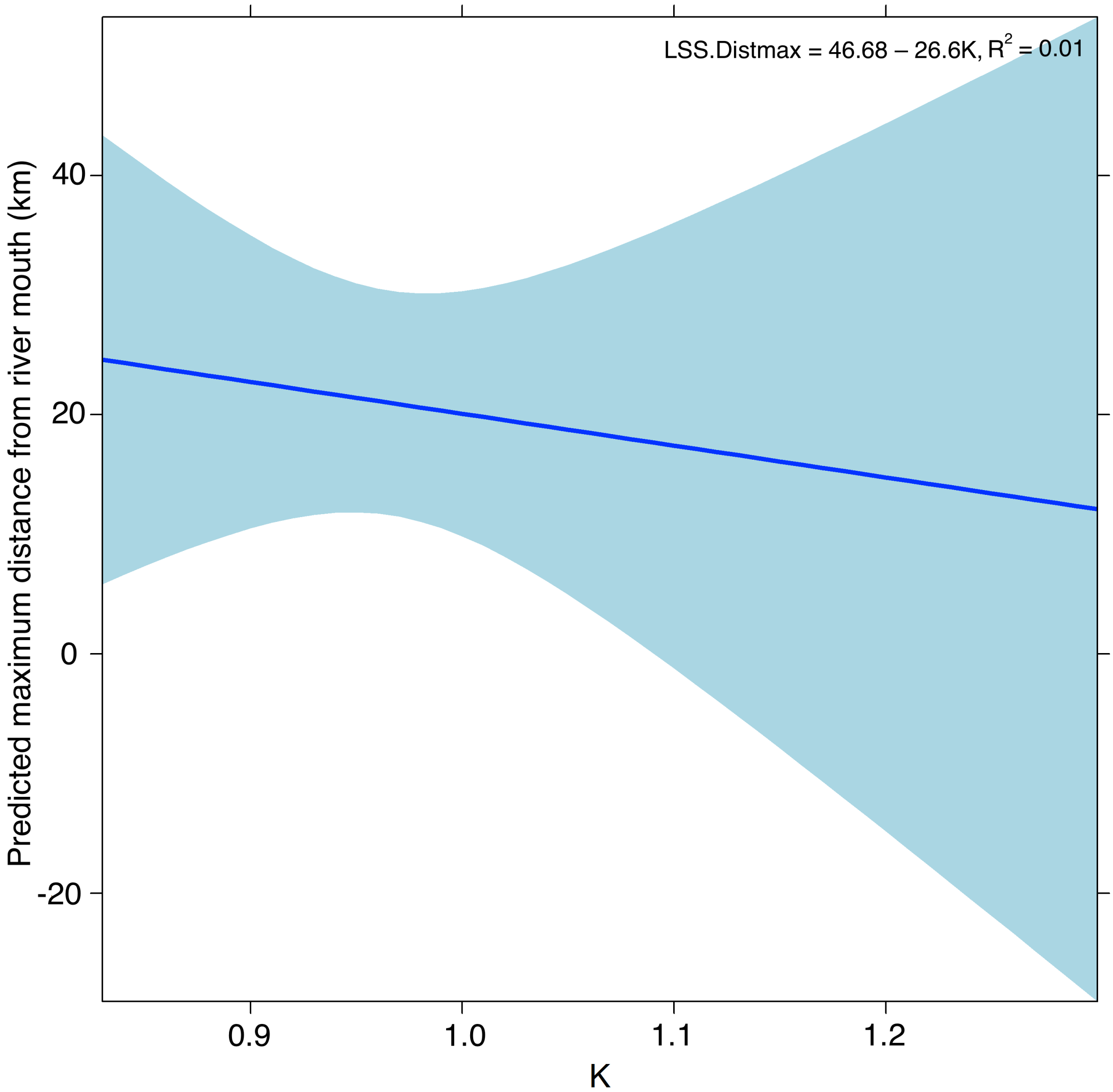

Figure 16 Predicted maximum distance away from river mouth as a function of K-factor for smolt from the Lier, Sande and Selvik rivers 2017. X-axis represent K-factor and y-axis is the predicted maximum distance away from river mouth in km.

Table 3 Model selection for estimating the determinates of arrival in the river mouth for the Årung River (Å.mig), arrival in the river mouth for the Lier River (L.mig), maximum migration distance for the Årung River (Å.Distmax) and maximum migration distance for the Lier, Sande and Selvik rivers (LSS.Distmax). The top five models according to corrected Akaike's Information Criterion (AICc)

Model number	Model structure[a]	*k*[b]	AICc	ΔAICc[c]	AICcWt[d]
	Å.mig				
9	Temp + Pres	3	53.41	0	0.88
7	Pres	2	58.22	4.8	0.08
8	Temp	2	61.49	8.1	0.02
1	diffP	2	62.25	8.8	0.01
4	rel.diffP	2	62.49	9.1	0.01
	L.mig				
5	rel.diffP * rel.diffT	4	57.67	0	0.36
3	rel.diffT	2	59.36	1.69	0.16
2	diffT	2	59.52	1.85	0.14
7	Pres	2	59.64	1.97	0.14
6	rel.diffP + rel.diffT	3	61.13	3.46	0.06
	Å.Distmax				
6	L1	3	90.70	0	0.51
7	g2	3	92.98	2.28	0.16
9	L1 + Reach	4	93.89	3.20	0.10
5	arrival.time	3	94.61	3.91	0.07
1	Reach	3	94.66	3.96	0.07
	LSS.Distmax				
12	K	3	174.85	0	0.42
13	K * arrival.time	5	175.70	0.85	0.27
14	K + arrival.time	4	176.40	1.55	0.19
18	L1 + K	4	178.11	3.26	0.08
16	K + River2	5	181.26	6.41	0.02

[a]The models estimate the relative contributions of mean daily water temperature (Temp), mean daily water discharge (Pres), the difference between the pressure between two days (diffP), the difference between the pressure between two days divided by pressure (rel.diffP), the difference between the temperature between two days divided by the temperature (rel.diffT), the difference between the temperature between two days (diffT), back-calculated length of the 1st winter of the smolt individual (L1), the logarithm of L1 minus the logarithm of the back-calculated length of the 2nd winter of the smolt individual (g2), which part of the river the smolt individual was caught and tagged (Reach, n=2, upper or lower), the date of 1st arrival in river mouth (arrival.time), the total length of the smolt individual (TL.mm), condition factor of the smolt individual (K).

[b]Number of estimated parameters

[c]Difference in AICc of the actual model and the one with the lowest AICc (ΔAICc= AICc*i*-AICcmin)

[d]AICc-weight

3.4 K-factor

The mean K-factor value of all the fish with weight measurements were 0.97 (Figure 17). The minimum for Lier, Sande and Selvik rivers were 0.91, 0.94 and 0.83 and maximum 0.99, 1.11 and 1.16. None of the fish from the Årung River had weight measurements and therefore had no K-factor calculations. The hatchery fish had a mean K-factor of 1.15 and maximum of 1.35.

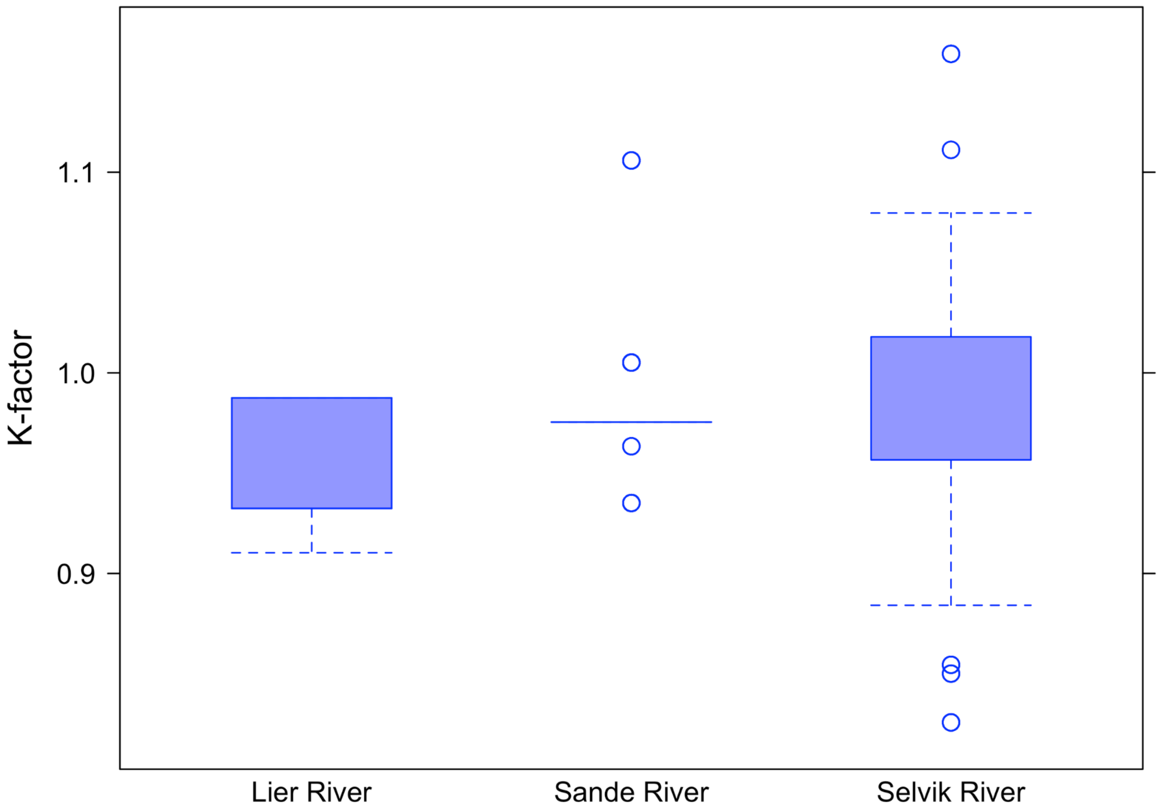

Figure 17 K-factor values at tagging for wild brown trout individuals from the Lier, Sande and Selvik rivers in The Oslofjord. X-axis gives the dates for first arrival, and y-axis is for the different rivers. The boxplot marks the 0.25 to 0.75 quantile, with median as a continuous line in the boxplot.

3.5 Depth and large-scale area use

The brown trout smolts mainly stayed close to the surface, but had some deeper dives (Figure 18). The smolts from Sande River never went below 15 meters below surface. The mean depth for all the fish were 2.8. The maximum depth for the Lier, Sande, Selvik and Årung rivers were; 50.8, 13.2, 51.0 and 49.2 m and mean±SD for each river were; 1.0±1, 1.7±0.7, 21.9±22.0 and 1.5±0.9 m.

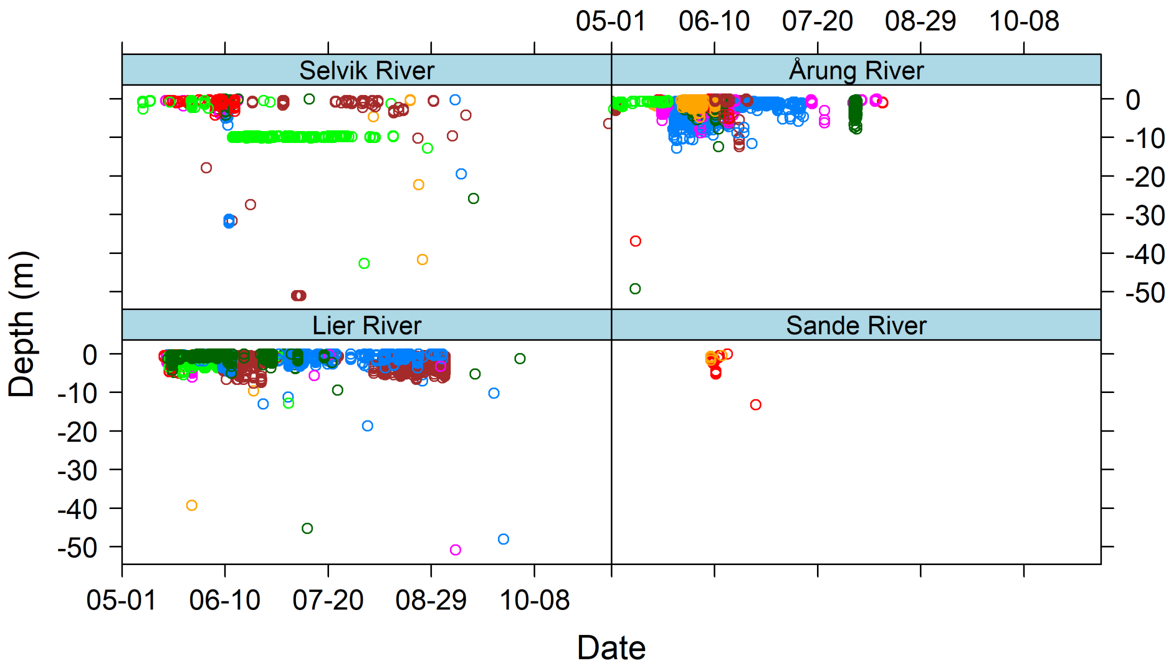

Figure 18 Depth use for brown trout smolts in the Selvik (N = 12), Årung (N = 14), Lier (N = 10) and Sande (N = 2) rivers in 2017. X-axis is the date (mm-dd) and y-axis is depth in meters below surface. The different colors mark different individuals.

The smolt from Lier, Sande and Selvik rivers are mainly detected on receivers near land and on the west side of the Oslofjord (Figure 19). There are, however, detections of individuals from Lier and Selvik on the east side near land.

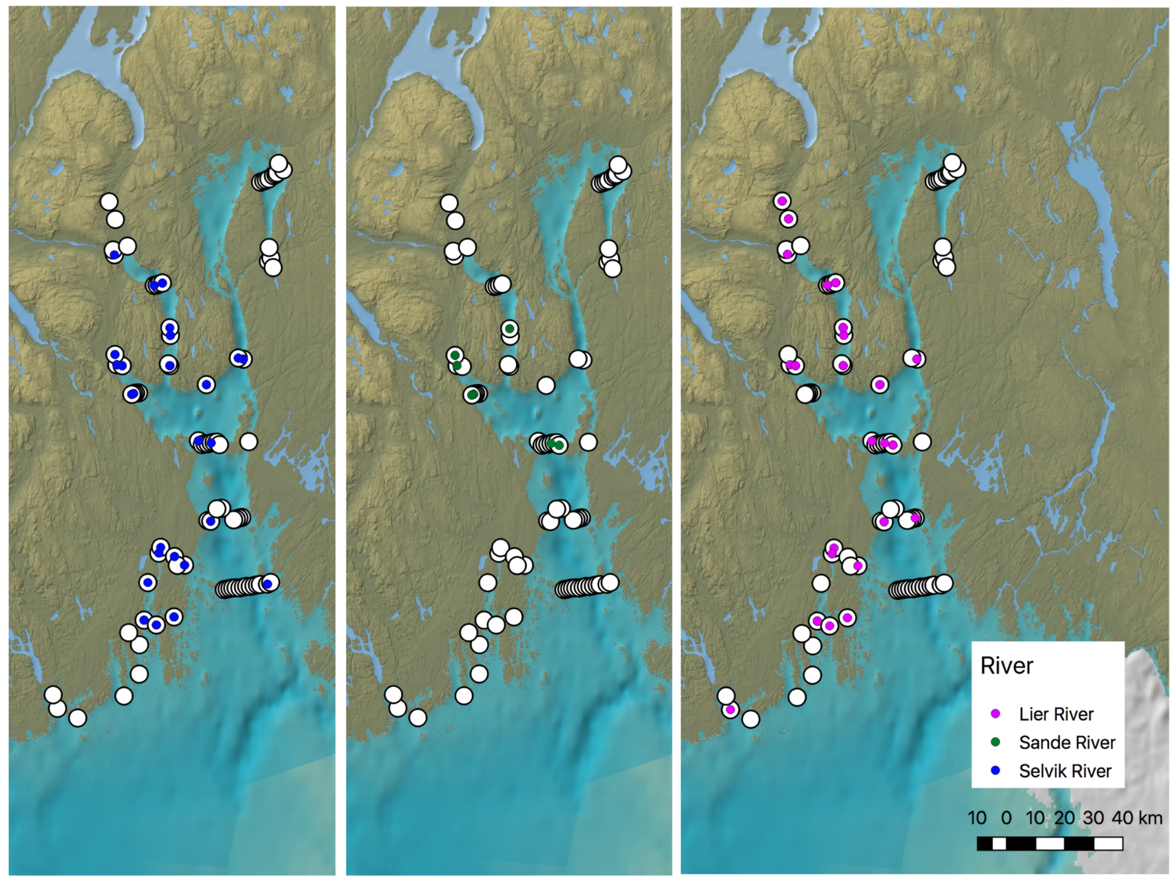

Figure 19 Detections of smolt from the Lier, Sande and Selvik rivers on the receivers of the Oslofjord 2017. Coloring in the white dot circle means a detection from one or more individuals caught and tagged in the Lier (pink), Sande (green) or Selvik (blue) rivers.

4. Discussion

Water temperature and discharge explained 28% in the Lier River and 42% in the Årung River regarding timing of arrival in the river mouth. Increasing temperature and discharge lead to an increase in the probability of migrating downstream and into the river mouth. As for maximum distances travelled away from natal rivers, there was a negative correlation between back-calculated length at 1st winter, and how far away from the river mouth an individual travelled in the Årung River. For the Lier, Sande and Selvik rivers the condition factor (K-factor) had the negative correlation with maximum distance. This means that what goes on in fresh water of the first years of the brown trout's life, does have an impact on how it later in life utilizes the marine system. These findings are of relevance to managers, who should have the entire life span of the brown trout in mind when making decisions affecting brown trout stocks. Smolt also stayed in shallower water close to land. Smolt from *G. salaris*-infected rivers utilized river mouths of non-natal rivers free from *G. salaris*, causing a potential risk for spreading the parasite during flooding events in the Oslofjord causing low salinity levels, and improved survival of the parasite.

4.1 Environmental cues for migration into river mouth

I hypothesized that increasing water discharge and temperature would facilitate migration into the river mouth, which the results of the AICc predictions supported. In the model for the Årung River we found that temperature and water discharge accounted for 42% of the variation in when the fish entered the river mouth. Previous studies have also shown that temperature and water discharge are good parameters for modelling this. In a study over three years in Stjørdalselva discharge and temperature accounted for between 28% and 61% of the variation in arrival in the river mouth (Hembrel et al. 2001). In the Lier River, it was the relative difference in the temperature and water discharge that according to AICc had the highest ranking, and accounted for 28% of the variation. These results on what affects the migration into the river mouth are therefore in accordance with several other studies findings (Jonsson & Jonsson 2011c; Klemetsen et al. 2003; Urke et al. 2018) and tell us that water temperature and water discharge are key environmental factors the smolt react to when descending the river. Jonsson and Jonsson (2011c) also discovered that migration numbers back into natal river increased up to a certain level of water discharge. Because of the findings in the migration model of the Lier River (Figure 12) it might be that this relationship also is true for upstream migrations. The reason for water discharge's importance can in smaller streams, like the Årung River, be due to avoidance of draught, meaning the fish have to migrate at higher levels of discharge to be able to pass at all (Borgstrøm & Heggenes 1988). Temperature influences the energy use for movement and physiological processes, by easing them, up to a certain temperature, before too high temperatures again restrict (Wootton 1991). Temperature will facilitate migration to an optimum, and then decline, as in accordance with the migration model of the Lier River.

4.2 How far and how deep do the smolt go?

For maximum distance travelled away from natal river I hypothesized that increasing body length increased this distance, however this was not what the results for this study showed. In my prediction model for maximum distance back-calculated length at 1^{st} winter (L1) was the parameter of the model with the lowest AICC-value for the Årung River. This explained 26% of the variation. Other studies have linked length at migration to maximum distances, with a positive correlation between body length and maximum distance (Flaten et al. 2016; Urke et al. 2018). However, there seem to be no studies that have found a link between back-calculated parr lengths and maximum migration distances. This might be because the studies have not included this as a parameter, or that this link is unique to the brown trout populations of the Årung River. For the Lier, Sande and Selvik rivers the condition factor (K-factor) was the parameter in the prediction model with the lowest AICc. Previous studies have also shown a negative correlation between condition factor and maximum distance, but this was also connected to body length, meaning long individuals with low condition factor travelled the furthest (Hawley et al. in press; Urke et al. 2018). However, three of the rivers in the study in Sognefjord had condition factor as the main explaining factor (Hawley et al. in press). The R^2 for this model was however only 0.01, meaning this does not explain much of the variation. One reason for this could be that there were three different populations from different rivers in the analysis, and it might have been beneficial to analyze them separately. In my study, none of the five models with the lowest AICc-value included body length at capture, however was back-calculated length at 1^{st} winter and arrival time in the river mouth factors in the models. Therefore, the hypothesis is not supported by the results in this study.

The last hypothesis of this study was that the smolt utilized shallow near-shore areas, and mainly areas close to their natal river. This hypothesis was partially supported by the results. The brown trout smolt from the four rivers stayed mostly close to the sea surface, with mean depth values under 2 m. The Selvik River did however, have a mean of around 20 m, but this might be due to an individual dying close to a receiver (green dots, Figure 18). These findings are therefore also in accordance with previous studies (Berg & Berg 1987; Flaten et al. 2016; Jonsson & Jonsson 2011c; Urke et al. 2018).

Brown trout are known for staying in brackish waters and estuaries, and not far offshore, due to their ionic regulation which is harder to execute in colder seawater (Jonsson & Jonsson 2011b). Therefore, the smolt is also known and expected to use the natal river mouths. The individuals in the Lier, Sande and Selvik rivers did not however just stay close to their natal river. They were found all along the western coast of the Oslofjord (Figure 19). For example, individuals from the *G. salaris*-infected Lier River were detected on several receivers close to the *G. salaris*-free Aulivassdrag river mouth in Tønsberg and the Numedalslåg river mouth in Larvik. This means that the hypothesis was supported in the fact that the smolt stayed close to land and in shallower waters. However, it also travelled far and was detected in mouths of non-natal rivers.

4.3 Shortcomings, suggestions of improvement and reproducibility

As there were only 51 individuals detected in this study the N is not too high, and therefore this might have had an impact on the outcome of the statistical comparisons of effects. The corrected AIC (AICc) was used, this being recommended for ecological studies with low N (Burnham et al. 2011), but the N within the parameter groupings might still be too low. Also, this study was done over one year, and the results should therefore be handled as explanations of what occurred in the four rivers in 2017.

Tagging more individuals would be beneficial, but this is a challenge. Although electro-fishing was carried out almost continuously in the period when migration was expected it was hard to catch large numbers due to high water level, making the electro-fishing less efficient. To increase the N of the study seven individuals from the DOFA hatchery were tagged. This can also be a cause of error, because hatchery-reared brown trout has in previous studies shown different behavior from wild brown trout (Alvarez & Nicieza 2003). It has been suggested that low condition factor is a proximate driver for choosing an anadromous lifestyle (Davidsen et al. 2014a). Therefore, tagging hatchery brown trout, with their high condition factor (mean: 1.15), may result in an incorrect assessment in the proportion of anadromous brown trout within the river population, and in practice, not a higher N in the fjord system to strengthen the data. Three of the 7 hatchery fish were not detected, and in total 23 individuals were not detected on the receivers. One of the reasons for this could be because visually determining smoltification can be a challenge on certain individuals (Wedemeyer 1996). That could be why some were not detected, because they simply did not migrate from the river at all. A study from a reservoir in Denmark reported 90% of the tagged smolt dying, mainly because of predation, within 3 weeks of tagging (Jepsen et al. 1998). This might be one more reason explaining the 31 % of tagged individuals that were not detected in this study. Surgical implantations in wild fish is complicated, because it is hard to study the possible behavioral changes, or post-surgery complications in the fish after release (Mulcahy 2003). In this study, there were a lot of small individuals (total length; median:185 mm, smallest: 126 mm) compared to the study from Hemne (total length; mean: 202 mm, smallest: 150 mm) (Flaten et al. 2016). Previous studies have not recommended putting transmitters into fish with fork length smaller than 120 mm, because of ability to avoid predators (Adams et al. 1998a; Adams et al. 1998b; Bendall et al. 2005; McCleave & Stred 1975). However, another study on salmon had no correlation between mortality and tag weight: body mass ratios (Newton et al. 2016), thus, this also might be applicable to brown trout, because they are so closely related.

Range testing of the receivers would have been beneficial to determine the actual range of the receivers in different conditions at the actual locations, to make sure there was a decent overlap and certainty of detecting an individual passing by a transect. This might have been helpful if wanting to e.g. look at residence time, because one could have been more certain that an individual would be detected. It would have been an improvement of the study to look at residence time in different river mouths, but this was hard to execute because of the size of the study area and the loss of several receivers. Upstream migration back into the natal river would be interesting to explore, but there were only three individuals detected returning in the river. A solution to this is using tags with longer battery time, but to extend the battery capacity the tag 'pin rate' would have to be reduced, and therefore detection probability may be compromised. The Selvik River did not have a receiver in the river at all. An explanation for the loss and relocation of 61% of the receivers might at least partially, be due to several of the receiver transects being placed in the middle of areas regulated for shrimp trawl in the Oslofjord (Appendix Figure A- 1).

The dataset for detections went through several processes of cleaning before analysis. Even though this was carried out using known ecological facts about brown trout, like maximum swimming speeds to pick out impossible detections, there still might have been erroneous removals or detections that should have been removed, but stayed in the dataset. Because of the study area being at sea in a large fjord system, it was challenging to cover the area with desired number of receivers to make sure there weren't detection gaps. Also because of the study area size, the chance of having more detections from one individual over time, were smaller, making the cleaning of detections harder. It was suggested from Thelma Biotel to reject all single detections, but doing that would have led to almost no detection data for this study. False detections from surrounding activities were also an issue, and even though most of these were easily filtered out due to non-existent ID numbers or code types, some of these false detections might also have had actual IDs present in the study. Thelma Biotel is working on software and methods for improving this in future use of their acoustic telemetry technology.

Back-calculations of length from the fish scale also might be a source of errors. The scales could have been read wrong, marking false annuli, giving wrong impressions of parr lengths back in time. Scale reading is hard, especially when the experience is limited, therefore all scale readings were verified by an experienced person. Other methods for back-calculations, like otoliths, were not an option since the individuals were being released after capture. Weight was not measured on all individuals, weakening the N of K-factor values. The use of Fulton's condition factor is also debated, and questions are being asked whether this truly is a good indicator of actual condition (Froese 2006).

Data on temperature and water discharge should also have been collected from the Sande and Selvik rivers to explore migration triggers for these rivers as well. Several studies have looked at diurnal vs. nocturnal linkage for explanation of downstream migration (Flaten et al. 2016), and this could also have been further explored in this study.

4.4 Management implications

Because fjord area use is affected by individual growth performance in freshwater stage eventual changes in freshwater environment that affect individual growth may have implications for the fjord use. The brown trout smolt also travel long distances from their natal river mouths in the Oslofjord. Therefore, it is important that the management of the species is conducted on a regional scale, considering both the marine and the fresh water environments into the management equation.

The fact that individuals from *G. salaris*-infected rivers are detected near healthy watercourse's river mouths is worrying. If the salinity of the Oslofjord is at a low enough level, due to extreme flooding events, it might be possible for the *G. salaris* to survive on the brown trout smolt long enough to transfer into e.g. the Numedalslåg, which is not infected. The climate changes our planet is facing is expected to increase the number and magnitude of flooding events (Milly et al. 2002), and therefore because of the Oslofjord's previously known fluctuations in salinity (Røed et al. 2016), we can expect them to be even greater. Due to the Oslofjord's unique geography, with several large watercourses on both the west and east side of the fjord, great flooding events can lead to corridors of fresh water in the fjord, where individuals of infected rivers can travel to non-infected watercourses, spreading the parasite further. Individuals were also detected on receivers on the east side of the Oslofjord. Because of this further research, with more receivers closer to land and river mouths of interest on the east side, should be done. Tagging smolt from the east side watercourses is advisable to explore if they also spend time in mouths of infected rivers on the west side of the fjord.

5. Conclusion

Migration into river mouth and fjord use is driven by a mixture of both internal effects, like condition factor and growth history and environmental drivers, like temperature and discharge. The brown trout smolt of the Lier, Sande, Selvik and Årung rivers in the Oslofjord is mainly found in shallow waters close to land, but can travel distances as far as 100 km away from natal river, and utilize non-natal river mouths. Smolt from rivers infected with the parasite *G. salaris* were also detected in mouths of *G. salaris*-free rivers, meaning that the parasite might spread to healthy rivers, like the Numedalslåg.

This is important knowledge for managers, so that they can have the entire life span of the brown trout in mind when making decisions, and consider the large area the brown trout utilizes. *G. salaris* is a threat towards wild Atlantic salmon populations and the potential risk of spreading should be limited as much as possible.

This was a one year study, and the results should therefore only be interpreted for 2017. However, the number of studies on brown trout smolt being so few makes the findings interesting, and of value to both ecologist and managers, and these connections should be further explored in similar studies in the consecutive years.

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Appendix

Table A- 1 All tagged fish with river and part of river, acoustic telemetry Id, total length in mm (TL), weight, if they were wild or from a hatchery, reach and if they were detected or not. Weight was not measured in all fish and Reach is only applicable to the Årung River.

Date	River	AT-type	AT-number	TL	Weight	Wild/ Hatchery	Reach	Detected
24/04/2017	Lier-grøtte	ID	10	132		W		No
24/04/2017	Lier-grøtte	ID	11	126		W		No
24/04/2017	Lier-grøtte	D	14	215		W		No
24/04/2017	Lier-grøtte	D	15	160		W		Yes
24/04/2017	Lier-grøtte	D	16	135		W		Yes
24/04/2017	Lier-grøtte	D	17	142		W		Yes
24/04/2017	Lier-grøtte	D	18	140		W		Yes
24/04/2017	Lier-grøtte	D	19	149		W		Yes
24/04/2017	Lier-grøtte	D	20	141		W		Yes
24/04/2017	Lier-grøtte	ID	69	137		W		Yes
29/04/2017	Sande	ID	44	53	31	W		Yes
29/04/2017	Sande	ID	46	55	30	W		No
29/04/2017	Sande	ID	49	58	28	W		No
29/04/2017	Sande	D	126	134	125	W		No
29/04/2017	Sande	D	127	135	32	W		No
29/04/2017	Selvik	ID	35	44	29	W		Yes
29/04/2017	Selvik	ID	37	46	33	W		No
29/04/2017	Selvik	ID	41	50	29	W		Yes
29/04/2017	Selvik	ID	42	51	25	W		Yes
29/04/2017	Selvik	D	120	128	39	W		Yes
29/04/2017	Selvik	D	121	129	45	W		Yes
29/04/2017	Selvik	D	122	130	43	W		Yes
29/04/2017	Selvik	D	123	131	56	W		Yes
29/04/2017	Selvik	D	124	132	35	W		Yes
29/04/2017	Selvik	D	125	133	43	W		Yes
02/05/2017	Sande-Veslebekken	D	130	138	36	W		Yes
02/05/2017	Sande-Veslebekken	D	131	139	38	W		Yes
02/05/2017	Selvik	D	143	151	68	W		No
02/05/2017	Selvik	D	144	152	33	W		Yes
02/05/2017	Selvik	D	145	153	47	W		Yes
02/05/2017	Selvik	D	146	154	44	W		Yes
02/05/2017	Selvik	D	147	155	35	W		Yes
02/05/2017	Selvik	D	148	156	31	W		Yes
02/05/2017	Selvik	D	149	157	31	W		Yes
02/05/2017	Selvik	D	150	158	31	W		Yes

02/05/2017	Selvik	D	151	159	32	W		No
03/05/2017	Lier	ID	30	130	20	W		Yes
03/05/2017	Lier	D	177	186	60	W		Yes
03/05/2017	Lier	D	178	151	34	W		Yes
03/05/2017	Lier-DOFA	D	180	180	65	H		No
03/05/2017	Lier-DOFA	D	172	190	77	H		Yes
03/05/2017	Lier-DOFA	D	173	212	129	H		Yes
03/05/2017	Lier-DOFA	D	174	210	105	H		Yes
03/05/2017	Lier-DOFA	D	175	201	91	H		No
03/05/2017	Lier-DOFA	D	176	168	54	H		Yes
03/05/2017	Lier-DOFA	D	181	195	87	H		No
03/05/2017	Sande	ID	1623	127	23	W		No
03/05/2017	Sande	ID	1624	135	24	W		Yes
03/05/2017	Sande	ID	1625	133	22	W		Yes
03/05/2017	Selvik	D	181	165	46	W		No
03/05/2017	Selvik	ID	1614	135	21	W		No
03/05/2017	Selvik	ID	1619	139	23	W		No
03/05/2017	Selvik	ID	1620	134	22	W		Yes
03/05/2017	Selvik	ID	1621	133	20	W		Yes
03/05/2017	Selvik	ID	1622	138	20	W		No
10/04/2017	Årung	D	50	222		W	Upper	Yes
10/04/2017	Årung	D	51	217		W	Upper	Yes
10/04/2017	Årung	D	52	237		W	Upper	Yes
10/04/2017	Årung	D	53	190		W	Upper	Yes
10/04/2017	Årung	D	54	229		W	Middle	No
10/04/2017	Årung	D	55	208		W	Middle	Yes
10/04/2017	Årung	D	56	267		W	Middle	Yes
10/04/2017	Årung	D	57	194		W	Middle	No
19/04/2017	Årung	D	58	277		W	Lower	Yes
19/04/2017	Årung	D	59	207		W	Lower	Yes
19/04/2017	Årung	D	60	232		W	Lower	Yes
19/04/2017	Årung	D	61	216		W	Lower	Yes
19/04/2017	Årung	D	62	220		W	Lower	No
19/04/2017	Årung	D	63	158		W	Lower	No
19/04/2017	Årung	D	64	171		W	Lower	Yes
19/04/2017	Årung	D	66	282		W	Lower	Yes
19/04/2017	Årung	D	67	198		W	Lower	Yes
19/04/2017	Årung	D	68	171		W	Lower	No
19/04/2017	Årung	D	69	154		W	Lower	Yes

Table A- 2 Model selection for estimating the determinates of arrival in the river mouth for the Årung River (Å.mig), arrival in the river mouth for the Lier River (L.mig), maximum migration distance for the Årung River (Å.Distmax) and maximum migration distance for the Lier, Sande and Selvik River (LSS.Distmax).

Model number	Model structure[a]	*k*[b]	AICc	ΔAICc[c]	AICcWt[d]
	Å.mig				
9	Temp + Pres	3	53.41	0.00	0.88
7	Pres	2	58.22	4.81	0.08
8	Temp	2	61.49	8.08	0.02
1	diffP	2	62.25	8.84	0.01
4	rel.diffP	2	62.49	9.08	0.01
6	rel.diffP + rel.diffT	3	64.12	10.71	0.00
5	rel.diffP * rel.diffT	4	66.23	12.82	0.00
2	diffT	2	66.34	12.93	0.00
3	rel.diffT	2	67.31	13.91	0.00
	L.mig				
5	rel.diffP * rel.diffT	4	57.67	0	0.36
3	rel.diffT	2	59.36	1.69	0.16
2	diffT	2	59.52	1.85	0.14
7	Pres	2	59.64	1.97	0.14
6	rel.diffP + rel.diffT	3	61.13	3.46	0.06
9	Temp + Pres	3	61.58	3.91	0.05
4	rel.diffP	2	62.34	4.67	0.04
1	diffP	2	62.75	5.09	0.03
8	Temp	2	63.12	5.46	0.02
	Å.Distmax				
6	L1	3	90.70	0	0.51
7	g2	3	92.98	2.28	0.16
9	L1 + Reach	4	93.89	3.20	0.10
5	arrival.time	3	94.61	3.91	0.07
1	Reach	3	94.66	3.96	0.07
10	L1 + arrival.time	4	94.95	4.25	0.06
8	L1 * Reach	5	97.90	7.21	0.01
11	L1 * arrival.time	5	98.58	7.88	0.01
3	Reach + TL.mm	5	103.76	13.06	0.00
4	Reach + arrival.time	5	104.15	13.45	0.00
2	Reach * TL.mm	6	111.13	20.43	0.00
	LSS.Distmax				
12	K	3	174.85	0	0.42
13	K * arrival.time	5	175.70	0.85	0.27
14	K + arrival.time	4	176.40	1.55	0.19
18	L1 + K	4	178.11	3.26	0.08

16	K + River2	5	181.26	6.41	0.02
17	L1 * K	5	181.42	6.57	0.02
15	K * River2	7	188.92	14.07	0.00
11	L1 * arrival.time	5	196.39	21.54	0.00
5	arrival.time	3	203.51	28.66	0.00
6	L1	3	205.83	30.98	0.00
10	L1 + arrival.time	4	206.51	31.66	0.00
7	TL.mm	3	206.65	31.80	0.00
1	River2	4	207.67	32.82	0.00
4	River2 + arrival.time	5	208.26	33.41	0.00
3	River2 + TL.mm	5	210.75	35.90	0.00
9	L1 + River2	5	210.81	35.96	0.00
2	River2 * TL.mm	7	218.76	43.91	0.00
8	L1 * River2	7	218.81	43.97	0.00

[a]The models estimate the relative contributions of mean daily water temperature (Temp), mean daily water discharge (Pres), the difference between the pressure between two days (diffP), the difference between the pressure between two days divided by pressure (rel.diffP), the difference between the temperature between two days divided by the temperature (rel.diffT), the difference between the temperature between two days (diffT), back-calculated length of the 1st winter of the smolt individual (L1), the logarithm of L1 minus the logarithm of the back-calculated length of the 2nd winter of the smolt individual (g2), which part of the river the smolt individual was caught and tagged (Reach, n=2, upper or lower), which river the smolt individual was caught and tagged (River2, n=3, Lier, Sande or Selvik), the date of 1st arrival in river mouth (arrival.time), the total length of the smolt individual (TL.mm), condition factor of the smolt individual (K).

[b]Number of estimated parameters

[c]Difference in AICc of the actual model and the one with the lowest AICc (ΔAICc= AICc*i*-AICcmin)

[d]AICc-weight

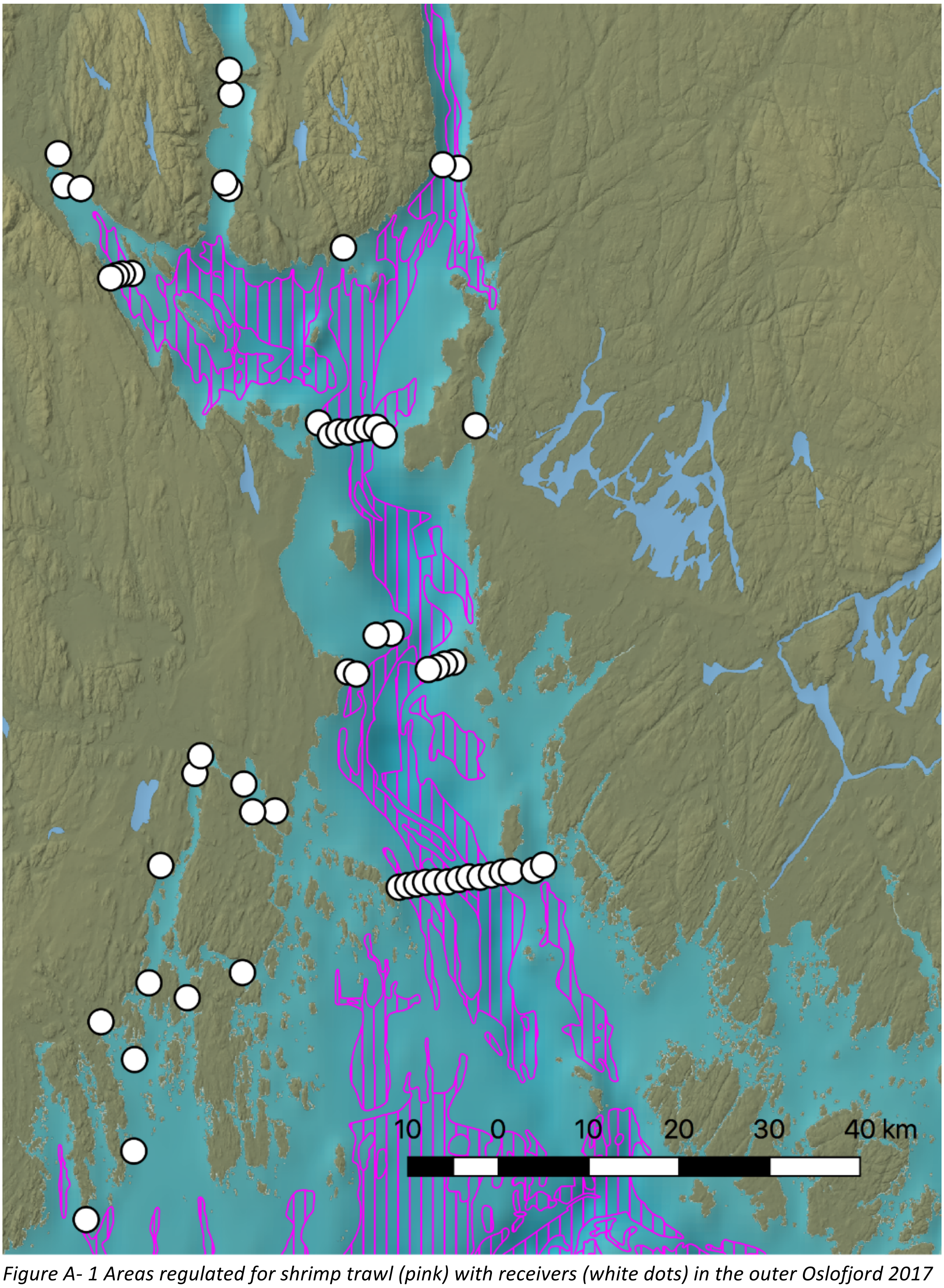

Figure A- 1 Areas regulated for shrimp trawl (pink) with receivers (white dots) in the outer Oslofjord 2017

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