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# Behavioral Study of Coexisting Populations of Anadromous Brown Trout and Arctic Char that Overwinter in a Subarctic Lake

Geir-Johnny Monsen
Natural Resource Management

# Acknowledgements

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# Abstract

This was an acoustic telemetry study on winter ecology and migratory behavior of anadromous brown trout *(salmo trutta)* and arctic char *(salvelinus alpinus)*. The two species are coexisting in a subarctic lake of northern Norway called Botnvatnet. There is little research conducted on winter-behavior of these two species, and the aim of this study was to enlighten some of the secrets that were kept in the dark and cold life under the ice.

To get a better picture of the behavioral patterns 24 acoustic receivers were constantly logging signals from acoustic tags operated into the fish. There was a great difference in the habitat utilization between the two species. Arctic char utilized water at a median depth of 12-15 meters during the coldest months, while the brown trout stayed at 3-5 meters. Estimations of both swimming distance and home range size revealed that the arctic char was most active during the study period, swimming a median length of 30 kilometers each day. However, the brown trout showed that it also was surprisingly active with an average swimming distance of 20 kilometers a day. Some individuals of both species even swam an average distance of 70-80 kilometers each day for some months during the study. Parameter estimates of the most fitted models revealed that the factors species, sex, month and length was important influences on the habitat utilization. The effect of length had complicated interactions and varied from month to month between species and genders.

It is likely to believe, considering the activity level of the fish during the winter, that they were gaining energy in form of eating. All the tagged individuals survived the winter which indicates that wintering in freshwater may be beneficial and improve the survival rate of these salmonids.

The candidate fish was captured and tagged in their spawning river which ran into the lake on the south end. All the tagged individuals returned to the lake after spawning and utilized the lake as a winter refuge. As spring unfolded a big part of the tagged individuals migrated to the sea. Parameter estimates of the most supported GLMsea-migration timing model predicted that increased water temperature (4°C) and raised water level (136 kPa) triggered the marine migration of the arctic char. There was not conducted a sea-migration model on the brown trout due to lack of individuals, but data on migration, water flow and water temperature *(figure 4.8)* strongly suggest the same pattern that were shown on the arctic char. The brown trout started the descend to the sea roughly two weeks (20.05.2016) before the arctic char (08.06.2016).

# CONTENTS

# 1 INTRODUCTION

Migration within animal populations involves large or small-scale bi-directional movements by individuals between different habitats. The animals migrate to habitats that fulfill competing needs within and between different life-stages which maximizes growth, reproductive success and survival (Tamario et al., 2019). Benefits of migratory movements may come in form of access to resources, refuge against predators, strategic placement of gametes in places that has good conditions to develop embryos and offspring. Potential costs of migration include predation, extra use of energy associated with moving to another habitat, straying, osmoregulatory stress and reduced reproduction success due to genetic incapability associated with inter-population hybridization (Tamario et al., 2019).

Brown trout (*Salmo trutta*) and Arctic char (*Salvelinus articus*) are species belonging to the Salmonidae family. The two species have important ecological, economical and recreational functions (Jonsson and Jonsson, 2011b, Klemetsen et al., 2003a). Both species has complicated life cycle with different strategies based on growth rate, diet, habitat, size of maturation and migratory behavior within the same population (Jonsson and Jonsson, 2011b). Freshwater habitats hold few predators and the risk of being exposed to pathogens is lower than in the marine environment. The freshwater habitat is utilized as nursing areas and early-life growth for all salmonids (Klemetsen et al., 2003a).

Anadromy is when fish spawn in freshwater and migrate to the sea (Jensen, 2013). In populations of brown trout and arctic char with free access to the sea, some individuals may become anadromous. At northern latitude the sea is often more productive than the freshwater habitats (Gross, 1987), this makes the growth potential for the migratory individuals greater than the freshwater resident fish. Reproductive success favors large body size and good fitness, especially with the female specimen, which makes the seasonal migration to the sea worth the risk (Klemetsen et al., 2003a, L'Abee-Lund et al., 1989). The benefits of becoming a migrant fish is however balanced out by the risk of being eaten by predators, exposure to pathogens, deceases and osmo-regulatory stress (Klemetsen et al., 2003a).

Arctic char is the northernmost freshwater fish species globally with a circumpolar distribution. Brown trout has a native distribution in Europe, north Africa and the western parts of Asia, but is by help of humans spread to most parts of the world (Elliott, 1994, Klemetsen et al., 2003a). In the north of Norway (north of 65°N) arctic char can form anadromous populations that migrates to the sea for some weeks in the summer to feed in the rich habitats close to its home river. Sea run brown trout populations on the other hand is found in most coastal streams all along the Norwegian coastline (Klemetsen et al., 2003a). The main difference of the two species is that arctic char is restricted to fresh water residency during winter due to low salinity tolerance at lower water temperatures (Hoar, 1976). Normally anadromous char individuals stay in coastal areas for 45-55 days in the early summer (May – July) (Berg and Berg, 1989, Finstad and Heggberget, 1993, Kirkemoen, 2016), while most of the trout are sea resident for 45-70 days (Jensen, 2013, Klemetsen et al., 2003a, Flaten et al., 2016). Some individuals of brown trout may even stay at sea for two years or longer before returning to their home river to spawn (Klemetsen et al., 2003a).

As mentioned, both anadromous arctic char and brown trout return to freshwater during the fall. At lower water temperatures, the saltwater tolerance gets reduced in both species, available feed organisms in the sea decrease, and the risk of getting eaten by a predator still remains. This makes the reward of staying in saltwater probably not worth the risk (Jonsson and Jonsson, 2011b, Klemetsen et al., 2003a). By using freshwater as a winter refuge, the fish eliminates the risks that the marine environment represent. The problem of food availability on the other hand is not eliminated, something that is considered to make winter a bottleneck period for salmonid species (Jonsson and Jonsson, 2011a, Cunjak and Power, 1986). Water temperature is often colder in freshwater during the winter months than the sea. This may be beneficial to the two species as the cold water slow down the metabolic rate and energy reserves is exploited more efficient (Jonsson and Jonsson, 2011b).

Wintertime is argued to be a bottleneck for survival for salmonid populations and overwintering in freshwater is an important adaptation for anadromous populations that live in the arctic. Very few studies have investigated the behavior of salmonids that seek refuge in freshwater during the winter. The reason may be that cold weather, hard conditions, short daylight, snow and ice makes it harder to conduct good studies in a safe way. Most studies that are conducted mainly focus on winter-activity in rivers under various ice conditions (Linnansaari et al., 2008, Linnansaari and Cunjak, 2010, Stickler et al., 2010), or on one species only like studies on arctic char in Svalbard and Bjørnøya (Svenning et al., 2007, Hawley et al., 2016). We know that the arctic char is active during the winter and foraging in low temperatures (Klemetsen et al., 2003b). A comparative study of the relationship between light intensity and feeding ability in brown trout and arctic char indicate that the brown trout has reduced food intake at lower temperature and light conditions (Elliott, 2011). There is reason to believe that the brown trout also has reduced activity level compared to the arctic char during the coldest months to save energy. Other aspects of overwintering in freshwater such as when they return in the lake after spawning, how long they stay in the lake and what controls the migration to the sea is key elements that we need to understand. More studies of winter behavior in systems containing freshwater resident and anadromous populations of both arctic char and brown trout is important to get a greater understanding of the lifecycle to these two species.

Acoustic technology has made it possible to study the behavior of aquatic organisms in their natural habitat, providing information beyond what can be directly observed (with water binoculars, underwater film, scuba diving) (Kessel et al., 2014). The first studies with acoustic telemetry was conducted in the 1970s, and was based on active tracking of a target organism that carried an acoustic tag (Kanwisher et al., 1974). The method was laborious, but provided one of the only methods to track real-time movements of aquatic organisms (Kessel et al., 2014). In the 1980s, passive acoustic telemetry evolved which made it possible to collect unique data of fish behavior without the same manpower needed (McKibben and Nelson, 1986, Klimley et al., 1988). In passive acoustic telemetry studies, one or multiple receivers with battery are deployed into the study area. The receivers are constantly logging signals from acoustic tags mounted to the candidate animals for the study. Detections are stored in the receiver until their downloaded and used in later analysis (Kessel et al., 2014). This technology is well suited to study behavior on species like brown trout and arctic char during the winter months (Bass et al., 2014, Hawley et al., 2016), providing new information that previously was impossible to retrieve.

The population of both arctic char and brown trout in the watercourse of Botn has never been studied before. Besides aquaculture in Skjerstadfjorden where Botnelva connects the system to the sea, the area is kept relatively untouched by human impact. This makes the whole system suitable to use as an important reference to how populations of both brown trout and arctic char utilize and overwinter in freshwater during the winter.

This is an exploratory study that aims at describing the behavior of sea run arctic char and brown trout that seek refuge in freshwater (lake in particular) during the winter months. Through this study I will try to enlighten and compare the habitat utilization between the two species. More specific I will try to describe 1) how active is brown trout that overwinter in freshwater after spawning compared to the arctic char, 2) how large fraction of the anadromous brown trout population remains in freshwater after spawning, 3) what environmental factors affect initiation of migration to the sea, and finally, 4) is the lake habitat utilization different between the two species.

# 2 MATERIALS AND METODS

## 2.1 Study area

The watercourse Botenvassdraget is located just north of the polar circle in the middle of Nordland county at 74$^{o}$42`N and 52$^{o}$25`E *(Figure 2.1).* The system contains one lake (Botnvatnet) measuring 1.96 km$^{2}$, and two rivers that drain into the lake. The river Knallerdalselva runs into the lake from south east true Knallerdalen, while Ingeborgelva drains to Botnvatnet from northeast *(figure 2.2)*.

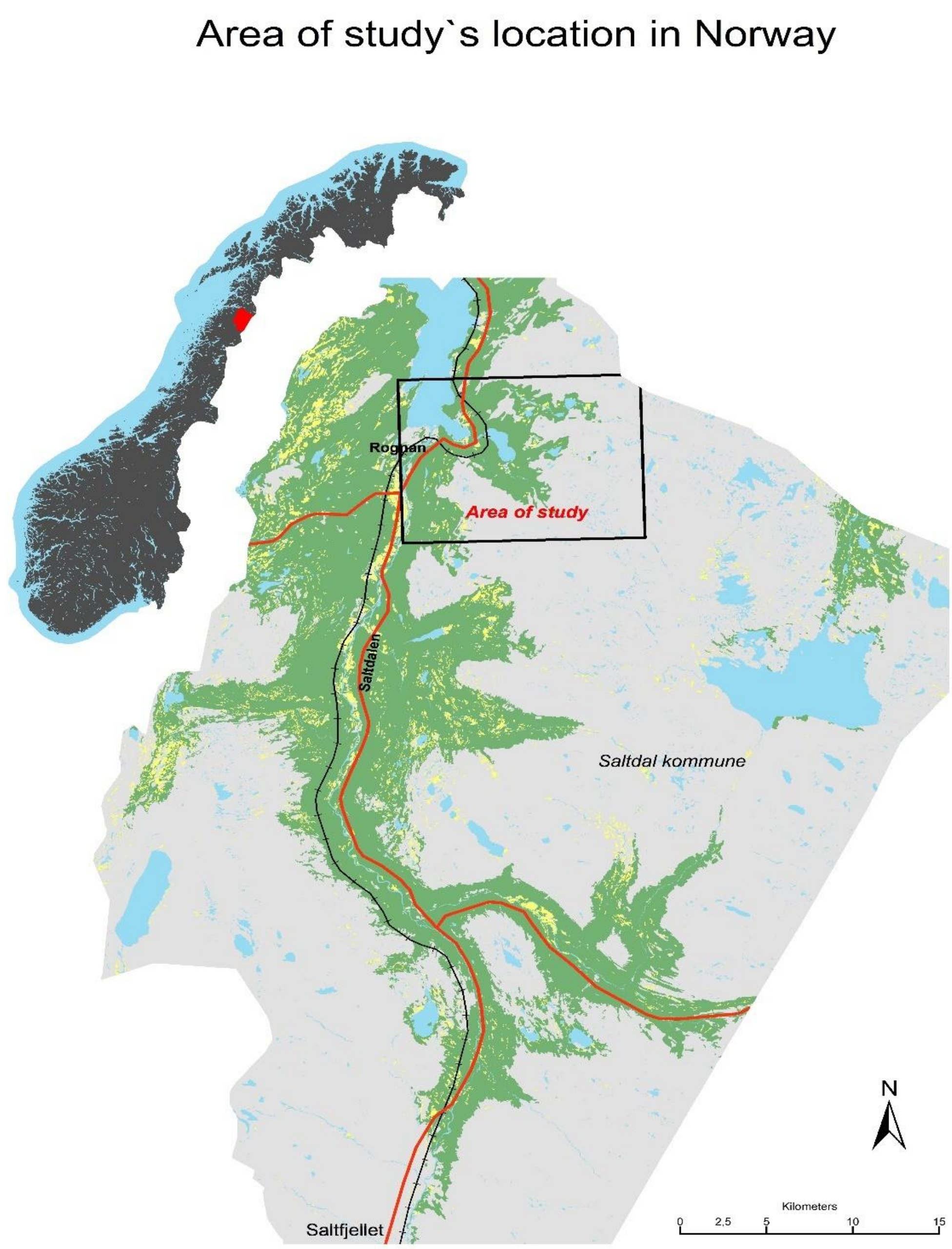


*Figure 2.1: The study areas location in Norway*

From Botnvatnet the main river Botnelva runs out of the lake true a smaller and more shallow part of the lake called Litlevatnet and into the sea in Saksenvika, the inner part of Skjerstadfjorden. The lake is located 12 meters above sea-level, and measures 114 meters at its deepest. Knallerdalselva is the main spawning river in the system, and it`s also here we collected the study-fish. The river is relatively shallow (0.5 – 1 m) with deeper pols (2-5 m) and crystal clear water. Upstream the anadromous part, the river runs fast with whitewater and small waterfalls. The anadromous part of Knallerdaslelva is 3.2 km and has a few rapids with faster flowing water in the upper part, in the lower parts it forms meanders and runs slowly.

The study system is close to pristine with no influence by power plants, dams or agriculture. There is one small road on the east side of the lake which leads to a few houses in the south end where Knallerdalselva runs into the lake. The most important human encroachment of the system is probably fishing as the landowners sell fishing license to the public.

The fjord, Skjerstadfjorden, which some of the fish migrates to is influenced by human activities. Skjerstadfjorden has considerable production of farmed salmon. There are 20 locations for producing food-fish and 12 locations for brood stock production. The production rotates from location to location so that some production locations have no fish production from time to time. There is also two hatcheries for farmed salmon in connection with the fjord (Busch et al., 2014). Other factors that may influence the marine environment in the fjord is sewage discharge and runoff from agriculture (Busch et al., 2014).

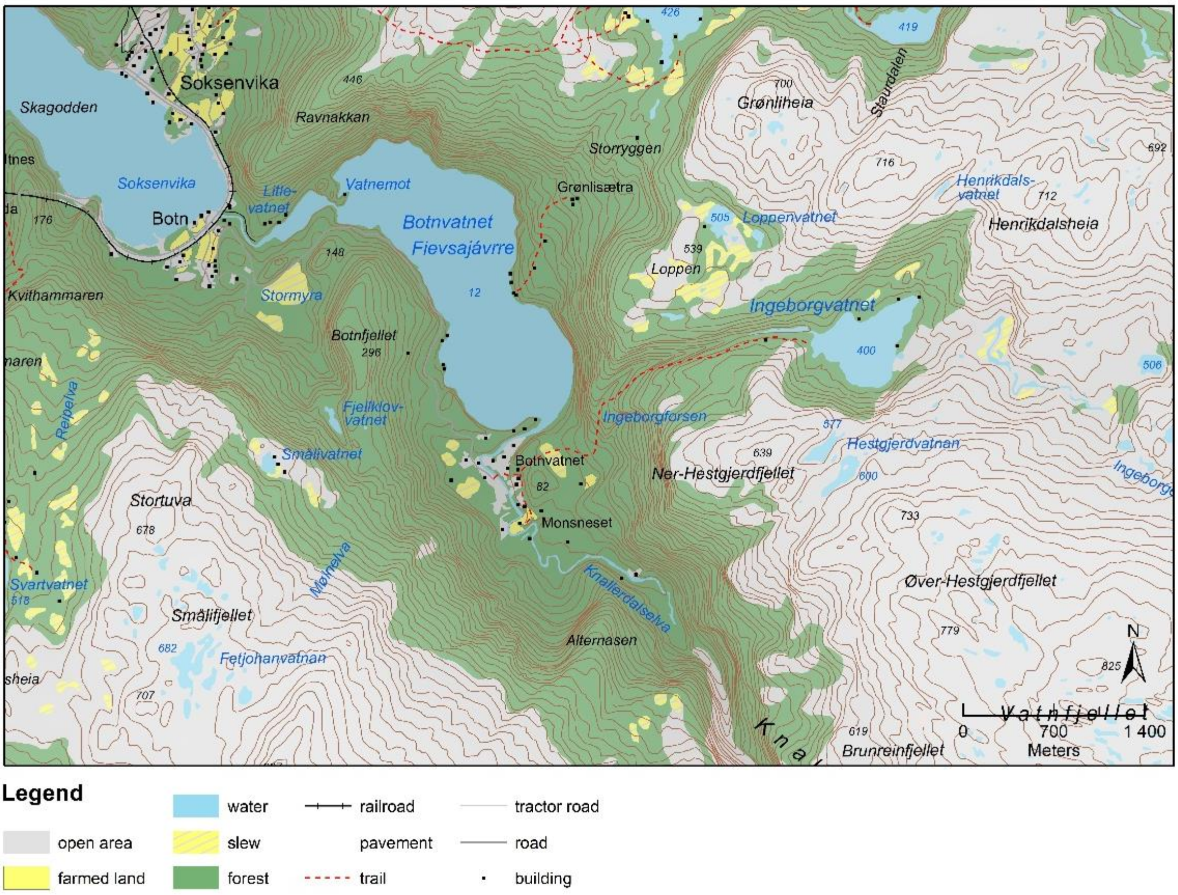


*Figure 2.2 Map showing the study area and its near surrounding area.*

## 2.2 Study species

### 2.2.1 Brown trout

Brown trout is an Atlantic species that natively occurs in Europe, North Africa and the western part of Asia. The species has with help of humans been spread to new countries and continents outside this area, and is considered a global species (Elliott, 1994). The species shows tremendous variation in individual growth rate, size, feeding niche and habitat use within the same population (Pakkasmaa and Piironen, 2001). If conditions as suitable spawning substratum, temperature and water quality is acceptable the species can occupy a variety of habitats covering large rivers, lakes, small tarns, tiny creeks, fjords and coastal waters (Klemetsen et al., 2003a).

Brown trout spawn mostly in running water in the autumn or winter. Time of spawning varies with the water temperature; lower water temperature gives the eggs longer incubation period and earlier spawning dates (Scott and Irvine, 2000). Lake spawning has also been observed in places that are influenced by groundwater influx (Brabrand et al., 2002). Also brackish-water spawning has been observed in the Baltic sea where eggs and young individuals can be able to survive at salinities up to 4-5 ‰ (Limburg et al., 2001) Female specimens dig their nests in stone and gravel substrate on the riverbed. One female is often courted by several competing males, but normally the majority of the eggs are fertilized by one large male (Klemetsen et al., 2003a). Shortly after spawning, the female covers the fertilized eggs with substrate.

The fertilized eggs remains in the gravel even after they hatch as a yolk-sac larvae the following spring. After yolk-sac resorption is completed, the fry , which is around 2 cm in length, emerge from the gravel and starts feeding on drifting invertebrates near the spawning ground. (Klemetsen et al., 2003a). The fry is aggressive, defends a territory and form dominance hierarchies after emerging from the gravel. Those who is unable to catch food may drift downstream in search of better feeding grounds, many of these individuals will probably die (Elliott, 1994) (Lahti et al., 2001).

In systems with connection to the sea the brown trout can form anadromous populations. There is difference in migratory distance among populations because of heredity and environment, but normally the fish stays within 100 km from the mouth of their home river (Klemetsen et al., 2003a, Jonsson, 1985). The migration to the fjord may be for the summer only or they can stay at sea for two years or more before they come back to their home river to spawn (Jonsson and Jonsson, 2002). Some fish chose to stay in freshwater during the cold winter months. By doing this they eliminate risks like predation and parasites that the marine environment inhabits. The water temperature is low in the subarctic lakes during wintertime. This slows down the metabolic rate and energy reserves is exploited more efficient (Jonsson and Jonsson, 2011a).

### 2.2.2 Arctic char

The arctic char is a species that thrives in cold water. It is found throughout the arctic, subarctic, boreal and temperate climate regions of the Holarctic. Most arctic char are found in Scandinavia with around 30,000 populations in Norway and 13,000 in Sweden (Klemetsen et al., 2003a). They are often found in cold lakes with depauperate fish communities. In alpine or northern lakes, it is often the only fish species present. The most northern populations live in lakes that are covered in ice throughout the entire summer most years (Reist et al., 1995). Arctic char probably colonized most areas that were ice-covered during the last glacial times but is currently absent from many lakes in southern parts of these areas. It may be due to climatic reasons (too warm), eutrophication or negative interactions with increasingly complex fish assemblages (Hartmann, 1984, Maitland, 1995, Hammar, 1998).

The arctic char that lives in the northern parts of its range may form anadromous populations *(figure 2.3)* if the lake or river has sea access. The anadromy is complex because both sexually mature and immature fish can migrate to the sea during summer (Nordeng, 1983). This is observed in brown trout as well, but in contrast, the Arctic char cannot survive in saltwater during the wintertime. In a population with three coexisting forms of arctic char (anadromous, small and large freshwater residents) all individuals can belong to the same gene pool, even the same parents. Parr of each form segregate into all three forms, and individuals may manifest all tree forms during their lifetime (Nordeng, 1983). Studies from the island Senja in the north of Norway (Jensen and Berg, 1977) and in Nauyuk, Canada (Gyselman, 1984) show that the arctic char stay in the sea for approximately six weeks. The largest individuals descend first, right after ice out. The main population migrates from early May to the middle of June. Arctic char stays close to the home river while they are at sea. On Senja, the annual survival rate for the migrating population was 0.50, but they found significantly lower survival for smaller fish (Jensen and Berg, 1977). The benefits of migrating to the sea is more pray to feed on which results in increased body size and fitness. In Nauyuk the arctic char had a mean weight gain of 42% during the weeks at sea (Rikardsen et al., 2007, Rikardsen and Amundsen, 2005, Gyselman, 1984).

The maturation pattern varies extremely among populations and individuals. Documentation of mature arctic char covers individuals from 3 g to 12 kg or more for both sexes (Klemetsen et al., 2002). Such a difference between the smallest and the largest adults is found in very few, if any, other species of fish. The size variation in the Arctic char can be explained with the large variation in habitat, niche shifts, migration and other ecological traits of the species (Klemetsen et al., 2003a). Normally the species spawn in lakes although some individuals or populations may spawn in rivers (Klemetsen et al., 2003a).

*Figure 2.3: Anadromous arctic char caught in the sea*

## 2.3 Fish capture and tagging:

The fish were sampled while they were in the river Knallerdalselva to spawn (*figure 2.4).* We tested different methods for capturing the fish; gillnets, fly fishing, regular fishing rod with lures and headlamp and dipnets. The sea trout were caught with small-meshed gillnets *(figure2.5)*, while the arctic char where captured with headlamp and landing net at nighttime. We held the fish in keepnets until the tag were implanted. The first species to arrive was the brown trout. This occurred in the middle of September. We started capturing the fish at 22.09.2016 and tagged them on 24.09.2016. The arctic char arrived at the spawning grounds in the middle of October and were tagged on the 19.10.2016 and 20.10.2016.

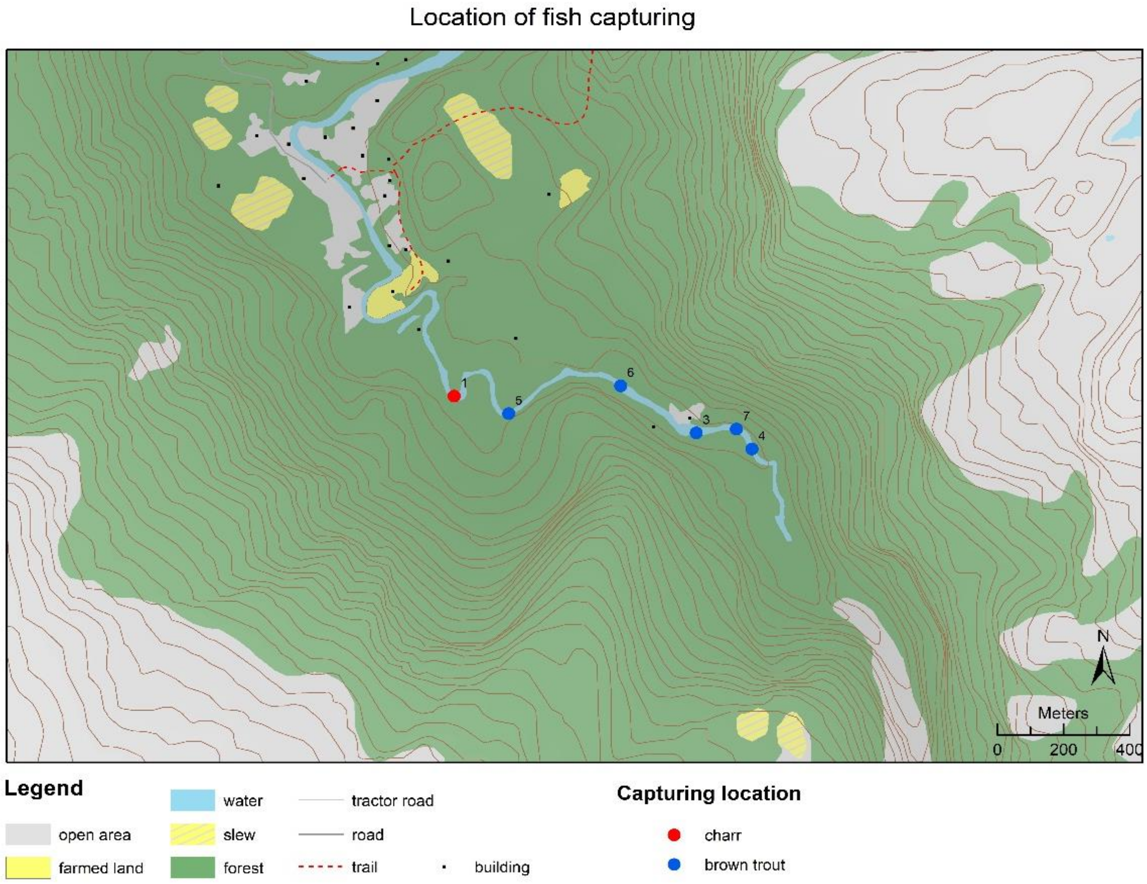


*Figure 2.4 Capture, tagging and release sites in Knallerdalselva for the brown trout and arctic char individuals that were included in the study. The red and blue dots show arctic char and brown trout locations, respectively.*

*Figure 2.5 Fish capturing with gillnets in Knallerdalselva*

## 2.4 Brown trout

In the deeper pools of the river two persons were walking with the same speed as the current downstream with the gillnet. In shallower parts the gillnet was stretched across the river and 2-3 persons walked on a line towards it scaring the fish into the net.

When fish got caught it was gently cut out of the net and put in a keepnet until the tagging procedure took place.

The tagging followed the general recommendations given by Mulcahy (2003) and was done by my co supervisor Torstein Kristensen from Nord university. I assisted him with sterilized tools and fish handling before and after surgery. The brown trout were anesthetized one at the time in a 60 L plastic tank containing 60 mg $l^1$ MS 222 (tricaine methane sulphonate) anesthetic. When the fish showed signs of full anesthesia (belly up, gentle ventilation, no reflex reaction when gently squeezing the caudal peduncle) it was length measured (total length, mm) and weighted (g). After this, the fish was put into a U-shaped tube that was about 80 cm long and 15 cm diameter *(figure 2.6)*. Wet rags were used to adjust the fish into a good position to perform the surgery. During surgery, the fish were ventilated by pumping aerated water containing 40 mg $l^{-1}$ MS 222 constantly over the gills. The fish got equipped with id-coded acoustic transmitters (ADP-LP-13, length 31mm, diameter 13 mm, weight in air 9.7 g, weight in water 5.7 g, power output 150 dB re 1µPa at 1 atm; Thelma Biotel AS, www.thelmabiotel.com). All tags were equipped with depth sensors. The tag was implanted to the abdominal cavity of the fish anteriorly to the pelvic fin-bone through a 1.5-2 cm long incision. The incision was closed by a single-layer, simple interrupted suture pattern using monofilament material (Resolon, 3/0 usp; www.resorba.com)(Mulcahy, 2003). The surgical area was sealed using tissue adhesive (Histoacryl; www.tissueseal.com). A small piece of the adipose fin was removed and stored in 96 % alcohol, for genetics analysis. Scales (1-3) were gently collected from right below the adipose fin and filed in individ.specific paper envelopes.

After surgery, the fish were put in a 60 l plastic container filled with fresh water and monitored until they gained consciousness. When they were fully recovered, the fish was released back into the river. An acoustic receiver (TBR700) were placed in the holding tank to confirm that the transmitters were correctly activated.

## 2.5 Arctic char:

The arctic char was captured at nighttime in one pool of the river Knallerdalselva. In total 21 individuals were tagged. To capture the fish, powerful headlamps and big landing nets were used. Two persons walked slowly in the river looking for fish. When the char was lit with the headlamp it got paralyzed for a short moment and it was possible to catch them with the landing net. The fish were gently placed in a keepnet before tagging.

The surgical procedure was conducted by Sindre Eldøy and Aslak Sjursen from NTNU which I cooperated with during my fieldwork. The fish were put into a 60 liter container, anaesthetized with 2-phenoxyethanol (EC No. 204-589-7; SIGMA Chemical Co., USA; 0.5 mL·$L^{-1}$ water). When the fish showed signs of full anesthesia (belly up, gentle ventilation) it was measured, weighted and the gender was confirmed **Error! Reference source not found.**. The fish got surgically implanted with the same acoustic tag as the brown trout. A 1.5–2 cm incision was made in the body cavity on the ventral surface anterior to the pelvic girdle. The incision was closed by 1-3 stitches of simple interrupted suture pattern using monofilament material (Resolon, 3/0 usp; www.resorba.com). During surgery the fish were constantly ventilated by pouring water from a cup over the gills. All fish were externally tagged with a modified carlin tag providing the address and phone number to the project leader.

The fish were placed into a 60 liter holding tank containing fresh water to wake up from the anesthesia (3-5 minutes). When the char was fully recovered it got released in a calm part of the river close to the capture site.

*Figure 2.6: picture showing an arctic char ready to get surgically implanted with an acoustic tag*

## 2.6 Monitoring:

A network of 20 TBR700 receivers produced by Thelma Biotel A/S that receive signals at 69 kHz were deployed in Botnvatnet to monitor the tagged fish *(figure 2.7)*. An additional two receivers were deployed in Knallerdalselva (spawning river) and one receiver in Botnelva to monitor the movement in and out of the lake. The receivers in the rivers were mounted on metal anchors that were placed on the riverbed with the hydrophones pointing upwards.

*Figure 2.7: Picture of how the TBR receiver deployed in the rivers were mounted*

The receivers were constantly logging transducer signals sent from acoustic transmitters operated into the fish. A mooring was made with concrete rocks anchored to the bottom and an 8 mm braided rope to a buoy on the surface. Two meters of stainless-steel chain with shackles connected the rope to the mooring rock. The buoy was deployed at 1-2 meters below the surface so that the ice sheet could not move or destroy the mooring. Receivers were mounted on the rope with strips about 1 meter below the buoy with the hydrophone pointing downwards. The receivers were distributed in a way that gave a good coverage of the lake, and close enough so that we could triangulate the signals that were sent from acoustic transmitters inside the fish (*figure 2.8)*. The receivers collected data from 24.09.16 until they ran out of battery in July 2017.

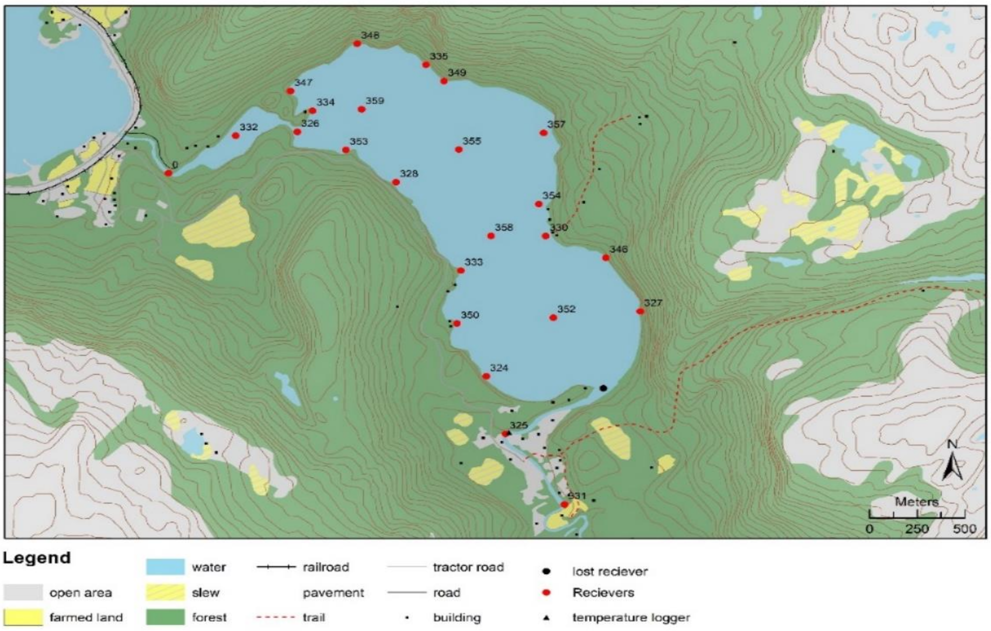


*Figure 2.8: Map showing the individual TBR receivers' location in the study system. Numbers indicate TBR IDs.*

## 2.7 River water temperature data

A combined HOBO water temperature and pressure logger (https://www.onsetcomp.com/products/data-loggers/u20-001-04) was deployed to measure both the temperature and the water level (hence the pressure), measured every sixth hour throughout the study period *(figure 2.9)*. The logger was placed in Knallerdalselva, logging physical data on the water that came into the lake. These data where downloaded to a computer and included in further data analyses.

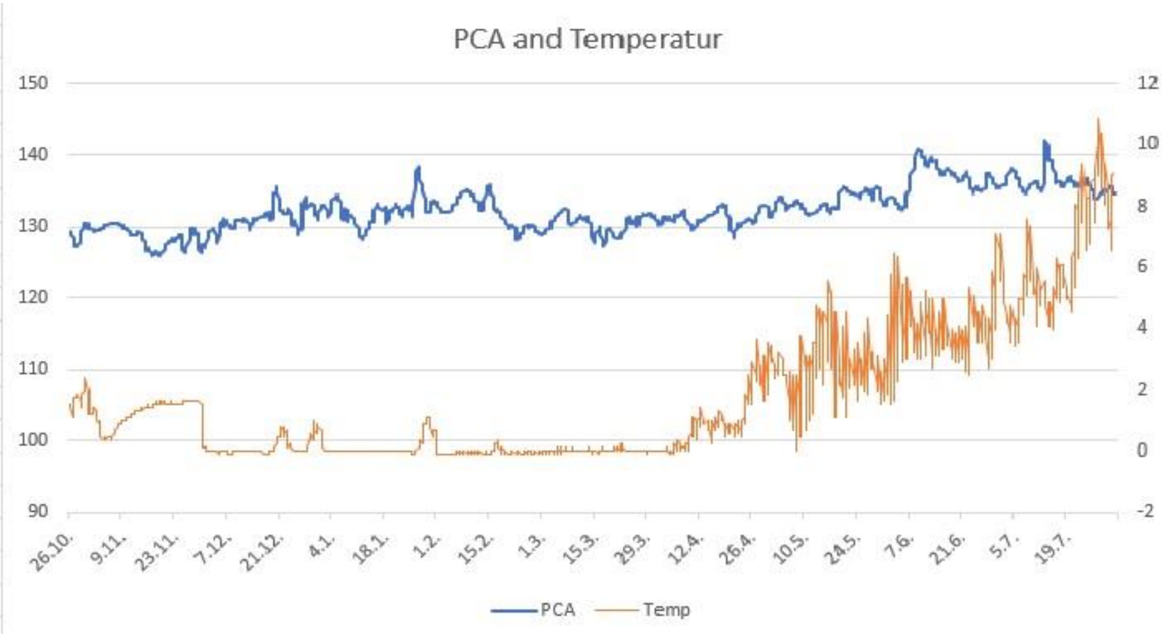


*Figure 2.9: The blue graph is showing the external pressure (kPa) while the orange graph shows the water temperature during the study period.*

## 2.8 Weather station data

Average precipitation, snow depth and average temperature was collected from the met.no eklima service (eklima.no) *(figure 2.10)*. The weather station that was used is placed in Setså (67°09'54"N 15°29'20"E), approximately six km from the study area. The data collected was from 19. September 2016 to 31. October 2017.

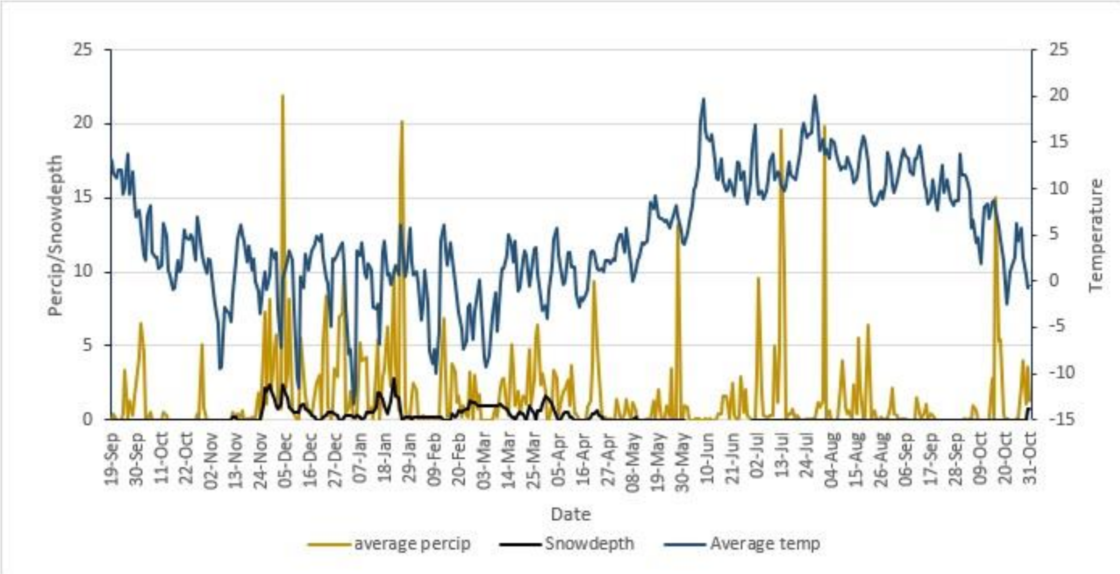


*Figure 2.10 : graph showing average precipitation, snow depth and average temperature during the study period for the Setså Meterological station (met. Station number: 82000)*

## 2.9 Migration to sea

Transmissions received in Saksenvika (by receivers mounted by Jan Grimrud Davidsen and collegues at NTNU) for the individual fish was extracted to confirm migration to the sea.

## 2.10 Spawning

Since fish were captured and tagged in their spawning river, estimations for when the fish started their migration up the river Knallerdalselva were unattainable. The end of the spawning period however was determined based on when the receivers started receiving transmissions from the individual fish in the lake.

## 2.11 Detailed habitat use

In this study, 21 TBR receivers with omni-directional hydrophones were deployed into the lake. The receivers were deployed relative to each other so that the ping signal from the fish could be detected by multiple hydrophones on the surface. The receivers probability to detect a transmitters signal is according to Simpfendorfer (2002) linearly related to its distance to the receiver. This means that the number of receptions over a given time period (here 10 minutes) is higher when the source signal is closer to the hydrophone. When a signal is detected by multiple receivers it is possible to estimate the signal source distance relative to each hydrophone by counting how many detections hydrophones receives from this single transmitter. From this, an average estimate of the transmitters position (a so-called PAV) over this 10-minutes time slot could be made. The number of received signals and hydrophones involved increases the accuracy of the estimated position (Simpfendorfer et al., 2002). I used these PAVs to estimate key space-use metrics such as the utility distributions ("home range"), distance moved and delta displacement (distance moved/"home range") for the individual fish.

All the individuals in my study was equipped with dept sensors which made it possible to estimate volumetric utilization throughout the winter. The volumetric utilization was conducted by adding z (depth) as a new variable to the existing XY-average position data. The mean depth position within every 10-minute timeslots was used to combine with the corresponding estimated PAVs. Using the R packages adehabitatLT and adehabitatHR, estimates of daily swum distances and daily 50% and 95% utilization distributions (UD50 and UD95) could be estimated, respectively (Calenge, 2006).

Univariate linear mixed effect models (LME), (Zuur et al., 2009) was fitted to explore and quantify temporal and individual characteristics' effects on the space-use trait variables (depth, UD50, UD95, distance and delta displacement. This was done by fitting trait-specific fully factorial linear mixed effects models according to the following general model:

$$y_{i,t} = \alpha_{S,G,M} + \beta_{S,G,M} L_i + a_i + \varepsilon_{i,t}$$

, where *y* represents the respective space use variables, L = length, M = month, G=gender, S= species and a is a random intercept factor (for taking within-individual data dependency into account) and $\varepsilon$ is the independent random residual variation. $\alpha$ represent intercept estimates and $\beta$ represent slope estimates. Model validation was conducted by exploring residual plots. The models were fitted using the lme4 package in R (Bates et al., 2014).

To quantify effects from water temperature and water level (i.e., discharge), candidate models of daily migration data to Saksenvika (see paragraph 3.11) was fitted for Arctic charr. Unfortunately, too few detections were registered to fit a similar model for brown trout. The candidate models were fitted as generalized linear models GLM (McCullagh and Nelder, 1989, McCullagh and および JA) under an assumption of binomial distribution where the response constituted of daily values of migrants divided by the corresponding values of individuals available for migration (i.e., number of individuals that eventually would migrate (and get registered) minus cumulated number of migrants). Both temperature and water level were included in some candidate models as quadric effects (i.e., temperature$^2$ and (water level)$^2$) to allow for fitting possible maximum or minimum effect values. The candidate models constituted combinations of single effect, additive and multiplicative effects of the two environmental variables, and model selection was undertaken by using Akaike's information criterion (AIC, (Akaike, 1974) following routines outlined in Zuur et al. (2009).

# 3 RESULTS

All the 40 tagged individuals included in this study survived the surgery and sent signals that was stored in TBR receivers deployed in the lake. All the TBR receivers worked perfectly except from one which got lost during the project. Results from the post-spawning migration also includes fish tagged by NTNU, it was 82 individuals in total.

## 3.1 Migration from Knallerdalselva to Bottenvatnet

All the tagged individuals returned to the lake after spawning within a five-day period during 22-27 October *(figure 3.1)*. 67 out of 82 tagged individuals of both species returned to the lake on the same day (22.10). There was no clear relationship between post-spwaning migration timing and changes in airtemperature or precipitation. The full spawning migration period was not covered by this study since the fish was captured and tagged in Knallerdalselva after the upstream migration had taken place.

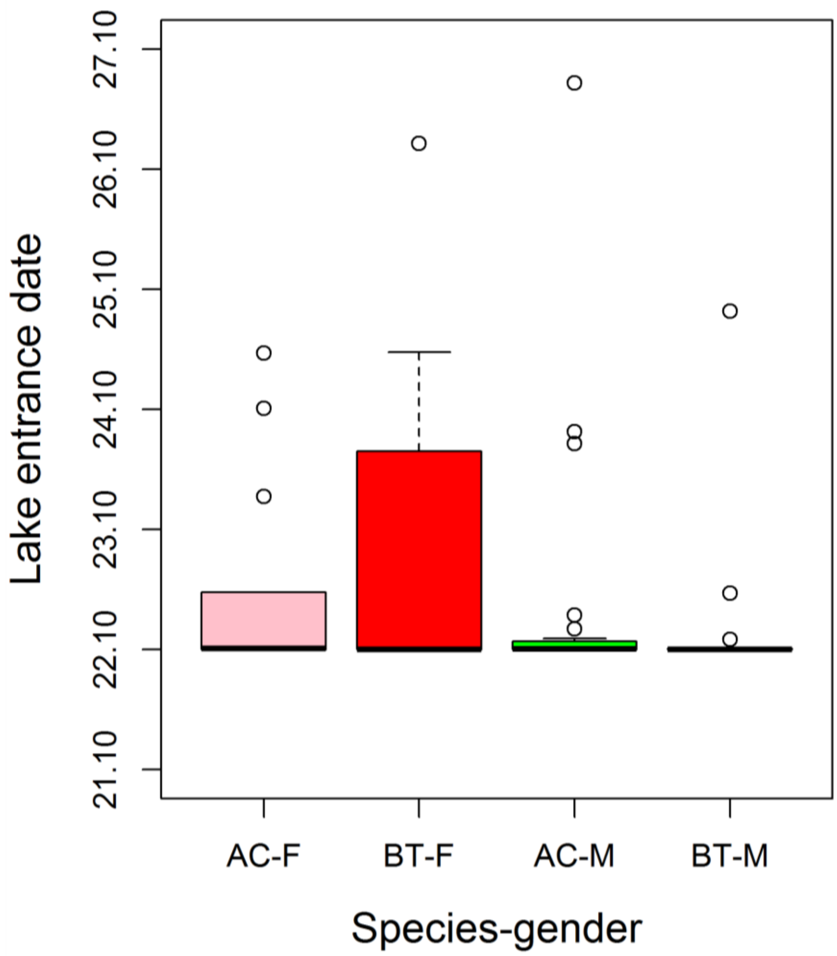


*Figure 3.1 Boxplot of timing of first detection of tagged fish after it returned to Botnvatnet from Knallerdalselva. AC-F = arctic char female, BT-F = brown trout female, AC-M = artic char male and BT-M = brown trout male. The boxes include 50 % of the observations, the thick horizontal line witin the boxes represents the median and whiskers 10 and 90 % percentiles.*

## 3.2 Swimming distance while in lake

The data revealed that most of the fish swam a great distance, the most active individuals for some periods swam 75-80 kilometers a day *(Figure 3.2 and 3.3).* During the coldest months (November-March) the Arctic charr was most active with an average swimming distance of 30 kilometers every day. There was no appreciable difference in swimming distance between the genders. The brown trout had an average swimming distance of 20 kilometers a day during the same time. During November and December, the female brown trout swam shorter than the male brown trout.

The fully factorial LME model fitted to swimming distance data revealed that the body length effect on swimming distance was significantly different between species and sexes among months *(Table 1, Figure 3.3)*. In arctic char body length had a positive effect on swimming distance for the male individuals. In the females, the effect of body length was the opposite: increased body length resulted in decreased swimming distance. The effect of body size within the tagged individuals of brown showed that increased body length resulted in longer daily swimming distance among the females, while the body length of the males made no large difference in swimming distance.

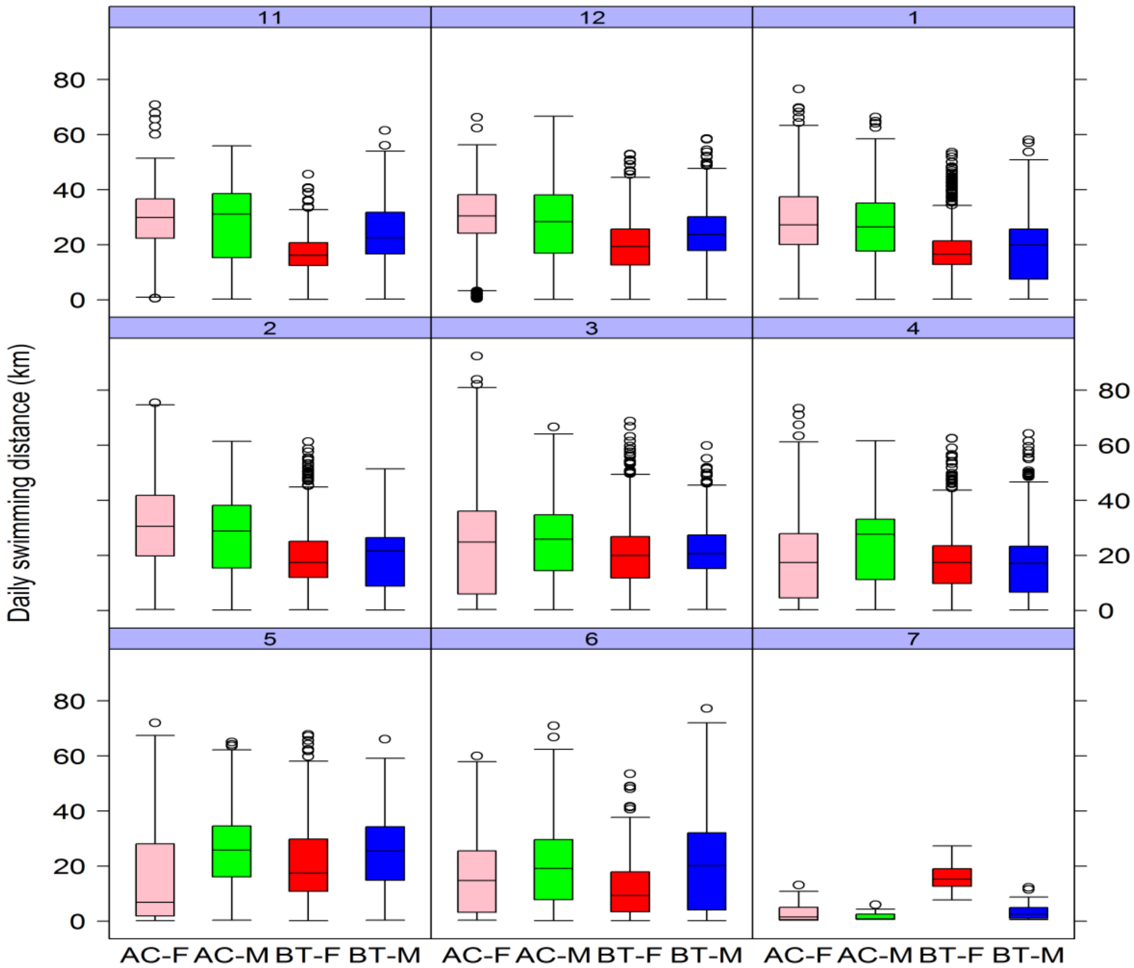


*Figure 3.2: Box plot showing monthly distributions of daily swimming distance (km) of the fish during the study period. Numbers in figure headers display month number. AC-F = arctic char female, AC-M = arctic char male, BT-F = brown trout female, BT-M = brown trout male.*

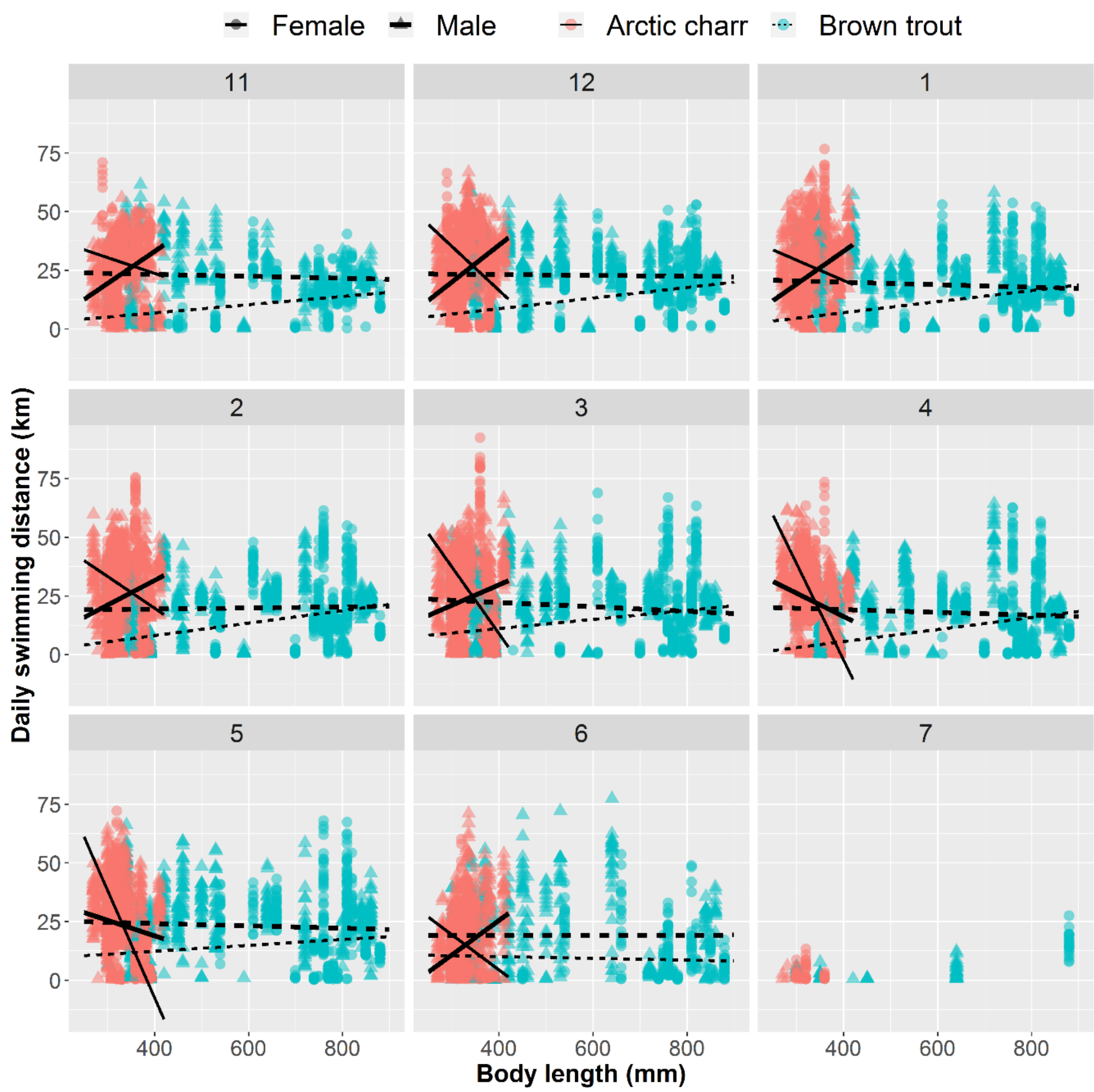


*Figure 3.3: Scatterplot showing daily swimming distances of the tagged fish during the study period as function of body length, species, sex and month. Lines represent model predictions for the fully factorial LME-model presented in Table 1 (and in Appendix table 1), where dashed lines are for brown trout and solid lines for Arctic charr and fat lines for males. Numbers in figure headers display month number (11 = November 2016 and so on).*

*Table 1: Anova tests statistics of the fully factorial mixed effects model fitted to estimate effects on daily swimming distance in brown trout and arctic char*

| Term | $\chi^2$ | Df | p |
|---|---|---|---|
| Length | 0.23 | 1 | 0.63 |
| Species | 2.66 | 1 | 0.10 |
| Sex | 0.82 | 1 | 0.37 |
| month | 677.47 | 7 | <0.0001 |
| Length*Species | 0.07 | 1 | 0.79 |
| Length*Sex | 0.31 | 1 | 0.58 |

| | | | |
|---|---|---|---|
| Species*Sex | 3.17 | 1 | 0.07 |
| Length*month | 64.16 | 7 | <0.0001 |
| Species*month | 118.77 | 7 | <0.0001 |
| Sex*month | 80.02 | 7 | <0.0001 |
| Length*Species*Sex | 8.04 | 1 | 0.00 |
| Length*Species*month | 699.93 | 7 | <0.0001 |
| Length*Sex*month | 20.15 | 7 | 0.01 |
| Species*Sex*month | 25.88 | 7 | <0.0001 |
| Length*Species*Sex*month | 53.75 | 7 | <0.0001 |

## 3.3 50 and 95 % Utilization distribution (UD50, UD95)

### 3.3.1 50% utilization distribution

Estimates of 50% utilization distribution of the different species and genders *are shown in figure 3.4*.

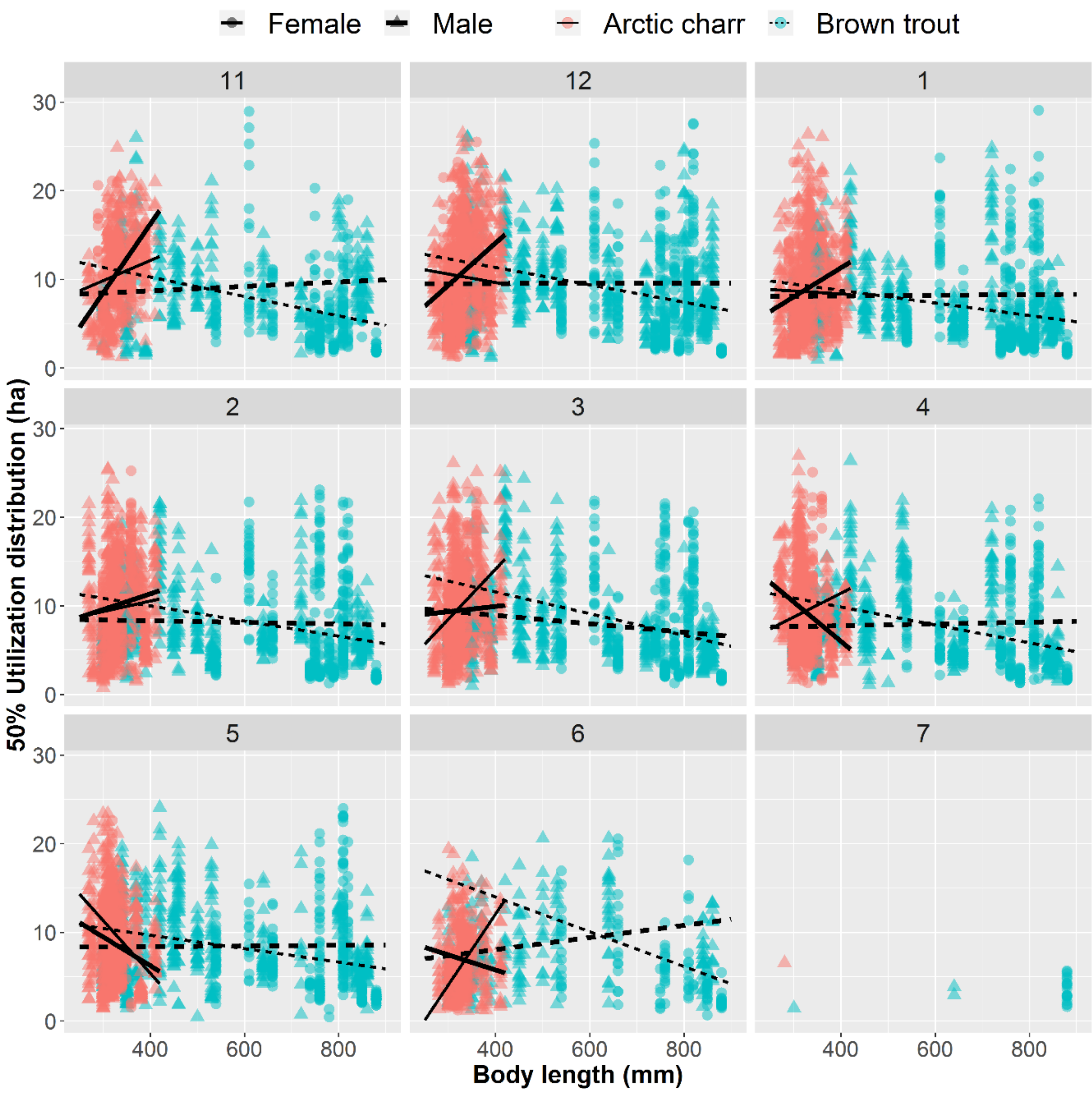

*Figure 3.4: Scatterplot showing monthly distributions of daily 50 % utilization distribution areas of the fish during the study period. Lines represent model predictions for the fully factorial LME-model presented in Table 3 (and in Appendix table 2), where dashed lines are for brown trout and solid lines for Arctic charr and fat lines for males. Numbers in figure headers display month number.*

Utility distribution 50% estimation from both genders of the arctic char and brown trout in the lake reviled that the arctic char has the largest home range. During November – March the arctic char has a daily utility distribution area of 10 hectare (mean±SD). During April and May, the home range decreases to eight hectares. The males utilization area were slightly larger than the females, but the difference is small. The difference in home range size between the genders of the brown trout is considerable larger during the study period. Female brown trout utilize an area of approximately 5 hectares while the males utilizes 8 hectares.

Parameter estimations of the most supported utility distribution 50% model showed that the factors species, sex, month and length was important influences on the utilization distribution *(table 2)*. The effect of length has complicated interactions and varies from month to month between species and genders.

Table 2: Anova tests statistics of the mixed effects model fitted to estimate effects on 50% utilization distribution in brown trout and arctic char.

| Term | $\chi^2$ | Df | p |
|---|---|---|---|
| Length | 0.228 | 1 | 0.63 |
| Species | 1.121 | 1 | 0.29 |
| Sex | 0.715 | 1 | 0.40 |
| month | 310.040 | 7 | <0.0001 |
| Length*Species | 1.294 | 1 | 0.26 |
| Length*Sex | 2.620 | 1 | 0.11 |
| Species*Sex | 1.358 | 1 | 0.24 |
| Length*month | 39.992 | 7 | <0.0001 |
| Species*month | 68.396 | 7 | <0.0001 |
| Sex*month | 43.003 | 7 | <0.0001 |
| Length*Species*Sex | 0.376 | 1 | 0.54 |
| Length*Species*month | 301.341 | 7 | <0.0001 |
| Length*Sex*month | 23.786 | 7 | <0.001 |
| Species*Sex*month | 14.690 | 7 | 0.04 |
| Length*Species*Sex*month | 93.477 | 7 | <0.0001 |

### 3.3.2 95% utilization distribution

Estimates of 95% utilization distribution of the different species and genders are shown in figure 3.5.

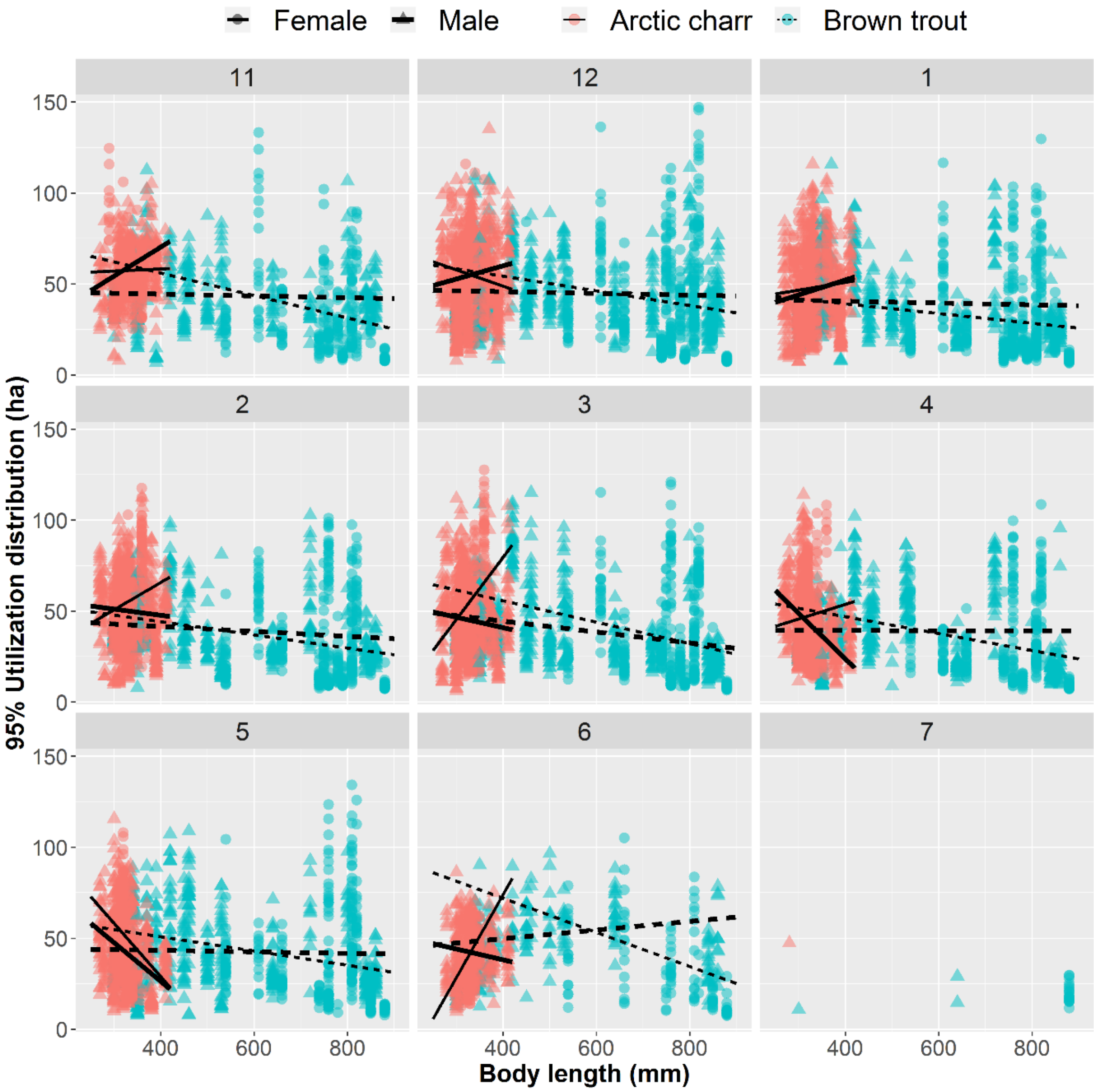


*Figure 3.5: Scatter plot showing monthly distributions of daily 95 % utilization distribution area of the tagged fish during the study period. Lines represent model predictions for the fully factorial LME-model presented in Table 3 (and in Appendix table 3), where dashed lines are for brown trout and solid lines for Arctic charr and fat lines for males. Numbers in figure headers display month number.*

Plots of the estimated 95% utilization distributions of the fish was affected by various factors such as month of the year, species, body length and gender. During the coldest months arctic charr utilized the largest home range of roughly 95 hectares. As the spring unfolded the home range size decreased. The 95 % utilization distribution area of the brown trout varied much between the individuals and between the months. Some brown trout`s utilized an area of 120-150 hectars while others utilized 30-50 hectars.

Parameter estimates of the fully factorial 95 % utilization distribution LME model showed that there was a significant interaction effect between length, sex, month and species, indicating that the length effect on utilization distribution area varied among months, sex and species *(table 3)*. The LME model predicted that there was a negative length effect in 95 % utilization distribution of female brown trout (i.e., large individuals used smaller UD95`s) throughout the study period. The predicted length effect on male brown trout was weak and varied from month to month. During the first three months of this study (November-January), the length effect of female arctic char was positive on the UD95 (i.e., large individuals used larger UD95`s than the smaller individuals). After January however, the model predicted that large body size of the females decreased the 95 % utilization distribution. The model predictions of the male arctic char were variating between the months. From January to April the predictions estimated that large body size increased the UD95, before it shifted again in May predicting that large body size decreased the home range.

*Table 3: Anova tests statistics of the mixed effects model fitted to estimate effects on 95 % utilization distribution in brown trout and arctic char.*

| Term | $\chi^2$ | Df | p |
|---|---|---|---|
| Length | 1.096 | 1 | 0.30 |
| Species | 0.637 | 1 | 0.42 |
| Sex | 0.017 | 1 | 0.90 |
| month | 381.175 | 7 | <0.0001 |
| Length*Species | 0.003 | 1 | 0.96 |
| Length*Sex | 1.113 | 1 | 0.29 |
| Species*Sex | 0.286 | 1 | 0.59 |
| Length*month | 43.189 | 7 | <0.0001 |
| Species*month | 149.386 | 7 | <0.0001 |
| Sex*month | 97.760 | 7 | <0.0001 |
| Length*Species*Sex | 0.025 | 1 | 0.88 |
| Length*Species*month | 230.915 | 7 | <0.0001 |
| Length*Sex*month | 34.650 | 7 | <0.0001 |
| Species*Sex*month | 34.084 | 7 | <0.0001 |
| Length*Species*Sex*month | 115.495 | 7 | <0.0001 |

## 3.4 Delta displacement

There was large variation in the swimming activity within the home range, i.e., the delta displacement, among individuals in both species throughout the study period and the delta displacement appeared as increasing with size in both species *(figure 3.6)*.

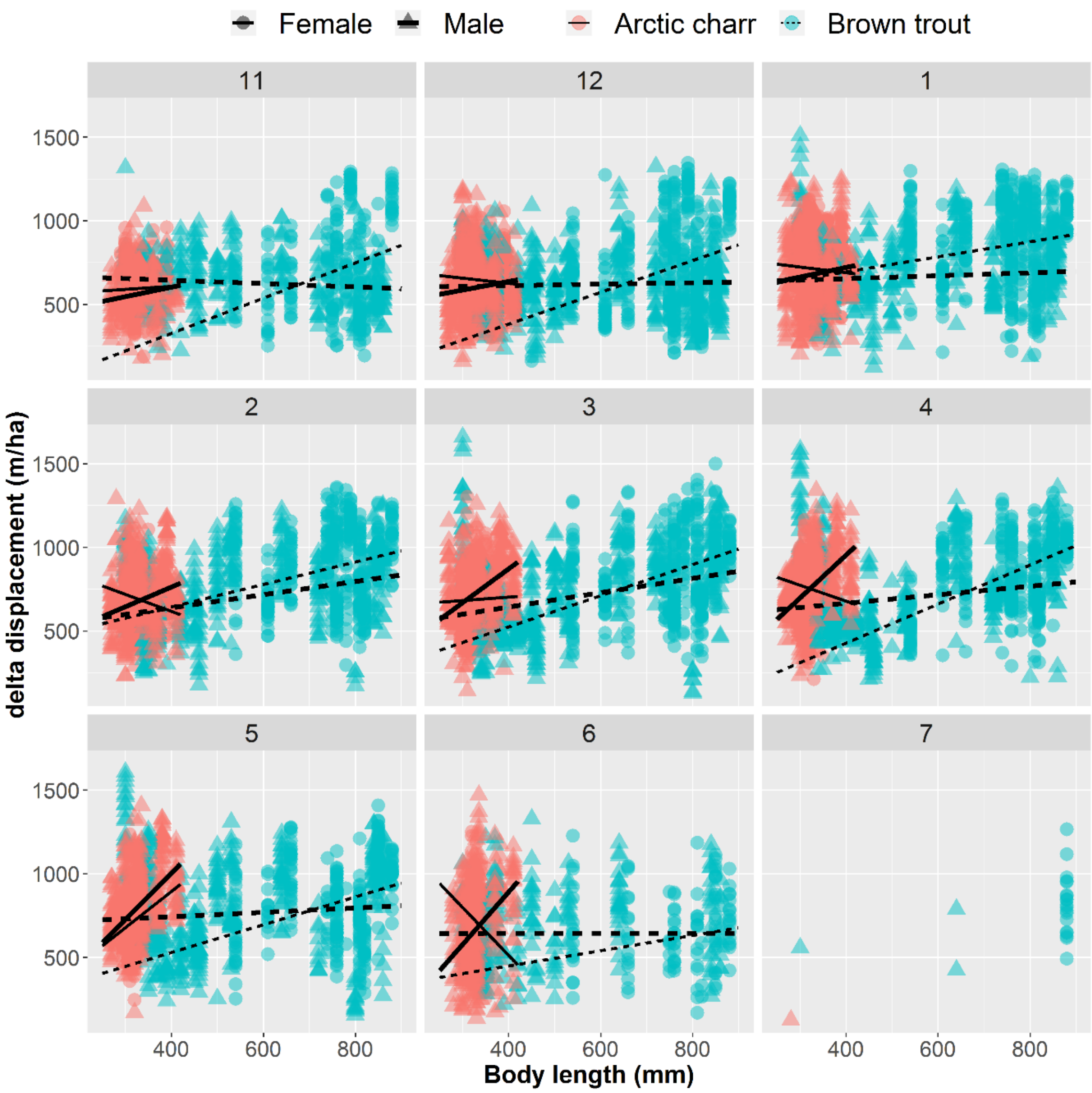


*Figure 3.6: Scatterplot of monthly distributions of the delta displacement as function of species, sex, month and body length to the tagged fish during the study period. Lines represent model predictions for the fully factorial LME-model presented in Table 4 (and in Appendix table 4), where dashed lines are for brown trout and solid lines for Arctic charr and fat lines for males. Numbers in figure headers display month number.*

The fully factorial delta displacement LME model revealed a significant interaction effect between species, sex, month of year and body on the delta displacement *(Table 4, figure 3.6)*. The model predicted delta displacement to increase with body size for female brown trout throughout all months whereas the males were estimated to have less pronounced size effect. This sex-related size effect was the opposite in Arctic charr where males had the most pronounced size effect on delta displacement.

*Table 4: Anova tests statistics of the mixed effects model fitted to estimate effects on delta displacement in brown trout and arctic char.*

| Term | $\chi^2$ | Df | p |
|---|---|---|---|
| Length | 6.7 | 1 | 0.01 |
| Species | 3.0 | 1 | 0.08 |
| Sex | 0.3 | 1 | 0.62 |
| month | 1027.9 | 7 | <0.0001 |
| Length*Species | 1.1 | 1 | 0.29 |
| Length*Sex | 3.6 | 1 | 0.06 |
| Species*Sex | 2.1 | 1 | 0.15 |
| Length*month | 98.3 | 7 | <0.0001 |
| Species*month | 120.2 | 7 | <0.0001 |
| Sex*month | 87.5 | 7 | <0.0001 |
| Length*Species*Sex | 1.9 | 1 | 0.17 |
| Length*Species*month | 105.1 | 7 | <0.0001 |
| Length*Sex*month | 53.1 | 7 | <0.0001 |
| Species*Sex*month | 70.0 | 7 | <0.0001 |
| Length*Species*Sex*month | 30.7 | 7 | <0.0001 |

## 3.5 Depth use

Figure 3.7 shows that the arctic char utilizes deeper water (12-15 meters median depth) than the brown trout (3-5 meters median depth) from November to the end of February. Both species tend to stay deeper during wintertime and slowly ascend during the spring. From March until the end of May the brown trout utilized a mean depth of one meter, while the arctic char`s mean depth varied from ten to eight meters until the end of June. The brown trout that remained in the lake during June utilized a mean depth of 4-5 meters. There was no clear difference in depth utilization between the sexes of the same species. Some individuals of both arctic char and brown trout performed deep dives (>30m) during this study. The arctic char had this behavior throughout the study period while the brown trout tended to perform these dives during the spring when the median water temperature was higher.

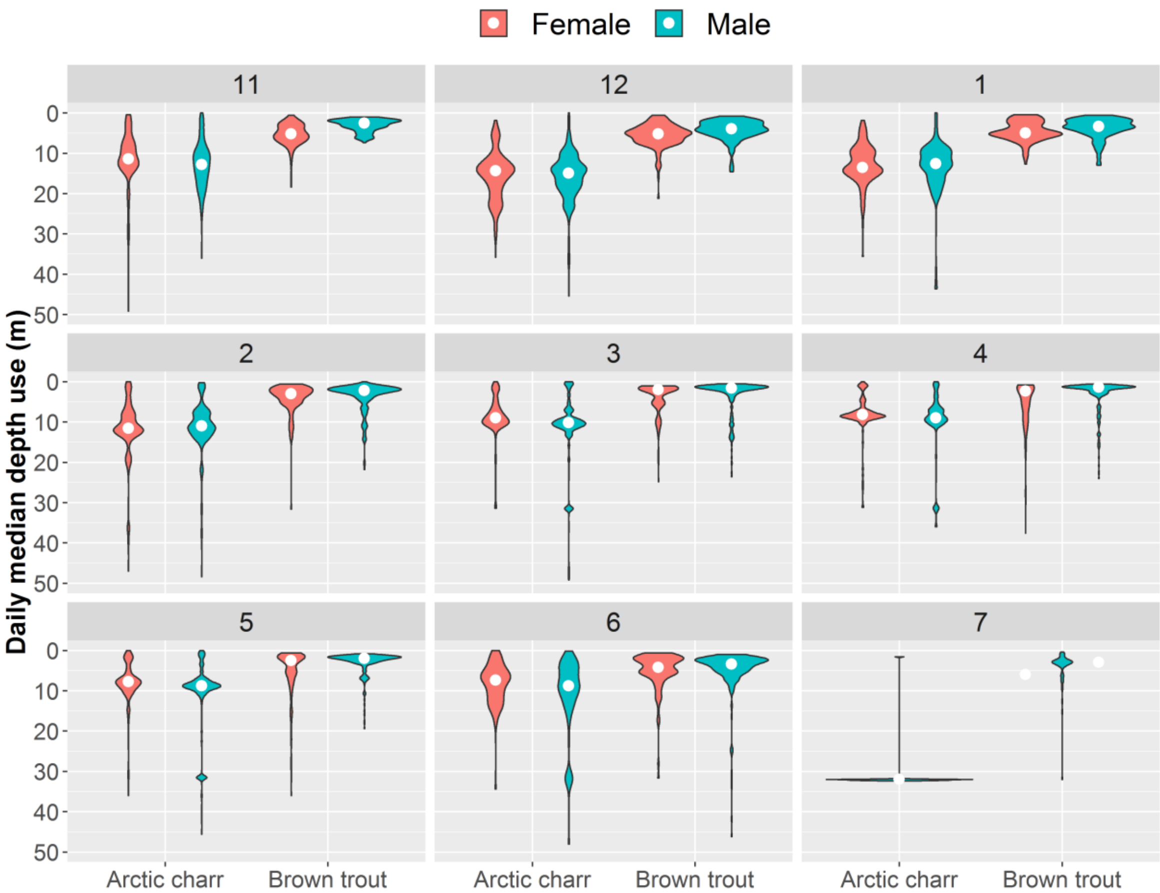


*Figure 3.7: Average daily depth use of brown trout and arctic char divided into months throughout the study period. Number in figure headers display month number. The numbers on the left side of the figure represent depth in meter.*

The fitted fully factorial LME model showed that there was a highly significant interaction effect between length, sex, species and month, indicating that the length effect on depth use varied among moths and sex and species *(table 5).* The LME model predicted that length effect was very weak and pretty much the same between the two brown trout sexes during the November to March period, after which the females started to deviate from the males to initiation of fjord descent. In Arctic charr, females showed a negative length effect on depth use (i.e., large individuals used shallower water layers) throughout the study period (apart from February), whereas the length effect varied from month to month in the male conspecifics *(figure 3.8)*.

*Table 5: Anova tests statistics of the fully factorial mixed effects model fitted to estimate effects on daily median depth use data in brown trout and arctic char. Df = degrees of freedom.*

| Term | $\chi^2$ | Df | p |
|---|---|---|---|
| Length | 0.896 | 1 | 0.34 |
| Species | 31.813 | 1 | <0.0001 |
| Sex | 0.002 | 1 | 0.97 |
| month | 516.017 | 7 | <0.0001 |
| Length*Species | 0.002 | 1 | 0.96 |
| Length*Sex | 0.148 | 1 | 0.70 |
| Species*Sex | 1.000 | 1 | 0.32 |
| Length*month | 52.671 | 7 | <0.0001 |
| Species*month | 317.480 | 7 | <0.0001 |
| Sex*month | 25.396 | 7 | <0.0001 |
| Length*Species*Sex | 0.619 | 1 | 0.43 |
| Length*Species*month | 217.452 | 7 | <0.0001 |
| Length*Sex*month | 101.651 | 7 | <0.0001 |
| Species*Sex*month | 120.013 | 7 | <0.0001 |
| Length*Species*Sex*month | 86.443 | 7 | <0.0001 |

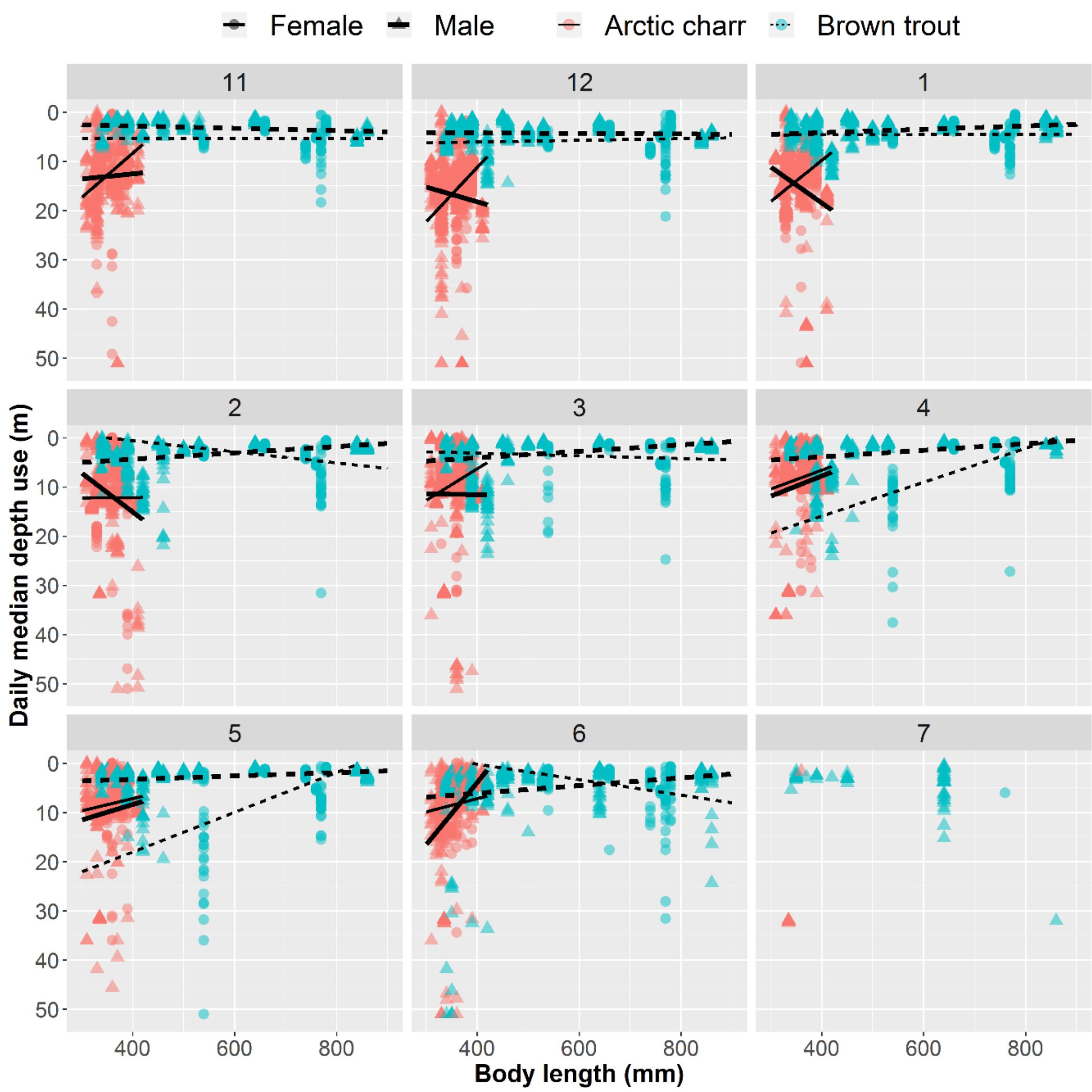


*Figure 3.8: Scatterplot of daily median individual depth use in Botnvatnet as function of month (month number in panel headers), species, sex and body length for the tagged individuals with depth sensors (i.e., > 300 mm). Corresponding lines represent model predictions from the fitted fully factorial LME-model presented in Table 5 (and Appendix Table 5).*

## 3.6 Sea-migration timing

Sea-migration of the tagged individuals unfolded from 20.05.19 until 17.09.19 with a clear peak between 20.05-18.06. Most of the brown trout entered the sea late May while most of the arctic char migrated two weeks later *(figure 3.9)*. The seaward migration of the arctic char was further concentrated than the brown trout with a clear peak from eight throughout ninth of June with 19 migratory individuals. The peak in the migration has a context to increased temperature and waterflow. The kPa went from seven on the morning sixth of May and raised to over 13 kPa throughout ninth and tenth of May before it gradually declined back to seven kPa on the twenty-third of May.

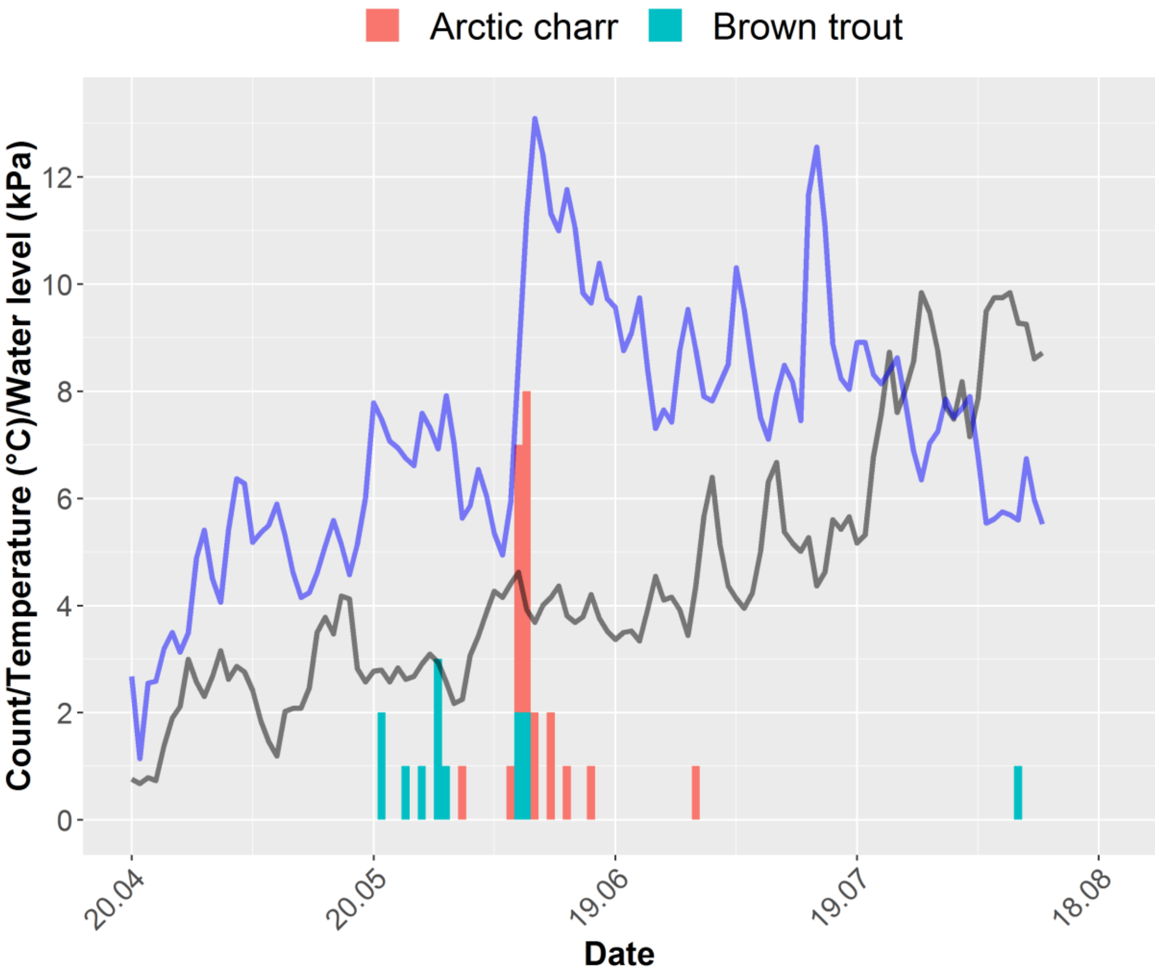


*Figure 3.9: shows first detection of the tagged fish that was registered on the TBR receiver in Saksenvika (saltwater). The grey graph display water temperature, the purple graph display water level measured in kPa.*

Parameter estimates of the most supported GLMsea-migration timing model,attaining AIC values more than 4 AIC units lower than the second-most supported candidate model, display a strong combined effect between the factors water temperature, water level (kPa) on migration time *(Table 6, Figure 3.10).* The most supported GLM-model fitted the sea sojourn data included an interaction effect between water level and a quadratic effect of water temperature (Temperature$^2$, *Table 6 and Figure 3.10*). The most supported model predicted migration to peak at high water levels when water temperature was close to 4 °C, and at about 136 kPa when water temperature is higher *(figure 3.10).*

*Table 6: Logit parameter estimates and corresponding likelihood ratio (LR) test statistics for the most supported generalized linear model fitted to estimate daily entrance to fjord probability as function of water level (kPa) and water temperature (Temp) in Knallerdalselva for the tagged Arctic charr individuals.*

| Parameter estimates | | | LR-test | | | |
|---|---|---|---|---|---|---|
| Term | Estimate | SE | Effect | Chisq | df | p |
| Intercept | 3205.9 | 1813.4 | kPa | 12.32 | 1 | <0.0001 |
| kPa | -23.8 | 13.5 | Temp$^2$ | 23.27 | 2 | <0.0001 |
| Temp | -1721.9 | 937.9 | kPa*Temp$^2$ | 7.21 | 2 | 0.0271 |
| Temp$^2$ | 225.1 | 120.7 | | | | |
| kPa*Temp | 12.7 | 7.0 | | | | |
| kPa*Temp$^2$ | -1.7 | 0.9 | | | | |

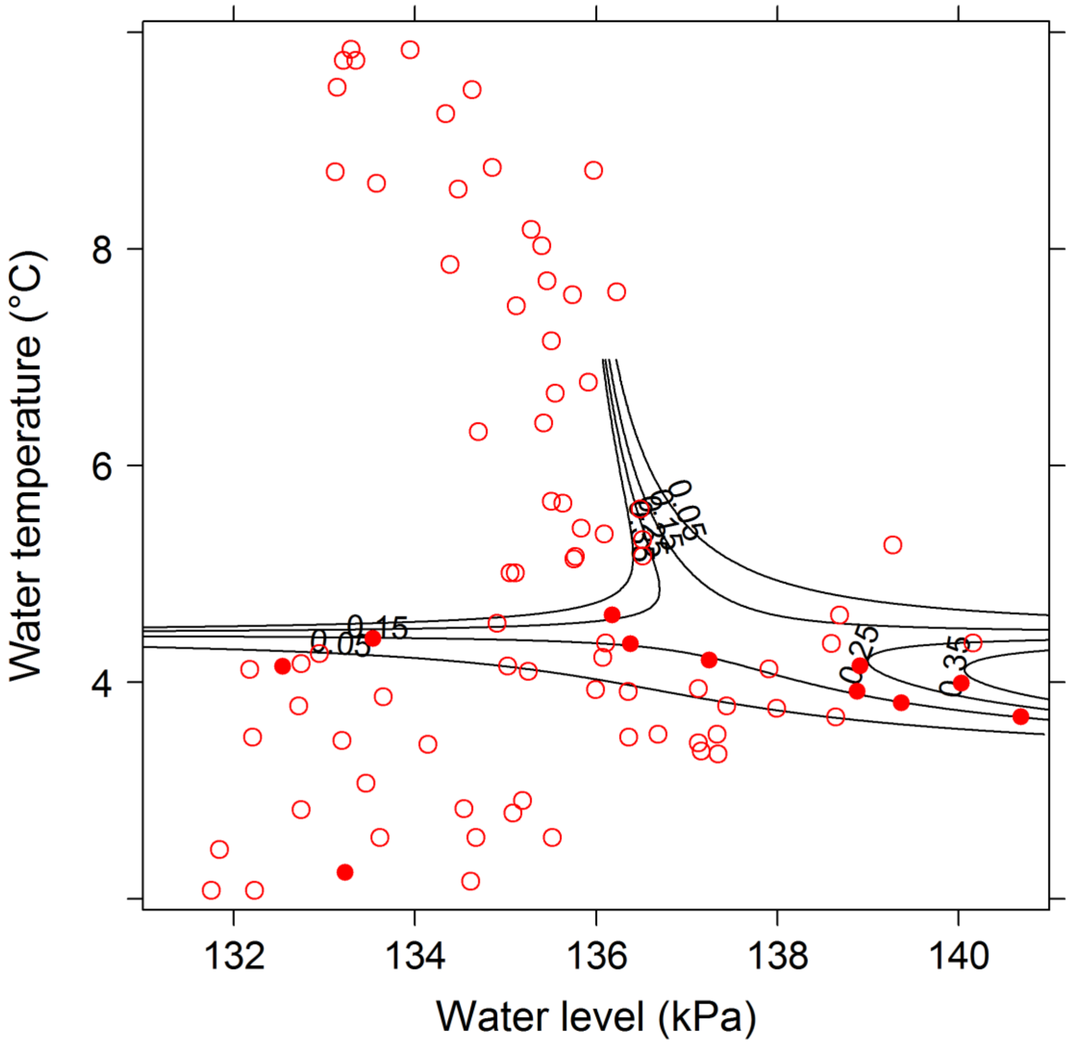


*Figure 3.10: Contourplot of the predicted daily migration-to-fjord probabilities as function of water level and water temperature in Knallerdalselva. Contours represent the predicted probabilities as estimated from the model presented in Table 6. Filled dots represents daily measurements of water temperatures and water levels for days where at least one individual migrated to fjord. Open dots are for days with no observed river-to-fjord migrations.*

# 4 DISCUSSION

The habitat utilization of the fish included in this study was affected by different factors such as size, sex, species and month. There was a significant difference in the habitat use between the arctic char and the brown trout throughout the winter. The arctic char was, as predicted, the most active species during the cold winter months. It was also the species that utilized the largest average depth. The brown trout on the other hand revealed that it as well was moving considerable distances under the ice, covering an average daily swimming distance of 20 kilometers. While initiation of sea migration was influenced by both water temperature and discharge in Arctic char, the latter seemed a more important factor for the brown trout.

## 4.1 Habitat utilization

Estimates of daily swimming distance revealed that the arctic char was the most ardent swimmer of the two species in this study *(figure 4.3)*. The difference was most visible during the cold and dark months from November until the end of February. Arctic char had a median daily swimming distance of 30 kilometers, while the brown trout elapsed 20 kilometer a day. The arctic char also had a significant larger home range (UD50 and UD95) than the brown trout during the same time. Laboratory experiments conducted by Helland et al. (2011) showed that both arctic char and brown trout reduced their resting metabolic rate under simulated ice-cover (darkness) compared to no ice (6-h daylight). In contrast to brown trout, the arctic char was able to obtain a positive growth rate in darkness and had a general higher food intake than the brown trout. Arctic char also had lower energy loss under a similar experiment in a semi natural environment with natural food supply. The difference in swimming distance between the two species may have a context with the fact that arctic char is better adapted to cold water, and therefore has a bigger surplus to forage for food. However, the activity level revealed on the brown trout during this study suggest that the brown trout as well is hunting and eating during the winter.

Delta displacement is a way to quantify the activity level within the home range. Brown trout was the species that utilized it`s home range the most. However, there was large variation in delta displacement among the individuals of both species during the study period *(figure 4.6)*. The LME model revealed that the delta displacement tended to increase with body size of female brown trout whereas the males had less pronounced size effect. Among the arctic char the opposite sex related size effect was observed where the males had this size effect. Sex, gender, size and species related patterns like this is hard to explain. There is few if none other studies like this conducted, so that observations like this only generates new questions. More studies are needed to conclude with anything regarding these observations.

Brown trout and arctic char had a significant difference in dept utilization throughout this study. The arctic char utilized a median depth of 12-15 meters during the winter while the brown trout was utilizing a median depth of 3-5 meters. As spring unfolded the median depth of both species decreased. Rune Lunde (2014) found similar observations during the 2013-2014 season in his MSc study of brown trout in the lake Vassbygdvatnet, Sogn og fjordane county. One of the drivers for dept utilization according to Lunde's study was temperature. An extension of the Lunde study showed that during winters without an ice sheet on Vassbygdvatnet, the typical thermal stratification that you get under ice-sheet conditions, increasing temperature with increasing depth, disappears. Under non-stratified conditions the entire water column became cold and the brown trout became far more active in terms of vertical migrations (Haugen et al 2019). The authors suggest this behavior to indicate thermal stress where they search for temperatures at around 4 C, but these temperatures are not available under unstratified winter conditions. Hence, as the temperature decreased to about zero degrees the brown trout utilized deeper water. However, this was a regulated system containing only brown trout, so that the interspecific competition between two species was not considered. The brown trout is typically more aggressive than the arctic char and forces the arctic char away from the most profitable habitat of the littoral zone during summer time (Jansen et al., 2002, Forseth et al., 2003). Less is known about their interspecific competition during winter. A study conducted by Amundsen and Knudsen (2009) in lake Fjellrøsa showed that large brown trout (>20 cm) mainly fed on small arctic char (<20cm) during the winter.

The water temperature in this study was measured in the surface water and in Knallerdalselva *(Appendix Figure 1)*. It's hard to say, due to lack of temperature data in the deeper water layers of the lake, if the fish utilized deeper water because of temperature differences. My main theory of the difference in dept utilization is that the arctic char avoids the shallower littoral zone to reduce the predation risk from the larger brown trout.

All the tagged individuals returned to the lake after spawning within five days. There was a major peak on the first day the fish started to descent (22.10.2016) with 67 out of 82 fish registered in the lake. Since there was no change in air temperature, water flow or precipitation the trigger of the post-spawn migration timing is hard to pinpoint. During fieldwork in the lake and rivers there was done several observations of both Sea eagle *(filii aquilae) and otter (Luter)* (pers. Obs). Since there was no obvious environmental impact due to weather conditions it`s likely to believe that there was an unpredicted event like an otter came up the river creating chaos that triggered the migration.

There was a strong relationship between raised water flow, raised water temperature and marine migration. The brown trout migrated approximately two weeks before the arctic char. This corelates with other observations like (Haugen et al 2019, (Haraldstad et al., 2017, Haraldstad et al., 2018) Studies of brown trout like (Jonsson and Jonsson, 2002, Jonsson, 1991), suggested that water temperature was the main driver for migration to the sea. In this study, Botnelva which connects the water system to the sea is a shallow river which can be difficult to migrate through on low waterflow (pers.obs). It is likely to believe that the water flow and time of year may be a just as important factor as the water temperature regarding what triggers the fish to migrate.

## 4.2 Shortcomings and suggestions of improvements

Acoustic telemetry studies are well suited to passively observe animal behavior in their natural habitat. By using enough stationary receivers, positioned correctly in the study area, position of tagged individuals can be located by triangulation at all time (Kessel et al., 2014). Receivers and transmitters have a detection range which can vary allot from system to system. Factors like high flow, air bubbles, turbidity and waves may have a large impact on the detection range (Donaldson et al., 2014). During this study sync tags were not used, and range tests were not performed. Deployment of sync tags would have improved the precision and time resolution of position estimates (Heupel et al., 2006). All the TBR receivers were placed relatively close to each other *(figure 3.7)*, so that the probability of blind spots in this study is relatively small. Range was not measured in Botnvatnet, but during winter conditions in the lake Lesjaskogsvatnet, central Norway, a comparable oligtrophic lake, ranges of 350-500 m were retrieved using similar tags as I did in a study by (Bass et al., 2014). However, one TBR located in the south end of Botnvatnet close to the outlet of Knallerdalselva was lost *(figure 3.7)*. This was an important TBR location which may have caused inferior quality of the data from that part of the lake.

This was a “one-season” study that took place from fall of 2016 until the spring of 2017. Many interesting behavioral patterns like timing of post-spawning migration, swimming distance and dept utilization was revealed. This study should have been conducted for more than one winter to test if these observed patterns were robust across years or just a unique result. For example, 82 % of all the tagged individuals returned to the lake after spawning on the same day. There were no environmental effects that explained this concentrated migration. Data from several years is necessary to fully understand the trigger of this concentrated migration.

Throughout this study, water temperature was an important factor for some of the observed patterns. For example, models predicted that the water temperature was one of the main drivers of marine migration. Other studies like (Lunde,2014, Haugen et al, 2019) strongly indicates that water temperature is connected to depth utilization. In Botenvatnet the water temperature was measured in the surface water. Sync tags, constantly monitoring water temperature each five meters or so of the lake`s depth would have improven the study. This accurate water temperature data may have contributed to better explaining the dept utilization of the fish.

The activity level documented throughout this study indicated that both species probably were feeding during the winter. Individuals of both arctic char and brown trout should have been caught during the winter, and stomach samples could have verified that the fish were feeding.

## 4.3 Relevance of fish management

The population of anadromous arctic char has like in most of the other rivers, declined drastically the last decades (Klemetsen et al., 2003a). Ten to twenty years ago thousands of arctic chars migrated up the river Knallerdalselva to spawn (pers mes. Jan Karsten Pedersen). While catching candidate char to this study approximately hundred fish were observed on the spawning grounds in the river. Analysis of sea-migration showed that a large part of the arctic char tagged in Knallerdalselva migrated to the sea (9 out of 21). It is strongly recommended that the arctic char that spawns in Knallerdalselva is protected and not harvested.

The spawning-river Knallerdalselva is very shallow many places and crystal clear. This makes it easy to spot fish. This also makes it easy to catch fish in illegal ways like snagging, gillnets, harpooning and so on. This kind of illegal fishing has been observed in the river before (pers mes. Jan Karsten Pedersen). It is important to maintain control in the river so that these things do not happen.

During this study the activity level observed on the brown trout strongly indicates that they are feeding during the winter. This also makes it possible to catch these fish during the ice fishing that takes place in the lake. Introduction of rules that impose the fisherman to release large brown trout’s may be a measure that secures the anadromous population of brown trout.

# 5 CONCLUDING REMARKS

In conclusion, acoustic telemetry conducted on Arctic char and brown trout in the Botn watercourse during winter 2016-2017 provided data with highly valuable and novel information. In particular, I want to highlight:

- Arctic char was the most active species during this study; however, the activity level of the brown trout was surprisingly high, suggesting that both species are foraging for food during the winter.
- All the tagged individuals of anadromous brown trout remained in freshwater during the winter
- Water flow and water temperature triggered migration to the sea
- The habitat utilization during winter showed large variation between the two species, indicating that there is large interspecific competition

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# 7 APPENDIX

### 7.1.1 Appendix Table 1

Parameter estimates for the fully factorial model fitted to estimate effects on daily swimming distance in tagged brown trout and arctic char in Botnvatnet.

```
Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 102.5    10.13
 Residual             110.5    10.51
Number of obs: 14935, groups:  ID, 81

Fixed effects:
                                          Estimate Std. Error t value
(Intercept)                               50.54481   32.70216   1.546
Length                                    -0.06709    0.09644  -0.696
SpeciesBrown trout                       -50.71393   34.88073  -1.454
SexMale                                  -72.04896   38.19044  -1.887
month212                                  40.65381    9.59431   4.237
month21                                    4.79183    9.71022   0.493
month22                                   23.31416   10.61920   2.195
month23                                   71.85106   10.40418   6.906
month24                                  111.36411   10.49040  10.616
month25                                  124.83401   10.67574  11.693
month26                                   13.66654   13.18291   1.037
Length:SpeciesBrown trout                  0.08465    0.09789   0.865
Length:SexMale                             0.20347    0.11351   1.792
SpeciesBrown trout:SexMale                97.12643   40.77352   2.382
Length:month212                           -0.11977    0.02831  -4.230
Length:month21                            -0.01959    0.02863  -0.684
Length:month22                            -0.06806    0.03116  -2.184
Length:month23                            -0.21676    0.03053  -7.101
Length:month24                            -0.34366    0.03078 -11.165
Length:month25                            -0.39007    0.03133 -12.449
Length:month26                            -0.08254    0.03943  -2.093
```

| | | | |
|---|---|---|---|
| SpeciesBrown trout:month212 | -40.87900 | 10.74267 | -3.805 |
| SpeciesBrown trout:month21 | -7.09151 | 11.06171 | -0.641 |
| SpeciesBrown trout:month22 | -25.66569 | 11.96071 | -2.146 |
| SpeciesBrown trout:month23 | -68.28278 | 11.79879 | -5.787 |
| SpeciesBrown trout:month24 | -115.90746 | 11.99470 | -9.663 |
| SpeciesBrown trout:month25 | -117.36663 | 12.30180 | -9.541 |
| SpeciesBrown trout:month26 | -1.92782 | 14.68468 | -0.131 |
| SexMale:month212 | -46.09530 | 11.46751 | -4.020 |
| SexMale:month21 | -6.23024 | 11.57121 | -0.538 |
| SexMale:month22 | -12.21090 | 12.41871 | -0.983 |
| SexMale:month23 | -55.36493 | 12.17944 | -4.546 |
| SexMale:month24 | -33.92874 | 12.26008 | -2.767 |
| SexMale:month25 | -57.89036 | 12.45715 | -4.647 |
| SexMale:month26 | -25.24774 | 14.89610 | -1.695 |
| Length:SpeciesBrown trout:SexMale | -0.22511 | 0.11557 | -1.948 |
| Length:SpeciesBrown trout:month212 | 0.12484 | 0.02906 | 4.296 |
| Length:SpeciesBrown trout:month21 | 0.02558 | 0.02950 | 0.867 |
| Length:SpeciesBrown trout:month22 | 0.07706 | 0.03202 | 2.407 |
| Length:SpeciesBrown trout:month23 | 0.21851 | 0.03142 | 6.955 |
| Length:SpeciesBrown trout:month24 | 0.35175 | 0.03174 | 11.082 |
| Length:SpeciesBrown trout:month25 | 0.38508 | 0.03236 | 11.899 |
| Length:SpeciesBrown trout:month26 | 0.06123 | 0.04035 | 1.517 |
| Length:SexMale:month212 | 0.14011 | 0.03403 | 4.117 |
| Length:SexMale:month21 | 0.02341 | 0.03431 | 0.682 |
| Length:SexMale:month22 | 0.03671 | 0.03667 | 1.001 |
| Length:SexMale:month23 | 0.16729 | 0.03598 | 4.649 |
| Length:SexMale:month24 | 0.10804 | 0.03622 | 2.983 |
| Length:SexMale:month25 | 0.18734 | 0.03683 | 5.086 |
| Length:SexMale:month26 | 0.09262 | 0.04465 | 2.074 |
| SpeciesBrown trout:SexMale:month212 | 45.27625 | 12.63714 | 3.583 |
| SpeciesBrown trout:SexMale:month21 | 5.72159 | 12.91815 | 0.443 |
| SpeciesBrown trout:SexMale:month22 | 8.18043 | 13.77028 | 0.594 |
| SpeciesBrown trout:SexMale:month23 | 52.89089 | 13.57215 | 3.897 |
| SpeciesBrown trout:SexMale:month24 | 35.05186 | 13.75042 | 2.549 |
| SpeciesBrown trout:SexMale:month25 | 51.67903 | 14.05632 | 3.677 |

| | | | |
|---|---|---|---|
| SpeciesBrown trout:SexMale:month26 | 7.63108 | 16.42501 | 0.465 |
| Length:SpeciesBrown trout:SexMale:month212 | -0.14279 | 0.03489 | -4.093 |
| Length:SpeciesBrown trout:SexMale:month21 | -0.03071 | 0.03528 | -0.870 |
| Length:SpeciesBrown trout:SexMale:month22 | -0.03936 | 0.03763 | -1.046 |
| Length:SpeciesBrown trout:SexMale:month23 | -0.17439 | 0.03697 | -4.717 |
| Length:SpeciesBrown trout:SexMale:month24 | -0.11786 | 0.03726 | -3.163 |
| Length:SpeciesBrown trout:SexMale:month25 | -0.18326 | 0.03793 | -4.831 |
| Length:SpeciesBrown trout:SexMale:month26 | -0.06701 | 0.04569 | -1.467 |

### 7.1.2 Appendix table 2

Parameter estimates for the fully factorial model fitted to estimate effects on 50% utilization distribution in tagged brown trout and arctic char in Botnvatnet.

Random effects:

| Groups | Name | Variance | Std.Dev. |
|---|---|---|---|
| ID | (Intercept) | 6.255 | 2.501 |
| Residual | | 15.201 | 3.899 |

Number of obs: 11462, groups: ID, 70

Fixed effects:

| | Estimate | Std. Error | t value |
|---|---|---|---|
| (Intercept) | 3.023124 | 8.634778 | 0.350 |
| Length | 0.022775 | 0.025551 | 0.891 |
| SpeciesBrown trout | 11.620081 | 10.017504 | 1.160 |
| SexMale | -17.803000 | 10.260637 | -1.735 |
| month212 | 10.450262 | 4.101364 | 2.548 |
| month21 | 6.645425 | 4.195744 | 1.584 |
| month22 | 2.777063 | 4.681542 | 0.593 |
| month23 | -11.404913 | 5.744514 | -1.985 |
| month24 | -2.308128 | 6.240380 | -0.370 |
| month25 | 26.141952 | 6.602942 | 3.959 |
| month26 | -22.857908 | 8.427633 | -2.712 |
| Length:SpeciesBrown trout | -0.033719 | 0.026429 | -1.276 |
| Length:SexMale | 0.054754 | 0.030509 | 1.795 |
| SpeciesBrown trout:SexMale | 10.890897 | 11.613521 | 0.938 |

| | | | |
|---|---|---|---|
| Length:month212 | -0.032343 | 0.012224 | -2.646 |
| Length:month21 | -0.026028 | 0.012473 | -2.087 |
| Length:month22 | -0.010913 | 0.013892 | -0.786 |
| Length:month23 | 0.033530 | 0.017362 | 1.931 |
| Length:month24 | 0.004000 | 0.018997 | 0.211 |
| Length:month25 | -0.082197 | 0.020187 | -4.072 |
| Length:month26 | 0.057001 | 0.025425 | 2.242 |
| SpeciesBrown trout:month212 | -9.834033 | 4.809833 | -2.045 |
| SpeciesBrown trout:month21 | -9.689713 | 4.896791 | -1.979 |
| SpeciesBrown trout:month22 | -4.003307 | 5.344083 | -0.749 |
| SpeciesBrown trout:month23 | 13.231456 | 6.285661 | 2.105 |
| SpeciesBrown trout:month24 | 1.583902 | 6.742728 | 0.235 |
| SpeciesBrown trout:month25 | -28.070637 | 7.099055 | -3.954 |
| SpeciesBrown trout:month26 | 30.035911 | 9.007440 | 3.335 |
| SexMale:month212 | -0.559345 | 4.983452 | -0.112 |
| SexMale:month21 | 6.350700 | 5.065365 | 1.254 |
| SexMale:month22 | 16.313866 | 5.515281 | 2.958 |
| SexMale:month23 | 33.763861 | 6.431334 | 5.250 |
| SexMale:month24 | 40.795685 | 6.910402 | 5.904 |
| SexMale:month25 | 7.824598 | 7.238801 | 1.081 |
| SexMale:month26 | 50.197599 | 9.094936 | 5.519 |
| Length:SpeciesBrown trout:SexMale | -0.041343 | 0.031450 | -1.315 |
| Length:SpeciesBrown trout:month212 | 0.033500 | 0.012664 | 2.645 |
| Length:SpeciesBrown trout:month21 | 0.029879 | 0.012908 | 2.315 |
| Length:SpeciesBrown trout:month22 | 0.013312 | 0.014300 | 0.931 |
| Length:SpeciesBrown trout:month23 | -0.034837 | 0.017684 | -1.970 |
| Length:SpeciesBrown trout:month24 | -0.003166 | 0.019293 | -0.164 |
| Length:SpeciesBrown trout:month25 | 0.085549 | 0.020476 | 4.178 |
| Length:SpeciesBrown trout:month26 | -0.065660 | 0.025766 | -2.548 |
| Length:SexMale:month212 | 0.002315 | 0.014872 | 0.156 |
| Length:SexMale:month21 | -0.018755 | 0.015103 | -1.242 |
| Length:SexMale:month22 | -0.048999 | 0.016408 | -2.986 |
| Length:SexMale:month23 | -0.105160 | 0.019416 | -5.416 |
| Length:SexMale:month24 | -0.125812 | 0.021011 | -5.988 |
| Length:SexMale:month25 | -0.027679 | 0.022088 | -1.253 |

```
Length:SexMale:month26                          -0.151557   0.027411  -5.529
SpeciesBrown trout:SexMale:month212              1.708708   5.652546   0.302
SpeciesBrown trout:SexMale:month21              -3.043645   5.735097  -0.531
SpeciesBrown trout:SexMale:month22             -14.139646   6.162498  -2.294
SpeciesBrown trout:SexMale:month23             -32.493482   6.980072  -4.655
SpeciesBrown trout:SexMale:month24             -40.430988   7.427751  -5.443
SpeciesBrown trout:SexMale:month25              -5.377674   7.749987  -0.694
SpeciesBrown trout:SexMale:month26             -59.785426   9.696767  -6.166
Length:SpeciesBrown trout:SexMale:month212  -0.005843   0.015317  -0.381
Length:SpeciesBrown trout:SexMale:month21    0.012797   0.015553   0.823
Length:SpeciesBrown trout:SexMale:month22    0.043235   0.016841   2.567
Length:SpeciesBrown trout:SexMale:month23    0.099251   0.019773   5.020
Length:SpeciesBrown trout:SexMale:month24    0.123502   0.021348   5.785
Length:SpeciesBrown trout:SexMale:month25    0.022212   0.022414   0.991
Length:SpeciesBrown trout:SexMale:month26    0.164578   0.027800   5.920
```

### 7.1.3 Appendix Table 3

Parameter estimates for the fully factorial model fitted to estimate effects on 95% utilization distribution in tagged brown trout and arctic char in Botnvatnet.

```
Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 168.6    12.98
 Residual             273.6    16.54
Number of obs: 11455, groups:  ID, 70


Fixed effects:
                                       Estimate Std. Error t value
(Intercept)                           5.366e+01  4.362e+01   1.230
Length                                1.147e-02  1.290e-01   0.089
SpeciesBrown trout                    2.696e+01  5.031e+01   0.536
SexMale                              -4.716e+01  5.177e+01  -0.911
month212                              3.091e+01  1.742e+01   1.774
month21                              -1.982e+01  1.782e+01  -1.112
month22                              -4.808e+01  1.989e+01  -2.418
month23                              -1.106e+02  2.440e+01  -4.532
month24                              -3.208e+01  2.651e+01  -1.210
month25                               9.249e+01  2.804e+01   3.298
month26                              -1.615e+02  3.578e+01  -4.515
Length:SpeciesBrown trout            -7.307e-02  1.332e-01  -0.548
Length:SexMale                        1.480e-01  1.539e-01   0.961
SpeciesBrown trout:SexMale            1.294e+01  5.837e+01   0.222
Length:month212                      -1.009e-01  5.194e-02  -1.942
Length:month21                        3.113e-02  5.300e-02   0.587
Length:month22                        1.389e-01  5.902e-02   2.353
Length:month23                        3.296e-01  7.376e-02   4.469
Length:month24                        6.887e-02  8.069e-02   0.854
Length:month25                       -3.046e-01  8.574e-02  -3.552
Length:month26                        4.429e-01  1.079e-01   4.103
SpeciesBrown trout:month212          -4.110e+01  2.043e+01  -2.012
SpeciesBrown trout:month21           -1.102e+01  2.080e+01  -0.530
SpeciesBrown trout:month22            2.615e+01  2.270e+01   1.152
```

| | | | |
|---|---|---|---|
| SpeciesBrown trout:month23 | 1.092e+02 | 2.670e+01 | 4.090 |
| SpeciesBrown trout:month24 | 1.697e+01 | 2.863e+01 | 0.593 |
| SpeciesBrown trout:month25 | -1.066e+02 | 3.015e+01 | -3.537 |
| SpeciesBrown trout:month26 | 1.904e+02 | 3.825e+01 | 4.977 |
| SexMale:month212 | -6.338e+00 | 2.116e+01 | -0.299 |
| SexMale:month21 | 3.280e+01 | 2.151e+01 | 1.525 |
| SexMale:month22 | 1.028e+02 | 2.342e+01 | 4.390 |
| SexMale:month23 | 1.681e+02 | 2.732e+01 | 6.152 |
| SexMale:month24 | 1.495e+02 | 2.935e+01 | 5.093 |
| SexMale:month25 | 1.251e+01 | 3.074e+01 | 0.407 |
| SexMale:month26 | 2.169e+02 | 3.861e+01 | 5.617 |
| Length:SpeciesBrown trout:SexMale | -9.126e-02 | 1.585e-01 | -0.576 |
| Length:SpeciesBrown trout:month212 | 1.221e-01 | 5.381e-02 | 2.270 |
| Length:SpeciesBrown trout:month21 | 3.781e-03 | 5.484e-02 | 0.069 |
| Length:SpeciesBrown trout:month22 | -1.136e-01 | 6.075e-02 | -1.869 |
| Length:SpeciesBrown trout:month23 | -3.269e-01 | 7.513e-02 | -4.351 |
| Length:SpeciesBrown trout:month24 | -5.371e-02 | 8.195e-02 | -0.655 |
| Length:SpeciesBrown trout:month25 | 3.270e-01 | 8.697e-02 | 3.761 |
| Length:SpeciesBrown trout:month26 | -4.750e-01 | 1.094e-01 | -4.342 |
| Length:SexMale:month212 | 1.373e-02 | 6.317e-02 | 0.217 |
| Length:SexMale:month21 | -1.088e-01 | 6.415e-02 | -1.695 |
| Length:SexMale:month22 | -3.321e-01 | 6.970e-02 | -4.765 |
| Length:SexMale:month23 | -5.467e-01 | 8.247e-02 | -6.629 |
| Length:SexMale:month24 | -4.785e-01 | 8.924e-02 | -5.362 |
| Length:SexMale:month25 | -6.787e-02 | 9.380e-02 | -0.724 |
| Length:SexMale:month26 | -6.616e-01 | 1.164e-01 | -5.685 |
| SpeciesBrown trout:SexMale:month212 | 1.783e+01 | 2.401e+01 | 0.743 |
| SpeciesBrown trout:SexMale:month21 | -5.820e+00 | 2.435e+01 | -0.239 |
| SpeciesBrown trout:SexMale:month22 | -8.037e+01 | 2.617e+01 | -3.071 |
| SpeciesBrown trout:SexMale:month23 | -1.566e+02 | 2.964e+01 | -5.281 |
| SpeciesBrown trout:SexMale:month24 | -1.413e+02 | 3.154e+01 | -4.481 |
| SpeciesBrown trout:SexMale:month25 | 2.204e-01 | 3.291e+01 | 0.007 |
| SpeciesBrown trout:SexMale:month26 | -2.519e+02 | 4.117e+01 | -6.117 |
| Length:SpeciesBrown trout:SexMale:month212 | -3.483e-02 | 6.506e-02 | -0.535 |
| Length:SpeciesBrown trout:SexMale:month21 | 7.376e-02 | 6.606e-02 | 1.117 |

| | | | |
|---|---|---|---|
| Length:SpeciesBrown trout:SexMale:month22 | 2.982e-01 | 7.153e-02 | 4.169 |
| Length:SpeciesBrown trout:SexMale:month23 | 5.189e-01 | 8.399e-02 | 6.178 |
| Length:SpeciesBrown trout:SexMale:month24 | 4.680e-01 | 9.067e-02 | 5.162 |
| Length:SpeciesBrown trout:SexMale:month25 | 4.623e-02 | 9.519e-02 | 0.486 |
| Length:SpeciesBrown trout:SexMale:month26 | 7.223e-01 | 1.180e-01 | 6.120 |

### 7.1.4 Appendix Table 4

Parameter estimates for the fully factorial model fitted to estimate effects on delta displacement in tagged brown trout and arctic char in Botnvatnet.

Random effects:

| Groups | Name | Variance | Std.Dev. |
|---|---|---|---|
| ID | (Intercept) | 14263 | 119.4 |
| Residual | | 30657 | 175.1 |

Number of obs: 11455, groups: ID, 70

Fixed effects:

| | Estimate | Std. Error | t value |
|---|---|---|---|
| (Intercept) | 5.359e+02 | 4.086e+02 | 1.312 |
| Length | 1.820e-01 | 1.209e+00 | 0.151 |
| SpeciesBrown trout | -6.297e+02 | 4.731e+02 | -1.331 |
| SexMale | -1.592e+02 | 4.853e+02 | -0.328 |
| month212 | 2.141e+02 | 1.843e+02 | 1.162 |
| month21 | 2.896e+02 | 1.885e+02 | 1.536 |
| month22 | 4.871e+02 | 2.103e+02 | 2.316 |
| month23 | 8.464e+01 | 2.581e+02 | 0.328 |
| month24 | 5.225e+02 | 2.803e+02 | 1.864 |
| month25 | -5.082e+02 | 2.966e+02 | -1.713 |
| month26 | 1.121e+03 | 3.785e+02 | 2.960 |
| Length:SpeciesBrown trout | 8.708e-01 | 1.250e+00 | 0.697 |
| Length:SexMale | 3.854e-01 | 1.443e+00 | 0.267 |
| SpeciesBrown trout:SexMale | 9.378e+02 | 5.486e+02 | 1.709 |
| Length:month212 | -4.904e-01 | 5.492e-01 | -0.893 |
| Length:month21 | -5.202e-01 | 5.604e-01 | -0.928 |
| Length:month22 | -1.196e+00 | 6.241e-01 | -1.917 |
| Length:month23 | 2.260e-02 | 7.800e-01 | 0.029 |
| Length:month24 | -1.132e+00 | 8.534e-01 | -1.327 |

| | | | |
|---|---|---|---|
| Length:month25 | 1.982e+00 | 9.069e-01 | 2.186 |
| Length:month26 | -3.042e+00 | 1.142e+00 | -2.664 |
| SpeciesBrown trout:month212 | -1.174e+02 | 2.161e+02 | -0.543 |
| SpeciesBrown trout:month21 | 3.195e+02 | 2.200e+02 | 1.452 |
| SpeciesBrown trout:month22 | -1.787e+01 | 2.401e+02 | -0.074 |
| SpeciesBrown trout:month23 | 1.610e+02 | 2.824e+02 | 0.570 |
| SpeciesBrown trout:month24 | -4.680e+02 | 3.029e+02 | -1.545 |
| SpeciesBrown trout:month25 | 7.990e+02 | 3.189e+02 | 2.505 |
| SpeciesBrown trout:month26 | -7.600e+02 | 4.047e+02 | -1.878 |
| SexMale:month212 | -1.578e+02 | 2.239e+02 | -0.705 |
| SexMale:month21 | -1.735e+02 | 2.275e+02 | -0.763 |
| SexMale:month22 | -5.716e+02 | 2.478e+02 | -2.307 |
| SexMale:month23 | -3.987e+02 | 2.889e+02 | -1.380 |
| SexMale:month24 | -9.709e+02 | 3.104e+02 | -3.127 |
| SexMale:month25 | 2.507e+01 | 3.252e+02 | 0.077 |
| SexMale:month26 | -1.859e+03 | 4.085e+02 | -4.550 |
| Length:SpeciesBrown trout:SexMale | -1.538e+00 | 1.487e+00 | -1.034 |
| Length:SpeciesBrown trout:month212 | 3.874e-01 | 5.690e-01 | 0.681 |
| Length:SpeciesBrown trout:month21 | -8.271e-02 | 5.799e-01 | -0.143 |
| Length:SpeciesBrown trout:month22 | 8.148e-01 | 6.425e-01 | 1.268 |
| Length:SpeciesBrown trout:month23 | -1.439e-01 | 7.945e-01 | -0.181 |
| Length:SpeciesBrown trout:month24 | 1.246e+00 | 8.668e-01 | 1.438 |
| Length:SpeciesBrown trout:month25 | -2.204e+00 | 9.199e-01 | -2.397 |
| Length:SpeciesBrown trout:month26 | 2.445e+00 | 1.157e+00 | 2.112 |
| Length:SexMale:month212 | 4.349e-01 | 6.681e-01 | 0.651 |
| Length:SexMale:month21 | 5.252e-01 | 6.785e-01 | 0.774 |
| Length:SexMale:month22 | 1.805e+00 | 7.371e-01 | 2.448 |
| Length:SexMale:month23 | 1.432e+00 | 8.723e-01 | 1.642 |
| Length:SexMale:month24 | 3.128e+00 | 9.439e-01 | 3.314 |
| Length:SexMale:month25 | 2.248e-01 | 9.922e-01 | 0.227 |
| Length:SexMale:month26 | 5.606e+00 | 1.231e+00 | 4.553 |
| SpeciesBrown trout:SexMale:month212 | -2.813e+01 | 2.539e+02 | -0.111 |
| SpeciesBrown trout:SexMale:month21 | -5.009e+02 | 2.576e+02 | -1.944 |
| SpeciesBrown trout:SexMale:month22 | -1.010e+02 | 2.768e+02 | -0.365 |
| SpeciesBrown trout:SexMale:month23 | -5.981e+01 | 3.136e+02 | -0.191 |

| | | | |
|---|---|---|---|
| SpeciesBrown trout:SexMale:month24 | 7.956e+02 | 3.337e+02 | 2.384 |
| SpeciesBrown trout:SexMale:month25 | -3.083e+02 | 3.482e+02 | -0.885 |
| SpeciesBrown trout:SexMale:month26 | 1.456e+03 | 4.357e+02 | 3.342 |
| Length:SpeciesBrown trout:SexMale:month212 | -1.891e-01 | 6.881e-01 | -0.275 |
| Length:SpeciesBrown trout:SexMale:month21 | 2.648e-01 | 6.987e-01 | 0.379 |
| Length:SpeciesBrown trout:SexMale:month22 | -9.310e-01 | 7.566e-01 | -1.231 |
| Length:SpeciesBrown trout:SexMale:month23 | -7.832e-01 | 8.883e-01 | -0.882 |
| Length:SpeciesBrown trout:SexMale:month24 | -2.888e+00 | 9.590e-01 | -3.011 |
| Length:SpeciesBrown trout:SexMale:month25 | 2.255e-01 | 1.007e+00 | 0.224 |
| Length:SpeciesBrown trout:SexMale:month26 | -4.907e+00 | 1.249e+00 | -3.930 |

### 7.1.5 Appendix Table 5

Parameter estimates for the fully factorial model fitted to estimate effects on depth use in tagged brown trout and arctic char in Botnvatnet.

Random effects:

| Groups | Name | Variance | Std.Dev. |
|---|---|---|---|
| AT.ID | (Intercept) | 9.256 | 3.042 |
| Residual | | 30.226 | 5.498 |

Number of obs: 8673, groups: AT.ID, 40

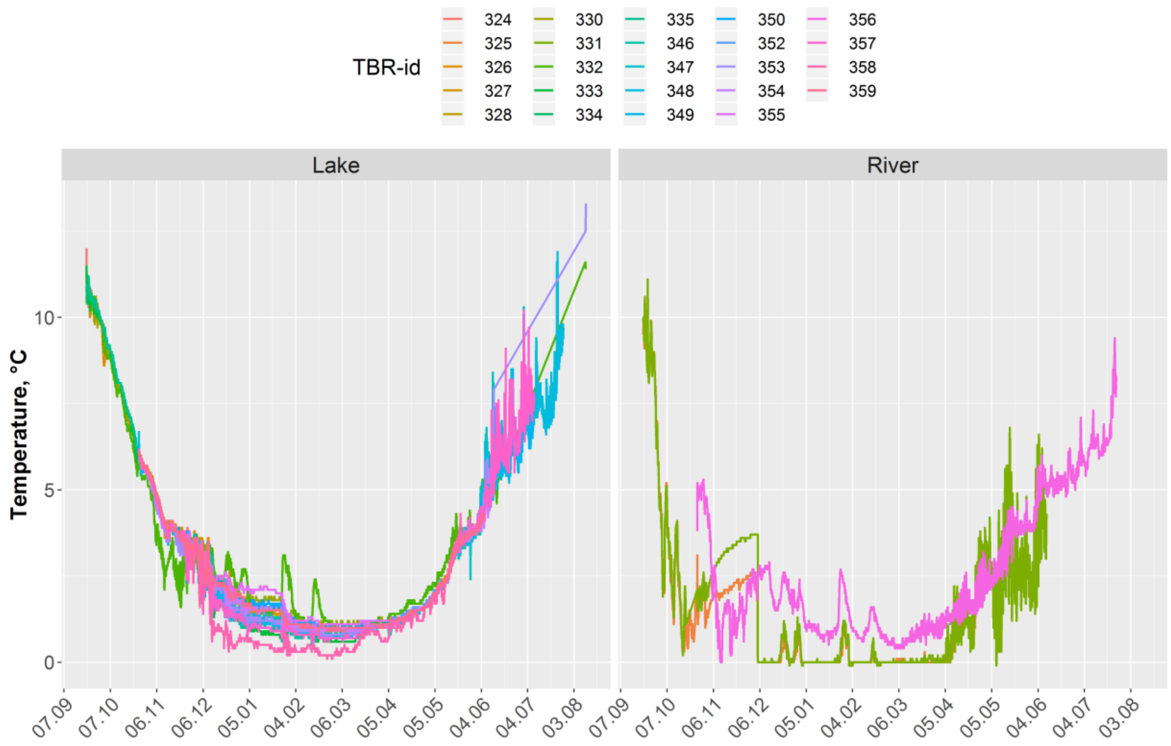
Fixed effects:

| | Estimate | Std. Error | t value |
|---|---|---|---|
| (Intercept) | 4.436e+01 | 2.487e+01 | 1.783 |
| Length | -8.998e-02 | 6.867e-02 | -1.310 |
| SpeciesBrown trout | -3.894e+01 | 2.730e+01 | -1.426 |
| SexMale | -2.772e+01 | 2.704e+01 | -1.025 |
| month212 | 1.115e+01 | 1.196e+01 | 0.932 |
| month21 | -1.104e+00 | 1.195e+01 | -0.092 |
| month22 | -3.197e+01 | 1.222e+01 | -2.617 |
| month23 | -1.241e+01 | 1.200e+01 | -1.034 |
| month24 | -2.249e+01 | 1.206e+01 | -1.865 |
| month25 | -2.728e+01 | 1.207e+01 | -2.260 |
| month26 | -2.646e+01 | 1.351e+01 | -1.958 |
| Length:SpeciesBrown trout | 8.990e-02 | 7.046e-02 | 1.276 |
| Length:SexMale | 7.975e-02 | 7.505e-02 | 1.063 |
| SpeciesBrown trout:SexMale | 2.417e+01 | 2.943e+01 | 0.821 |

| | | | |
|---|---|---|---|
| Length:month212 | -2.069e-02 | 3.303e-02 | -0.626 |
| Length:month21 | 6.433e-03 | 3.300e-02 | 0.195 |
| Length:month22 | 8.941e-02 | 3.373e-02 | 2.651 |
| Length:month23 | 2.590e-02 | 3.315e-02 | 0.781 |
| Length:month24 | 5.180e-02 | 3.329e-02 | 1.556 |
| Length:month25 | 6.517e-02 | 3.335e-02 | 1.954 |
| Length:month26 | 6.316e-02 | 3.762e-02 | 1.679 |
| SpeciesBrown trout:month212 | -9.839e+00 | 1.313e+01 | -0.749 |
| SpeciesBrown trout:month21 | 3.816e-01 | 1.312e+01 | 0.029 |
| SpeciesBrown trout:month22 | 2.262e+01 | 1.341e+01 | 1.687 |
| SpeciesBrown trout:month23 | 8.997e+00 | 1.317e+01 | 0.683 |
| SpeciesBrown trout:month24 | 4.680e+01 | 1.323e+01 | 3.537 |
| SpeciesBrown trout:month25 | 5.605e+01 | 1.323e+01 | 4.237 |
| SpeciesBrown trout:month26 | 1.490e+01 | 1.474e+01 | 1.011 |
| SexMale:month212 | -2.158e+01 | 1.303e+01 | -1.656 |
| SexMale:month21 | -2.635e+01 | 1.302e+01 | -2.024 |
| SexMale:month22 | -1.216e+00 | 1.331e+01 | -0.091 |
| SexMale:month23 | 6.586e+00 | 1.308e+01 | 0.504 |
| SexMale:month24 | 3.006e+01 | 1.315e+01 | 2.286 |
| SexMale:month25 | 3.159e+01 | 1.317e+01 | 2.398 |
| SexMale:month26 | 6.433e+01 | 1.467e+01 | 4.386 |
| Length:SpeciesBrown trout:SexMale | -7.735e-02 | 7.688e-02 | -1.006 |
| Length:SpeciesBrown trout:month212 | 1.909e-02 | 3.389e-02 | 0.563 |
| Length:SpeciesBrown trout:month21 | -6.589e-03 | 3.386e-02 | -0.195 |
| Length:SpeciesBrown trout:month22 | -7.802e-02 | 3.460e-02 | -2.255 |
| Length:SpeciesBrown trout:month23 | -2.305e-02 | 3.401e-02 | -0.678 |
| Length:SpeciesBrown trout:month24 | -8.621e-02 | 3.416e-02 | -2.524 |
| Length:SpeciesBrown trout:month25 | -1.055e-01 | 3.420e-02 | -3.085 |
| Length:SpeciesBrown trout:month26 | -4.735e-02 | 3.852e-02 | -1.229 |
| Length:SexMale:month212 | 6.093e-02 | 3.616e-02 | 1.685 |
| Length:SexMale:month21 | 7.693e-02 | 3.613e-02 | 2.129 |
| Length:SexMale:month22 | -1.233e-04 | 3.693e-02 | -0.003 |
| Length:SexMale:month23 | -1.379e-02 | 3.631e-02 | -0.380 |
| Length:SexMale:month24 | -8.265e-02 | 3.650e-02 | -2.265 |
| Length:SexMale:month25 | -8.643e-02 | 3.659e-02 | -2.362 |

| | | | |
|---|---|---|---|
| Length:SexMale:month26 | -1.795e-01 | 4.101e-02 | -4.377 |
| SpeciesBrown trout:SexMale:month212 | 2.238e+01 | 1.418e+01 | 1.579 |
| SpeciesBrown trout:SexMale:month21 | 3.072e+01 | 1.417e+01 | 2.168 |
| SpeciesBrown trout:SexMale:month22 | 1.562e+01 | 1.447e+01 | 1.079 |
| SpeciesBrown trout:SexMale:month23 | 1.658e+00 | 1.422e+01 | 0.117 |
| SpeciesBrown trout:SexMale:month24 | -4.972e+01 | 1.430e+01 | -3.477 |
| SpeciesBrown trout:SexMale:month25 | -5.765e+01 | 1.431e+01 | -4.029 |
| SpeciesBrown trout:SexMale:month26 | -4.543e+01 | 1.588e+01 | -2.862 |
| Length:SpeciesBrown trout:SexMale:month212 | -6.110e-02 | 3.704e-02 | -1.649 |
| Length:SpeciesBrown trout:SexMale:month21 | -8.250e-02 | 3.701e-02 | -2.229 |
| Length:SpeciesBrown trout:SexMale:month22 | -2.001e-02 | 3.782e-02 | -0.529 |
| Length:SpeciesBrown trout:SexMale:month23 | 2.028e-03 | 3.719e-02 | 0.055 |
| Length:SpeciesBrown trout:SexMale:month24 | 1.081e-01 | 3.738e-02 | 2.892 |
| Length:SpeciesBrown trout:SexMale:month25 | 1.211e-01 | 3.746e-02 | 3.232 |
| Length:SpeciesBrown trout:SexMale:month26 | 1.535e-01 | 4.192e-02 | 3.661 |

### 7.1.6 Appendix Figure 1




*Appendix Figure 1: Temperature visualized in a plot conducted with the retrieved temperature data from the TBR receivers.*

**Norges miljø- og biovitenskapelige universitet**
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway