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2 Abstract

Managing migratory fish species is a major conservational and scientific challenge, due to the diverse habitat requirements of these species and the required connectivity between the habitats. Little is known about the ecology and behavior of wintering trout and as it is believed to be a bottleneck period for salmonids (*Salmonidae*), new knowledge is needed (Greenberg et al. 2007). The aim of this study was to explore the among-individual spatio-temporal variation in habitat use in post-juvenile sea trout (*Salmo trutta morpha trutta*) living in the regulated Aurland river-system in Western Norway. This was done using acoustic telemetry technology and triangulation. The lake Vassbygdvatnet is located 6 km upstream from the estuary with Vassbygdelvi River running inn and Aurlandselva running out. The in-lake habitat use and the connectivity in the freshwater phase of sea trout attained the main focus in this study and was determined using vertical, 2D and 3D utilization distribution (UD) methods and the UDs were used to model the behavior of the trout using linear mixed models. The trout was tagged during four periods over the course of 21 months and assigned into three groups: smolt, finnock (i.e., immature individuals that has been to sea) and mature trout according to fish lengths and anadromous traits.

Finnocks and mature trout returning from the sea arrived to Vassbygdvatnet during August- September and stayed there for the entire winter, before emigrating in May. A large proportion of the sea trout of all the tagged size groups utilized Vassbygdvatnet during several life stages, where they displayed pelagic behavior mainly utilizing the upper 15 meter depth stratum. Also assigned mature trout stayed within the lake through from September until May and spawning is believed to have occurred within the lake.

Adfluvial migrations in the Aurland river and lake system were observed where smolt and finnock migrated downstream from their river-release sites to open waters during spring. Individuals tagged in the river downstream Vassbygdvatnet (Aurlandselva) migrated to the fjord, whereas smolt and finnock released upstream Vassbygdvatnet (Vassbygdelvi) ended up in the lake where just a few migrated further downstream to the fjord.

The trout that wintered in the lake was obstructed from downstream migrations during spring by being attracted by the outgoing discharge water leading into Vangen hydropower station. There is a fish ladder between Aurlandselva and Vassbygdvatnet that functions well for migrations in itself but the attraction towards the discharge water of Vangen prevents the trout from finding it. When the water

flow was naturalized in Aurlandselva during early summer the trout immediately migrated downriver to the fjord.

Detailed analyses of the acoustic telemetry data revealed that 2D and 3D lake habitat use was affected by a complex interplay between fish size, water temperature and the prevailing water maneuvering regime. The trout seemed to prefer the warmest available water temperature during winter. The depth utilization was highly influenced by the temperature, but is also directly influenced by the maneuvering of the hydropower plant and different size groups responded differently towards the different discharge levels. Large variations in the depth use and temperature conditions in Vassbygdvatnet between the two seasons caused the trout to winter at different depths the consecutive winters. The lake was stratified at 4.2°C during the 2012-13 winter where the trout showed little variation in depth use and isothermal at <1°C the following year giving large variation in the depth use of the trout. The behavior of the trout during the two winters revealed that the trout preferred the warmest available temperature in the lake.

The findings in this study have provided novel insights into the role of freshwater habitat use in the sea trout life cycle and the findings have important management implications pertinent to aspects such as estimation of spawning stock (lake spawning) and maneuvering of water discharge during winter and spring to secure relevant thermal regimes in the lake and allow for down-stream migration, respectively.

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3 Introduction

The teleost fish family *Salmonidae* (Salmonids) is characterized by a considerable flexibility in their life histories with high variability in growth rate, size at reproduction and migratory behavior, both within and between species. Freshwater habitats have few predators and fewer potential pathogens than marine waters, and are utilized as nursing areas and growth for the juvenile populations of anadromous salmonids, but both resident and migrant life histories may be present as evolutionary stable strategies within the same population of salmonids (Jonsson & Jonsson 2011). Size is perhaps the most important life-history trait of salmonids and is directly linked to fitness and reproductive success of salmonid populations (Jonsson & Jonsson 2011). Growth benefits in the more productive marine environment is a key ecological factor favoring migratory behavior, and the individual decision to become a migrant seems to be based upon energetic status and growth in the juvenile freshwater phase (Boel et al. 2014). The benefit of increased growth rate in marine waters is however balanced out by the increased mortality risk by predation, diseases and osmo-regulatory stress of this migratory lifestyle (Jonsson & Jonsson 2011).

Anthropogenic pressures and environmental variability may strongly impact these life history strategies, and population status of salmonids. During the last decades, a marked decline in most anadromous salmonid populations in Norway has been observed. A number of factors in the sea phase, such as climate change, reduced prey availability and increased infection pressure from sea-lice (*Lepeophtheirus salmonis*), have been proposed (Taranger et al. 2014; Thorstad et al. 2014b). Furthermore, loss and degradation of habitat due to pollution, infrastructure and river regulation in freshwater environments are contributing factors to the population decline. Managing migrating fish species is a major scientific and conservation challenge, due to the diverse habitat requirements of these species, as well as the required connectivity between the different habitats.

Sea trout (*Salmo trutta* morpho *trutta*) is named from its utilization of sea habitats, even though it spends most of its life in fresh water. Fresh water is where they hatch, spend their juvenile years, spawn and spend their winters. The sea trout can, after spending their juvenile period (2-6 years) in fresh water and after undergoing several morphological and physiological changes (smoltification), utilize the sea as feeding habitat. The seaward migration normally occurs during spring; when the seas are rich in feeding opportunities and rivers are flooded from snow melt. The reward of migrating to the sea is fast growth as marine waters hold more potential feed organisms and intraspecific competition is reduced. However, sea migrations increase the risk of predation and diseases compared to trout that remain in freshwater resident throughout their life. Sea trout normally return to freshwater during fall in order to spawn and for winter refuge. Sexual maturity is normally reached after 1-3 sea summers. Seawater tolerance of sea trout is reduced at low temperatures, (Jonsson & Jonsson 2011) and as

temperature and available feed organisms at sea decrease during fall and winter, and as predation remains a threat, the reward of staying in seawater may not be worth the risk involved. By migrating back to freshwater, and using it as winter refuge until spring, also by the population that is not sexually mature, enable the trout to eliminate the risk marine habitats represent, but the problem of food availability is not eliminated, and is a main reason why winter is believed to be a bottleneck-period for trout (Cunjak & Power 1986). Alongside temperature stress, floods and various threats from stranding, oxygen depletion e.g., fresh water generally have lower temperatures through winter than marine environments. The low temperatures in freshwater can give metabolic benefits are achieved in freshwater when food are unavailable. Low temperatures slow down the metabolic rate of ectothermal species, prolonging the longevity of energy reserves (Jonsson & Jonsson 2011).

Even though winter has been argued to be a bottleneck for salmonids populations, few studies have been undertaken that describe the winter activity in fresh water of salmonids and the few that are done, mainly focus on the winter-activity in the rivers under various ice conditions (Fette et al. 2007; Linnansaari et al. 2008; Linnansaari & Cunjak 2010; Stickler et al. 2010) and few in lakes. Winter activity of salmonids was reviewed as a “life in the ice-lane” by Greenberg et al. (2007) more studies of winter activity of salmonids should be undertaken in order to fully understand the lifecycle of salmonids. Most studies of salmonids are undertaken from spring until fall, due to ice, short days and harsh weather making study conditions difficult, and therefore little is known about the behavior of trout during winter.

With all the benefits of hydropower: renewability, being a predictable and stable power-source that in most cases is highly profitable, the local environmental damages hydropower causes is often neglected. In the case of hydropower, there is a clear conflict between environmental cost and benefit, depending on what scale it is measured. Negative environmental impacts caused locally by hydropower are weighed against the demand for renewable energy that can replace greenhouse gas emitting energy sources and reduce global warming. The ecological function of regulated rivers is often severely reduced due to loss of habitat features, water-covered area, altered temperatures and bottom freezing, resulting in reduced production in the rivers and low fish biomass (Ellis & Jones 2013; Fette et al. 2007). Altered waterways and fluctuations in discharge over short time-periods, seasonal discharge deviations from what is natural caused by hydropeaking, are well documented for having negative effects on fish production and biomass and are often a direct cause of the altering of natural processes in rivers (Fette et al. 2007). Direct mortality for migrating fish in hydropower turbines is also common for fish migrating downstream in regulated rivers (Kraabol et al. 2008). Measures like the construction of weirs, restocking, spillways and fish ladders can be useful tools to mitigate some of the negative effects caused by the development of hydropower on fish populations (Brittain 2003), but the positive

effects from mitigating measures seldom outweighs the negative effects caused by altering the natural processes in rivers on which the organisms that live there are adapted to and really on.

Telemetry technology allows us to study animal behavior in their natural environment (Krejcar 2011). Recent advances in biotelemetry and analysis tools give a more nuanced view of animal behavior and movement patterns (Simpfendorfer et al. 2002). Acoustic telemetry is a well-established technology that makes it possible to follow fish behavior accurately and observe fish in a great range of habitats, including both freshwater and saltwater where it previously was difficult and without permanently damaging or killing fish as data is collected (Adams et al. 2012). The technology is well suited to study winter behavior of fish in fresh water systems (Bass et al. 2014). The ability to track live fish in its natural environment can give insight in the natural behavior of fish under hostile conditions, where it previously was impossible, and help us understand winter behavior of sea trout in fresh water and lakes in particular.

Various studies have been carried out on the sea trout population in the regulated Aurland river system, Western Norway. Fish density surveys and the counting of spawners have been carried out on numerous occasions (Jensen et al. 1993; Pulg et al. 2013; Sægrov 2000) alongside recent river habitat evaluations (Pulg et al. 2013). Common for all these studies is that the individuals that reside in Vassbygdatnet have been understudied and in most cases not included at all. As Vassbygdatnet is a large part of the anadromous stretch of the in the Aurland discharge area there is a knowledge gap for the freshwater habitat use of the trout population Aurland. In this study, I intend to fill some of these knowledge gaps for Aurland population and suggest new ideas of the use of lakes by sea trout in general.

This is an exploratory study, aiming to determine the seasonal utilization of freshwater habitats for post juvenile sea trout. Furthermore, to determine the in-lake habitat use on a temporal and three-dimensional scale and identify factors that governs the habitat utilization. By identifying behavioral responses to environmental changes and monitor changes in the habitat use over time and space more precise management strategies can be implemented.

The aim for this study is therefore to quantify freshwater habitat utilization for different life stages of sea trout over time and space, in the Aurlandsvassdraget watercourse by using acoustic telemetry technology. I will identify and quantify the effect from the most important environmental factors affecting the habitat use. Finally, the fish management implications of my findings will be discussed and suggestions for further study topics will be proposed.

4 Material and method

4.1 Area description

Lake Vassbygdatnet (Vassbygdatnet) is located in the Discharge area Aurlandsvassdraget (Aurlandsvassdraget). The lake has a surface area of 1.84 km² and is located 54 meters above sea level. The average depth is 40 m and maximum depth is 65m. The lake is located in the Valley Aurlandsdalen that is flanked by steep mountainsides with one main entrance river, River Vassbygdelvi (Vassbygdelvi), with its tributary, the River Midjeelvi (Midjeleva). The lake is oligotrophic and classified as a lime-poor clear lake, and the ecological state is the water quality and ecological state is classified as “good”, but this assessment is based on incomplete information (Vann-nett 2014). The River Aurlandselva (Aurlandselva) runs out of Vassbygdatnet and connects the watercourse to the marine habitat the Fjord Aurlandsfjorden (Aurlandsfjorden), a branch of the Fjord Sognefjorden in Sogn og Fjordane County.



Figure 1 The study area (Norges Kartverk 2014)

Aurlandsvassdraget comprises 818 km² with a mean annual discharge of 40 m³s⁻¹ and the catchment area to Vassbygdatnet is 759 km² with a mean annual incoming discharge of 37.6 m³s⁻¹ (NVE 2014) and originates from a high-mountain plateau that originally, drained through steep ravines and

waterfalls in the higher parts of Midjeelvi and Vassbygdelvi before the valley levels out and the river widens. Aurlandsvassdraget is, however, regulated for hydropower purposes so most of the water, both in and out of Vassbygdvatnet, does not follow its natural course, but runs through tunnels and turbines to the Hydropower plant Aurland I (Aurland I). The water is then lead into Vassbygdvatnet and continues through the Hydropower plant Vangen (Vangen) to Aurlandsfjorden. The construction of the hydropower scheme started in 1969 and was developed through several stages until completion in 1980 (Vinjar 2011). The ecological state of Aurlandselva is classified as “poor” due to hydro-hydropower-induced morphological changes and altered water flow regime (Vann-nett 2014).

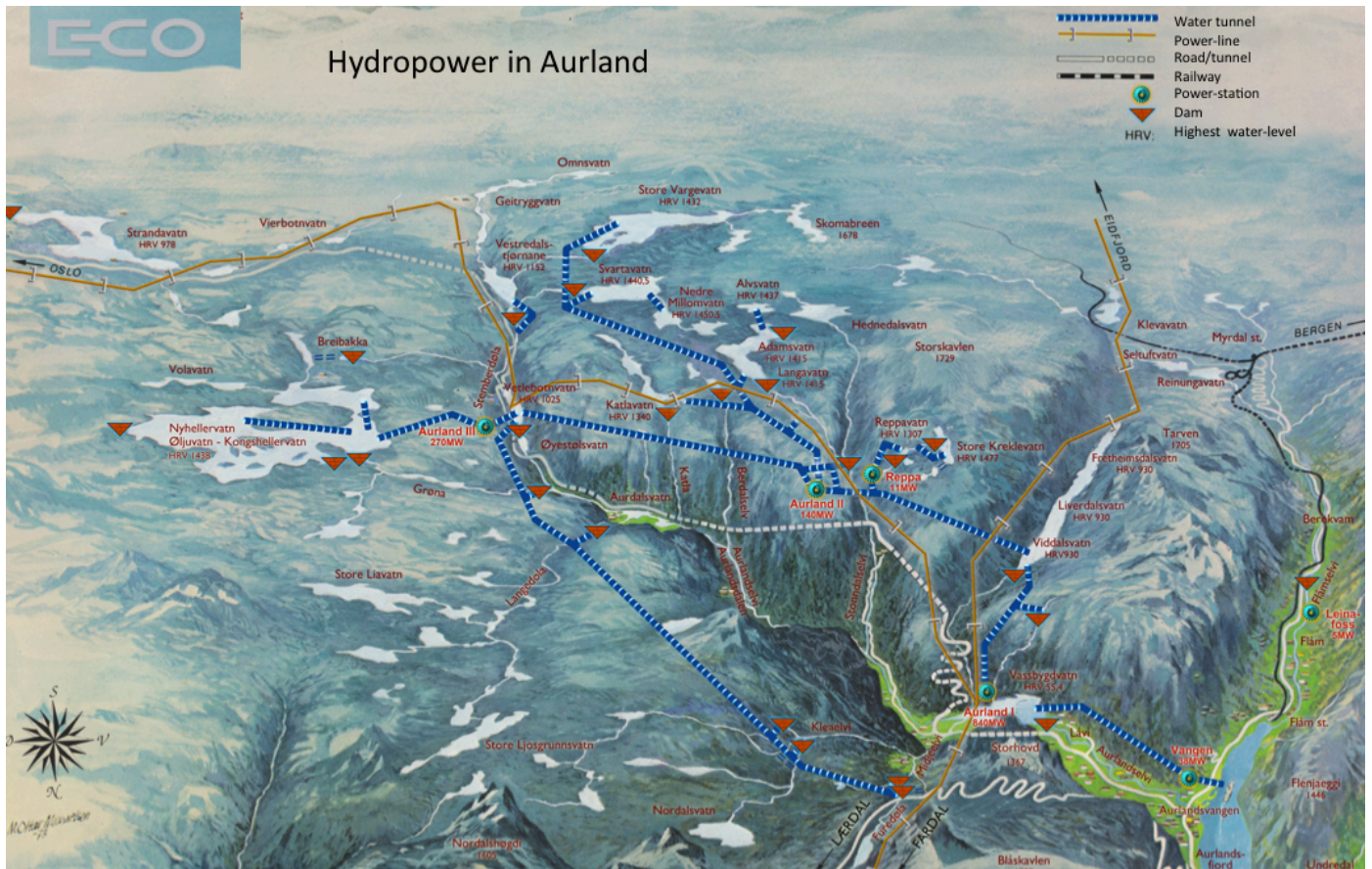


Figure 2 Map over the watershed and the regulation scheme in Aurland provided by E-CO Energi

The residual watershed that is not regulated for hydropower draining into Vassbygdvatnet is 166 km². The minimum discharge to Vassbygdelvi from the headwater Lake Viddalsvatnet is 0.3 m³s⁻¹. Summer discharge in Aurlandselva is from May 1 to September 15. During this period Vangen is inoperative and the dam holding water back from Aurlandselva is lowered, so the discharge in Aurlandselva is not regulated but the discharge is still affected by the maneuvering of Aurland I. The inlet tunnel to Vangen is located at 15 m depth of Vassbygdvatnet and a maximum water intake volume is 100m³s⁻¹.

During winter, September 15 until May 1, the minimum discharge in Aurlandselva is 3m³s⁻¹. A total of 90% of the discharge water running into Vassbygdvatnet originates from Aurland I and is released at surface-level of Vassbygdvatnet. The anadromous stretch of Aurlandsvassdraget is 10.4 km including Aurlandselva (6 km), Vassbygdvatnet (1.4 km) and 3 km of Vassbygdelvi. Prior to regulation for

hydropower, Midjeelevi entailed an anadromous stretch of 1.4 km that currently is unsuitable for fish production as it frequently runs dry (Sægrov 2000). The dominant fish species in Aurlandsvassdraget is brown trout (*Salmo trutta*), but European eel (*Anguilla anguilla*), Atlantic salmon (*Salmo salar*) and three-spined stickleback (*Gasterosteus aculeatus*) are also present in the system (Jensen et al. 1993; Ola Ugedal (pers.com) 2014; Ulrich Pulg (pers.com) 2014).

4.2 Study Species

4.2.1 Brown trout

The brown trout is a European species of salmonid fish. It includes anadromous forms, known as the Atlantic brown trout (*Salmo trutta morpha trutta*), also called sea trout. In addition it includes exclusively freshwater reciding populations, often referred to in general as brown trout or lake trout or river trout, (in the same order, *Salmo trutta morpha fario* and *Salmo trutta morpha lacustris*) depending on whether it belongs to a lake or a river population (Jonsson & Jonsson 2011; Klemetsen et al. 2003a). Most trout spawn in running water, but lake spawning has been observed in areas that are influenced by groundwater influx e.g., (Brabrand et al. 2002). Furthermore, brackish-water spawning has been documented in the Baltic Sea (Jonsson & Jonsson 2011). Anadromous forms migrate to the ocean after smoltification, the development of salt-water tolerance, and returns to fresh water to spawn and for winter refuge (Jonsson & Jonsson 2011).

Atlantic brown trout ranges from: in the northeast, the tributaries of the White Sea, Iceland in the Northwest and, in the south, the river Douro on the border between Spain and Portugal. Brown trout have also been introduced to many regions around the world beyond their natural distribution range and established self-sustaining, wild populations in many of the introduced countries (Jonsson & Jonsson 2011). Brown trout are opportunistic predators, while in freshwater, their diets mainly consist of invertebrates and crustaceans, other fish and invertebrates (Jonsson & Jonsson 2011). As they grow larger, brown trout change their diet from small invertebrates to larger pray like crustaceans and larger fish. The migratory and anadromous forms of brown trout grow significantly larger than stationary forms mainly due to abundance of forage fish in the waters where they migrate (Klemetsen et al. 2003b). Shifts in the diet and habitat during their lifetime reduce intra-specific competition and cannibalism in the population and is an adaptive trait that can sustain a larger population both in numbers and biomass than a non-migratory population (Jonsson & Jonsson 2011). My study focus on anadromous brown trout, but also include some freshwater-stationary resident lake trout.

Sea trout is currently under threat along the Norwegian west-cost from pollution (acid rain, and local water pollution), habitat loss (river regulation, fragmentation of rivers by roads and other infrastructure, anti-flood measures, and canalization in agricultural areas), and high levels of

aquaculture-induced pathogens, with sea lice being one of the main threats (Taranger et al. 2014). Brown trout is characterized as “least concern” on the international red list but for the sea trout is characterized as “markedly declined” (The IUCN Red List 2014). Many of the threats from pollution and habitat loss are currently improving or the rate of deteriorating has slowed down. However, rivers that are heavily regulated maintain a low production and the mitigating measures that often are done after regulation like restocking mainly focus on Atlantic salmon and not on sea trout (Sægvog 2000). The threat from aquaculture-induced pathogens are increasing and are in areas that are heavily developed for aquaculture the main threat to sustain a healthy sea trout population (Taranger et al. 2014). The threat from aquaculture is relatively new in contrast to river regulation for hydropower in the larger rivers, where most are and have been regulated for the past 30 years along the Norwegian west coast. In that sense the threat from aquaculture affects an already diminished trout population and gravely threatens the population as a whole.

4.2.2 The trout in Aurland

Aurlandsvassdraget was known for being one of the best sea trout (from this point referred to as: trout) rivers in the world. Historical data shows catches of trout prior to hydropower regulation in the period 1969-1984 with reported catches up to six tons annually but also show steady decline after the construction was started. The regulation of Aurlandsvassdraget has led to a severe deterioration of the Atlantic brown trout habitat and population. Atlantic brown trout in Aurlandselva is famous for having large individuals with frequent catches of fish up to 9 kg (Jensen et al. 1993). Aurlandselva still has large individuals, but the biomass and productivity is very low compared to previous grandeur, the trout population is presently characterized as reduced but sustainable (Vann-nett 2014). Large efforts have been done to try to restore some of the damages the construction of hydropower has done to the population the last years (Pulg et al. 2013).

The trout population in Aurland is one of the more studied trout populations in Norway with fish-scale archives as far back as 1911 (Jensen et al. 1993) long time series of counting spawning fish in the rivers (Jensen et al. 1993), mark and recapture studies carried out in 1970 (Jensen et al. 1993) and radio telemetry study in 1992 (Økland et al. 1995), various biological surveys of the status of the fish populations in Aurland and habitat evaluations with emphasis on fish production (Jensen et al. 1993; Pulg et al. 2013; Sægvog 2000). An ecological study of the changes in Vassbygdelvi in following hydropower regulation (Raddum et al. 2008) has been done and more technical research on the temperature regimes in Aurland before and after regulation has been carried out (Bakken et al. 2011).

The growth-rate of the trout in Aurland is relatively low for the freshwater phase with a relatively high average smolt age (Jonsson & Jonsson 2011) of 3-5 years at an average 14.1cm length and reach sexual maturity after 1-3 sea-summers giving a generation time of 5-7 years (Jensen et al. 1993; Sægvog 2000).

The smolt age is high for this latitude, but comparable to what is found in similar cold-water systems (Jonsson & Jonsson 2011; Kristensen 2011). The majority of the sea trout in Aurland migrates in May and returns in August-September and stay in freshwater until next spring when they start a new sea migration (Jensen et al. 1993) as commonly described in the literature (Jonsson & Jonsson 2011).

Altered temperature conditions alongside long-term regulation effects such as: lack of suitable spawning habitats, diverted water, habitat fragmentation and deterioration have been blamed for the severe population decline in Aurlandselva alongside speculations of direct mortalities in Vangen. The combination of these factors has been used to explain the low fish production and rapid deterioration of the trout population in Aurland after the hydropower scheme was constructed (Jensen et al. 1993; Sægrov 2000) Individual growth is also poorer after regulation (Jensen et al. 1993) Elevated winter temperatures as a result of bottom water from Viddalsvatnet holding 4°C is drained in large amounts to the surface of Vassbygdatnet during winter making Vassbygdatnet and Aurlandselva unnaturally warm during winter and the continued discharge of cold melt-water that is not allowed to heat as it runs through the warmer valleys, during spring and summer leads to cold temperatures in Vassbygdatnet and Aurlandselva during summer. The high temperatures during winter are believed to cause phenological shifts of critical life-stages as swim-up timing for hatching juveniles (Sægrov 2000) and the availability of feed organisms and the low summer temperatures is a limiting factor for growth and biomass production in general as there is a large temperature dependence for metabolism and primary production for most of the aquatic organisms present in the system (Jensen et al. 1993). Mortalities by kelts through Vangen from Vassbygdatnet were not observed in the first telemetry study performed in Norway (Økland et al. 1995). A study performed in 2012, where the different habitats within Aurland were mapped, concluded that only 0.2% of the river area was suitable for spawning (Pulg et al. 2013). On the basis of this study efforts have been done to improve the spawning conditions in Aurland alongside other river restoration efforts (reopening channels, removal of migration barriers, renewing of the riverbed).

The temperatures in Vassbygdeldvi has however been elevated after the hydropower was constructed due to groundwater-influx and less melt-water during spring witch have lead to a higher relative insect production (Raddum et al. 2008) than before the hydropower scheme was constructed. However, the total production has decreased much more than the contribution from the increase in relative production, as the river is reduced to a shade of its former grandeur, with a reduction in annual discharge of approximately 80%.

As a mitigating measure for the river regulation, smolt was released from a hatchery, located by Aurlandselva owned by E-CO Energi, in the rivers but did not increase the catches. A total of 30 000

trout smolt and 10 000 salmon smolt was released annually in the period 1980-2000. Poor smolt quality was believed to be the reason and a large proportion became residents instead of sea trout and therefore became a competitor of natural recruits of trout and salmon (Sægrov 2000). The smolt release program in Aurland was terminated in year 2000. An egg burial program replaced the smolt-release program but the efficiency of this practice remains enigmatic.

4.3 Study design

For this study trout were caught in Aurlandsvassdraget at four different time periods and tagged with acoustic transmitters. Hydrophones, able to detect signals from the transmitters, were placed in an array to track the movement and behavior of the trout within Aurlandsvassdraget and the connecting fjords. For this study the trout is classified by fish-lengths; smolt is defined as trout <20cm, finnocks 21-39cm and mature 40cm.

4.3.1 Sampling and surgical protocol

Individual trout from Aurlandsvassdraget were captured with hook and line or electrofishing during four different sampling and tagging periods. (**Figure 3**) Smolts and finnocks at >25cm were caught using electric fishing equipment by certified operators. Finnock and mature trout larger than 25cm were efficiently caught by experienced anglers, using floater and fly. The trout was carefully transported in suitable transport-containers to 6.0 m³ holding tanks located at the hatchery by Aurlandselva, owned by the power company E-CO Energi. The fish was observed from hours to several days depending on the sampling success and intensity during the different sampling periods. Large emphasis on inducing as little strain as possible on the fish throughout the chain of operations.

Sea trout that was large enough for the intended transmitter (**Table 2**), and without any visible signs of physical damage or poor general condition, were selected for tagging. During the spring-tagging periods in April, fish were selected based on visual inspection assessing anadromous appearance only (i.e., silvery body) - and not by size. Larger specimens of the sampled material was preferred during tagging of finnocks and mature trout during fall, as larger trout are believed to a higher survival rate than smaller specimens. An overview of the tagging schedule and transmitter types deployed is provided in **Figure 3**.

The protocol for anesthesia, analgesia and surgery is described by Urke et al. (2013) Fish were anesthetized using Metakain (Finquel ®), (Scan-Aqua), in ventilated water before it is brought to the surgical table. The trout was visually inspected for damages and length was measured. For trout <25 cm, weight was also measured. During surgery, aerated water with 50% dose of anesthesia Anesthesia

and aerated, was supplied through a tube placed in the oral cavity to ventilate the gills. Surgical equipment was sterilized before use, and care was taken to maintain conditions as clean as possible during the procedure. Transmitters were carefully placed in the abdominal cavity of the trout through an incision made in the abdomen in front of the pelvic fin-bone. The incision was closed by two to three suture stitches, and acryl-based adhesive (Histoacryl ®) was added as a sealant to the closed up wound. A small piece of the pelvic fin (2-3 mm) was then cut of and placed in 70% alcohol for genetic analysis and scale samples were taken and filed individually in envelopes. (Urke 2014)

After surgery the trout were placed in a 60-liter recovery tank, with aerated fresh water, and monitored until they gained consciousness. An acoustic receiver (VEMCO VR-100) was placed in the holding tank to confirm that the transmitter was functioning correctly. The handling time was approximately 2 min per fish in total and the fish regained consciousness and showed swimming behavior after 0.5–2 min of recovery. Water temperature during surgery varied from 3.9 to 9.6 °C depending on the sampling period. The trout was released 15 minutes to 24 hours after recovery varying from different sampling and tagging periods. Finnocks and mature tagged during September both years were caught in Aurlandselva and Vassbygdvatnet and for the April tagging-periods, trout was caught in Vassbygdelvi and Aurlandselva. For all tagging-periods the trout was released in the vicinity of where they were captured.

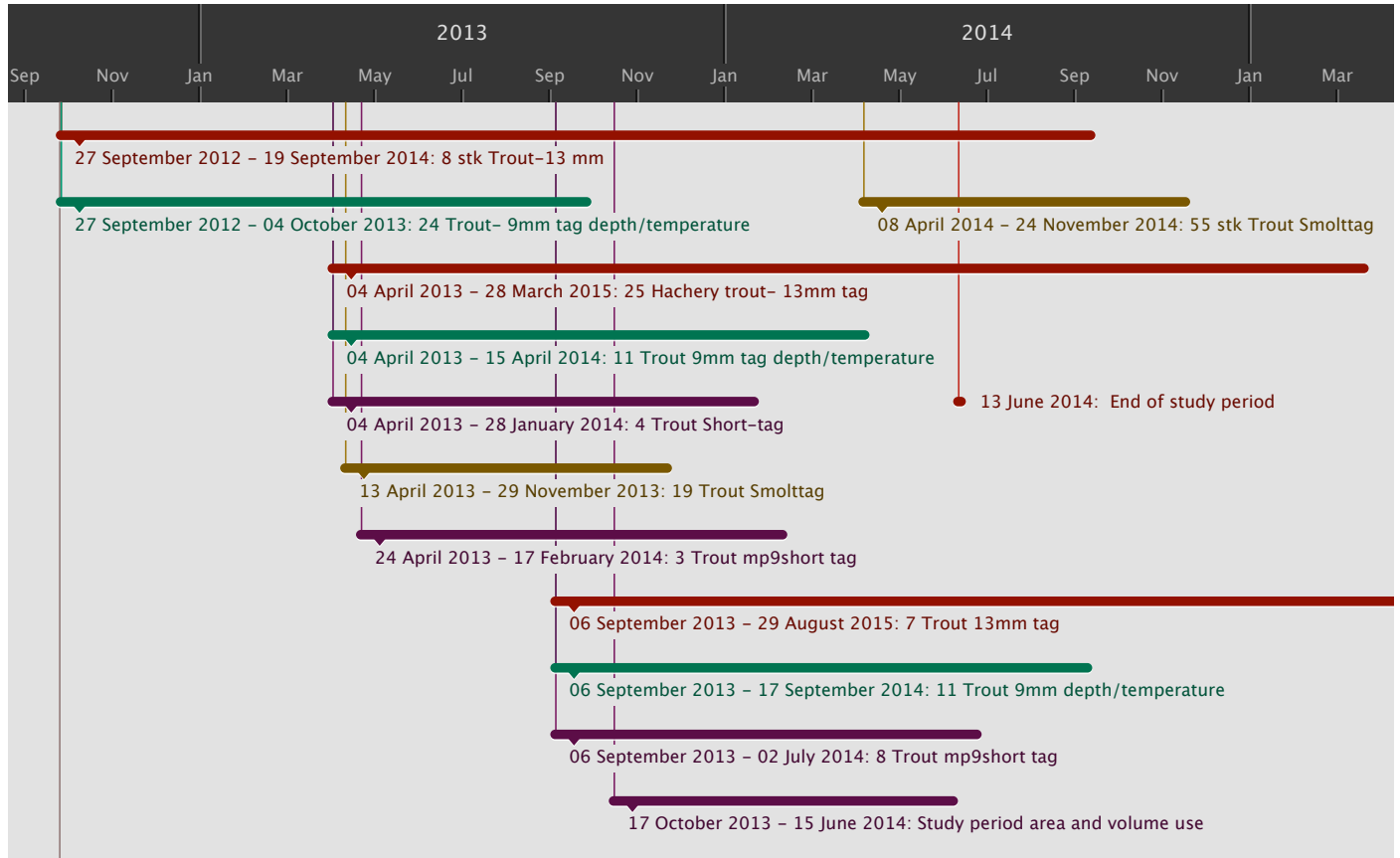


Figure 3 Tagging program of trout in Aurland and the life expectancy of the transmitters used with the end of study period illustrated.

Invasive animal experiments requires approval from animal welfare authorities and this project was granted by the Norwegian Animal Research Authority ID12/4638 and 13/5648 (Mattilsynet 2012; Mattilsynet 2013)

Table 1 The tagging periods, dates and transmitter types, with their specifications, used during this study and the fish lengths of the trout the transmitters were used on.

Tagging period	Date	Transmitter	Transmitter type	(n)	Length average \pm sd cm	Min/Max length
Fall 2012	27-30.09.12	9 mm	Instant-ID/depth/temp	24	34.2 \pm 4.1	44 / 28
		13 mm	Instant-ID + depth/temp data-storage	9	48.1 \pm 10.6	59 / 37
Spring 2013	13.04.13	smolt	Instant-ID	30	20.3 \pm 3.8	15.0 / 28.5
		mp9short	Instant-ID	7	29.0 \pm 3.1	29.0 / 36.0
Fall 2013	06.09.13	9 mm	Instant-ID/depth/temp	4	37 \pm 5.6	24/46
		13 mm	Instant-ID + depth/temp data-storage	7	52 \pm 10.1	41/72
		mp9short	Instant-ID	4	30 \pm 4.2	24 /46
Spring 2014	13-24.04.14	smolt	Instant-ID	56	16.4 \pm 4.1	12,0/28,2

4.3.2 Acoustic transmitters

In this project, acoustic transmitters developed by Thelma Biothel were used. These transmitters transmit a number of acoustic pulses, where the inter-distance between pulses makes an ID-code used to identify the individual fish. The delay time between signals are randomized to reduce code collisions with an average time interval of 3 minutes between transmitter signals. (Thelma Biotel 2013). Depth, temperature and other sensor data can also be collected in accordance to the specification provided by the Thelma Biothel transmitters.

Transmitter-range was measured in Vassbygdatnet during September 2014 on the smolt- and mp9short-transmitters. The transmitter range was tested, by placing a VR2W-receiver at a fixed point, and gradually moving away from the receiver. By measuring the distance to the receiver, and keeping precise control over the time at a given distance. Transmitted signals were frequently detected at 150m and giving inconsistent detections at 180m for both transmitter types. No signals were received at 200m, giving a range of 150-180m (Table 2).

Table 2 Transmitter-type specifications of transmitters used for this study with transmitter-range and the fish-lengths they are applicable. *Range was not measured in Vassbygdatnet but during winter conditions in Lake Lesjaskogvatnet, a comparable oligotrophic lake, retrieved from Bass et al. (2014).

Transmitter type	Fish size	Specification	Battery life guaranteed	Battery life expectancy	Range m
9 mm	>24cm	ID depth/temp inst	282 Days	471	350-500*
13 mm	>30cm	ID depth/temp data-storage	572 Days	955	350-500*
smolt	>12cm	ID	173 Days	289	150-180
mp9short	>15cm	ID	173 Days	289	150-180

The Mp9Short and the smolt-transmitter provide instant ID while the 9 mm transmitters provide alternating temperature and depth information and instant ID on every signal transmitted. The 13 mm transmitter is a data storage transmitter that provides information about the average temperature and depth the fish have used over the preceding eight days (Thelma Biotel 2013). Sensor information from

the data storage transmitters is not used in this study as they are designed for less frequently received transmissions than in the case of my Vassbygdvatnet receiver set-up, However, information on ID from and position from these transmitters was used.

4.3.3 Acoustic receivers

I used acoustic VR2W receivers produced by VEMCO Division AMIRIX Systems Inc. Halifax, NS, Canada and receive signals at 69 kHz. (Vemco). The VR2W receivers receive signals from passing tagged fish that are within the transmission range. To confirm that all transmitters were working the VR2W records the identification number and time stamp from acoustic transmitters as a tagged trout travels within transmission range. The VR2W data were downloaded *in situ* to an ordinary laptop PC via Bluetooth wireless connection. The VR2Ws were placed in a triangulation set-up securing coverage of transmitter signals throughout the lake (Figure 4)

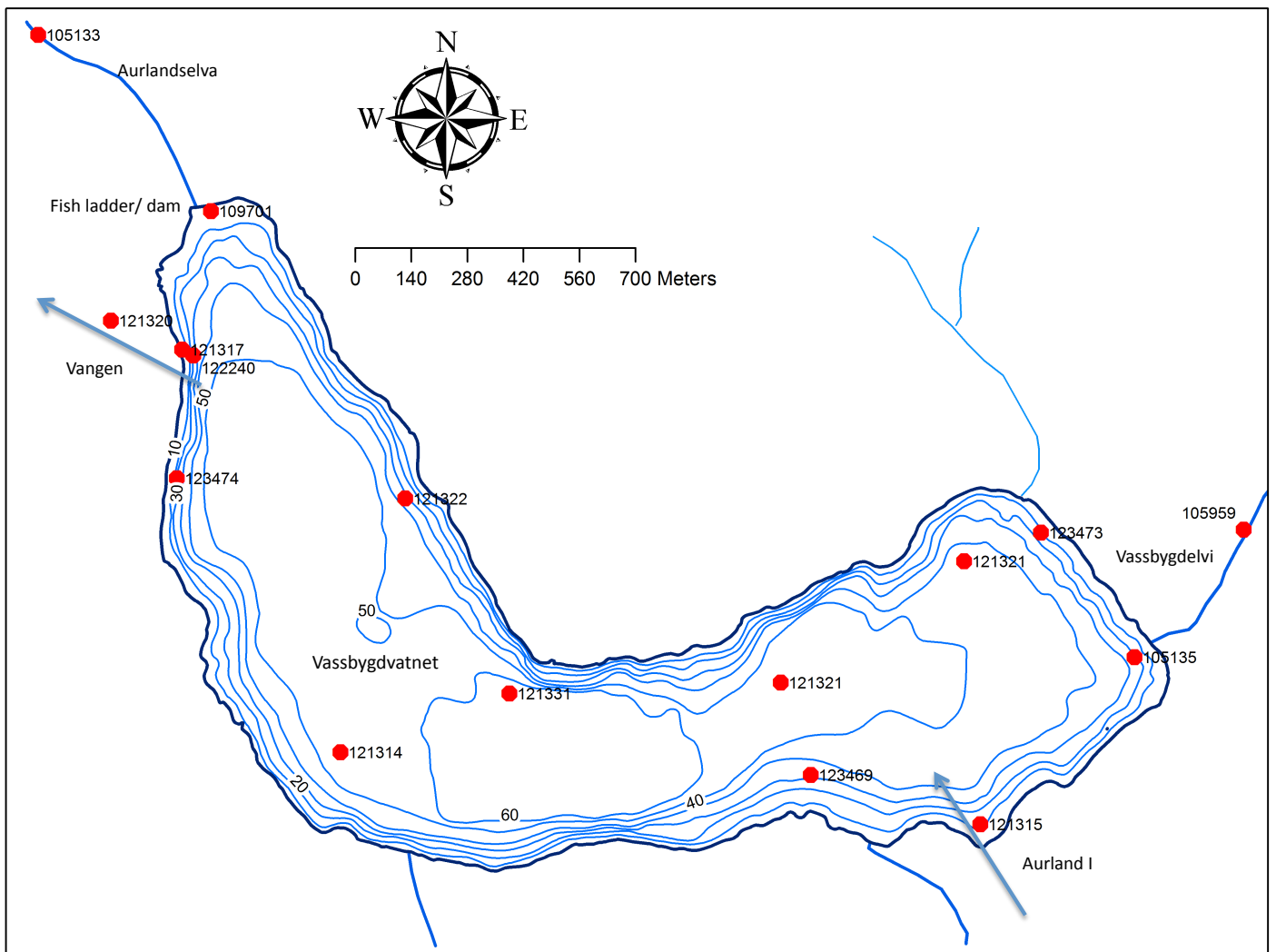


Figure 4 Bathymetric map of Vassbygdvatnet with the rivers running in and out. The hydropower outlet and inlet is shown for Aurland I and Vangen with the arrow indicating direction of flow. The receiver network drawn in indicated with red dots with VR2W-ID.

The VR2W receivers were placed in the lake and fjord moored to the bottom by anchor and rope and strapped to the rope at 3-4 meter depth with the hydrophone pointing downwards with a buoy keeping the device upright in the water. The VR2W receivers mounted in shallow water (rivers and estuaries) were mounted to a metal anchor placed on the bottom with the hydrophone pointing upwards.

In total, 12 acoustic receivers were placed in Vassbygdatnet in the estuary and rivers to record fish as they passed by within detection range. Receiver 121317 was lost due to ice during December-January and was replaced in April 4, by receiver 122240.

The receiver array in Vassbygdatnet is part of a larger system of receivers including the rivers Lærdalselva, Årdalselva and Fortunselva and the entire Sognefjorden with the fjord-branches leading to the mentioned rivers in the KUSTUS project that will be completed in 2015. The loggers placed in the rivers and ocean is not included in the core analyses of this study, but data from the fjord were used to verify sea-ward migration (i.e., anadromy).

4.3.4 Hydroacoustic survey

A hydroacoustic survey was carried out in Vassbygdatnet on March 20, 2014 using a Simrad EK60 transceiver and Simrad ES70-11 transducer at 70kHz. The spit-beam transducer was set up to ping twice pr second during both the daytime and nighttime survey. Survey length day was 13.1 km during daytime and 9.8 km during night yielding coverage of 9.7 and 7.2 %. Prior to the survey, in situ equipment calibration was undertaken following recommendations given in by the European Union for Standardization CEN-EN 15910 (2014)

The hydroacoustic data was analyzed in the Sonar5 software (Balk & Lindem 2000). In this study, -62 dB was used as threshold target strength – which corresponds roughly to 2 cm fish targets. For estimation of length (TL) from single echo detection (SED) target-strengths (TS) data the following formula was employed:

$$TS = 20\log(TL) - 68$$

In order to estimate biomass from the total echo energy combined with the SED TS-distribution, I used the following Length-Weight (LW) relationship formula:

$$W = 0.0085 L^{3.03}$$

Only data collected during the nighttime survey was used for the estimates carried out.

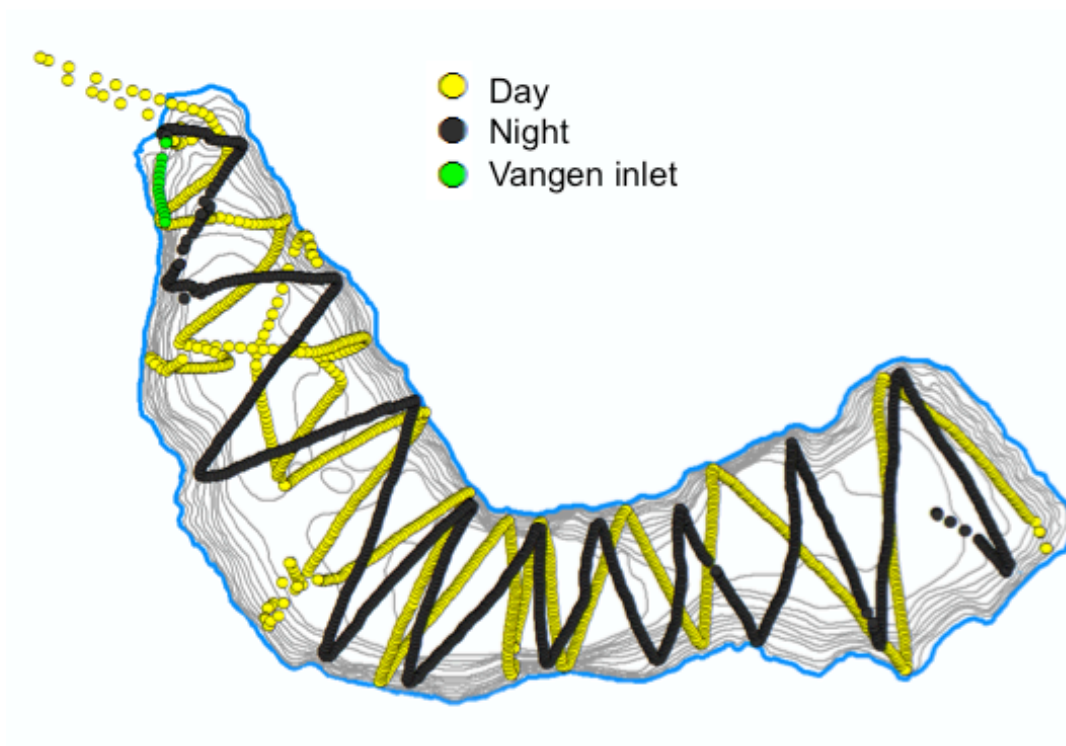


Figure 5 Hydroacoustic survey route during night and day from Vassbygdatnet on March 20, 2014

4.4 Environmental data.

4.4.1 Water temperature data

I measured conductivity, water temperature and depth (CTD) monthly throughout the study period in the lake to get temperature data at different depths. This was undertaken using an SD204 (SAIV A/S) that measures, calculates and records water conductivity (salinity), temperature, depth (pressure) and water density. Data were recorded in physical units and uploaded to a computer via the software, SD200W.

Temperature profile °C Vassbygdvatnet September 2013 – June 2014

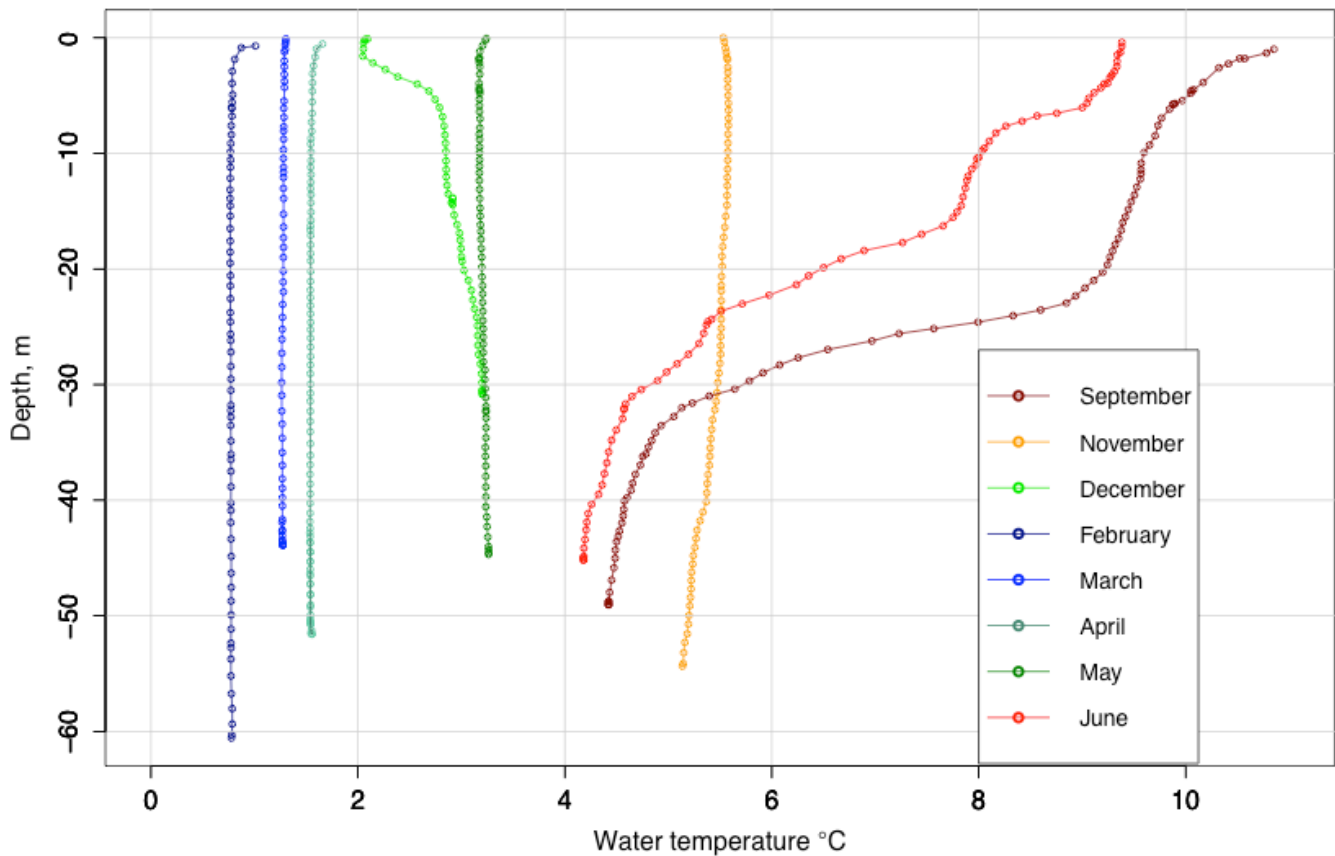


Figure6 Temperature profiles from Vassbygdvatnet September 2013 -June 2014. Data were retrieved from the Saiv204 CTD-sonde.

Temperature loggers (Tinytag) were installed in Vassbygdelvi and Aurlandselva logging water temperature of the incoming and outgoing water to and from the lake once a minute throughout the study period. These data were downloaded to a computer via a serial download pad. TinyTag loggers in Vassbygdelvi and Aurlandselva at 1 m depth in Vassbygdvatnet provide water temperature logs for the entire study period.

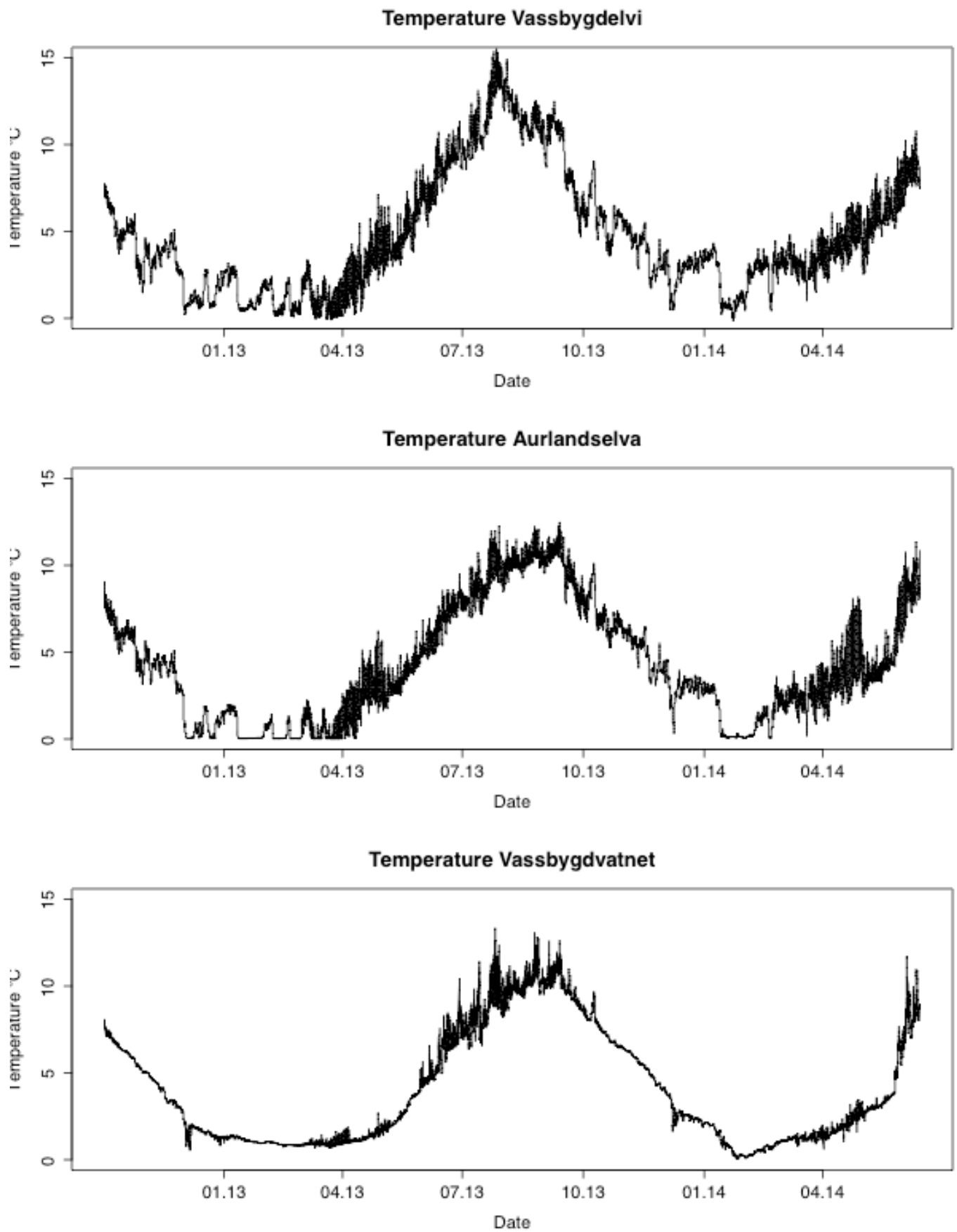


Figure 7 Temperature from Vassbygdelvi, Aurlandselva and Vassbygdvatnet (1m) through the study period gathered from TinyTemp loggers.

The 9 mm transmitter that transmits temperature and depth data also provide temperature data from the lake and rivers when the trout is within receiver detection range (**Figure 19**).

4.4.2 Discharge measurements

E-Co Energi provided data from the discharge water volume from Aurland I running in to Vassbygdvatnet and from Vangen running out. Norwegian Water Resources and Energy Directorate provided discharge water from Vassbygdelvi and Aurlandselva.

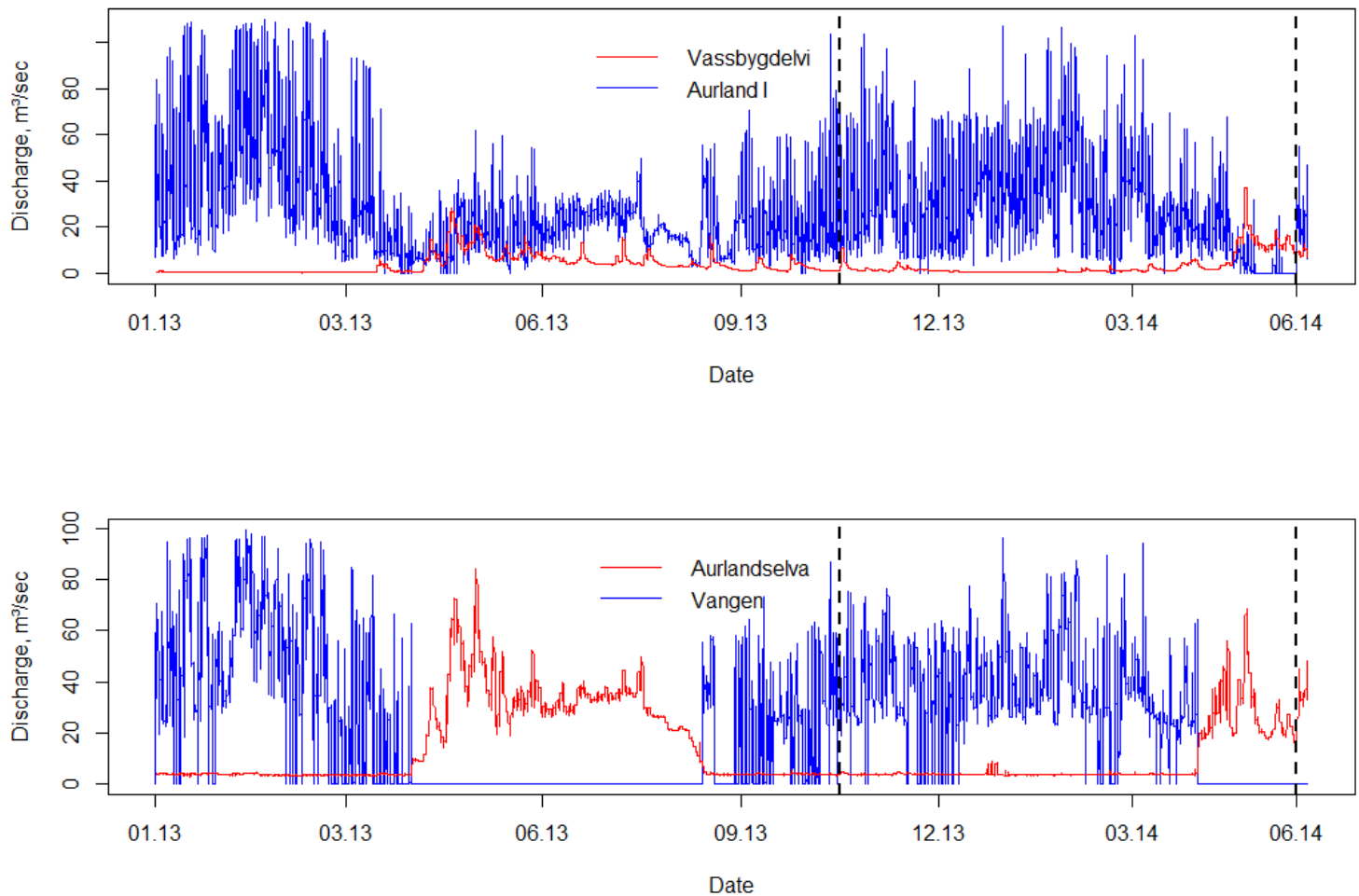


Figure 8 Discharge into Vassbygdvatnet from Vassbygdelvi and Aurland I hydropower plant (top) and discharge out of Vassbygdvatnet from Aurlandselva and Vangen hydropower-plant (bottom) throughout the study period. The dotted line indicates period where area and volume distribution utilization was used

4.5 Fieldwork

The original receiver network, from 2012, comprised of 8 receivers in Vassbygdvatnet including one inside Vangen hydropower tunnel. On 15 November 2013, I added five additional receivers, to the original eight, to the receiver-network in Vassbygdvatnet bringing it to a total of thirteen receivers in the lake including one in the Vangen tunnel.

VR2W data were retrieved, and CTD- profiles measured every month, with the exception of January where ice conditions prevented such operations.

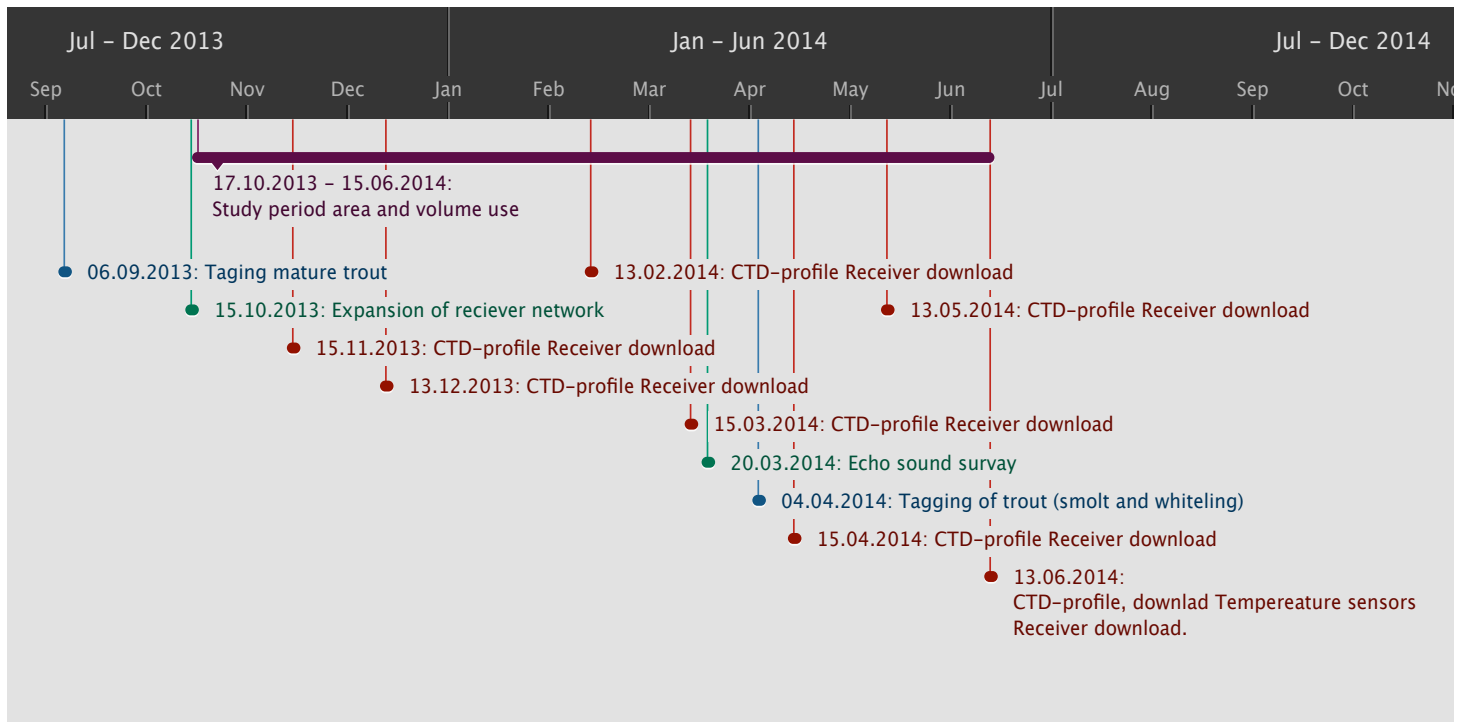


Figure 9 Fieldwork schedule through the study period for area and volume analyses and the tagging date for the trout and time for the hydroacoustic survey. The horizontal line shows the period where distribution utilization analysis were used.

4.6 Quantitative analyses

4.6.1 Large-scale habitat use

In order to estimate large-scale habitat use probabilities four main habitats were selected: Vassbygdeldvi, Vassbygdvatnet, Aurlandselva and Fjord. To estimate the probability of utilizing the selected habitats, a multinomial modeling approach was undertaken. The aim was to estimate these probabilities at any given point in time over the study period, which was not likely to change in a linear fashion over this entire time span. This was achieved by using a vector-generalized additive model approach (VGAM, (Yee & Wild 1996)). This modeling approach allows for non-linear and non-parallel response-trajectories among the response categories. The response trajectories were fitted as spline functions constrained to produce total habitat allocation probabilities = 1 on probability scale. The probabilities were fitted on logit-scale so as to secure fulfillment of this constraint. The models were fitted using the VGAM-package in R (Yee 2010) and model selection (i.e., optimal number of spline knots, k) was conducted using the built-in generalized cross validation procedure (Gu & Wahba 1991).

The last detection for individual trout, each day, - where there was a detection, was extracted and generalized to count for that entire day in order to see how the habitat-use changed throughout the

seasons. The detection-probability in Vassbygdatnet is much higher than in the rivers and in the fjords, so gaps were filled in manually for days missing signals for individual trout to produce a more accurate estimate of where a fish was located over time. To counter for this, gaps in detections were filled manually for individual trout, so if there were two consecutive signals from the same habitat it was assumed that there was no habitat-change for the “missing days”. The habitat of release was used for the time prior the first detection limited by the tagging date. If there was a gap over several days and a change in habitat during that period the habitat for the previous signal was chosen. When signals disappeared from the receivers located in the river-mouth for several days it was interpreted as a move up or down the river. No estimates were done past the last registered detection or before the trout was tagged. The VGAM model time frame is the from the time of tagging and guaranteed battery life of the transmitters for the trout tagged during April 2013, and for the trout tagged during September 2013 and April 2014, the study-period limit was used as cut-of day as it precedes the battery life expectancy for the transmitters. This analysis was only preformed on trout that had detections on receivers.

4.6.2 Migrations

Transmissions received in succession for individual trout in the different habitats was extracted to confirm migration in and out of Vassbygdatnet, Aurlandselva, Vassbygdeldvi and to the fjord. The time of the first registered transmission in the new habitat was used to confirm shifts in habitat. For this analysis, confirmed migrations by the receivers were used only. If there was a habitat shift between two habitats that are not in succession (i.e., Fjord – Vassbygdatnet) no estimate of the migration timing was done. This method was applied for the period July 2013 – June 14.

4.6.3 Spawning

The spawning season was defined 1 October- 1 January. The habitat use throughout the spawning period for suspected mature trout (>40 cm) was extracted from the dataset and the migrations and habitat use was analyzed manually for these trout.

4.6.4 Detailed habitat use

The study system was based on omni-directional hydrophones (VR2W) that were deployed relative to each other so that their detection ranges overlap and the same ping signal can be received by multiple hydrophones. According to Simpfendorfer et al. (2002), a receivers’ probability to detect a transmitters’ signal is linearly related to its distance to the receiver. Hence, the number of receptions over a given time period is higher, the closer the source signal is to the hydrophone. When a signal is detected by multiple hydrophones it is possible to calculate signal source distance relative to each hydrophone by counting how many detections from an individual transmitter, each hydrophone receives. This gives an average estimate of the transmitter position (PAV) over a set time period. The accuracy of the estimated position increases whit the number of received signals and number of hydrophones involved. (Simpfendorfer et al. 2002). Movement patterns and home ranges for tagged individuals can be

constructed by using this data. In my study, such individual-based PAVs were estimated over 30-minutes time slots.

The estimated PAVs were used for estimating individual utilization distributions (UDs), for the area within one removes outliers and only includes the area mostly used by the individual (Rogers & White 2007). I estimated UD's using the same smoothing parameter, $h=50$, across all individuals. The gridding parameter was set to 500. This approach allowed for direct comparison of home range sizes among individuals, without having to consider eventual effects from differential smoothing parameter on the UD's. Weekly UD's were estimated using the kernelUD function embedded in the R package adehabitatHR (R- Core Team 2012)

Volumetric UD's were estimated for individuals with depth-sensor transmitters implanted (**Table 2**). This was conducted using the same 30-minutes slots of XY-position averaging, just by adding the Z-dimension (depth) as the mean depth position within each time slot. The 3D UD's were fitted using the kde function embedded in the ks-package in R (R Core Team 2012).

Space-use variables (depth, XY UD's and XYZ UD's) were included in univariate linear mixed effect models (LME) fitted to estimate effects from a range of external (e.g., water temperature, water discharge) and internal (size) variables on the within-Vassbygdatnet habitat use. For UD's, the 50% distribution levels (i.e., the core distribution area/volume) were used as responses in the LME's. Individual IDs were used as random effect to account for within-individual dependency of observations (Nakagawa & Schielzeth 2010) with model selection following procedures described in Zuur et al. (2009) utilizing Akaike's information criteria (Akaike 1974) for model selection. Model selection tables along with parameter estimate using tables of the selected models are shown in the appendix (section 8.3), and corresponding prediction plots of the selected models are displayed in the results chapter.

For the in-lake habitat use analysis five "seasons" were defined dependent of the dam in Aurlandselva was opened or closed: fall.open 15 August-15 September, Fall.closed 15 September – 15 December, Winter 15 December- 15 March, spring.open 16 March – 30 April and Spring.open, 1 May – 13 June. The x-y axis of the plotted LME-models was, depending on the model, scaled to relevant fish-lengths, discharge volumes from Aurland I and relevant water temperatures for the seasons, in order to avoid predictions beyond the observed values the models are based on.

5 Results

5.1 Large-scale habitat use

5.1.1 Habitat use of trout released in Aurlandselva and Vassbygdvatnet during April 2013

The large-scale habitat use of 34 out of the 35 trout (15-36cm), tagged during April 2013 involved in the VGAM-analysis and revealed that Vassbygdvatnet was the most utilized habitat from April to October. Fjord migrations only occurred during summer months from May-September, and 15 out of the 34 trout tagged had marine migrations (**Figure 10**). Number of observations decreased gradually as time passed and ending up with 17 individuals in October. Hence, the accuracy of the analyses is higher in the early phase than towards the end.

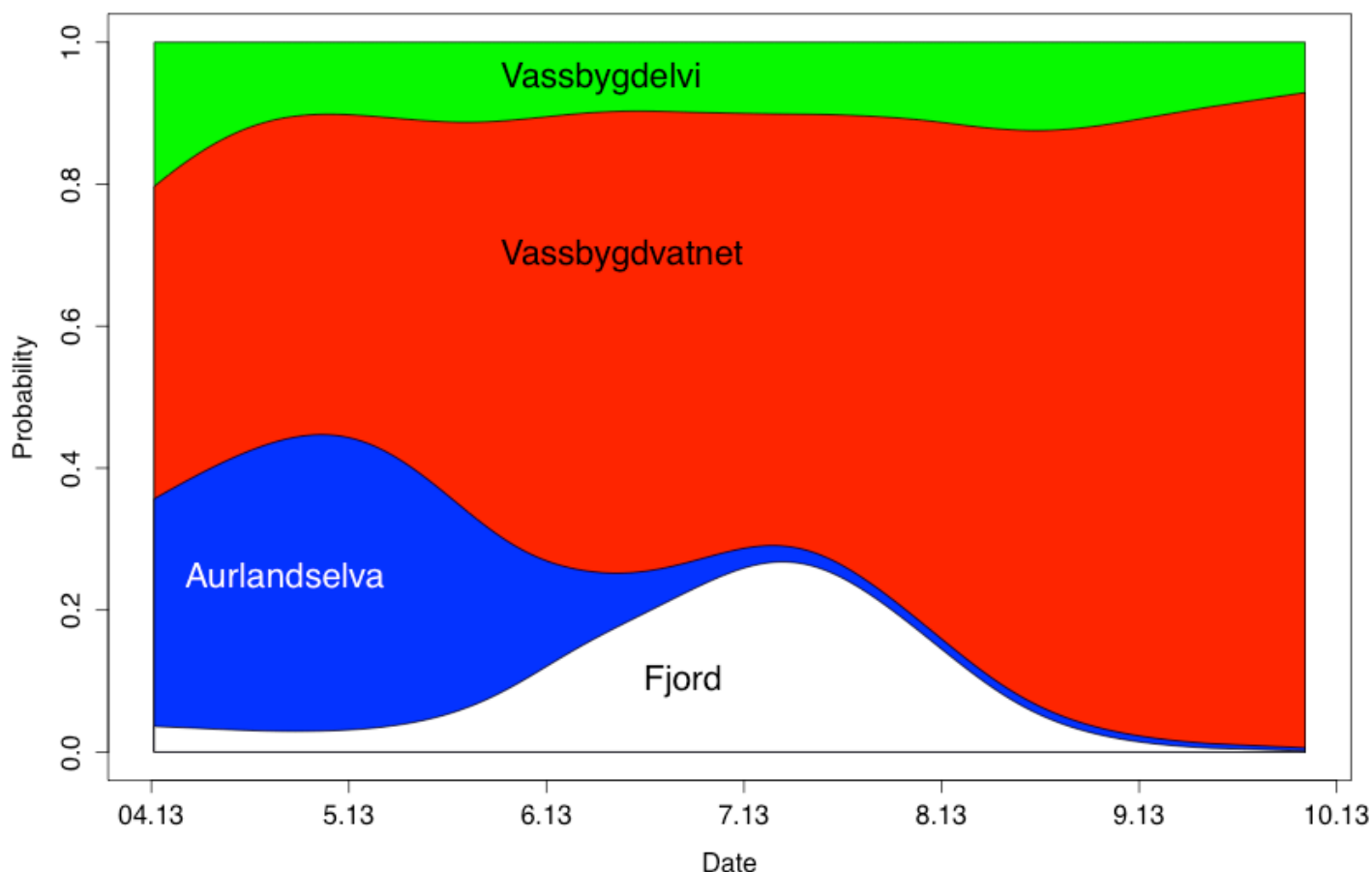


Figure 10 VGAM prediction plot showing the estimated the large-scale habitat use for trout 15-36 cm, tagged during April 2013, for the period April to October 2013 (n=34)

5.1.2 Habitat use of trout released in Aurlandselva and Vassbygdvatnet during September 2013

The VGAM-analyses for the large-scale habitat use from 26 out of 26 trout 24-72 cm, tagged during September 2013 with detections to undergo this analysis. The analysis shows that Vassbygdvatnet is

the preferred habitat during this period accounting for 80% of the tagged populations for the period from September 2013 to May 2014 (**Figure 11**). During early May the trout started migrating to the fjord where 18 individuals had registered fjord migrations. Number of observations decreased gradually as time passed and ending up with 11 individuals in June. Hence, the accuracy of the analyses is higher in the early phase than towards the end.

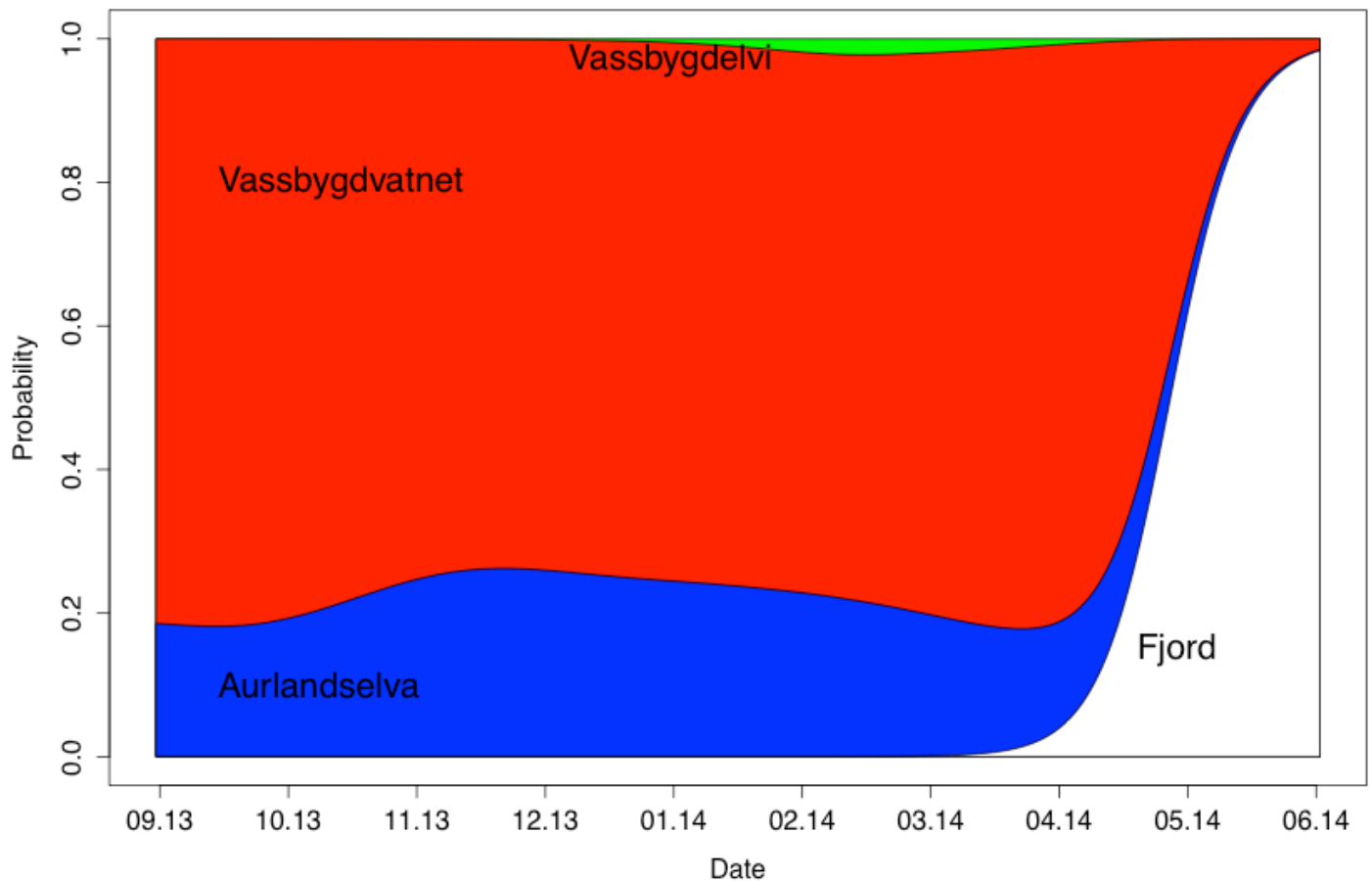


Figure 11 VGAM prediction plot showing the estimated large-scale habitat use for 26/26 mature and finnock (24-72 cm), tagged during September 2013, for the period September 2013 to June 2014.

5.1.3 Habitat use of trout released in Aurlandselva and Vassbygdvatnet during April 2014

VGAM- detection prediction plots for the smolt and finnock tagged during April 2014 were separated on release site in order to see the large-scale habitat use after release. From 22 out of 24 smolts and finnock released in Vassbygdvatnet (12-22 cm), only two smolts migrated to the fjord and were 17.5 and 15.5 cm. All smolt and finnock released in Aurlandselva for 8 out of the 32 (17-28 cm) with detections to undergo this analysis migrated had marine migrations. For this group no upstream migrations to Vassbygdvatnet were observed. The trout migrated downstream during the same time-period but the trout released in Vassbygdvatnet stopped in Vassbygdvatnet whereas the trout that was released in Aurlandselva migrated to the fjord (**Figure 12** and **Figure 13**) For the trout released in Aurlandselva, no upstream migrations were observed. The first fjord migration from the trout released in Vassbygdvatnet occur 46 days later than for the trout released in Aurlandselva. For the trout released in Vassbygdvatnet the number of observations decreased gradually as time passed and ending up with 17 individuals in

June. Hence, the accuracy of the analyses is higher in the early phase than towards the end. For the plot for release in Aurlandselva the number of observations *increased* gradually as time passed due to known release site the location for Aurlandselva is given, before the accuracy decrease as with the other analysis. The plot (**Figure 13**) fails to illustrate the majority of trout that remain in Aurlandselva undetected by the receivers, and fail to meet the criteria for this analysis, and excluded from the plot.

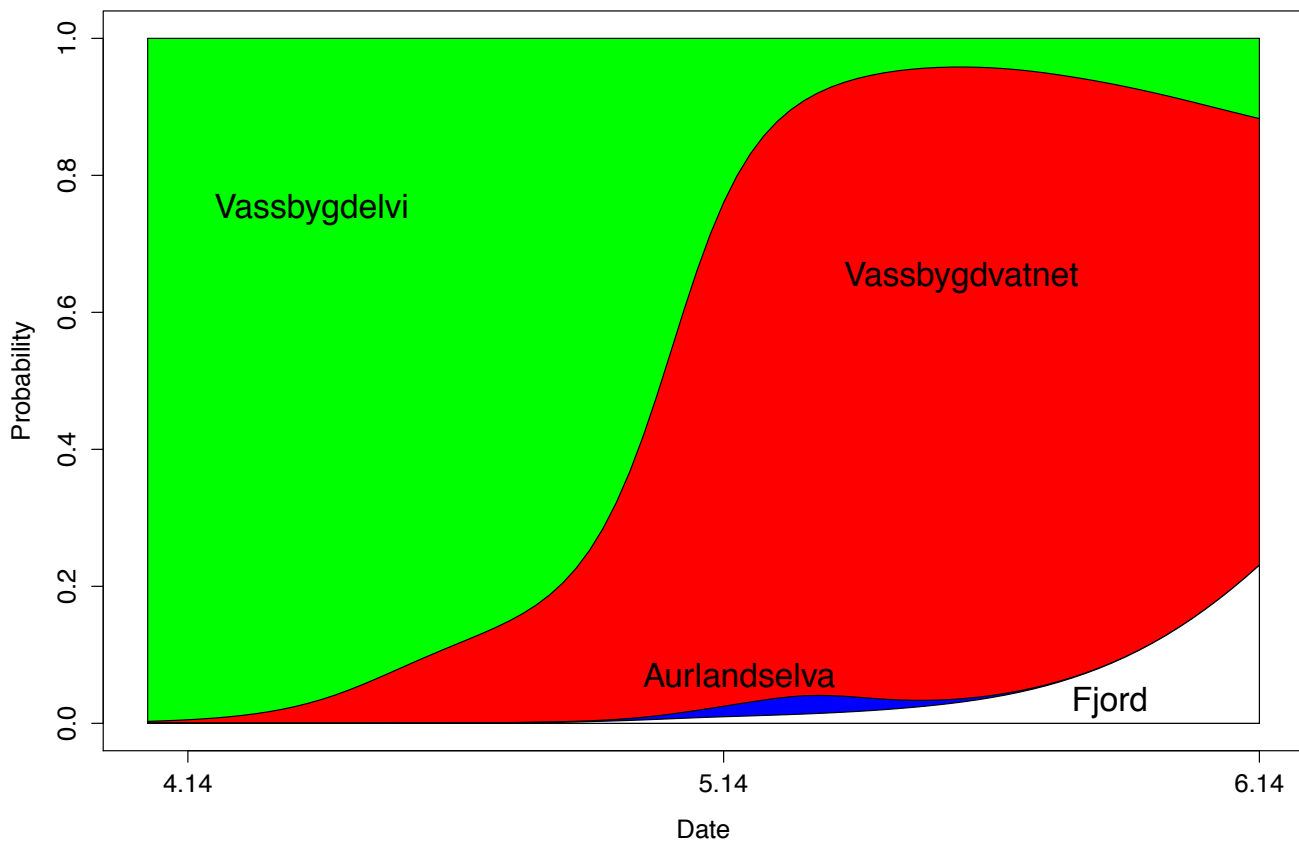


Figure 12 The VGAM- detection prediction plot shows the large-scale habitat use for 22/24 tagged trout (12-22cm) and released in Vassbygdelvi during April 2014, for the period April to June 2014.(n=22)

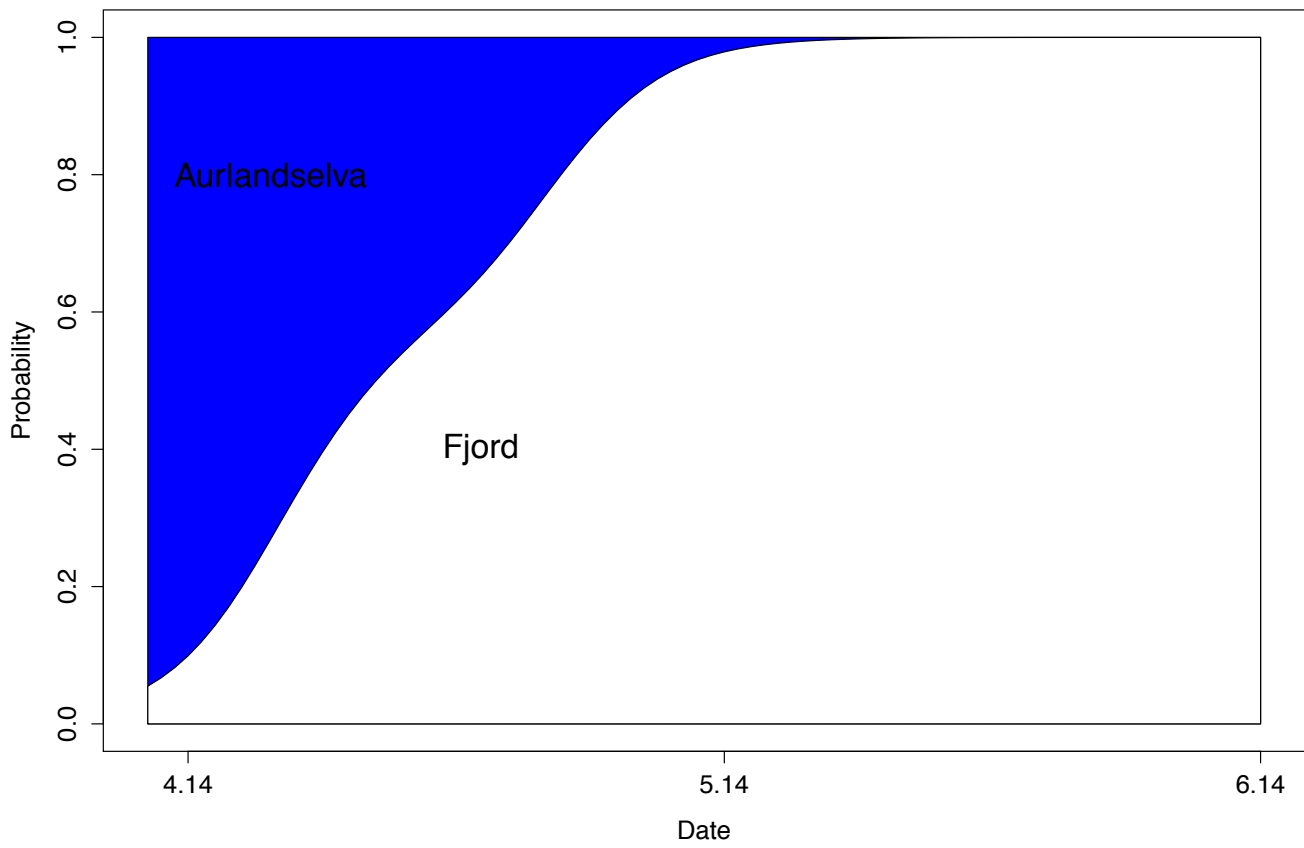


Figure 13 VGAM- detection prediction plot shows the large-scale habitat use for 8/32 trout (17-28 cm), in Aurlandselva during April 2014, for the period April to June 2014.(n=8)

5.1.4 Return from marine habitat

The sea-return timing was recovered for 9 trout during the period 13 July to 28 August, four originated from tagged during September 2012 and 5 from the April 2013 tagging. All registered returns were in the period of naturalized discharge in Aurlandselva, before the dam was elevated and minimum discharge was implemented. The data material for return is limited as it only contains the 8 trout (37-59cm) tagged with 13 mm transmitters during fall 2012 and 15 trout (12-36cm) tagged during spring 2013 that had marine migrations. With 9 out of 21 trout returning from the marine habitat the return rate is 42%.

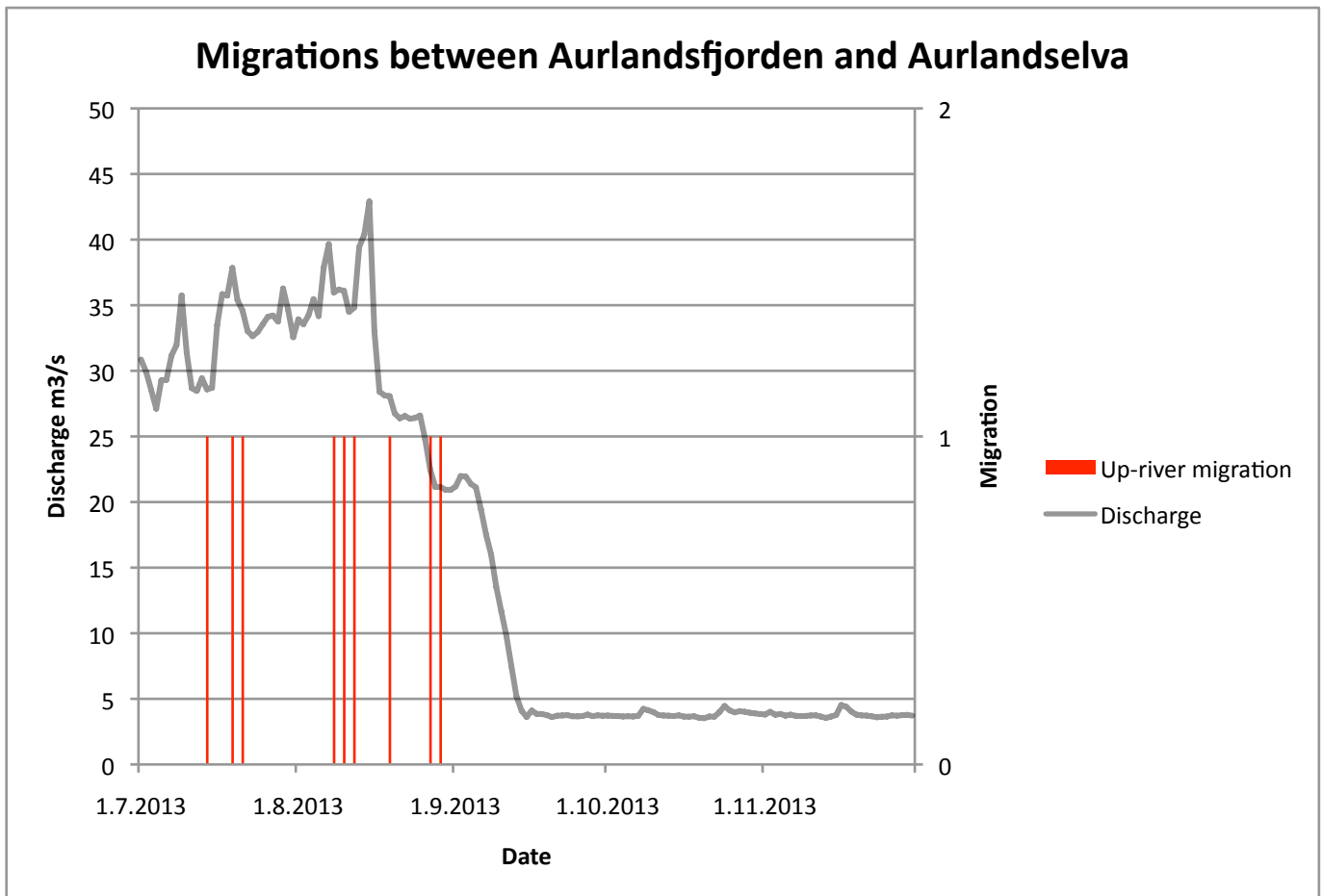


Figure 14 Migrations from marine environment to Aurlandselva from 01.07.13-01-12-13 from trout tagged during September 2012 and spring 2013

5.1.5 Migrations between Aurlandselva and Vassbygdvatnet

The majority of individual trout tagged during fall 2013 migrated into Vassbygdvatnet shortly after release in Aurlandselva and stayed in the lake until spring. In total, 20 individuals that were detected by a river- and lake-receiver migrated between Vassbygdvatnet and Aurlandselva during fall. The recorded habitat shifts were dominantly up-river from Aurlandselva to Vassbygdvatnet, with a peak shortly after tagging 06.09.13 (Figure 15) In total, 19 out of the 26 trout tagged during fall 2013 moved upstream to Vassbygdvatnet from Aurlandselva shortly after release. In addition, two upstream migrations were

observed for trout tagged during September 2012. 13 downstream migrations were observed for trout during fall 2013. Downstream migrations through the fish-ladder were only recorded for fish over 25cm. There were 13 downstream migrations during late spring and winter but no downstream migrations from Vassbygdvatnet was registered during spring before the dam was lowered. After the dam was lowered 01.05.14, five trout moved downriver the first week during two days and 10 followed throughout May and early June with one registered migration per day.

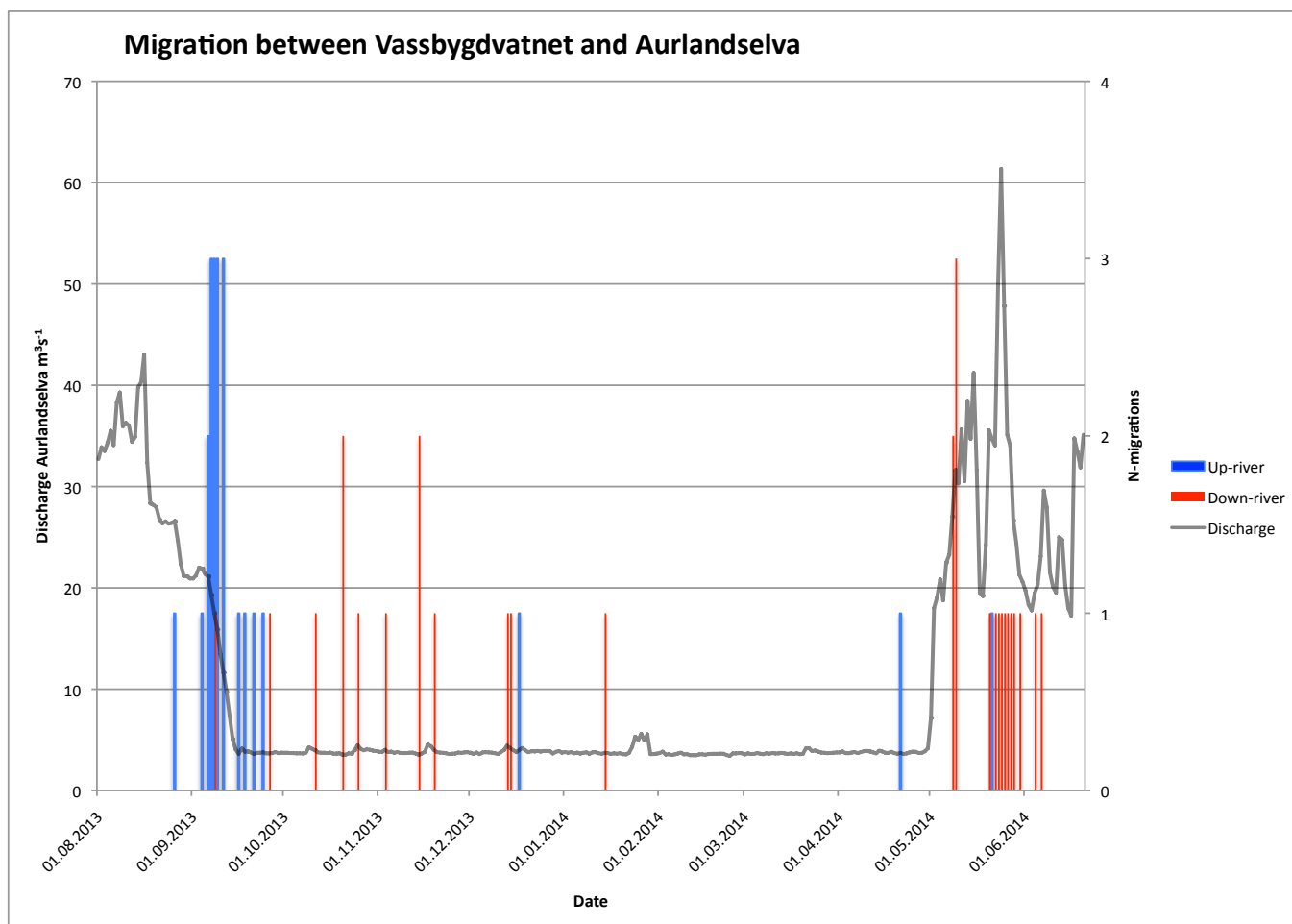


Figure 15 Confirmed migrations between Vassbygdvatnet and Aurlandselva, and the discharge in Aurlandselva.

5.1.6 Upstream migration to Vassbygdelvi from Vassbygdvatnet

From the 24 trout that was released upstream the receiver in Vassbygdelvi, (VR2W-ID 105959) (Figure 4) eight downstream migrations were recorded. Seven recorded migrations occurred during spring and one in January. (Figure 16) There was just one registered up-river migration for the entire study period and 8 registered downstream migrations just prior to release upstream the receiver in Vassbygdelvi. There was only one registered upstream migration between Vassbygdelvi and Vassbygdvatnet during the study period. The one up-river migration was a 26cm finnock that returned to the lake 6 weeks later. All down-stream migrations registered are trout that were caught, tagged and released above the receiver in Vassbygdelvi in April 2014.

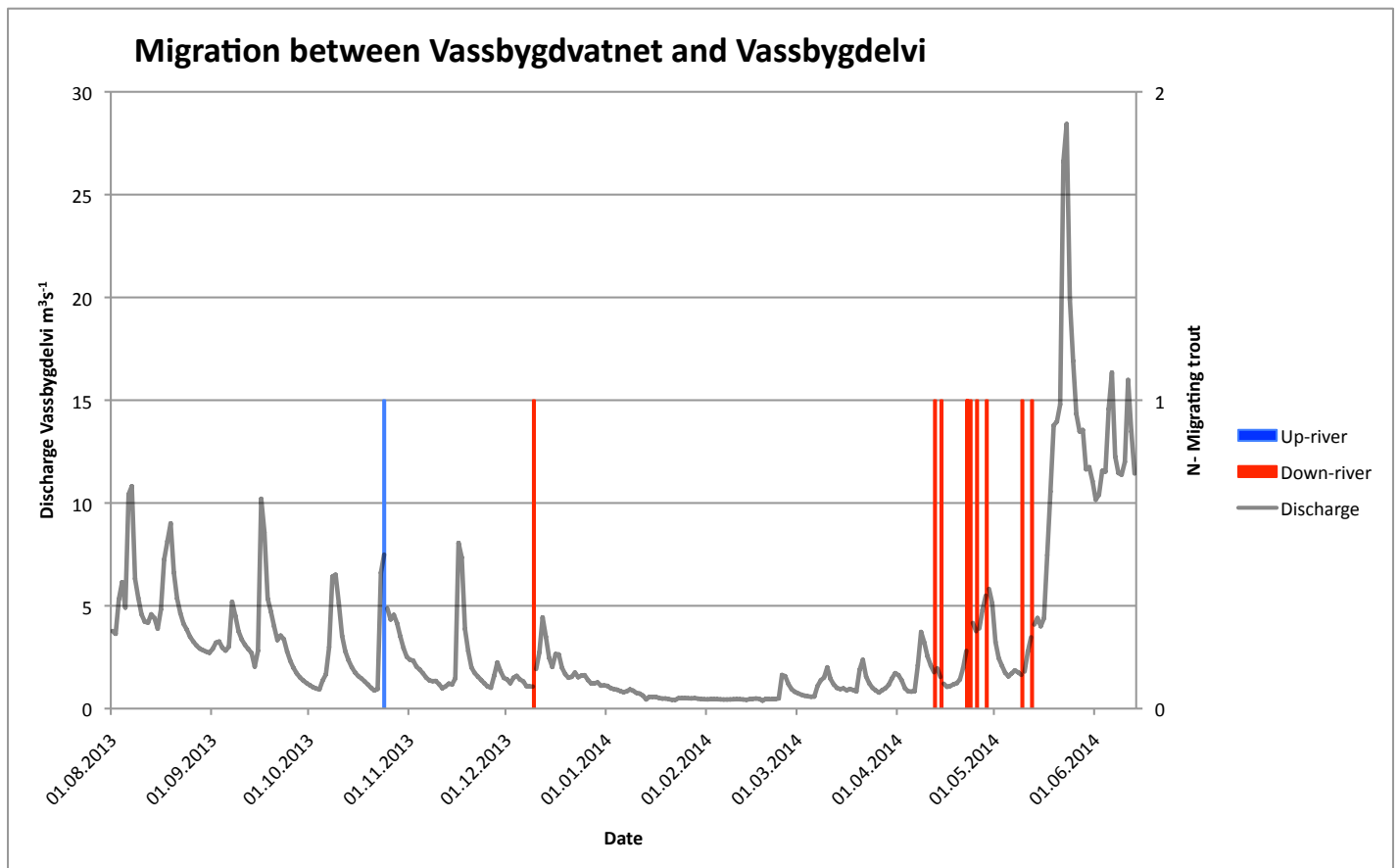


Figure 16 Confirmed migrations between Vassbygdvatnet and Vassbygdelvi and the discharge in Vassbygdelvi. Showing only 2014 as there was no observed migrations during the fall 2013.

5.1.7 Seaward migrations

Seaward migration endured several weeks and had no apparent peak (**Figure 17**). There were 34 registered where 27 occurred after the dam was lowered in Vassbygdvatnet during spring. For nine of these migrations were detected on the estuary receivers and registered the timing of the migration where six occurred between 00:00 and 02:00 and two occurred during daytime. No apparent grouping was found, where several fish migrated during the same time of day. The relationship between changes in discharge and temperature, and the timing of migration is not clear. The trout that migrated before the dam was lowered was trout that had stayed in Aurlandselva through the winter. The full migration history for the summer 2014 is not included as this study was concluded 13 June 2014. During winter 2013-2014 winter migration was observed on four trout, two in December (not plotted in **Figure 17** and two in January.

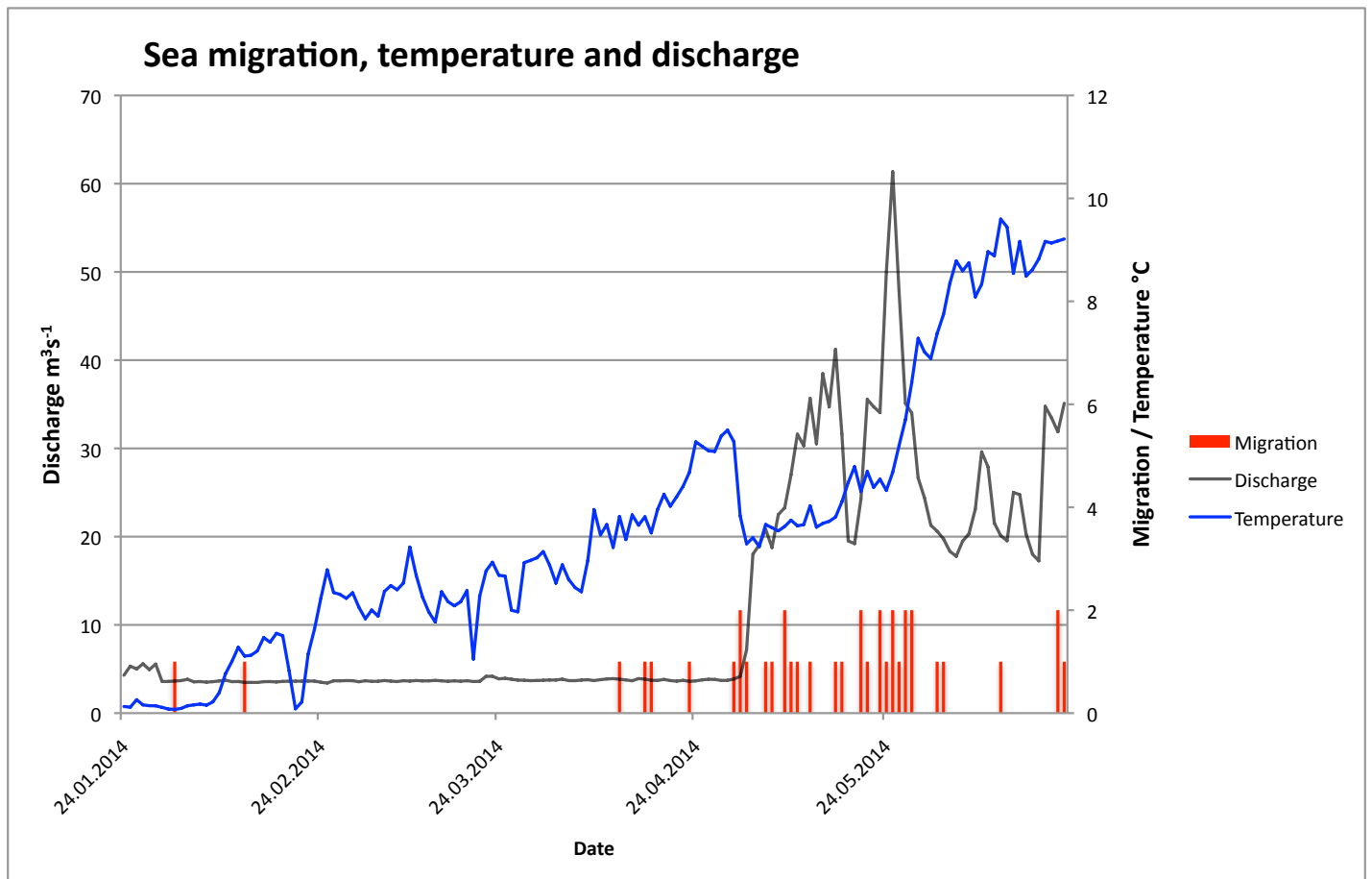


Figure 17 Seaward migrations of trout, during the period January-June in 2014, in relation to river discharge and water temperature in Aurlandselva

5.1.8 Spawning histories

In total 20 spawning histories from 18 individuals was retrieved during the study period, where 10 were suspected to have spawned Aurlandselva and 8 in Vassbygdvatnet. Two trout are suspected to have spawned in the lower stretches of Vassbygdelvi but they were not registered on the receiver located in Vassbygdelvi (VR2W-ID 105959), 408m upriver.

During 2012, five trout stayed in Aurlandselva throughout the spawning period and three stayed in Vassbygdvatnet throughout the period, whereas two possibly migrated up the lower stretches of Vassbygdelvi and spawned there.

During the 2013 spawning season, six out of the eleven trout that were tagged during fall 2013, (>40 cm) stayed in Aurlandselva throughout the spawning season and five in Vassbygdvatnet. Two trout that were tagged in 2012 returned to the same area in which they had spawned the previous year, one to Aurlandselva and the other to Vassbygdvatnet. The trout from 2012 that returned to Vassbygdvatnet in 2013 is suspected to have spawned at different localities the two years.

5.2 Spatial distribution in Vassbygdvatnet

5.2.1 Depth use

The temperatures and depths retrieved from the sensor-transmitters from seven trout 2012-13 (26-46cm) and seven trout 2013-2014 (24-46cm) from Vassbygdvatnet reveal that the trout utilize the full depths of the lake during but chiefly occupy upper 15 meters (**Figure 18**). There was a large difference in depth use temperature the trout endured varied greatly the two studied winters. During 2012-2013, individuals stayed in shallow waters (<3-5 m) throughout winter, with low inter-individual variation, whereas 2013-2014 individuals generally used deeper waters (5-10 m) over long periods and displayed large inter- and intra-individual variation. During the 2012-13 winter the average experienced temperature from the sensor-transmitters never dropped below 4 °C whereas in the 2013-14 winter the average experienced temperature dropped to 0.2°C. The trout wintered at a deeper and more variable depth during the last than during the first winter (**Figure 19**). The temperatures decrease gradually, follow the same pattern during both falls but stabilize at 4.2 °C during the 2012-13 winter but continues to drop during December and January during the 2013-14 winter reaching a minimum in late January before the temperature increased. The experienced temperatures started to increase sharply during April both years.

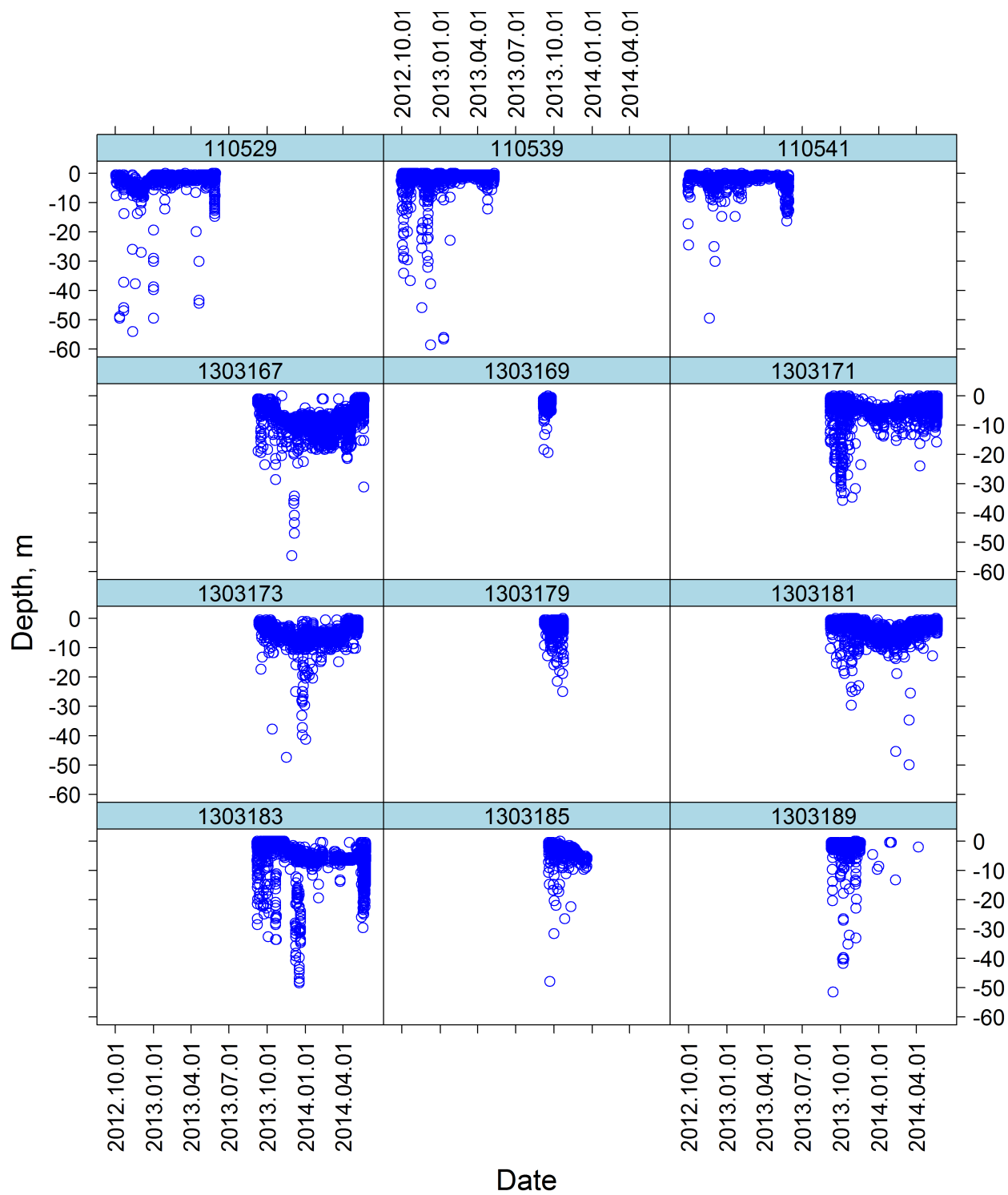


Figure 18 In lake depth use of 12 individual trout (24-46cm) throughout their winter stays in Vassbygdvatnet ID for individual trout is shown. The data on individual trout is found in the appendix (Table 3-Table 5)

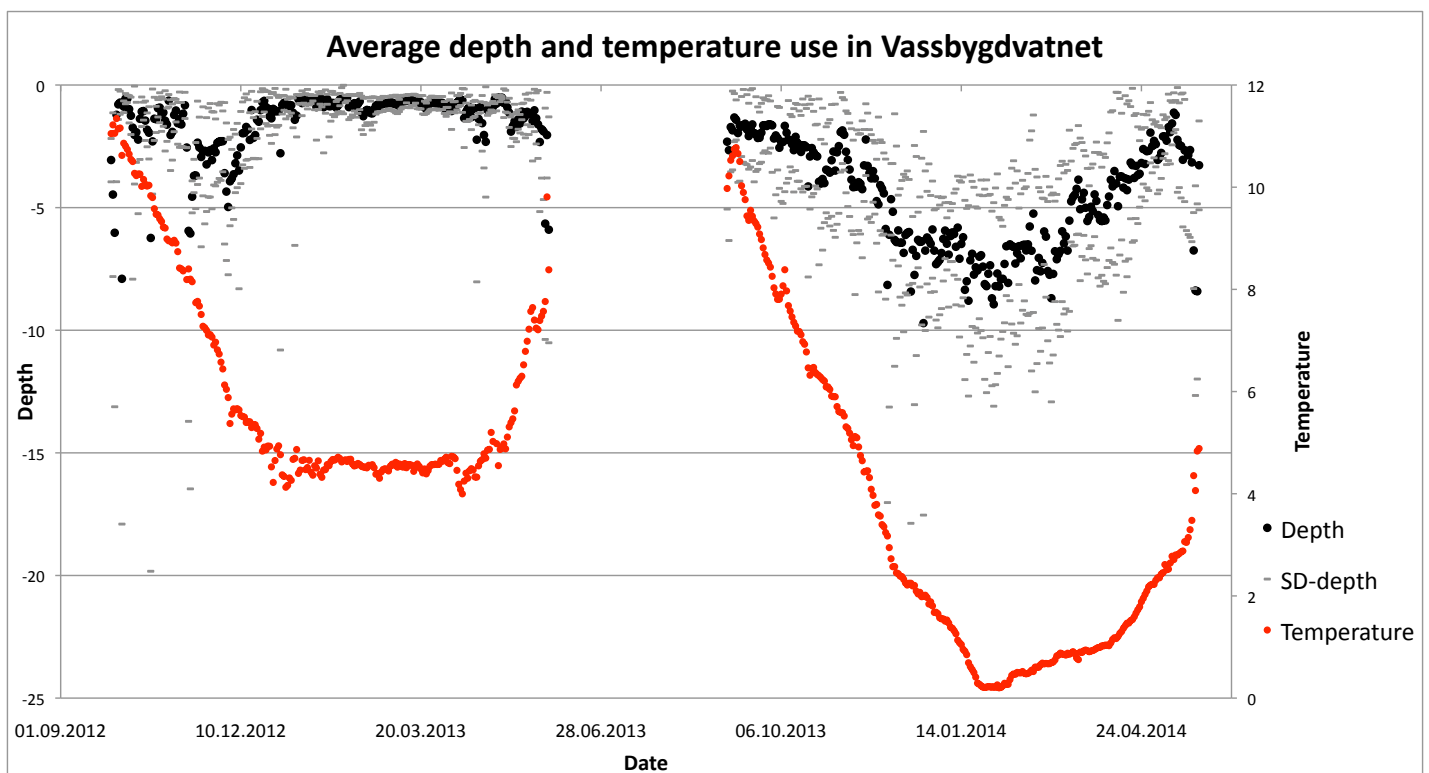


Figure 19 Daily average depth and temperatures of 14 trout, 24-46 cm (n=7) in 2012-13 and 2013-14 (n=7) retrieved from 9mm sensor-transmitters from winters 2012-13 and 2013-14 in Vassbygdvatnet

The main imprint from the most supported LME-model fitted to predict trout depth use in Vassbygdvatnet, is that the predictor structure is complex (**Figure 20**). The model estimates that smaller fish move deeper as temperature decreases and as the discharge in Aurland I increases. In general, the decreasing temperatures seem to affect the depth use highly, but there is a substantial interaction with the discharge from Aurland I. In particular, when the temperature-difference between the discharge water and Vassbygdvatnet is presumed to be high during fall and spring. During early fall (fall open) the discharge has an opposite effect on large and smaller trout as the smaller trout move very deep at high discharge but the larger fish move up in the water-column with increased discharge. During late fall the larger fish move deeper with higher discharge but the depth use of smaller fish is largely affected by temperature and there is no effect by increased discharge. During early spring the smaller trout is more affected by increased discharge than larger trout but also here the larger trout move higher in the water-column as discharge increases in Aurland 1, as seen during fall. During late spring the depth use of larger trout is dominantly affected by temperature. Smaller fish move higher in the water-column when the water temperature is low, but when the water temperature is higher the fish move deeper with increased discharge in Aurland I. There were no trout with depth/temperature transmitters in Vassbygdvatnet during summer.

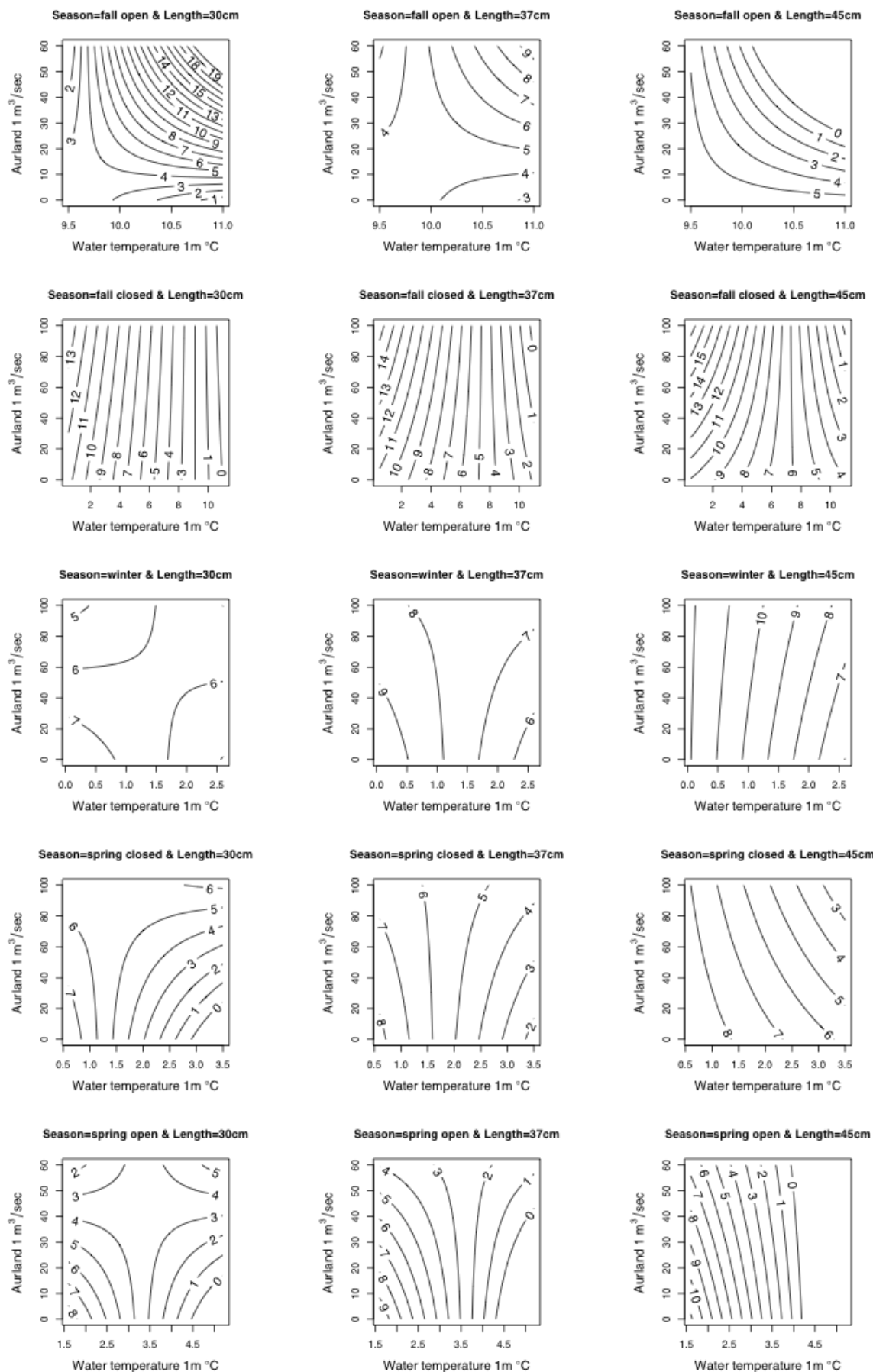


Figure 20 Predicted depth utilization for trout, showing how depth utilization changes in relation to water temperature and discharge from Aurland I at different fish lengths throughout the seasons. Axes are scaled to relevant water temperatures and discharge from Aurland I hydropower plant. Predictions were estimated from the most supported LME-model (appendix section 8.3.1). Predictions are on data collected from dept/temperature transmitters from the 2012-13 and the 2013-14 winters. (n=14)

5.2.2 Area utilization distributions

The Vassbygdvatnet trout were distributed in the entire lake with two core areas towards the western and eastern end of the lake. The UDs decreased in area in the winter and increased as spring unfolded. The trout was largely stationary and stayed within the same area for long periods of time. The trout aggregated in the west end of the lake toward the intake of Vangen during April and the majority of the trout left soon after the dam was lowered in week 18.(appendix section 8.2)

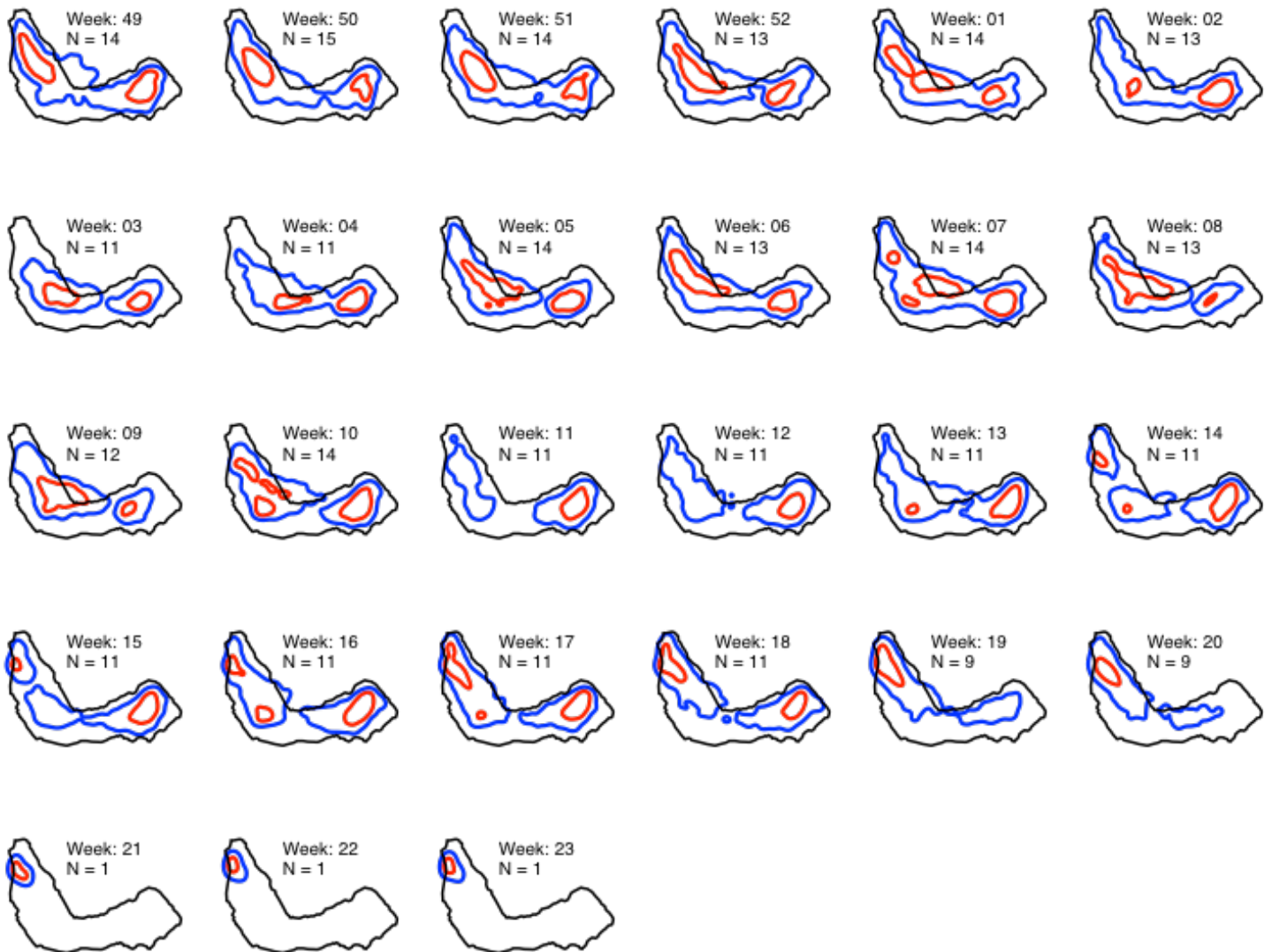


Figure 21 Pooled weekly utilization distributions of >30cm trout during November 2013-June 2014 with the number of individuals involved in the analysis provided. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

Area UDs was determined for 31 trout with 50% and 95% UDs. The UDs varied throughout the year with a decrease in activity from fall to winter and an increase during spring (Figure 22). The home ranges of the trout was not evenly distributed trough out the lake but had two clear hotspots towards in both ends of the lake. During the winter the main proportion of the trout was located in the east end of the lake towards the backwaters of Vassbygdelvi with a gradual increase in home range size towards

spring. The main distribution of trout shifted during spring as they moved westward towards the outlet of the lake and aggregated close to the inlet of Vangen and stayed there until the dam in Aurlandselva was opened 1 May. The trout rapidly left the lake when the dam was lowered. The home ranges decreased during late April period as the trout moved closer to the outlet.

From the area utilization LME prediction plot (**Figure 23**) the home range of trout increases as the temperature drops during fall with little variation of between the different fish-length during fall. During winter the larger fish utilize a larger area than smaller fish, and the low temperature affect the area use of the smaller fish negatively to a larger extent, than for smaller fish. Late winter early spring (spring.open) the trout of different length have different behavior at the same temperature. Smaller fish (<30 cm) utilize a fairly large area in late winter and their area utilization decrease as the temperature increases during early spring and the same impression continues in spring.

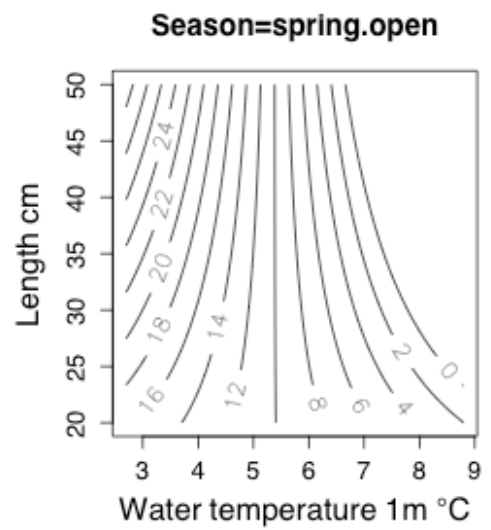
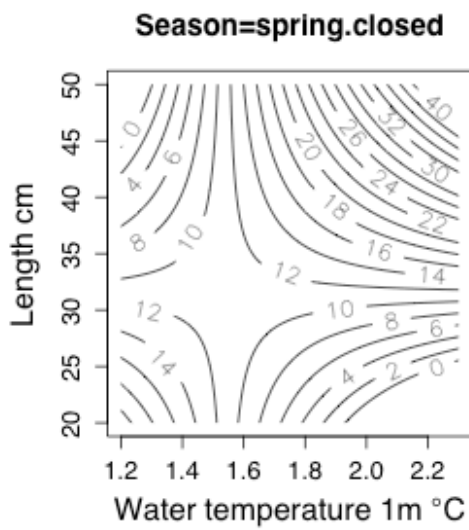
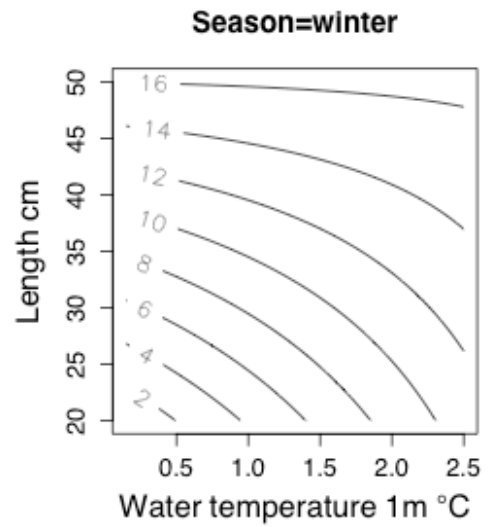
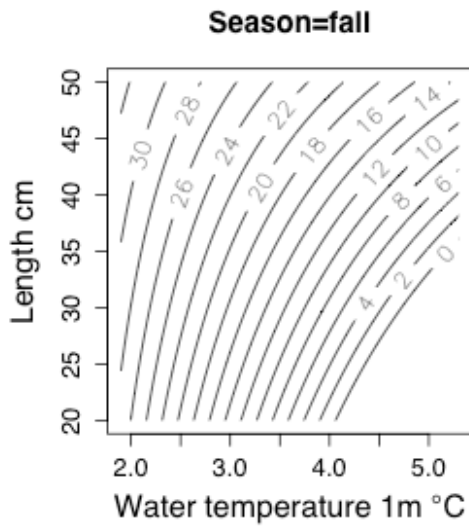


Figure 22 LME model prediction for 50% area utilization distribution in hectare for different fish lengths and temperatures on the basis of the area distribution from 31 trout. . Axes are scaled to relevant water temperatures and fish lengths. Predictions were estimated from the most supported LME-model (appendix section 8.3.2). Predictions are on data collected from November 2013- June 2014 . (n=31)

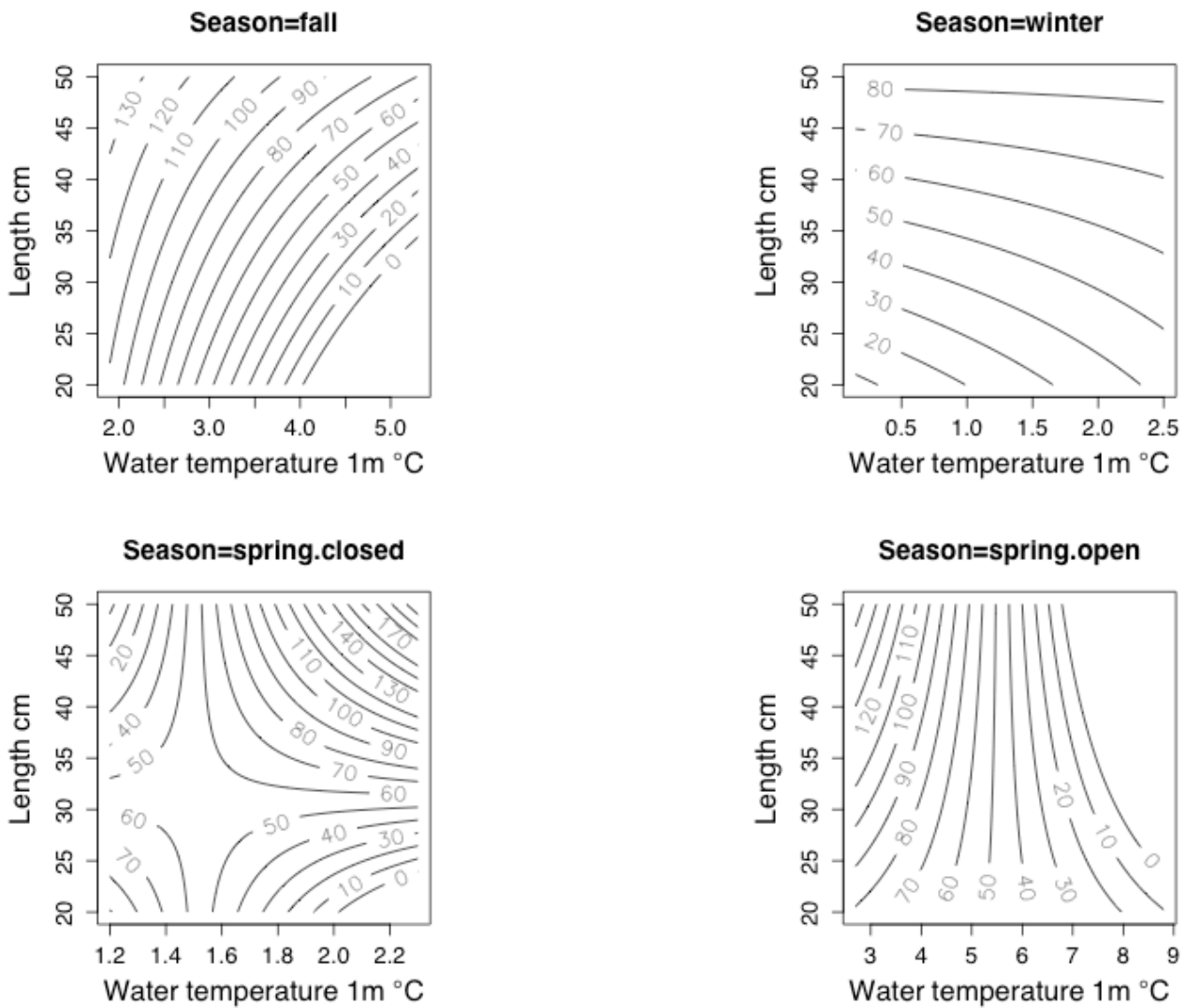


Figure 23 LME model prediction for 95% area utilization distribution in hectare for different fish lengths and temperatures on the basis of the area distribution from 31 trout. . Axes are scaled to relevant water temperatures and fish lengths. Predictions were estimated from the most supported LME-model (appendix section 8.3.2). Predictions are on data collected from November 2013- June 2014 . (n=31)

5.2.3 Volumetric utilization distributions

Nine trout, with depth sensor transmitters had sufficient area distribution data (>20 calculated positions in a week) to calculate utilization volume for the 2013-14 winter. The volume was stably small throughout the winter compared with the spring season. The volumetric UDs increased exponentially during spring reaching volumes 10 times the volume during fall and winter. An example trout (36cm) was located relatively deep throughout the winter as seen in **Figure 24**. The volume use is illustrated in **Figure 24** showing the different weeks in different colors moving from blue in November via green towards red as time progress towards May.

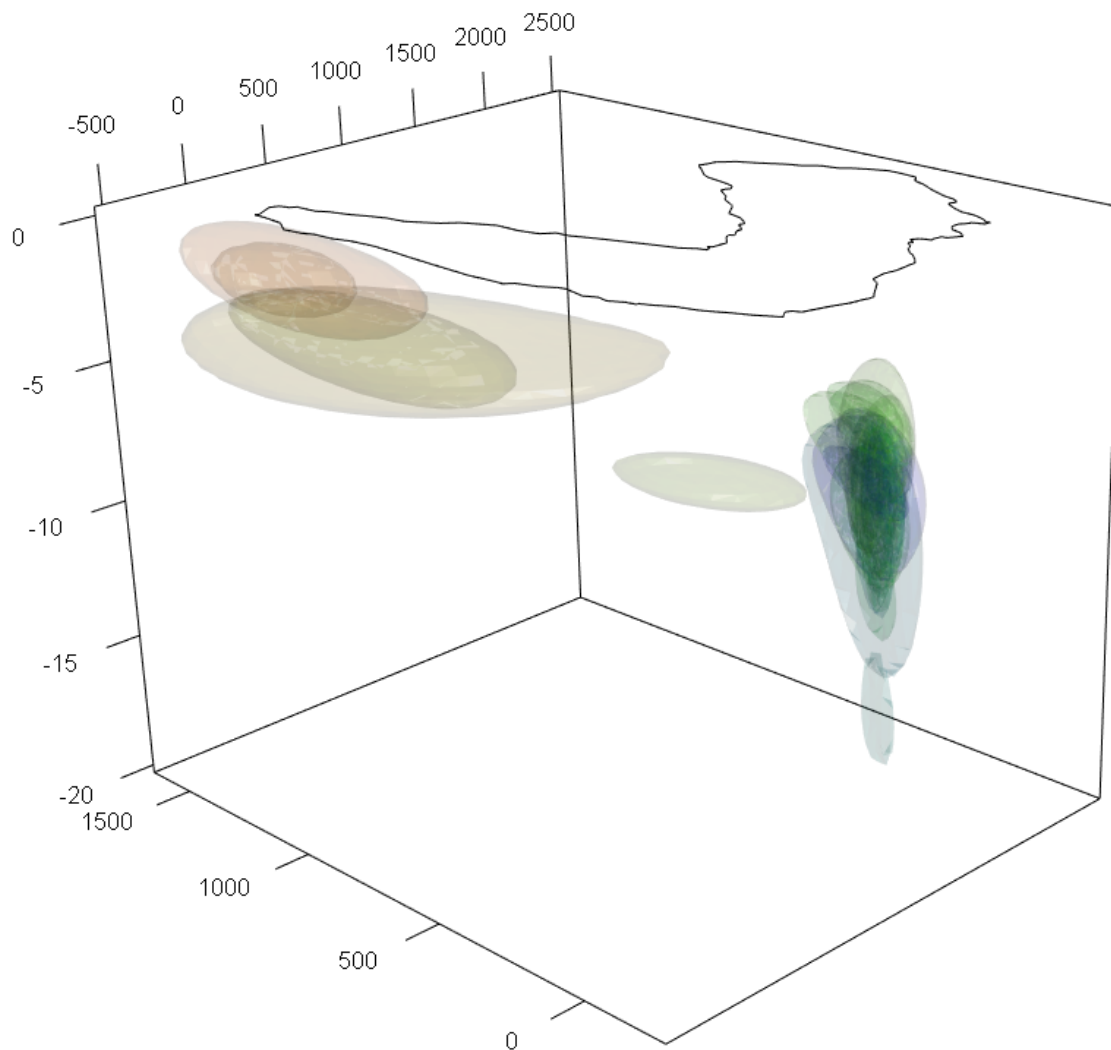


Figure 24 Average volume use of trout from one individual in Vassbygdvatnet for each week. Blue is first study week (week 48, 2013) moving through green toward red indicating last study week (week 22, 2014). Scale is in meters but the xy-axes are not drawn to scale in relation to the z-axis. The xy-axes have been zeroed at Aurlandelva outlet area. (Fish ID 1303173, 35 cm)

The predicted volume UD's (**Figure 26** and **Figure 27**) are similar to the area UD's (**Figure 22** and **Figure 23**) showing increasing volume for larger fish length and for increasing temperatures. The predicted volume is relatively stable for fall, winter and early spring, before increases sharply during spring.

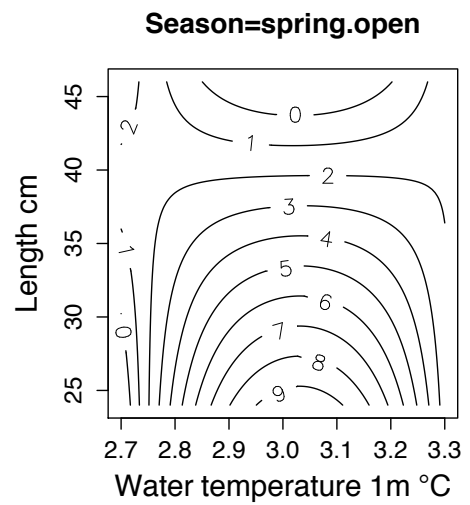
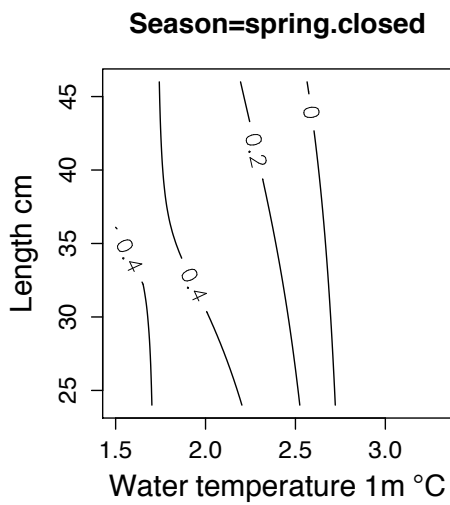
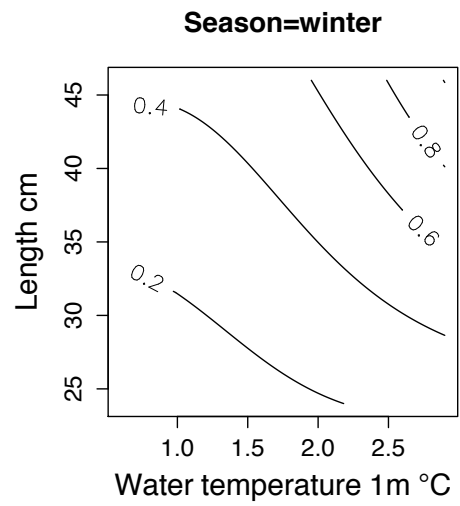
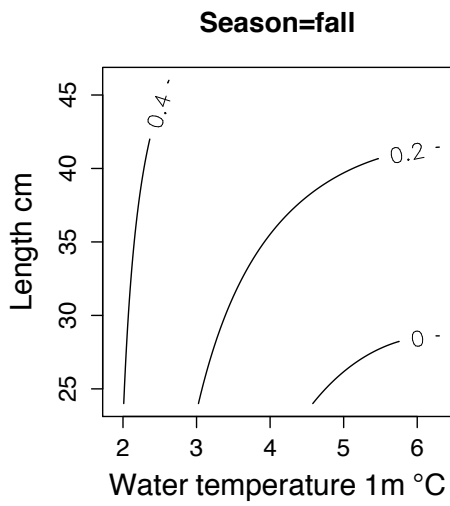


Figure 25 Volume use prediction model for 50% volume use in gigaliters (10^9 L) for different fish-lengths over different seasons at different temperatures at one meter. Volumes utilization is predicted using an LME-model selected as shown in Appendix section 8.3.3.

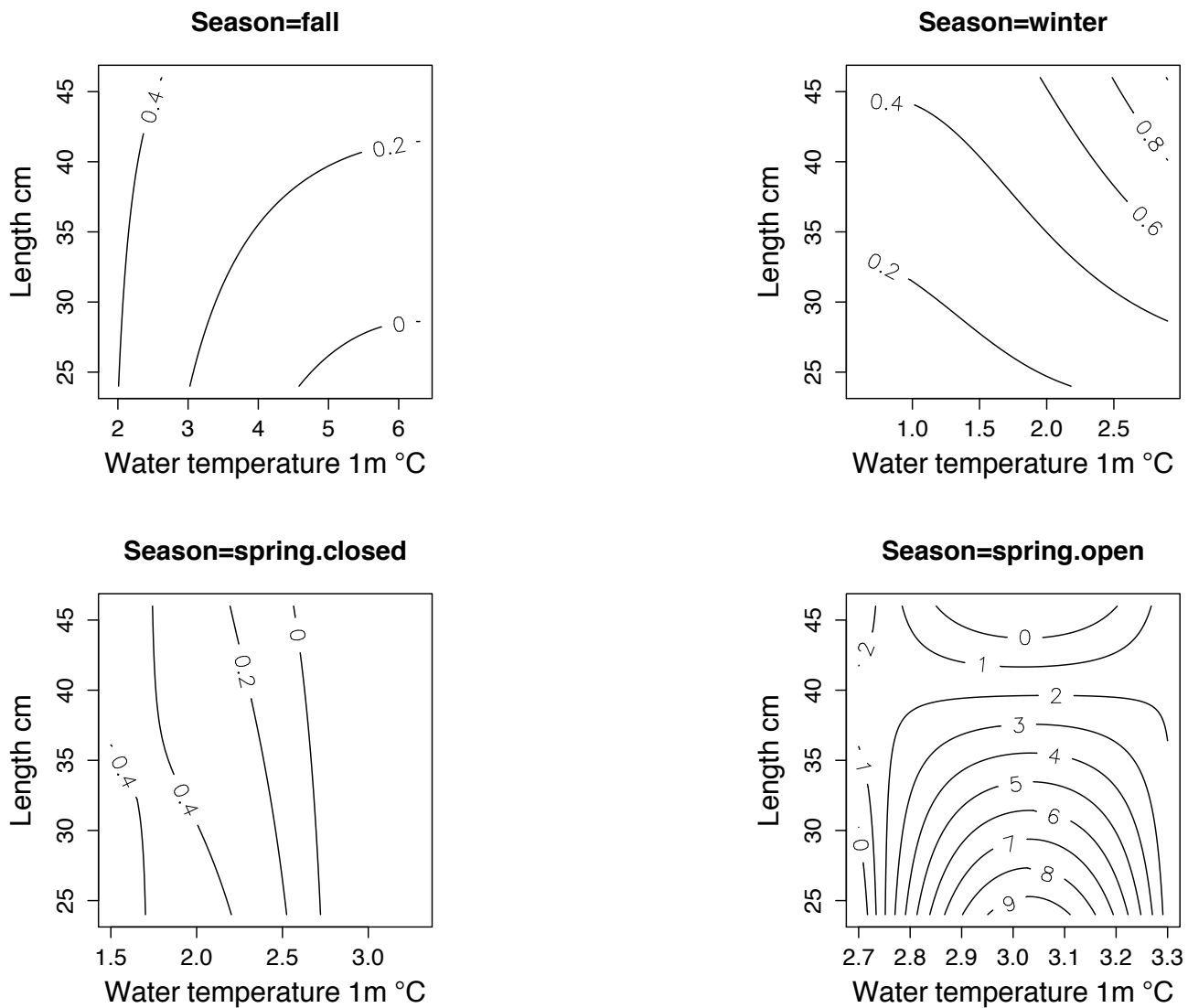


Figure 26 Predicted volume utilization distributions for trout modeled for 95% volume use in gigaliters (10^9 L) for different fish-lengths and water temperatures at one meter over the seasons at different temperatures at one meter. Volumes utilization is predicted using an LME-model selected as shown in Appendix section 8.3.3. Axis are scaled to relevant fish lengths and water temperatures.

The UD's volume model predicts a gradual decrease in volume use during fall, and remaining relatively small throughout the winter compared to spring. The utilized volumes as winter are smaller for small trout than for larger trout throughout the winter. During spring the utilized volume increase with increasing temperatures reaching 10 times the values shown during winter.

5.3 Hydroacoustic survey

The distribution of fish in is concentrated towards the east end of Vassbygdatnet (**Figure 27** and **Figure 28**) with no detections in the vest end detected (**Figure 27**) There was a grouping of three relatively similar lengths found on to localities during the survey.).

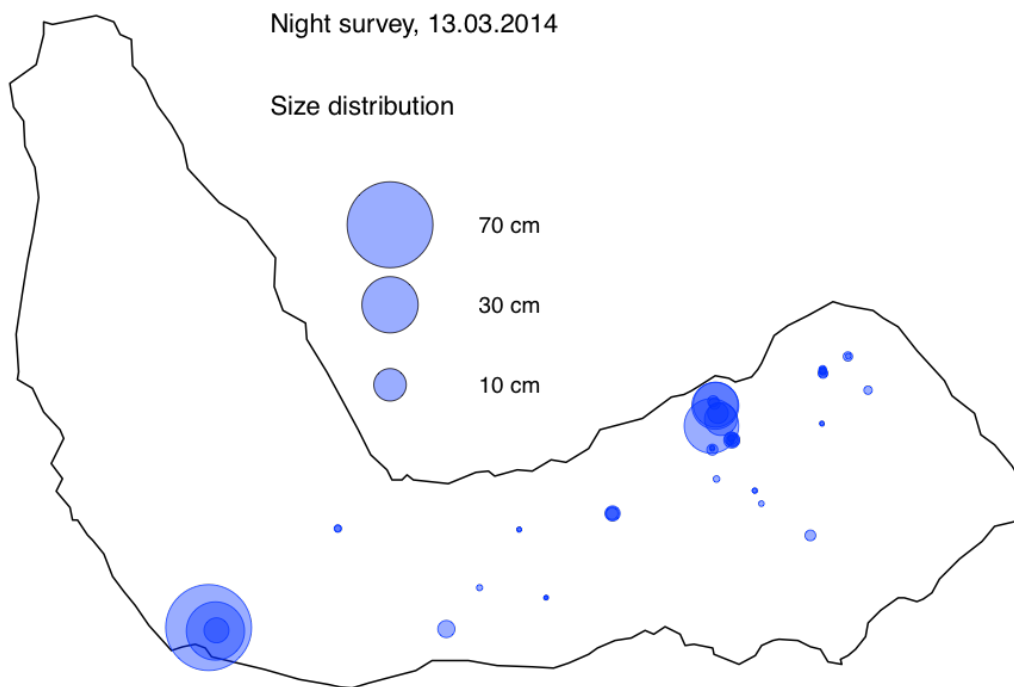


Figure 27 Individual positions and size of single-echo detections (SED) in Vassbygdvatnet 13.03.2014 (week13) from hydro-acoustic night survey. Circles indicate individual fish.

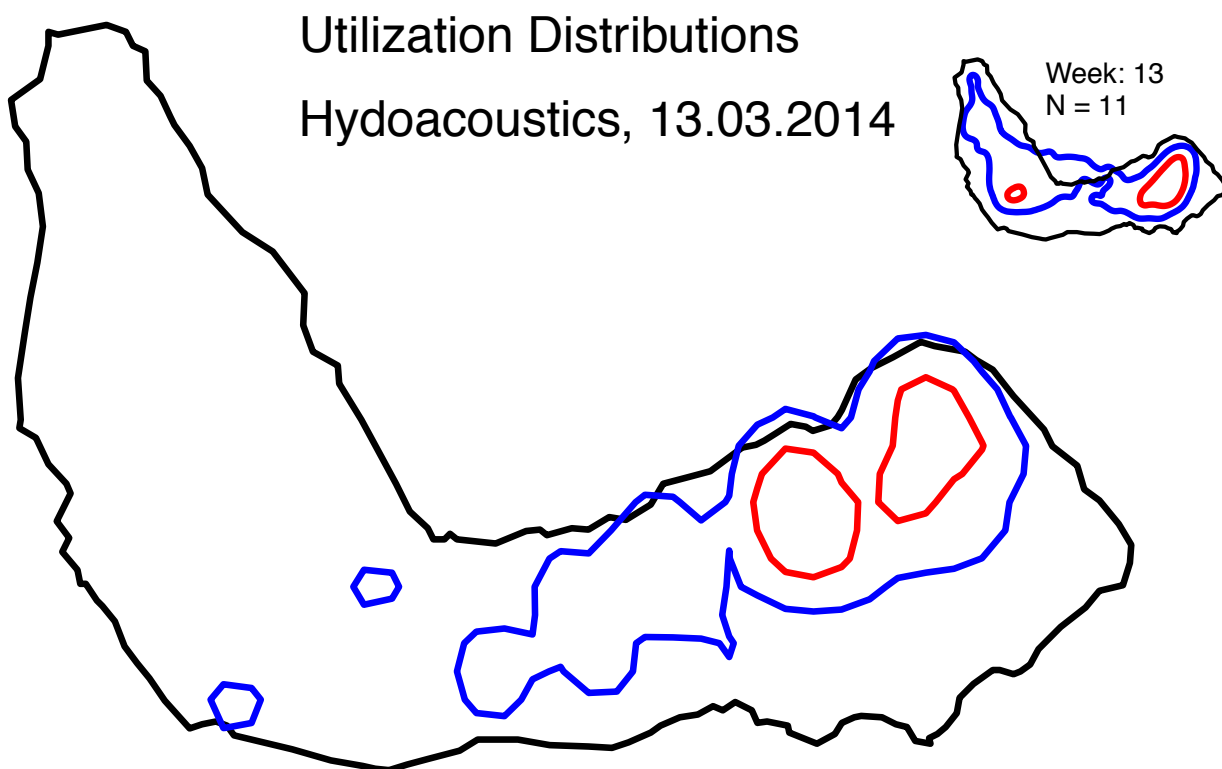


Figure 28 Utilization distribution in Vassbygdvatnet estimated from SED Hydroacoustic data (large), red indicating 50% utilization area and blue indicating 95% utilization area. Small map shows the utilization distribution for the same week as the hydroacoustic survey was undertaken, gathered from the pooled weekly utilization distributions of >30cm trout.

5.4 Fish migrating into Vangen

Three trout (40-50cm) were registered in the Vangen tunnel during summer 2013 and one during summer 2014 (before 13 June), but not during production periods and none of the registered trout passed through the hydropower plant. The three trout were and stayed in the tunnel from one to eleven days before returning to the lake. The three trout were observed in Vassbygdvatnet and Aurlandselva after being registered in the tunnel showing that they found their way out.

6 Discussion

6.1 Habitat use

This study quantifies large-scale habitat use by sea trout showing that Vassbygdvatnet is the most utilized habitat by the post-juvenile population in Aurland holding 80% of the sea migrating fraction of the population from September to May and 50% of the smolts and finnocks throughout the summer. Migrations between the different habitats have been identified on a longitudinal and temporal scale and identifying different phases of migration by trout in Aurland and identified possible migration barriers. The models of the in-lake habitat use and identified behavioral differences over the seasons and for different fish lengths. Furthermore showed that different sizes of the trout respond differently to environmental change and that the maneuvering of Aurland I affects the habitat use of trout directly. This study quantifies large-scale habitat use by sea trout showing that Vassbygdvatnet is the most utilized habitat by the post-juvenile population in Aurland holding 80% of the sea migrating fraction of the population from September to May and 50% of the smolts and finnocks throughout the summer. Migrations between the different habitats have been identified on a longitudinal and temporal scale and identifying different phases of migration by trout in Aurland and identified possible migration barriers. The models of the in-lake habitat use and identified behavioral differences over the seasons and for different fish lengths. Furthermore showed that different sizes of the trout respond differently to environmental change and that the maneuvering of Aurland I affects the habitat use of trout directly.

6.1.1 Large scale habitat use

Vassbygdvatnet is a very important habitat for a large proportion of the trout population in Aurland throughout the year. The VGAM model shows that close to 80% of the finnocks and mature trout (24-72) cm that was tagged during September arrived in Vassbygdvatnet shortly after release and stayed in Vassbygdvatnet during the both years. All remaining trout of this group migrated to the fjord in May. For the smolt and finnocks tagged in April 2013, 50% stayed in Vassbygdvatnet throughout the summer and did not have marine migrations showing that Vassbygdvatnet is used for summer feeding by both smolt and finnocks. The large-scale habitat use for the smolt and finnocks tagged during April 2014 shows great variability dependent on the release site (**Figure 12** and **Figure 13**). The trout released in Vassbygdsvi mainly migrates to Vassbygdvatnet, but did not migrate further and the trout released in Aurlandselva migrated to the fjord. The similarity between the two plots demonstrates that smolt and finnock migrate downstream from both release sites during the same period showing that the rheotaxis of the trout is negative during spring as described in numerous previous studies, summarized in Jonsson and Jonsson (2011).

Only two out of the 24 trout that was released in Vassbygdelvi in April 2014 migrated to the fjord before the study period was concluded 13 June. A study performed in the River Gudena in Denmark concluded that migrating trout stop their migration in order to feed, at the first available feeding opportunity, if the energy reserves are depleted (Boel et al. 2014). The trout stopping in order to feed in Vassbygdvatnet can be a plausible explanation for the lack of marine migrations for the trout that was released in Vassbygdelvi. In 2013, only 50% of the smolt and finnocks that was tagged during spring migrated to the fjord. No finnocks or mature trout tagged during September 2013 however, stayed in Vassbygdvatnet during summer during 2014, leaving the freshwater environment in early May. This indicates that a large proportion of the trout migrate to the fjord the following year, after spending one summer in Vassbygdvatnet.

The lack of marine migrations from the trout tagged in Vassbygdelvi show adfluvial migratory behavior within the Aurland system as described in land locked systems by Saraniemi et al. (2008) and leads to the speculation whether or not there are subpopulations within Aurland; giving genetic explanations for the variability in behavior observed or if the behavioral differences observed could be accounted for by the phenotypical plasticity trout is known for (Jonsson & Jonsson 2011). This behavior is not accounted for in previous studies from Aurland, that include fish-scale analysis, (Jensen et al. 1993; Sægrov 2000) so if there is sufficient available food in Vassbygdvatnet for the trout to archive fast growth during summer, the sea age revealed from these studies from Aurland underestimates the actual sea age. The observed behavior indicates that a large proportion of the trout in Aurland, migrate one year later than described previously in the literature. In order to verify and quantify the extent of this behavior, the use of element analysis as described in Clarke et al. (2007) for the fish scales collected during tagging could be used. As there are old scale-archives from before the rivers were regulated for hydropower, old scales could be used in order to find out if this is a regulation effect or was common also before the river was regulated.

The survival rate is not estimated from the VGAM analysis but a life history is established from a proportion of the tagged trout. For instance, for the trout tagged during September 2013 (24-72 cm) the life history was available for 70% of the tagged population until data sampling was concluded 13 June. The remaining 30% loss can be accounted for by the combination of mortality and malfunctioning transmitters. In addition, loss of transmitters by excretion by the spawning population have been observed in previous studies and can account for some of the loss (Jensen & Rikardsen 2012). These factors lead to the assumption that a winter survival of 70% is a conservative estimate for this group. For the trout tagged during September 2012 the same analysis was performed (but not plotted) for the same time span giving a fish/transmitter survival of 57% for the guaranteed battery life of the transmitters. However, inconsistencies in the reliability of the transmitters used the two seasons inhibit

direct comparison of the two seasons directly, and inhibit survival/mortality analysis. Due to high mortality and low detection rate in the marine environment the VGAM-plots are skewed, favoring Vassbygdatnet as predicted habitat. For the trout tagged April 2013, 15 out of 34 (44%) had marine migrations whereas the VGAM- model predicts only 35%. For the trout tagged in Aurlandselva, as displayed in **Figure 12**, eight out of 32 trout migrated to the fjord shortly after release, but the analysis used, fails to take in account the majority of trout that remain in Aurlandselva due to the low detection probability in Aurlandselva for this group. A more robust and relevant approach like multi-strata mark-recapture analysis, e.g., Conditional Arnason Schwarz model, would probably handle this issue better (Schwarz et al. 1993), and should therefore be elaborated in future analyses. Despite the shortcomings in the applied VGAM approach as the detection probability is not taken into account, the method used is applicable for picking up interesting large-scale habitat use in the acoustic telemetry data.

6.2 Migrations and connectivity

Migrations or habitat shifts, within Aurlandsvassdraget occur throughout the year with some very clear peaks during spring and fall. Downstream migrations peak during spring for downstream migrations and upstream migrations primarily occurs during fall. There are few habitat shifts during summer and winter so the majority of trout stay within the habitat they selected until the next migration period.

6.2.1 Sea return

All the trout that returned from marine migrations that was registered, returned in the 13 July to 28 August during naturalized discharge in Aurlandselva. The limited number of individuals available for this analysis inhibits me to generalize with certainty for the population as there may be individual returns by the untagged population but I believe that the return window shown in **Figure 14** represent a mean of the population as it is in the window of return commonly described in the literature, summarized by Jonsson and Jonsson (2011). That all the returns occurred during the period of naturalized discharge in Aurlandselva indicated that the period of naturalized discharge is sufficiently long to insure returns, if discharge is a criterion for successful returns during fall. There were no trout at sea registered by any of the fjord receivers after 29 August, before 2 migrated out to the fjord in December, indicating that the trout that wanted to return did so. With 9 out of 21 trout returning from the marine habitat the return rate is 42%, but these figures are conservative, as there can also be malfunctioning transceivers unaccounted for by in this analysis as previously discussed.

6.2.2 Lake-river migrations during fall

The majority of migrations between Aurlandselva and Vassbygdatnet occurred during spring and fall both before and after the dam was elevated showing that the fish ladder functions in both directions. Data from 2012 indicated that the fish ladder is well functioning for upstream migrations as tagging was performed after the dam was elevated and trout released downstream of the dam appeared in

Vassbygdvatnet shortly after. During September 2013, tagging was performed during naturalized flow in Aurlandselva and the migrations into Vassbygdvatnet from Aurlandselva chiefly occurred shortly after tagging (**Figure 15**). There were 16 upstream migrations before dam elevation and four individuals through the fish ladder. There are no obvious migration barriers in the river between the hatchery (1 km down-river) and Vassbygdvatnet when the dam is lowered. Due to the timing of release, 9 days before the dam was elevated, it is probable that the majority of trout that wanted to migrate to Vassbygdvatnet had sufficient time to do so before the dam was elevated.

The connectivity between Vassbygdvatnet and Aurlandselva is, as expected, higher when the dam is lowered and there is a more natural flow of water between the two systems and can be explained by the fish ladder acting as a migration barrier between the two habitats. This is a common observation in regulated rivers (Calles & Greenberg 2009; Larinier & Travade 2002). The documented migrations in both directions, when the dam was elevated, show that the fish ladder comprises no absolute migration barrier. After the trout had migrated into Vassbygdvatnet there were 13 registered downstream migrations out of the lake during fall 2013 - all by trout larger than 30 cm. It is possible that the fish ladder is a larger migration barrier for trout smaller than this size. However, the downward migrations during this period can be considered as spawning migrations, and that the tagged finnocks that are not sexually mature, lack the motivation for downstream migrations during fall and account for the lack of <30cm trout, migrating downstream. Downstream migrations will be addressed further under spring migrations (section 6.2.4).

There was one registered up-stream migrations from Vassbygdvatnet to Vassbygdelvi from the receiver in Vassbygdelvi. For the VGAM analysis, possible migrations were estimated from fish that move out of receiver range manually, indicates that there was a large number of finnocks that move up the river far enough to be out of transmitter range for the receiver located in the estuary of Vassbygdelvi. This indicates some upstream migration, but they stop somewhere between the receiver in the river and estuary. One possible explanation is that a weir that is located 70 meter upstream from Vassbygdvatnet is a migration barrier. The weir is not large enough to obstruct mature trout motivated to migrate upstream, but could be an obstacle for juvenile fish. Lack of motivation for upstream migration was observed in the River Nidelva (Fjeldstad et al. 2012) where a constructed weir, that was no real barrier for spawning salmon, was demolished and lead to the advancement of the ascent of salmon by one month than observed before the weir was demolished. This study showed that even small obstacles might pose as a real migration barrier if the fish lack the motivation to migrate further. It is nevertheless peculiar that none of the fish caught and tagged downstream from Vassbygdelvi on their upriver migration, migrated up Vassbygdelvi in order to spawn or over-winter.

As no upstream migrations were observed or estimated for the VGAM- predictions for trout that was assigned mature (>40cm). Two mature trout were suspected to migrate up Vassbygdeldvi did not migrate past the receiver located 408 meter upriver (**Figure 5**) (VR2W-ID 105959), so migrations up Vassbygdeldvi was not confirmed, but based on detections in the vicinity of the estuary in Vassbygdvatnet. Vassbygdeldvi was the assumed destination for the majority of mature trout arriving in Vassbygdvatnet before I started analyzing the data. Vassbygdeldvi has long stretches of suitable spawning sites and every year a large number of spawners are observed in Vassbygdeldvi (Jensen et al. 1993; Pulg et al. 2013; Sægrov 2000). This shows that potentially a large proportion of mature trout remain in Vassbygdvatnet throughout the spawning period. Furthermore, the lack of tagged trout that migrated up Vassbygdeldvi indicates that the sampling method used was selective. For future telemetry studies in Aurlandsvassdraget, finnocks and mature trout must also be sampled from Vassbygdeldvi during fall, and not only from Aurlandselva and Vassbygdvatnet, in order to get the full understanding of the migration patterns of the trout. It is possible that the tagging procedure was invasive and interrupts the natural migratory behavior of the trout, but similar studies (Saraniemi et al. 2008; Thorstad et al. 2014a; Urke et al. 2013), indicate the contrary, and also findings from this study shows that the trout tolerates the tagging procedure well.

Transmission signals have a longer range in still than running water, registrations of migrating fish can therefore be bias towards lake resident fish than towards river resident fish. The first receiver downstream from Vassbygdvatnet is located at Saurea (VR2W-ID 105133) (**Figure 4**), 560 m downstream the lake, where most migrants were registered both in and out of the lake. Since the receiver is located so far downstream from the lake there is a time lag between when the first received signal and the actual timing of migration onset. It can be argued that last lake registration is a better measure for when the migration actually occurred for downstream migrations, but the first registration was chosen in order to use the same method for all migration figures. For upstream migration the time of arrival is a more accurate as there is a higher detection probability in the lake and there is a receiver at the river mouth both off Aurlandselva and Vassbygdeldvi.

6.2.3 Spawning migration and behavior

The majority of mature trout that migrates up into Vassbygdvatnet stays there throughout the spawning season as previously discussed. Ulrich Pulg observed in lake spawning nests during a diving survey in Vassbygdvatnet at 15m depth in the north east end of the lake (Ulrich Pulg (pers.com) 2014). For six out of the 20 trout that possibly spawned in Vassbygdvatnet, there were no prolonged stays near the spawning habitats described in a study to map spawning habitats in Aurlandsvassdraget (Pulg et al. 2013). The described spawning habitats in this study are: the Aurlandselva outlet and Vassbygdeldvi inlet. These six trout are believed to spawn within the lake, a behavior that has to my knowledge, never previously been recorded for sea trout.

Groundwater influx has been described as a requirement for successful in-lake spawning on lake resident brown trout (Brabrand et al. 2002) and such conditions are believed to occur in Vassbygdvatnet. The unregulated section of Midjeelva is 30km², a discharge area large enough to sustain year round surface discharge in other areas (NVE 2014). Midjeelvi is partly dried up for most of the year due to the geological conditions of the riverbed where water seeps through (Pulg et al. 2013). This indicates that there is substantial groundwater seepage through the valley that drains into Vassbygdvatnet below the surface creating habitats similar to what is described in (Brabrand et al. 2002) from Lake Røldalsvatnet. These findings show that lake spawning may be a common phenomenon in Vassbygdvatnet, and a strategy used by a large proportion of the population in Aurlandsvassdraget. The lack of searching behavior up Vassbygdelvi, which does not have any large migratory barriers from Vassbygdvatnet, indicate that lake spawning may be a preferred strategy for a large proportion of the trout population in Aurland. If this has been going on since before the regulation, or is an adaptation to the lack of suitable spawning habitat in the rivers as described by Pulg et al. (2013) is not known.

For two trout that was tagged with 13 mm transmitters in 2012, the spawning history for two spawning seasons was available where one trout (size at tagging- 50 cm) returned to Vassbygdvatnet to spawn two consecutive seasons and one to Aurlandselva for two consecutive seasons. This is consistent with previous studies that show that the homing of trout is strong and that they frequently return to the same area for many consecutive years, summarized by Jonsson and Jonsson (2011). The trout that returned to Vassbygdvatnet seemed to spawn at two different locations in 2012 and 2013: in the Vassbygdelvi estuary in 2012 and in the Aurlandselva outlet area in 2013. Hence, they returned to Vassbygdvatnet to spawn but did not seem to choose the same spawning area within Vassbygdvatnet the two consecutive years.

Monitoring of salmonid spawning numbers has been done in Aurland in several studies on both salmon and trout spawners are manually counted by drift dives (Pulg et al. 2013; Sægrov 2000) and from the riverbank (Jensen et al. 1993). Drift-dive counts are considered to provide conservative estimates, as all river-stretches are not equally suitable for this method. Although the method of using drift dive counts is suitable to find annual variations in the population. However, the findings from my study indicate that using drift dives alone to estimate the spawning population alone, may underestimate size of the spawning population as a whole.

In this study, spawning season was defined as the 15 October- 1 January period. November has been described as the peak spawning period for Aurland (Jensen et al. 1993), but observations of spawning

has been done until mid January. The spawning size was set at 40 cm (length after 2-3 sea summers) and described as a likely size of sexual maturity in Aurland (Jensen et al. 1993). It is probable that there are trout that spawn before they reach this size, especially among males, but in order to eliminate “false spawners”, and since the sex of the fish was not determined for all the trout, a conservative size of mature trout was set for this analysis.

6.2.4 Downstream migrations during spring

Downstream migrations were chiefly observed during spring with the first sea migrations during April from Aurlandselva and from Vassbygdelvi with a peak in May from both rivers. There were no downstream migrations from Vassbygdatnet before the dam was lowered. The timing of the downstream spring migrations was similar to what is found in the neighboring River Lærdalselva (Kristensen 2011) and comparable to what is commonly described in the literature summarized in Jonsson and Jonsson (2011).

During spring no downward migrations through fish ladders was observed. As previously discussed there are both upstream and downstream migrations during fall through the fish ladder showing that it is well functioning in it self. There is however a period after the dam is elevated, where the hydropower station is inactive in order to fill Vassbygdatnet reservoir, shown by the discharge plot for water running out of Vassbygdatnet (**Figure 8**). All the downstream migrations occurred in a timeframe connected to this period. This leads to speculations whether or not the intake water for Vangen attracts the trout that are seeking downstream and diverts the trout from finding the fish ladder leading to Aurlandselva. The discharge through the fish ladder is $3\text{m}^3\text{s}^{-1}$ and through Vangen the discharge can vary from 0-100 m^3s^{-1} . The large masses of water that runs through Vangen is enough to create currents in Vassbygdatnet and may divert the fish from finding even though the inlet is located at a depth of 15 meter.

A radio-telemetry study was performed in 1994 on both sea trout and presumed stationary trout ranging from 34-78 cm in Vassbygdatnet. In this study there was no fish registered in the Vangen intake and they concluded that loss of large fish through Vangen is not a problem, (Økland et al. 1995) this study is consistent with their findings. Radio-telemetry is believed to be a more appropriate approach to document loss directly through Vangen, as the conditions are believed not to be favorable for acoustic telemetry due to the noise created by the water running through the tunnel. In 1997, five trout were caught in the tunnel and due to their poor condition and pale appearance they concluded that the fish had been there for a long time. In 1998, 31 trout was caught inside the tunnel in May (after Vangen was shut down) where 23 (average length 26.9cm) was classified as sea trout in a study performed by Sægrov (2000) indicating some loss through Vangen.

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A radio-telemetry study was performed in 1994 on both sea trout and presumed resident trout ranging from 34-78 cm in Vassbygdvatnet. In this study, there was no fish registered in the Vangen intake and they concluded that loss of large fish through Vangen is not a problem (Økland et al. 1995). My results are consistent with their findings. Radio-telemetry is believed to be a more appropriate approach to document loss directly through Vangen, as the conditions are believed not too favorable for acoustic telemetry due to the acoustic noise created by the water running through the tunnel. In 1997, five trout were caught in the tunnel and due to their poor condition and pale appearance they concluded that the fish had been there for a long time. In 1998, 31 trout was caught inside the tunnel in May (after Vangen was shut down) where 23 (average length 26.9cm) was classified as sea trout in a study performed by Sægrov (2000) indicating some loss through Vangen.

The reason why there were no downstream migrations before the dam is lowered may be that the water running into Vangen attracts the trout, obstructing the trout from finding the fish-passage leading to Aurlandselva - a phenomenon previously described from the River Gudbrandsdalslågen by Kraabol et al. (2008). There was a distinct shift in the area distribution utilization during April with suspected migratory trout moving from the east end towards the Vest end, and aggregating towards Vangen (appendix section 8.2). This indicates that the trout seeks downstream, but is unable to find the fish

ladder when Vangen is running at high discharge. Downstream migration fishways have been proven to be more difficult to work than upstream migration fishways when dams are constructed (Calles & Greenberg 2009; Kraabol et al. 2008). Even though downstream migrations through the fish ladder was observed during fall the lack of downstream migrations during spring show that the fish-ladder does not function well for spring migrations. The timing of smolt migrations has been reported to be later for smolt than for kelts (Kristensen 2011) in the neighboring Lærdalselva river, so it is not certain an earlier lowering of the dam would shift the migration timing for this group. The VGAM analysis for spring 2014 indicated that the smolt that resides in Vassbygdelvi utilize Vassbygdvatnet as feeding habitat before they migrate further, and thereby delaying their seaward migration as previously described.

The rapid downstream migration into Aurlandselva following dam lowering (**Figure 15**), and the aggregation of trout of trout towards the downstream end of Vassbygdvatnet (towards Vangen inlet and Aurlandselva (appendix section 8.2)), indicates that the timing of dam lowering may take place a bit late in the spring and that an earlier lowering of the dam would shift the migration time to occur earlier. This was also concluded in the previous radio telemetry study performed in Vassbygdvatnet, (Økland et al. 1995), where the timing of dam lowering and kelts migration was well synchronized. Findings from Sægrov (2000), indicate that earlier migration in Aurland trout impose higher individual growth rates while at sea. Hence, since the trout seem to be obstructed from migrating early by the dam, it is possible that sea growth can be increased by shifting the dam lowering to an earlier time during spring. Fast growth and size are described as being perhaps the most important life-history trait of salmonids, increasing both the fitness and the survival rate of individuals and their offspring, and thereby the population as a whole (Jonsson & Jonsson 2011) Therefore, to introduce a regulation regime that allows maximization of the sea growth is recommended. More studies should be done in order to evaluate migration timing to show the effect of lowering the dam two to three weeks earlier in a controlled experiment to see if the migration timing shifts in response to such a change.

In this study three trout stayed in the tunnel leading to Vangen for 1-11 days during June 2013 before they found their way out. All detections occurred when the hydropower station was inactive. The acoustic conditions inside Vangen are not ideal as noises from the discharge water greatly influence the detection probability, so mortality through Vangen so it cannot be ruled out as a possibility. Several trout appeared in the fjord after being registered on the receiver located at the mouth of the tunnel leading in to Vangen in Vassbygdvatnet during winter, without being registered in Aurlandselva or inside the tunnel. This study reveal that mortality through Vangen is not a major threat for the trout over tagging size. From the VGAM-analysis it is clear that a large number of trout simply disappear from receiver-range, as there is a large decline in number of trout to base the estimate on as time passes. This

could be accounted for by natural mortality or that the trout is out of range, but the signal from the transceiver should be possible to pick up for at least a proportion of deceased trout as the transmitter is not dependent on the trout being alive to send out signals, and that there is a dense receiver network in Vassbygdvatnet. The inability to separate malfunctioning transmitters and mortality remain a problem but the malfunction-probability could be quantified by comparing with other studies performed with the same technology. The *individual* life history and migrations was not in focus for this study as it mainly focuses on the different groups.

Four sea migrations were registered in December-January, during winter 2013-14, but it does not seem to be a dominating strategy for the trout in Aurland as observed in Skibotn river (Jensen & Rikardsen 2012) where 91% utilized estuary and marine waters during winter. The two fish registered were in the period when Aurlandselva was very cold and bottom freezing was reported. A sea lice monitoring program in Sognefjorden, caught trout in throughout the winter in fish-traps (Vollset & Barlaup 2014), so there is clearly sea trout present in the fjords during winter, but none of the trout tagged in Aurland was in the vicinity of these fish-traps during period the sea-lice monitoring program was conducted.

6.3 Winter habitat use in Vassbygdvatnet

The in-lake habitat use is dependent on numerous factors and intra species variations. The depth distribution (**Figure 18**) and UDs plots (appendix section 8.3.2) illustrate that the trout utilize the entire lake. The areas utilized expand during spring as feeding opportunities increase. The depth use of the trout varies greatly between the two studied winters, largely accounted for by different temperature conditions. The LME-habitat use prediction models show that the factors that govern the habitat use is complex with varying behavior for different fish lengths and temperatures. The discharge water from Aurland affects the depth use of the trout showing that the trout is directly influenced by the regulation regime.

6.3.1 Depth utilization distribution

The trout seemingly chooses the warmest available temperature during winter. During the 2012-13 the daily average utilized water temperatures the trout wintered in, revealed from the depth/temperature transmitters, shows that the daily average utilized temperatures never dropped below 4.2 degrees. The temperature in Vassbygdvatnet had available water temperatures that were colder than this temperature (**Figure 7**) but did not utilize these temperatures. The variability in depth use during the 2012-13 winter was low and suggests that the trout stayed in the strata where the warm temperatures were available. During this winter vertical movement represented a large shift in thermal habitat and can explain the consistency of the depth use seen. During the 2013-14 winter however, Vassbygdvatnet was isothermal at $<1^{\circ}\text{C}$ (**Figure 6**) and the daily average utilized temperature dropped to 0.2°C in

January. The lack of strata during the 2013-14 winter can explain the large variability in depth seen, as a stratum holding a more desirable temperature did not limit the trouts' vertical movement. Under such conditions, a shift in depths use does not represent a shift in thermal habitat giving the trout a more variable depth use. Furthermore the average depth utilized during the 2013-14 winter was deeper than the first winter, and as there were no options in thermal habitat selection, it can indicate that the trout prefer to winter at a deeper depth than seen in 2012-13 but that temperature is a stronger driver of behavior than depth in itself. The deeper depth use that was seen during the 2013-14 winter is possibly an anti-predatory behavior as there are predatory birds present in Aurland (personal observation). However, the large variability during the 2013-14 winter shows that this is not a strong preference. During 2012-13 there was a thick ice cover on Vassbygdvatnet preventing overhead predators to pose a threat for the trout; this was not the case during 2013-14 where the ice-cover was inconsistent.

The discharge in Aurland I also contributed to the variations seen in depth use during the winters I studied. Derived from the LME-model selection process (appendix section 8.3), the processes governing the depth use are complex and factors such as season, and the discharge in Vassbygdelvi, alongside water temperature as discussed earlier, contribute to the depth distribution in Vassbygdvatnet. The depth utilization prediction model (**Figure 20**) shows that the water temperature and discharge in Aurland I affects the depth distribution of trout in Vassbygdvatnet. The general picture is, that the trout move deeper when temperatures drops, especially when the discharge water has a different temperature than the still water in Vassbygdvatnet, during spring and fall. However, during spring and fall, the larger trout move higher in the water-column with increased discharge indicating that they utilize the discharge water as feeding habitat at lower temperatures than smaller trout. Larger trout have lower optimum growth temperature and feed at lower temperatures than small trout. (Jonsson & Jonsson 2011) The smaller fish move deeper with increased discharge during the fall and clearly tries to avoid the discharge waters moving to depths of >18 meters at $60\text{m}^3\text{s}^{-1}$ when the larger trout stay close to the surface water. This is also the case during late spring where smaller trout move deeper at high discharge when the water temperature is low whereas the larger trout move higher in the water column.

When the temperature increases to above a $3.2\text{ }^\circ\text{C}$ threshold smaller trout show the same tendency as larger trout and move higher in the water-column with increased discharge at low temperatures but deeper when the temperature is under this threshold. This shows that the smaller fish avoid the discharge water when the temperature difference between the lake and the discharge water is high, but utilizes it as feeding habitat when the water temperature is high, or that the temperature in the discharge water during snow-melt periods in the spring as and the temperature is lower in Vassbygdvatnet than the discharge water in Aurland I. Larger fish utilize the discharge water more than

smaller fish and possibly feed on drift exhausted from Viddalsvatnet through discharge water at lower temperatures than smaller fish, and endure a higher temperature difference between the present water in Vassbygdatnet and Aurland I. Studies from the river Rohne in Switzerland on trout (Fette et al. 2007) shows that smaller trout are more negatively affected by hydropeaking than larger trout in rivers. However, the effects of hydropeaking on the physical habitat of rivers is much larger than in lakes as it alters the discharge volume and velocity alongside the water-covered area causing stranding and loss through drift. In lakes, hydropeaking can induce changes in turbidity, temperatures and the stratification of the lakes and alter the supply of feed organisms from the discharge water, but problems such as stranding and drift are avoided.

Are low summer temperature and high winter temperature negative as metabolism is temperature dependent and that the trout expire their energy resources during winter faster at high temperatures? The trout seem to prefer the warmer water during the 2012-13 winter, (**Figure 19**) and could easily avoid the warm water present by staying close to the discharge water from Vassbygdelvi or close to the surface where there was a severe ice cover in 2012 that sustained until spring. However, the trout choose the highest available temperature during the entire winter. Whether or not this is what is best for the trout over the seasons is unclear, as the trout prefers the temperature where they consume most energy resources. The metabolism for trout is low even at 4.2°C, but the degree-day sum that is highly linked to metabolism (Jonsson & Jonsson 2011), is over four times higher for the 2012-13 winter than for the 2013-14 winter. Few studies on metabolism have been done at comparable temperatures but a study performed on wild Atlantic salmon (Bacon et al. 2005) show that Atlantic salmon can grow at temperatures >1.5°C but have a negative growth rate below this temperature. If the species respond similarly, the trout would be unable to grow even if feed organisms were available during the 2013-14, where the average experienced temperature dropped to 0.2°C. However, feed opportunities during winter are believed to be infrequent in a cold oligotrophic lake during winter. Sub-thermo cline temperature in ice covered lakes are commonly 4°C and are shown to be utilized by trout during winter in lake studies (Jonsson & Jonsson 2011).

The data material for the depth utilization analysis was limited by failing sensors in the depth/temperature transmitters. From the 24 trout that was tagged with 9mm transceivers during September 2012, unachievable sensor values from the depth/temperature sensors was received, and lead to the exclusion of these transmitters from the depth analysis and models. The transmitters continued to emit instant ID far beyond the failure of the sensors within the transceivers but did not last the guaranteed life expectancy. For 14 trout tagged with 9mm transmitter during September 2013, 5 transmitters had the same problem leading to the assumption that the transmitters used during September 2013 were more reliable than the transmitters used in 2012.

6.3.2 Volumetric and area utilization distributions

The UD plots (appendix section 8.2) illustrate that the individual trout utilize the entire lake but prefer certain core areas towards the ends of the lake, using the middle section of the lake less actively. During spring there was a sharp increase in spatial utilization distribution for all fish lengths in contrast to what was seen during fall and winter. This shows that the trout was largely dormant throughout winter and become more active as spring unfolds and feeding opportunities become more frequent. Larger trout increase their area utilization earlier than smaller trout supporting the observations previously discussed under depth use. Larger trout have a lower optimum feeding temperature than smaller trout as discussed previously under depth utilization (Page 57).

The trout in Aurland utilized the entire lake in the November 2013 to June 2014 period with core utilization area (UD50) towards the ends of the lake using the middle of the lake mainly for migration between the two, presumed more desirable habitats (Figure 18). During late winter and spring there was a tendency for the trout to occupy the northeastern end of Vassbygdvatnet, the area of Vassbygdvantet that are believed to be least influenced by the discharge water from Aurland I indicating that the trout avoids the discharge water.

From the area UD prediction model it appears that larger fish (>30 cm) decrease their area UD as temperature decrease during fall revealing that they are more active during early fall, when they first arrive than later in the season. The temperature decrease for this period was only 1.1 °C but the area UD decreased by a factor of ten during this period indicating that other factors such as time of year, day length, and decreasing feed opportunities alongside spawning behavior contributes to the decrease in area UD, so the temperature and fish length is not believed to account for the decrease in area UD alone. The predicted volume for season spring is however calculated from only four individual fish as some have left the system as the dam was lowered and all migrate down-river during this period so the data for the season spring.open is limited.

The hydroacoustic survey was performed 23 March 2014 (week 13) and reveal that the trout was mainly located in the northeast end of the lake when the survey was conducted as seen by **Figure 28**. By comparing the UD plot from the hydroacoustic survey and the kernel UD for week 13; there is a slight discrepancy between the two methods used but that the general picture is similar. This discrepancy can be explained partly by that different methods generally give different results, but also by the kernel distribution utilization is based on weekly distribution and that the Hydroacoustic survey illustrated in **Figure 28** was collected during one night. The consistency between the two methods used supports the kernel utilization methods relevance for the entire study period where this method was used.

Malfunctioning depth-sensors in transmitters limits the number of volumetric utilization distributions analysis in the same manner as discussed under depth utilization (section 6.3.1).

The kernel-based UD method developed used, (Simpfendorfer et al. 2002) does not take the physical limitations of the lake into account but the size of areas created for individual fish (appendix section 8.2) are mainly used as measures of activity and not for exact localizations of individual trout. During fall and spring as river migrations skews the predicted area utilized as few detections the first week after arrival or the last week before departure are involved in the analysis, making a relatively small calculated utilization area, and might not be a representative prediction of the utilized area and volume.

6.4 Study design

Temperatures from discharge water, and the temperature difference between Vassbygdatnet and the discharge water from Aurland I is probably an important factor affecting trout habitat use in Vassbygdatnet and temperature profiles from Vassbygdatnet the 2012-13 winter would be helpful in order to understand why there is such a large difference in depth use between the two years.

Area and volume predictions were based on one winter only and with a small number of individuals ($n = 31/n=7$). Area distribution in Vassbygdatnet has more individuals and with a relatively large variation in size groups of trout but only for one winter. The differences in depth use from the two winters indicate that there can be large variations between in the physical conditions trout experience in Vassbygdatnet so in order to get a complete picture of the factors that govern the habitat use in Vassbygdatnet the data generated winter 2014-15 should also be analyzed in the same manner.

6.5 Management implications and further study

The aggregation in of trout towards Vangen in April before it was shut down 1 May and naturalized flow in Aurlandselva was implemented, shows that the currents towards the inlet of Vangen attract trout seeking to migrate downriver during spring. The findings from this study indicate that the trout is obstructed to migrate out for several weeks. This obstruction in migration possibly limits the potential growth the sea trout can achieve during summer, as growth is directly linked to the duration and timing of the marine migrations (Jonsson & Jonsson 2011). In the fall however, the trout returning from sea migrations arrive well within the window of naturalized discharge with no returns after August, whereas the naturalized flow lasts until September 15. On the basis of these findings a pragmatic approach could be to shift the season of naturalized discharge in Aurlandselva by two to three weeks to insure seaward migrations from Vassbygdatnet earlier in the spring. This will not affect the annual

production of hydropower and at the same time ensure sea migrations at a time when the trout is ready to leave Vassbygdvatnet. Another approach that could be applicable is to have periods where Vangen shuts down during spring. This would make the fish ladder easier to find for the trout, as it is believed the current towards Vangen caused by the current from the discharge water and not that the fish ladder is a migration barrier that hinders the migration. Furthermore, the timing of downstream migrations are in other systems described as a critical periods for hydropower induced mortalities (Kraabol et al. 2008). Migrations through Vangen are not believed to be a large problem for kelts (Økland et al. 1995), but turbine loss for other size groups are not evaluated properly and cannot be ruled out as a possibility. This approach would thereby also limit the risk for turbine loss in Vangen hydropower plant.

As data is continually being generated until fall 2015 in Vassbygdvatnet, the foundation for a good evaluation of mortality through Vangen is possible, and further investigation on the individual life history of the tagged trout is strongly recommended. The mortality through Vangen could be quantified by following the life history of individual fish utilizing appropriate analytical methods. Such studies should include transmitter malfunction probability and detection probability within a dense network of receivers, allowing precise triangulation. In addition it is possible to use a stationary echo sound device or Didson sonar technology during critical periods, like during spring before the dam opens. This approach can give a conclusive answer for all size groups of fish and not only for fish large enough for telemetry transmitters.

Monitoring of salmonid spawning numbers has been done in Aurland in several studies on both salmon and trout spawners using drift dives (Pulg et al. 2013; Sægrov 2000) and observations from the riverbanks (Jensen et al. 1993). In order to assess the size of the spawning population in Aurland, drift-dive counts should be combined with hydroacoustic surveys in the same time period in order to get a more accurate estimate of the spawning population. Diving surveys in Vassbygdvatnet should also be undertaken in order to get an understanding the quantity of trout to use this strategy as well as identifying utilized spawning sites.

As in lake spawning is believed to be a frequently used strategy by the trout population in Aurland, and due to the few studies undertaken that have observed this behavior, new knowledge is needed. Assessment of the extent and success of this behavior and Whether or not in-lake spawning strategy is a suboptimal strategy for the trout and a result of the lack of suitable spawning sites in the rivers described in (Pulg et al. 2013) or a well functioning strategy that can help sustain the population. Furthermore, nest-site monitoring and experimental studies should be undertaken to document the survival rate and success of eggs and juveniles from in lake spawning.

The adfluvial migrations performed by smolt and finnocks tagged in Vassbygdeldvi could be useful findings for the egg-burial program in Aurland. The main goal for this program is to produce sea trout. The large site dependency seen on the migratory patterns by the smolt and finnocks that was tagged in April 2014 shows that there is a risk of producing freshwater resident trout if they are released in Vassbygdeldvi. The further life history of smolt and finnocks from Vassbygdeldvi should be investigated further in order to establish the relationship between the different migratory strategies observed. The question remain open whether or not the large proportion of trout from Vassbygdeldvi that utilize Vassbygdvatnet as feeding habitat observed, migrate to the fjord later in the summer. Moreover, do they continue to perform adfluvial migrations or migrate to the fjord the following year? Further studies are needed to find the behavior of mature trout that spawn in Vassbygdeldvi and should be included in future telemetry studies undertaken. Smolt and finnocks could be tagged with transmitters with longer battery life than what was used for this study in order to understand the full life history of these trout. Element analysis methods of fish scales from trout caught in the different habitats in Aurlandsvassdraget could be used to establish the predominance of different migratory strategies based on the localities they are captured.

LME- depth utilization model based on data collected from the depth sensor transmitters reveal a direct response to the discharge water from Aurland I, showing that the maneuvering of the hydropower plant affects the habitat utilization of the trout directly. Furthermore, the aggregation of trout in the northeast end of the lake- suggests that the trout responds negatively to the discharge water from Aurland I. The implications of these findings are not clear, and further studies are needed in order to understand what these effects these responses have on the metabolism, individual growth and fitness, and for the population fitness of the trout population in Aurland in general.

The large variation in available water temperature the two studied winters show that the maneuvering of the hydropower plants highly affects the physical environment in Vassbygdvatnet. More studies are needed in order to find what conditions create the best suitable environment for the trout. Furthermore, to find out how the maneuvering of the hydropower plants can be run in order to create these conditions. In response to the conclusion reported by Jensen et al. (1993) claiming that the fish population is limited by low water temperatures during summer, Bakken et al. (2011). This study purpose a lowered outlet of the discharge water from Aurland I in order to elevate the temperatures during summer would create a warmer surface layer in the lake but before such an endeavor is undertaken.

7 Concluding remarks

- Vassbygdvatnet the most utilized habitat for post juvenile trout in Aurlandsvassdraget and an important habitat for the trout population in Aurland, accounting for the majority of the post juvenile population for large proportions of the year.
- In lake spawning was observed in Vassbygdvatnet, supporting previous findings of such behavior in Vassbygdvatnet.
- The trout is obstructed from migrating during spring and seem unable to find the fish ladder leading towards Aurlandselva and the Fjord. The fish ladder is well functioning in itself, but the trout seem unable to find the fish ladder leading out of the lake, causing the trout to aggregate towards Vangen hydropower plant during spring.
- The trout show behavioral changes to fluctuations in the discharge water from Aurland I, and observation of trout seeking to avoid the discharge water was done.
- Regulation effects from the discharge water caused large variations in the observed temperatures the trout inured the two consecutive winters resulting in variable depth use by the trout an prefers to utilize the warmest available water temperatures.

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8 Appendix

8.1 Temperature profiles from Vassbygdvatnet

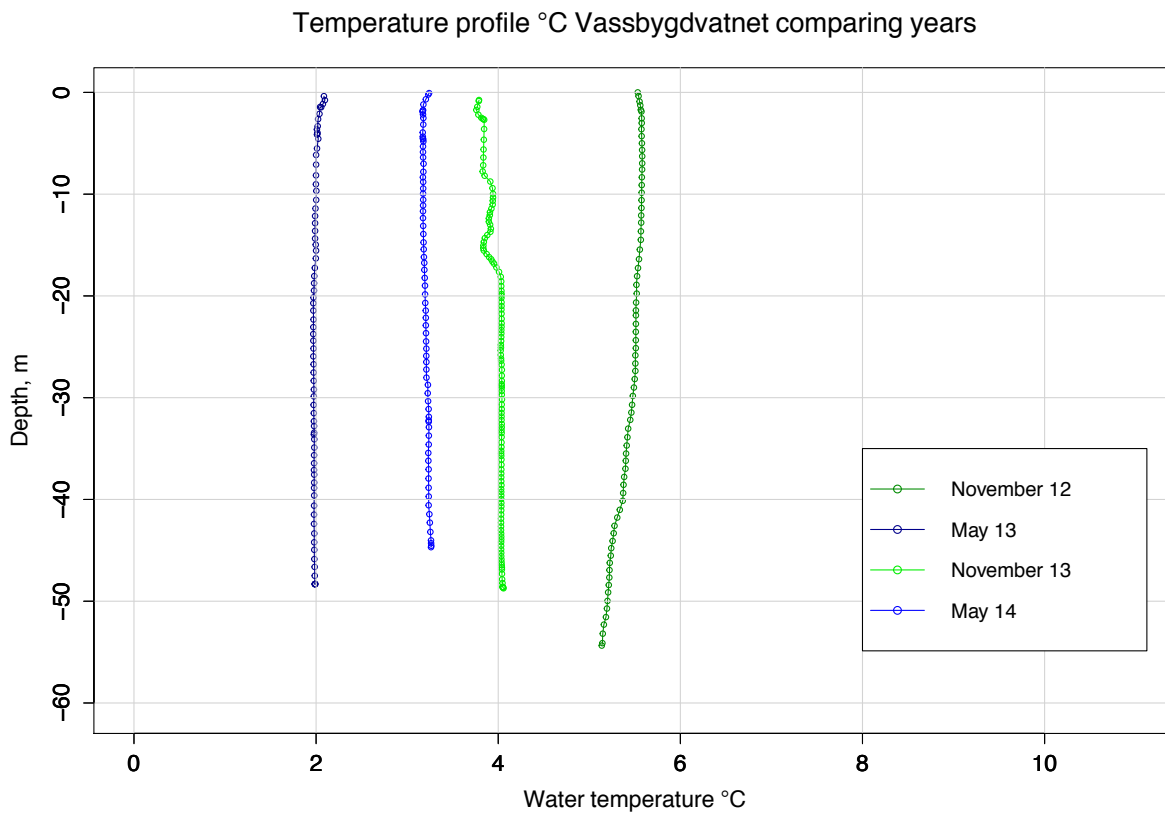


Figure 29 Comparing water temperature profiles from November and May 2012 and 2013

Table 3- Fish ID, the tagging periods and fish lengths, habitat the fish was released and the transmitter type that was used for individual fish

Fish ID	Tagging period	Realece site	Length cm	Weigt g	Transmitter type
11051	fall.12	Aurlandselva	38		9 mm
11053	fall.12	Aurlandselva	35		9 mm
11055	fall.12	Aurlandselva	33		9 mm
11057	fall.12	Aurlandselva	32		9 mm
11059	fall.12	Aurlandselva	40		9 mm
110511	fall.12	Aurlandselva	38		9 mm
110513	fall.12	Aurlandselva	35		9 mm
110515	fall.12	Aurlandselva	44		9 mm
110517	fall.12	Aurlandselva	28		9 mm
110519	fall.12	Aurlandselva	28		9 mm
110521	fall.12	Aurlandselva	36		9 mm
110523	fall.12	Aurlandselva	28		9 mm
110525	fall.12	Aurlandselva	35		9 mm
110527	fall.12	Aurlandselva	36		9 mm
110529	fall.12	Aurlandselva	41		9 mm
110531	fall.12	Aurlandselva	32		9 mm
110533	fall.12	Aurlandselva	31		9 mm
110535	fall.12	Vassbygdatnet	33		9 mm
110537	fall.12	Vassbygdatnet	36		9 mm
110539	fall.12	Vassbygdatnet	29		9 mm
110541	fall.12	Aurlandselva	32		9 mm
110543	fall.12	Aurlandselva	34		9 mm
110545	fall.12	Aurlandselva	33		9 mm
110563	fall.12	Aurlandselva	33		9 mm
1105101	fall.12	Aurlandselva	59		13 mm
1105103	fall.12	Aurlandselva	68		13 mm
1105105	fall.12	Aurlandselva	38		13 mm
1105109	fall.12	Vassbygdatnet	43		13 mm
1105113	fall.12	Vassbygdatnet	55		13 mm
1105115	fall.12	Vassbygdatnet	45		13 mm
1105125	fall.12	Aurlandselva	38		13 mm
1105127	fall.12	Aurlandselva	40		13 mm
1105129	fall.12	Aurlandselva	60		13 mm
1105131	fall.12	Aurlandselva	37		13 mm
1105133	fall.12	Aurlandselva	46		13 mm
12062041	spring.13	Aurlandselva	26,0	201,0	smolt
12062042	spring.13	Aurlandselva	22,5	105,0	smolt
12062043	spring.13	Aurlandselva	25,5	106,0	smolt
12062044	spring.13	Aurlandselva	25,5	120,0	smolt
12062045	spring.13	Aurlandselva	20,5	104,0	smolt
12062046	spring.13	Aurlandselva	18,0	70,5	smolt
12062047	spring.13	Aurlandselva	23,5	90,0	smolt
12062048	spring.13	Aurlandselva	23,5	111,0	smolt
12062049	spring.13	Aurlandselva	28,5	156,0	smolt
12062050	spring.13	Aurlandselva	21,5	80,0	smolt
12062051	spring.13	Aurlandselva	22,0	92,0	smolt
12062052	spring.13	Aurlandselva	20,0	70,0	smolt
12062053	spring.13	Aurlandselva	21,0	61,0	smolt
12062054	spring.13	Aurlandselva	22,0	72,0	smolt
12062055	spring.13	Aurlandselva	20,5	67,0	smolt
12062056	spring.13	Aurlandselva	20,5	62,0	smolt

Table 4 Fish ID, the tagging periods and fish lengths, habitat the fish was released and the transmitter type that was used for individual fish

Fish ID	Tagging period	Realece site	Length cm	Weigt g	Transmitter type
12062662	spring.14	Aurlandselva	24,0	152,0	smolt
12062663	spring.14	Aurlandselva	12,7		smolt
12062664	spring.14	Aurlandselva	18,1	47,0	smolt
12062665	spring.14	Aurlandselva	20,3	70,1	smolt
12062666	spring.14	Aurlandselva	14,4	26,2	smolt
12062667	spring.14	Aurlandselva	25,0		smolt
12062668	spring.14	Aurlandselva	20,6	73,4	smolt
12062669	spring.14	Aurlandselva	19,1	49,5	smolt
12062670	spring.14	Aurlandselva	19,6	46,7	smolt
12062671	spring.14	Aurlandselva	24,0	89,9	smolt
12062672	spring.14	Aurlandselva	16,2	31,8	smolt
12062673	spring.14	Aurlandselva	20,9	80,6	smolt
12062674	spring.14	Aurlandselva	19,8	63,9	smolt
12062675	spring.14	Aurlandselva	21,9	63,2	smolt
12062676	spring.14	Aurlandselva	16,1	35,9	smolt
12062677	spring.14	Aurlandselva	21,9	68,2	smolt
12062678	spring.14	Aurlandselva	24,5	10,3	smolt
12062679	spring.14	Aurlandselva	26,0		smolt
12062680	spring.14	Aurlandselva	25,0		smolt
12062681	spring.14	Aurlandselva	25,5		smolt
12062682	spring.14	Aurlandselva	19,2	56,1	smolt
12062683	spring.14	Aurlandselva	20,8	67,4	smolt
12062684	spring.14	Aurlandselva	18,2	43,1	smolt
12062685	spring.14	Aurlandselva	17,8	43,2	smolt
12062686	spring.14	Aurlandselva	22,5	83,2	smolt
12062687	spring.14	Aurlandselva	23,5	83,2	smolt
12062688	spring.14	Aurlandselva	17,5	45,8	smolt
12062689	spring.14	Aurlandselva	28,0		smolt
12062690	spring.14	Aurlandselva	23,8	86,8	smolt
130331	fall.13	Aurlandselva	58		13 mm
130333	fall.13	Aurlandselva	51		13 mm
130335	fall.13	Aurlandselva	52		13 mm
130337	fall.13	Aurlandselva	72		13 mm
130339	fall.13	Aurlandselva	53		13 mm
130341	fall.13	Aurlandselva	42		13 mm
130343	fall.13	Aurlandselva	41		13 mm
130345	fall.13	Aurlandselva	46		13 mm
1303167	fall.13	Aurlandselva	42		9 mm
1303169	fall.13	Aurlandselva	40		9 mm
1303171	fall.13	Aurlandselva	33		9 mm
1303173	fall.13	Aurlandselva	35		9 mm
1303175	fall.13	Aurlandselva	39		9 mm
1303177	fall.13	Aurlandselva	38		9 mm
1303179	fall.13	Aurlandselva	38		9 mm
1303181	fall.13	Aurlandselva	46		9 mm
1303183	fall.13	Aurlandselva	24		9 mm
1303185	fall.13	Aurlandselva	35		9 mm
1303189	fall.13	Aurlandselva	35		9 mm

Table 5 Fish ID, the tagging periods and fish lengths, habitat the fish was released and the transmitter type that was used for individual fish

Fish ID	Tagging period	Release site	Length cm	Weight g	Transmitter type
12062662	spring.14	Aurlandselva	24,0	152,0	smolt
12062663	spring.14	Aurlandselva	12,7		smolt
12062664	spring.14	Aurlandselva	18,1	47,0	smolt
12062665	spring.14	Aurlandselva	20,3	70,1	smolt
12062666	spring.14	Aurlandselva	14,4	26,2	smolt
12062667	spring.14	Aurlandselva	25,0		smolt
12062668	spring.14	Aurlandselva	20,6	73,4	smolt
12062669	spring.14	Aurlandselva	19,1	49,5	smolt
12062670	spring.14	Aurlandselva	19,6	46,7	smolt
12062671	spring.14	Aurlandselva	24,0	89,9	smolt
12062672	spring.14	Aurlandselva	16,2	31,8	smolt
12062673	spring.14	Aurlandselva	20,9	80,6	smolt
12062674	spring.14	Aurlandselva	19,8	63,9	smolt
12062675	spring.14	Aurlandselva	21,9	63,2	smolt
12062676	spring.14	Aurlandselva	16,1	35,9	smolt
12062677	spring.14	Aurlandselva	21,9	68,2	smolt
12062678	spring.14	Aurlandselva	24,5	10,3	smolt
12062679	spring.14	Aurlandselva	26,0		smolt
12062680	spring.14	Aurlandselva	25,0		smolt
12062681	spring.14	Aurlandselva	25,5		smolt
12062682	spring.14	Aurlandselva	19,2	56,1	smolt
12062683	spring.14	Aurlandselva	20,8	67,4	smolt
12062684	spring.14	Aurlandselva	18,2	43,1	smolt
12062685	spring.14	Aurlandselva	17,8	43,2	smolt
12062686	spring.14	Aurlandselva	22,5	83,2	smolt
12062687	spring.14	Aurlandselva	23,5	83,2	smolt
12062688	spring.14	Aurlandselva	17,5	45,8	smolt
12062689	spring.14	Aurlandselva	28,0		smolt
12062690	spring.14	Aurlandselva	23,8	86,8	smolt
130331	fall.13	Aurlandselva	58		13 mm
130333	fall.13	Aurlandselva	51		13 mm
130335	fall.13	Aurlandselva	52		13 mm
130337	fall.13	Aurlandselva	72		13 mm
130339	fall.13	Aurlandselva	53		13 mm
130341	fall.13	Aurlandselva	42		13 mm
130343	fall.13	Aurlandselva	41		13 mm
130345	fall.13	Aurlandselva	46		13 mm
1303167	fall.13	Aurlandselva	42		9 mm
1303169	fall.13	Aurlandselva	40		9 mm
1303171	fall.13	Aurlandselva	33		9 mm
1303173	fall.13	Aurlandselva	35		9 mm
1303175	fall.13	Aurlandselva	39		9 mm
1303177	fall.13	Aurlandselva	38		9 mm
1303179	fall.13	Aurlandselva	38		9 mm
1303181	fall.13	Aurlandselva	46		9 mm
1303183	fall.13	Aurlandselva	24		9 mm
1303185	fall.13	Aurlandselva	35		9 mm
1303189	fall.13	Aurlandselva	35		9 mm

8.2 Area distribution utilizations from Vassbygdvatnet

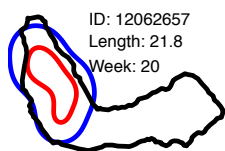


Figure 30 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

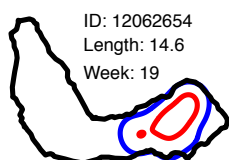


Figure 31 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

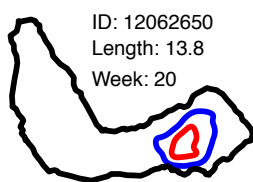


Figure 32 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

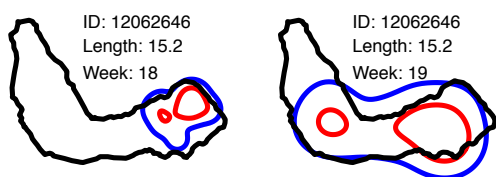


Figure 33 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

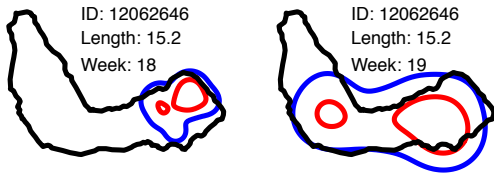


Figure 34 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.



Figure 35 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

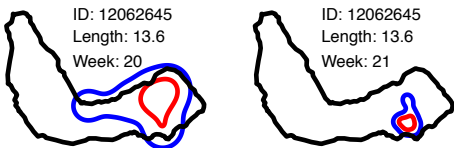


Figure 36 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

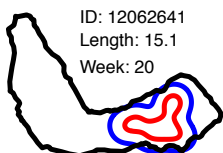


Figure 37 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

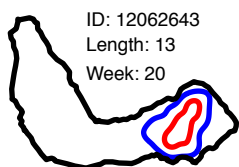


Figure 38 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

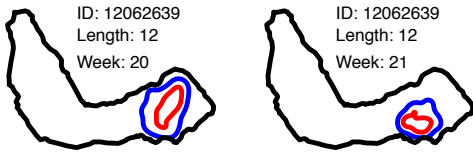


Figure 39 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

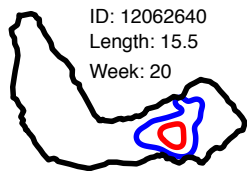


Figure 40 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

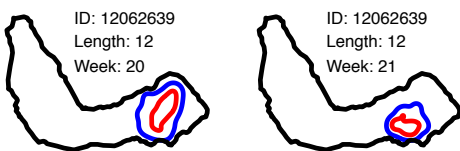


Figure 41 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

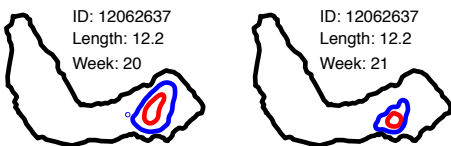


Figure 42 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

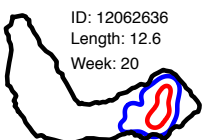


Figure 43 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

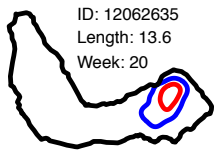


Figure 44 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

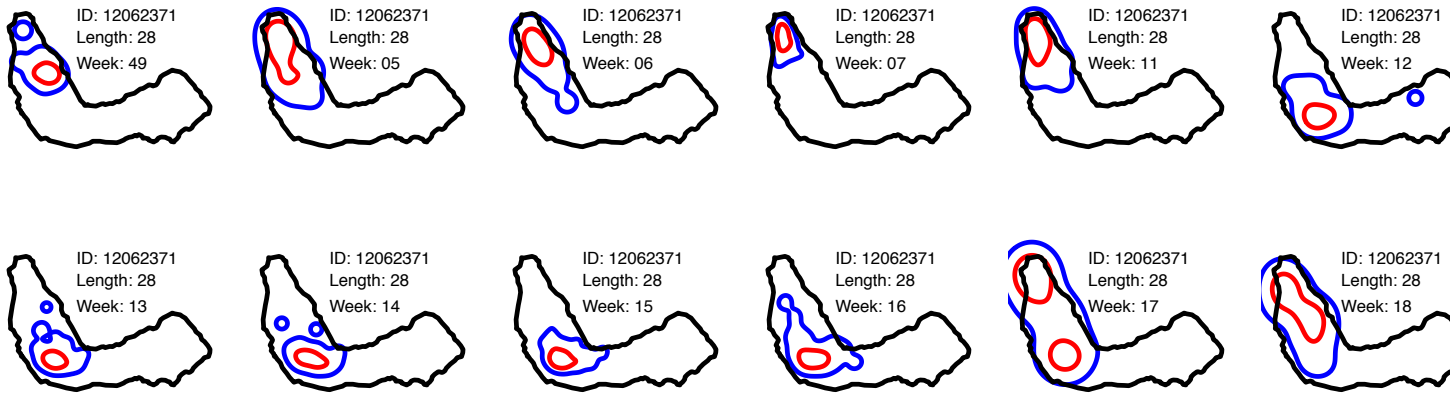


Figure 45 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

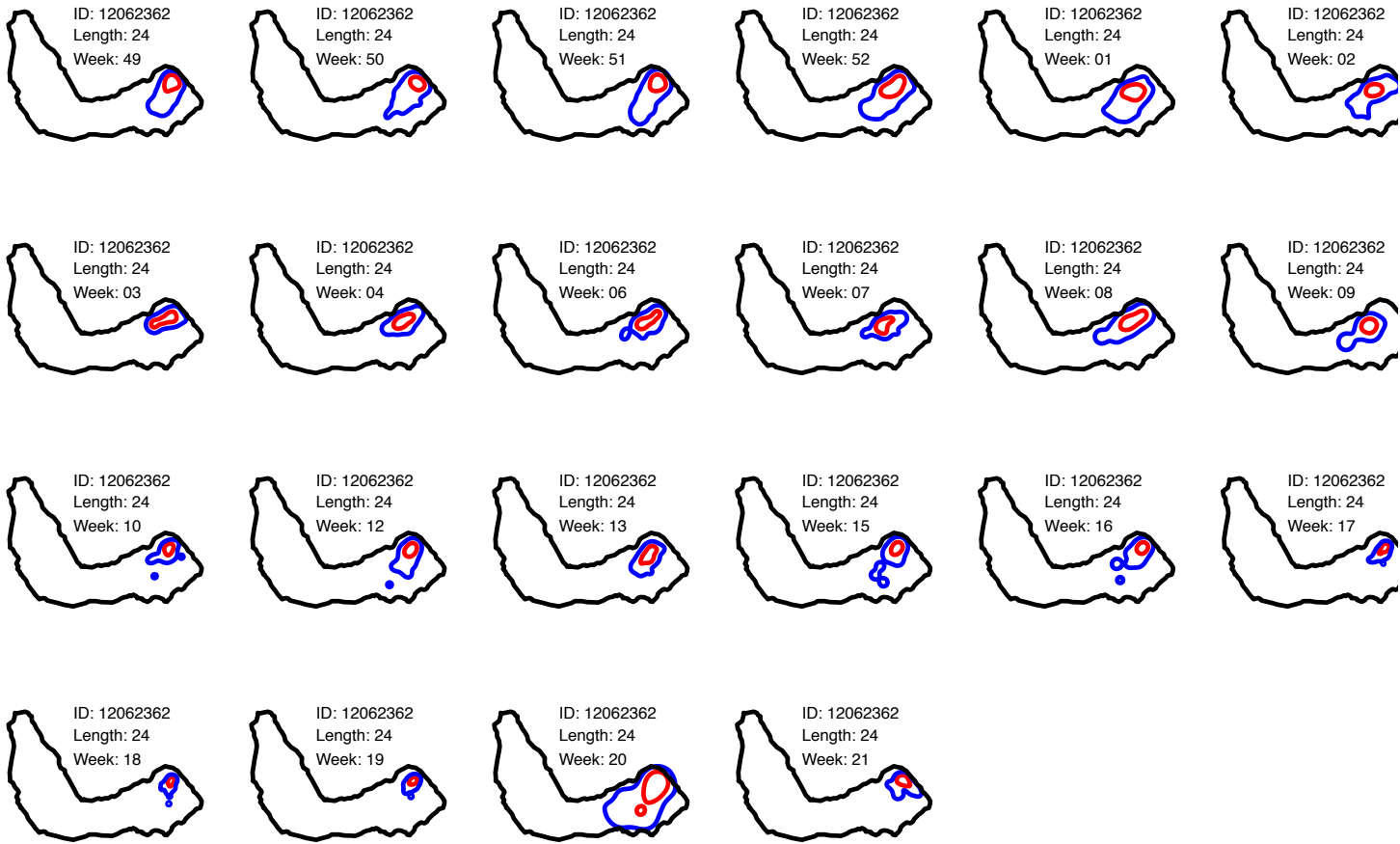


Figure 46 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

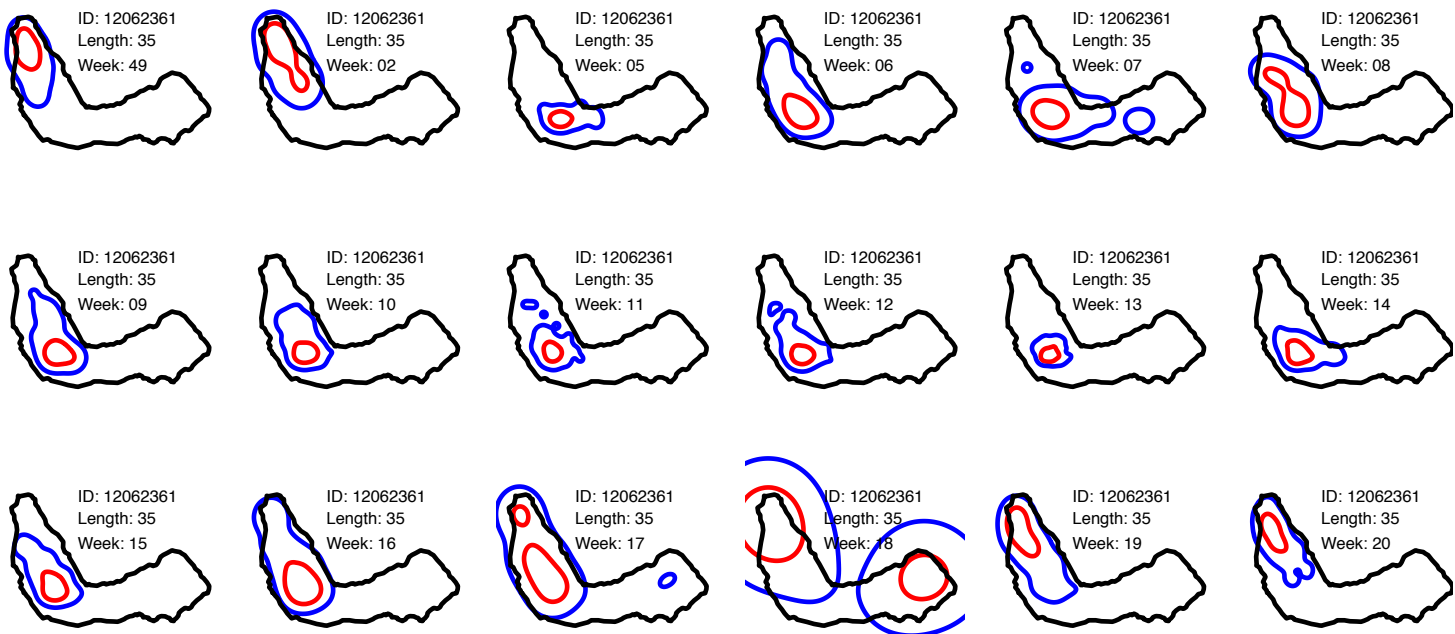


Figure 47 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

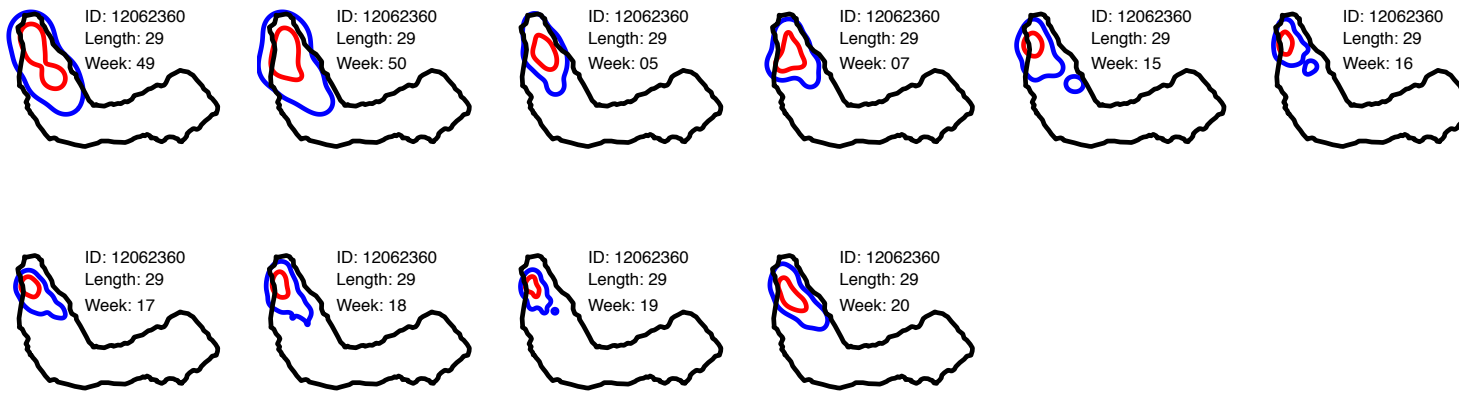


Figure 48 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

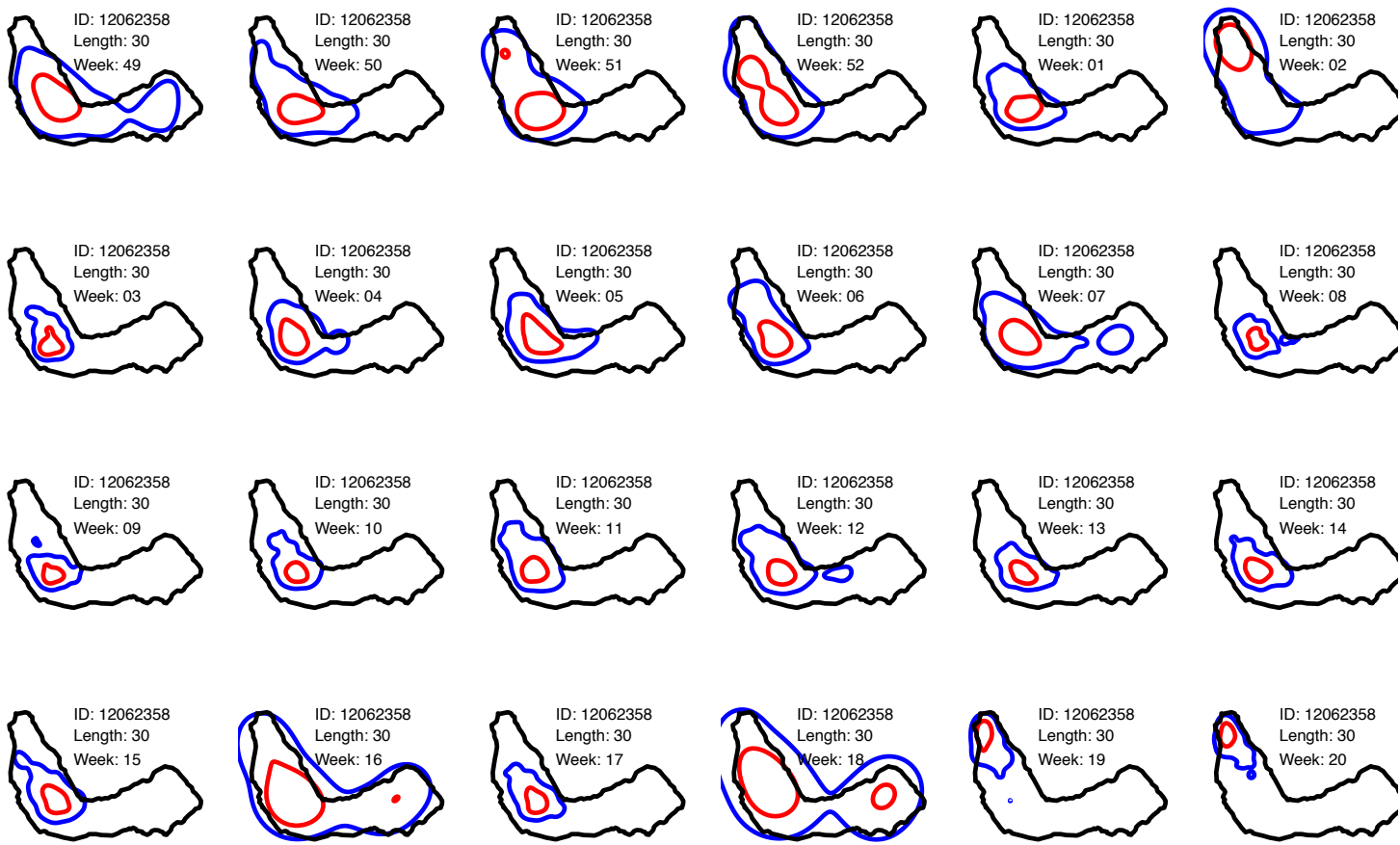


Figure 49 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

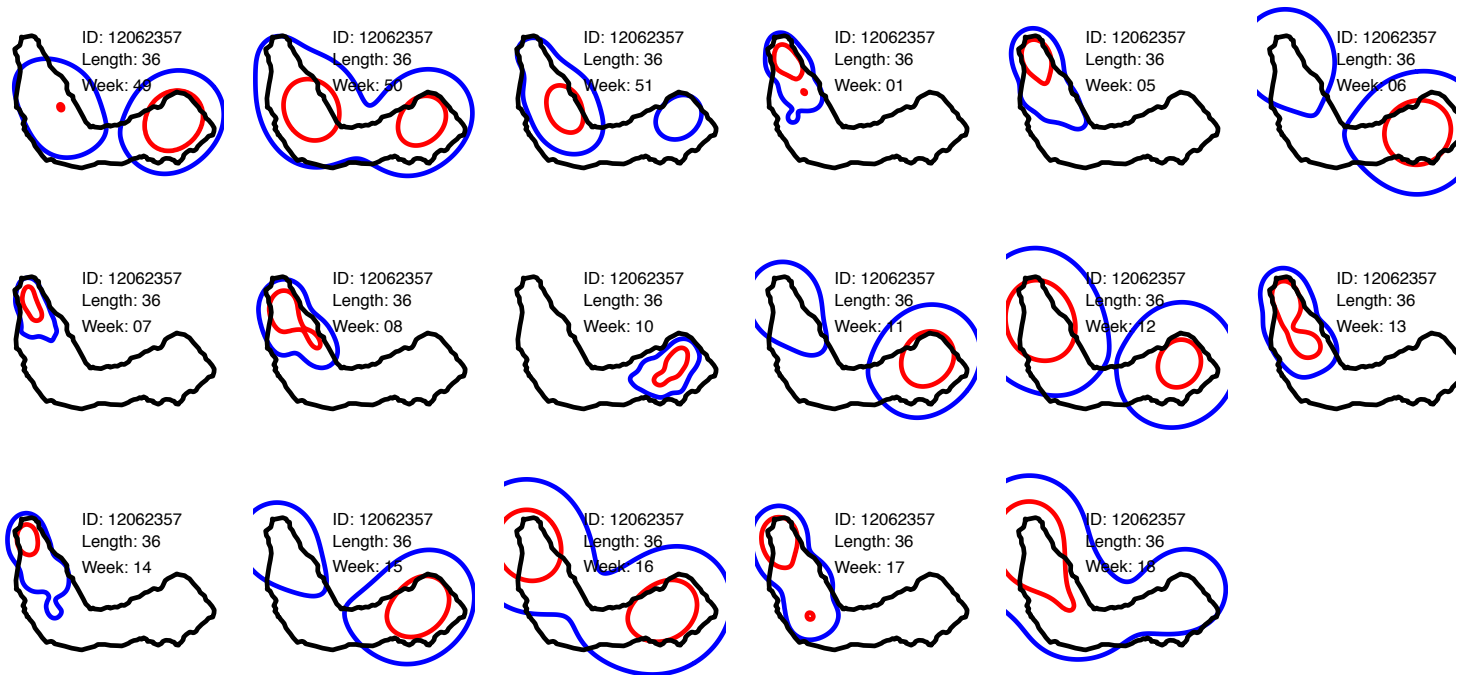


Figure 50 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

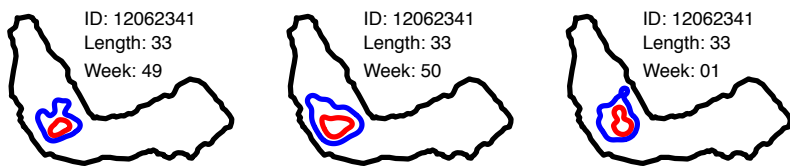


Figure 51 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

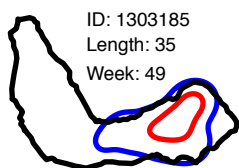


Figure 52 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

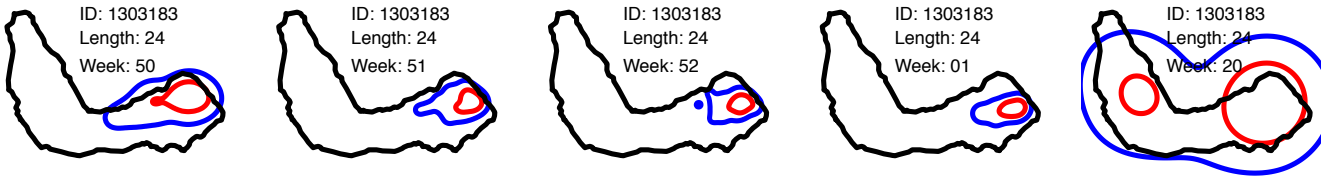


Figure 53 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

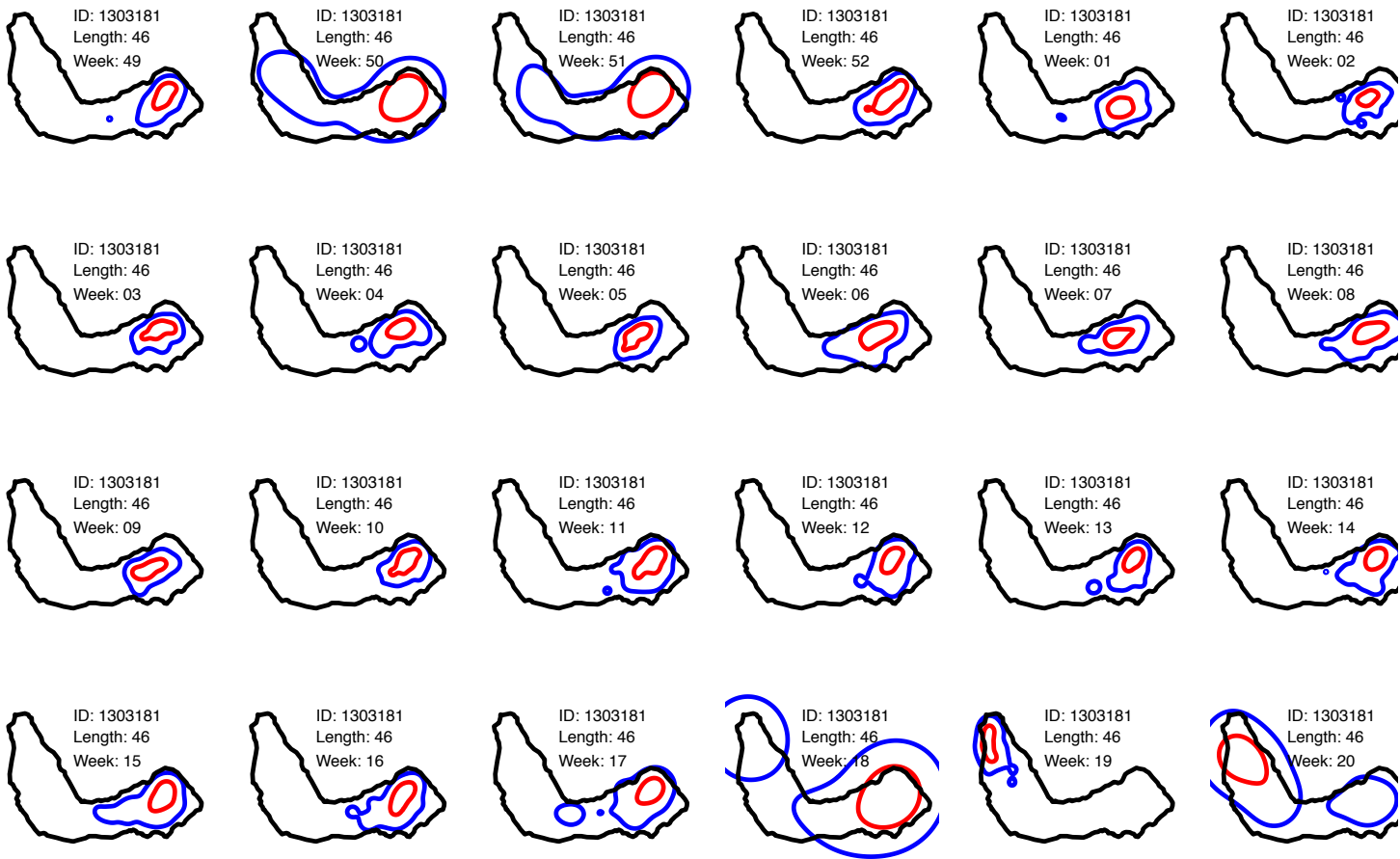


Figure 54 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

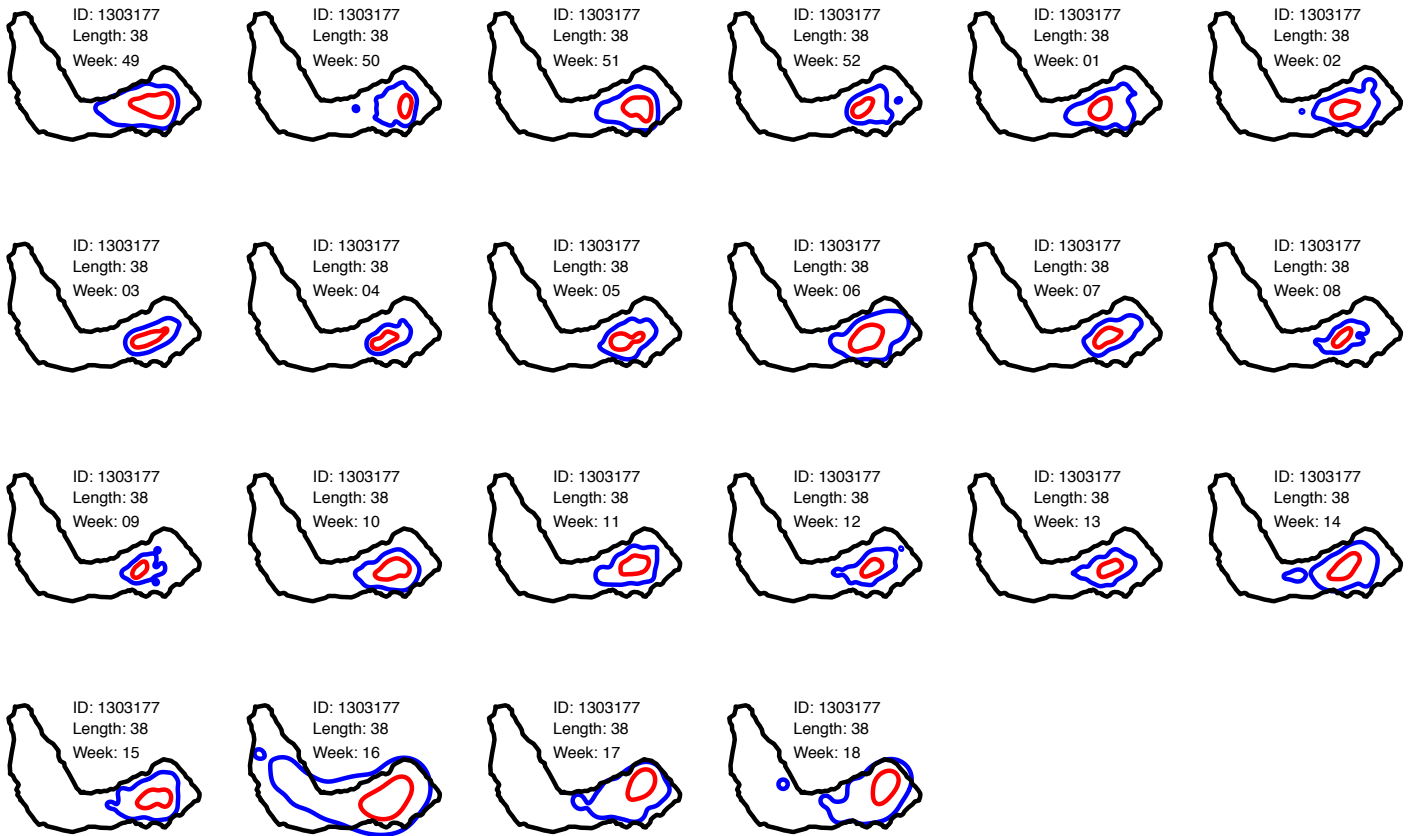


Figure 55 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

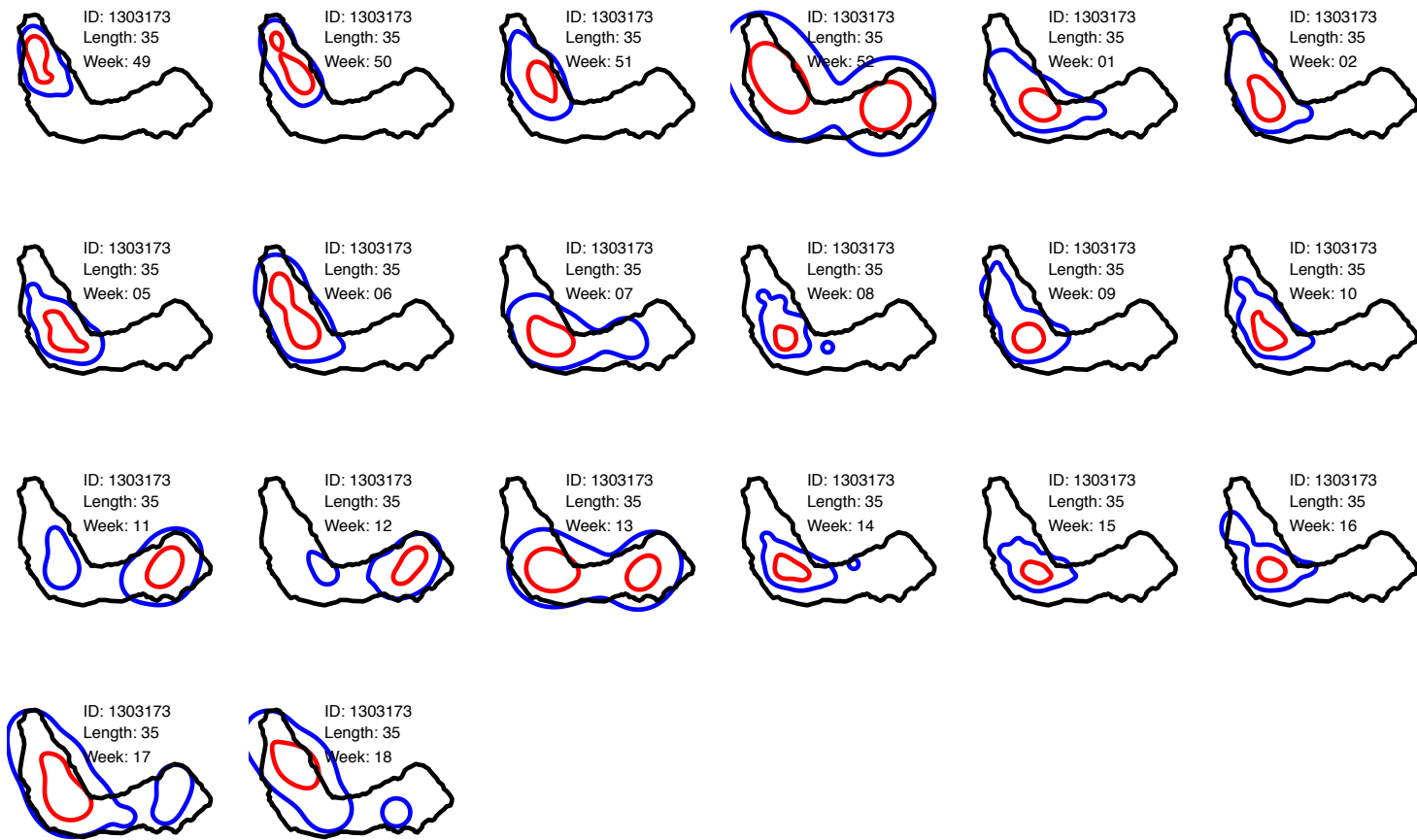


Figure 56 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

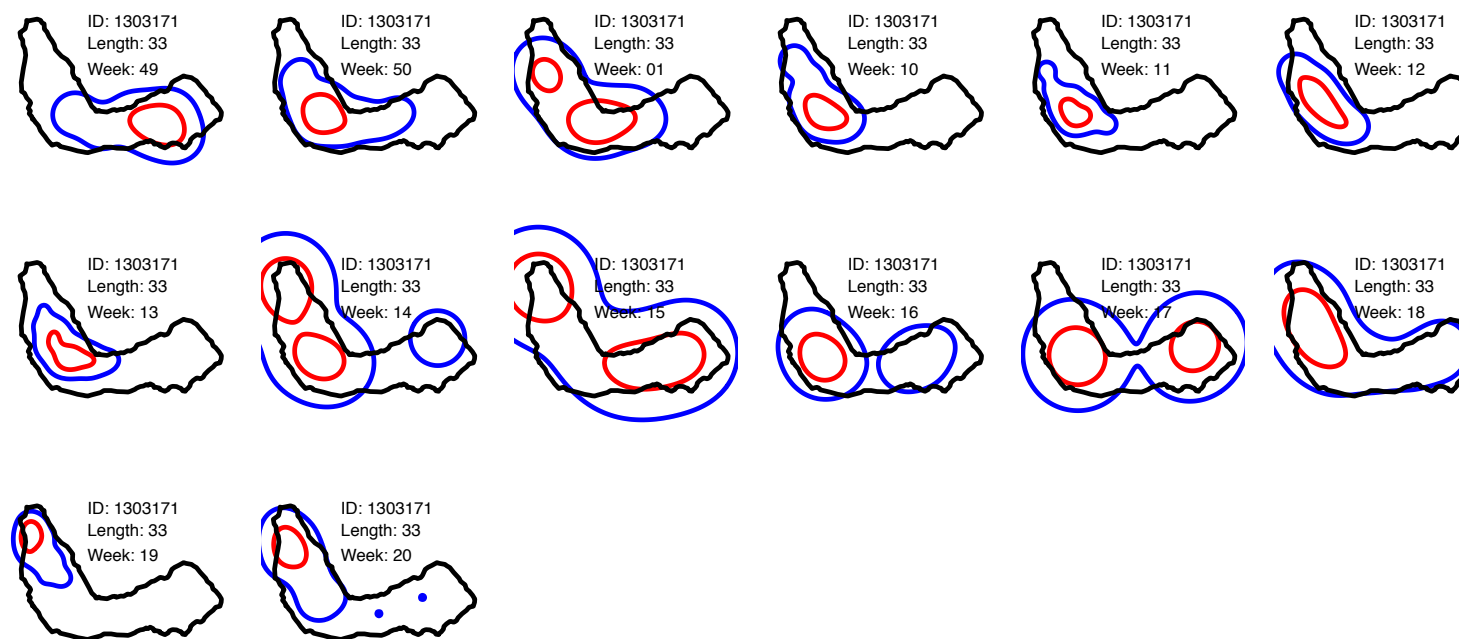


Figure 57 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

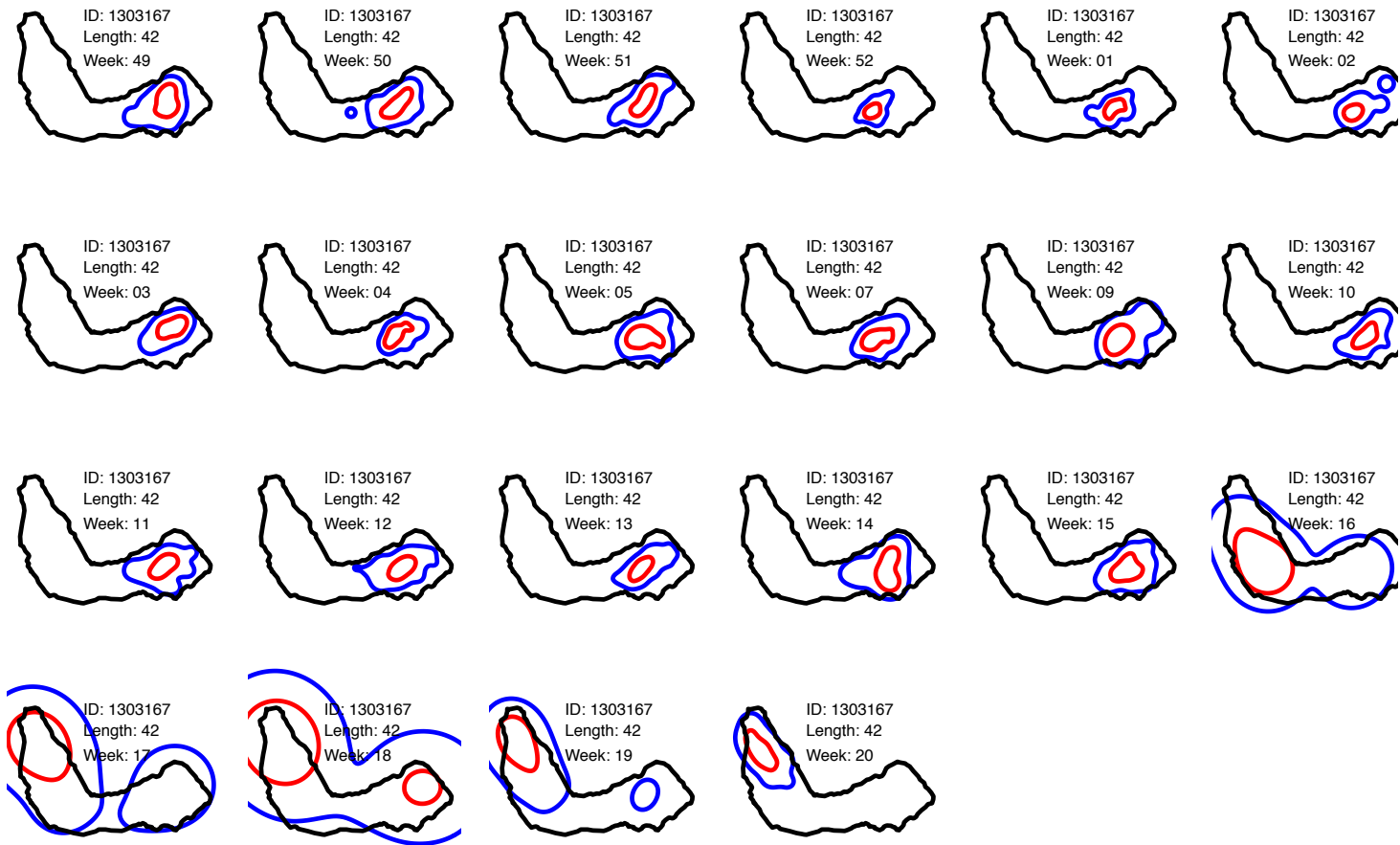


Figure 58 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

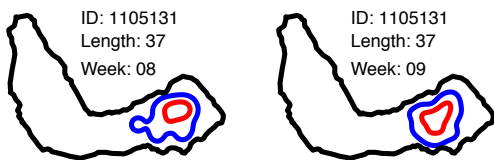


Figure 59 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.



Figure 60 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

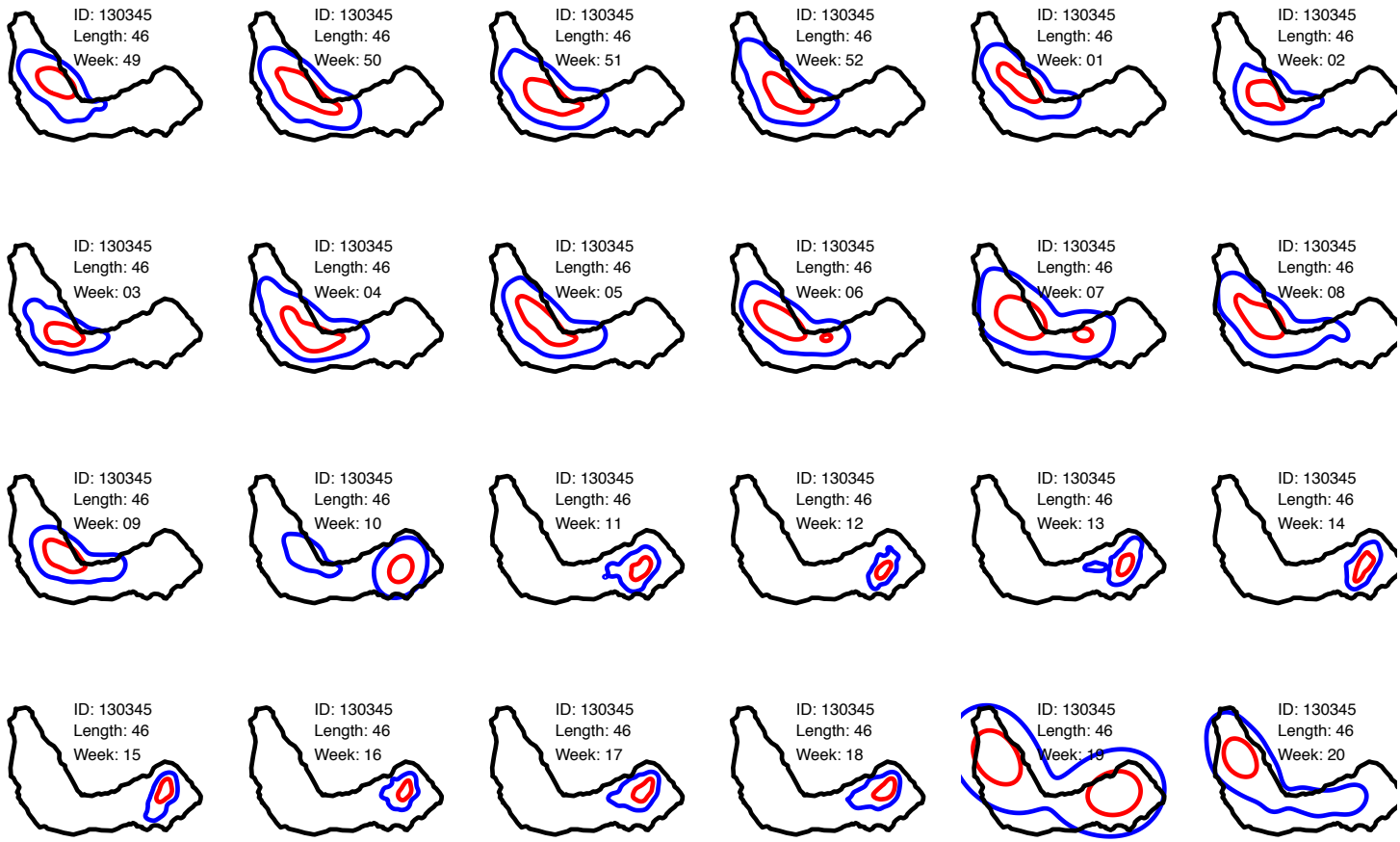


Figure 61 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

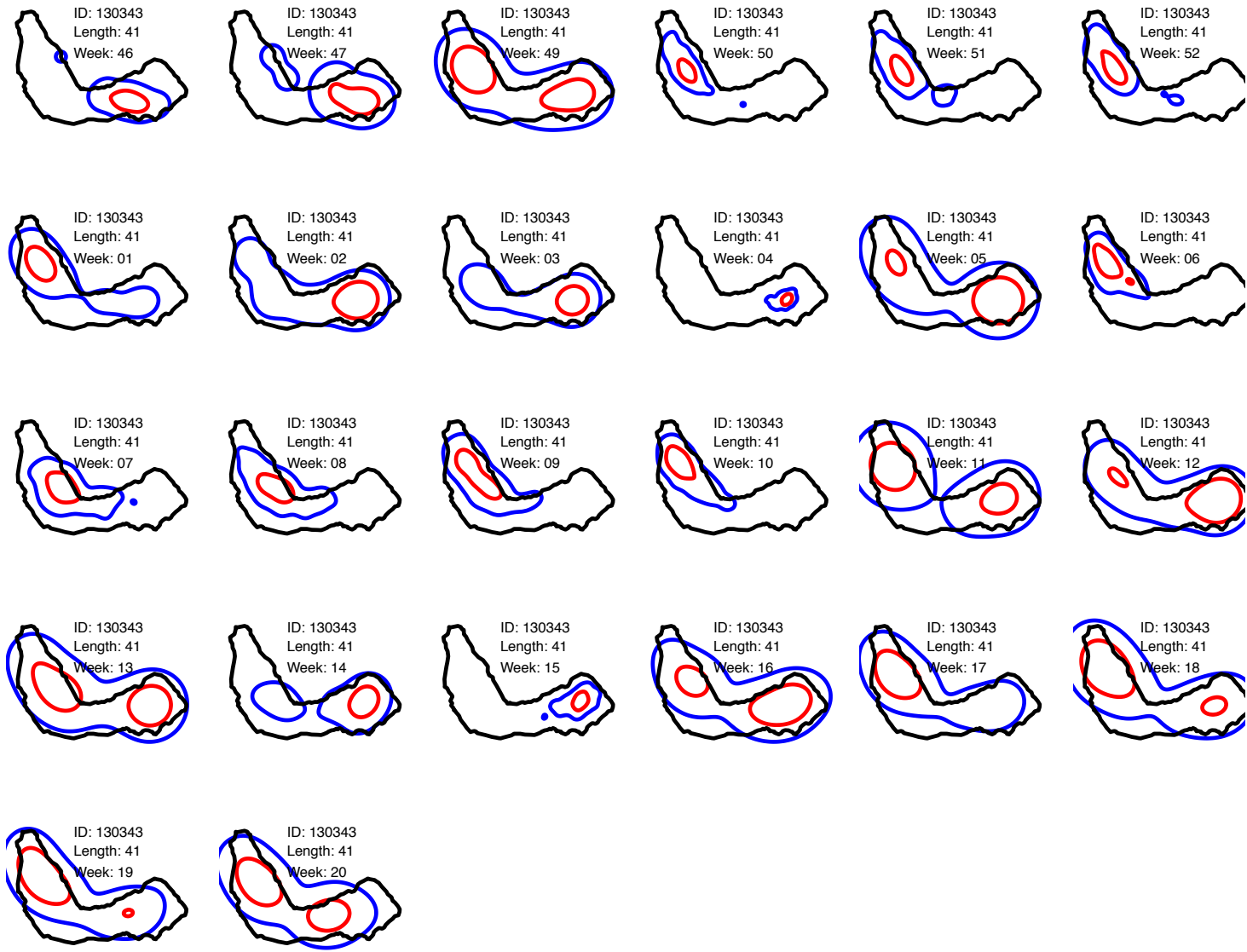


Figure 62 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

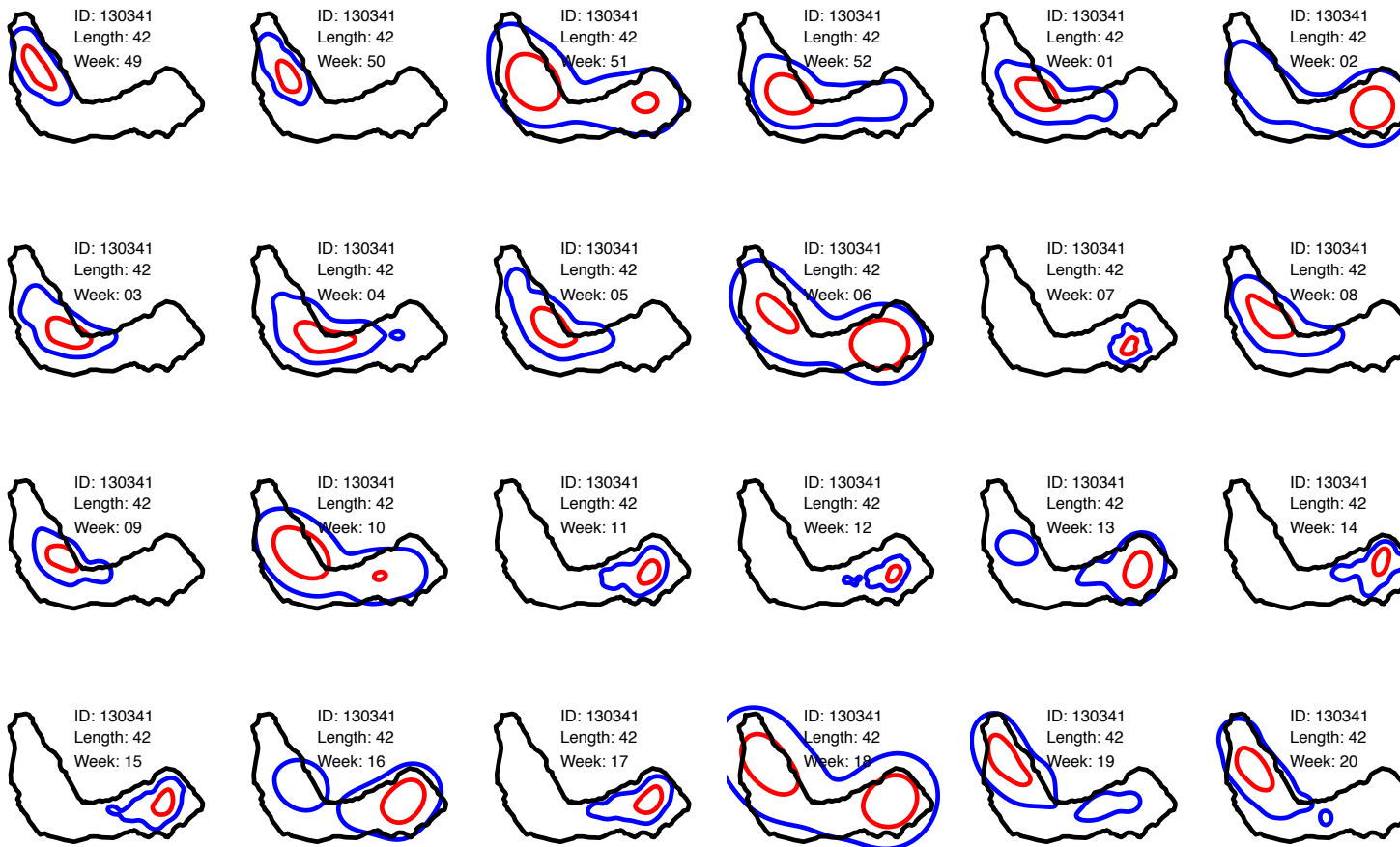


Figure 63 Weekly utilization distributions of one individual trout showing fish ID, length. Red area indicates the 50% utilization distribution and blue indicates the 95 percent utilization distribution for a given week.

8.3 Model selection

8.3.1 Depth utilization distribution

Table 6 The ten best-fitted models for predicting depth utilization Predictions are on data collected from dept/temperature transmitters from the 2012-13 and the 2013-14 winters. (N=14)

Model	Explanatory Variables	Degrees of freedom	AIC-Value	AIC-diff
1	Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*	100	877060,8	0
2	Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*season	100	877218,8	158
3	Discharge Aurland I*Water.use.vangen*water temperature 1m*fish length*sunrise*season	100	877895,8	835
4	Discharge Aurland I*water temperature 1m*fish length*sunrise*season	52	878645,8	1585
5	Discharge Aurland I*fish length*water temperature 1m*season*sunset	52	878722,8	1662
6	water temperature 1m*fish length*day length*day length	53	879075,8	2015
7	Water.use.vangen*water temperature 1m*fish length*sunrise*season	52	879111,8	2051
8	Water.use.vangen*water temperature 1m*fish length*sunset*season	52	879118,8	2058
9	Discharge Aurland I*water temperature 1m*fish length*	148	879446,8	2386
10	Discharge Aurland I+Discharge Vassbygdeldvi*water temperature 1m*fish length*sunrise*season	53	879670,8	2610

Table 7 residuals for predicting depth utilization distribution

Random effects			
Groups	Variance	Std.Dev.	Corr
Spec.fiskeID	1.901e+01	4.35980	
DoY	6.632e-04	0.02575	-0.66
Residual	3.260e+00	1.80542	
Number of observations	217668		
n=	14		

Table 8 Utilization distribution model for predicting depth use for trout in Vassbygdvatnet (on the following two pages)

(Intercept)	-7.283e+00
Discharge Aurland I	2.489e-01
Discharge Vassbygdelvi	4.061e+00
water temperature 1m	-2.855e+00
fish length	4.566e-01
day length	3.620e+00
fall.open	2.183e+03
spring.closed	-6.489e+00
spring.open	1.219e+02
winter	1.609e+01
Discharge Aurland I*Discharge Vassbygdelvi	-1.688e-01
Discharge Aurland I*water temperature 1m	1.921e-02
Discharge Vassbygdelvi*water temperature 1m	3.442e-01
Discharge Aurland I*fish length	-1.086e-02
Discharge Vassbygdelvi*fish length	-8.931e-02
water temperature 1m*fish length	4.671e-02
Discharge Aurland I*day length	-6.187e-02
Discharge Vassbygdelvi*day length	-9.208e-01
water temperature 1m*day length	-9.400e-02
fish length*day length	-9.321e-02
Discharge Aurland I*fall.open	-4.248e+02
Discharge Aurland I*spring.closed	-8.970e-01
Discharge Aurland I*spring.open	3.132e+01
Discharge Aurland I*winter	4.363e-01
Discharge Vassbygdelvi*fall.open	-8.558e+02
Discharge Vassbygdelvi*spring.closed	5.349e+01
Discharge Vassbygdelvi*spring.open	-2.194e+01
Discharge Vassbygdelvi*winter	7.472e+00
water temperature 1m*fall.open	-1.999e+02
water temperature 1m*spring.closed	2.944e+01
water temperature 1m*spring.open	-7.700e+01
water temperature 1m*winter	-9.688e+00
fish length*fall.open	-5.256e+01
fish length*spring.closed	-1.242e-01
fish length*spring.open	-4.812e+00
fish length*winter	-8.721e-01
day length*fall.open	-1.875e+02
day length*spring.closed	-2.856e+00
day length*spring.open	-9.838e+00
day length*winter	-5.415e+00
Discharge Aurland I*Discharge Vassbygdelvi*water temperature 1m	7.970e-03
Discharge Aurland I*Discharge Vassbygdelvi*fish length	5.297e-03
Discharge Aurland I*water temperature 1m*fish length	-1.277e-04
Discharge Vassbygdelvi*water temperature 1m*fish length	-1.055e-02
Discharge Aurland I*Discharge Vassbygdelvi*day length	2.848e-02
Discharge Aurland I*water temperature 1m*day length	2.609e-03
Discharge Vassbygdelvi*water temperature 1m*day length	3.284e-02
Discharge Aurland I*fish length*day length	2.380e-03
Discharge Vassbygdelvi*fish length*day length	2.252e-02
water temperature 1m*fish length*day length	3.320e-03
Discharge Aurland I*Discharge Vassbygdelvi*fall.open	1.501e+02
Discharge Aurland I*Discharge Vassbygdelvi*spring.closed	-5.801e-01
Discharge Aurland I*Discharge Vassbygdelvi*spring.open	-7.097e-01
Discharge Aurland I*Discharge Vassbygdelvi*winter	-1.311e+00
Discharge Aurland I*water temperature 1m*fall.open	4.322e+01
Discharge Aurland I*water temperature 1m*spring.closed	5.726e-01
Discharge Aurland I*water temperature 1m*spring.open	-8.991e+00
Discharge Aurland I*water temperature 1m*winter	-3.187e-01
Discharge Vassbygdelvi*water temperature 1m*fall.open	8.122e+01
Discharge Vassbygdelvi*water temperature 1m*spring.closed	-5.634e+01
Discharge Vassbygdelvi*water temperature 1m*spring.open	4.421e+00
Discharge Vassbygdelvi*water temperature 1m*winter	9.009e-01
Discharge Aurland I*fish length*fall.open	1.068e+01
Discharge Aurland I*fish length*spring.closed	2.934e-02
Discharge Aurland I*fish length*spring.open	-5.127e-01
Discharge Aurland I*fish length*winter	-8.171e-06
Discharge Vassbygdelvi*fish length*fall.open	2.108e+01
Discharge Vassbygdelvi*fish length*spring.closed	-1.373e+00
Discharge Vassbygdelvi*fish length*spring.open	8.131e-01
Discharge Vassbygdelvi*fish length*winter	3.141e-01
water temperature 1m*fish length*fall.open	4.856e+00
water temperature 1m*fish length*spring.closed	-7.648e-01
water temperature 1m*fish length*spring.open	2.261e+00
water temperature 1m*fish length*winter	5.324e-01
Discharge Aurland I*day length*fall.open	3.425e+01
Discharge Aurland I*day length*spring.closed	1.153e-01
Discharge Aurland I*day length*spring.open	-1.904e+00
Discharge Aurland I*day length*winter	6.300e-03
Discharge Vassbygdelvi*day length*fall.open	7.067e+01
Discharge Vassbygdelvi*day length*spring.closed	-2.644e+00
Discharge Vassbygdelvi*day length*spring.open	1.942e+00
Discharge Vassbygdelvi*day length*winter	2.208e-01

water temperature 1m*day length*fall.open	1.728e+01
water temperature 1m*day length*spring.closed	-1.532e+00
water temperature 1m*day length*spring.open	4.734e+00
water temperature 1m*day length*winter	2.319e+00
fish length*day length*fall.open	4.534e+00
fish length*day length*spring.closed	9.437e-02
fish length*day length*spring.open	3.594e-01
fish length*day length*winter	1.921e-01
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length	-2.965e-04
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*day length	-2.126e-03
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*day length	-8.928e-04
Discharge Aurland I*water temperature 1m*fish length*day length	-1.470e-04
Discharge Vassbygdeldvi*water temperature 1m*fish length*day length	-7.245e-04
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fall.open	-1.542e+01
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*spring.closed	7.669e-01
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*spring.open	2.936e-01
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*winter	7.208e-01
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*fall.open	-3.763e+00
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*spring.closed	1.606e-02
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*spring.open	1.301e-03
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*winter	2.535e-02
Discharge Aurland I*water temperature 1m*fish length*fall.open	-1.087e+00
Discharge Aurland I*water temperature 1m*fish length*spring.closed	-1.481e-02
Discharge Aurland I*water temperature 1m*fish length*spring.open	1.470e-01
Discharge Aurland I*water temperature 1m*fish length*winter	2.311e-03
Discharge Vassbygdeldvi*water temperature 1m*fish length*fall.open	-2.015e+00
Discharge Vassbygdeldvi*water temperature 1m*fish length*spring.closed	1.480e+00
Discharge Vassbygdeldvi*water temperature 1m*fish length*spring.open	-2.144e-01
Discharge Vassbygdeldvi*water temperature 1m*fish length*winter	-2.973e-01
Discharge Aurland I*Discharge Vassbygdeldvi*day length*fall.open	-1.206e+01
Discharge Aurland I*Discharge Vassbygdeldvi*day length*spring.closed	1.639e-02
Discharge Aurland I*Discharge Vassbygdeldvi*day length*spring.open	3.204e-02
Discharge Aurland I*Discharge Vassbygdeldvi*day length*winter	1.044e-01
Discharge Aurland I*water temperature 1m*day length*fall.open	-3.485e+00
Discharge Aurland I*water temperature 1m*day length*spring.closed	-5.136e-02
Discharge Aurland I*water temperature 1m*day length*spring.open	5.556e-01
Discharge Aurland I*water temperature 1m*day length*winter	1.421e-02
Discharge Vassbygdeldvi*water temperature 1m*day length*fall.open	-6.722e+00
Discharge Vassbygdeldvi*water temperature 1m*day length*spring.closed	3.492e+00
Discharge Vassbygdeldvi*water temperature 1m*day length*spring.open	-3.087e-01
Discharge Vassbygdeldvi*water temperature 1m*day length*winter	-7.710e-01
Discharge Aurland I*fish length*day length*fall.open	-8.620e-01
Discharge Aurland I*fish length*day length*spring.closed	-3.923e-03
Discharge Aurland I*fish length*day length*spring.open	3.002e-02
Discharge Aurland I*fish length*day length*winter	-1.864e-03
Discharge Vassbygdeldvi*fish length*day length*fall.open	-1.742e+00
Discharge Vassbygdeldvi*fish length*day length*spring.closed	6.713e-02
Discharge Vassbygdeldvi*fish length*day length*spring.open	-6.421e-02
Discharge Vassbygdeldvi*fish length*day length*winter	-6.407e-02
water temperature 1m*fish length*day length*fall.open	-4.214e-01
water temperature 1m*fish length*day length*spring.closed	3.631e-02
water temperature 1m*fish length*day length*spring.open	-1.426e-01
water temperature 1m*fish length*day length*winter	-1.016e-01
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length	7.193e-05
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*fall.open	3.868e-01
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*spring.closed	-2.108e-02
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*spring.open	-3.997e-03
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*winter	-1.305e-02
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*day length*fall.open	1.238e+00
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*day length*spring.closed	-4.518e-02
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*day length*spring.open	-1.789e-02
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*day length*winter	-5.607e-02
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*day length*fall.open	3.023e-01
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*day length*spring.closed	-4.157e-04
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*day length*spring.open	3.823e-04
Discharge Aurland I*Discharge Vassbygdeldvi*fish length*day length*winter	-1.566e-03
Discharge Aurland I*water temperature 1m*fish length*day length*fall.open	8.772e-02
Discharge Aurland I*water temperature 1m*fish length*day length*spring.closed	1.408e-03
Discharge Aurland I*water temperature 1m*fish length*day length*spring.open	-8.899e-03
Discharge Aurland I*water temperature 1m*fish length*day length*winter	5.186e-04
Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*fall.open	1.669e-01
Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*spring.closed	-9.148e-02
Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*spring.open	1.377e-02
Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*winter	5.766e-02
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*fall.open	-3.107e-02
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*spring.closed	1.244e-03
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*spring.open	2.046e-04
Discharge Aurland I*Discharge Vassbygdeldvi*water temperature 1m*fish length*day length*winter	6.602e-04

8.3.2 Area utilization prediction model selection

Table 9 The ten best-fitted models for predicting area utilization distribution Predictions are on data collected from dept/temperature transmitters from the 2013-14 winters. (N=31)

Area utilization distribution		Degrees of freedom	AIC	
Model				
1	water temperature 1m*fish length*day length	34	5206,849	0
2	water temperature 1m*.opening+fish length,2)	8	5216,466	9,617
3	water temperature 1m+study.week,2,	9	5219,261	12,412
4	water temperature 1m*season*fish length*day length	26	5233,057	26,208
5	water temperature 1m*.opening	6	5234,579	27,73
6	water temperature 1m+Water.use.vangen+fish length,3)	8	5239,598	32,749
7	water temperature 1m*Water.use.vangen+fish length,3)	9	5244,497	37,648
8	water temperature 1m*Water.use.vangen+fish length,3)	9	5244,497	37,648
9	water temperature 1m+.opening*study.week	7	5249,487	42,638
10	water temperature 1m+Water.use.vangen+fish length,2)	7	5253,861	47,012

Table 10 residuals for predicting area utilization distribution

Random effects		
Groups	Variance	Std.Dev.
ID	76.91	8.77
Residual	291.71	17.08
Number of observations	606	
n=	41	

Table 11 Utilization distribution model for predicting area use for trout in Vassbygdvatnet

Fixed effects*	
	Estimate
(Intercept)	1.328e+00
fish length	-1.546e-02
water temperature 1m ¹	-5.795e-01
water temperature 1m ²	4.729e-02
spring.closed	-7.193e+00
spring.open	-2.223e+03
winter	-2.032e+00
fish length*water temperature 1m ¹	1.037e-02
fish length*water temperature 1m ²	-8.636e-04
fish length*spring.closed	1.585e-01
fish length*spring.open	5.550e+01
fish length*winter	4.177e-02
water temperature 1m ¹ *spring.closed	6.717e+00
water temperature 1m ² *spring.closed	-1.497e+00
water temperature 1m ¹ *spring.open	1.481e+03
water temperature 1m ² *spring.open	-2.443e+02
water temperature 1m ¹ *winter	1.180e+00
water temperature 1m ² *winter	-2.418e-01
fish length*water temperature 1m ¹ *spring.closed	-1.433e-01
fish length*water temperature 1m ² *spring.closed	2.979e-02
fish length*water temperature 1m ¹ *spring.open	-3.696e+01
fish length*water temperature 1m ² *spring.open	6.099e+00
fish length*water temperature 1m ¹ *winter	-2.793e-02
fish length*water temperature 1m ² *winter	7.936e-03

8.3.3 Volume utilization prediction model selection

Table 12 The ten best-fitted models for predicting volume utilization distribution. Predictions are on data collected from dept/temperature transmitters from the 2012-13 and the 2013-14 winters. (n=9)

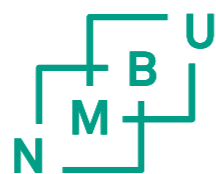
Volume utilization Distribution			
Model	Explanatory variables	Degrees of freedom	AIC
1	Fish length*Water temperature 1m ² *season	26	612,6377 0
2	Fish length+Water temperature 1m*season+ open/closeding	10	617,3649 4,7272
3	Fish length+season*Water temperature 1m	9	619,1902 6,5525
4	Fish length*season*Water temperature 1m	18	619,9173 7,2796
5	Fish length* open/closeding*study.week	10	620,1644 7,5267
6	Fish length* open/closeding+study.week	7	620,8933 8,2556
7	Fish length+Water temperature 1m+ open/closeding+study.week	7	622,0212 9,3835
8	Water temperature 1m+ open/closeding+Fish length+study.week	7	622,0212 9,3835
9	Water temperature 1m+ open/closeding*study.week+Fish length	8	623,7275 11,0898
10	Water temperature 1m*study.week	6	623,9783 11,3406

Table 13 residuals for predicting volume utilization distribution

Random effects			
Groups	Variance	Std.Dev.	Corr
Spec.fiskeID	1.901e+01	4.35980	
DoY	6.632e-04	0.02575	-0.66
Residual	3.260e+00	1.80542	
Number of observations	217668		
n=	14		

Table 14 Utilization distribution model for predicting area use for trout in Vassbygdvatnet

Fixed effects		Estimate
(Intercept)		1.328e+00
fish length		-1.546e-02
water temperat	1m^1	-5.795e-01
water temperat	1m^2	4.729e-02
spring.closed		-7.193e+00
spring.open		-2.223e+03
winter		-2.032e+00
fish length*wa	temperature 1m^1	1.037e-02
fish length*wa	temperature 1m^2	-8.636e-04
fish length*spr	g.closed	1.585e-01
fish length*spr	g.open	5.550e+01
fish length*wi	r	4.177e-02
water temperat	1m^1*spring.closed	6.717e+00
water temperat	1m^2*spring.closed	-1.497e+00
water temperat	1m^1*spring.open	1.481e+03
water temperat	1m^2*spring.open	-2.443e+02
water temperat	1m^1*winter	1.180e+00
water temperat	1m^2*winter	-2.418e-01
fish length*wa	temperature 1m^1*spring.closed	-1.433e-01
fish length*wa	temperature 1m^2*spring.clos	2.979e-02
fish length*wa	temperature 1m^1*spring.open	-3.696e+01
fish length*wa	temperature 1m^2*spring.open	6.099e+00
fish length*wa	temperature 1m^1*winter	-2.793e-02
fish length*wa	temperature 1m^2*winter	7.936e-03



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