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Growth, survival and migration of juvenile brown trout (*Salmo trutta*) in six tributaries to river Verdalselva: connectivity and source sink dynamics

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Environment and Natural Resources

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Vekst, overlevelse og vandring hos ørretunger (*Salmo trutta*) i seks sidebekker til Verdalselva: konnektivitet og source-sink dynamikk

"The gift of God shall wander from seashore to the mountains if she wants to"

("*Ganga skal Guds gava til fjells som til fjøre om ganga ho vil*")

– Gulatingsloven, the oldest written law in Norway

Preface

This thesis is written as a part of the project "Ny giv for sjøørreten" ("A new impetus for the sea trout") in river Verdalselva with its tributaries and is a vital part of my master's degree in Nature management at the Faculty for Environmental Science and Natural Resources, Norwegian University of Life Science, NMBU.

All photos are taken by the author unless else stated.

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Norwegian University of Life Science

Ås, 14. May 2019

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Abstract

Brown trout (*Salmo trutta L.*) in dendritic river systems mainly use smaller tributaries as spawning- and nursery grounds. The juveniles exhibit territorial behavior and compete over resources of food and shelter. Interactions between density-dependent and density-independent factors influence their life-history traits in intricate ways. Owing to the possibility for inter-tributary movement and inter-tributary variation in habitat quality in such dendritic river systems, survival, growth and migration can be investigated with a metapopulation approach. Differences in habitat quality and juvenile brown trout density among the tributaries may induce migratory behavior and source-sink dynamics. The aim of this thesis was to provide evidence of density-dependent and density-independent differences in growth, survival and migration and reveal source-sink dynamics processes in brown trout inhabiting the river Verdalselva tributaries.

Data was collected by electric fishing and capture-mark-recapture analysis was used to investigate growth, survival and migration within and among six neighboring tributaries to Verdalelva, at four occasions; May, August and October 2018 and in January 2019. Altogether, 1685 juvenile brown trout was caught, out of which 582 were PIT-tagged, 35 recaptured and 101 redetected. Based on previous data, high and low juvenile brown trout densities assigned three tributaries as source and three as sink sub-populations.

Recapture probabilities were generally low, most probably due to difficult fishing conditions (water turbidity, dense vegetation) and due to undetected migration, but there was some variation among the tributaries. As expected, comparing habitat characteristics among tributaries showed significant differences between the source and sink groups. Source tributaries had higher water current velocity and were wider whereas sink tributaries had smaller substrate size and less woody debris. Density estimates of both 0+ and >0+ age classes of juvenile brown trout supported these results and the pre-classification into source and sink groups as the density was significantly lower in sink than in source tributaries.

Sink 0+ individuals were on average larger than source individuals in both August and October, but individuals from source tributaries had higher growth rates (though not significantly so) over the same time span. The estimated monthly survival was negatively associated with juvenile density in the source group but not in the sink group, indicating density-dependent survival in the former. Density-independent effect of drought was found to be most pronounced in the sink tributaries where downstream migration probability increased

with decreasing rainfall. The finding of negative correlation between population density and downstream migration probability was not expected and may indicate that density-independent factors overruled density-dependent factors during the warm and dry 2018 summer.

In conclusion, this study has provided results that in varying degree proved useful for enlightening the addressed hypothesis. There was some support for density-dependent survival in source-subpopulations, but no or enigmatic support for density-dependent growth and dispersal. Density-independent survival in sink subpopulations was largely supported and downstream migration was largely density-independent (maybe drought driven). Four individuals migrated between tributaries, which strengthens the hypothesis of source sink dynamics and calls for further research.

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1. Introduction

Sea trout populations decline in large areas of Norway, where largely anthropogenic activities, such as aquaculture and agricultural and infrastructural land use, have been suggested as key causal factors (Bergan & Solem, 2019; Thorstad et al., 2014). Agricultural and infrastructural land use may potentially inflict connectivity and habitat quality in this species' nursery areas that largely comprises small streams or tributaries of larger river systems (Jonsson & Jonsson, 2011). Not much is known about migration patterns and survival of juvenile sea trout (*Salmo trutta*) in dendritic river systems. Due to inter- and intra-cohort competition, they may explore different habitat opportunities that influence survival and growth. Sea trout juveniles exhibit territorial behavior, where dominant and larger individuals occupy preferred habitat with the best opportunities for foraging and shelter (Heggenes et al., 1999; Jonsson & Jonsson, 2011). Less dominant individuals are believed to move downstream and possibly migrate into the main river. There they may meet competitors of greater size, which might encourage search for new feeding grounds, perhaps in adjacent tributaries. However, the evidence supporting this theory is poor.

Therefore, a metapopulation approach might be helpful when studying migration patterns and life cycles of juvenile seatrout in river systems. In population biology, the term metapopulation describes an assembly of spatial delimited local populations. River systems and adjacent tributaries which are inhabited with subpopulations (demes) of juvenile sea trout, demonstrate such a metapopulation structure.

Source-sink population dynamics is defined by the existence of high-quality habitats producing a surplus of individuals that may disperse to sink habitats where habitat quality is poorer, and density is lower. This metapopulation and source-sink-dynamics may apply to river systems and tributaries that support sea trout populations. However, these river structures are in constant danger due to human interference. During the last century a substantial amount of water ways have been cut off by roads and railways fragmenting and degrading habitat. The once numerous sea trout is today reduced to such a low stock that fishing is prohibited in the rivers that flow out into Trondheimsfjorden (Anonymous, 2007; Bergan & Solem, 2019).

Over the last decades, awareness has risen, and actions have been put into operation to rescue the sea trout populations. However, the measures of environmental measures are often not thoroughly evaluated, and uncertainty exists regarding the best approaches. From a nature

management perspective, investigations on metapopulation processes in sea trout systems and how they respond to habitat measures will bring important knowledge to policy makers. The river system Verdalselva, in region Trøndelag in Norway, has been subjected to several studies that have revealed large inter-tributary variation in juvenile brown trout densities and is therefore well suitable for such a study.

This thesis is the first sub-study in Verdalselva that aims to investigate the metapopulation structure and source-sink dynamics as well as density and survival using capture-mark-recapture analysis in six neighboring tributaries. Through my master's thesis I aim at enlightening the following research questions and hypotheses:

Q1: Is there evidence for density-dependent/density-independent growth, survival and migration between the source and sink tributary groups?

> H1.1: The source tributaries exhibit evidence of density-dependent growth, survival and migration.

> H1.2: The sink tributaries exhibit evidence of density-independent growth, survival and migration.

Q2: Is there evidence of source-sink dynamics between the source and sink tributary groups in river Verdalselva?

> H2.1: Juvenile sea trout migrate from tributaries with high-density and high-quality habitats.

> H2.2: Juvenile sea trout migrate to tributaries with low-density and lower habitat quality.

At first, I will introduce a brief history of the role of salmonids in the Norwegian management and highlight the most precarious issues. Then I will introduce short on the theory this study derives from according to those issues. Then I will present the methods and materials used to yield my presiding results. At last I will try to justify the findings in relation to existing knowledge and draw some cautious conclusions.

1.1. The history of importance

Thousands of years ago, humans most likely harvested and nourished from anadromous salmonids as they followed the ice edge north during the end of the last ice-age (Halffman et al., 2015). Petroglyphs forms drawings of salmonids that reaffirms the importance of these fisheries. In Norway, the first known descriptions of the property rights to salmonid fisheries are found on rune stones from the 10th century (Anonymous, 1993). Gulatingsloven, the oldest law in Norway, states "*Ganga skal Guds gava til fjells som til fjøre om ganga ho vil*" which prohibits blocking of the waterways ensuring free migration routes from mountain to sea for the salmonids. These provisions were brought on by Magnus Lagabøters country laws from 1274 and Christians V´s Norwegian legislation written in 1687 (Anonymous, 1993). In the following centuries, the rules were tightened by new legislations that all had in common the importance of open migration routes ensuring that salmonids could reproduce and persist (Anonym, 2010; Anonymous, 1993). In the 19th century, salmon (*Salmo salaris*) and brown trout became very popular objects for sport fisheries. The first form of known tourism in Norway was by the English upper-class commonly known as "fishing lords" which anticipated the development of modern sport fishing. Sea trout as well as salmon, have been the most desired fish for sports fisheries which has strongly influenced how Norway manages salmonids (Bergan & Solem, 2019). The salmonids have an important cultural, historical and socio-economic role in the Norwegian society and have been a part of the management of nature as far back as we know. Open migration routes have been the key factor in this management.

1.2. The history of impacts

During the 20th century, profound land-use changes were conducted rapidly (Bergan & Nøst, 2017). In line with the growth and development of human population, the demand of energy, food and materials increased substantially which led to an escalating exploitation of natural resources. Along followed infrastructure that seized area and affected rivers and streams with severe environmental effects. Development of hydropower plants led to changes in water discharge, while roads and railways were built with impassable culverts. As agricultural areas expanded nursery streams were led into ditches and underground piping. Rivers and streams were transformed from natural meandering systems to channels with none, or small, riparian zones changing the ecological functions of the systems. In addition, acidification from sulphur-

pollution, contamination of freshwater from leaking sewage, industries and mining, and nutrient enrichment from artificial fertilizer from cultivated land lead to a reduction in water quality (Bergan & Nøst, 2017; Thorstad et al., 2014 and references therein). During the last century, water ways have been subject to detrimental human impacts. The sea trout suffers as they depend on reproducing in small streams and tributaries that has been ignored by the nature and resource management for many years (Bergan & Nøst, 2017).

The water quality has improved since the worst period in the 1990th (Bergan & Nøst, 2017) and it is believed that negative impacts in the fresh water phase are reduced and the sea trout smolt production is stable (Jonsson et al., 2011; Thorstad et al., 2015). Nevertheless, catches of sea trout still have a negative trend in most coastal regions, indicating that the mortality in the sea water phase has increased the last decades (Finstad et al., 2011; Jonsson et al., 2009; Thorstad et al., 2014). Rising temperatures (e.g. global warming), abundance of prey, predation and the growing threat of sea lice infection pressure induced by open net cages fish farms are suggested to influence mortality in a complex interaction., but it is not well established what are the determining factors (Finstad et al., 2011; Jonsson et al., 2009; Thorstad et al., 2015).

1.3. Sea trout population and river fragmentation in Trøndelag

Fishing sea trout is prohibited in rivers connected to Trondheimsfjorden because the population is at a historically low level (Jonsson et al., 2009). The river Verdalselva has been investigated several times since the 80s exhibiting fragmentation and bad conditions in the tributaries (Haukeland et al., 1986; Hol, 2018; Kristiansen & Rikstad, 2007; Lyngstad, 1992; Vårhus, 2016). Verdalselva runs into Trondheimsfjorden, which serves as a national protected salmon fjord since 2003 (Anonymous, 2007), and thus fish farming is not allowed in the fjord and the infection pressure from sea lice should be minor (Thorstad et al., 2015). Still the number of both "catch and release" and killed sea trout had a negative trend until 2011, and have since then more or less stabilized at a low level (Anonymous, 2018a) (Figure 1).
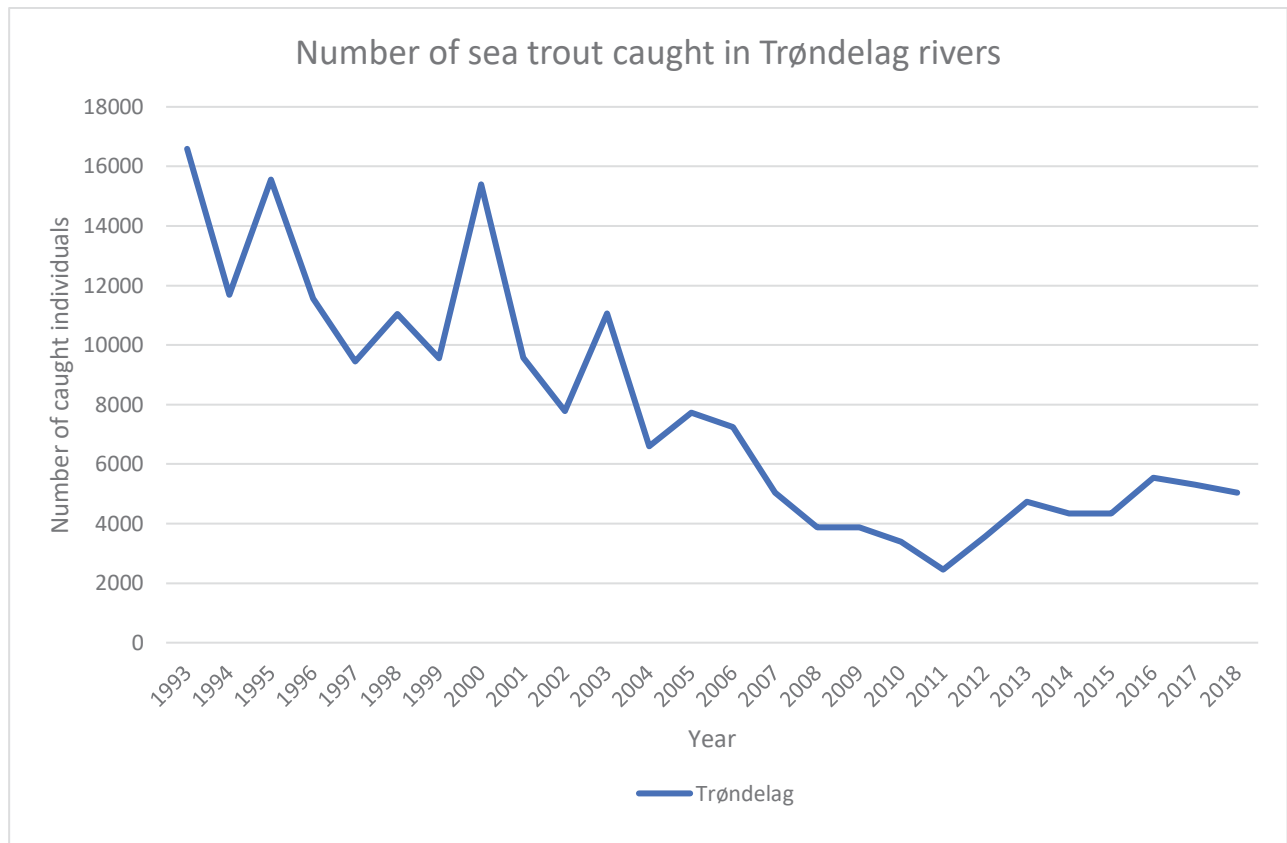
Figure 1: Total catches of sea trout in Trøndelag county rivers from 1993 to 2018 (Anonymous, 2018a).

Fragmentation of habitat, i.e. barriers and obstacles in the waterways, constrains migration and influence life history traits, growth and survival. Migration behavior of sea trout is driven by evolutionary processes where the cost of migrating is compensated by benefits such as faster growth and raised fecundity (Jonsson & Jonsson, 2011 and references therein). In a river system where tributaries become inaccessible, or difficult to access for the adult spawning sea trout, the hindrances may lead to low recruitment as well as alter local extinction in upstream areas. Hol (2018) investigated 34 tributaries in river system Verdalselva in Verdal municipality and estimated a 35 percent reduction of nursery streams habitat because of closed stream areas, barriers and blocked migration routes. When including degradation of habitat- and water quality (assumed status before 1940), an 80 percent reduction in juvenile sea trout productivity were estimated (Hol, 2018). Bergan and Nøst (2017) conducted a similar study in 37 streams in Trondheim municipality and found a 70 percent habitat loss and a total of 90 percent reduction in production of juvenile sea trout. Both studies highlighted the effects of fragmentation as causing increased patchiness in these habitats.

1.4. Metapopulation theory applied on sea trout

Structures with patchiness of habitat can be acknowledged as a metapopulation structure (Hanski et al., 2004). A dendritic river system in its natural condition has a structure where the different tributaries reflect defined patches of environment. The sea trout inhabiting these tributaries are likely to have a metapopulation structure where demes (subpopulations) inhabit the different tributaries. The sea trout usually performs homing (migrates back to spawn in the stream where it grewup) thus they are genetically differentiated among streams (Hovgaard et al., 2006; Jonsson & Jonsson, 2011; Knutsen et al., 2001; Thorstad et al., 2014). As most of the individuals in a sea trout population migrate to the sea to grow and mature, the different demes have common feeding grounds where they mix. Sea trout straying when returning to spawning areas is common (Berg & Berg, 1987) and enables genetic exchange, colonization as well as recolonization of extinct populations (Hanski et al., 2004; Jonsson & Jonsson, 2006; Knutsen et al., 2001; Thorstad et al., 2014). Newly colonized streams have a mixture of genes from individuals of different origin (Jonsson & Jonsson, 2011; Knutsen et al., 2001). In a metapopulation structure, this behaviour of spreading may contribute to distribute individuals evenly through the habitat according to local carrying capacity.

The tributaries often differ in habitat quality implying that a source-sink population dynamic may also occur among the brown trout populations inhabiting them. Hanski et al. (2004) defines a source-sink structure to be based on the difference between immigration and emigration between habitats, where the good quality source habitat produces a surplus of individuals that disperse to lower quality sink habitat. Such a structure requires a great dispersal rate of individuals, and the connectivity between the tributaries are of great importance (Hanski et al., 2004). Different densities among juvenile sea trout subpopulations facilitates source-sink processes. As density-dependent factors are known to regulate the population of juvenile brown trout in early stages (Elliott, 1993; Jonsson & Jonsson, 2011), competition may trigger active dispersal of individuals from tributaries with high density seeking better feeding ground in habitats with lower density. Such migratory behaviour may distribute the fish so that the density reaches the carrying capacity of both habitats if the cost of migration is lower than the gain (Jonsson & Jonsson, 2011). Density-independent factors influenced of seasonal changes and hydrological processes as drought, flood, high temperatures and ice covering may as well play a central role in movement (Elliott, 1994; Heggenes et al., 1999; Vøllestad & Moland, 2008).

In general, source-sink dynamics in age structured metapopulation remain rather unexplored (Hanski et al., 2004), and we do not know how human impacts of fragmentation will interfere with source-sink processes in a metapopulation of sea trout. A source-sink dynamic between tributaries in a river system may enhance production and be of great importance in management of these waterways. There is a need for knowledge of how the metapopulation structure are influencing the migration, survival and growth of the sea trout.

2. Materials and methods

2.1. Study species

The investigated species in this study is the brown trout[1]. Brown trout is iteroparous (spawns multiple times during a lifetime) and belongs in the family of Salmonidae. The species originates from Europe but today the geographical distribution is worldwide due to human introduction (Elliott, 1994; Lowe et al., 2000). Where brown trout populations have access to marine environment, they exhibit partial migration were some individuals may be stationary whilst others become anadromous sea trout (del Villar-Guerra et al., 2014; Jonsson & Jonsson, 2006; Klemetsen et al., 2003). The juvenile sea trout spends between one and seven years in fresh water before they exhibit physiological and morphological changes (smoltification) and migrate to the sea to grow and mature (Jonsson & Jonsson, 2011). The sea trout can spend from some months during summer to several years in the sea before maturing (Jonsson & Jonsson, 2011). In Verdalselva, most of the brown trout are considered to be sea trout as they co-exists with Atlantic salmon that can impose interspecific competition as their spatial habitat niches overlap (Heggenes et al., 1999; Jonsson & Jonsson, 2011). However, in the tributaries, the juvenile sea trout is dominating.

Sea trout inhabiting dendritic river systems is known to use smaller tributaries as spawning- and nursery grounds but can use large rivers (Armstrong et al., 2003; Crisp, 1993; Jonsson & Jonsson, 2011). Spawning usually occurs in the period October to December where they seek to shallow running water with gravel and pebbles mean size of approximately 10 percent of its body length (Armstrong et al., 2003; Jonsson & Jonsson, 2011). The eggs are deposited and buried in a series of nests that aggregated forms a redd. Access to oxygen are of importance and kept by ventilating water flow through the substrate, but may be blocked by fine substrate from erosion that cause increased mortality (Armstrong et al., 2003).

Density-dependent factors are expressed when the alevins emerge from the gravel in large numbers during spring, usually in May. When the yolk sac is consumed, the alevins exhibit an ontogenetic shift where they start to feed on drifting invertebrates and locate suitable shelter. In this critical period the mortality rate can be up to 90 percent (Elliott, 1994; Heggenes et al.,

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[1] Brown trout and sea trout are the same species, but the latter also includes migration to the sea. As we don't know the faith of the investigated juveniles, the brown trout term is used in this study.

1999; Jonsson & Jonsson, 2011). The juvenile brown trout exhibit size dependent territorial behavior and the fry meet intense intra- and inter-cohort competition from its relatives and older age-classes (Heggenes et al., 1999). As the juveniles grow they show tendency to form size structured dominance hierarchies and exhibit spatial niche selection, i.e. the larger fish wins the best feeding- and sheltering ground (Heggenes et al., 1999; Jonsson & Jonsson, 2011). The young fry is often found in shallow water and larger individuals in deeper areas and pools (Heggenes et al., 1999). Heterogenous habitat with a variability of larger structures may sustain higher densities as visual isolation between individuals reduce territorial sizes and aggression as well as provide shelter and hiding from predators (Heggenes et al., 1999). The early mortality rate and later available resources and shelter is proposed to regulate the population at an equilibrium density (Elliott, 1993; Jonsson & Jonsson, 2011).

Natural and seasonal events of drought and flooding may also regulate the population. There are indications of that density-independent factors can overrule density-dependent factors and be the main determinant of the population density in some cases under harsh environmental conditions (Cattanéo et al., 2002; Elliott, 1993; Vøllestad & Moland, 2008). It is recognized that impact from hydrological factors not only depends on magnitude but also the timing of the events relative to the development of the inhabitants (Cattanéo et al., 2002; Elliott, 1993) and that early stages (0+ and 1+) of brown trout were most vulnerable (Cattanéo et al., 2002 and references therein). Elliott (1993) 25-year study of brown trout in Black Brows beck revealed that summer drought had the most severe impact on the population, probably as the drought reduced suitable habitat and increased interaction between individuals. Cattanéo et al. (2002) found that high discharge and velocity at the time when the fry emerge reduced the density significantly, most likely by flushing them out of the system. When density-dependent and density-independent factors act together, the outcome is rather unpredictable and lead to fluctuation in the juvenile trout density regardless of the number of spawning adults and deposit eggs.

2.2. The study system

Verdalselva is designated as a national wild salmon river, located in Verdal municipality in Trøndelag county (Anonymous, 2007). The watershed area is 1468 km^2 and stretches from the Swedish boarder to the river outlet at Verdalsøra, in the north-east part of the designated national wild salmon fjord Trondheimsfjorden (Anonymous, 2007; Anonymous, 2018b). The

annual inflow is estimated to 1781 million m^3 of water (Anonymous, 2018b). The upper parts of the river are named Helgåa, but changes name to Verdalselva the last 20 km downstream where the river converges with the river Inna. The original stretch available for anadromous salmonids where approximately 33 km. In 1990, various environmental measures were conducted in the waterfall Grunnfoss and a fish ladder was constructed in waterfall Granfossen. Together, these efforts opened an additional 19 km upstream where now the waterfall Kløftafossen stops anadrome migration today (Berger et al., 2007; Øksenberg, 2013). Rainfall data were collected from the nearby weather station Buran. The tributaries with the corresponding watersheds are shown in Figure 2.
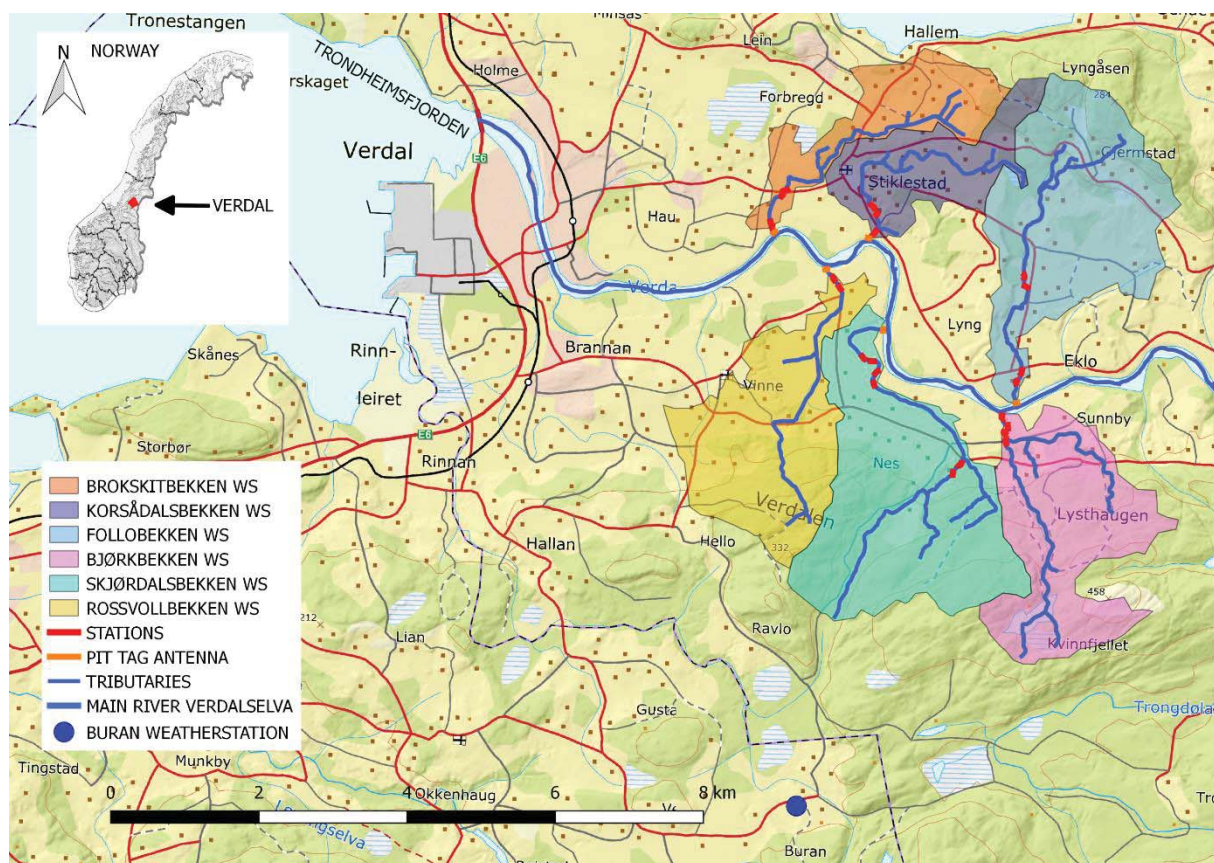
Figure 2: Map overview of the investigated part of river Verdalselva, Buran weather station and the watershed of the investigated tributaries on different colors.

According to Øksenberg (2013), various native species are found in the river system, amongst others resident and anadromous brown trout, Atlantic salmon, three-spined stickleback (*Gasterosteus aculeatus*), European eel (*Anguilla anguilla*), burbot (*Lota lota*) and Artic charr

(*Salvelinus alpinus*). The non-native species brook charr (*Salvelinus fontinalis*) and invasive species common minnow (*Phoxinus phoxinus*) are also present in the river system as a result of human introduction, and rainbow trout (*Oncorhynchus mykiss*) which escapes from nearby fish farms (Rikstad, 2016; Øksenberg, 2013).

2.3. Study tributaries and design

Tributaries varied strongly in a number of physical characteristics and previous data also show marked differences in juvenile brown trout densities (Hol, 2018; Vårhus, 2016). Details on tributary characteristics is provided in appendix 1 (Table 9 to 20).

The six neighboring tributaries were located within a 5.4 km stretch of the main river Verdalselva, three on the north side and three on the south side (Figure 2). In the design of this study, the tributaries were divided in source- and sink-groups based on density estimates from previous studies (Hol, 2018; Vårhus, 2016). Three of the tributaries had dens subpopulation of juvenile sea trout and were treated as sources whilst three had a less dens subpopulations and was treated as sinks.

The source tributary group: Follobekken, Bjørkbekken and Skjørdalsbekken

The sink tributary group: Brokskitbekken, Korsådalsbekken and Rossvollbekken

All tributaries provide migration access to the main river and thus also between the tributaries. Due to the relatively few years of juvenile density estimates available, this group assignment is to be considered a tentative one and history may show this to be wrong, as it is well known that juvenile densities in brown trout vary considerably among years (Jonsson & Jonsson, 2011).

2.3.1. Location and numbering of fishing stations

The aim was to place four fishing and tagging stations were used in each tributary, although Skjørdalsbekken had a total of six stations, Korsådalsbekken had three and Rossvollbekken only had two stations as the length of the anadromous stretch varied. All fishing stations were numbered by rising numbers from downstream closest to the outlet to Verdalselva, e.g. the station closest to the main river is number 1, further upstream number 2 and so on. All fishing stations intended to cover approximately 100 m^2 and were located at suitable habitats based

on assessment at low water level during first fishing round in May. Two stations were located close to Verdalselva, station 1 and 2, and additional two stations further upstream, station 3 and 4.

The stations were set up to study small-scale migration between adjacent neighboring stations and the inter-pair distance between pairwise stations to monitor large-scale within-tributary movement. The distance between the two stations in one pair ~100 meters and a distance > 100 meters between the pairs of stations. The PIT-antenna (see below) were placed close to the main river to monitor up- and downstream migration i.e. in and out from the tributary (Figure 3).
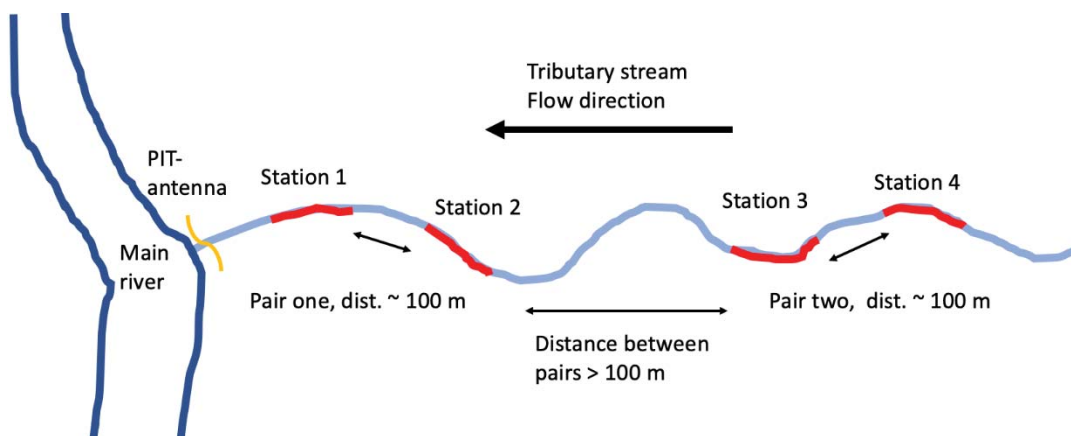
Figure 3: Illustration of placement for the PIT-antenna to detect emigration and the pairwise fished stations to reveal small-scale and large-scale movement within the tributaries.

2.3.2. PIT telemetry

Passive Integrated transponder (PIT) technology have been a huge advance in tracking animals and have become a common technique in tracing stream dwelling fish. PIT tags are made without battery and can be made very small to suit implantation in e.g. fish. The PIT tags act as a lifetime barcode with a unique alpha-numeric code for each tag and are activated by a low-frequency radio signal from a scanner or reader antenna which the tag sends back the code (Andrews & Gibbons, 2004). The reading range vary with natural conditions, but have increased as a result of effective antenna technology over the last decade. Linnansaari et al. (2007) found a detection range up to 90 cm (23 mm tags) and that the signal was penetrating water, ice, wood and rocks at winter conditions using a portable backpack reader.

Weber et al. (2016) found similar result with detection rate >80 cm (23 mm tags) but that 12 mm tags only had a range <50 cm, and that the reading range decreased with increasing ice cover (<0.5 m). PIT-tags used in this study are explained in section 2.4.2.

In this study, stationary PIT-antennas (LF HDX RFID Multi-Antenna reader, ISO 11784) were mounted at the outlet of the tributaries to the main river, except in Bjørkbekken as we run out of time and the battery was spoiled. In general, the reader box and batteries were placed in a plastic container (Figure 5) in safe distance from floods. The antenna tuner box was attached outside the container in a tree at the same height with connection to the antenna wires. The antenna wires were placed in a loop that covered the streambed overflow area in case of flood and secured with sticks and stones (Figure 4).

Figure 4: Antenna cable secured in the stream bed. *Figure 5: The container with reader box and battery.*

After installation the system was tuned with simulating a passing fish holding a PIT tag in horizontal position and sweeping up- and downstream in different ranges from the antenna wire. We achieved a detection range that varied from 10 to 50 cm between the readers in the different locations.

An Oregon RFID portable backpack reader (ORSR LF HDX RFID long range single antenna PIT tag reader, IOS 11784 + Mobile Reader Kit) were used in the last round (round 4 in January 2019) to detect tagged individuals. The tributaries were mostly covered with thin ice that could barely hold the weight of a person. The thin ice cover should not represent a barrier for the signal (Linnansaari et al., 2007; Weber et al., 2016).

2.3.3. Habitat characterizations and registrations

Each fishing station was divided into five cross-sectional transects where the first and the last was at the beginning and end of the station, as illustrated in Figure 6. E.g. a 40-meter-long station has five transects, with 40/4 = 10 meters between each transect. At each transect, canopy cover, branches over the riverbank and riverbank vegetation were registered. In the tributary the amount of moss and algae (if present), streambed substrate composition (clay, silt, gravel- and rocks-size), width, velocity and depth were noted. Depth was measured at 10, 25, 50, 75 and 90 percent of the width range of the water cover in the tributary. The percentage of substrate for each substrate size group were subjectively estimated to compare streambed conditions among stations.
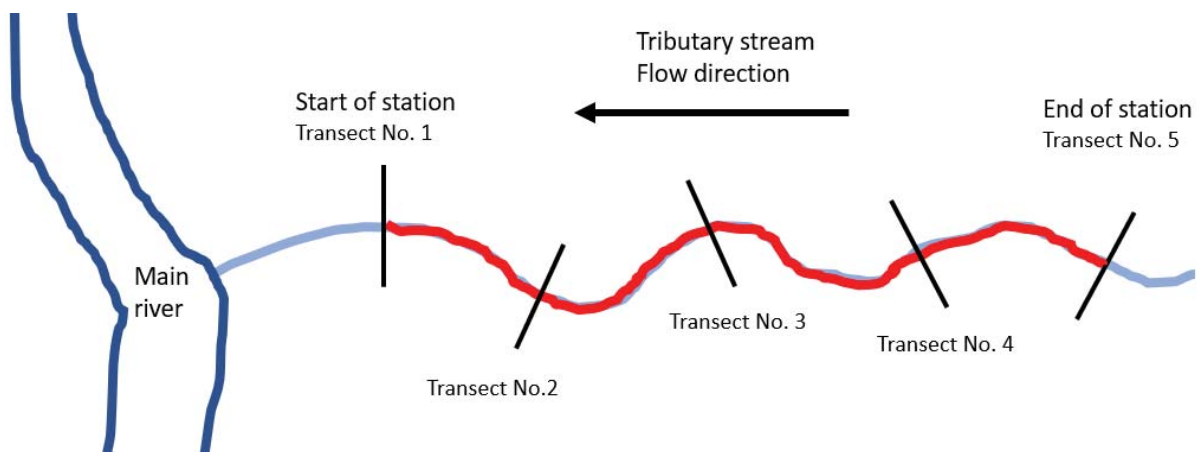
Figure 6: Illustration of a fishing station divided into transects where the habitat characteristics is measured. Canopy cover, branches over the riverbank and riverbank vegetation were registered. In the tributary, the amount of moss and algae (if present), streambed substrate composition (clay, silt, gravel- and rocks-size), width, velocity and depth were noted. Depth was measured at 10, 25, 50, 75 and 90 percent of the width range of the water cover in the tributary.

2.4. Capture, handling and tagging

In all tributaries, fishing was conducted in the three rounds in 2018 whilst in round 4 in 2019 only detections were performed. Round 1 was conducted in late May, round 2 in late August, round 3 in late October 2018 and the last round 4 in January 2019. Altogether 1685 juvenile sea trout was captured and of those 582 were PIT-tagged. Details on tagging and recapture numbers for the different study tributaries can be found in the appendix 1 (Appendix tables 9-19).

2.4.1. Electric fishing

Electric fishing is a well-known and widely used method which use is investigated in many studies and explained thoroughly by Bohlin et al. (1989). The probability for catchment of fish depends on several factors. Forseth and Forsgren (2009) suggest the following steps to fulfil a catchment: "*1) the fish must to be affected by the electric current, 2) the fish has to be pulled towards the anode or be stunned, 3) the fish has to be spotted by the fishers and 4) the fishers has to be able to capture the fish with the dip nets*". Failure was experienced several times during the fieldwork at one or several of these steps as a result of turbid water, branches blocking capture and fish swimming outside the electric field and disappearing.

The capture was conducted starting from the downstream end of a station moving upstream. Minimum two persons were always present, both for safety reasons and to maximize the probability of successful catch. One person would be equipped with the backpack portable electroshock gear, with the anode-net in one hand and a dip net in the other hand, and the second person would carry a dip net and a bucket to contain the captured fish (Figure 7). Electroshocking pulses were given for five to ten seconds and the affected fish was attempted captured with the dip net. All fish were kept in the bucket during

Figure 7: My colleague Hanne Marie and the helper Marianne Rønning Råbakk conducting electro fishing in stream Follobekken.

fishing and water was changed if the temperature was high or/and high density of fish in the bucket.

All fish where captured with electric fishing equipment, and a GeOmega FA-4 35-70 Hz, pulsed-DC from Terik Technology was used in all rounds. In round 2 in August, additional equipment type IG200/2C 10-100 Hz pulsed-DC from Schneider electric was borrowed from the Akvaplan-NIVA (Norwegian Institute for Water Research) to enhance effectivity with two teams conducting the electric fishing. Both fishing gear consisted of a backpack with battery and a control box, connected to a hand-held anode net and a cathode wire, which both should be kept in water during usage.

2.4.2. Handling and tagging

After capturing, the fish was held in a bucket with water, and an operating table with all necessary equipment was made ready before handling the fish. Snout to fork length (FL) of all fish was measured with a measuring tape glued to a tube cut in half. Fish <60 mm were not tagged and immediately put in separate a bucket after registering the species and length. Fish with FL >60 mm and <120 mm was tagged with 12 mm half duplex PIT tags (12.0 mm x 2.12 mm HDX ISO 11784/11785, read-only, air weight 0.1 g), and fish > 120 mm FL was tagged with 23 mm PIT tags (23.0 mm x 3.65 mm HDX ISO 11784/11785, read only, air weight 0.6 g). Before tagging, the fish were put individually in a bucket with a seductive mixture (5-7 ml of benzocaine per 10 liters of water) until sedated. The respective PIT-tag was scanned with a handhold PIT tag reader (Oregon RFID DataTracer Proximity reader), sterilized with 96 percent ethanol and washed in chlorhexidine before inserted surgically. A scalpel was used to apply a 2-3 mm long incision slightly through the skin in the abdomen region between the pectoral- and pelvic fins adjusted slightly to one side of the mid-ventral line. The PIT mark was then pressed through the incision and in to the abdominal cavity. The fish were then kept in a bucket of water until the sedative wore off before being randomly distributed back in to the tributary within the station it was caught.

2.4.3. Density fishing removal method

Density estimation (round 2, August) was performed by using the removal method as described carefully by Bohlin et al. (1989). Fishing was conducted at each station in three

rounds and the fish from the different catch rounds was then kept in separate buckets. If less fish than two were caught in either round 1 or 2, we assumed a low density and did only two passes. Determination of species (salmon or trout) and fork length on the fish to tag, or else total length (TL), were measured before the fish was released. These density estimates are not to be mixed with the first-pass number of individuals that has been used in some of the analysis.

2.5. Data processing and analysis

Model selection were based on Akaike's information criteria (AIC) (Akaike, 1974; Anderson, 2007) where the model that explains most of the variation while using fewest model parameters has the best outcome. The selection of possible models was based on an ecological approach where the experienced conditions were assessed. All dataset were prepared in Microsoft Excel before imported to statistical software R Studio and MARK (R Core Team, 2018; White, G C & Burnham, K P, 1999). As both fork length and total length were used as measurement units, all lengths where converted to total length (TL) in the dataset. The formula TL=0.9364 + 0.9896 * FL (R^2 = 0.997) were used and estimated with data from the project Gyrofri (personal message, Thrond Haugen).

2.5.1. Capture-mark-recapture analysis (CMR)

The mark-recapture data was analyzed using the software MARK version 9.0 (White, G. C. & Burnham, K. P., 1999). The data consisted of four mark-recapture occasions i.e., k_{max}=4). According to the design of study, and the initial plan, between-station migration (ψ), along recapture probability (p) and with survival (S) was modeled. A constrained approach had to be undertaken due to the short time-series of the data and the relatively low recapture rate. A multistate approach was used, where the initial individual encounter histories comprised of 4-digit arrays of either "0", "1", "2", "3", "4", "5" or "6" depending on whether the individual was encountered during an encounter occasion or not ("0" if not) – and if encountered, in what station (i.e., "state") the encounter took place (see Figure 19). An encounter history like "4041" would signify that the individual was captured, tagged and released in station 4 at first occasion, not detected during the second occasion, but detected in station 4 during occasion three, and finally detected in station 1 during the last occasion. Even though '0' signifies a lack of detection during occasion 2, and could indicate demise, subsequent detections confirm

that the individual was still alive. This exemplifies the nature of mark-recapture-analysis where incomplete detection histories are analyzed by simultaneously analyzing both processes related to detection and survival (Lebreton et al., 1992). The process of migration is also analyzed. The initial multistate design was simplified and deployed in this study, specifically to include three states: "Tag zone", "Upstream" and "Downstream". Unique "tag zone" states were assigned to each tributary, so regardless of which station the fish was tagged and released in within the tributary, they got the same tag-zone assignment (i.e., attaining values 1-6). Subsequent recaptures downstream (including other tributaries) or upstream got values of 7 and 8, respectively.

The parameterization of the multi-state model deployed is visualized in a fate diagram in Figure 8. From the fate diagram, we can follow individuals tagged at occasion k that get captured (and tagged and released) in some station in tributary 2. In the diagram, you can follow the Markovian steps describing survival and dispersal processes involved over two capture occasions, following the Conditional Arnason-Schwarz parameterization (Arnason, 1973). S_k^2 is the survival probability over the k to the k+1 period for individuals that stayed in zone 2 at occasion k, ψ_k^{27} is the probability of dispersing from zone 2 to a downstream zone during the k to the k+1 period (ψ_k^{22} is the probability of staying, ψ_k^{28} is the probability of going upstream), and p_k^2 is the probability of being captured in zone 2 at occasion k. Encounter histories for some example fates (corresponding to fates on the same line in the figure) are provided in curly brackets to the right; 0, not caught; 2 caught in zone 2; 7 caught in downstream zone; 8 caught in upstream zone; -2 means assigned as caught, as well as those caught and killed in zone 2 (i.e., right censored).

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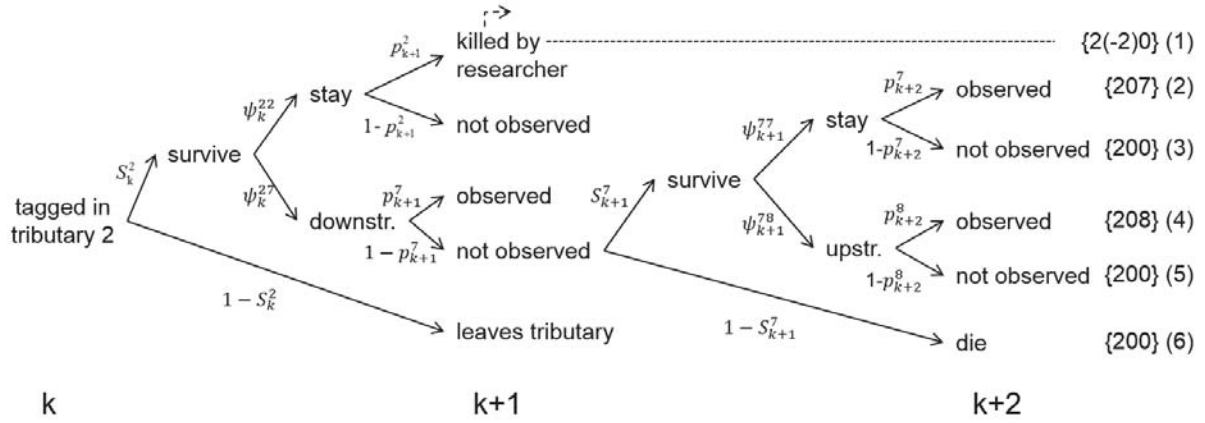
Figure 8: Fate diagram with corresponding Conditional Arnason-Schwarz (CAS) parameterization for a three-occasion study system (see text for a detailed description). Angled and dashed right-pointing arrows indicate right-censoring (i.e., data is used up to this occasion, but censored out of study beyond this point).

Figure 9 provides a comprehensive overview of parameters from the four occasions for the study system, apart from the ψ-parameter for which just two examples are presented to ease readability. The red and blue rings represent two different individual encounter histories where both encounter histories using the conventional CAS (CAS$_{orig}$) and the applied upstream/downstream CAS approach (CAS$_{adj}$) are shown at the bottom of Figure 9.
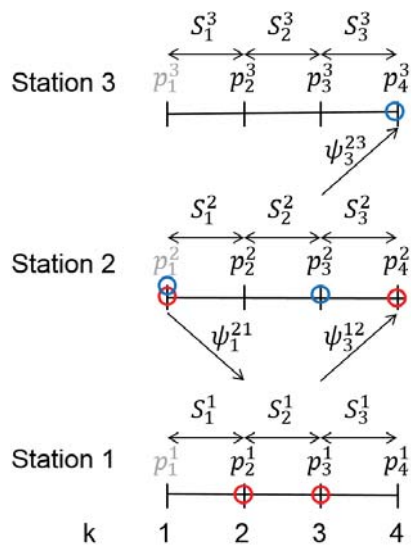
Figure 9: Overview of potential CAS parameters fitted for this study for individuals caught, tagged and released in tributary #3. k = occasion number; S_k^i represents survival over the k to k+1 period in zone i (Figure 8); p_k^i represents (re)capture probability at occasion k in habitat i (p1 are indicated in grey as these are not estimable); ψ_k^{ij} represents the dispersal probability from state i to j over the k to k+1 period. The red and blue circles denote two example encounter trajectories ((2112) and (2023)) described further in the main text.

Parameters were fitted using the maximum log likelihood method. All parameters can in theory be estimated as being constant over all occasions/periods, or to be time dependent. In addition, and more relevant from an ecological perspective, the parameters can be estimated as functions of covariates and factors of interest. Covariates can both be occasion-specific (e.g.,

temperature and discharge), and individual-specific (e.g., size). In this study, population density was used as an individual covariate allowing for population density to vary among occasions irrespective of where the individual was residing (i.e., it was kept track on which station it was recaptured at the different occasions).

Candidate model structures with combinations of individual and environmental covariates were fitted and subjected to model selection by means of Akaike's Information Criterion, AIC (Akaike, 1974; Anderson, 2007)

2.5.2. Other statistical analyses

All other statistical analyses were performed in statistical software R (3.5.2) (R Core Team, 2018). The parameter estimates from the most supported CAS-model in program MARK was used for further plotting in R. Habitat characteristics analysis were conducted using ordination analysis where the habitat registrations were standardized with mean =0 and standard deviation =1. The analyses were conducted using envfit, with the R-package vegan (Oksanen et al., 2015). Effects of sink-source grouping was explored by performing permutation test in a redundancy analysis setting.

Differences in juvenile brown trout density between the source and sink groups was performed using Welch ANOVA: One-way analysis of means ($\ln(x+1)$-transformed) allowing for unequal variances between the groups. Further, generalized linear models (GLM) and linear models (LM) approach where conducted to fit and test models (McCullagh & Nelder, 1989).

Differences in 0+ growth between source and sink tributaries were tested using linear models using 0+-length as response and month and source-sink group as effects in a fully factorial design. Significant group*month effect would be interpreted as differential growth rates.

3. Results

3.1 Habitat characteristics

The permutation test yielded a significant difference in habitat between the source and sink tributary groups ($p<0.001$) and a significant tributary effect ($p<0.001$) derived of the scaled habitat characteristic data from the tributaries. The principal component axis 1 (PC1) explain 31.7 % of the variance and PC2 axis explain 13.9 %, that give cumulative proportion 45.6 % of the variance explained in PC1 and PC2 axis (Table 1). When including source-sink as an explanatory variable to the PCA in a redundancy permutation test, an additional 11.2 % of the variation was explained. Substituting source-sink with tributary yielded 27.1 additional variation explained in the habitat characteristics

Table 1: Proportion explained of the principal components (PC) in the unconstrained ordination of the scaled characteristics from the tributaries.

Importance of components:	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalue:	3.1687	1.3917	1.3488	0.9753	0.9254	0.7080	0.6157	0.4274	0.3026	0.1368
Proportion explained:	0.3169	0.1392	0.1349	0.0975	0.0925	0.0708	0.0616	0.0427	0.0302	0.0137
Cumulative Proportion:	0.3169	0.4560	0.5909	0.6885	0.7810	0.8518	0.9134	0.9561	0.9863	1.0000

Biplot of the permutation test of the scaled habitat characteristic data from the tributaries visualizes where the respectable tributaries are located hence to the load from the different characteristics (Figure 10). Axes pointing in the same direction are positively correlated e.g. moss and width, and opposite direction are negatively correlated e.g. algae and shade. Axes perpendicular to each other has no correlation. Follobekken are correlating positively towards velocity and width, i.e., it seems to have higher velocity and be wider. Korsådalsbekken seems to correlate negatively towards mean substrate, e.g. smaller substrate size. The source tributary group tend to load against width, more moss growing and larger mean substrate, and opposite with the sink tributary group.
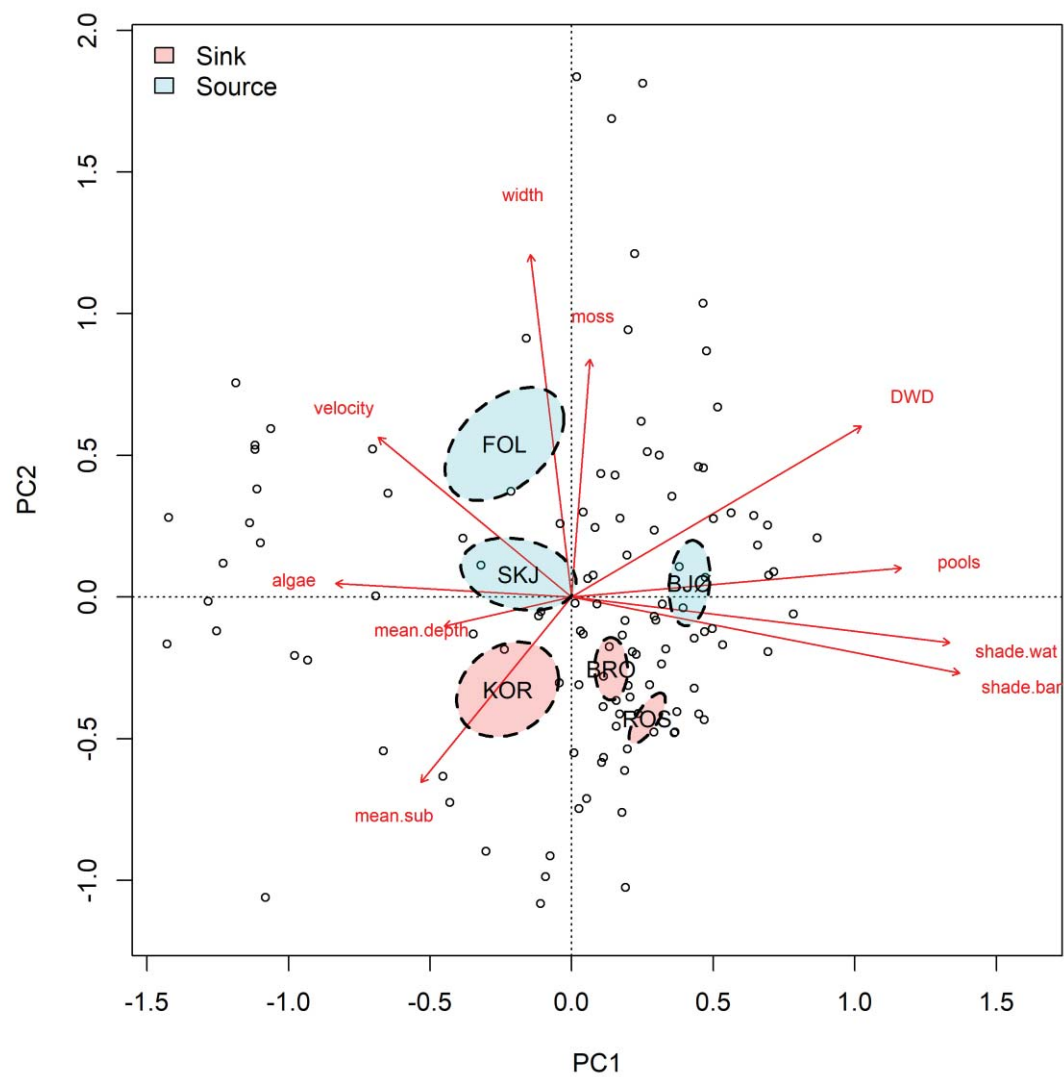
Figure 10: Biplot of the RDA-analysis of the scaled habitat characteristic data displays a significant difference between source and sink tributaries ($R^2 = 0.271$, $P = 0.001$) Centroids display 95% confidence bounds for the respective tributaries (abbreviated). DWD = dead woody debris.

3.2 Size distributions

In round 2 conducted in August a total of 1173 juvenile trout were caught. The cohort size limit between 0+ and >0+ was determined to be divided between 7 and 9 cm total length (TL) which varied among the different tributaries (Figure 11).
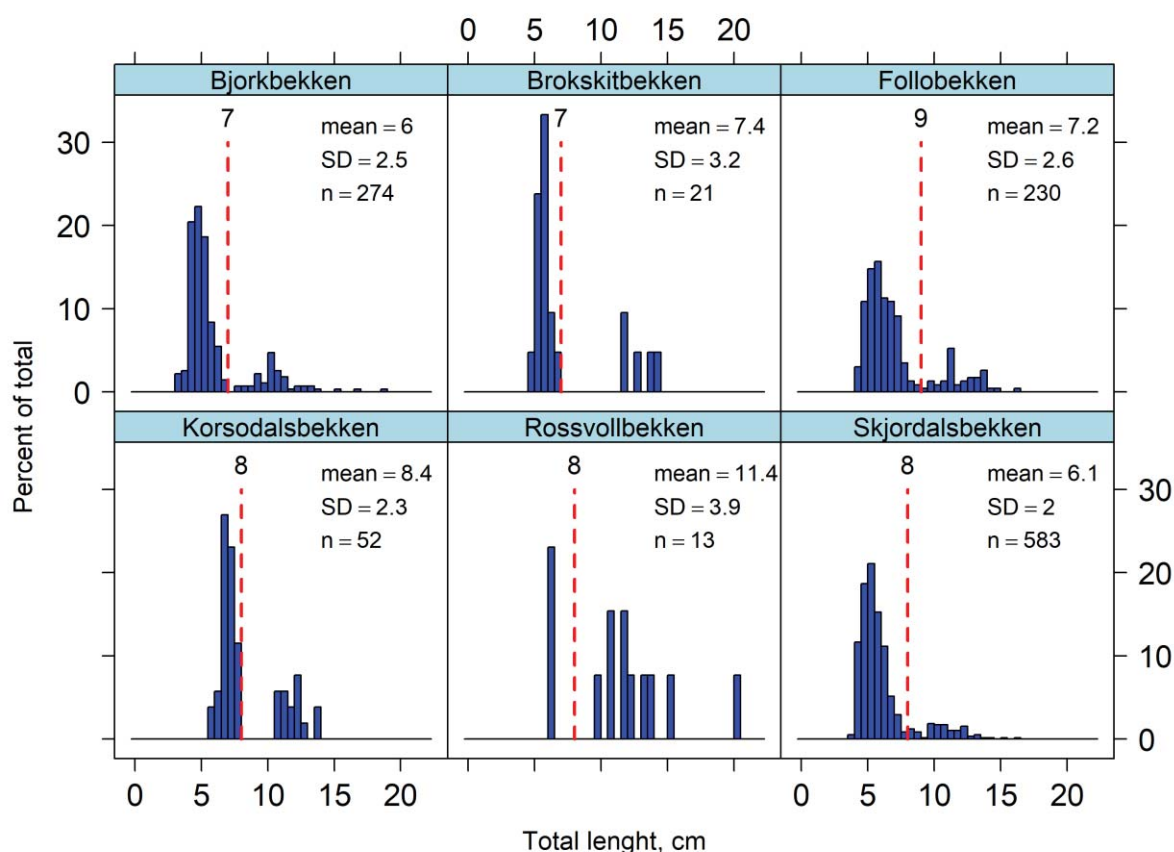
Figure 11: Age Length distribution of juvenile trout where the split assessed size limits between the cohort 0+ and >0+ are fixed are indicated as dashed vertical red lines between 7 and 9 cm.

3.3 Intra- and inter tributary 0+ growth and length by month

The variation in 0+ length distributions for all tributaries in August and October 2018 is displayed in Figure 12. This shows the growth in length between the periods, where the median length of juvenile sea trout in the source tributaries are somewhat ending at the same level, whereas the sink is slightly larger (Figure 12).
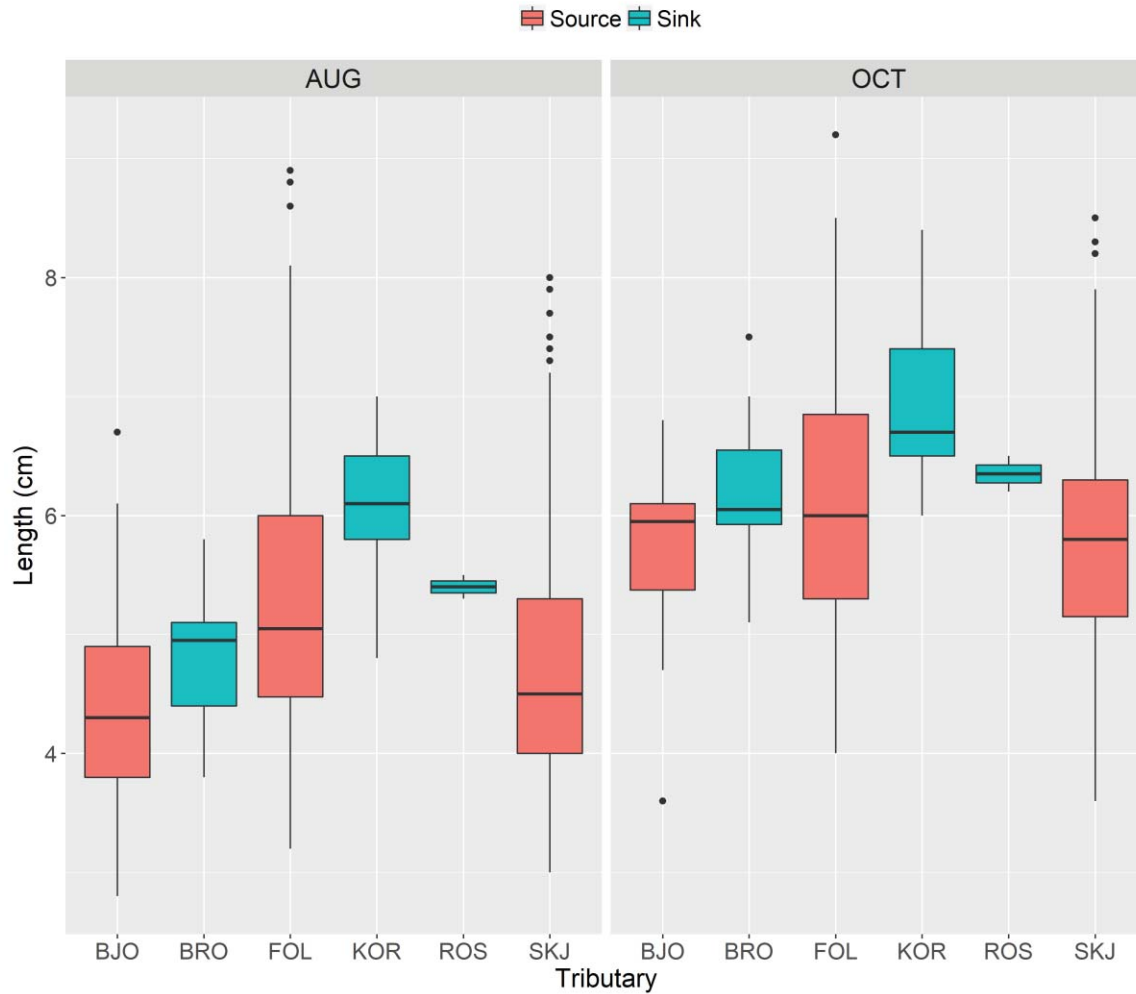
Figure 12:Boxplot of 0+ length distribution for each tributary in August to the left and October to the right that shows the growth pattern in this period. Y-axis = length in cm, x-axis = tributary. Boxes entail 50% of the observations and the whiskers span 90% of the observations. Thick horizontal lines represent the median value. Dots are outliers.

The analysis of 0+ growth between the source and sink tributary groups from round 2 in August to round 3 in October yielded a statistically non-significant interaction effect (R^2=0.06, P = 0.178), Table 2.

Table 2: Linear model parameter estimates for the analysis of 0+ growth between round 2 in August and round 3 in October 2018.

Parameter estimates

Coefficients	Estimate	SD.error	t value	P value
Intercept	5.532	0.074	74.44	2.00E-16
Month OCT	0.873	0.185	4.71	2.77E-06
SourceSinkSink	2.122	0.276	7.69	2.78E-14
Month OCT: SourcesinkSink	-0.686	0.509	-1.35	0.178
Multiple R-squared: 0.06644				

Prediction plot of 0+ growth for each tributary sink and source group which visualizes the differences in growth between round 2 in August and round 3 in October for the tributary source and sink groups. (Figure 13).
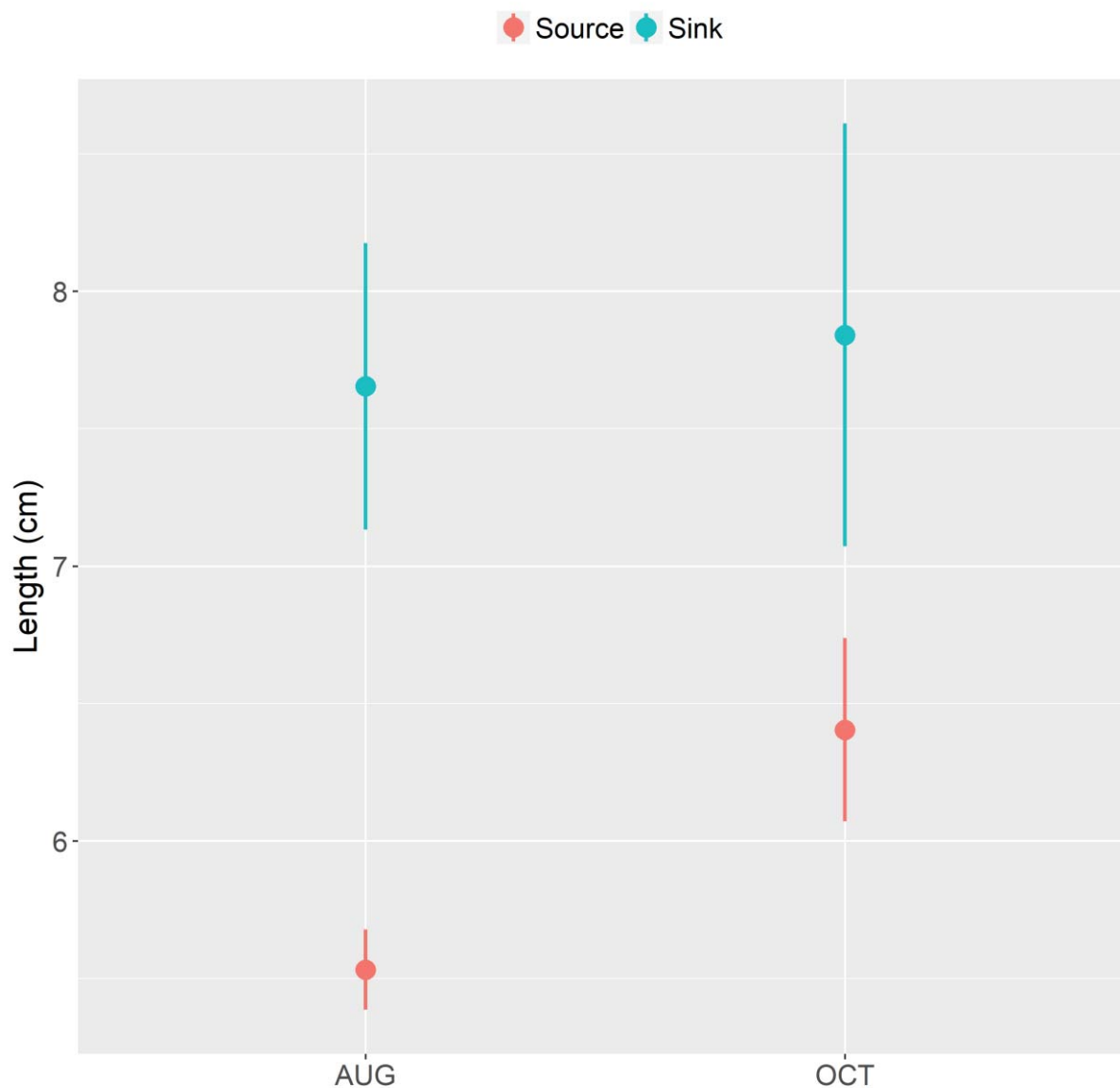
Figure 13: Prediction plot of 0+ length for sink and source groups where x-axis displays month and y-axis displays mean length in cm. Predictions are retried using the linear model presented in Table 2. Error bars represent 95% confidence intervals.

3.4 Differences in juvenile densities

There was a significant difference between the source and sink groups in juvenile densities. Juvenile densities varied considerably among the six study tributaries (Boxplot Figure 14 and

15). Parameter estimates for generalized linear model (GLM) and ANOVA, pointing to variation between the source-sink groups in 0+ densities, yielded significant difference in density between the source and sink tributary groups ($R^2 = 0,85$, P = <0.0001) (Table 3).

Table 3: Parameter estimates of the generalized linear model for the 0+ density. Parameter estimates are on ln-scale.

Parameter estimates

Parameter	Estimate	SD.error	z value	P value
Intercept	4.803	0.024	198.35	2.00E-16
SourceSinkSink	-2.109	0.09	-23.43	2.00E-16

0+ density estimates for each tributary for round 2 in August was used to test for differences between source and sink tributary groups where x-axis = ln(density+1), y-axis = tributaries. Sink tributaries Brokskitbekken and Rossvollbekken have clearly the lowest density, whereas tributary Korsrådalsbekken overlaps with the source tributary group that has a higher density (Figure 14).
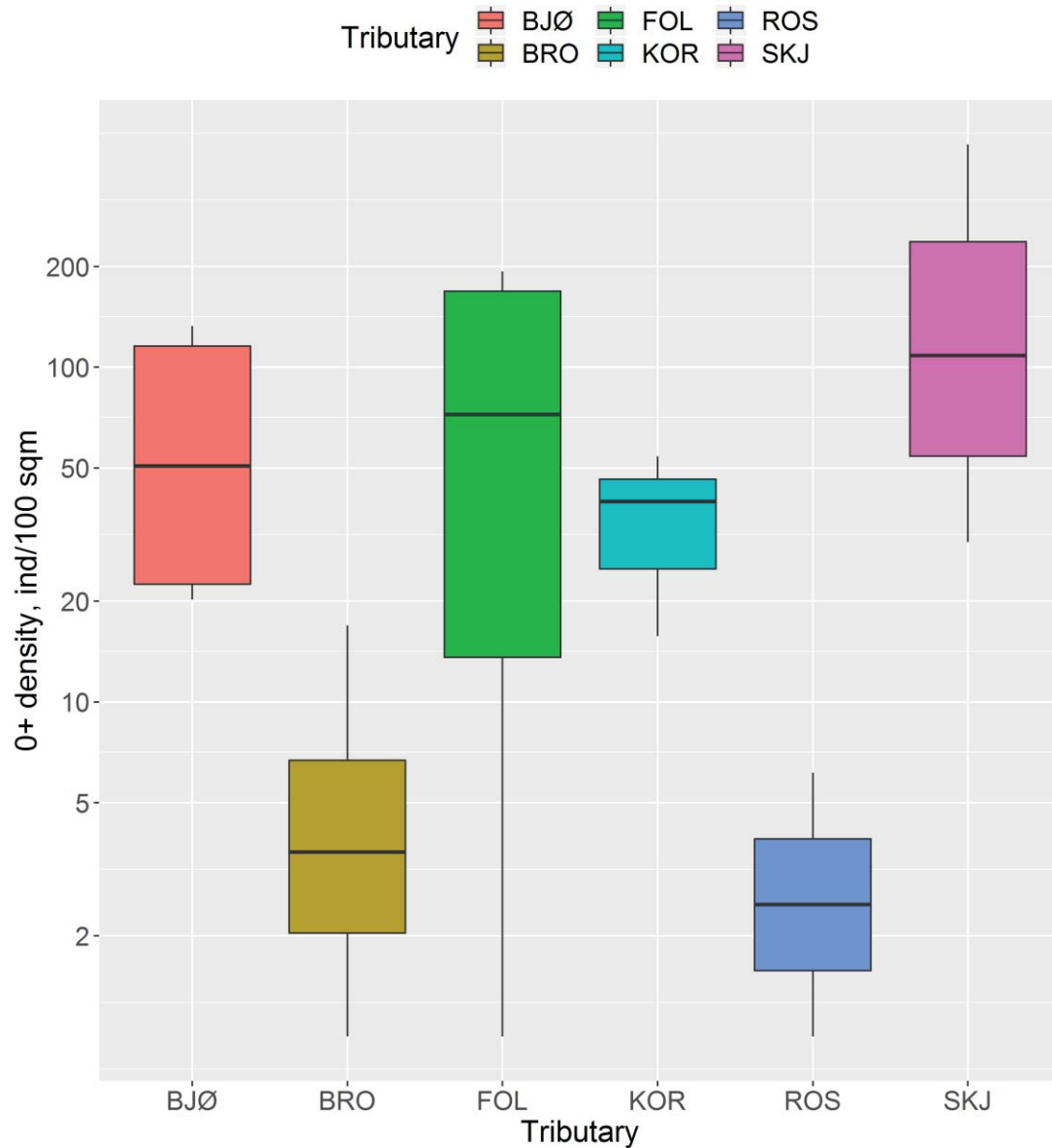
Figure 14: Boxplot of 0+ density estimates for each tributary for round 2 in August to test differences between source and sink tributary groups where y-axis is log-transformed. Boxes entail 50% of the observations and the whiskers span 90% of the observations. Thick horizontal lines represent the median value. Dots are outliers.

Parameter estimates for generalized linear model (GLM) and ANOVA, pointing to variation between the source-sink groups in >0+ densities provides similar results as the 0+ analysis, and yielded significant difference in density between the source and sink tributary groups (R^2=0.86, P = <0.0001) (Table 4).

Table 4: Parameter estimates for the GLM fitted to estimate effect of source-sink on 0+ densities in the six study tributaries in Verdalselva 2018. The model was fitted as Poisson model with log-link.

Parameter estimates

Coefficients	Estimate	SD.error	z value	P value
Intercept	2.962	0.061	48.77	2.00E-16
SourceSinkSink	-1.194	0.15	-7.937	2.08E-15

Boxplot of >0+ density estimates for each tributary for round 2 in August demonstrates a similar pattern where the sink tributary group are representing the lowest mean densities. Sink tributary Brokskitbekken has clearly lowest density of >0+ (Figure 15).
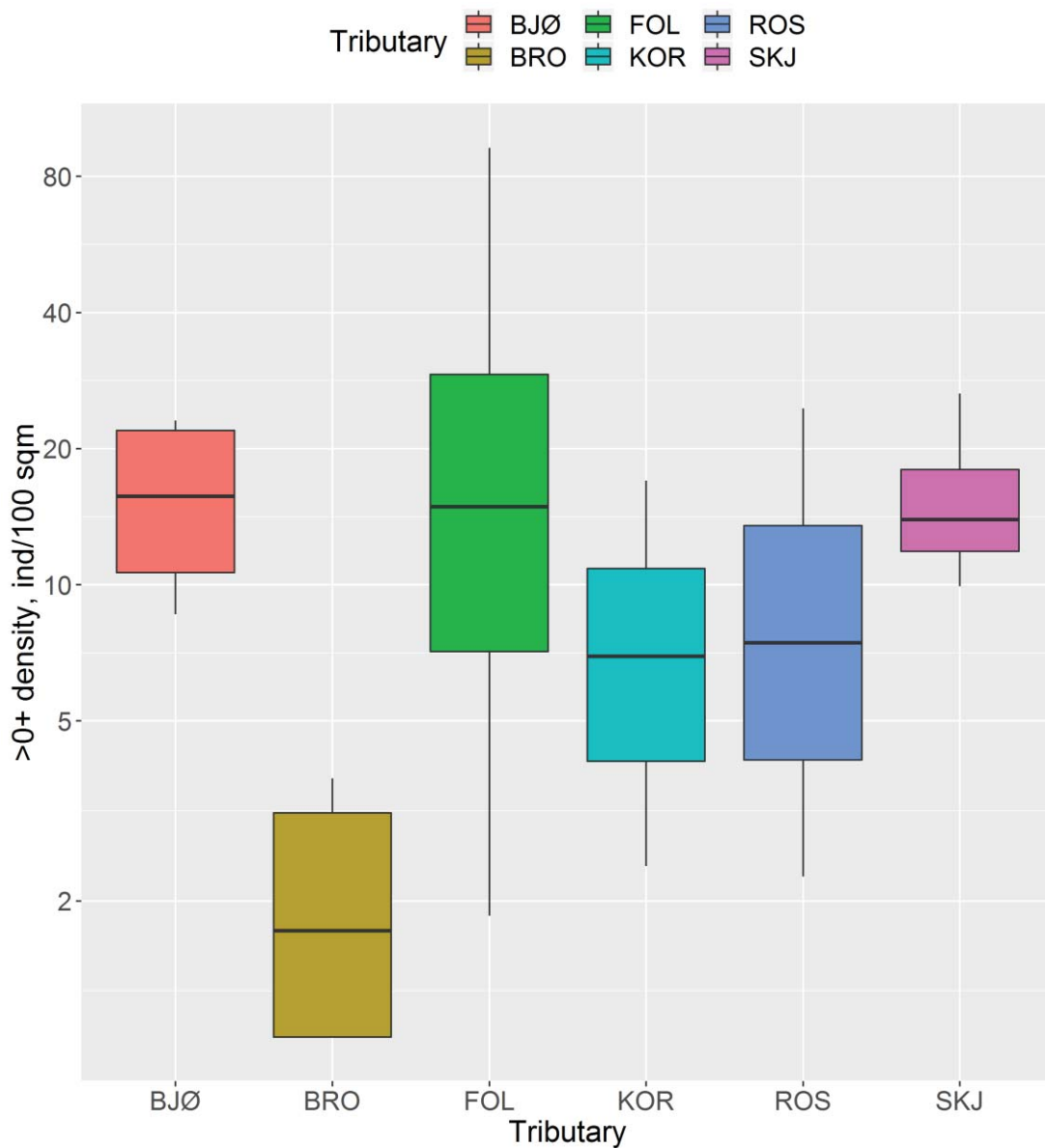
Figure 15: Boxplot of >0+ density estimates for each tributary for round 2 in August to test differences between source and sink tributary groups where y-axis is log-transformed. Boxes entail 50% of the observations and the whiskers span 90% of the observations. Thick horizontal lines represent the median value. Dots are outliers.

Tributary Rossvollbekken has the lowest density for the 0+ cohort, but the >0+ has much higher density in line with Korsådalsbekken. Brokskitbekken has also very low density for the 0+ cohort and the lowest density for >0+ cohorts.

3.5 Capture-mark-recapture analysis (CAS)

The most supported CAS model suggest survival to respond differently to juvenile density between source and sink systems; and recapture probability to be tributary-specific. Upstream migration varied over time and downstream migration showed different density- and precipitation effects between source and sink systems. The CAS model with most support in the data was used in the further analysis. The model estimated 18 of 26 beta parameters (1 were fixed) and had an AIC weight of 0.318 which was 1.77 units lower than the second-most supported model. The eleven most supported candidate models are listed in Table 5 and parameter estimates for the most supported model is provided in Table 6.

Table 5: Model selection table for the ten most supported CAS models. Par. = Number of parameters estimated, SourceSink = grouped tributaries in source and sink tributaries, density = density of trout, t = time, down = downstream migration, BuranMax = maximum rainfall in a 24 hours period at Buran weather station, SS = SourceSink, stL = standardized length. N-S-Maxrain= max rainfall in a 24 hours period in Egge weather station (north) and max rain in in a 24 hours period at Buran weather station (south).

	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	(S(SourceSink*density)p(stream)psi(Up(t),Down(Density*SouceSink*BuranMaxrain))	979.306	0.000	0.318	1.000	18.000	942.145
2	(S(SourceSink*density)p(stream)psi(Up(t),Down*Density*SouceSink*N-S-Maxrain))	981.075	1.769	0.132	0.413	18.000	943.913
3	(S(SourceSink*density)p(stream)psi(Up(t),Down*Density*SouceSink*BuranMaxrain+SS*stL))	981.112	1.806	0.129	0.405	20.000	939.681
4	(S(SourceSink*density)p(stream)psi(Up(t),Down*Density*SouceSink+BuranMax))	981.356	2.050	0.114	0.359	18.000	944.195
5	(S(SourceSink*density)p(stream)psi(Up(t),Down*Density*SouceSink+N-S-rainMax))	981.585	2.280	0.102	0.320	18.000	944.424
6	(S(SourceSink*density)p(stream)psi(Up(t),Down*Density*SouceSink*N-S-rainMax*stL))	981.896	2.590	0.087	0.274	20.000	940.465
7	(S(SourceSink+density+Buran)p(stream)psi(Up(t),Down*Density*SouceSink*BuranMax))	983.010	3.704	0.050	0.157	20.000	941.579
8	(S(ROS-VS-rest)p(stream)psi(Up(t),Down*Density*SouceSink*stL))	984.400	5.094	0.025	0.078	16.000	951.479
9	(S(SourceSink*density*stL-ROS-VS-rest)p(stream)psi(Up(t),Down*Density*SouceSink*stL))	985.133	5.827	0.017	0.054	17.000	950.096
10	(S(SourceSink*density+SS*stL)p(stream)psi(Up(t),Down*Density*SouceSink*BuranMax))	985.535	6.229	0.014	0.044	21.000	941.958
11	(S(SourceSink*density)p(stream)psi(Up(t),Down*Density*SouceSink*EggeMax))	986.046	6.740	0.011	0.034	19.000	946.754

Table 6: Beta estimates (logit scale) from the most supported CAS model (model 1). S = Survival, P = recapture probability, PSI = migration probability. 1 parameter were fixed due to estimation problems.

Type	Term	Group	Estimate	SE	LCL	UCL
S	Intercept	Sink	3.830	0.540	2.772	4.888
S	Density	Sink	0.113	0.085	-0.054	0.279
S	Intercept	Source	5.049	0.437	4.192	5.906
S	Density	Source	-0.018	0.010	-0.038	0.002
S	Intercept	Up/Down	0.881	1.207	-1.485	3.247
P	Intercept	BRO	-2.472	0.629	-3.704	-1.240
P	Intercept	KOR	-2.498	0.438	-3.356	-1.640
P	Intercept	FOL	-1.428	0.258	-1.934	-0.921
P	Intercept	BJO	-2.954	0.376	-3.691	-2.217
P	Intercept	SKJ	-1.805	0.237	-2.269	-1.340
P	Intercept	ROS	-3.351	1.038	-5.386	-1.316
P	Intercept	Up/Down	0.000			
PSI	Intercept	Between Streams	0.000			
PSI	Intercept	Sink (down)	1.158	0.983	-0.769	3.085
PSI	Density	Sink (down)	-0.224	0.117	-0.453	0.005
PSI	Rainfall	Sink (down)	-0.124	0.054	-0.230	-0.017
PSI	Intercept	Source (down)	11.072	0.000	11.072	11.072
PSI	Density	Source (down)	-0.042	0.026	-0.093	0.009
PSI	Rainfall	Source (down)	-1.056	0.000	-1.056	-1.056
PSI	Intercept	Up(1-2,2-3)	-6.034	1.003	-8.000	-4.068
PSI	Intercept	Up(3-4)	-2.505	0.241	-2.977	-2.032

3.5.1   Recapture probability (p)

The recapture rates in the most supported CAS model were nicely estimated, and in general low, although different among streams. CAS-derived predicted recapture probabilities show that tagged trout juveniles in Follobekken clearly had the highest probability of recapture, close to 0.2, and Rossvollbekken had the lowest below 0.05 (Figure 16).
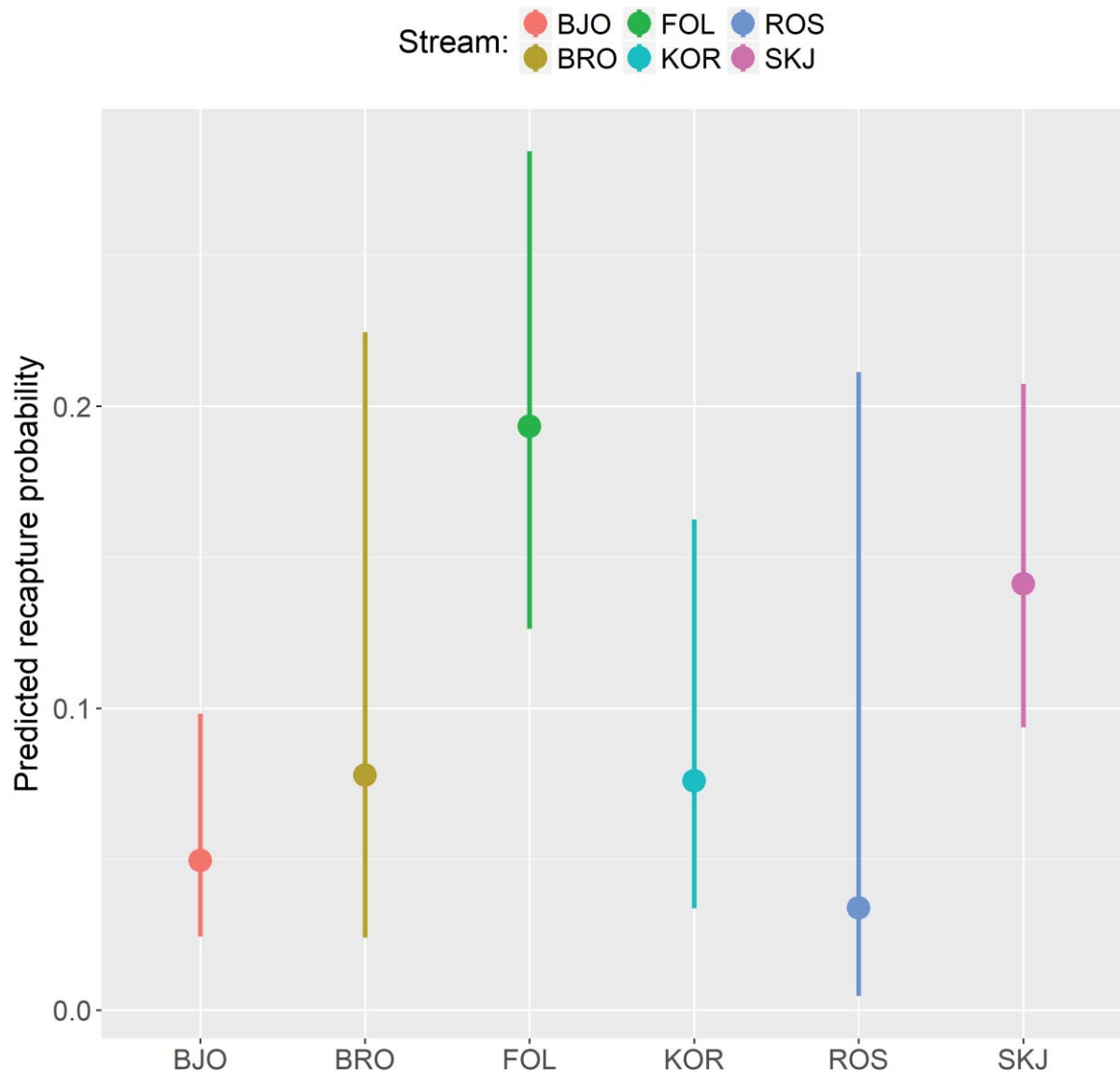
Figure 16: Prediction plot with 95% confidence interval error bars of recapture probability for each stream based on the most supported CAS model presented in Table 6.

3.5.2 Survival (S) and migration (psi)

The source tributaries survival estimate was negatively associated with density (S = -0.018, SE = 0.01) indicating a weak density-dependent survival. Survival in the sink tributaries was positively correlated with density (S = 0.113, SE= 0.085) and show no sign of density-dependent survival. Predicted monthly survival (lines) modeled from number of captures from the first-pass rounds of capture hence to source and sink tributaries with corresponding 95

percent confidence intervals (colored fields) are shown in Figure 15. The sink tributary group in red are limited to the maximum of 20 individuals caught in the first-pass round and the source tributary group in blue had a maximum of 80 caught individuals (Figure 17).
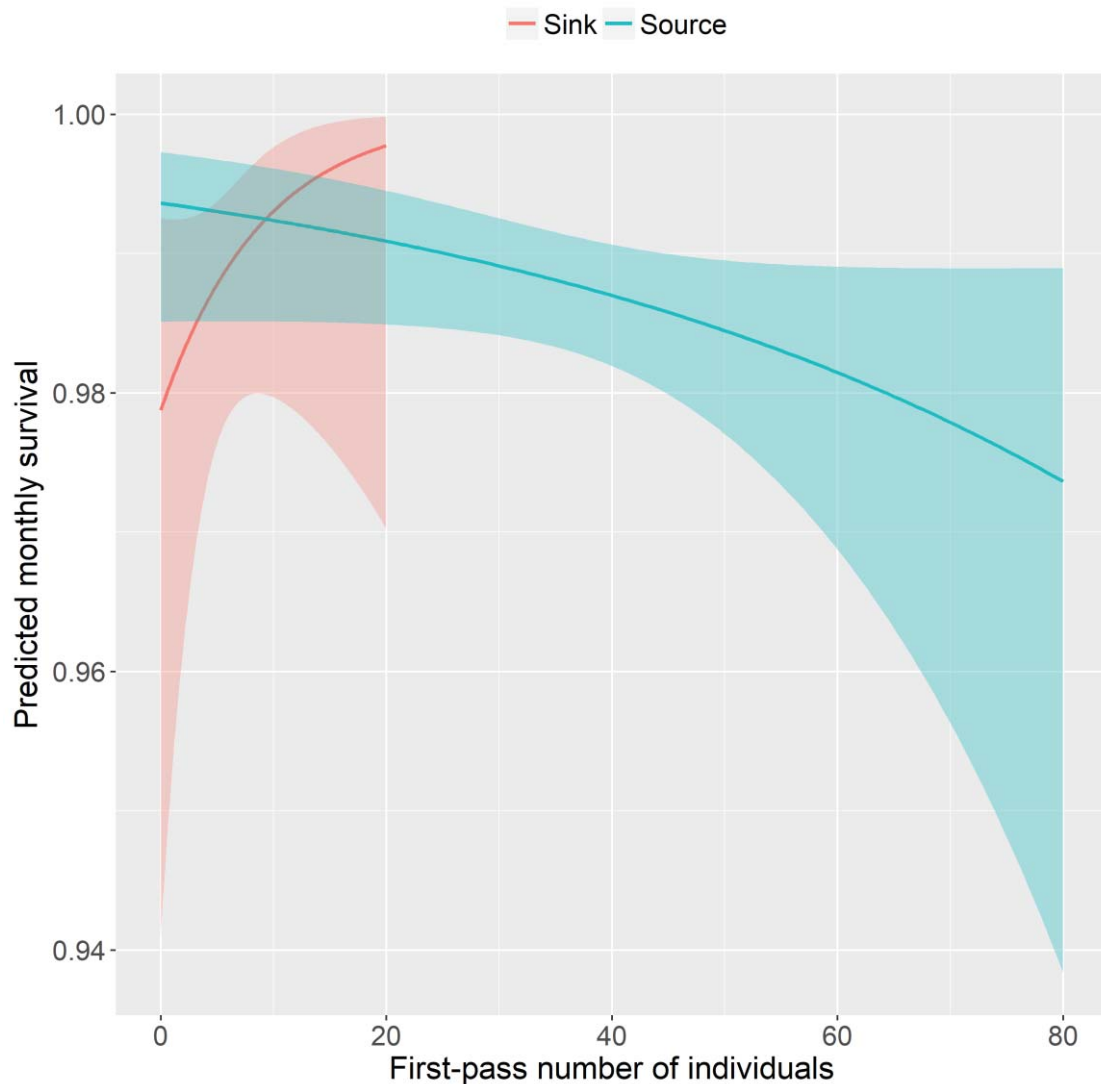
Figure 17: Prediction plot of monthly survival for (lines) first-pass fishing rounds, upper- and lower 95 percent confidence intervals (colored fields). Predictions were derived from the most supported CAS model presented in Table 6.

The downstream migration (psi) estimates for both the source and sink tributaries were negatively correlated with density and indicates inverse density-dependent migration i.e. lower migration probability with higher density. Additionally, the signal was strongest in the sink group but not at a significant level. The predicted downstream migration probability increased with decreasing precipitation (rainfall, proxy for discharge) and was negatively

associated to number of first-pass individuals (proxy for density) (Figure 18). The effect is most pronounced in the sink tributaries.
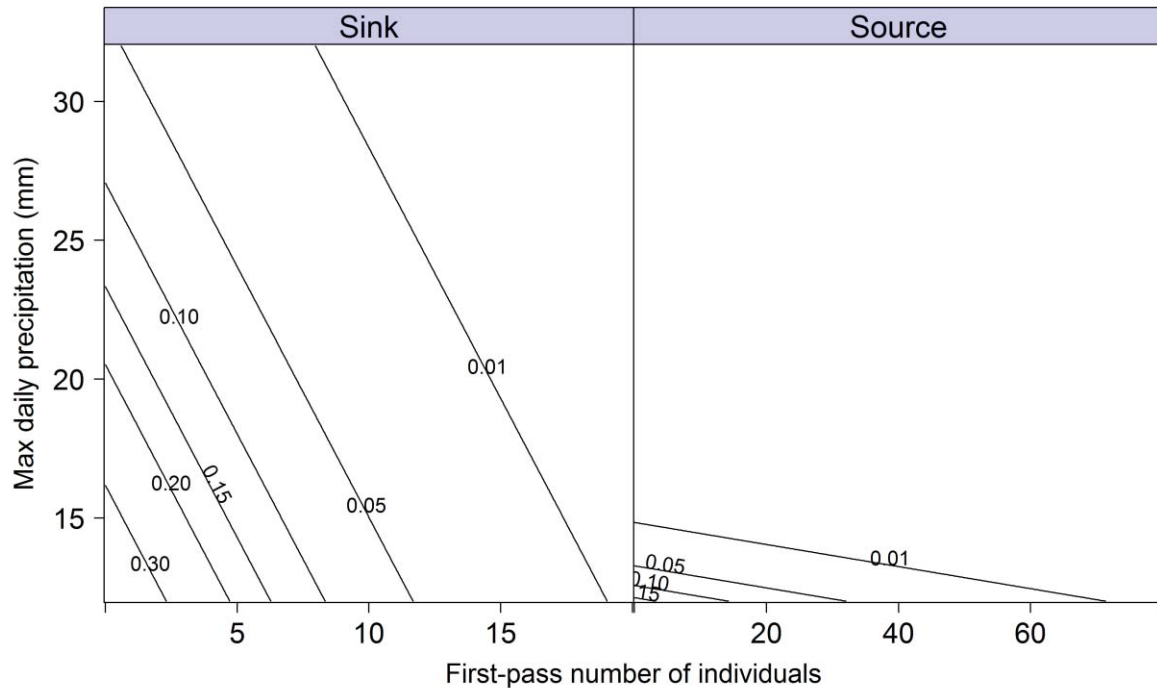
Figure 18: Contour plot of predicted downstream migration probabilities (psi), shown as contour lines, as a function of max daily precipitation and first-pass numbers of individuals for source and sink tributary groups. Predictions were derived from the most supported CAS model presented in Table 6.

3.6 Intra- and inter-tributary displacement

Displacement within tributaries was detected when collecting data with the portable back-pack PIT-antenna in round 4 in January. Many of the detections were located outside the stations, and maps with the detection locations can be found in the attached appendix 2.

Four individuals of juvenile sea trout migrated between tributaries. Two of them were redetected in Follobekken,of which one was tagged in Brokskitbekken (station 3, FL 7.0 cm in May) having migrated 1.33 km and the other one was tagged in Skjørdalsbekken (station 4, FL 7.2 cm in May) indicating that it had migrated 7.44 km. The other two sea trout were redetected in Rossvollbekken,of which one was tagged in Korsodalsbekken (station 3, FL 6.1 cm in August) having migrated 2.23 km and the last was tagged in Brokskitbekken (station 3, FL 6.5 cm in May) and migrated 2.66 km (Figure 19).
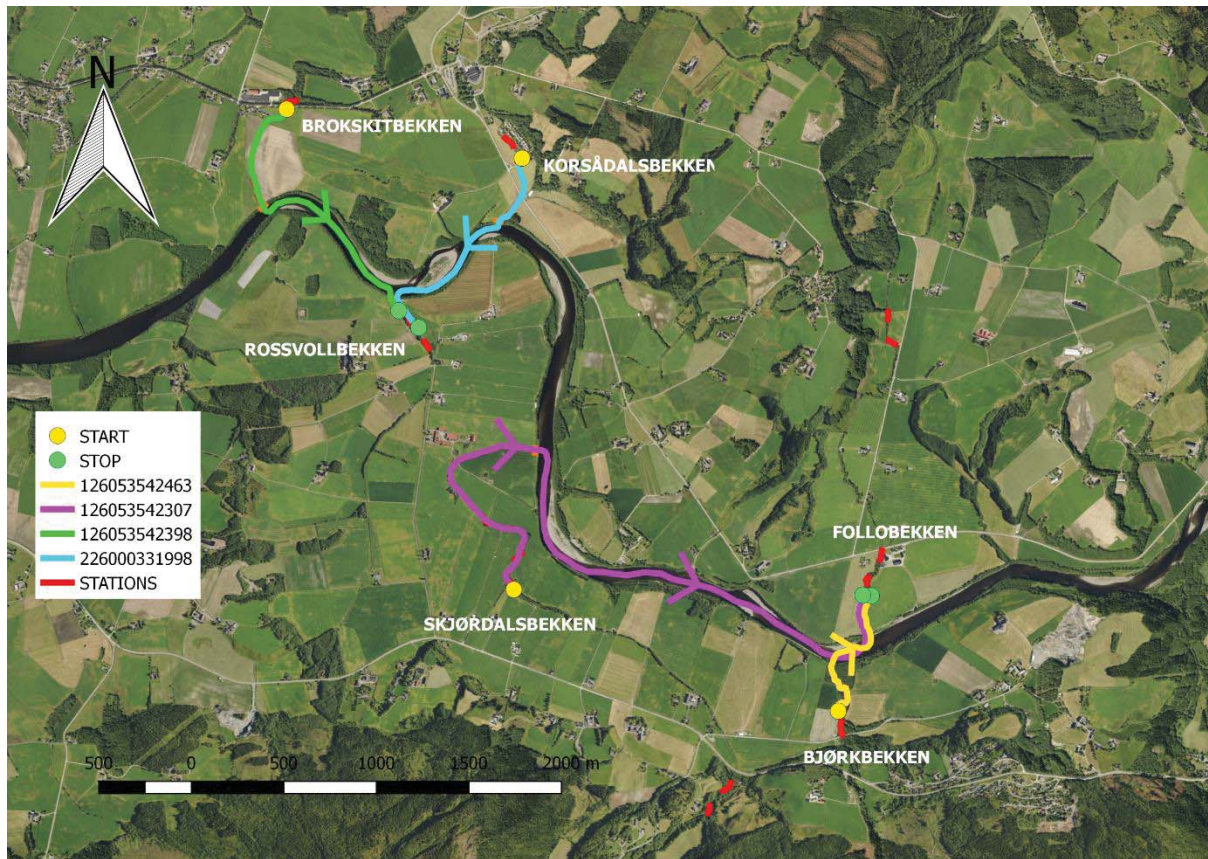
Figure 19: Between tributary migration were four individuals moved between tributaries. The yellow dots are the tagging location (start) and the green dots are the location of redetection (stop). Colored lines with arrows show the distance and direction of migration.

4 Discussion

This study has provided partial evidence supporting the assignment of Verdalselva brown trout subpopulations into source and sink populations. It was found that the sources generally had higher juvenile densities than the sinks and that inter-tributary movement do occur. Little evidence was found to support that growth and downstream migration were density-dependent in both source and sink populations, but survival tended to be density-dependent in source populations. Downstream migration was not density-dependent in 2018 and rather seemed to be related to low water levels in both source and sink populations, especially in the latter.

4.1 Habitat differences in source and sink tributaries

The permutation test yielded a significant difference in habitat characteristics between the source and sink tributary groups. The ordination analysis of tributary habitat characteristic seems to represent reality, as the correlation of the characteristics make logical sense, e.g. more shade less algae. The source and sink tributary groups load significantly different and is thus located differently in the PC1-PC2-biplot. This further indicate environmental differences between habitat characteristics in the groups, which was also supported by the perturbation test.

Among tributaries, differences in habitat characteristics are widely acknowledged since variation of environmental conditions are common (Armstrong et al., 2003; Vøllestad et al., 2002). These differences can originate from both natural and man-made impacts (Bergan & Nøst, 2017). Bergan and Nøst (2017) found that most of the streams in Trondheim municipality were influenced by urbanization, channelizing and/or enclosing streams in pipes/ditches as a result of modern agriculture. The results from the current study give the same impression and confirms that there are differences in habitat characteristics that can be measured and quantified in the investigated tributaries in Verdalelva. The investigated tributaries' ecological status has been classified using both ASPT-index and fish density by Vårhus (2016) and Hol (2018) on which the assignment into source and sink tributary groups in this study rests.

Hol (2018) classified the tributaries following the EU Water Framework Directive (WFD)[2] classification status system of salmonid densities, where the sink tributary Rossvollbekken and Brokskitbekken were classified with "bad" status and Korsådalsbekken as "poor". The source tributary Skjørdalsbekken and Bjørkbekken were classified as "high" status but Follobekken was no clear case as there was a prominent density difference. Thus, the lower part was classified as "poor" but the upper part as "high".

4.2 Age and size distribution

The age-specific length divide of cohort 0+ and >0+ were assigned length limits between 7 and 9 cm, which largely correspond to findings in Hagstrøm (2012) and Hol (2018). Several age classes of juvenile trout are known to coexist in streams and tributaries where juvenile cohorts have a similar growth rate that make it possible to separate the young of the year (0+) from older individuals (Heggenes et al., 1999; Jonsson & Jonsson, 2011). Growth of 0+ rarely exceeds 10 cm the first summer, but there are individual variations due to various biotic and abiotic factors, e.g. available territories, shelter, food and temperature (Jonsson & Jonsson, 2011). >0+ individuals, at the time of capture, were believed to have a greater size, which is demonstrated as a distinction in the bar plot whereby the division between 0+ and >0+ cohorts could be made.

4.3 Growth variation

Growth for the 0+ cohort (and thus length) between the source and sink tributary groups were not statistically significantly different, but there was a tendency (p=0.178) that August-to-October growth was higher in source than sink subpopulations. Nevertheless, the sink populations seemed to end up with larger individuals than source population individuals in October (Figure 12). This supports the expectations of higher growth in the sink tributaries due to less density-dependent competition. It was a noticeable result that the significant

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[2] The Water Framework Directive 2000/60/EC is an EU directive which commits European Union member states to achieve good qualitative and quantitative status of all water bodies.

denser population in the source tributaries had a higher growth rate than the less dens populations in the sink tributaries.

Several studies demonstrate density-dependent growth of juvenile brown trout and pronounced intra- and inter-cohort competition, e.g. access to food and shelter due to territorial behavior (Bohlin et al., 2002; Grant & Imre, 2005; Jenkins Jr et al., 1999; Lobón-Cerviá, 2007; Vøllestad & Moland, 2008). Vøllestad et al. (2002) investigated seven neighboring streams in the Rena region and found significant growth variation among streams and that the predicted growth rate decreased with increasing brown trout density. Bohlin et al. (2002) conducted an experimental study of wild stream-living and released hatchery brown trout, that found compensational growth of juvenile brown trout when the density decreased. These results correspond with Jenkins Jr et al. (1999) results from two Californian streams where they found a strong negative relationship between brown trout density and average size of 0+ in fall.

Elliott (1994) conducted a 25-year study in Black Brows Beck, Lake District where evidence of density-dependent growth in juveniles was not found. Still, only one stream was investigated, implying that those results cannot be directly compared to this study. High density may increase social interactions and energetic cost which suppress growth (Jensen et al., 2000). It might lead to increased competition for available food resources which can be scarce (Jenkins Jr et al., 1999). Jenkins Jr et al. (1999) observed that the growth rates were negatively influenced even at very low densities (0.26-0.44 fish/m^2) both in an artificial channel experiment and in a natural habitat.

There is no straight forward explanation to the faster growth rate in the denser source tributaries yielded in this study. Juvenile brown trout do not grow faster due to higher density which implies that there are other determining factors at play. Neighboring watersheds should eliminate differences among tributaries of drought and flood which is known to have severe impact (Cattanéo et al., 2002; Elliott, 1993; Vøllestad & Moland, 2008).

There may be environmental factors that influence the habitat quality of the sink tributaries, such as e.g. allochthone and autochthone production of available food. Substrate characteristics may also influence the density related to shelter and territorial behavior, suggesting that a lack of suitable habitat cannot support higher densities (Heggenes et al., 1999). Human-induced effects cannot be excluded when the tributaries are mostly located in

agricultural area. During fieldwork, spreading of manure was observed close to tributary Rossvollbekken during fishing, a practice that can have a tremendous negative short-term effect on water quality. Such events are unpredictable and may occur but would have been detected through perceived drops in density and density estimates.

Another explanation for the unexpected results may be that the sink tributaries provide such poor habitat conditions that the growth rate is lower at low density than the source tributaries at high densities. In that case, the length distribution would probably have demonstrated a considerable shorter length and slower growth rate, which was not found to be the case.

A different temperature regime may also cause differences in growth rate. Higher temperature are found to increase growth (optimum growth rate perceived at temperatures between 13-14 °C) and the effect minimizes the effect of high density (Bærum et al., 2013). Nonetheless, the tributaries in this study are adjacent which argue for delimited temperature differences. Still, a great proportion of cold ground water supply could have changed these similarities and contributed to a significant lower temperature in the measurements taken when conducting fieldwork. This turned out not to be the case in this study. These results should imply that the juveniles may had obtained growth in the dens source tributaries.

It may be that mechanism of compensatory growth could explain late summer growth rate differences between the groups. The source group individuals exhibited shorter lengths in August than the sink group, and it seems that the sink group had a higher early season growth rate, whilst in October the juveniles in the source group had improved length growth as to almost reach the sink group juveniles.

It can be suggested that the high density in the source group depressed growth between May and August. When conditions improved in August, with increased precipitation and normalization of discharge (Skaland et al., 2019), the surviving individuals may have been left with greater space and less competition of resources and could probably proceed with (compensatory) growth (Bohlin et al., 2002; Bærum et al., 2013; Vøllestad & Moland, 2008). Such compensatory growth may appear when individuals are small for their age and accessible food resources suddenly gets abundant (Bærum et al., 2013). This suggestion is supported by the observation of an abundance of fry in Skjørdalsbekken and Bjørkbekken in May, but they were too small to catch and are therefore not included in this study. Density-dependent processes may be rough during summer and these processes increase with

conditions of drought (Elliott, 1993), such as experienced in the summer of 2018 (Skaland et al., 2019). Many individuals may have demised or emigrated out from the tributaries.

Altogether, these findings support the hypothesis that density-dependent growth is pronounced in the source tributary group and that density-independent growth may have occured in the sink tributaries at the time of study.

4.4 Differences in juvenile density

The density-based assignments, based on previous density estimates, into source and sink tributaries largely corresponded with the density estimates derived in the current study. Density estimates from both 0+ and >0+ cohort showed a significant higher density in the source tributary group than in the sink tributary group. As mentioned above, the 0+ fry was generally too small to be caught in round 1 (May) and are therefore not included in the estimates. We observed considerable numbers of fry in source tributaries Bjørkbekken and Skjørdalsbekken.

The results support that the tributaries may have been reasonably grouped in source and sink groups based on juvenile density estimates. Cattanéo et al. (2002) investigated 30 different reaches in different environmental areas and revealed that there was a substantial difference in density between the streams: They also found evidence that events of flood during emergence of alevins influenced the density across all reaches. Studies have also found that stochastic and intrinsic events of unknown proportions can influence and even deplete strong cohorts in one stream, but not others, within a defined area (Lund et al., 2003). Variation in density among tributaries, as well as age classes, has been shown to occur due to natural conditions and local carrying capacity as well as a result of human interaction and fluctuations over time (Bergan & Nøst, 2017; Cattanéo et al., 2002; Vøllestad & Moland, 2008). As population density largely result from survival, growth and migration, these events are discussed further in the following chapters.

4.5 Survival differences

The predicted monthly survival was positively correlated with first-pass density of all cohorts in the sink tributary group and negative correlated with density in the source tributary group. These results may indicate that density-dependent survival can influence the source tributary populations and that density-independent survival is pronounced in the sink tributary group.

Density-dependent survival is widely acknowledged as a main determinant for regulating brown trout populations (Cattanéo et al., 2002; Elliott, 1994; Lobón-Cerviá, 2007; Vøllestad & Moland, 2008). Elliott (1994) 25-year time series from one stream found strong indication of density-dependent survival in the early life stages after the alevins emerge from the gravel, and that later stage trout were not affected similarly. The aforementioned study by Cattanéo et al. (2002) found evidence for density-dependent survival for 0+ cohort that suggest intracohort competition, which results correspond well with Vøllestad and Moland (2008) study of 8 streams.

However, there are also studies with contradicting results. For instance, when Bohlin et al. (2002) conducted a density-manipulation study in streams with both residential wild fish and hatchery fish, they found evidence that density affected survival also in later life stages, corresponding with the results from the manipulation study conducted by Jenkins Jr et al. (1999). Hagstrøm (2012) detected significant negative correlation between 0+ versus 1+ densities, and an alternating dominance structure among years, implying that a strong competitive relationship between the two cohorts affected the survival and density heavily. Thus, it seems that both density-dependent (i.e. high density) and density-independent effects can increase mortality of the early stages of juvenile sea trout populations but less evidently so for older stages.

Density-independent mechanisms may also regulate trout populations with respect to survival when conditions are harsh (Cattanéo et al., 2002; Elliott, 1994; Vøllestad & Moland, 2008). As mentioned above (4.4), severe impacts such as drought (Elliott, 1993; Vøllestad & Moland, 2008) and floods, e.g. high discharge in the early life stages (Cattanéo et al., 2002), are known to overrule density-dependent factors and regulate the density of brown trout within the same stream.

High temperatures may also cause trouble and will increase metabolic rate in fish so that general demand of food increases, making the available resources and quality in each stream become extra important. When the water temperature exceeds the optimal growth temperature

(13-14 °C), it may increase density-dependent stressors in an already stressed environment (Bærum et al., 2013). Unfortunately, it was not possible to find any of the temperature loggers placed out and the exact temperature regime in the tributaries is not known. Nevertheless, the air temperature, in general, often correspond with water temperature, and in periods during the summer of 2018 the air temperature was higher than normal. The summer months of 2018 were very dry (Skaland et al., 2019), and drought may have reinforced density-dependent mechanisms as the water covered area decreased and thus may have increased density and influenced survival.

4.6 Migration differences

According to the most supported CAS model, the migration probability increased with decreasing rainfall and unexpectedly more so in the sink group. More surprisingly, the migration probability was negatively associated with the first-pass number of individuals.

At first, it was assumed that heavy rainfall had led to a sudden rise in discharge that possibly had increased migration by flushing out the juveniles and decreasing the density (and thus the recapture probability) as described by Cattanéo et al. (2002). Nonetheless, the results are more or less pointing towards that the increased downstream migration probability with decreasing rainfall may be an effect of drought, and the acknowledged evidence of drought as a negative effect (Elliott et al., 1997) that ultimately drives the fish out of the tributary.

Severe drought made the data deviate and impacted the population density strongly, but can only be speculated whether it had an impact on migration, as shown in the study by Elliott et al. (1997). Vøllestad and Moland (2008) found a strong negative effect of drought stress on growth and contemplated that the effect may be utterly intensified with high density. However Jonsson and Jonsson (2011) mention that salmon parr can move as their feeding opportunities gets poor and seek to deeper pools or richer adjacent tributaries. The juvenile trout immigration is proposed to be triggered when the energetic surplus on an individual level drops to a level where they seek new feeding opportunities to enhance survival (Jonsson & Jonsson, 2011).

The results from this study partly correspond to earlier findings concerning drought which causes hash conditions. Low discharge decreases available water-covered habitat and reduce feeding opportunities, and along with high temperatures the conditions gets rough. The fish

may have to relocate and seek to deeper pools where this is available. Dry conditions and low discharge are forcing the trout to change habitat and can trigger migration.

A contradiction appears when the effect of density is negatively correlated with migration probability and does not correspond with earlier findings. As the density increases, the logic result would be that available resources decrease, and the competition increase. The effect of higher density was expected to increase migration as, above mentioned; the fish seeks better opportunities. Why the effect of drought is most pronounced in the less dense sink tributaries is not known, but environmental differences between the source and sink group may play a role, and here access to shaded pools may differ between the two groups. The ordination analyses did not show clear differences among sample stations, but data on total pool densities in the tributaries will be needed to elucidate this in the future, i.e., access to refuge under drought conditions.

These findings support the hypothesis that density-dependent survival exists in the source tributaries at the time of study. The sink tributaries show no sign of density-dependent survival and survival may be stronger influenced by density-independent factors. There is no support for density-dependent migration in the source tributaries with high density, but the experienced drought has probably increased density-independent migration in the sink tributaries. It is worth mentioning that the drought in summer 2018 was sever and the worst since 1947 (Skaland et al., 2019).

Further, it is difficult to separate emigration from mortality which influence the results in the analysis. Individuals are not recaptured if they move outside stations and such movement were confirmed with the portable backpack reader survey in round 4. The purpose with the PIT-antenna at the outlet was to detect individuals emigrating from the tributaries but unfortunately the PIT-antennas did not work properly. Assumed demised individuals may therefor still be alive in habitats elsewhere.

4.7 Evaluating method, results and shortcomings

Habitat difference errors may occur both as the result of changing characteristics due to weather conditions and time of year, and because registrations are conducted by different people that may have a subjective opinion of the study objects. Higher or lower discharge will influence several of the measurements, such as e.g. velocity and water depth. Canopy and

vegetation cover differ vastly during the year, and since the last habitat characteristics were conducted in October, we had to conduct a subjective qualified assumptions/judgement, which could potentially change some of the effects in the statistical analysis. Nonetheless, it should not be undermined that a tributary is a changing eco system.

The growth rate may decline during summer season (Vøllestad et al., 2002). As the 0+ were too small to catch in May, only the late seasonal growth between August and October was investigated and the growth rate may have declined which could have influenced the result.

Conducting electrofishing in a successive way require that the conditions are well suitable. The characteristics of the tributaries made a great effort to make this part of the field work challenging. All the investigated tributaries have sections located in ravine landscape that forms deep V-shaped stream channels were trees are falling constantly into the riverbed, branches are blocking passage and sighting and make it difficult to conduct electrofishing in an appropriate way. There was a great deal of climbing, and some deeper pools that were impossible to reach into with the dipnets. The riparian zone and the streambed consisted of patches with clay and silt, so that even a small proportion of rain decreased visibility. Low recapture probability is most probably linked to the characteristics of the tributaries and turbid water that reduce sight and it becomes difficult to discover and catch the fish. We also had some helpers with different level of experience to electrofishing and catching with dip-nets which may have decreased the catchability. These implications of catchability and recapture may have influenced the estimates of density, migration and survival.

The handling and tagging were mostly done smoothly, but we did experience some mistakes. Altogether three juvenile sea trout died during the process due to movement when using the scalpel and was cut open, and one did never wake up after the anesthesia treatment. When exploring the data set there was altogether five double-noted PIT-tags that I could not find any obvious solution of wrongs. The hypothesis is that the scanner has been taken in a signal from a nearby PIT-tag in the tagging process and that the tag we implanted never was detected. The take home message is to keep the unused PIT-tags out of range from the reader.

The recapture probability was lower than we had expected and hoped for due to revealing knowledge. The estimates were relatively precise (i.e. small standard errors) - estimating precise p-values allows more confidence in the estimates of survival (S) and migration (psi) (Lebreton et al., 1992).

Detection of migration relays on that we recaptured the tagged individuals to reveal movement. As fishing were only conducted in the stations the fish had to be present in a station and be recaptured. The low recapture rate did not make it easy to detect such movement and individuals emigrating from the tributaries where not detected as the PIT-antennas did not work properly and assumed dead individuals may still be alive in another habitat. However, in round 4 in January the portable backpack enabled longer detection routes through and between stations and detected individuals without catching them and was a huge advantage. The ice cover made it easy to slide over large areas rapidly and revealed a great deal of tagged individuals that had never been detected without this equipment. Thus, the integrated GPS switched of in Korsådalsbekken. Luckily, we carried a hand hold GPS that enabled us to recreate the locations comparing the time of detections. However, the GPS locations have an error range that has to be considered when using the locations of detections. The take home message is to always have a backup GPS around the neck and double check the that the integrated GPS works properly.

A sever error I experienced was that the all of the five temperature loggers that were placed out disappeared. Unfortunately, it was not possible to relocate and find any of those. Comparing the temperature in the different tributaries were than impossible.

Several results in the present study differ from what was expected based in acknowledged science. The investigated tributaries have demonstrated highly differentiated juvenile brown trout densities at the period of investigation. The dry conditions in the summer months of 2018 may have led to a population circumstance where density-independent factors have over-ruled density-dependent factors as lower discharge and higher temperatures were prominent; both of which are key stressors for juvenile brown trout. In August there was an increase in precipitation and normalization of the conditions and the juvenile brown trout that had been depressed may have compensated delayed growth. This natural variation is likely to exhibit a year-to-year fluctuation, but 2018 can be seen as a deviating period of study with the worst drought experienced since 1947 (Skaland et al., 2019). To understand more on the dynamics of the tributaries to Verdalselva more investigation should be conducted.

4.8 Conclusion

In summary, this study has provided data that in varying degree proved useful for enlightening the addressed hypothesis. The hypotheses attained the following support from the data:

H1.1: Some support for density-dependent survival in source-subpopulations, but no or enigmatic support for density-dependent growth and dispersal.

H1.2.: Density-independent survival in sink subpopulations was largely supported and down-stream migration was largely density-independent (may have been drought driven).

H2.1: Some support for emigration from the source tributaries.H2.2: Some migration into sink tributaries (n=2) were documented from the back-pack reader survey.

This study is time-limited and thus not able to cover superior processes. Nevertheless, it is the first step of an investigation that will continue in the tributaries in river system Verdalselva and can contribute with data for comparison with ensuing results. The provided density estimates correspond well with the categorization of source and sink tributaries. Still, the study found that the brown trout do perform micro migration within the particular tributary. The four individuals that migrated between tributaries can also alter the question of importance of source sink dynamics that can be examined in later studies. Well-functioning PIT-antennas are of great importance to reveal more of this knowledge.

4.9 Consequences for management

The over-arching impression left by this study is that connectivity is of importance in Verdalselva and that connectivity is also one of many elements to be considered in the tutors of the EU Water Framework Directive classification of river systems. All tributaries are of importance in a well-functioning dendritic river system. Tributaries with poor or no spawning habitat may provide supplementary habitat qualities and be put to use due to the migratory behavior. Habitat niche shift during seasons and over wintering habitat are of great importance.

Open migration routes are of importance to increase the total habitat area and should be prioritized in further environmental measures in management and to achieve the goal in the Water Framework Directive.

4.10 Further research

- PIT antenna must work. As above mentioned, the purpose of the PIT-antennas is to detect emigrating individuals that will provide useful data of migration pattern. Further, it is difficult to separate migration and mortality in the analysis, which detection of emigrating individuals may exclude some "unknown" mortality.

- Extensive use of the portable backpack reader. This useful tool makes detection of tagged individuals fast and easy and can provide information from areas impossible to cover with recapture. Large detection reaches may provide information of small-scale and large-scale migration and thus among tributaries to reveal source sink dynamic.

- Tag more individuals. To tag a larger proportion of individuals will provide more recaptures and redetections that can reveal the migration dynamic and provide knowledge of this dendritic river system.

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Appendix

Appendix 1 Investigated tributaries

The distance from the main river outlet in Trondheimsfjorden to the tributaries range from 5.8 km (Brokskitbekken) to 11.2 km (Follobekken). The tributary lengths ranged from 3.9 km (Brokskitbekken) to 6.2 km (Skjørdalsbekken), and watershed are from 2.75 km^2 (Brokskitbekken) to 7.38 km^2 (Skjørdalsbekken). In tributary Korsådalsbekken, migration was improved by changing the culvert under the road Vukuvegen (county road 757) and in tributary Follobekken boulders were used to construct several elevation steps (pools) to ease migration through the culvert under road Vukuvegen. The watersheds are dominated of both cultivated and forest landcover with a smaller percentage of marsh and urban surfaces (Table 7).

Table 7: Tributaries and watershed characteristic (Anonymous, 2015).

Tributary	Distance from outlet	Length km	Watershed Km²	Gradient m/km	Mean discharge l/s	Land cover (percent in catchment)			
						Cultivated	Marsh	Forest	Urban
Brokskit-	5.8	3.9	2.75	22.3	58.0	65.2	1	24.2	0.1
Korsådals-	7.4	4	2.81	13.9	54.7	60.9	1.2	30.1	1.5
Follo-	11.2	4.9	6.38	43.2	130.8	49.7	0.3	42.4	0.3
Bjørk-	11.1	3.9	5.29	79.3	101.0	10.7	3.3	76.3	2.1
Skjørdals-	8.8	6.2	7.38	27.9	126.9	28.2	1.1	67.8	0
Rossvoll-	6.7	4.3	5.23	54.6	85.2	45.1	0.3	47.7	0.6

Density of salmonids and water quality of the tributaries in Verdalselva have been subjected to investigations several times. The research of Haukeland et al. (1986), Lyngstad (1992), Bergan et al. (2007), Kristiansen and Rikstad (2007), Rikstad (2016), Vårhus (2016) and Hol (2018) indicates that these tributaries have a various density of fish in the different investigations though a consistent method is not used (Table 8).

Table 8: Previous research of the study tributaries where juvenile densities of brown trout and salmon (in brackets) is given per 100 m2. 0 is no fish found, and - is not investigated or no data found.

Year/ Tributary	1984[1]	1985[1]	1992[2]	2005[3]	2006[3]	2015[4]	2017[5]	2018[6]
Brokskit-	-	0	144	36	-	18.5	-	6.5

Korsodals-	-	19.3	40.4	10	-	-	26.27	33.90
Follo-	-	0	55.3	6	35	75.5	-	126.3 (4.2)
Bjørk-	23.9 (1.4)	15.3 (3.5)	-	20 (4)	-	86.5	-	77.8 (0.89)
Skjørdals-	33.4	8 (0.7)	79.7	22 (4)	-	-	244.99	179.9 (3.3)
Rossvoll-	-	0	1.3	-	0	-	14.37	13.30

[1]1984-85 Haukeland et al. (1986), density per 100 m^2 of >0+ (0+ not included) ,fished 3 times and used Zippins method.

[2]1992: Lyngstad (1992), density per 100 m^2 of >0+ (0+ not included), fished 3 times and used Zippin's method.

[3]2005-06: Kristiansen and Rikstad (2007), density per 100 m^2, fished only one pass.

[4]2015: Vårhus (2016), density per 100 m^2, fished 3 times and used Zippin's method.

[5]2017: Hol (2018), density per 100 m^2, fished 3 times and used Zippin's method.

[6]2018: This study, density per 100 m^2, fished 3 times and used Zippin's removal method (Zippin, 1956).

Tributary Brokskitbekken (sink)

In Brokskitbekken four fishing-stations have been placed out ranging from 47.1 to 58 meters in length (Figure 21).
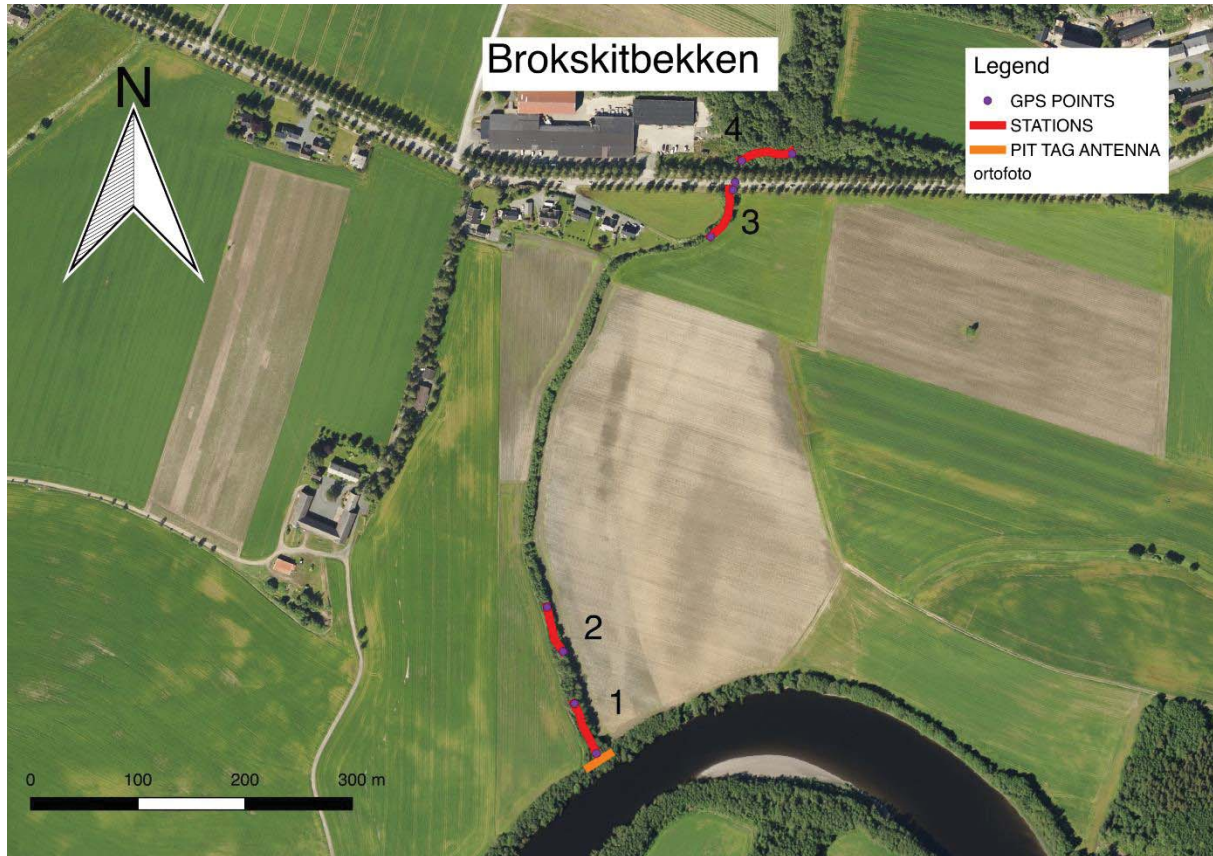
Figure 21:Lower part of the tributary Brokskitbekken where the four fishing stations are located.

Brokskitbekken is located on the north side of river Verdalselva. The original open migration route for brown trout was 3465 meters, but today the migration stretch is restricted to 1215 meters caused by a 180 meter long culvert which is a barrier for migration (Hol, 2018; Vårhus, 2016). Both ecological status and the Average Score per Taxon (ASPT-index) is classified as very "poor" by Vårhus (2016). The riparian zone downstream the road Vukuvegen constitute a narrow stripe consisting of a mixed tree species composition mainly of grey alder (*Alnus incana*), birch (*Pendula spp.*), bird cherry (*Prunus padus*) and goat willow (*Salix caprea*) (Figure 20).

Figure 20:The riparian zone at station 2 consisting of grey alder. Turbid water at the time the photo was taken.

A total of 59 brown trout were captured in Brokskitbekken. 35 of those were tagged and 26 were too small (length <60 mm) to tag. Seven trout were longer than 120 mm and tagged with large PIT-marks (23 mm). Only two fish were recaptured at station 3 and 4 in round 3 (Table 9). Five individuals were detected in round 4 in January 2019. The low total number of brown trout with an estimated density of 6.5 individuals per 100 m^2 suggest that the tributary has a small subpopulation of trout. The tributary is thereby classified as a sink in this study.

Table 9: Captured, PIT-marked and recaptured fish in the tributary Brokskitbekken.

Round	Date	Temp	Station	Fish captured	Fish tagged	Fish recaptured	PIT 23 mm
1	31.05.2018	13.2	1	9	8	-	
	31.05.2018	13.2	2	0	0	-	
	31.05.2018	13.2	3	8	8	-	1
	30.05.2018	13.2	4	5	5	-	
2	27.08.2018	10.4	1	11	0		
	27.08.2018	10.4	2	1	0		
	28.08.2018	10.6	3	5	1	1	
	28.08.2018	10.6	4	2	2	1	1
3	31.10.2018	4.4	1	9	3		1
	02.11.2018	5.1	2	4	4		2
	02.11.2018	5.1	3	4	3		
	02.11.2018	5.1	4	1	1		
4	23.01.2019		All	-	-	5	
Sum				59	35	7	5

Brokskitbekken

Table 10: Measurement and characteristics of Brokskitbekken

		Station		
Characterization	1	2	3	4
Distance from outlet (m)	18	120	593	675
Total length (m)	58	47.1	50	50
Area (m^2)	97	63	102	110

Mean width (cm)		168	134	205	220
Mean depth (cm)		8.4	10	4.6	7.6
Mean velocity (m/s)		0.28	0.19	0.27	0.23
No of pools		4	2	4	7
Large woody debris		8	4	3	10
Mean moss (%)		0	0	0	0
Mean algae (%)		9.6	0	3.2	3.2
Mean canopy cover (%)		90	94	83	87
Substrate composition (%)	<2 mm	26	63	37	50
	2-20 mm	22	16	18	24
	20-100 mm	28	13	11	15
	100-250 mm	12	5	21	0
	>250 mm	12	3	13	11

Tributary Korsådalsbekken (sink). Korsådalsbekken are located on the north side of Verdalselva and three fishing stations were placed out (Figure 23).
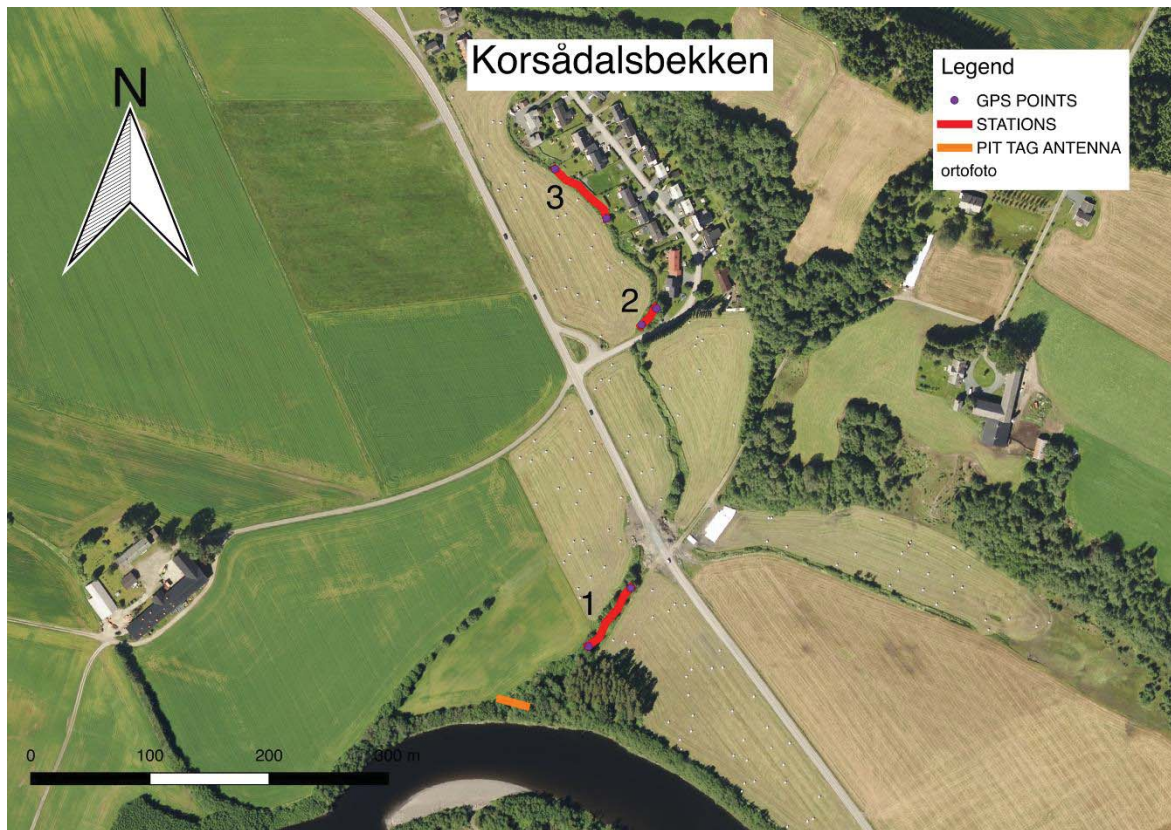
Figure 23: Tributary Korsådalsbekken and location of the three fishing stations.

Korsådalsbekken had a total of 4495 meter open migration route for brown trout, but the migration stretch is restricted to 750 meters before ending in a 440 meter closed area that makes a barrier for the fish (Hol, 2018). The ecological status and ASPT-index are classified as "bad" by Hol (2018). The riparian zone towards farmland and residential area in the investigated stretch of the tributary is partly absent or constitute a narrow zone except the upstream 100 meters from the main river where forest of spruce and pine (*Pinus sylvestris*). A mixed tree species composition of grey alder, birch, bird cherry goat willow and some spruce make up the remaining riparian zone (Figure 22).
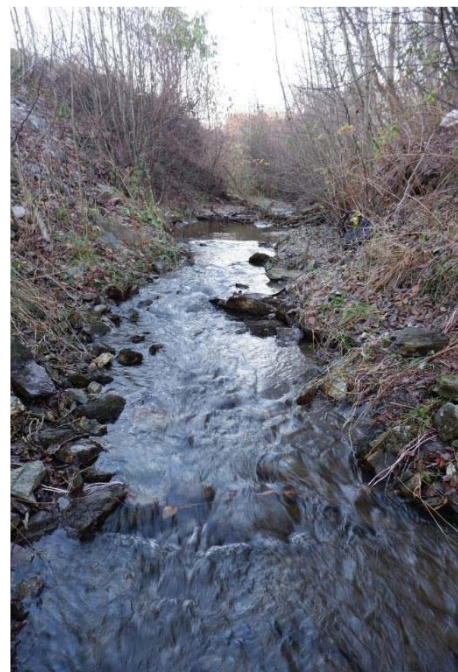
Figure 22:Station 1 in stream Korsodalsbekken near the outlet to Verdalselva.

A total of 100 brown trout were captured in Korsådalsbekken, of them 73 fish were tagged, whilst only three were longer than 120 mm and tagged with large PIT-marks (23 mm) and 27 were too small (length <60 mm) to tag. Only two fish were recaptured at station 1 in round 3 (Table 11). 20 individuals were detected in round 4 in January 2019. The low total number of brown trouts with an estimated density of 33.9 individuals per 100 m^2 suggest that the tributary has a small subpopulation of trout. Korsådalsbekken is thereby classified as a sink this study.

Table 11: Captured, PIT-marked and recaptured fish in the tributary Korsådalsbekken.

Round	Date	Temp	Station	Fish captured	Fish tagged	Fish recaptured	PIT 23 mm
1	30.05.2018	14.1	1	14	14	-	
	30.05.2018	14.1	2	11	9	-	
	30.05.2018	14.1	3	4	3	-	
2	24.08.2018	11.7	1	11	9		3
	24.08.2018	12.0	2	15	5		
	24.08.2018	12.0	3	26	15		
3	03.11.2018	4.3	1	8	7	2	
	03.11.2018	4.3	2	6	6		
	03.11.2018	4.3	3	5	5		
4	23.01.2019		All	-	-	20	
Sum				100	73	22	3

Korsådalsbekken

Table 12: Measurement and characteristics of Korsådalsbekken.

Habitat characterization	Station		
	1	2	3
Distance from main river (m)	95	400	510
Total length (m)	65	20	82
Area (m²)	125	34	144
Mean width (cm)	192	168	176
Mean depth (cm)	13	9.7	8
Mean velocity (m/s)	0.32	0.14	0.19

No of pools		4	1	1
Large woody debris		26	1	0
Mean moss (%)		0	0	0
Mean algae (%)		3.2	16.4	19.6
Mean canopy cover (%)		96	90	17
Substrate composition (%)	<2 mm	44	39	19
	2-20 mm	11	2	8
	20-100 mm	7	20	46
	100-250 mm	14	17	7
	>250 mm	22	22	20

Tributary Rossvollbekken (sink). Rossvollbekken only has two stations because the conditions upstream were not suitable for sea trout (Figure 25).
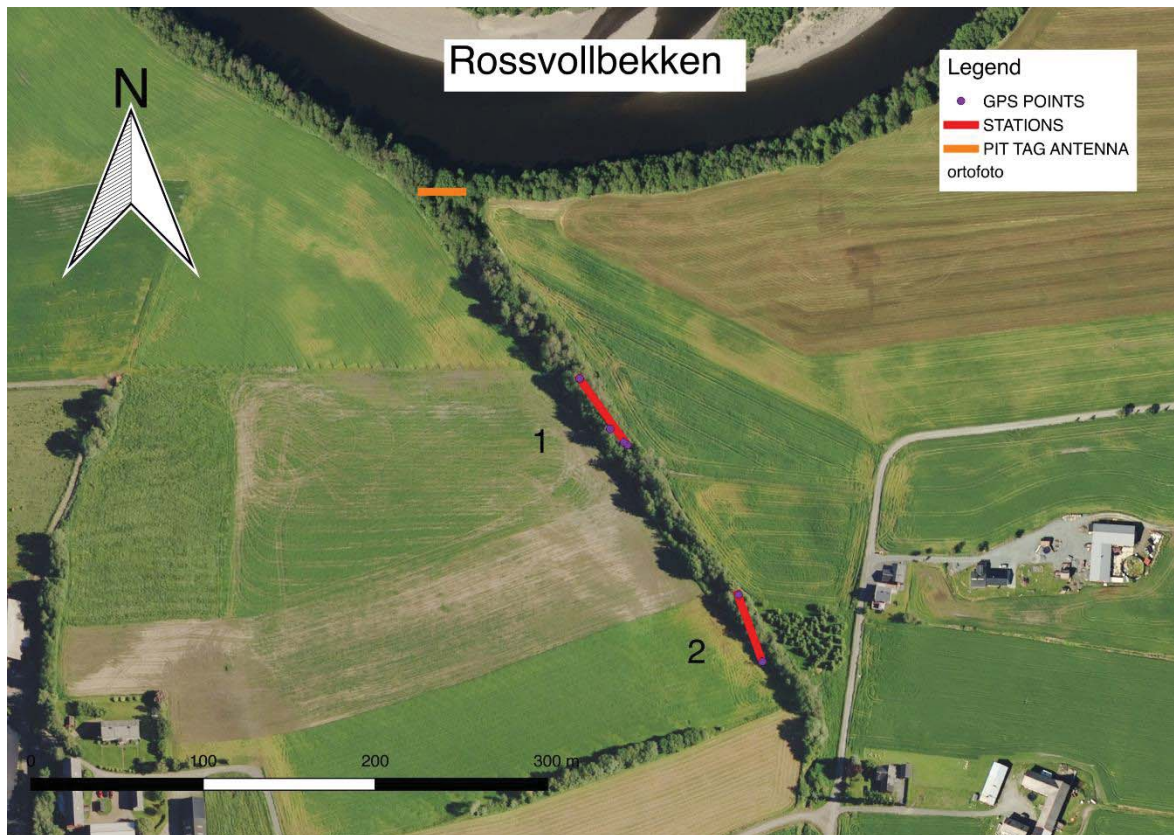
Figure 25: Location of the two stations in tributary Rossvollbekken.

The original migration route for brown trout is estimated to be 3570 meters but is today restricted to 2350 meters (Hol, 2018). The ecological status were classified as "poor" and ASPT-index were classified as "bad" by Hol (2018). Step and narrow streambed in most of the tributary (Figure 24).

A total of 33 brown trout were captured in Rossvollbekken. 29 of those were tagged, whilst only three was longer than 120 mm and tagged with large PIT-tags (23 mm), and four were too small (length <60 mm) to tag. Only one trout was recaptured at station 2 in round 3. Nine individuals were detected in round 4 in January 2019 (Table 13). The low total number of brown trout, with an

Figure 24: Station No 1 in stream Rossvollbekken.

estimated density of 13.3 individuals per 100 m^2, suggest that the tributary has a small subpopulation of trout. Rossvollbekken is thereby classified as a sink in this study

Table 13: Captured, PIT-marked and recaptured fish in the tributary Rossvollbekken.

Round	Date	Temp	Station	Fish captured	Fish tagged	Fish recaptured	PIT 23 mm
1	01.06.2018	14.3	1	7	7	-	
	01.06.2018	14.3	2	11	11	-	
2	26.08.2018	10.9	1	1	1		1
	26.08.2018	10.9	2	12	8		2
3	31.10.2018	4.6	1	1	1		
	31.10.2018	4.6	2	1	1	1	
4	24.01.2019		All			9	
Sum				33	29	10	3

Rossvollbekken

Table 14: Measurement and characteristics of Rossvollbekken.

			Station	
Habitat characterization			**1**	**2**
Distance from main river (m)			148	310
Total length (m)			54	33
Area (m^2)			79	60
Mean width (cm)			147	183
Mean depth (cm)			7.2	14.92
Mean velocity (m/s)			0.23	0.12
No of pools			6	3
Large woody debris			12	4
Mean moss (%)			0	0
Mean algae (%)			0	0
Mean canopy cover (%)			92	95
		<2 mm	37	37
		2-20 mm	20	4
Substrate composition (%)		20-100 mm	18	18
		100-250 mm	21	25
		>250 mm	4	16

Tributary Follobekken (source)

Follobekken has four fishing stations with a range between 39- and 52-meters length approximately 1500 meters between the pairs of stations (figure 26). The natural open migration route for brown trout were estimated to 5920 meter but today restricted to 2780 meters (Hol, 2018). The ecological status and ASPT-index were classified as "moderate" by Vårhus (2016). Measures are done to ease the migration through the culvert under road Vukuvegen at the end of station 2. Large boulders are set up to form a fish ladder with elevating pools, but flood and high discharge have relocated the boulders. Now it seems to be a hindrance for migratory sea trout with a 40 cm jump to reach the bottom of the culvert (Figure 27). Nonetheless juvenile trout was found upstream this culvert at station No 3 and 4. The riparian zone consisting mainly of birch, goat willow and grey alder.
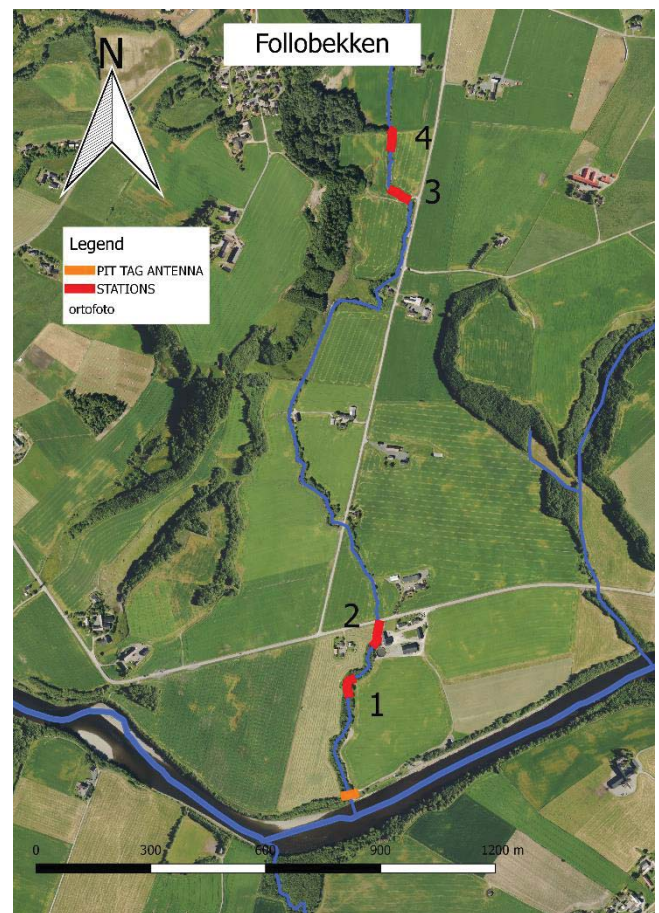
Figure 26: Tributary Follobekken with the pairs of station located in cultivated land.

A total of 332 brown trout were captured in Follobekken. 134 of those were tagged, only nine was longer than 120 mm and tagged with large PIT tags (23 mm) and 210 was too small (length <60 mm) to tag. 12 trouts were recaptured in total. Eight fish were recaptured at station 2, 3 and 4 in round 2, and four trout recaptured at station 2 and 4 in round 3. 29 individuals were detected in round 4 in January 2019 (Table 15). The high total number of brown trout with an estimated density of 126.3 individuals per 100 m^2 suggest that the tributary has a large subpopulation of trout. Follobekken is thereby classified a source in this study.
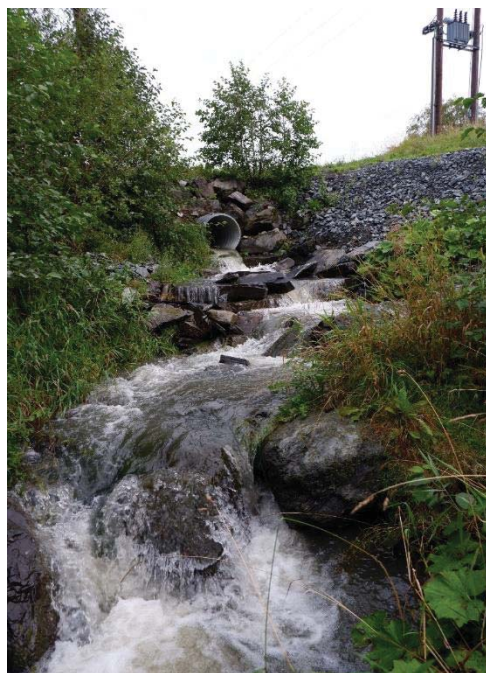
Figure 27: Culvert at the end of station 2 under road Vukuvegen in Follobekken.

Table 15: Captured, PIT-marked and recaptured fish in the tributary Follobekken.

Round	Date	Temp	Station	Fish captured	Fish tagged	Fish recaptured	PIT 23 mm
1	31.05.2018	13.8	1	4	3	-	
	31.05.2018	13.8	2	20	20	-	1
	31.05.2018	13.8	3	5	3	-	
	31.05.2018	13.8	4	15	15	-	
2	24.08.2018	11.9	1	1	1		
	24.08.2018	11.9	2	48	31	3	2
	26.08.2018	10.9	3	82	8	1	2
	26.08.2018	10.9	4	96	21	4	2
3	02.11.2018	4.7	1	3	3		
	02.11.2018	4.7	2	12	12	2	1
	02.11.2018	4.7	3	19	6		1
	02.11.2018	4.7	4	29	11	2	
4	23.01.2019		All	-	-	29	
Sum				332	134	41	9

Follobekken

Table 16: Measurement and characteristics of Follobekken.

Habitat characterization		Station			
		1	2	3	4
Distance from main river (m)		300	478	1970	2135
Total length (m)		47.6	50	37.8	43
Area (m^2)		117	119	82	119
Mean width (cm)		246	238	216	276
Mean depth (cm)		8.24	11.84	10.12	8.84
Mean velocity (m/s)		0.38	0.42	0.47	0.26
No of pools		3	1	1	3
Large woody debris		29	1	14	19
Mean moss (%)		0	0	3.2	6.4
Mean algae (%)		3.2	43.2	3.2	9.6
Mean canopy cover (%)		84	10	84	67
Substrate composition (%)	<2 mm	54	6	16	26
	2-20 mm	12	10	47	28
	20-100 mm	27	36	32	31
	100-250 mm	3	22	5	9
	>250 mm	4	26	0	6

Tributary Bjørkbekken (source). Bjørkbekken is located at the south side of main river Verdalselva and has four fishing stations with a range from 50 to 69 meters length (Figure 28).
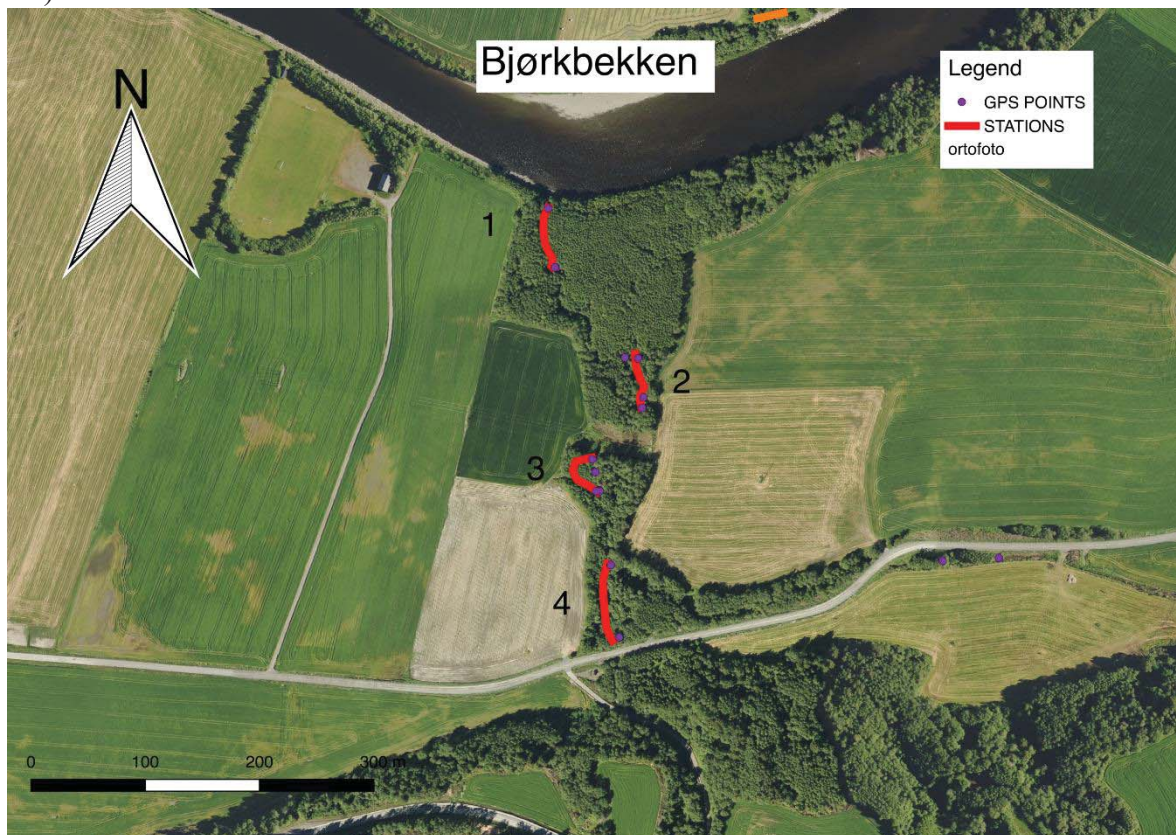
Figure 28: Location of stations in tributary Bjørkbekken.

The riperian zone of the tributary are wide and consist of forest with a mixed tree species composition with mostly grey alder, birch, spruce, bird cherry and goat willow. Bjørkbekken have some areas with meandering streambed and almost to natural conditions. A waterfall creates a natural migration barrier 75 meters upstream station 4 (Figure 29). The original migration route for brown trout including tributary Sundbybekken were estimated to 2050 meters but is today restricted to 1850 meters (Hol, 2018). The ecological status and ASPT-index in Bjørkbekken were classified as "moderate" by Vårhus (2016).

A total of 385 brown trout were captured in Bjørkbekken of which 120 were tagged, whilst only seven was longer than 120 mm and tagged with 23 mm

Figure 29: Upstream station No 4 were the waterfall makes a natural migration barrier.

PIT tags. 265 were too small (length <60 mm) to tag. Only two brown trout were recaptured, one in station 2 in round 2 in August, and one at station 1 in round 3 in October. 18 individuals were detected in round 4 in January 2019 (Table 17). The 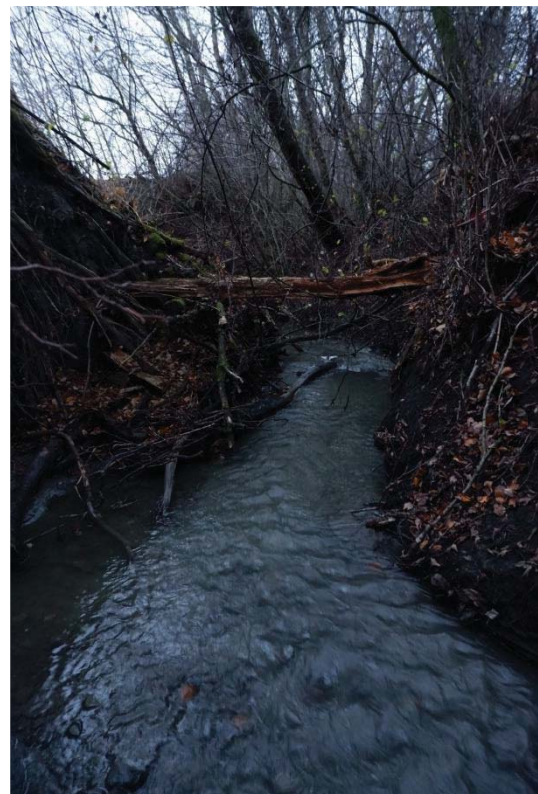high total number of brown trout with an estimated density of 77.8 individuals per 100 m^2 suggest that the tributary has a large subpopulation of trout. Bjørkbekken is thereby classified as a source in this study.

Table 17: Captured, PIT-marked and recaptured fish in the tributary Bjørkbekken.

Round	Date	Temp	Station	Fish captured	Fish tagged	Fish recaptured	PIT 23 mm
1	02.06.2018	11.1	1	17	17	-	2
	02.06.2018	11.1	2	20	20	-	1
	02.06.2018	11.1	3	29	23	-	
	02.06.2018	11.1	4	23	19	-	
2	22.08.2018	11.9	1	46	14		3
	22.08.2018	11.9	2	32	5	1	
	21.08.2018	12.3	3	72	7		1
	21.08.2018	12.3	4	125	4		
3	01.11.2018	3.9	1	1	1	1	
	01.11.2018	3.9	2	12	7		
	01.11.2018	3.9	3	5	2		
	01.11.2018	3.9	4	3	1		
4	24.01.2019		All	-	-	18	
Sum				385	120	20	7

Bjørkbekken

Table 18: Measurement and characteristics of Bjørkbekken.

Habitat characterization	Station			
	1	2	3	4
Distance from main river (m)	13	222	353	483
Total length (m)	53.5	61	49.1	63
Area (m^2)	113	117	109	125
Mean width (cm)	211	192	222	199
Mean depth (cm)	8.96	9.52	5.96	3.64

Mean velocity (m/s)			0.192	0.134	0.23	0.174
No of pools			5	10	6	4
Large woody debris			12	28	15	13
Mean moss (%)			0	0	0	0
Mean algae (%)			6.4	12.8	0	0
Mean canopy cover (%)			92	84	88	77
Substrate composition (%)	<2 mm		9	17	15	9
	2-20 mm		33	31	40	29
	20-100 mm		21	43	40	51
	100-250 mm		24	5	5	9
	>250 mm		11	0	0	0

Tributary Skjørdalsbekken (source)

Skjørdalsbekken has six fishing stations ranging from 40 to 55 meters length (Figure 30 and 31). Station 1 and 2 were included in the study in round 2. The original migration route for brown trout were estimated to be 6285 meters but is today restricted to 3870 meters (Hol, 2018). Both ecological status and ASPT-index were classified as "good" by Hol (2018).
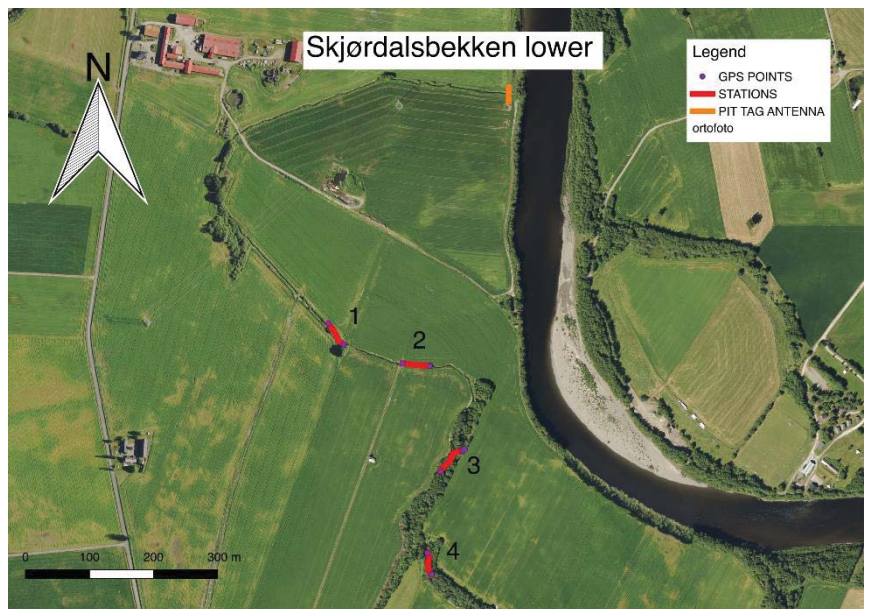
Figure 30: Location of downstream station 1-4 in stream Skjørdalsbekken.

Station 1 to 4 are located in agricultural land with a narrow riparian zone consisting of a mixed tree species composition with mostly grey alder, bird cherry and goat willow. Station 5 and 6 are located in a steeper area with forest growing in a greater distance from the cultivated land (Figure 31). This forest consists of more birch, grey alder and spruce, along with bird cherry and goat willow.

Figure 31: Location of upstream station 5 and 6 in stream Skjørdalsbekken.

A total of 776 brown trout were captured in Skjørdalsbekken. 191 of the fish were tagged, whilst only 10 was longer than 120 mm and tagged with large PIT-marks (23 mm) and 585 were too small to tag (length <60 mm). 16 trout were recaptured in total during electrofishing. 13 trout were recaptured at all previous tagged stations in round 2 (as station 1 and 2 were included in round 2) and 3 fish recaptured at station 2, 3 and 4 in round 3. 20 individuals were detected in round 4 in January 2019 (Table 19). The high total number of brown trout, with an estimated density of 179.9 individuals per 100 m^2, suggest that the stream has a large subpopulation of trout, and classified as a source in this study.

Table 19: Captured, PIT-marked and recaptured fish in the tributary Skjørdalsbekken.

Round	Date	Temp	Station	Fish captured	Fish tagged	Fish recaptured	PIT 23 mm
1	01.06.2018	15.4	3	26	23	-	
	01.06.2018	15.4	4	33	29	-	
	01.06.2018	12.4	5	10	8	-	
	01.06.2018	12.4	6	9	8	-	2
2	23.08.2018	9.8	1	40	11		
	23.08.2018	9.8	2	36	13		1
	23.08.2018	9.8	3	59	19	6	3
	21.08.2018	9.8	4	101	20	4	2
	21.08.2018	9.8	5	155	1	1	

	Date							
	21.08.2018	9.8	6	181	7	2		
3	31.10.2018	3.3	1	23	9			
	31.10.2018	3.3	2	37	13	1	1	
	01.11.2018	2.8	3	21	12	1		
	01.11.2018	2.8	4	9	4	1		
	01.11.2018	2.8	5	13	5		1	
	01.11.2018	2.8	6	23	9			
4	24.01.2019		All	-	-	20		
Sum				776	191	36	10	

Skjørdalsbekken

Table 20: Measurement and characteristics of Skjørdalsbekken.

Habitat characterization		Station					
		1	2	3	4	5	6
Distance from main river (m)		830	964	1194	1390	3150	3330
Total length (m)		41	40	60	50	50	57
Total area (m^2)		93	91	145	108	85	115
Mean width (cm)		226	228	241	216	170	202
Mean depth (cm)		19.52	20.28	9	10.16	9.96	9.88
Mean velocity (m/s)		0.55	0.46	0.25	0.24	0.26	0.27
No of pools		0	1	9	4	4	2
Large woody debris		0	3	17	15	9	12
Mean moss (%)		0	0	0	0	0	0
Mean algae (%)		0	9.6	0	0	12.8	6.4
Mean canopy cover (%)		6.6	12	92	86	90	66
Substrate composition (%)	<2 mm	29	36	32	16	16	10
	2-20 mm	32	18	32	18	10	12
	20-100 mm	39	34	34	48	52	23
	100-250 mm	0	2	2	12	14	33
	>250 mm	0	10	0	6	0	22

Appendix 2 Detection GPS locations round 4

Sink tributary group

Detection with GPS- locations from round 4
in January. Maps of each tributary were the
green line is the tracking route and the
yellow dots are detections.
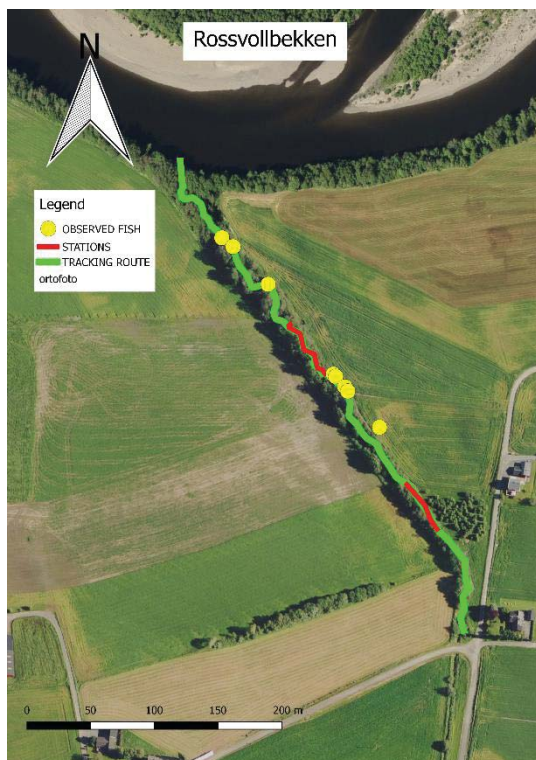
Source tributary group

Detection with GPS- locations from round 4
in January. Maps of each tributary were the
green line is the tracking route and the
yellow dots are detections.
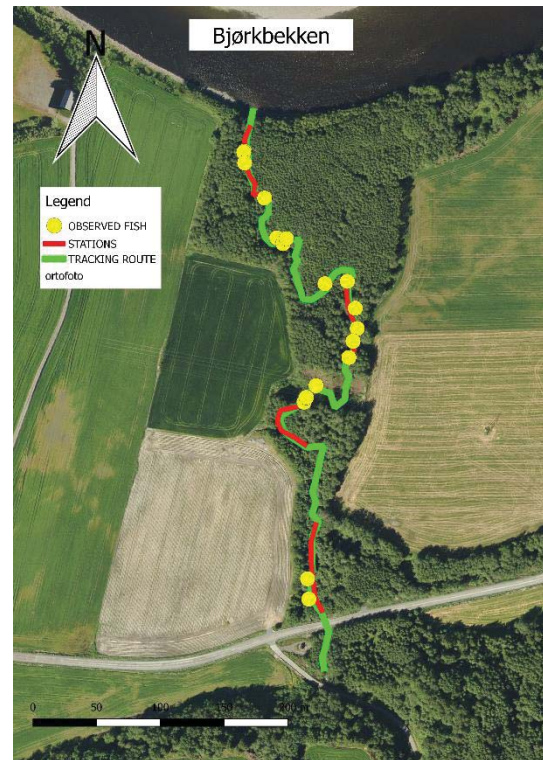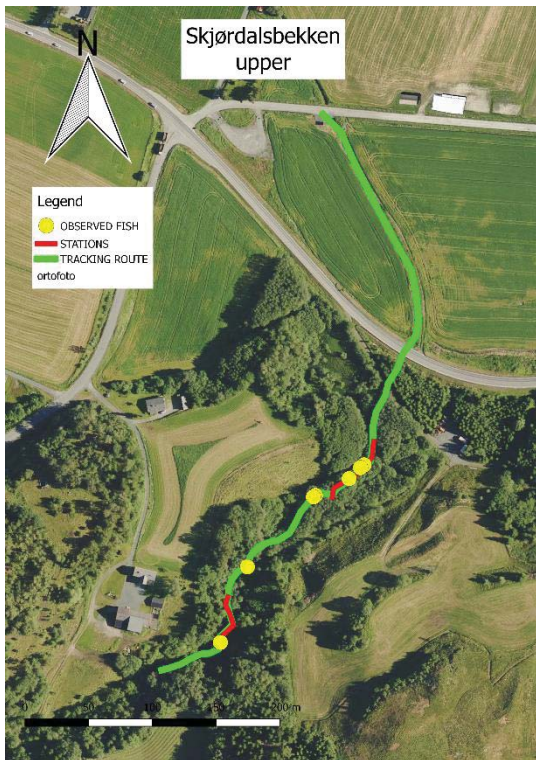
Appendix 3 Density estimates removal method

Tables of caught individuals from each tributary in round 2 in August, removal method is used.

Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Rossvoll-	Trout	2018	0+	1	54	1.47	0	0	0	0.0	0.0	0.0	0.00	0.0	3 times
Rossvoll-	Trout	2018	>0+	1	54	1.47	1	0	0	1.00	0.0	0.00	1.26	0.00	3 times
Rossvoll-	All	2018	All	1	54	1.47	1	0	0	1.00	0.0	0.00	1.26	0.00	3 times
Rossvoll-	Trout	2018	0+	2	32.7	1.83	2	1	0	0.71	0.29	0.01	5.14	0.60	3 times
Rossvoll-	Trout	2018	>0+	2	32.7	1.83	3	5	1	0.29	0.30	0.17	23.53	17.40	3 times
Rossvoll-	All	2018	All	2	32.7	1.83	5	6	1	0.41	0.22	0.08	25.34	8.27	3 times

Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Brokskit-	Trout	2018	0+	1	58	1.68	5	5	1	0.44	0.23	0.04	13.74	3.98	3 times
Brokskit-	Trout	2018	>0+	1	58	1.68	0	0	0	0.0	0.0	0.0	0.0	0.0	3 times
Brokskit-	All	2018	All	1	58	1.68	5	5	1	0.44	0.23	0.04	13.74	3.98	3 times
Brokskit-	Trout	2018	0+	2	47.1	1.34	1	0	-	1.00	0.00	0.00	1.58	0.00	2 times
Brokskit-	Trout	2018	>0+	2	47.1	1.34	0	0	-	0.0	0.0	0.0	0.0	0.0	2 times
Brokskit-	All	2018	All	2	47.1	1.34	1	0	-	1.00	0.0	0.00	1.58	0.00	2 times
Brokskit-	Trout	2018	0+	3	50	2.048	2	2	-	0.00	1.00	0.0	3.91	0.0	2 times
Brokskit-	Trout	2018	>0+	3	50	2.048	2	0	-	1.00	0.00	0.00	1.95	0.00	2 times
Brokskit-	All	2018	All	3	50	2.048	4	2	-	0.50	0.19	0.05	7.81	4.78	2 times
Brokskit-	Trout	2018	0+	4	50	2.2	0	0	-	0.0	0.0	0.0	0.00	0.0	2 times
Brokskit-	Trout	2018	>0+	4	50	2.2	3	0	-	1.00	0.00	0.00	2.73	0.00	2 times

Brokskit- | All | 2018 | All | 4 | 50 | 2.2 | 3 | 0 | - | 1.00 | 0.00 | 0.00 | 2.73 | 0.00 | 2 times

Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Follo-	Trout	2018	0+	1	47.6	2.46	0	0	0	0.0	0.0	0.0	0.00	0.0	3 times
Follo-	Trout	2018	>0+	1	47.6	2.46	1	0	0	1.00	0.0	0.00	0.85	0.00	3 times
Follo-	All	2018	All	1	47.6	2.46	1	0	0	1.00	0.0	0.00	0.85	0.00	3 times
Follo-	Trout	2018	0+	2	50	2.38	12	7	6	0.31	0.18	0.12	31.42	12.38	3 times
Follo-	Trout	2018	>0+	2	50	2.38	8	6	7	0.07	0.25	3.07	91.42	307.35	3 times
Follo-	Salmon	2018	>0+	2	50	2.38	1	1	0	0.57	0.44	0.01	1.83	0.62	3 times
Follo-	Salmon	2019	0+	2	50	2.38	3	0	0	1.00	0.0	0.00	2.52	0.00	3 times
Follo-	All	2018	All	2	50	2.38	24	14	13	0.28	0.13	0.22	68.28	22.18	3 times
Follo-	Trout	2018	0+	3	37.8	2.16	34	21	20	0.25	0.11	0.53	160.28	53.07	3 times
Follo-	Trout	2018	>0+	3	37.8	2.16	5	3	0	0.67	0.19	0.01	10.15	0.91	3 times
Follo-	All	2018	All	3	37.8	2.16	39	24	20	0.30	0.10	0.36	156.29	36.36	3 times
Follo-	Trout	2018	0+	4	43	2.76	29	37	20	0.15	0.11	1.28	192.32	127.86	3 times
Follo-	Trout	2018	>0+	4	43	2.76	7	3	4	0.28	0.24	0.12	18.87	11.81	3 times
Follo-	All	2018	All	4	43	2.76	36	40	24	0.17	0.10	1.04	201.12	104.45	3 times

Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Skjordals-	Trout	2018	0+	1	41	2.26	16	9	7	0.35	0.15	0.13	47.38	12.76	3 times
Skjordals-	Trout	2018	>0+	1	41	2.26	5	1	2	0.45	0.26	0.03	10.37	3.32	3 times

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Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Skjordals-	All	2018	All	1	41	2.26	21	10	9	0.37	0.13	0.12	57.33	12.37	3 times
Skjordals-	Trout	2018	0+	2	40	2.28	17	5	3	0.62	0.12	0.02	29.02	2.06	3 times
Skjordals-	Trout	2018	>0+	2	40	2.28	4	4	1	0.41	0.26	0.05	12.47	4.70	3 times
Skjordals-	Salmon	2018	0+	2	40	2.28	1	0	0	1.00	0.0	0.00	1.10	0.00	3 times
Skjordals-	Salmon	2018	>0+	2	40	2.28	2	0	0	1.00	0.0	0.00	2.19	0.00	3 times
Skjordals-	All	2018	All	2	40	2.28	24	9	4	0.60	0.10	0.03	43.30	2.79	3 times
Skjordals-	Trout	2018	0+	3	60	2.41	21	7	16	0.16	0.16	0.64	75.73	63.52	3 times
Skjordals-	Trout	2018	>0+	3	60	2.41	11	6	4	0.41	0.17	0.05	18.35	4.53	3 times
Skjordals-	All	2018	All	3	60	2.41	32	13	20	0.24	0.12	0.29	79.00	28.54	3 times
Skjordals-	Trout	2018	0+	4	50	2.16	40	33	22	0.25	0.10	0.44	152.00	43.77	3 times
Skjordals-	Trout	2018	>0+	4	50	2.16	4	3	3	0.14	0.34	0.53	25.48	52.53	3 times
Skjordals-	All	2018	All	4	50	2.16	44	36	25	0.24	0.09	0.51	173.13	50.64	3 times
Skjordals-	Trout	2018	0+	5	50	1.7	60	46	44	0.15	0.09	2.27	461.37	226.84	3 times
Skjordals-	Trout	2018	>0+	5	50	1.7	3	2	1	0.41	0.32	0.04	8.92	4.12	3 times
Skjordals-	All	2018	All	5	50	1.7	63	48	45	0.16	0.08	1.97	451.40	197.26	3 times
Skjordals-	Trout	2018	0+	6	57	2.02	70	59	41	0.23	0.07	0.68	273.50	68.30	3 times
Skjordals-	Trout	2018	>0+	6	57	2.02	8	2	3	0.46	0.20	0.03	13.43	3.20	3 times
Skjordals-	All	2018	All	6	57	2.02	78	61	44	0.25	0.07	0.59	278.17	59.36	3 times
Korsådals-	Trout	2018	0+	1	65	1.92	12	1	1	0.81	0.11	0.00	11.30	0.28	3 times

Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Korsådals-	Trout	2018	>0+	1	65	1.92	5	4	2	0.34	0.25	0.06	12.29	5.94	3 times
Korsådals-	All	2018	All	1	65	1.92	17	5	3	0.62	0.12	0.02	21.21	1.51	3 times
Korsådals-	Trout	2018	0+	2	20	1.68	12	1	0	0.93	0.07	0.00	38.71	0.21	3 times
Korsådals-	Trout	2018	>0+	2	20	1.68	2	0	0	1.00	0.0	0.00	5.95	0.00	3 times
Korsådals-	All	2018	All	2	20	1.68	14	1	0	0.94	0.06	0.00	44.65	0.19	3 times
Korsådals-	Trout	2018	0+	3	82	1.76	9	8	7	0.12	0.22	0.88	53.06	88.00	3 times
Korsådals-	Trout	2018	>0+	3	82	1.76	2	0	0	1.00	0.0	0.00	1.39	0.00	3 times
Korsådals-	All	2018	All	3	82	1.76	11	8	7	0.21	0.19	0.26	35.84	26.36	3 times

Tributary	Species	Year	Age	Station	Length	Width	c1	c2	c3	Est catchability (p)	SE(p)	SE(#fish/sqm)	fish/100m2	se	Method
Bjork-	Trout	2018	0+	1	53.5	2.11	15	8	1	0.64	0.11	0.01	22.31	1.44	3 times
Bjork-	Trout	2018	>0+	1	53.5	2.11	12	7	2	0.54	0.14	0.02	20.55	2.42	3 times
Bjork-	Salmon	2018	>0+	1	53.5	2.11	1	0	0	1.00	0.0	0.00	0.89	0.00	3 times
Bjork-	All	2018	All	1	53.5	2.11	28	15	3	0.60	0.09	0.02	43.44	2.47	3 times
Bjork-	Trout	2018	0+	2	61	1.92	11	7	2	0.52	0.15	0.03	19.20	2.65	3 times
Bjork-	Trout	2018	>0+	2	61	1.92	5	5	3	0.21	0.27	0.23	22.08	22.97	3 times
Bjork-	All	2018	All	2	61	1.92	16	12	5	0.41	0.14	0.07	35.60	7.01	3 times
Bjork-	Trout	2018	0+	3	49.1	2.22	25	22	15	0.22	0.12	0.49	109.48	48.91	3 times
Bjork-	Trout	2018	>0+	3	49.1	2.22	6	0	3	0.41	0.26	0.04	10.43	3.93	3 times
Bjork-	All	2018	All	3	49.1	2.22	31	22	18	0.24	0.11	0.40	115.10	40.26	3 times
Bjork-	Trout	2018	0+	4	63	1.99	59	32	27	0.34	0.08	0.20	131.62	19.61	3 times

| Bjork- | Trout | 2018 | >0+ | 4 | 63 | 1.99 | 3 | 3 | 1 | 0.36 | 0.31 | 0.04 | 7.60 | 4.26 | 3 times |
| Bjork- | All | 2018 | All | 4 | 63 | 1.99 | 62 | 35 | 28 | 0.34 | 0.08 | 0.20 | 139.20 | 20.05 | 3 times |