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Adult Atlantic salmon (*Salmo salar*) spawning migration and behaviour in the lower Skienselva

An investigation into the behavior of Atlantic salmon below the Skotfoss hydropower plant

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This thesis is worth 60 study points

Abstract

Atlantic salmon swim upstream from the sea through Frierfjorden to spawn in the Skien watershed, the third largest in Norway. There are two hydroelectric power plants in the lower reaches of the Skienselva: Klosterfoss and Skotfoss. Salmon caught swimming up the fish ladder at the downstream power plant were tagged, released, and tracked from the beginning of the upstream migration to the end of the spawning period in the entire anadromous watershed. Salmon spent unequal amounts of time at the four spawning areas in the main river and a tributary between Klosterfoss and Skotfoss. Salmon spent less time at the Vadrette spawning site compared to the Fossum and Grøtsund spawning sites. Salmon which swam upstream to the Skotfoss hydroelectric power plant did not all ascend the fish ladder there, 26% did. In this study, 16% of all salmon tagged at Klosterfoss ascended the fish ladder at Skotfoss and swam to upstream spawning sites. This is much smaller than the what is expected based on the fry populations in the rivers of the Skien watershed. Salmon which ascended the Klosterfoss ladder relatively early, swam upstream to Skotfoss more quickly than salmon that arrived relatively late at the Klosterfoss ladder. Short and repeated movements upstream to Skotfoss, and downstream to areas in the Farelva, and back again to Skotfoss were observed in the majority of tagged salmon that approached Skotfoss. The “yo-yo” migration of salmon in the Farelva is for the most part unexplained, but the movement costs the salmon valuable energy before and during the spawning season and so would seem to be a negative behavior. These results indicate that salmon find the entrance to the fish ladder and do not remain stuck at the tunnel outlet, but most do not successfully ascend it. This could be the result of poor ladder construction, too low flow from the ladder, low survival of fry from upstream of Skotfoss reducing the number of salmon that are homing to upstream spawning areas, or that not all salmon which approach Skotfoss are homing to areas above the ladder. The possibility exists that salmon which will eventually spawn in areas downstream of the ladder engage in searching behavior near the fish ladder. If efforts to restore the populations in the upper watershed are to continue, issues salmon have with ascending the Skotfoss fish ladder must be addressed first.

Contents

1 Introduction

1.1 Problem Statement

We chose the Atlantic salmon (*Salmo salar*), in the Skien watershed for this study because they have experienced great physical changes in the freshwater environment in the last 150 years, due to human impact. Atlantic salmon is the most important fish species in Norway, both economically and culturally (Norwegian Seafood Council 2019). Approximately 25% of the total healthy populations of salmon in the world are in the rivers of Norway. These populations have been fished on a large scale for food and on a small scale for recreation, which ties them strongly to the economy (Hindar et al. 2011). Norway is also one of the world's leaders in hydropower energy, producing 144 terrawatt-hours (Twh) of energy in 2016, 22 Twh more than the country's annual consumption [hydropower.org] [worlddatainfo.org]. As Europe fulfills promises to become more sustainable in the areas of energy production and consumption, Norway, as the largest producer of hydropower in Europe, is getting ready to increase its energy export of this excess. It already exports around 10% of all the energy produced, and 99% of total production is hydropower [hydropower.org].

The life history of anadromous fish like salmon relies very heavily on their ability to migrate between the sea and freshwater river system. Nearly all major river systems in Norway, approximately 2/3 of watersheds, are in some way regulated by hydropower, which can disrupt or halt the migration of salmon. Of all the self-reproducing populations of salmon in Norway, 19% are significantly affected by hydropower (Forseth et al. 2017). Hydropower development has greatly decreased since a peak in the 1950s, mostly due to the fact that the major river systems were all developed. Further degradation of populations due to the impacts of hydropower is unlikely as extensive protections have been in place since 2001 and fewer permissions have been granted to hydropower projects after 2003 (Forseth et al. 2017). Nonetheless, the Skien watershed salmon population, is still recovering from the effects of the initial damming in 1860, which cut off much of the available habitat.

Other factors affecting the salmon population in Norway include escaped fish from sea-ranching and a period of acid rain degradation in the 20th century. Escaped salmon have the capability to alter the genetic diversity of wild salmon, possibly negatively, and acid rain decimated the salmon population in southern Norway. The recovery of salmon stocks in the southern counties is ongoing, but previously "extinct" populations of salmon, have rebounded since a liming program for 21 acidified rivers (Hesthagen and Larsen 2003). Managing escaped salmon is an ongoing project. There is less genetic evidence of escapes in water bodies that were designated National Salmon Fjords or National Salmon rivers in the last 20 years, which indicates that these designations are beneficial (Karlsson et al. 2016). The focus of salmon conservation is shifting from waterways where salmon have become extinct, to maintaining and rebuilding existing populations, using stocking of fry and renovating fish ladders, such as has been done in the Skienselva and of maintaining populations in undeveloped rivers.

Atlantic salmon are anadromous and iteroparous, and it follows that environmental changes can impact the species drastically. Salmon are reliant on ocean feeding areas and spawning habitat in freshwater, including traversable waterways to reach those spawning areas, both upstream for adults and downstream for smolts (Primmer et al. 2006). The precise timing of the upstream migration varies between and among populations. In Norway, salmon enter rivers between May and October and the spawning period is from October to December (Thorstad et al. 2008). The spawning migration occurs in two major phases. The first phase is a movement towards the coast. This phase was previously thought to be imprecise and that salmon would swim to the nearest coastline and then travel along it until they reach the river they are homing to, but it is actually a quite accurate migration (Ulvan et al. 2018). The second phase is a precise journey to the natal spawning area that includes the upstream, freshwater migration. Most individuals return to their natal river and spawning area, but studies show that some stray to other rivers or sites within the river (Jonsson et al. 2003). This upstream migration is further broken into phases, including a migration phase of steady progress upriver with resting periods, followed by a searching phase, and finally a holding phase, although there is considerable individual variation in this pattern (Økland et al. 2001; Thorstad et al. 2008). These phases may, however, not exist or be different in rivers with alterations such as dams and hydropower plants.

Salmon can use manmade fish ways, also known as fish ladders to ascend dams. As of 2002, approximately 500 fish ladders were installed at dams in Norway, 406 of which were for anadromous species (Direktoratet for Naturforvaltning 2002). However, many of the ladders are imperfect and a significant amount of salmon do not pass through them, in part for reasons unknown to fish biologists. Some studies show that the salmon are unable to find the entrance to the ladder, instead staying at hydropower station outlets for days or weeks (Thorstad et al. 2003; Lundqvist et al. 2008). Studies have correlated this phenomenon with the low flow of water from the fish ladder and bypass route compared to the flow from the power plant tunnel outlet (Rivinoja et al. 2001). Others have theorized that fish which enter the tunnel of an un-screened outlet are not aware of the bypass at all, and will remain unaware even if artificial freshets are produced as a countermeasure (Thorstad et al. 2003). The fish ladder at Skotfoss has been partially or completely renovated multiple times, but a study in 2010 on juvenile salmon and sea trout populations in the watershed asserted that in order to increase the population size in the upper watershed, the intake of the fish ladder should be widened to allow for greater flow (Hvidsten 2010). While the biological mechanism of these delays is still being identified, so too are the impairments this may cause to adult spawning salmon in their upstream migration. This study hopes to contribute to understanding both the mechanism and the impairments.

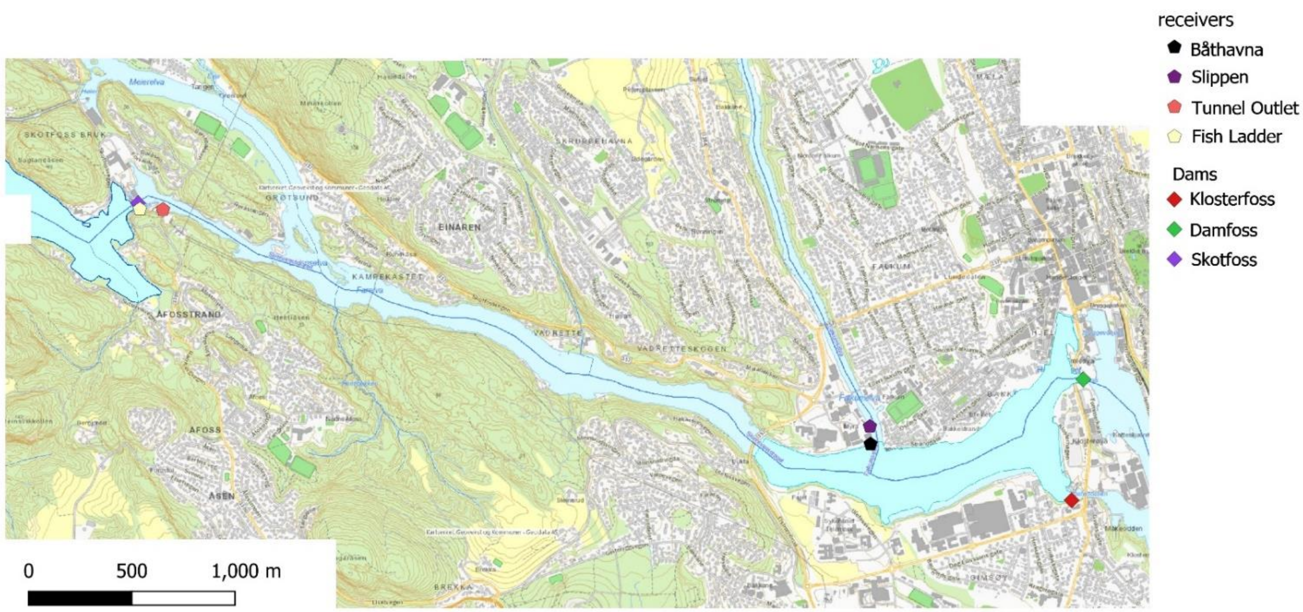

Figure 1. Close up map of study area between Skien and Skotfoss with the four stationary receivers shown, placed at the mouth of the tributary, Falkumelva, and at the tunnel outlet and fish ladder at the Skotfoss hydroelectric power dam. Basemap from NVE atlas (Norges vassdrags og energi direktoratet) [atlas.nve.no]

The studied river system, the Skien watershed, has two major barriers in the very lower end (Figure 1). These barriers were once passable waterfalls, but the dam built in 1860 at Skotfoss blocked passage completely, followed by a dam at Klosterfoss in 1862. A fish ladder mandated by the State was briefly installed with the new hydropower plant in 1952, but it was not designed to fit the conditions as Skotfoss and few if any fish used it. In the 1980s, a large restoration effort was undertaken, including building a new ladder and stocking the upper reaches of the watershed. The efforts had some positive impacts on the Skienselva salmon population, as seen in Figure 2.

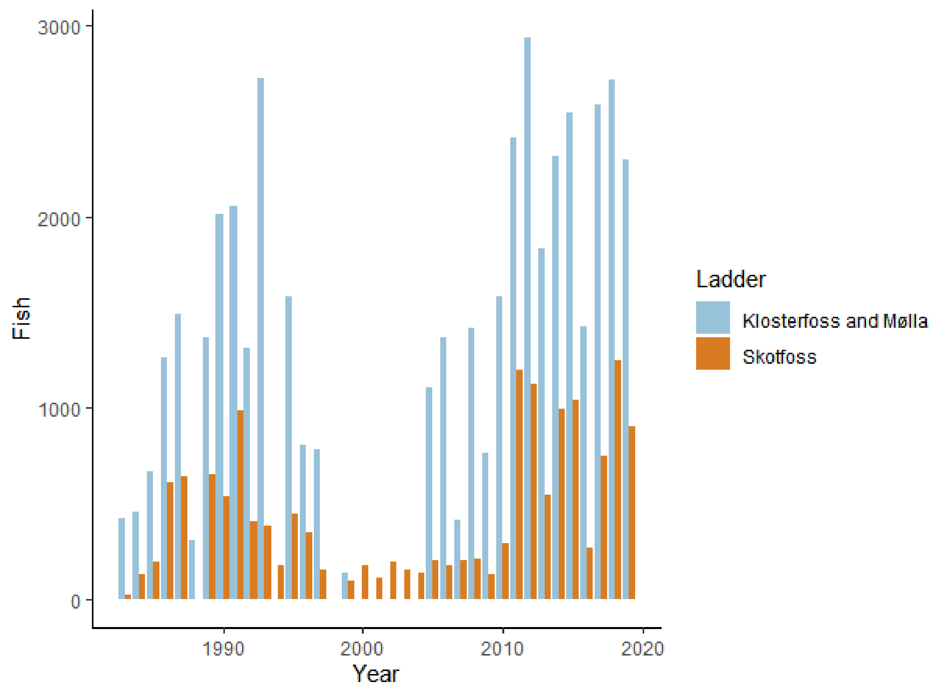

Figure 2. Counts of salmon using the fish ladders at Skotfoss, Klosterfoss and Mølla (or Damfoss) over the years 1983-2019 (pers.comm. Dag Natedal). Data on species is taken from fish counters which may not always correctly identify species.

The figure also shows that there is a far larger number of salmon which enter the Hjellevannet above Klosterfoss and Mølla than pass Skotfoss and swim into Norsjø. This is true despite Hvidsten's investigation into juvenile populations in Bøelva, Heddøla, and Bliva/Falkumelva which showed that the largest production comes from Heddøla (2010). The second largest fraction was from unspecified areas downstream of Skotfoss and upstream of Klosterfoss, but if all the smolt from upstream of Skotfoss successfully returned to their natal river, more than 50% of salmon entering the Skien watershed would ascend the Skotfoss fish ladder. This study will investigate where in the available area they spawn; what percentage spawn in the tributary branch Falkumelva. Using the tracking data, the behavior and movement of salmon between Klosterfoss and Skotfoss can be analyzed.

1.2 Objectives and Research Questions

Past studies in the literature have addressed the ability of salmon to ascend a fish ladder, and the demographics of fish that pass versus fish that do not. However, none address the behavior of fish which are unable or approach but do not ascend a fish ladder (Karppinen et al. 2002; Gowans et al. 2003; Thorstad et al. 2003). As Figure 2 shows, many adult Atlantic salmon do not enter or ascend the fish ladder at Skotfoss. The possibility should be considered that some attempt to ascend the ladder but are unable to. These salmon may be homing to a spawning area that they cannot reach. It is also possible that some salmon approach the dam as they explore the area above Klosterfoss, in the way that wandering or straying salmon might. The tracking data from this study applied to the questions listed above will provide conclusions about the overall behavior of salmon downstream the hydropower plant at Skotfoss.

Atlantic salmon blocked by an impassable barrier may spawn in unsuitable places with inadequate flow or poor substrate, leading to recruitment failure (Thorstad et al. 2008). For instance, migration delays in another salmonid, Arctic grayling (*Thymallus arcticus*), induced the displacement of fish to lower quality spawning habitat downstream of their natal spawning site (Scruton et al. 2007). Salmon that originate from areas upstream of Skotfoss and Norsjø, and are returning to their natal areas may find themselves in a similar situation. Between Skotfoss and Klosterfoss there are fewer available spawning areas and those spawning areas are possibly of lower quality that those upstream, in Tinnåa, for example (Heggenes and Dokk 1995). The spatial distribution of redds and thus offspring, is, at least to some extent, determined by the spatial distribution of the breeding adults (Finstad et al. 2010). High levels of genetic differentiation can occur between populations of freshwater salmonids that are geographically very close to one another (Primmer et al. 2006). A small amount of salmon will stray to other rivers, colonizing new habitats and possibly counteracting inbreeding, but the percentage is low, 6% for wild conspecifics, higher for hatchery-raised and sea ranched salmon released on an undeveloped river (Jonsson et al. 2003). With the "forced straying" that results from an impassable barrier, these genetic variations may vanish, reducing differentiation among salmon populations. If the salmon in the Skienselva are choosing to or out of necessity must spawn in subpar spawning sites, or at least not their natal spawning area, then this may have consequences for the genetic diversity and overall genetic health of the Skienselva salmon stock. By analyzing their movements to and from the dam, and in and out of nearby spawning areas, we can make inferences about their behavior, though not their intent or motives. If a considerable number of salmon are being stopped by the dam, either because they cannot find the entrance or they cannot ascend the ladder, then their behavior downstream may either be to continually rest at the fish ladder or the tunnel outlet of the dam, or to make many trips in between Skotfoss and the near spawning sites in the Farelva (Laine 1995; Rivinoja et al. 2001; Lundqvist et al. 2008). This should be reflected in the total number of observations in each of these spawning areas as well as the number of observations per fish. If, however, many of the salmon which approach the Skotfoss dam are "wandering" salmon in a search phase – exploring all of the Skienselva and Falkumelva before choosing a spawning site, then there should be a large amount of movement between all four spawning sites and total observations and observations per fish will correlate to the size or quality of the spawning area (Økland et al. 2001). The observations of erratic behavior may be found both in salmon that are wandering and salmon that have been halted in their migration by the dam and determining the difference between these two is difficult. Though by analyzing the lengths of movement, and the time spent at the dam, we can infer which group these salmon may belong to.

The objectives of this study are to investigate:

1) When the time comes to spawn what do salmon that do not ascend the ladder, but were present at Skotfoss do?
2) Wil these salmon remain in the stretch of river directly below the dam, possibly spawning in the two suitable spawning areas: Vadrette and Grøtsund?
3) Will these salmon stray to the tributary river, the Falkumelva, and spawn there?
4) Will salmon be observed equally at the four available spawning sites, or will some be more populated than others?
5) Finally, could we view the tunnel outlet and the pool below the fish ladder as a "holding site" because of favorable temperature and flow conditions, where even salmon that mean to spawn in the near downstream sites come to rest for a time?

In the present study, Atlantic salmon were tagged in the summer of 2019 and tracked from July to December. Movements in the area between the two dams at Klosterfoss and Skotfoss are especially the focus of this study, with emphasis on movements relative to fish ladders and the spawning sites within this area. A subset of the tagged Atlantic salmon was closely monitored during the height of spawning season and the time spent in known spawning habitat calculated. This group of intensively tracked salmon is also referred to as the IT group for the rest of this paper. Their movements will help shed light on the various aspects of the spawning migration of salmon in the Skien watershed.

This thesis will begin with a description of the study area, followed by an outline of the various methods. The results of the study will then be presented, with a discussion including what questions the results provide an answer for. Finally, an outlook to discuss further research and a conclusion to summarize the most important findings.

1 Study Area & Methods

2.1 Description & History

The Skien watershed is located in southeast Norway and is the country's fifth largest watershed (Hvidsten 2010). It has a total precipitation field of 10807.66 km^2 that stretches from the Kvenna watershed in Hardangervidda to its mouth at Frierfjorden (Norges vassdrags og energi direktoratet). The watershed drains 8646.12 million m^3 of water per year (Norges vassdrags og energi direktoratet). The river runs free for 11 km from the mouth of the river to the city of Skien. Anadromous fish may then ascend fish ladders at either Klosterfoss or Møllefoss, also known as Damfoss, as shown in Figure 1, which are branches of the river divided by a natural island (Gimsøy Is.). Upstream of these two dams is the small lake Hjellevannet, off of which branches the tributary river Falkumelva (305 km^2, 219.34 mill m^3/yr, 7.96 m^3/s) , also known as Bliva (Norges vassdrags og energi direktoratet). At Fossum (5 km from Hjellevannet), the Falkumelva branches into two tributaries, one of which has a dam less than a kilometer from the fork, while the other continues until Svartufs waterfall above Royevannet. The main branch of the river which runs into Hjellevannet, however, is a short stretch known as the Farelva (283.9 m^3/s), between the city of Skien and the Skotfoss hydropower plant. If fish ascend ladder at Skotfoss, then they are free to cross the lake Norsjø (55.12 km^2, 15.3 meters above sea level, 5100 million m^3, and average depth 87 meters) and access several tributaries.

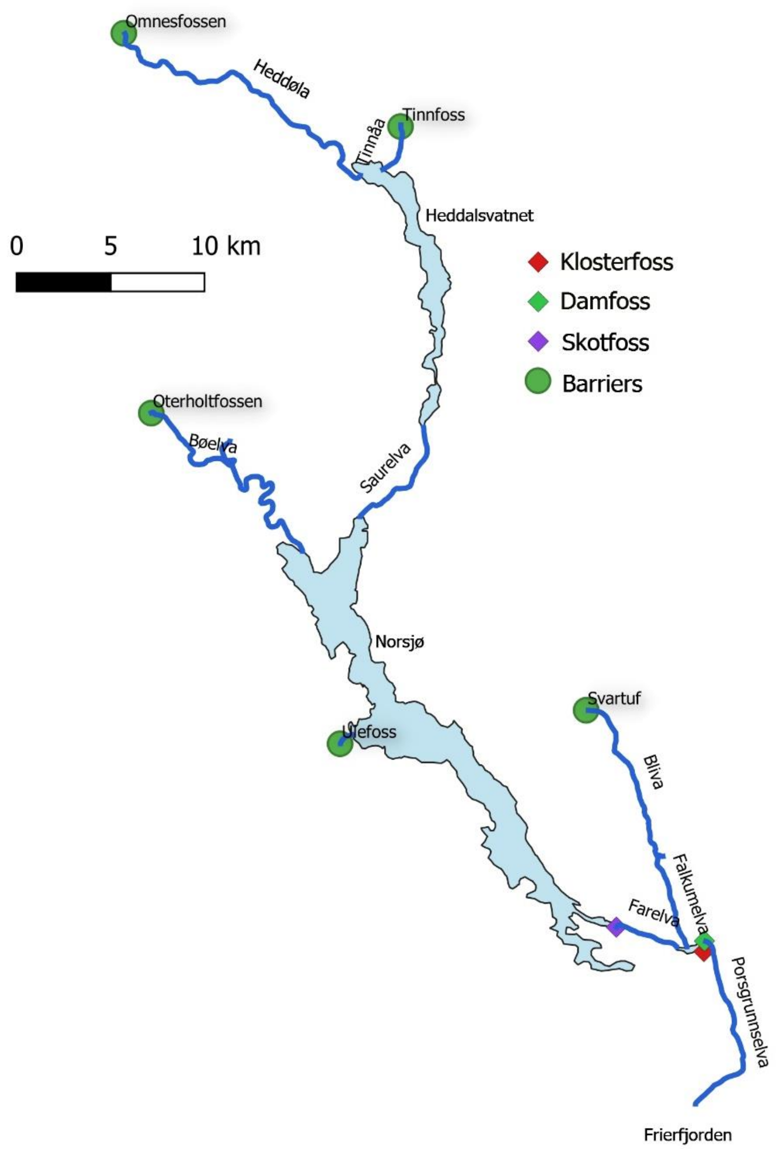

Figure 3. Map of the Skien watershed from Frierfjorden in the south to the anadromous extent at Oterholtfossen and Omnesfossen. Barriers are all naturally impassable waterfalls.

The three major rivers Eidselva, Bøelva (aka Gvarvelva) and Sauerelva flow into the Norsjø, as shown in Figure 3. The Sauerelva is fed by the rivers Heddøla and Tinnåa. Historically, the available reaches of the Bøelva (18 km), the Sauerelva (6 km), Heddøla (18 km), and Tinnelva (1 km) constituted the main spawning and recruitment areas for anadromous fish. These areas remain the same today, with natural waterfalls as barriers (Bøelva: Oterholtfossen; Heddøla: Omnesfossen; Tinnåa: Tinfos). The Eidselva has natural waterfalls 11 m in height, 700 meters from the mouth that fish have never been able to ascend. The river was dammed at these falls and subsequently developed for industry in 1891 (Norges vassdrags og energi direktoratet).

Klosterfoss is the name of the formerly passable 5 meter high falls and the current hydropower plant in Skien, shown in Figure 1. This plant was built in 1969, though the reservoir at Hjellevannet was formed in 1862 (Norges vassdrags og energi direktoratet). It has an annual flow of 1541 million m^3 and a maximum flow of 240 m^3/s. Since 1886 there have been many fish ladders installed at Klosterfoss. The current ladder is a denil-type that was built in 1976 (Kraabøl 2014).

The dam at Skotfoss sits on what was a set of waterfalls that were historically passable to anadromous fish species. The original dam was finished in 1861, 200 meters upstream from where the current dam sits (Petterson 1998). This dam completely blocked salmon from entering the the lake Norsjø and all tributaries upstream. The current power plant was completed in 1953 and modified in 1969 and has a height change of 10 meters. Annually, 1434 million m^3 of water pass through the Skotfoss hydropower plant and the maximum amount of the water the plant can handle at any given time is 280 m^3/sec (akershusenergi.no). The fish ladder at Skotfoss was originally constructed in 1952 with the construction of the new hydropower plant and the moving of the dam 100 meters from Firingfossen to Skotfoss. This ladder had the entrance just under the dam and functioned poorly possibly because of this- the entrance was thought to be too far from the tunnel outlet. In 1977, a new entrance was constructed nearer to the tunnel outlet. This was the first time in over 100 years that salmon returning to the upper reaches of the Skien watershed became a possibility. The fish ladder was modified further in 2013, but this new section also functions poorly so, for the last several years, the old entrance below the dam has been used instead.

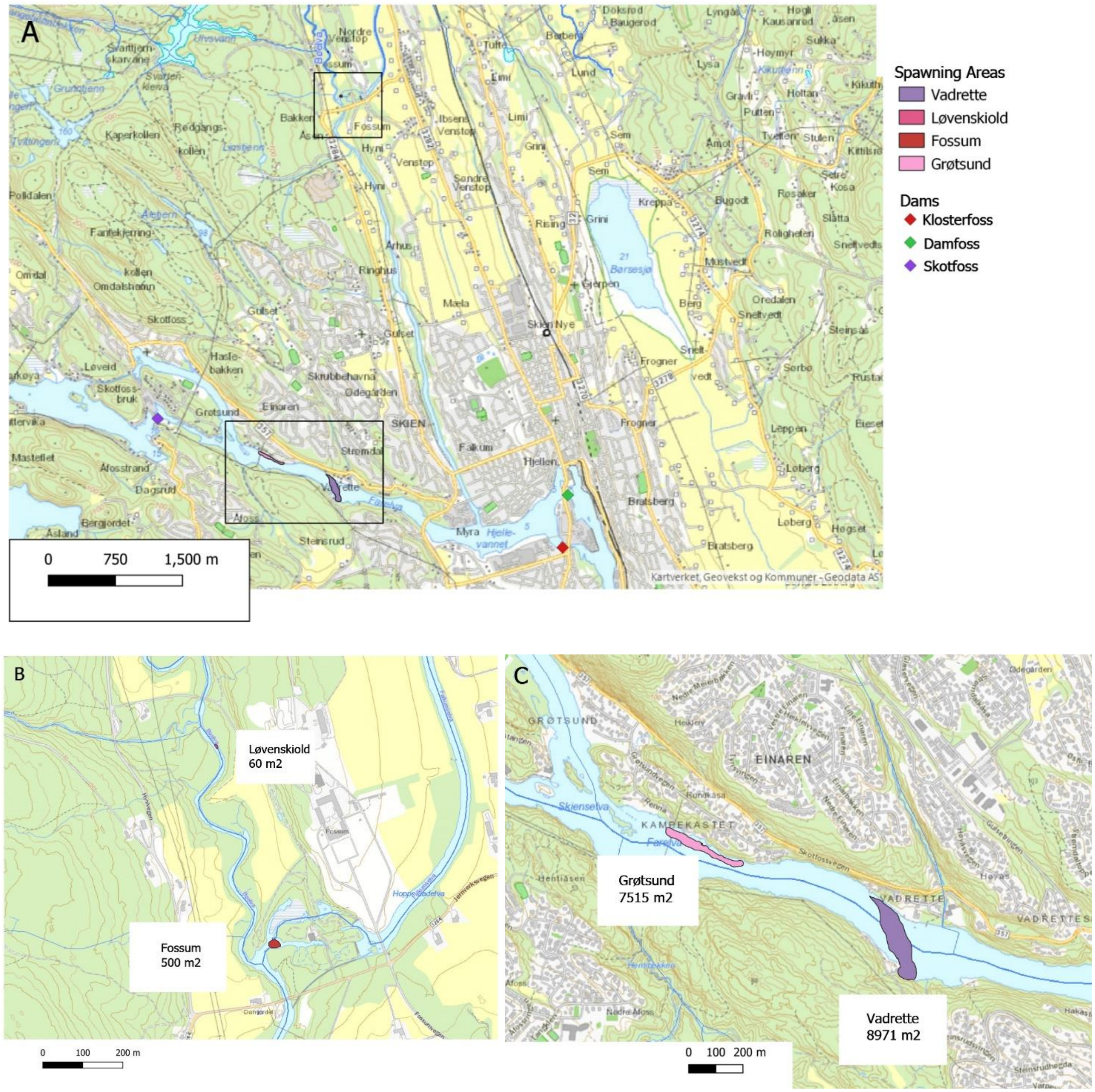

Figure 4. A. Map of the larger Skien and Skotfoss area; **B.** Detailed map of the two spawning areas in the tributary branch, Falkumelva; **C.** Detailed map of the two spawning areas in the main branch, Farelva. Basemap from NVE atlas [atlas.nve.no].

In the 1980s, local entities worked together and began a stocking campaign that included setting out 270,000 sea trout and salmon fry in the upper watershed every year beginning in 1988 (Carm and Langkaas 1993; Akershus Energi 2018). The Bøelva and Heddøla continue to each receive over 10,000 summer old salmon, hatchery-raised from stock at Klosterfoss and Skotfoss (pers. comm. J. Heggenes). Despite this, the Falkumelva remains the densest area of growing salmon (Hvidsten 2010).

The focus of this thesis is on the four spawning areas available to Atlantic salmon in the waters between Skotfoss and Klosterfoss without needing to ascend the fish ladder at the Skotfoss hydroelectric power plant, of which there are four that are known (Figure 4). Grøtsund, Vadrette, Fossum, and Løvenskiold spawning sites are believed to be the main spawning areas. Grøtsund (7151 m^2) and Vadrette (8971 m^2) are located on the Farelva (Figure 4C), Fossum (500 m^2) and Løvenskiold (60 m^2) are located on the Falkumelva (Figure 4B).

2.2 Capture & Tagging

At the Klosterfoss hydroelectric power plant , 62 Atlantic salmon (33 males and 29 females) and 38 sea trout (10 males and 28 females) were captured ascending the fish ladder and tagged with ATS radio-tags. None of these salmon were from the stocked population in the upper watershed. This was done in three separate rounds in July, August and September. The rounds were spread out to allow for more precise tracking and to include fish arriving at Klosterfoss at different times in the upstream migration period, which spreads across these months. Most of the fish were captured by closing the fish ladder the day before tagging; the resulting standing fish were netted and placed in a holding tank with circulated water from the river. Some fish were also caught just below the dam by experienced anglers from the local sportfishing chapter, as few fish were attempting to pass through the ladder. Fish were held in the holding tank for up to two days before being placed in an oxygenated anesthetic bath. The anesthetic used was benzocaine in a concentration ranging from 50-100 mg/L. Individual fish remained in the anesthetic bath until their equilibrium was lost, indicating that they were properly anesthetized, from 1:50 to 5:00 minutes. They were then sexed, photographed, and measured before being placed in a specially designed, V-shaped, adjustable case, where the fish were kept upside down, with their heads and gills in flowing, anesthetized water (Figure 5a). A small incision was made in the ventral body cavity of the fish, 15-20 mm long. The transmitter (F1800, Advanced Telemetry Systems, ATS, USA) was inserted into the incision, while the whip antenna was led through another hole in the ventral area, pierced with a hollow needle. The incision was closed with two to three separate sutures with silk thread. After the surgery was completed, the fish were taken to another holding tank and watched closely until they recovered. Once they could swim normally (0:40 -4:30 min), they were released just upstream of the dam using a carrying-bag.

2.3 Tracking the radio-tagged salmon and trout

ATS transmitters were used for all fish in this study. These transmitters send a frequency of 142.242 - 142.442 Mhz, with unique codes allowing for multiple fish to send signals on the same frequency. Tracking occurred through a combination of manual tracking and four permanently mounted stationary receivers (model 4500C). The stationary receiver placement is shown in Figure 1. The receiver at the mouth of the Falkumelva, shown as “Båthavna” in Figure 1 was placed there to detect fish which passed the mouth and swam up the main river. The receiver just upstream of the mouth of the Falkumelva at Slippen was placed to detect fish which swam up that tributary. The direction of movement was identified using two antennae at this location. At Skotfoss receivers were placed both at the tunnel outlet of the hydropower plant and in and above the fish ladder itself. The two antennae at the fish ladder helped identify the difference between fish which actually swam up the ladder, fish which were in the ladder, but did not swim all the way up, and fish which were holding just below the ladder. Stationary receivers were deployed from June 5, 2019, before the first fish were tagged. The stationary receivers were able to track fish up to 1 km from location, while manual tracking was precise between 25-400 m. Manual tracking was accomplished using either a car-mounted dipole antenna or a handheld Yagi-antenna connected to an ATS receiver (model R4500C).

Tracking of the entire anadromous-available watershed above Klosterfoss occurred every other day from July 5 through December 18. Below Klosterfoss, however, the water was too briny for the radio signal to be heard well, so only a few attempts were made to track in that area. Most of the tracking was done from using the car-mounted antenna, but around Hjellevannet and along the Farelva, the handheld antenna was often used for better accuracy. Between October 19 and November 18, the intensive spawning time, tracking of a selection of the fish four times a day, every six days, occurred. The four shifts were categorized as morning (6-12), afternoon (12-18), evening (18-24), and night (24-6) (Figure 5f). This tracking was done to better quantify the time the salmon spent in known spawning areas. The chosen salmon in the Falkumelva had been tracked in and around the spawning areas before the intensive period began and the chosen salmon in Farelva had been observed either at the tunnel outlet or below the fish ladder at Skotfoss. The intensively tracked fish (hereafter referred to as the IT group) were tracked to within 50 m, where possible.

The tracked salmon and trout first had their positions placed on paper maps, then entered onto a newly developed app from the Norwegian Institute of Nature Research (NINA). This allowed for the data to be shared between all the relevant parties. The intensive spawning period tracking went straight to the app, instead of the paper maps.

2.4 Spawning Sites

The entirety of the river from the tailrace at Skotfoss to Vadrette, just up from the Elstrøm bridge, was investigated in an earlier study (Heggenes and Dokk 1995). At Grøtsund, the water flow speed and the substrate was observed to be moderately favorable and there were five small redds. Downstream at Vadrette the water flow speed was slower and the substrate size was smaller and more favorable (Figure 4C). There were 18 large redds observed across the river at Vadrette. This is considered the best place for spawning in the Farelva (Heggenes and Dokk 1995).

On the Falkumelva the investigation of active spawning areas was carried out during this project. The length of the river was walked on the following days at the end of the spawning period days: November 6, 12, 17, 18, 27, and 30. Redds appear lighter than the surrounding area because the movement generated by the female salmon as she creates the redd shifts fine materials downstream (Wollebæk et al. 2008; Pedley 2018). The substrate in the area becomes more well sorted than the area around it, and in streams with uniform substrate, the characteristic build-up of gravel upstream of the redd, with trailing upturned gravel downstream will be apparent (Pedley 2018). These characteristics are typical of new redds created during the spawning time and were used to identify spawning sites (Fossum and Løvenskiold) in the Farelva and Falkumelva (Figure 4B).

2.5 Other Sources of Data

The Skotfoss and Klosterfoss fish ladders are both equipped with fish counters and video monitoring of the fishway. These are monitored by riverwatchdaily.is and the Skien sportfishing chapter. All fish that successfully pass the fish ladder are recorded. Water flow data for both of the hydropower plants were also made available to us (pers.comm Sverre Revhaug). Temperature data from Fossum and Skotfoss was taken with submerged loggers. Temperature data was also used from the fish counter online data [riverwatchdaily.is].

2.6 Data Analysis

All statistical analysis was done using R, version 3.6.2. Analysis of salmon “nearness” to the spawning areas was computed using ArcMap 10.7.1. Variation in arithmetic mean is reported as standard deviation.

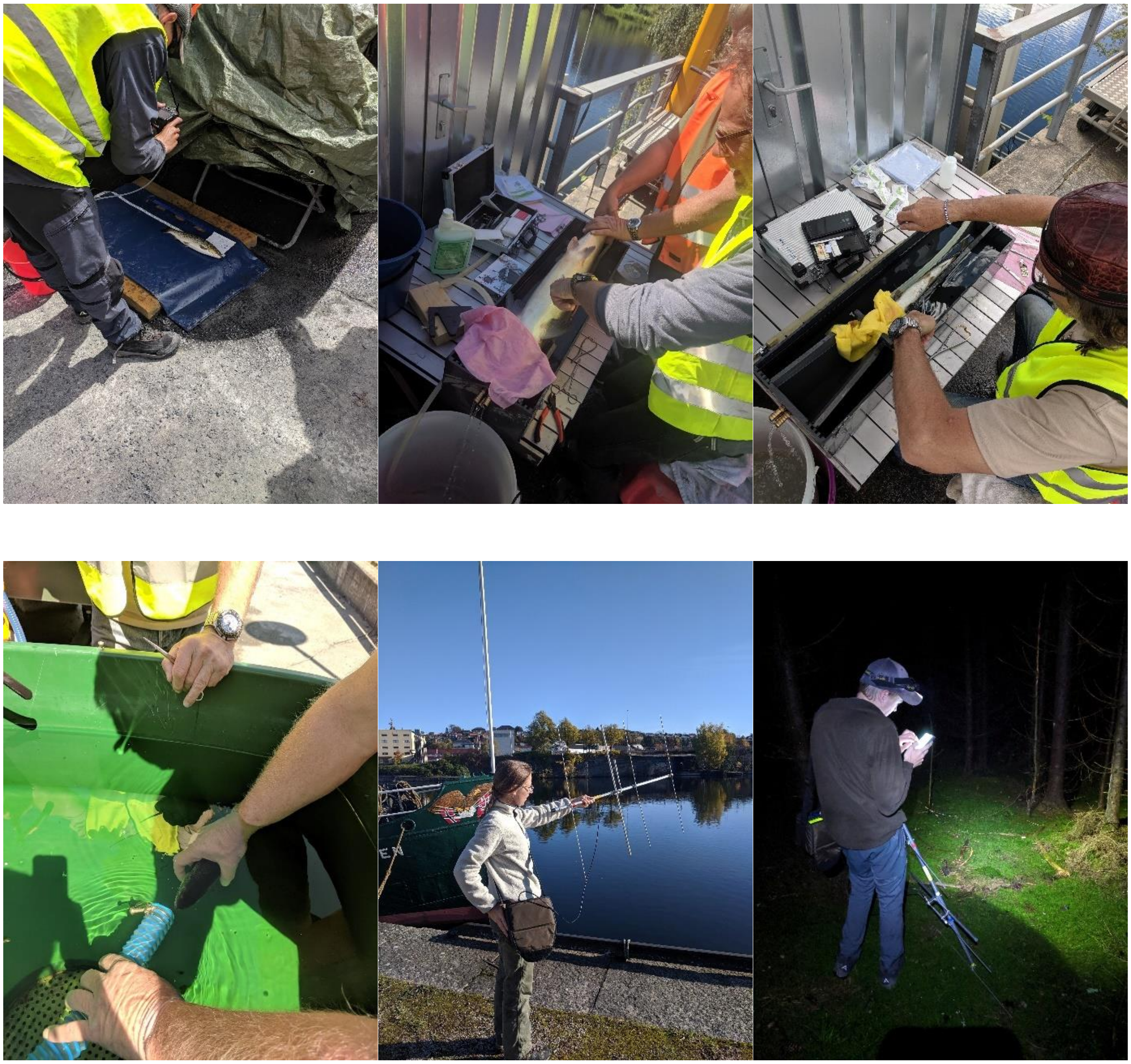

Figure 5. a) Photographing fish after anaesthetization, b-c) inserting the tracking tag in a large salmon, and a small trout, d) monitoring the recovery process, e) manual tracking in the city of Skien, f) manual tracking in the dark during the intensive tracking/spawning period.

2 Results

Altogether, 5,516 manual tracking observations and over 371, 000 observations from the stationary receivers of 62 adult Atlantic salmon were used in this study. The positions are spread geographically across the available anadromous habitat in the Skien watershed and temporally from July through December. Tagging was completed in July, August, and September, and few fish were entering the Klosterfoss fish ladder by the beginning of September. One of the salmon was found dead near Klosterfoss and one salmon was caught by an angler in August, so statistical analysis uses a sample size of 60 salmon.

3.1 Water flow and temperature

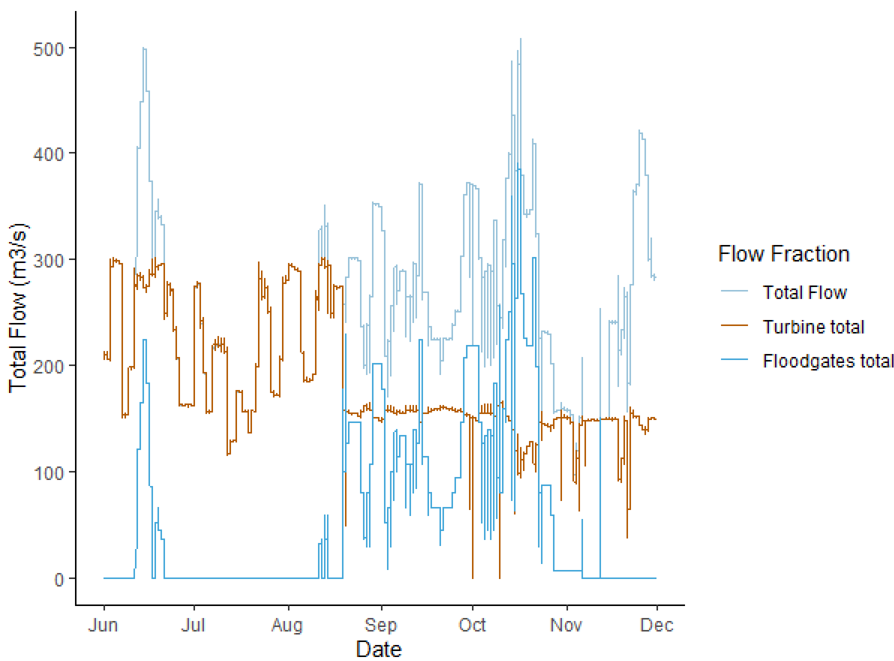

Figure 6. Plot of flow volume from the Skotfoss hydroelectric power plant and dam 280 m^3/s is the maximum amount of water the plant can handle. However, the floodgates can open to allow more water into the Farelva.

The average volume of water released through the Skotfoss hydroelectric power plant in July was 198.9 ± 50.5 m^3/sec, in August was 213.8 ± 61.9 m^3/sec and in September was 156.6 ± 5.97 m^3/sec. The floodgates were open the most in the month of October, with an average of 150.26

± 99.3 m^3/sec. The peak combined flow was in late October and then dropped sharply in early November. The water temperature peaked at the end of July and remained relatively constant for the rest of the migration season, before dropping significantly before the spawning season (Figure 7 & 9).

The tributary Falkumelva is much smaller than the main branch, Farelva and this, along with its length and steeper gradient, causes the water temperature to be cooler. This may help to make it a more favorable spawning area.

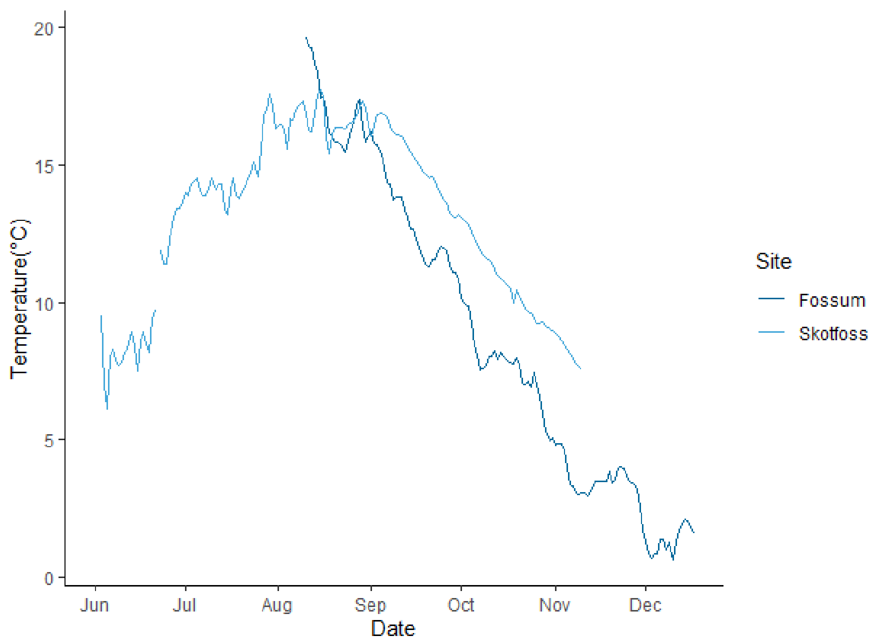

Figure 7. Plot of water temperatures at Skotfoss and in the spawning area known as Fossum on the Falkumelva branch.

3.2 Passage of the Skotfoss Fish Ladder

3.2.1 Length Selectivity

According to the Skotfoss fish counter, 919 salmon passed the ladder from July 1 to November 30 [riverwatchdaily.is]. Of these, 229 were classified as small, 690 were medium, and none were large as shown in Figure 6 (small <45 cm, 45> medium < 120 cm, and large >120 cm). A steady amount of migration up the ladder occurred through July, but in August, the passage occurred in waves, as seen in Figure 8-9. Passage of the Skotfoss fish ladder stopped almost entirely by November (Figure 8 and 9). Passage of the fish ladder at Klosterfoss ended almost completely by October (Figure 10). There is no correlation between the flow of water from the floodgates at Skotfoss and the count of fish ascending the ladder on any given day (Kendall's rank correlation, Z=-4.47, p-value=7.66×10^{-6} , tau=-0.27; Figure 8). There is no correlation between the flow of water at the tunnel outlet of the hydropower plant and the count of fish ascending the ladder (Kendall's rank correlation, Z=3.14, p-value=0.0016, tau=0.177).

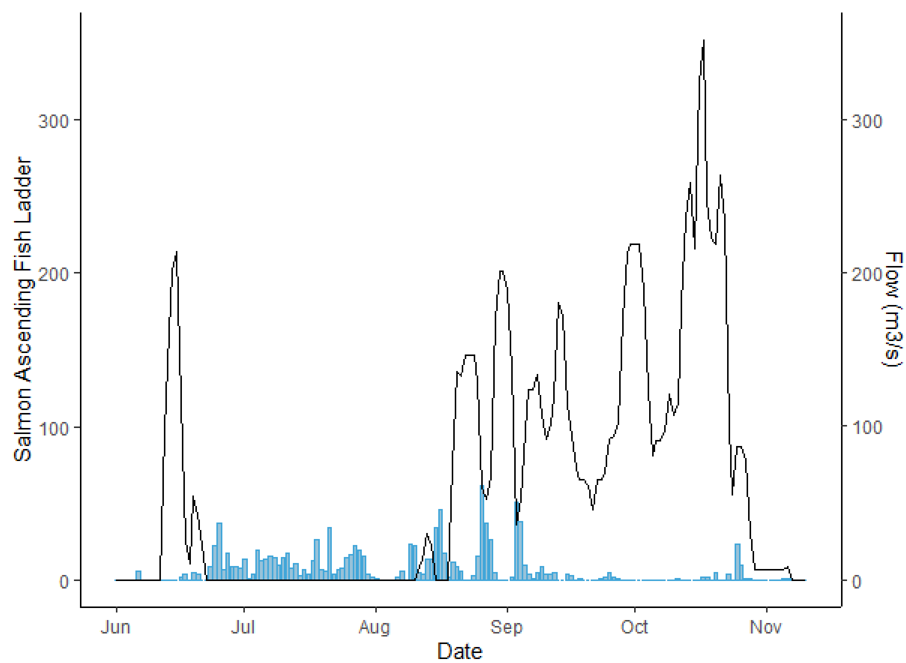

Figure 8. Plot of salmon ascending the fish ladder at Skotfoss throughout the study period (columns, left-axis, with the flow over the floodgate, near the fish ladder (line, right-axis). Counts of salmon taken from the fish counter at Skotfoss [riverwatchdaily.is].

There is a weak correlation between the temperature measured at Skotfoss and the number of fish ascending Skotfoss on a daily basis (Kendall's rank correlation, Z=6.091, p-value=1.23×10^{-9}, tau=0.346; Figure 9).

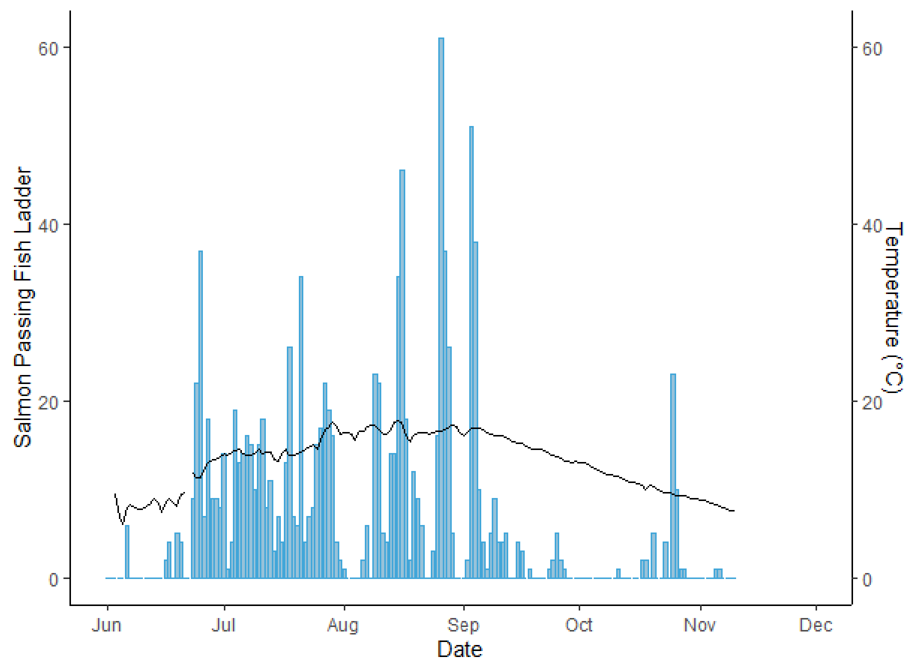

Figure 9. Plot of salmon ascending the fish ladder at Skotfoss throughout the study period (columns, left-axis) with the water temperature at Skotfoss (line, right-axis). Counts of salmon taken from the fish counter at Skotfoss [riverwatchdaily.is].

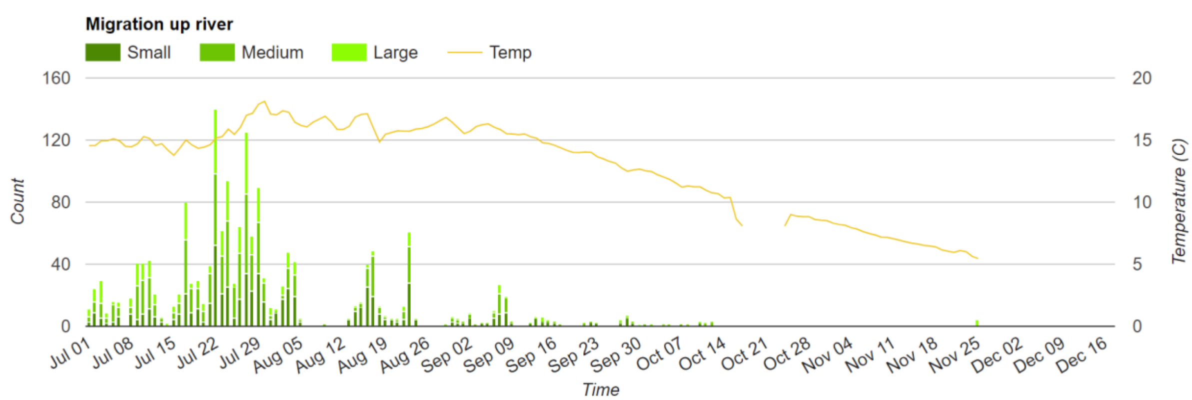

Figure 10. Histogram of all fish which were recorded successfully ascending the fish ladder at Klosterfoss [riverwatchdaily.is]. There is no differentiation between species at the Klosterfoss fish counter.

Salmon that passed the fish ladder at Skotfoss were bimodal in length, with a peak at 50 cm and 70 cm (Figure 12). The lengths of salmon that ascended Klosterfoss are also somewhat bimodal.

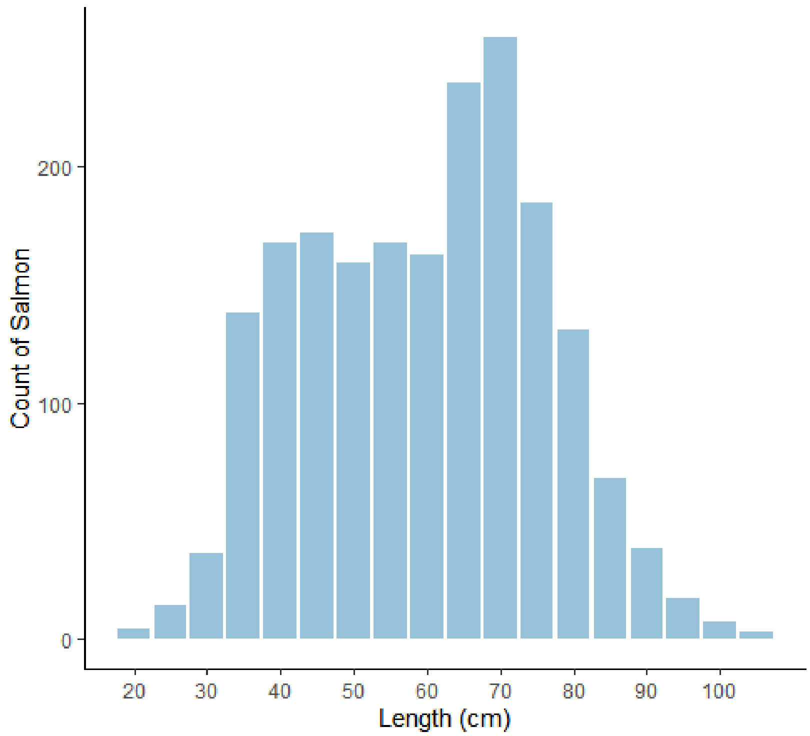

Figure 11. Histogram of lengths of all fish observed by the fish counter at the fish ladder at Klosterfoss during the upstream migration period (N=1966). Includes anadromous sea trout.

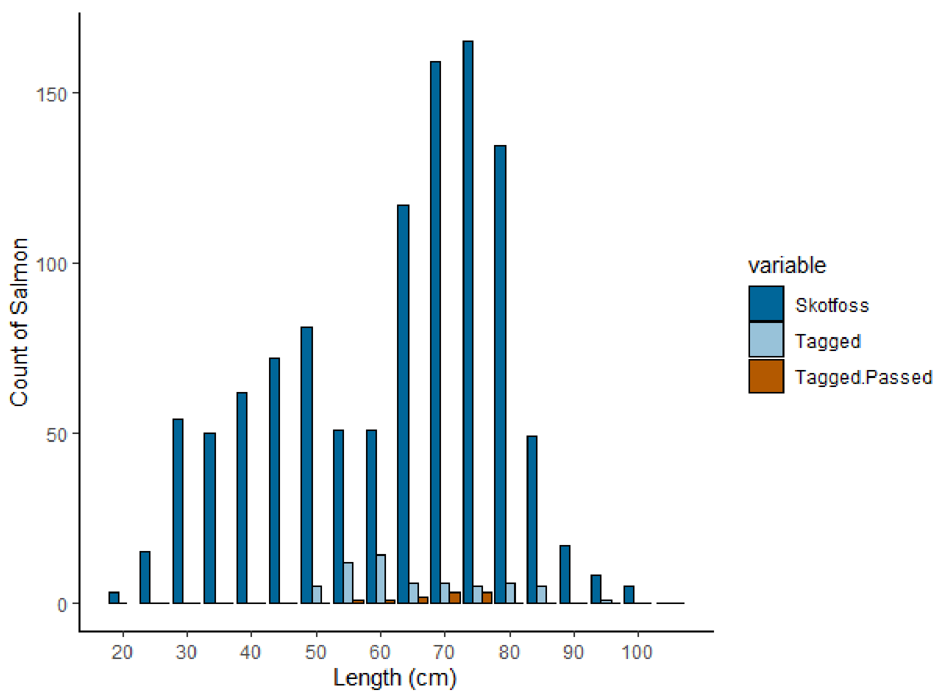

Figure 12. Histogram of lengths of all salmon which were observed to pass the Skotfoss fish ladder by the fish counter, all of the salmon tagged in this study, and all of the salmon tagged in this study which ascended the Skotfoss ladder and swam into Norsjø. ($n_{skotfoss}$=1094, n_{tagged}=60, $n_{tag.passed}$=10)

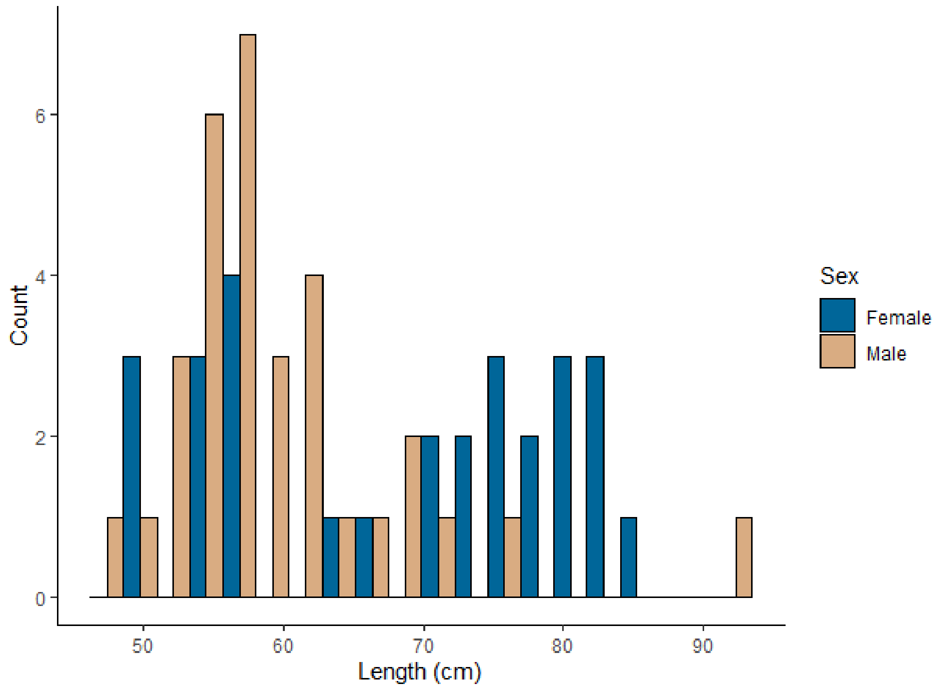

Figure 13. Histogram of lengths of all salmon tagged in this project. (n_{fem}=28, n_{male}=32)

Overall, 63% of all tagged salmon were observed by the receiver at the tunnel outlet at Skotfoss over the course of the study and 26% of the salmon which approached Skotfoss eventually ascended the fish ladder. All but two of the salmon observed at the tunnel outlet were also observed at the fish ladder. The mean body length of all salmon tagged (N=60) was 63.8 ±11.1 (Figure 12). Female salmon were significantly longer than male salmon (Wilcoxon rank sum test, W=627.5, p-value = 0.0079; Figure 13). Tagged salmon that successfully ascended the fish ladder at Skotfoss and swam into Norsjø (n=10) had a mean body length of 66 ± 6.8 cm. Salmon which approached the tunnel outlet but did not ascend the fish ladder had a mean body length of 63 ± 10.5 cm, and salmon which did not approach the dam at all had a mean body size of 64 ± 13.2 cm, all shown in Figure 11. Comparisons of the length frequency data from the two fish counters, all the of tagged salmon, and the tagged salmon which ascended Skotfoss were done with Kolmagarov-Smirnoff tests and are shown in Table 1. The Skotfoss and Klosterfoss length frequencies are not significantly different (p-value=0.13). The length distribution of all tagged fish was found to be significantly different than both the Klosterfoss and Skotfoss distributions. Interestingly, the salmon that were tagged and ascended Skotfoss had a significantly different length distribution that the length distribution noted by the fish counter at Skotfoss. All K-S tests performed were with ties, which may cause the p-value to be inaccurate.

Table 1. Results of the K-S tests between the four different frequency distributions of length of salmon in the Skienselva. The Klosterfoss data includes the lengths of sea trout which passed the fish counter.

x	y	Two-tailed p-value
Klosterfoss total	All Tagged	0.0002
Skotfoss total	All Tagged	0.0007
Tagged & Passed Skotfoss	All Tagged	0.0029
Klosterfoss total	Skotfoss total	0.13
Tagged & Passed Skotfoss	Skotfoss total	1.99×10^{6}

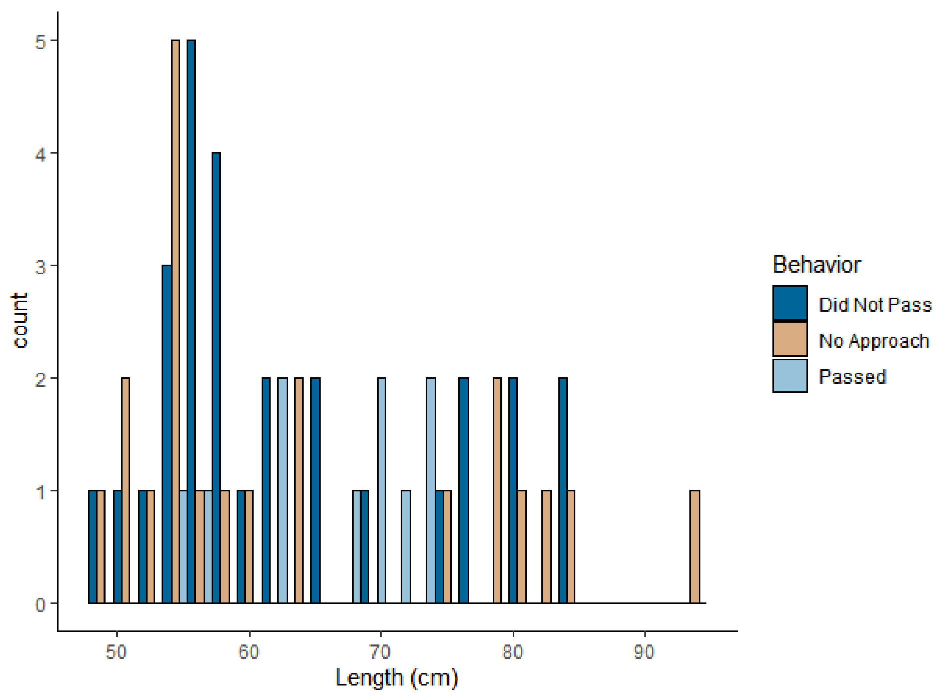

Figure 14. Histogram of the lengths of tagged salmon grouped by their behavior at Skotfoss, whether they: successfully ascended the fish ladder, did not attempt to ascend the ladder or attempted and failed, or did not approach Skotfoss at all. (n=28, n=22, n=10)

Based on only the tagged data, using two other non-parametric tests, there was not a significant difference of body lengths between the three different behavior groups (Kruskal-

Wallis rank-sum, df=2, chi-squared = 1.0439, p=0.593). There was also no significant difference between the lengths of fish which successfully ascended the ladder and those that did not, regardless of whether they approached the dam or not (two sample Wilcoxon rank-sum test, W=197.5, p-value=.3417, ties error present). There was a narrower range of body lengths in the salmon that passed the fish ladder. Taking into account the results of the K-S tests, the Wilcoxon signed rank test, and the Kruskal-Wallis test, there is nuance to whether or not the fish ladder at Skotfoss is size selective.

3.2.2 Other Factors

As can be seen in Figure 15, the majority of tagged salmon were observed by the tunnel outlet receiver at Skotfoss but did not successfully ascend the fish ladder. The 10 fish which did are shown in Table 2, along with the number of other tagged salmon also detected by the fish ladder receiver at that time. Most of the salmon were tagged in the month of August (n=35), and the greatest amount of salmon that approached the tunnel outlet at Skotfoss, but did not ascend the fish ladder was in that month. No fish tagged in the month of September (n=11) successfully passed the fish ladder. Furthermore, the majority of salmon tagged in September were never observed by the receiver at the Skotfoss tunnel outlet. The month with the highest number of salmon that ascended the ladder was July, and thus this group made up the largest proportion of salmon in that month, six out of 13 tagged. This is true even though more fish were tagged in August. Only four of the 35 fish tagged in August passed the ladder into Norsjø.

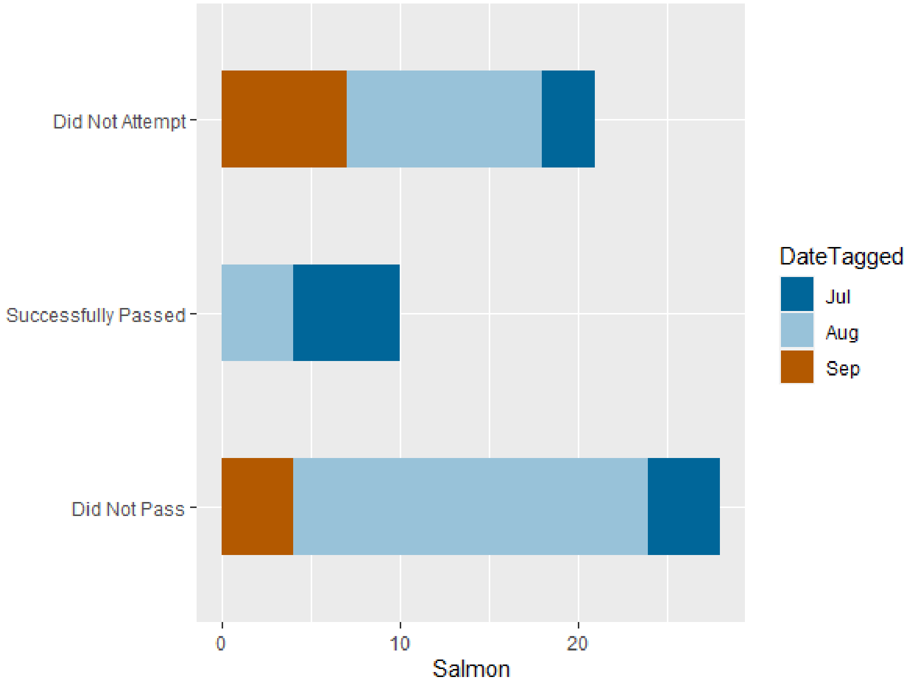

Figure 15. Stacked bar graph of the month tagged and the three behaviors: Were never observed at Skotfoss, ascended the ladder, or were observed at the tunnel outlet at Skotfoss but did not ascend the ladder. Dates for tagging were not random or evenly distributed. The greatest number of salmon were tagged in August(n_{aug}=35, n_{jul}=13, n_{sep}=11).

Table 2. Showing the number of fish present below the ladder, as observed by the stationary receiver there, when the 10 tagged fish were recorded swimming up the fish ladder at Skotfoss.

Frequency	Code	Date Ascended Skotfoss Ladder	Other fish present
343	75	7/17/2019	5
343	8	7/21/2019	4
273	11	7/28/2019	4
242	13	7/29/2019	4
302	13	8/16/2019	9
282	75	8/27/2019	12
252	13	8/28/2019	10
302	8	9/4/2019	6
273	8	9/13/2019	8
322	5	10/19/2019	4

The salmon took an average of 10 days to reach Skotfoss from the tagging site, Klosterfoss, with a minimum of a just under four hours and a maximum of 67 days. This results in speeds of .0031 km/h – 1.289 km/h. There is a moderate correlation between the date of tagging and the length of time the salmon took to get to Skotfoss (Pearson's correlation coef.= 0.38).

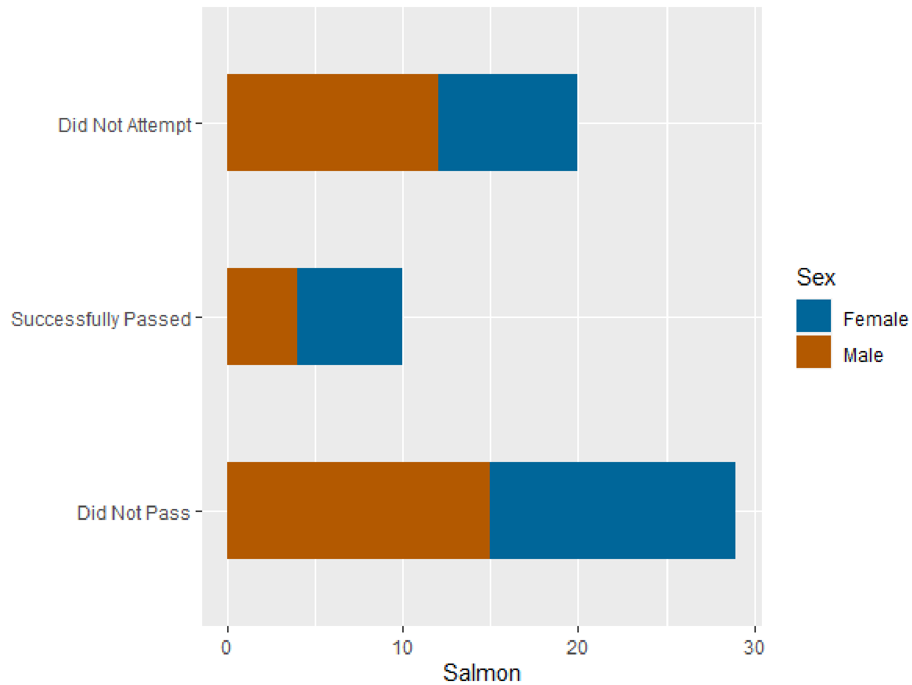

Figure 16. Stacked bar graph of fraction of male and female salmon and whether or not they approached the tunnel outlet at Skotfoss and whether they passed the Skotfoss fish ladder.

Approximately equal amounts of male and female salmon were found in each of the three groups (Figure 16). Slightly more tagged female salmon successfully passed into Norsjø: six females and four males.

Salmon remained for an average of 9.5 days (min=1, max=41 days) on their first visit at the tailrace (n=38) and 6.6 ± 8.6 days at (min=1, max=32) the fish ladder (n=36) of the hydropower plant at Skotfoss. Fish that were observed for less than 24 hours are classified as one day. Of the salmon that did not approach Skotfoss (n=22), eight swam up Falkumelva and were observed there by manual tracking. The rest remained in either Hjellevannet or the Farelva.

There were 38 salmon which approached and were recorded by the receiver at the tailrace. A majority of these 38 (n=29), left and returned at least once. On average these 29 returned three times (min=1, max=10, median=2) to the tailrace and their trips away from the tailrace lasted 11 days, (min=1, max=98, median=4). Most fish made 1-2 trips, and the average was pulled up by seven fish making 5 or more trips. Although the data suggests fish ascended the Skotfoss fish ladder before making many returns (Figure 17), there was a lot of variation in the data, and there was not a significant difference between number of returns and whether or not the salmon passed the fish ladder(two sample Wilcoxon rank-sum, W=96.5, p-value=0.31, ties error present).

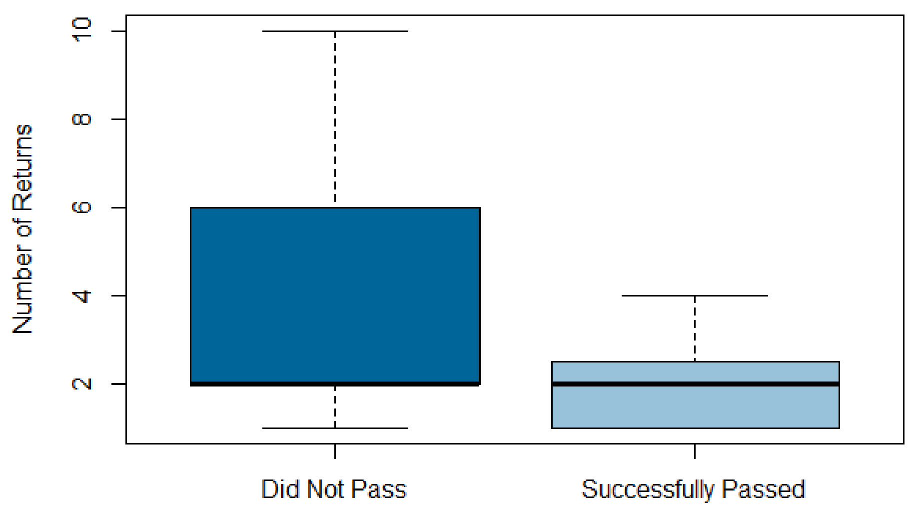

Figure 17. Boxplot of the count of returns salmon made to the Skotfoss tunnel outlet area comparing fish which did go on to successfully pass the fish ladder and those that did not.

The length of the initial stay at the outlet of the hydropower station was significantly longer for fish which successfully ascended the fish ladder than fish that did not. (two-sample Wilcoxon rank-sum, W=214, p-value=0.013, ties error present).

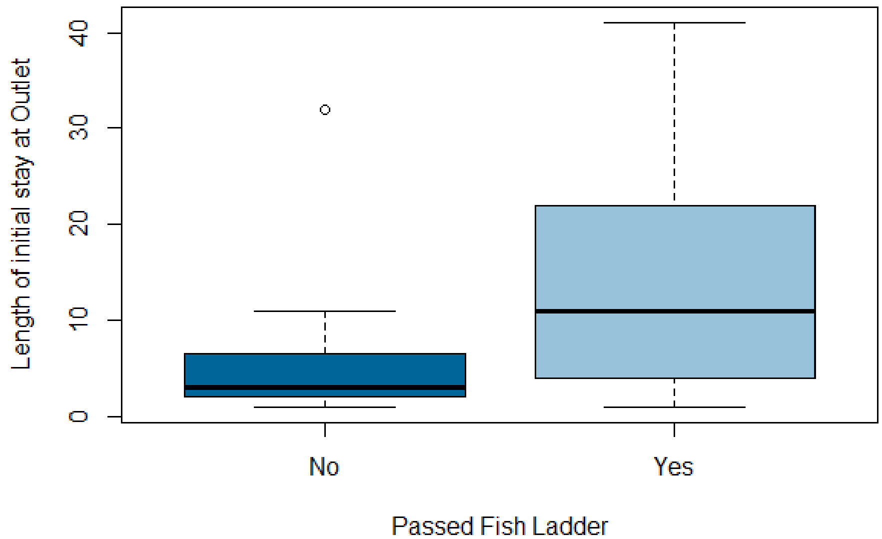

Figure 18. Boxplot comparing the length of the initial stay at the tunnel outlet at Skotfoss, in days, of salmon that eventually passed the fish ladder and those that did not.

3.2 Intensively tracked salmon at Skotfoss

Table 3. Total length and sex of the 19 Atlantic salmon in the IT group.

Frequency	Code	Length (cm)	Sex
242	5	56	Female
252	1	80	Female
273	1	59	Male
273	3	56	Male
273	4	81	Female
273	5	78	Female
273	9	76	Female
282	1	58	Male
282	5	76	Female
282	13	82	Female
302	2	61	Male
302	4	56	Male
302	9	66	Male
302	11	93	Male
302	75	55	Male
322	4	80	Female
322	5	69	Male
343	2	64	Male
343	5	55	Male

The IT salmon were tracked through the spawning period (Oct. 19- Nov. 18), four times a day, every six days, resulting in 387 observation points. The salmon were tracked mostly within and around the four spawning areas: two in the Farelva, and two in the Falkumelva. None of these fish successfully ascended the fish ladder. The lengths and sex are shown in Table 3.

3.2.3 Behavior at the Tailrace and below the Fish Ladder

Out of the 19 IT group salmon, 13 were observed by the stationary receiver at the tailrace of the hydroelectric plant. Only one salmon from the IT group was detected by the receiver at the tunnel outlet but not at the fish ladder. Of these 13 salmon, three were observed through manual tracking within 50 meters of the downstream spawning areas before the stationary receiver at the tunnel outlet detected them. However, considering that the river itself is only 100 meters wide in some places, these fish may have just been passing through.

Nine out of the 13 returned to the tailrace a second time after they were observed in spawning areas for an average of 3.1 ± 2.8 days. Only two salmon (302-2 and 273-9) did this within the spawning period (2, 1 days). These nine only visited the nearest spawning areas in the mainstem Farelva branch (Vadrette and Grøtsund), 1.5-3 km downstream of the dam, neglecting the spawning areas in the tributary Falkumelva 9-9.5 m away (Figure 4). Six of the nine which returned to the tailrace visited both Vadrette and Grøtsund spawning sites in the Farelva. Two salmon of the these nine returned to the tailrace in between visiting the two spawning areas and did not return after that.

As an anomalous example of a salmon visiting Skotfoss, then deciding to spawn in Falkumelva, one small male (55 cm;302-75) approached the Skotfoss tunnel outlet on July 19, stayed for 6 days, then 10 days later was manually tracked near the spawning area on the Falkumelva known as Fossum (Figure 19), 3.8 km downstream and then 6 km upstream in this tributary, all before the spawning season began. During spawning season, however, this salmon was undetected within 75 meters of either of the known spawning areas in Falkumelva, he remained 4 km upstream of the spawning areas.

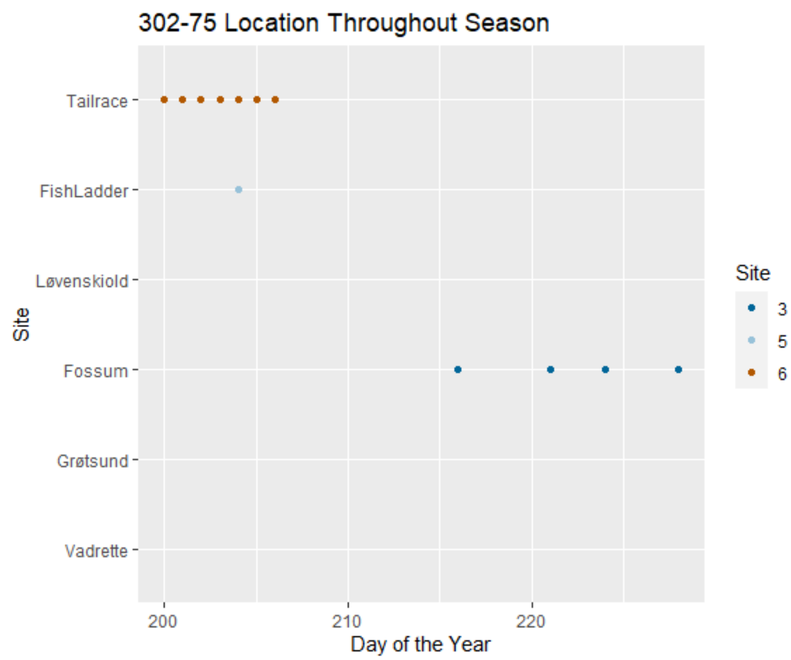

Figure 19. Plot of observations of an IT group salmon near either the fish ladder or the tailrace at Skotfoss, or within 50 meters of any four of the spawning areas. Atlantic salmon with tag 302-75 and the locations it was observed at either manually or by the stationary loggers throughout the season.

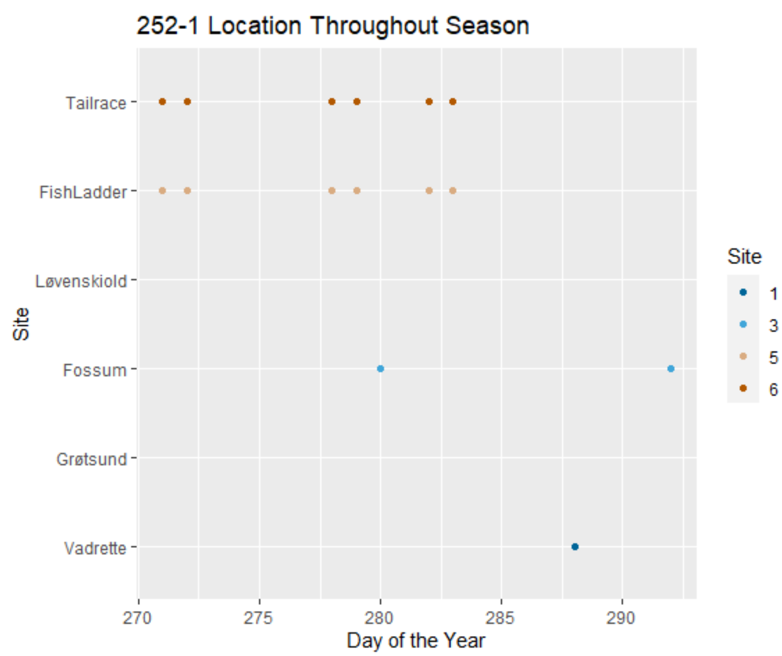

Figure 20. Plot of observations of an IT group salmon near either the fish ladder or the tailrace at Skotfoss, or within 50 meters of any four of the spawning areas. Atlantic salmon with tag 252-1 was unique among the intensively tracked fish.

One particular fish, a large female salmon (80 cm), made many long movements. After approaching the Skotfoss fish ladder early in the season, she was manually tracked at the Fossum spawning site, returned to Skotfoss, then to Grøtsund, but returned to Falkumelva again, at the end of the spawning season (Figure 20). This movement altogether is over 27 km beginning at Skotfoss. Including the journey from the initial tagging at Klosterfoss brings the distance to 31 km. She eventually settled just over 75 meters away from the Løvenskiold spawning area but was untracked after October 25.

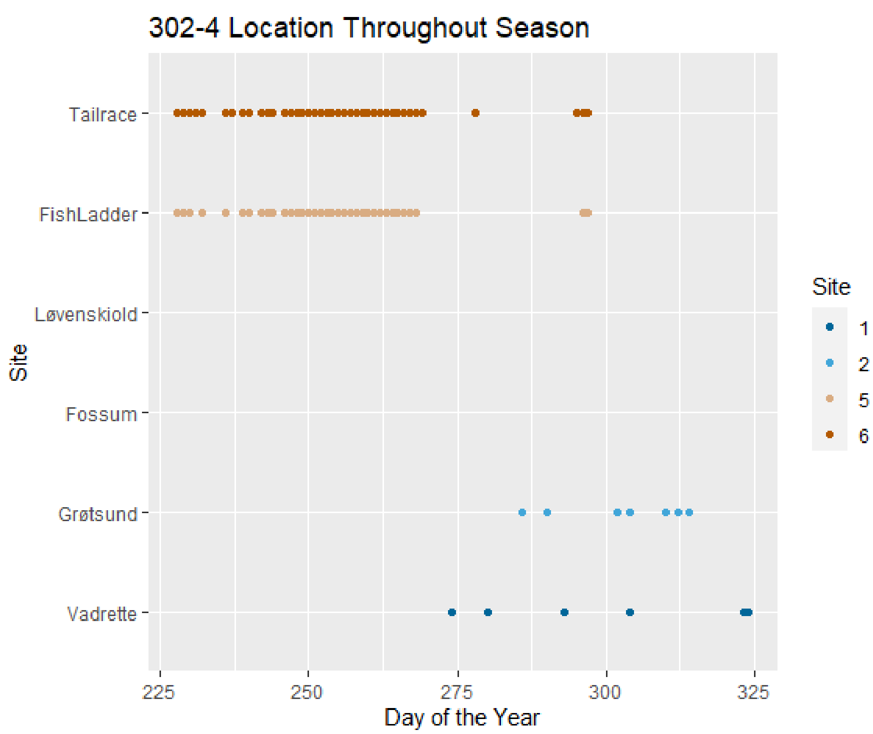

Figure 21. Plot of observations of an IT group salmon near either the fish ladder or the tailrace at Skotfoss, or within 50 meters of any four of the spawning areas. A small male salmon (56 cm).

The salmon tagged 302-4 rested at Skotfoss and was detected by both the tunnel outlet and fish ladder receivers from August 16 to September 26, but was undetected by either of the receivers at Skotfoss for four brief periods. In these periods, he was observed by manual tracking at points just downstream of the tunnel, but not near the spawning areas. After September 26, the salmon made many movements between the spawning sites in the Farelva

(1.5 and 3 km downstream) and the tunnel outlet and fish ladder (Figure 21). Eventually, 302-4 seemed to settle in Vadrette in November.

3.3 Spawning Site Nearness

The observation points of spawning site nearness were calculated using the "Near" tool in ArcGIS. Salmon within 50 and 75 m of the spawning sites throughout the entire tracking period (July 7-December 18) were identified. Of all the salmon tagged, 21 were observed at two or more spawning sites, one female was observed at three, and one male (302-11) was observed at all four. The average number of observations per fish, per site, was 9.1, however, the median was 4.5, because the majority were single observations. The most total observations of tagged salmon were at Fossum on the tributary branch, followed by Grøtsund on the main river branch (Figure 22).

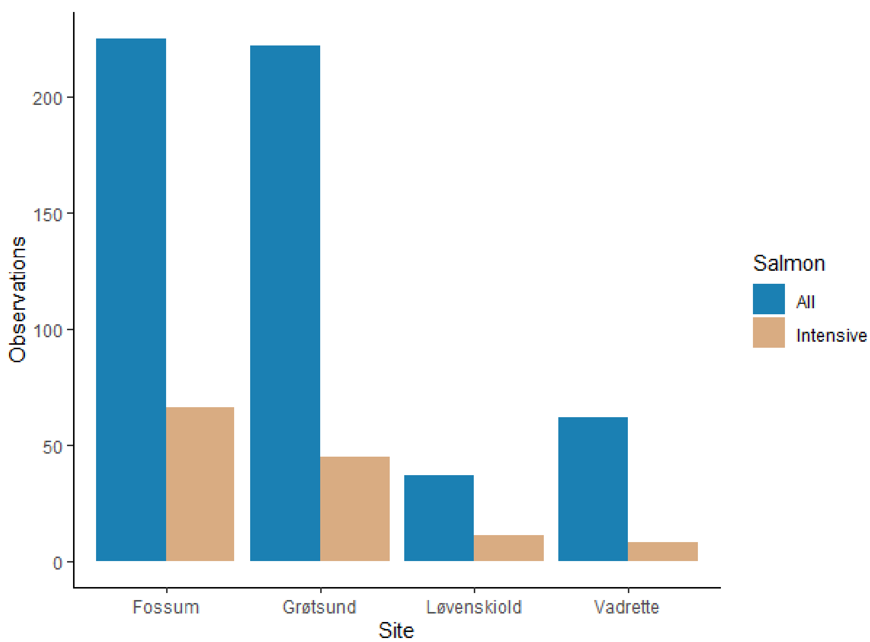

Figure 22. Bar plot of total count of observations at each site, with intensive tracking observations singled out.

3.3.1 All Tagged Salmon

There is a significant difference between the total number of observations per fish within 50 meters of Vadrette (mainstem, n=18, mean= 5.22± 10.3) and Fossum (tributary, n=11, mean = 20.54, ± 30.5;Pairwise Wilcoxon test, p-value =0.024, ties error present), and Vadrette and Grøtsund (mainstem, n=24, mean= 15± 33.7; Pairwise Wilcoxon test, p-value=0.024, ties error present). Fossum and Grøtsund had more total observations of tagged salmon within 50 meters than Vadrette (Kruskal-Wallis rank-sum, df=3, X^2 test statistic=11.12, p-value=0.01; Figure 23)). The fish which visited Vadrette spent less time there and/or returned fewer times than the fish which visited Fossum and Grøtsund spawning areas. These differences are repeated in the 75 meter near data as well, (Kruskal-Wallis rank-sum, X^2 test statistic= 13.49, df=3, p-value=.004; Figure 24)).

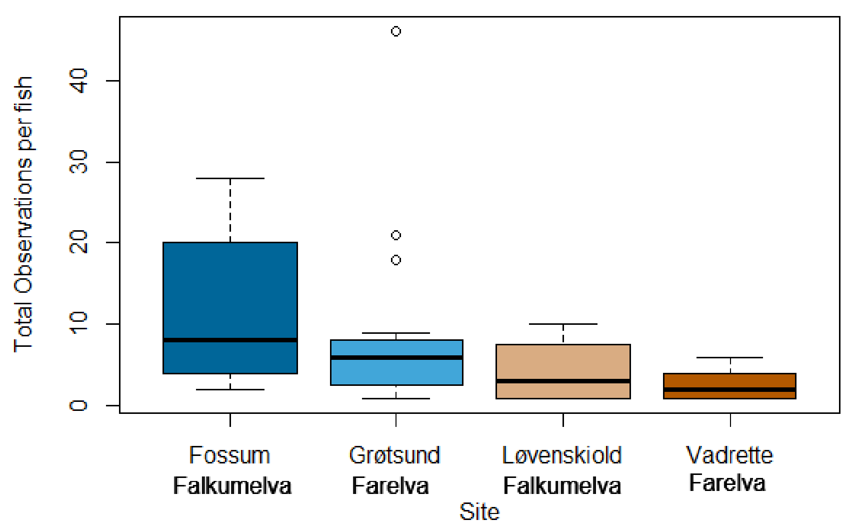

Figure 23. Boxplot of the total observations (both consecutive and nonconsecutive) of all salmon within 50 meters of each spawning site on the two river branches.

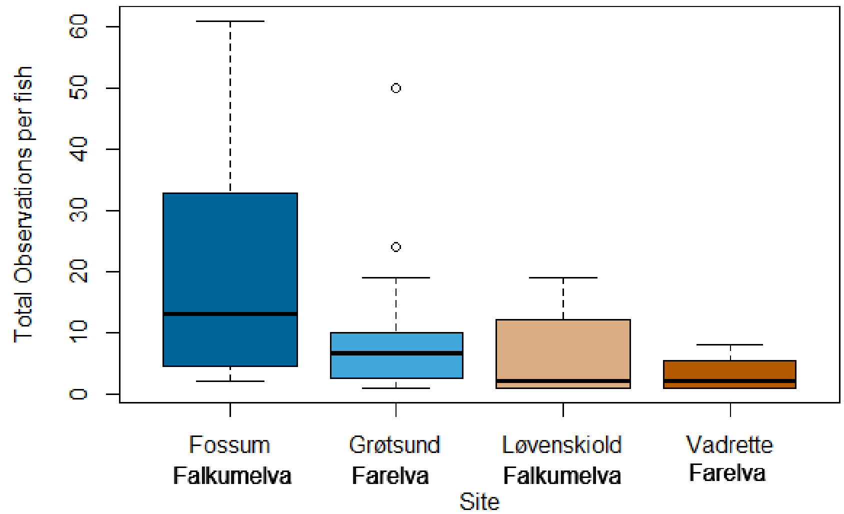

Figure 24. Boxplot of the total observations (both consecutive and non-consecutive) of all salmon within 75 meters of a spawning site for the entire season.

The arrival dates of salmon observed within 75 meters of the spawning sites were not significantly different (Kruskal-Wallis rank-sum test X^2=3.34, df=3, p-value=0.342). But as can be seen in Figure 25, Grøtsund and Vadrette have wider ranges than the others.

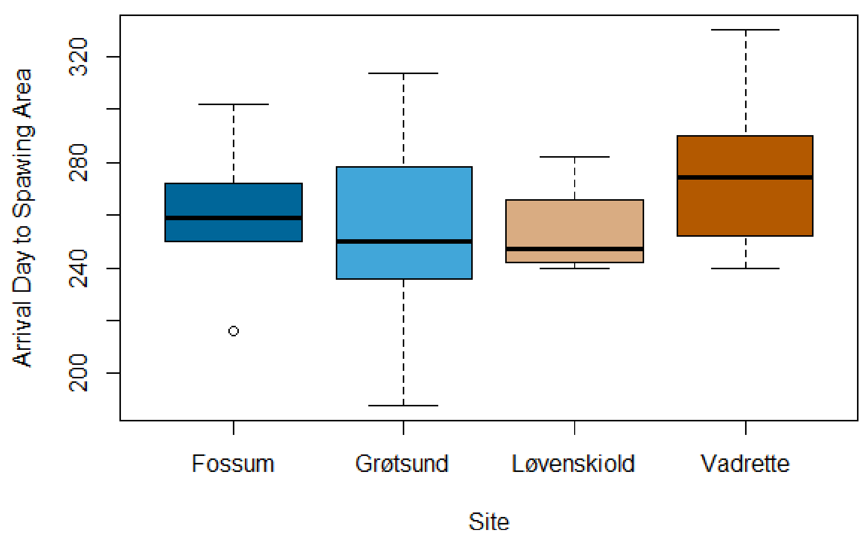

Figure 25. Boxplot of the arrival dates of all tagged salmon categorized by which spawning site which they were observed within 50 m of.

With a relaxed alpha, salmon spent significantly less time between their first and last sightings near the Vadrette spawning site (Kruskal-Wallis rank-sum, X^2=6.36, df=3, p-value=.095; Figure

26). Salmon may have left the spawning area in between their first and last sightings. The longest times were spent at Fossum and Grøtsund, though the two longest at Grøtsund are likely outliers.

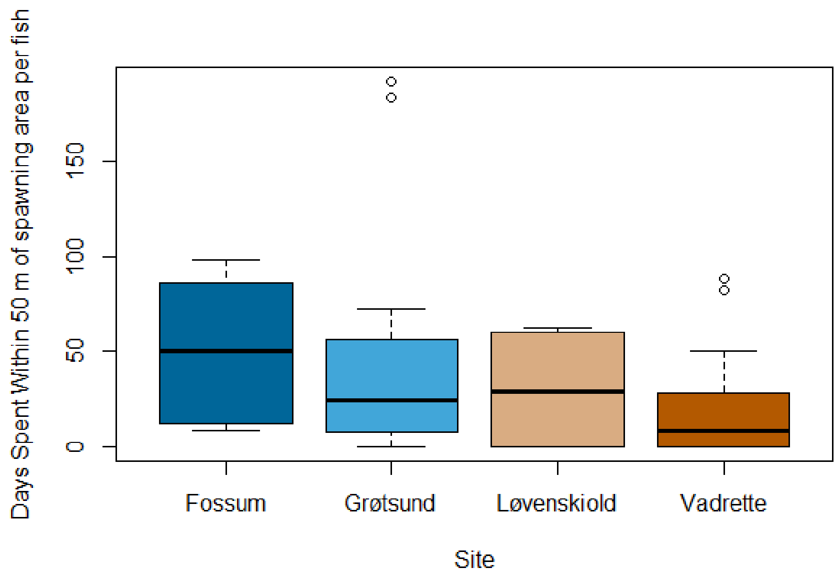

Figure 26. Boxplot of days between the first and last observations of salmon near each of the four spawning areas.

3.3.2 Intensively Tracked Group

The data below is from the days of intensive tracking during the spawning season only. Observations from regular days of tracking were not included.

There was not a significant difference between the total number of observations of the IT group salmon within 50 meters of the spawning sites in the tributary Falkumelva (n=8, mean=5.25± 4.2)and the mainstem Farelva (n=10, mean=4.9± 4.6) (two sample Wilcoxon rank-sum, df=2, W=42.5, p-value=.86) or among all spawning sites (Kruskal-Wallis rank-sum, df=3, X^2=1.24 , p-value=0.74; Figure 28). Neither was there a significant difference between the number of consecutive (2 or more in a row) observations of the IT group within 50 meters of the Falkumelva (n=8, mean=3.125± 3.7) and Farelva (n=10, mean=3.6±4.1) spawning sites (two sample Wilcoxon rank-sum,df=2, W=35.5, p-value=.71, ties error present) nor among all sites (Kruskal-Wallis rank-sum, df=3, p-value=.56; Figure 27). The values for salmon which were observed within 75 meters of a spawning sight were similarly non-significant (Figure 29).

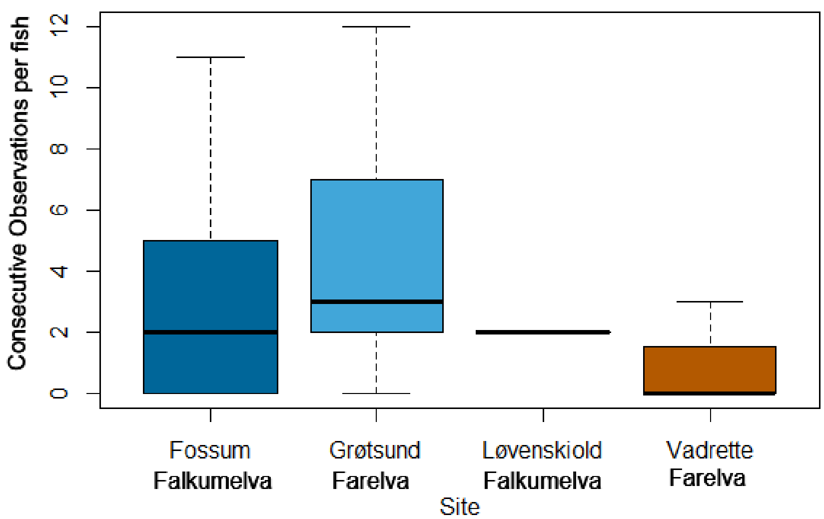

Figure 27. Boxplot of the number of consecutive (defined as two or more observations in a row) observations of the IT group within 50 meters of a spawning site on days of intensive tracking during the spawning season.

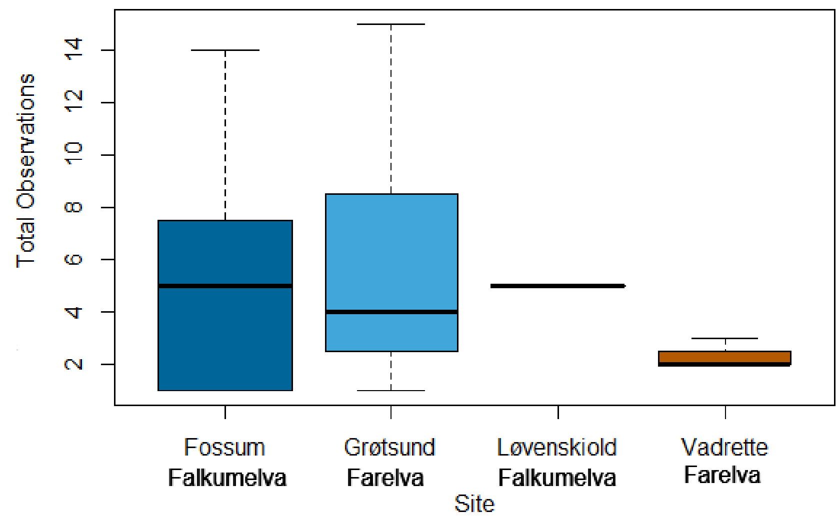

Figure 28. Total observations per fish, consecutive and non-consecutive, of IT group salmon near the four spawning sites on the two river branches, Falkumelva, the tributary branch, and Farelva, the main branch.

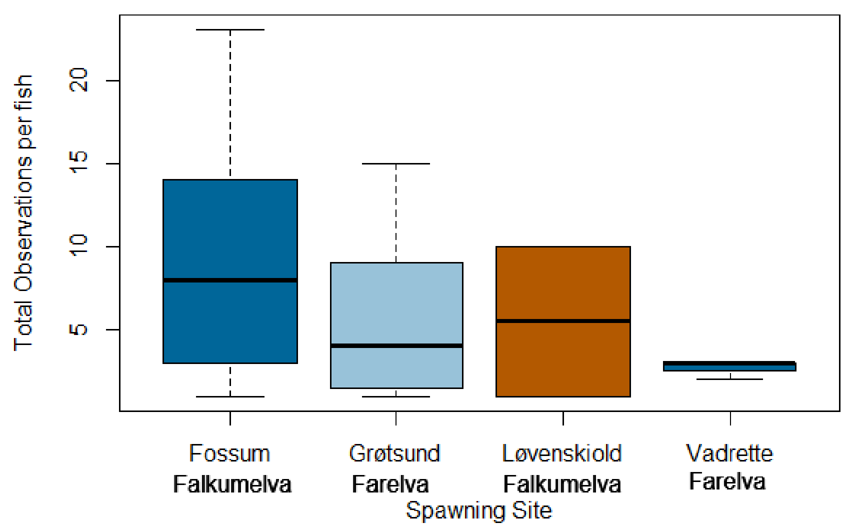

Figure 29. Boxplot of the total observations (both consecutive and non-consecutive) per IT group fish within 75 meters of a spawning area for the entire season.

There was not a significant difference between males (n=12, mean=5.1± 4.2) and females (n=6, mean=5.00±4.9) in the IT group in either total observations near spawning areas (two sample Wilcoxon rank-sum, p-value 0.77, ties present; Figure 30) or consecutive observations near spawning areas (males: mean=3.25± 3.6; females: mean=3.66± 4.5) (two sample Wilcoxon rank-sum, p-value= 0.96, ties present; Figure 31).

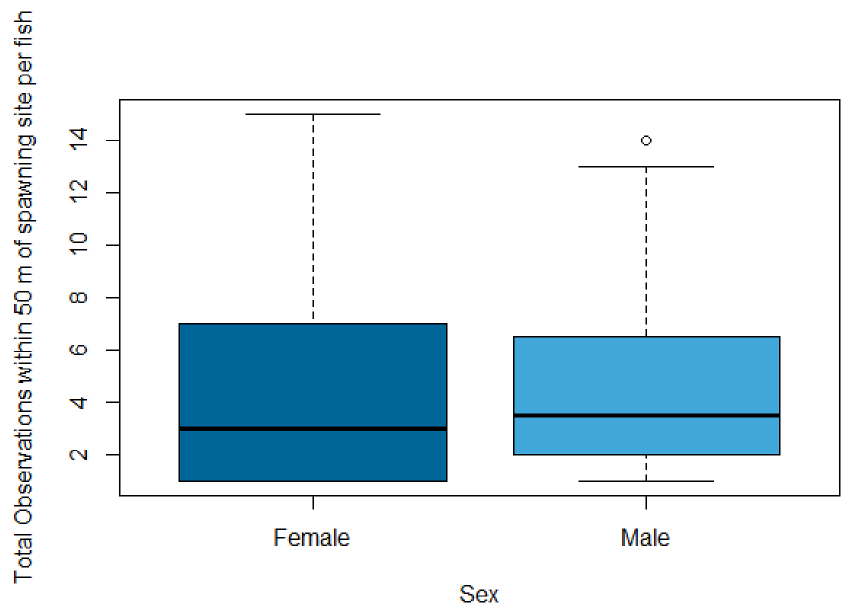

Figure 30. Boxplot of IT group; comparison of female and male fish total observations within 50 meters of a spawning area. No significant difference.

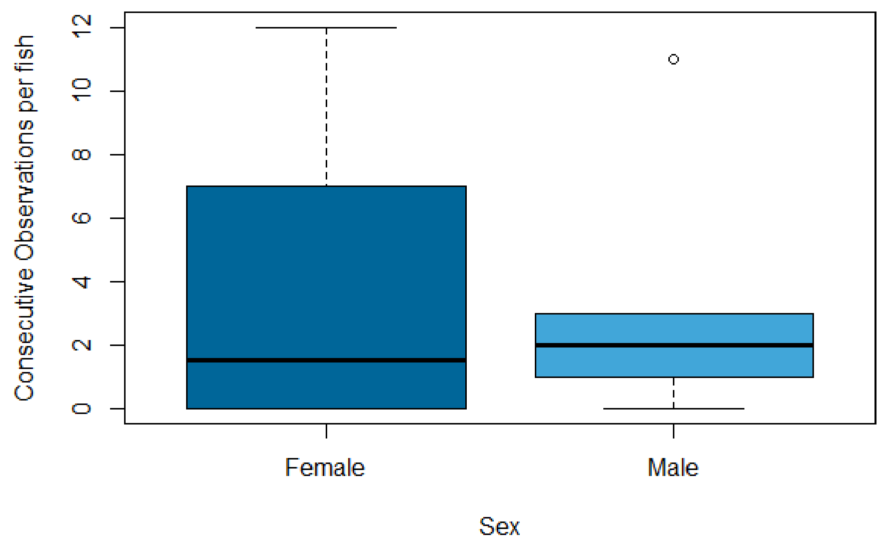

Figure 31. Boxplot of IT group; a comparison of female and male salmon observed for two or more consecutive rounds within 50 meters of the spawning area during the intensive tracking period. No significant difference.

4 Discussion

Most salmon (63%) in the Skienselva swam to the dam and power station at Skotfoss. However, the majority did not ascend the fish ladder (74%). Tagged salmon at the tailrace and fish ladder made on average three trips away from the ladder and some were tracked in spawning areas, mostly in the main river branch, with varying arrival times and stay lengths. Grøtsund spawning area had a much higher number of total observations and more observations per fish than Vadrette spawning site (Figure 22). Only four salmon approached the dam and then retreated downstream to the tributary Falkumelva to spawn. Depending on how we classify the erratic movements of salmon within the Farelva, the tunnel outlet could be viewed as simply part of the holding area of salmon that originate from the Grøtsund spawning area, or as "yo-yo" movements of indecisive salmon which wanted to continue upstream but were unable to do so. The results support that despite fish stocking in the upper reaches of the Skien watershed, in areas with larger spawning sites, the most used spawning sites are Grøtsund and Fossum, in the Farelva and Falkumelva. The fish ladder at Skotfoss is likely one of the reasons that the spawning sites in the upper watershed are used less than the sites below the dam. Size selectivity by the fish ladder may affect the demographics of the salmon that do ascend successfully to spawn in the Eidselva, Tinnåa, Bøelva, or Heddøla.

4.1 Arriving at the Dam

With later tag release dates, the time spent swimming up to Skotfoss increased generally, but the correlation is not strong, as was found in another study (Scruton et al. 2007). There is disagreement in the literature about the relationship between arrival time and other variables in the spawning migration of salmon, with some studies arguing that the further upstream salmon eventually spawn, the earlier they enter the river, and others finding no relationship between arrival time and migration distance (Thorstad et al. 1998). In the case of Skotfoss, salmon that arrive in the river early because their natal river is further from the sea may find themselves unable to get there. They then must choose whether to stay in the spawning areas available just downstream of Skotfoss or to explore other areas, such as Falkumelva. Especially if they choose to spawn at Vadrette or Grøtsund, they may find themselves competing for good redd sites with salmon for whom the Farelva is their natal river. These salmon could be better adapted to this area, and they may have stayed in the ocean for a longer period, as they did not need to migrate as far upstream to reach their natal river. On the other hand, earlier arrival times may be associated with a competitive advantage in access to spawning grounds or could be an effort on the part of the salmon to avoid unfavorable conditions such as warm water temperatures (Thorstad et al. 2008). Overall, the salmon which arrive early and eventually spawn in the Farelva have both advantages and disadvantages over salmon that arrive later.

4.2 Behavior at the Tailrace

The results from the stationary receivers at the Skotfoss power station outlet and the fish ladder are comparable in some ways to results from other studies of Atlantic salmon. For instance, depending on the study salmon have stayed, or gotten "stuck", at the outlet of hydropower stations anywhere from 0-71 days (median=20), 1-12 days, 1-22 days, 1-41 days (mean=19), .6-43 days (mean=23.7), a mean of 42 days, and a median of 12 days, (Rivinoja et al. 2001; Thorstad et al. 2003; Scruton et al. 2007; Lundqvist et al. 2008). For comparison, salmon at a natural waterfall stayed for 1-41 days (mean=19) below the falls before passing them (Johansen 2010). Salmon at Skotfoss stayed from 0-32 days, mean=7, but they were not confined to only the tunnel outlet area and swam between the area below the fish ladder and the tunnel outlet.

All but two of the salmon which approached the tunnel outlet or tailrace at Skotfoss, quickly approached the fish ladder and were observed by both receivers at the fish ladder and above the tunnel outlet while they stayed in the area. This could indicate either that the receivers ranges crossed, which is unlikely, or that the salmon swam between the tunnel outlet and the ladder at least once every day. If the latter is the case, then salmon at Skotfoss do not suffer from an inability to find the entrance to the fish ladder, and they do not remain "stuck" at the tunnel outlet, as has been the case in other studies.

The number and frequency of returns to the Skotfoss tailrace by salmon, on average three returns with 11 days in between, indicates a lot of movement and energy spent by fish after they arrive at this barrier. This agrees with Lundqvist et al (2007) and Rivinoja (2001) which both found that 40% of the salmon made at least 3 downstream movements. A study of salmon in Scotland also recorded results of descent downstream after time spent at the dam (Webb 1990). Their results indicated the possibility that recent arrivals at the dam are more likely to descend significantly further (10 kilometers) downstream than salmon which remain below the dam for longer periods. Since the distance downstream from Skotfoss to Klosterfoss is less than 10 km, the downstream distances are by necessity, shorter. It should also be considered that these are periods when the tag signals were lost as the salmon moved very far into the unscreened tunnel. Since fish that ascend the ladder can no longer make the back and forth movements, the significant difference in the number of returns between salmon that passed the ladder and salmon that didn't isn't surprising or novel. However, salmon which eventually ascended the fish ladder and swam in Norsjø also stayed longer at the tailrace before making their first trip back downstream (Figure 18). Other fish which approached the ladder, but left again quickly (mode=2 days), may have been “roaming” salmon in their search phase, but making erratic movements that are part of the search phase of the upstream migration (Økland et al. 2001). This expresses that even salmon that are homing to an upstream area engaged in some erratic movement, but they did not begin as quickly as salmon that were likely not homing to the upper watershed.

These short downstream movements have been coined as “yo-yo” movements by other researchers in the field (Lundqvist et al. 2008). This behavior is also known as “wandering behavior” (Scruton et al. 2007). These “yo-yo movements”, which occurred even during and after spawning season in this study, may indicate that these salmon are still homing to their natal spawning area upstream. These movements are costly, energy-wasting efforts for salmon which have a limited reserve of energy in freshwater, as they do not feed while in the natal river. It is possible that these movements correlate to changes in discharge from the power station, as was found by Rivinoja et al. (2001). Alternatively, these may merely be movements that are a part of the search phase of salmon, found in salmon on the river Tana, an undisturbed river with no human-made obstacles (Økland et al. 2001). In the Tana, 70% of salmon had a phase with erratic movement near the area they eventually spawned at. If this is the case in the Farelva, then these movements are not the frantic movements of salmon blocked from their natal river, but rather salmon making a search of the area for the best spawning grounds or possible mates.

4.3 Passage of the Fish Ladder

The tagged salmon in this study had an overall rate of ascending the fish ladder at Skotfoss of 16%. Comparably, Lundqvist et al found, on average, a 70% loss of potential salmon spawners because of inability to pass the fish ladder on the River Umeälven (2008). On the river Nidelva, also in the south of Norway, none of the salmon in the study successfully passed the fish ladder, which was 2.5 km upstream of the tunnel outlet. Salmon in both of these studies struggled to continue their upstream migration on account of the attraction of salmon to the tunnel outlet instead of the fish ladder. This does not explain the low rate of passage for the Skienselva salmon, as the fish ladder and the tunnel outlet are within 150 meters of each other, and nearly all salmon that approached the tunnel outlet, approached the ladder too. The fault in the fish ladder could lie in the amount of flow that runs through it. Hvidsten (2010) suggests that the opening to the ladder should be widened to allow for greater flow to improve the numbers of fish that ascend the ladder.

A steady amount of migration up the Skotfoss ladder occurred through July, but in August, the passage occurred in waves (Figure 8-9). The reason for this could be the pattern of flow volume changes at the hydropower plant and the flow allowed to release over the top of the dam near the fish ladder, as was found in Rivinoja et al., (2001). Though there was no correlation between either the flow through the floodgates nor the tunnel outlets at Skotfoss and the number of salmon ascending the ladder. The weak positive correlation between the temperature at Skotfoss and the number of salmon ascending the ladder, which agrees with a study of Atlantic salmon in Scotland but disagrees with two other studies in Sweden, which both found no correlation (Gowans et al. 1999; Rivinoja et al. 2001; Lundqvist et al. 2008).

Figure 15 implies that early arrival salmon were more strongly homing to rivers in the upper watershed than the salmon which arrived late. This could be due to the same phenomenon that caused salmon which entered the river at Klosterfoss later to swim more slowly up to Skotfoss than salmon which arrived earlier. However, as mentioned above, there is disagreement in the literature over this.

4.4 Length & Selectivity

Figure 12 expresses the bimodality seen in the salmon that ascended the Skotfoss ladder and were recorded by the fish counter, and salmon that were tagged in this study. This bimodality is lessened in the values seen from the Klosterfoss fish ladder, though some of the pattern is visible (Figure 11). In Figure 13, we see that almost none of the bimodal pattern exists in the lengths of fish which were captured and tagged. Importantly, the records from Klosterfoss do not differentiate between salmon and sea trout (*Salmo trutta*) which pass the counter. The fish counter at Skotfoss does determine species, but both the species data and the length measurements from Skotfoss and Klosterfoss may have a high amount of uncertainty, as these data are determined visually using photos taken of the fish against a white background they pass as they swim through the top of the ladder. With that uncertainty in mind, the bimodality could be a result of the two species, or of the different growth rates of multi-sea-year salmon and salmon which spent only 1 year at sea. The very large salmon could be individuals that are returning to spawn a second time, having spent a total of 3 – 6 years at sea (Jonsson and Jonsson 2011). It could also be the second peak is the significantly longer female salmon, and the first peak is the smaller males.

As far as length selection of the fish ladder is concerned, according to the length data from the fish counters, there is not a difference in the length frequency distributions of salmon that ascend Klosterfoss and Skotfoss. However, according to the length data from tagged salmon, there is a difference seen. As the fish counter data from Klosterfoss includes sea trout, and the Skotfoss counter differentiates between trout and salmon, it is more significant that the K-S test revealed the Skotfoss and Klosterfoss length distributions to be the same. This implies that the salmon which climb Skotfoss are of the same lengths as both the salmon and trout that ascend Klosterfoss. While the tagged data only included salmon and, even though the sample size is smaller, showed a difference. Slightly more female salmon successfully ascended the fish ladder as well, and were shown to be significantly longer than the tagged males in this study. Overall, it is not definite that the fish ladder is size selective, but these results suggest that it might be.

4.5 Spawning Sites & Implications

Given the erratic movements by salmon in this study, while it is possible this is a result of the salmon's search phase, it is also a possibility that salmon spawn in lower reaches than the spawning areas they originate from because they are unable to ascend the Skotfoss fish ladder. In the stretch between Skotfoss and Klosterfoss their options are between two sites on the main river and two sites on the tributary, but if they were not hatched in the Falkumelva branch, they may be unlikely to stray to this river. On the other hand, salmon who find themselves in unfamiliar rivers with unfamiliar populations will select a river with many other Atlantic salmon, in this case, the Falkumelva (Jonsson et al. 2003). In some cases, salmon may return to the sea without spawning: up to 35% and 22% left the river entirely in studies in Sweden and France (Rivinoja et al. 2001; Croze 2005).

Fossum is a very active spawning site given its small size and placement on the small tributary, Falkumelva. At only 500 m^2 it is the second smallest site of the four. However, it is at the outlet of a small dam and power station, which has no fish ladder. It has also been shown that the Falkumelva has the densest production of young trout and salmon in the Skien watershed (Hvidsten 2010). Therefore, it is not surprising that Fossum had the highest observations of mature adults before and during the spawning season (Figure 22). Though the site, Løvenskiold, which sits less than a kilometer upstream did not share in this abundance and had nearly as low numbers of observations as Vadrette. It is possible that the physical characteristics of Fossum make it a very suitable spawning ground because of the higher flow entering there, the water depth and presence of riffles, and the gravel substrate. However, Hvidsten left 33% of the total production of Skienselva unaccounted for, theorizing that there were sites in the Farelva and Falkumelva that were not included in their investigation (2010). This could be the accounted for by the spawning site Grøtsund, which had the second highest total observations. Overall, the results of this study do not agree with the juvenile population numbers, given that while Bliva/Falkumelva had the highest density, it contributed the smallest fraction of the total production in the watershed. This could be because either we or Hvidsten did not include all possible spawning areas, or because the fractions of adults returning to each of the rivers are different from the fractions of juvenile salmon.

Given the fact that Vadrette lies across the main branch of the river that fish ascending upstream to Skotfoss must pass and that it is the largest spawning site available, it was a surprisingly inactive site. It was assumed to be the more productive of the two sites, because it was shown to have more redds (Heggenes and Dokk 1995). However, it was the least active site in this study. This is shown in the significantly different amounts of time fish spent at Vadrette as compared to Fossum and Grøtsund (Figure 22-24). From the first observation at the site, to the last, salmon spent less time at the Vadrette site (Figure 26). This does not take into account that salmon may leave in between observations, but it is still an important factor to consider when or if the salmon left the spawning site to hold in another location over winter. However, the most likely reason that the average time spent at Vadrette is lower is that salmon were more likely to only have a single observation at Vadrette. This difference is not repeated in the data from the IT group, neither in the amount of total observations or consecutive observations. It must be considered, however, that none of the IT salmon ascended the fish ladder at Skotfoss and they were chosen because they had been observed previously in spawning areas. This could influence the differences in time spent at the spawning areas because these salmon were a not a random subset of the population. More of the non-IT group salmon had singular observations at Vadrette than the IT group, thus bringing the observations per fish at Vadrette up to the same level as the other spawning sites. The data used in the statistical test between the IT groups were also only from the intensive tracking days, so that consecutive observations could be identified. Moreover, when considering the differences in observation numbers at these sites, it is important to remember that the salmon in the Farelva includes salmon that may have attempted to ascend the ladder and failed, whereas the salmon in Falkumelva, may have homed there directly, without entering a search phase that included the Farelva.

If we connect the phenomenon of the “yo-yo” behavior at the tailrace, with the greater number of total observations at Grøtsund, the smaller, but closer site, an interesting theory develops. Despite the graininess of our data, it suggests that the salmon were going between the spawning site at Grøtsund and the power plant outlet. These may be the salmon that would like to spawn upstream of Skotfoss, but are unable to ascend the ladder and the result is, that they double back to the nearest downstream spawning site, not to stay, but instead to swim between the dam and the spawning site, even in the spawning season. A study on Chinook salmon in the US posited that salmon which find themselves in unfamiliar territory, surrounded by an unfamiliar salmon population, will simply go to a spawning area with many other salmon (Connor et al. 2019). This could include both the Grøtsund and Falkumelva populations, further increasing the production in those areas and creating a larger population of adult salmon that will home there.

This displacement could be damaging the salmon population in the Skien watershed. The homing process is an important part of the adaptation to the local conditions. It ensures that the salmon spawn in habitats that have already been proven to be successful (Heggberget et al. 1996). It follows that an altered distribution as caused by a man-made barrier such as a dam or weir could reduce the genetic variation within a river as a result of habitat fragmentation. Indeed, in anadromous Masu salmon, there was not a significant reduction in genetic diversity, but a reduction in the number of alleles in the isolated areas upstream of a dam, indicating a slower loss of diversity over time, not an immediate loss (Kitanishi et al. 2012). If, as it appears, Grøtsund is the default spawning place for salmon unsuccessful at ascending the fish ladder at Skotfoss, then it could become overcrowded and lead to recruitment failure. It will also likely impact the distribution of fish which spawn upriver of Norsjø. Thorstad et al (2008) also claim that a more spread out distribution of spawners may reduce the total population, as the survival of juvenile salmon is strongly density-dependent. This is a problem that could impact the salmon populations above the Skotfoss dam, as with fewer adult spawners, the sites will be less populated and/or further apart.

This is to say nothing of the fact that Grenland Sportfiskere continue to stock the upper reaches with salmon fry every year, without seeing an increase in passage of the Skotfoss ladder that is expected. If the ladder at Skotfoss hinders salmon from returning to the spawning sites upstream, then the efforts to re-populate the upper watershed will always be hobbled and may never see the salmon return to population levels found before the first dam at Skotfoss was built.

5 Outlook

With further study, the home range of salmon while they move within this section of river and the total amount and speed of movements could be analyzed. This would require more analysis of the observation points using geographic information systems software. The movement of salmon in and out of spawning areas throughout the spawning season and the yo-yo movements between the dam at Skotfoss and areas downstream need further investigation. Why do salmon move in this way? What is the biological purpose? Tracking studies are extremely useful to the study of species, but there are facets of biology that they are not suited to investigating. For example, a tracking study can determine how many times a salmon attempted to ascend a ladder, but they cannot determine how much body fat that salmon lost in the process and whether or not the offspring of that particular individual will survive to adulthood. More detailed observations of the salmon in the spawning sites, by mounting stationary receivers and antennas would be a good way to precisely identify the spawning areas in the Farelva particularly. This area of study, the analysis of salmon which fail to pass a fish ladder is novel and requires more research.

The method of tracking the IT group every six days, while still completing the tracking every two days, allowed a brief look into the fine details of daily movement of the salmon in the Falkumelva and Farelva. However, because of the length of time in between the intensive tracking days, the data does not lend itself easily to precise conclusions about total movement. Furthermore, reversing the choice to follow particular fish, rather than to track all of the salmon within or very near the four spawning areas, could not only be more efficient, but also be closer to what a detailed study of the spawning area’s needs. It would confine intensive tracking to specific areas, decreasing time spent driving and allowing for a more consistent schedule of tracking because it would not involve need to chase down fish which are on a list.

Also, the fish counters at both the Klosterfoss and Skotfoss ladders can contribute to any analysis by giving background information, but the available Klosterfoss data does not differentiate between sea trout and Atlantic salmon. Any truly definitive conclusions as to the length selectivity of the Skotfoss ladder cannot be made without this data. Since the counter uses video to identify length, it could have been a part of this project to identify the species from the video by eye, or to find a way to apply the program that the Skotfoss fish counter uses to identify species, to Klosterfoss.

In order to determine where the change happens, from the largest portion of new salmon coming from the upper watershed, to the vast majority of salmon spawning in the areas between Skotfoss and Klosterfoss, the survival of salmon migrating downstream through Skotfoss and Klosterfoss should be investigated. The issue may not be that the ladder does not allow salmon to ascend it, but that there are few salmon homing to areas upstream of Skotfoss. Alternatively, it is a combination of both issues that compound the problem and hinder efforts to repopulate the upper watershed.

Finally, to determine the source of the length bimodality, the salmon tagged in future should also be aged. In this way it could be decided if the bimodality is a result of the different lengths of single- and multi-sea-winter salmon or a result of the differing lengths between males and females.

6 Conclusion

Overall, we see a chain of events occur: Not all salmon which pass the Klosterfoss dam continue up the main branch to Skotfoss, but of those that do, 74% do not find and ascend the Skotfoss fish ladder. Not all of these are salmon that have an intent to spawn in the spawning areas in the upper watershed. The fish ladder may allow smaller salmon to ascend, while larger salmon are less able to ascend. Some of these salmon that do not ascend the ladder engage in energetically costly back and forth movements between Skotfoss and one or more of the spawning sites, most likely the Grøtsund site, as this site had significantly more total observations than Vadrette, the other site in the Farelva. This may be the result of salmon that originate from Grøtsund or Vadrette in a searching phase, looking for the best places to spawn or for mates. The Fossum spawning site on the small tributary, was the most active spawning site in the study, which is reinforced by this rivers status as the most productive in the Skien watershed. Altogether, the behavior of salmon below the Skotfoss dam indicates that there may be salmon that are prepared to spawn in the upper reaches of the watershed, and continue to recover the populations, but are unable to ascend the fish ladder. These fish instead appear to spawn in the small area at Grøtsund, with reduced likelihood of survival and recruitment of offspring to the next generation of salmon. Furthermore, the salmon that do survive to adulthood from these four sites are unlikely to stray into the upper watershed, so their offspring will continue to spawn in the Farelva as well. In conclusion, if the restoration efforts on the upper watershed are to continue, the issues at the Skotfoss fish ladder will have to be addressed first.

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