Upstream fishway performance by Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) spawners at complex hydropower dams

– is prior experience a success criterion?

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Abstract

Passage of hydropower plants by upstream-migrating salmonid spawners is associated with reduced migration success, and the need for knowledge of fish behavior downstream of dams is widely recognized. In this study, we examined fishway passage of landlocked Atlantic salmon in River Klarälven, Sweden and brown trout in River Gudbrandslågen, Norway, and the influence of prior experience on passage success in 2012 and 2013. Fishway trap efficiency varied from 18 to 88% and was influenced by river discharge. Most salmon (81%) entered the fishway trap on days without spill, and salmon moved from the turbine area to the spill zone when there was spill, with small individuals showing a stronger reaction than large fish. Analysis of fish with and without prior trap experience showed that a higher percentage of the “naïve” fish (70% of salmon and 43% of the trout) entered the fishway traps than the “experienced” ones (25% of the salmon and 15 % of the trout). Delays for fish that entered the trap ranged from 3-70 days for salmon and 2-47 days for trout.

Keywords; Atlantic salmon Brown trout, Fish migration, Spawning migration, Prior experience, Salmonid conservation.

Introduction

Habitat fragmentation is a major threat to biodiversity worldwide and an important topic in conservation biology (Nilsson 2005; Noss and RF 2006). Hydroelectric development, in which dams block, partly or completely, upstream migration of fishes such as salmonids, is one common cause of habitat fragmentation (Nilsson 2005; Clay and Eng 2017). As a result, fishways have often been implemented to restore connectivity in these fragmented rivers, with varying degrees of success (Mallen-Cooper and Brand 2007). The different kinds of fishways vary in their physical characteristics, and these differences may not only facilitate passage of certain species of fish over others, they may also favour passage of a subset of individuals within a species due to individual differences in behaviour and/or physiological status of the fish (Hinch and Bratty 2000; Pon et al. 2009). Moreover, it is not only the physical characteristics of the actual fishway that affect successful dam passage, but also the environment characterizing the headwater and tailrace above and below the hydropower station and dam, which often varies over time, so that even well-designed fishways may function poorly in certain situations, resulting in delayed or disrupted dam passage (Larinier 2001). This may be especially true during high flow conditions due to turbulent "white water" in the tailrace section, inadequate attraction flows at fishway entrances relative to turbine outflows and spillwater release as well as to the placement of fishways at hydraulically unsuitable locations (Larinier 2001; Larinier et al. 2002). Successful passage of dams might therefore be lower than expected, and fishways may not mitigate the fragmentation of the river caused by hydroelectric dams and power plants (Roscoe and Hinch 2010).

Anadromous salmon and brown trout (*Salmo trutta)* use considerable amounts of energy during migration, and it is important that they use energy efficiently, minimizing swimming costs when possible (Bernatchez and Dodson 1987). Fishways with low functionality may have severe consequences for both individual fitness and population resilience. Studies in the Fraser River showed that sockeye salmon (*Oncorhyncus nerka)* that failed to pass a fishway had high levels of physiological stress, made repeated attempts to locate and enter a fishway and exhibited long periods of intense swimming activity, often swimming in unfavourable areas with high water velocities and turbulence (Hinch and Bratty 2000; Cooke et al. 2006;

Young et al. 2006). The successful fish, on the other hand, often entered the fishway on their first attempt, spent little time searching for the fishway entrance and selected routes through areas where water velocity was low and thus less energy consuming. These results for sockeye salmon suggest that failure to pass fishways may be due to a combination of poor route choices, elevated stress and physical exhaustion. Thus, demanding migratory routes, combined with challenging fish passage solutions, may not only cause exhaustion and stress, but could ultimately also act as bottlenecks for survival and passage success of migrating fish (Stevens and Black 1966; Peake 2004). Prolonged searches for a passage route past an obstacle also expose fish to predators and anglers, which may cause surviving fish to consume even more energy in their struggle, energy that otherwise could be used for reproduction (Kinnison et al. 2001, 2003). As anadromous species feed less during their riverine migratory phase, energy-consuming migrations may increase mortality and act as evolutionary selection forces (Bernatchez and Dodson, 1987, Jonsson and Jonsson, 2011).

Upstream-migrating salmon and trout often seek areas with high velocities and flows. This behaviour is thought to be an evolutionary mechanism that ensures spawning success by enabling the fish to negotiate along the main river stem and reach suitable spawning grounds (Ferguson et al. 2002). Hence, discharge of water is probably the single most important factor for attracting upstream migratory salmonids to fishway entrances, and large variation in the operation scheme of flow and/or spill releases from dams may hinder or delay upstream migration (Larinier 2001 and references within; Rivinoja et al. 2001; Williams et al. 2011 and references within). In many cases, the main reason for upstream passage failure often occurs when turbine and/or spillway discharge flow masks attraction flow from fishway entrances (Vegar et al. 1996; Karppinen et al. 2002; Thorstad et al. 2003). For example, ascending fish may be steered towards blind alleys and interrupted or delayed in their upstream migration if attraction flow from turbine or spillway discharge is high relative to fishways, or if spill is released far from the fishway (Bjornn and Peery 1992; Kraabøl 2012). Therefore, application of optimal spillway manipulations seems to be a potentially cost-effective mitigative action to improve fishway performance. To survive, reproduce and maintain natural adaptations to the pre-regulated river environment, fish rely on the ability to make decisions that encourage behavioural patterns that lead to successful passage (Brown and Laland 2003; Laland et al. 2003). Thus, any fish passage solution should consider the behaviour of the fish, including their cognitive abilities and motivational state, as seen in Goerig and Castro-Santos' (2017) study of brook trout, where they found individual variability in attempts to pass even after accounting for the effects of hydraulics, diel period and physiology. Although individuals respond directly to the hydrodynamic and hydraulic environment in the tailrace section, behavioural responses may also depend on previous experience and the ability to learn from prior experiences during passage attempts. Kieffer and Colgan (1992), for example, describe how fish learn about their surroundings through trial and error, but also by observing the behaviour of conspecifics. Thus, the cognitive abilities of fish may enable them to modify their search behaviour from previous experiences. If so, this may entail searching for, or avoiding, certain objects or areas (Goodyear 1973).

Studies of fish passage typically involve some sort of tagging, which in turn involves capturing and handling of fish. Handling the fish during capture, anaesthesia, tagging procedures and transportation is associated with an increase in stress and may result in abnormal behaviour (Thorstad et al. 2008 and references within). Whether or not the stress generated from handling is related to learning, with subsequent effects on passage, is in need of further investigation. Nevertheless, stress associated with handling may not only have a negative effect on passage success, but may also lead to faulty evaluations of the performance of a given fish passage solution, potentially leading to poor management decisions (Nyqvist et al., 2017).

In this study, we investigated how mature wild spawners of large-bodied land-locked Atlantic salmon in the River Klarälven, Sweden, and brown trout in the River Gudbrandsdalslågen, Norway, performed during their attempts to locate and ascend fishways. The purpose of the study was to: (1) assess fishway trap efficiency at both study sites; (2) investigate the behaviour and performance of salmon and trout translocated from successful fishway entries with ascending salmon and trout without previous experience from successful entries of the fishway; and (3) describe and analyze behaviour and performance of adult salmon approaching a large and complex hydroelectric dam and power station in relation to spillway and turbine outlets in the tailrace area. The shortage of experimental studies on these topics represents a major knowledge-gap, and there is a need for descriptive as well as experimental studies dealing with the behavioural details during the migratory phase of salmonids in regulated rivers.

Material and methods

The study was conducted at the Forshaga dam in the River Klarälven and at the Hunderfossen dam in the River Gudbrandsdalslågen (Fig. 1). Both dams are associated with a run-of-the-river power plant and a dam section equipped with several spillways. The environmental conditions are characterized by several waterways across the dam and great variation in water discharge during the migratory season. The River Klarälven was investigated during 2012 and 2013 and the River Gudbrandsdalslågen during 2013.

Study area in Sweden, salmon

The River Klarälven (catchment area 11 800 km^2) stretches 460 km through Norway and Sweden before it empties into Lake Vänern (5 650 km^2), Sweden's largest lake. This river is the major spawning and nursery river for landlocked Atlantic salmon in Lake Vänern. The mean annual discharge at the river outlet is 162.5 m^3/s, with a mean annual high of 690 m^3/s (www.smhi.se). During the two study years, the average discharge for June to September was

265 m^3/s in 2012, and 165 m^3/s in 2013 (Fig. 2). The River Klarälven has been dammed for hydropower purposes since the beginning of the 1900s (Piccolo et al. 2012), and today there are eleven hydropower plants in the river, of which nine are situated in Sweden and two in Norway. The main available spawning areas occur above the eighth dam, within a free-flowing reach of 140 km. There are no known spawning grounds below the first hydropower plant.

All hydropower dams located in the Swedish portion of the River Klarälven lack fishways and are not passable for upstream migrating fish. Instead, the upstream migrating salmonid spawners are collected in a fishway equipped with a trap at the lowermost power plant in Forshaga, 25 river km upstream of Lake Vänern (Fig. 3). The maximum intake capacity at Forshaga power plant is 163 m^3/s, and water is spilled through four spillways and a log chute distributed across the dam, depending on river discharge (Fig. 3). Once captured, the fish are transported by truck and released upstream of the eighth power-plant where the spawning grounds are situated (see also Hagelin et al. 2016 for details of the system).

There are two entrances to the fishway, one facing the spill area and one facing the turbine outflow area. Both entrances lead the fish to a single large pool into which auxiliary water is released (Fig. 3 and 4). From each entrance, fish can ascend a Denil fishway to a false weir that empties into a downward-sloping tube that leads them into an indoor collecting basin where the fish are held up to a week until transported (Fig. 4). The fishway discharge is about 1 m^3/s in the ladder but the attraction flow can be up to 3 m^3/s. All spawners caught in the trap are netted, sorted by species and origin (hatchery-reared or wild, sorted by the absence of an adipose fin in reared fish) measured for body length and sex before transporting them further upstream.

The fish trap in Forshaga was open 106 days between 11 June and 27 September 2012 and 110 days between 21 May and 3 October 2013. From 2004-2013, an annual average number of 628 (range 292-1031) wild and 592 (range 124-992) hatchery-reared Atlantic salmon were caught in the trap (data from Fortum Generation AB).

Study area in Norway, trout.

The River Gudbrandsdalslågen (catchment area 11 500 km^2) is the major spawning and nursery river for the land-locked and large-bodied brown trout in Lake Mjøsa (365 km^2). The mean annual discharge is 248 m^3/s, with a mean annual high of 630 m^3/s (Fig. 2). A 78 km river section is available for ascending trout, of which 62 km is situated upstream of the dam and reservoir at the Hunderfossen power plant. In this study, we focused on trout movements downstream the dam. Out of 17 major and minor spawning areas recorded in the river, 10 are located upstream of the dam (Kraabøl and Arnekleiv, 1998); the rest located downstream of the power plant. In this study, however, we tagged fish in the fishway (termed experienced) and immediately downstream of the dam (termed naïve), so these fish are likely looking to reach areas further upstream.

Hunderfossen dam was constructed in 1960 – 64 (Fig. 5). The maximum intake capacity of Hunderfossen power plant is 320 m^{3}s^{-1}. After passing the turbines, the water is led back to the river, 4.4 km downstream of the dam. Spill water is released through seven spill gates, one timber gate and one ice and trash spillway (Fig. 5).

The fishway (1.8 m^3/s) at Hunderfossen dam consists of a pool-and-weir section (from the entrance to the fish trap) and a Denil section (from the fish trap to the outlet) (Fig. 5). From 2004-2013, the trap caught an annual average number of 508 (range 305 – 685) brown trout. The fishway empties directly into a deep pool below the dam, where there are three different entrances (Fig. 5).

Radio tagging and tracking Atlantic salmon in Sweden.

In 2012 we tagged 16 wild Atlantic salmon (Table 1) caught in fyke nets in Lake Vänern, approximately 5 km from the river mouth. The mean length of the tagged salmon was 71 cm (range: 61-79 cm, SD = 5.0 cm). The fish were tagged on a boat and then either released at the capture site in the lake (n=10) or transported in a tank and released 5 km upstream of the river mouth (a total transport distance of approximately 10 km) (n=6). Fish were tagged on four occasions, 19 and 26 June and 3 and 6 July. All fish in 2012 were tagged before they reached the fishway in Forshaga and are hereafter referred to as “naive”.

In 2013, 20 wild Atlantic salmon (Table 1) were caught in fyke nets at the same location as in 2012. The fish were removed from the fyke net, tagged and then immediately released back into the lake. We tagged fish on four occasions, 19, 24 and 27 June and 8 July. The mean length of the tagged salmon was 73 cm (range: 57-86 cm, SD = 5.5 cm). In addition, 20 “experienced” fish (Table 1) from the fish-trap in Forshaga were also tagged and then transported by truck in an aerated tank and released 4 km downstream of the power-plant. The mean length of the experienced tagged salmon was 74 cm (range: 62-85 cm, SD = 6.1 cm). Again, the fish caught in the lake were regarded as “naïve" fish, lacking experience from entering the fish trap in 2013, whereas the fish caught in the fishway trap were treated as experienced. The experienced fish were all tagged on 28 June.

All fish were inspected for injuries and measured to the nearest cm (total fish length, L_T), after which they were tagged with external radio transmitters (model F2120, Advanced Telemetry Systems (ATS), Isanti, MN, U.S.A.), with a mortality signal that becomes activated after 8 hours of no movements. The tags weighed 16 g, which is well below the recommended maximum of 2% of total body mass (Winter 1983, Thorstad et al. 2000), measured 21 x 52 x 11 mm, lying flat against the fish’s body. During the tagging procedure, in which two coated wires are pierced through the area below the dorsal fin, fish were kept in a dark plastic tube filled with river/lake water. As soon as the tagging was done the fish were put in a large tank to monitor their recovery. To minimize further stress, the fish were treated without anesthetics as described by Finstad (2005). All fish were tagged in temperatures below 19°C.

To track the tagged fish, we used stationary loggers and manual tracking. We placed three stationary data loggers, model R4500S (ATS), connected to 6-element Yagi-antennas, around the power-plant to detect movements in the area downstream of the dam. One was placed near the turbine outlet, one at the spill gate closest to the fish trap and one at the spill gate furthest away from the fish trap (Fig. 3). Before tagging we used the stationary loggers to provide a signal map of the area so the we could tell, more specifically, where the fish resided. Manual tracking, using receiver model R4000 (ATS) and a 3-element Yagi-antenna, was conducted approximately every third day from the time of release until the fish had either been caught in the trap or had moved back downstream to the lake. Manual tracking was primarily done on foot but also by boat and covered the area from the power plant to the river mouths. We also had additional antennas at the three mouths of the River Klarälven to detect river entry and downstream movements into Lake Vänern.

Radio tagging and tracking trout in Norway.

During the spawning migration season in 2013, artificial freshets were used to attract and capture brown trout at spillway 1 on the eastern side of Hunderfossen dam (Kraabøl 2012, Fig. 5). When flow through spillway 1 exceeds 10 m^3/s, ascending trout gather in the deep pool below the dam (Fig. 5). Trout were trapped in pots or stranded after spillway closure and netted and secured as quickly as possible in a 1 m deep pool. A total of 44 brown trout was captured, tagged and released into the deep recipient pool immediately below the fishway (Tab. 1, Fig. 5). All individuals were tagged with floy anchor tags and a subsample was radio-tagged (n=9) on 9 and 29 August 2013. The mean length of the tagged trout was 68 cm (range: 48-88 cm, SD = 9.9 cm). These fish were termed ”naive” as they had not entered the fish trap during 2013. In addition, 73 experienced brown trout were captured in the fish trap (Fig. 5, Tab. 1). All individuals were tagged with floy anchor tags and a subsample was radio-tagged (n=10). These individuals were released downstream of the dam in the same pool as the naive fish. The mean length of the experienced trout was 72.5 cm (range: 48-87 cm, SD = 9.6).

For all fish, origin (hatchery-reared or wild, sorted by the absence of an adipose fin in reared fish) of the fish was noted, and total fish length (L_T) was measured to the nearest cm. The hatchery-reared fish were stocked as 2-year-old (lengths 20-25 cm) and had been at least 3 growth seasons in Lake Mjøsa before they returned as spawners. Previous studies have shown no effect of origin on downstream or upstream migration and behavior of trout at the Hunderfossen dam (Kraabøl 2012), but we included nevertheless origin in the analysis of the trout in this study. The floy anchor tags (Floy tag, Seattle, WA, U.S.A.) were inserted in front of the dorsal fin by a floy-pistol. The unanesthetized fish were kept in a dark plastic tub filled with river water during tagging. Radio-tagging followed the same procedure as in Sweden. After tagging and measuring, all tagged naïve trout were carried in opaque, dark plastic bags filled with water and released in the deep pool below the dam. Experienced trout were put in a large fish tank and transported with a crane to the deep pool downstream of the fishway. The handling time was approximately the same for the naive and experienced fish. All fish were tagged in temperatures below 19^{o}C.

Tagged trout (floy- and radio tags) caught in the fish trap were identified on a daily basis by the staff at Hunderfossen trout hatchery. To follow the radio-tagged fish we used manual tracking. The fish were positioned by using an ATS R4500s receiver and a hand-held antenna from land (there are roads along both sides of the river, running from the dam to Lake

Mjøsa). The position of trout was identified on average every 2.7 days, i.e. 23 times in the period 30 August – 1 November 2013.

Statistics

We calculated *fishway efficiency* (Ebstaller et al. 1998), or to be more exact fishway trap efficiency, for the fishways in Forshaga (Atlantic salmon) and Hunderfossen (brown trout). Fishway trap efficiency was defined as the proportion of tagged fish, residing in the area, that entered the fishway and were captured in the fish trap. In Forshaga only fish actively approaching the dam were considered residing in the area, whereas in Hunderfossen all tagged fish were assumed to be residing in the area since they were captured and released immediately below the fishway.

Since experienced fish had already passed the fishway once, we only used recaptures of naïve salmon and trout (one year at Hunderfossen and both years at Forshaga) to estimate fishway trap efficiency, as this measurement best describes efficiency under “normal” conditions.

To make comparisons between naïve and experienced fish we also calculated fishway trap efficiency for tagged fish (i.e. capture rate for naïve fish and recapture rate for experienced fish) that were detected near the dam. These calculations were based on data from 2013 for both naïve and experienced Atlantic salmon and brown trout. Analysis of these data was done using a binary logistic regression model BSTEP, exploring the relationship between the probability (P) of observing captures in the fishway at the dam in Forshaga (Atlantic salmon) and Hunderfossen (brown trout) and three different fish state variables, namely the level of experience (experienced or naïve fish), sex and length. In addition, origin (wild or hatchery-reared) was included as a variable in the brown trout analysis.

The movement between areas 1 and 2 in the River Klarälven (Fig. 3) was analysed for naïve Atlantic salmon from 2012 and 2013 using a generalized linear model. “Occupancy of an area" was treated as a binary response variable and year as a factor. The spill difference during the time period between manual tracking occasions was quantified as either absolute or relative spill, i.e. absolute spill was set as maximum spill minus the minimum spill, and relative spill was set as the ratio of mean spill to mean flow (Q), and both were used as covariates together with fish length.

We also tested for behavioural differences between naïve and experienced fish. The behaviours tested were delay and motivation. Delay, i.e. the number of days from entering the area below the power plant (Fig. 3) (Sweden) or from being tagged (Norway) to entering the fish trap, was analyzed using a Mann Whitney test. For Atlantic salmon we used data from 2012 and 2013 and for brown trout we used data from 2013. Motivation, expressed as number of attempts to enter the trap, was calculated both totally and per day and tested using a Mann-Whitney test. An attempt is defined as an occasion when the fish resided in the vicinity of the fishway entrance, positioned by the automatic loggers. This metric was only computed for Atlantic salmon in Klarälven in 2012 and 2013.

A separate success rate was also analysed for the Atlantic salmon studied in 2012. Here, we compared the performance of naïve Atlantic salmon that were treated in two different ways, i.e. tagged and released directly into the lake or tagged, transported and then released into the river. This analysis was done using a binary logistic regression BSTEP. Whether or not the fish made attempts and/or passed the fishway was used as the response variable and handling of fish (released directly vs transported and released) and length were treated as factors. All statistical analyses were carried out in IBM SPSS Statistics 24.

All handling of fish in Sweden was performed in agreement with the animal welfare permit no. 2013/85 from the Swedish Board of Agriculture and in Norway in agreement with animal welfare permit no. 2013/116588.

Results

Fishway trap efficiency

For Atlantic salmon at Forshaga, eleven of the 16 radio-tagged naïve salmon made attempts to enter the fishway in 2012, i.e. they resided in the area. Two out of the eleven salmon eventually entered the fishway and were captured in the collecting basin in the fish trap. The transmitters switched to mortality mode for five of the salmon, indicating the fish died, became inactive or lost their transmitters before entering the fishway. Thus, fishway trap efficiency in 2012 was 18% if the fish with mortality signals are included and 33% if they are excluded. In 2013, 18 of the 20 naïve radio-tagged salmon made attempts to enter the fishway, i.e. they resided in the area. Of the 18 salmon, 14 were captured in the trap and two either died or lost their transmitter (for the same reasons as outlined above). Thus, fishway trap efficiency in 2013 was 78% if the fish with mortality signals are included and 88% if they are excluded. The average discharge for the migration period, i.e. when the fish were in the area, was higher in 2012 (276 m^3/s) than in 2013 (121 m^3/s) and consequently there was also more spill in 2012 (Fig. 7). Most fish (81%) entered the trap on days without spill (Figs 7a and b).

For brown trout at Hunderfossen in 2013, 19 of the 44 naïve tagged (floy and radio) trout were captured in the trap in the fishway. Thus, fishway trap efficiency was 43%.

Naïve vs experienced

There was a significant effect of level of experience (naïve vs experienced) on the number of salmon that entered the fish trap in Forshaga in 2013 ($Z=7.5$, $P = 0.006$). Of the 20 tagged naïve salmon, 70% were captured in the trap as compared to 25% of the 20 experienced ones (Table 2, Fig. 6). Further, 10% of the naïve and 45% of the experienced salmon ceased upstream migration, i.e. based on manual tracking and information from the dataloggers, they moved downstream and left the area after tagging and release, and they did not move upstream to the power plant area. A similar difference in success rate between naïve and experienced fish was found for brown trout at Hunderfossen dam (Z=10.35, P=0.001). Out of 44 tagged naïve brown trout, 43 % were captured in the fish trap, whereas only 15 % of the experienced (n=73) ones were captured in the fish trap (Fig. 6). Manual positioning of the radio-tagged fish revealed that 11% of the naïve and 50 % of the experienced brown trout ceased migration after tagging and release. We found no significant effects of sex and fish length on the success rate for salmon or trout (Table 2). In addition, we found no significant effects of origin (wild or hatchery-reared) for trout.

Searching behaviour

Based on telemetry data, we found that salmon searched for a passage route in waterways releasing the highest water discharges. When the majority of water discharge was released through the turbines, the salmon were mainly observed in turbine zone 2, and when the majority of water was released through the spill gates, the fish were more often located in spill zone 1 (Fig. 3). Periods of high spill water release (Z = 21.04, p= <0.001) and increasing spill (Z = 4.71, p= 0.03) stimulated the fish to move to zone 1 in both 2012 and 2013 (Figs 7a and b, Table 3). There was also a significant difference between years (Z= 8.68, p= 0.003), where more fish moved to the spill zone in 2012, and an effect of fish length (Z = 5.14, p= 0.023), where smaller fish responded by searching more actively towards the spill than larger individuals (Table 3).

Delays

Naïve salmon were delayed by a median of 15 days (3-70), whereas the experienced salmon were delayed by 7 days (7-70). For brown trout, the median delay for experienced and naïve trout was 26 (2-47) and 25 (4-43) days, respectively. The difference in delays between experienced and naïve fish was not significant for either species (Mann-Whitney U test, U=36.5, N_1=16, N_2 = 5, P = 0.771 for salmon, U=95.0, N_1=19, N_2=11, P = 0.698 for trout).

We found no differences in total number of attempts to enter the fishways between the naïve (median 1 attempt) and experienced (median 2 attempts) salmon (Mann-Whitney U test, U= 87.0 N_1=18 N_2 = 11 P = 0.444). The same was true if expressed as the number of attempts/day, with a median of 0.027 attempts day^{-1} for the experienced fish and 0.037 attempts day^{-1} for the naïve ones (Mann-Whitney U Statistics, U= 94.0 N_1=18 N_2 =11 P = 0.822).

Handling

There was a significant difference in the number of attempts between the two groups of naïve salmon that had been handled differently in 2012 (Logistic regression z=4.49, p= 0.034). Out of the 10 salmon that were released immediately after tagging, seven made attempts to enter the fishway and two succeeded in entering the trap. Out of the six salmon that were transported to the river, two made attempts to enter the fishway but none managed to enter it.

Discussion

All migratory salmonid populations are dependent on spawners reaching spawning grounds, and therefore in regulated rivers, it is paramount that spawners can successfully pass dams to reach them. Our study of Atlantic salmon and brown trout showed that the situations for single dam passages in two regulated rivers could potentially be improved as passage success varied in Klarälven and was unsatisfactorily low in Gudbrandsdalslågen. Our analyses also showed that previous experience, defined as prior successful entry into the fishway traps, had a negative effect on passage success for the same fishway later in the season.

Reproductive success is of fundamental importance for all populations, and for migrating fish it is tightly linked with both migration success and timing (Dingle, 1996). Within this context, well-functioning fishways are required, where functionality not only involves successful passage (i.e., the proportion of fish that enter and pass a fishway), but also passage with little delay. If delay is substantial, reproductive success may be negatively impacted due to aborted spawning migrations, reduced windows of opportunity to mate due to delayed arrival at spawning sites and forced spawning at sub-optimal and over-crowded areas below dams (Gorsky et al. 2009; Holbrook et al. 2009). While the observed delays for salmon (7-15 days) and trout (25-26 days) passing the dams at Forshaga and Hunderfossen may not have serious consequences for reproductive success, although one may question this for trout, there is seldom only one dam for fish to pass to reach their spawning grounds. In the River Klarälven, the fish would need to pass eight dams to reach the spawning grounds in Sweden and an additional three to the Norwegian spawning grounds. The cumulative delay associated with so many dams would undoubtedly have a negative effect on reproductive success, and thus the current truck and transport system seems to be the only viable alternative.

A well-functioning fishway must work well under a variety of flow conditions. We found that mean fishway (trap) efficiency in River Klarälven varied greatly, ranging from 18% in a high flow year to 88% in a year of normal flow conditions. Our measure of efficiency in Gudbrandsdalslågen may be an underestimate as we assumed all of the fish remained in the dam area after release (i.e. we did not radio-track all fish). Even if this is the case, the efficiency in Gudbrandsdalslågen (47%) was higher than a previous report of 21% to 39% for other years (Kraabøl et al., 2012). Fish used in these previous reports (Kraabøl et al., 2012) were all considered naïve. Hence, there was large annual variation in fishway performance at both dams, which have run-of-the river hydropower plants. Fishways at run-of river hydropower plants have previously been shown to have large interannual variation in their passage performance, which has been ascribed to differences in flow conditions, resulting from different patterns of spill in relation to flow (Rivinoja et al. 2001; Lundqvist et al.

2008). We found, for example, that Atlantic salmon were more likely to enter the fishway when spill was low or nil and moved from the tailrace to the spill area when spill increased, a pattern also reported by Rivinoja (2001). While we did not study in detail the behaviour of the trout at Gudbrandsdalslågen, previous studies here have estimated fishway performance to be optimal at flows of 2-20 m^3/s, sub-optimal up to 180 m^3/s and completely dysfunctional at higher flows (Jensen and Aass 1995). In Klarälven, we also saw a size-dependent effect of spill, where small fish responded by searching more actively towards the spill area than large fish. We can only speculate as to why this occurred, but it may be related to large individuals being more successful at holding position (Fleming 1996; Fleming et al. 1996).

The low efficiency at high spill observed in the River Klarälven will require one or more counter-measures to reduce the likelihood that fish become attracted away from fishway entrances. One way to increase fishway trap efficiency would be to establish operational schemes for releasing spill water near the fish trap entrance during spawning migrations. Such a spill plan was recently implemented in Klarälven (in 2018), but to date it has not been evaluated. Another counter-measure that one might consider is installation of physical screens along the tailrace to hinder fish from moving away from fishway entrances towards spill or turbine discharge areas. At the Pitlochry Dam, Scotland, Webb (1990) found that 55% of the ascending Atlantic salmon passed fishways successfully without screens, but 100% passed after screens had been installed (Gowans et al. 1999).

Catching, handling and transporting fish may affect the upstream migration behaviour and success due to stress (Jokikokko 2002, Potz et al.2006) and exhaustion (Cooke and Hinch 2013). Many studies looking at passage success have still used fish collected from passage facilities, i.e.“experienced”, fish that have been exposed to some degree of handling (e, g. Roscoe et al. 2011, Bunt et al. 2012). Unfortunately, the difficulties associated with capturing naïve spawners in large lakes and rivers often necessitates the need to use fish captured in fishways, i.e., it is the only viable option. Our study indicates that there may be biases associated with using ”experienced” fish. We do not know the reason for the lower passage success for experienced fish than for naïve fish. Nevertheless, it is important to consider that prior experience as defined here includes more than experience entering a fishway, it also includes effects from handling/transport procedures as well as other experiences such as delays in the fishway traps or exhaustion from migrating in a portion of the river for a second time. We believe that a likely explanation for the difference in fishway trap efficiency for naïve and experienced fish, which is consistent with the results for the two years of study in the River Klarälven and for the River Gudbrandsdalslågen, may be related to stress, and that stress reactions may have over-ruled the effects of prior success. Both naïve and experienced fish were subjected to stress associated with handling and tagging, but the experienced fish were also subjected to stress associated with being held in the collection basin and, for salmon, transportation from the fishway trap to the release site in the river. Further support for an effect of stress can be seen in the response of naïve and experienced salmon directly after release, where 10% of the naïve salmon and 45% of the experienced ones ceased migration after tagging and release and did not move up to the power plant area.

Even if a tenable explanation for this difference in behavior and performance of naïve and experienced salmon and trout is stress-related, we cannot rule out the possibility that this difference may be related to learning as well. Previous experimental studies have provided indications that fish can remember negative experiences for a substantial amount of time (Odling-Smee and Braithwaite 2003; Yue et al. 2004) and that the primary function of fear and stress is to help animals avoid danger (Paul et al., 2005), and thereby avoid certain places (Portavella et al. 2004; Yue et al. 2004). In the study conducted in 2012 we found that a larger percentage of the salmon released directly into the lake attempted to enter the fishway (70%) than fish transported 10 km into the stream before released (33%). Thus, it once again seems likely that the difference in behaviour and performance of naïve and experienced fish is stress-related and/or related to secondary effects such as energy consumption, where stress associated with transportation alone may be sufficient to produce behavioural differences.

Overall, our results suggest that evaluations of fishway performance (efficiency) should be tempered with caution, depending on the source of individuals used in such studies. More research is needed to understand the reason for the difference we observed, but the potential bias associated with prior experience appears to be general as we obtained similar results with two different species in two different river systems. Our results also underscore the need to consider fishway efficiency during multiple years, presumably related to interannual differences in flow conditions. There are many ways to deal with interannual flow variation, such as establishing a spill plan and using screens to influence route choice. Other possibilities are to increase attraction flow at the traps, design fishways with multiple entrances or in some cases, in particular in large rivers, to construct more than one fish passage solution, and in that way cover the broad range of flow conditions that the fish face (Larinier 2001).

Fishway efficiency and fish behaviour during passage is affected by a number of factors, factors that may cause cumulative responses and it is difficult to single out the importance of each factor. We have, in this study, made an attempt to illustrate the importance of prior experience to fishway efficiency, but we also recommend further research to continue to investigate and pinpoint the different factors affecting fishway efficiency to reduce losses during migration in the future.

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Tables

Table 1. Overview of the tagged Atlantic salmon and brown trout during 2012-2013 in the River Klarälven and the River Gudbrandsdalslågen.

	Year	**Sex**		**Length**		
		Females	Males	Average	Range	SD
Naive salmon	2012	x	x	71.3	64-79	4.5
Experienced salmon	2013	13	7	74.5	62-85	6.4
Naive salmon	2013	10	10	72.9	57-86	5.5
Experienced brown trout	2013	52	21	72.5	48-87	9.6
Naive brown trout	2013	32	12	68.3	48-88	9.9

Table 2. The results for the binary logistic regression model for the probability of captures in the fish trap, showing the Wald statistic and the odds ratios (Exp (β)) with 95 % C.I. for captures in the fish traps. A backward stepwise likelihood procedure suggested that the variables “sex” and “individual fish length” should be excluded from the model. The variable, group, refers to the experienced salmon and trout that either passed or failed to pass a fishway.

Captures in fish trap						
			Wald statistic			
Model	Predictor	Coefficients	Z	P	Exp	95%
Salmon	Intercept	-0.85	3.02	0.082	0.43	
	Group					
	Experienced				1	
	Naïve	1.95	7.50	0.006	7	0.43-28.17
Trout	Intercept	0.27	0.81	0.37	1.32	
	Group					
	Experienced				1	
	Naïve	1.44	10.35	0.001	4.22	1.75-10.12

Table 3. The results for the generalized estimating equations model for occupancy in an area, showing the Wald statistic and the odds ratios (Exp (β)) with 95 % C.I. Variables in the model are year 2012 and 2013, and individual fish length. Total spill and spill increase were measured during the time between two tracking occasions.

Occupancy of an area						
			Wald statistic			
Model	Predictor	Coefficients	Z	P	Exp (β)	95% C.I.
Salmon	Intercept	6.36	4.30	0.067	578.27	
	Movement					
	Year	1.65	8.68	0.003	0.19	-2.75- -0.55
	Length	-0.93	5.14	0.023	0.91	-0.17- -0.13
	Spill (m^3/s)	2.58	21.04	0.000	13.20	1.48-3.68
	Spill increase (m^3/s)	0.01	4.71	0.030	1.01	0.00-0.26

Figure 1. The catchment areas for lake Mjösa – river Gudbrandsdalslågen, Norway and lake Vänern – river Klarälven, Sweden. Map made using ArcMap 10.5.

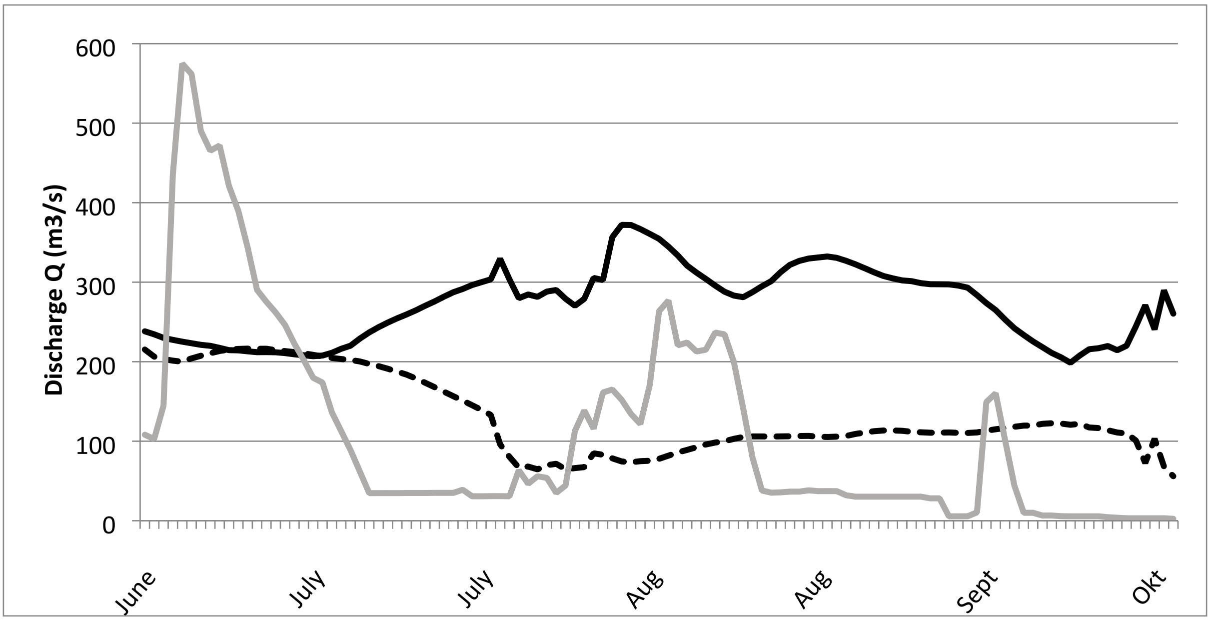


Figure 2. Discharge (m/s^3) in the River Klarälven during the migration period in 2012 (black line) and 2013 (dotted line) and in the River Gudbrandsdalslågen in 2013 (grey line).

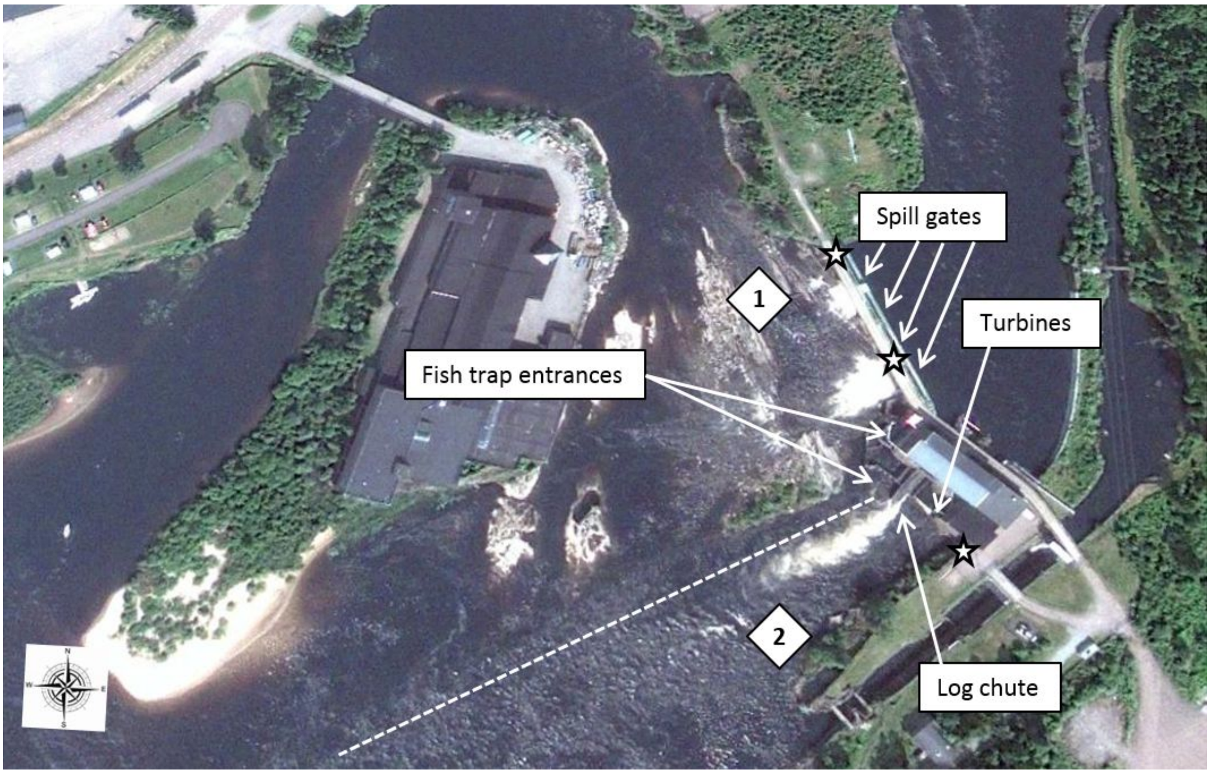


Figure 3. Aerial photo (google maps) of the power plant at Forshaga, River Klarälven, showing the location of the three turbines, four upward-opening spill gates and one downward-opening log-chute. There are two entrances to the fishway. The area depicted with “1” represents the spill area, and by “2” the turbine outflow area, with the dotted line showing the border between the two areas. The three stars show the location of the telemetry antennas.

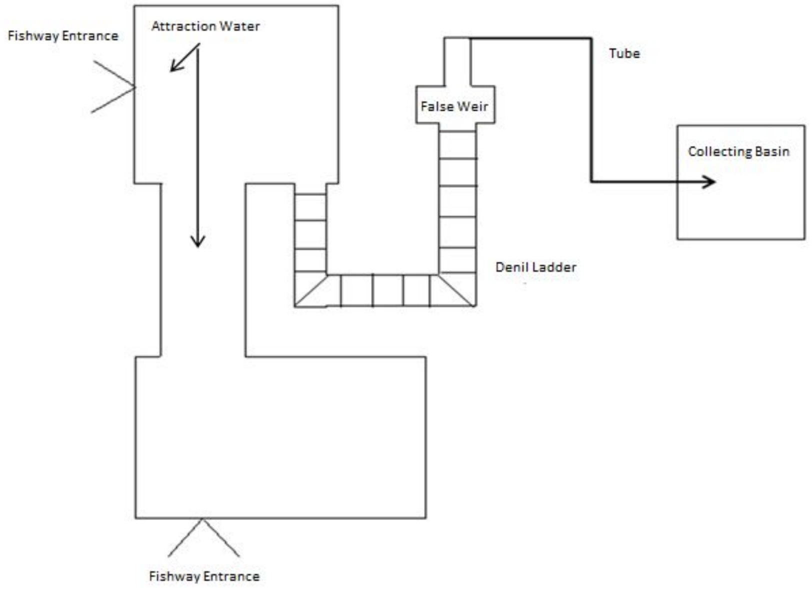


Figure 4. Schematic diagram of the fish trap in Forshaga.

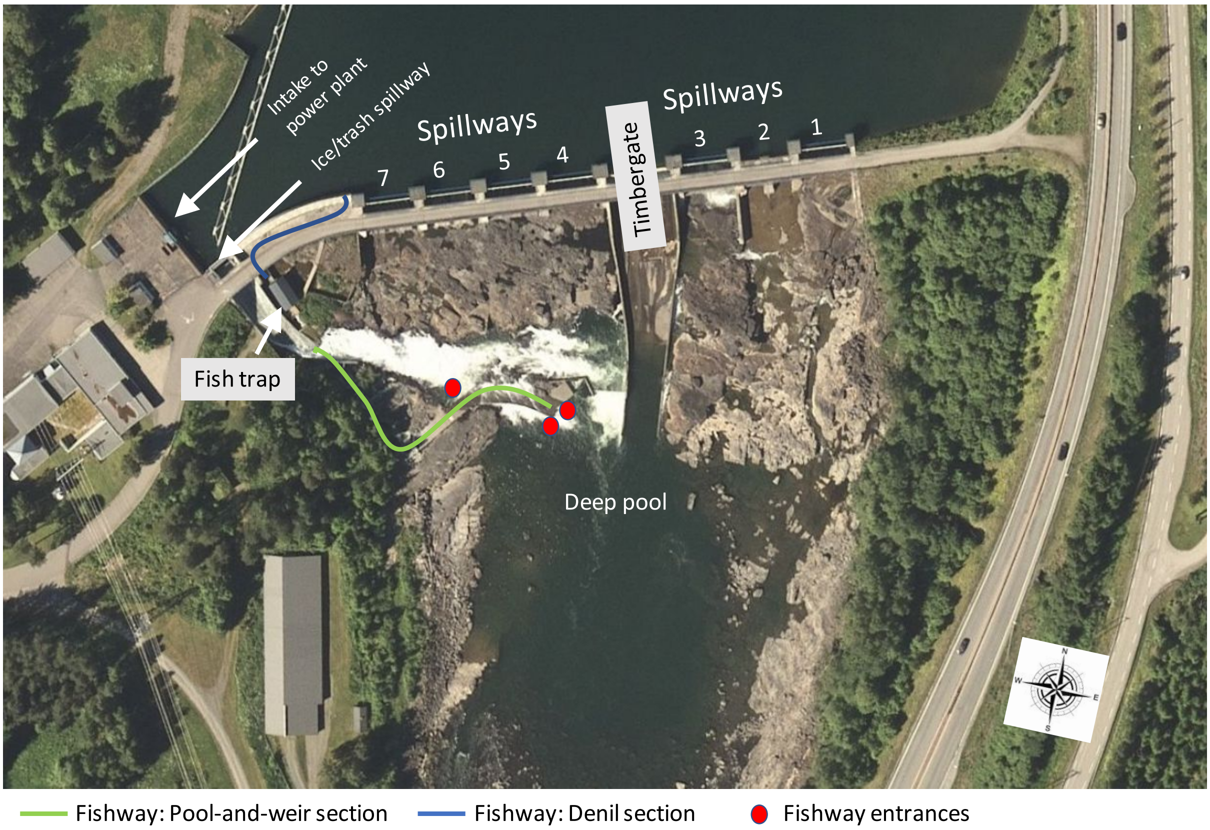


Figure 5. Aerial photo (google maps) of the power plant at Hunderfossen, Gudbrandsdalslågen, showing the intake to the power station and the placement of the seven spillways and the fishway solutions. The fish trap is located between the pool-and weir section (from the fishway entrances to the fish trap; in green) and the denil section (from the fish trap to the outlet; in blue).

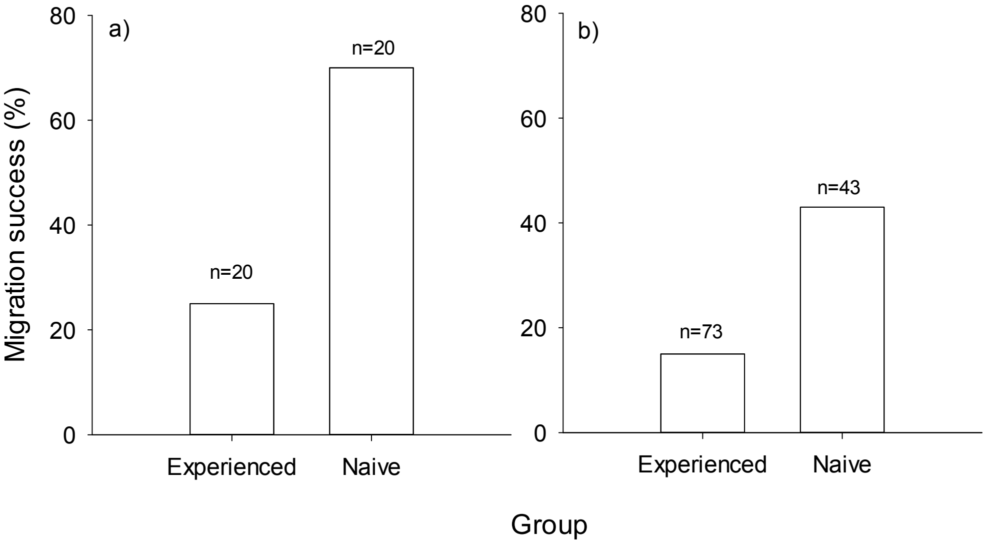
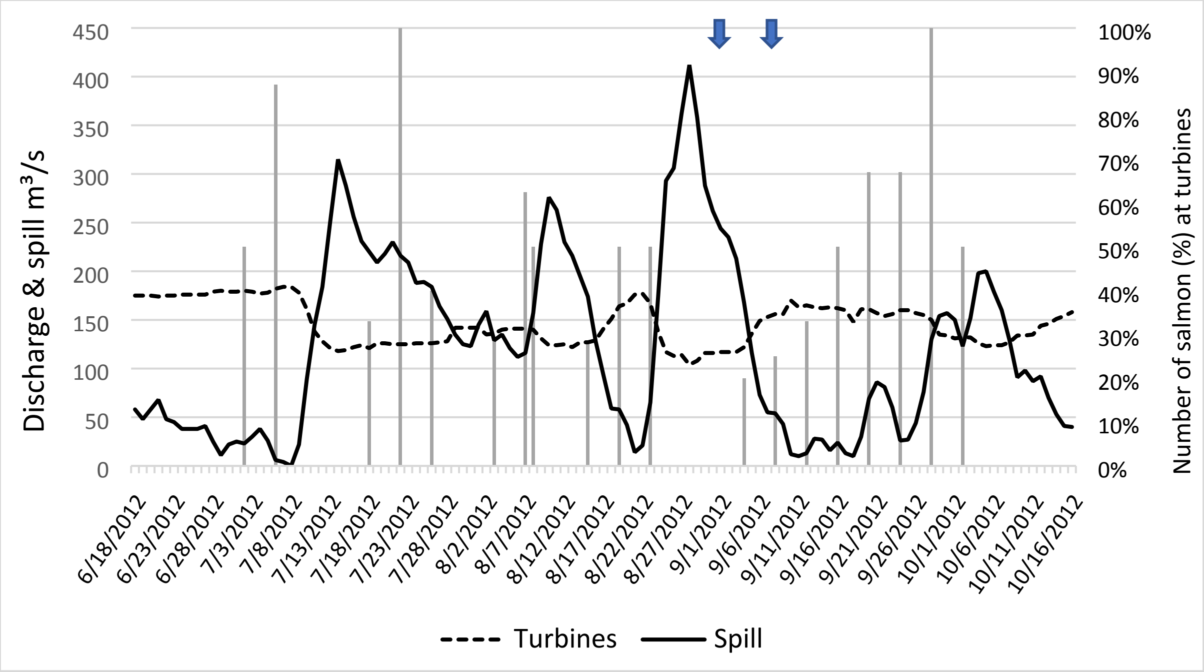
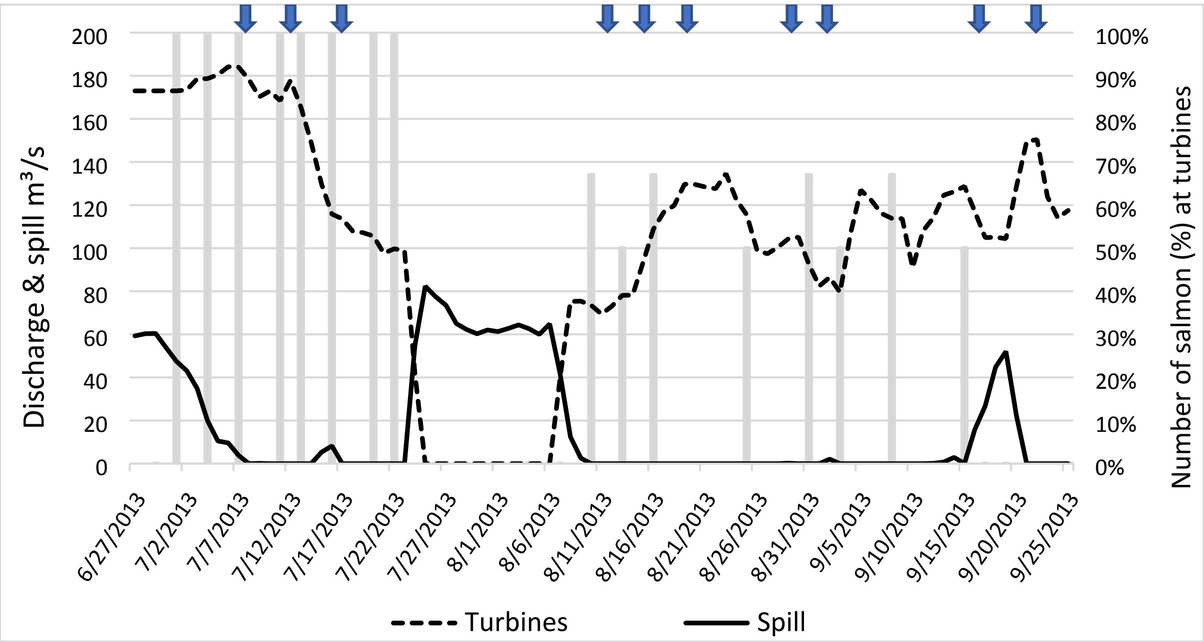


Figure 6. Percentage of naïve and experienced individuals of a) Atlantic salmon and b) brown trout that succeeded in entering the fishtrap at Forshaga and Hunderfossen dams, respectively. Total sample sizes are indicated above each histobar.



7a



7b

Figure 7. The number (% of the total number of salmon in the area at that time) of salmon (depicted by the histobars) observed in the vicinity of the turbine outlet (area 2 in Fig. 3) at Forshaga in 2012 (upper panel a) and 2013 (lower panel b). Arrows present times of salmon entering the fish trap.