Biotic and abiotic determinants of the ascent behaviour of adult Atlantic salmon transiting passable waterfalls

Authors

Robert J. Lennox[1, §], Eva B. Thorstad[2], Ola H. Diserud[2], Finn Økland[2], Steven J. Cooke[1], Ingar Aasestad[3], and Torbjørn Forseth[2]

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6

[2]Norwegian Institute for Nature Research, P. O. Box 5685, Sluppen, N-7485 Trondheim, Norway

[3]Lågendalsveien 2307, 3282 Kvelde, Norway

[§]Corresponding Author: Robert Lennox; Email: robertlennox9@gmail.com; telephone: 1-613-408-3474

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Abstract

The spawning migration of Atlantic salmon has been characterized by tracking salmon carrying electronic tags as they ascend rivers but still little is known about how natural obstacles such as waterfalls influence migratory behaviour and how such behaviours are mediated by various biotic (e.g., fish size) and abiotic (e.g., discharge, water temperature, barometric pressure) factors. The Norwegian river Numedalslågen is interrupted by natural waterfalls ranging in height from 2 to 6 m. We tagged 113 Atlantic salmon with radio transmitters in the estuary and used stationary radio telemetry stations to track fish. Ninety-one salmon were recorded in Numedalslågen, 39 of which remained in the river for spawning. Large salmon moved farther and faster upriver but also delayed longer and had lower daily probability to pass the second waterfall. Delay below and passage probability at the final, largest waterfall was affected by water discharge, wherein passage occurred when discharge was declining. Barometric pressure also influenced daily probability of ascent, albeit in opposite directions for each waterfall. Importantly, we also found that salmon with surgically implanted radio transmitters moved farther upriver on average and delayed less time below one of the waterfalls than those with externally attached transmitters. Although there is variance in timing arising from individual decision making, we showed that natural waterfalls delay progress of Atlantic salmon on their spawning migration and that both biotic (i.e. size) and abiotic (i.e. barometric pressure, discharge) factors influenced the salmon's decisions to pass waterfalls that they encounter.

Keywords- biotelemetry, waterfall, migration, exploitation, straying, salmonidae

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Introduction

Migration behaviour has evolved in all animal taxa and serves different functions among species (Dingle 1980, 2014). Migration behaviour often maximizes lifetime fitness (Dingle and Drake 2007), and migratory animals access multiple habitats to exploit spatiotemporal dynamic resources. Migratory animals are increasingly threatened by human developments that obstruct migration and limit access to key habitats (Lennox et al. 2016). Migratory barriers can include city buildings for birds (Hager et al. 2013), wind turbines for bats (Cryan and Brown 2007), and dams for fishes in freshwater systems (Kareiva et al. 2000; Roscoe and Hinch 2010; Noonan et al. 2012). Dams are constructed for flood control, irrigation, hydropower generation, among other reasons, and now number in the tens of thousands around the globe. These unnatural barriers can often delay (Jensen et al. 1986; Gowans et al. 1999) or disrupt (Tentelier and Piou 2011) migration (see Thorstad et al. 2008). Some dams are passable to fish by either being sufficiently small that jumping fish may ascend or by the provision of fish passage facilities intended to enable the upstream migration of migrants. Rivers are highly variable, and there are both local differences in gradient and hydrology as well as seasonal changes in river features, especially temperature and flow, that can be considered obstacles to migration (Thorstad et al. 2008).

Many rivers are now altered, challenging migration of many fishes (Lennox et al. 2016). Rivers also have natural challenges to migration, obstacles whose features provide important information about natural variation in migration behaviour within fish species. Atlantic salmon

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(*Salmo salar*) provides a good model species for studying migration behaviour because it is widely distributed in the North Atlantic Ocean (MacCrimmon and Gots 1979), is economically and culturally important throughout its range (Stensland 2010), is a species at risk in many jurisdictions (Parrish et al. 1998, ICES 2017), and has a well-studied upriver migration biology (Jensen et al. 1986; Økland et al. 2001; Baisez et al. 2011; Richard et al. 2014; Kristinsson et al. 2015). The current paradigm for Atlantic salmon migration has been developed from electronic tagging studies (Økland et al. 2001; Richard et al. 2014) in rivers with low gradient and relatively linear migrations between the tagging site and spawning grounds for fish. Økland et al. (2001) observed salmon rapidly ascending rivers in an active migration phase until they reached their eventual spawning site, where they held in pools for weeks or months until reproduction (Heggberget 1988). Richard et al. (2014) similarly suggested a rapid ascent of the river, albeit with holding occurring in favourable pools that may not necessarily be near the spawning sites. In many rivers, the spawning grounds are beyond natural obstacles such as high velocity gorges (Lennox et al. 2015) or waterfalls (Kennedy et al. 2013; Kristinsson et al. 2015) that many salmon ascend during the migration. How these natural obstacles alter the migration patterns of salmon in freshwater is under-represented as a component of the migration biology of salmon.

High gradient rivers may challenge salmon migration, and identification of the factors that influence upriver migration can therefore contribute to a more complete model of fish migration biology by contrasting patterns and strategies used by fish under different hydraulic environments. Moreover, documenting the passage patterns and success of salmon at natural obstacles will advance understanding of salmon behaviour at manmade obstacles such as fishways by providing evidence of natural behaviour for contrast (Jensen et al. 1986; Gowans et al. 1999). Numedalslågen River in southern Norway includes waterfalls that salmon can ascend to spawning grounds, providing a venue in which to investigate the migration behaviour of Atlantic salmon in a river punctuated by waterfalls. We used radio-tagging and linear regression models to investigate the rate of displacement, delays below waterfalls, and probability of waterfall passage during two migratory seasons in Numedalslågen.

Methods

Study Site

Numedalslågen measures 336 km and is Norway's third longest river, draining a total catchment area of 5670 km^2 and meeting the Atlantic Ocean at 59.043604, 10.064923. The main stem of the river consists of 72 km accessible to salmon up to Hvittingfoss, in addition to 55 km of major tributaries of the river including the Hagnes, Dale, and Herland Rivers. Salmon spawn throughout this 72 km stretch and in tributaries. In July and August, the maximum temperatures in the river attain 15-25 °C. The river is developed for hydropower production, but all power stations are upstream of the salmon producing stretch. The river has relatively high fish species richness and includes migratory Atlantic salmon, which are of high cultural importance, supporting recreational hook and line fishing in the river, and a method of traditional recreational fishing that is endemic to the watershed. The river is interrupted by waterfalls that salmon ascend before reaching the end of the migratory stretch at Hvittingfoss: Abyfoss (6 m), Holmfoss (2 m; Figure 1A), and Hoggtveita (3 m; Figure 1B). Flow in the river and at these waterfalls is partially controlled by release of water through the power generating station at rates set by Norwegian Royal Decree. Flow thresholds were updated in 2001 to stipulate minimum flow requirements at the town of Kongsberg (upstream of the salmon producing stretch), from May 25 – June 30 (65 $m^3 s^{-1}$), July 1 – July 30 (50 $m^3 s^{-1}$), and August 1 – August 31 (40 $m^3 s^{-1}$). The contribution from non-regulated parts of the watershed at the river mouth is more than 50%, so the river is largely impacted by natural variation in water discharge.

Sampling

A total of 113 salmon were intercepted before they entered the Numedalslågen River in 2003 (N = 64; 25 male, 38 female, 1 unknown; 72 ± 12.8 cm) and 2007 (N = 49; 11 male, 37 female, 1 unknown; 81 ± 9 cm) throughout the season (May 22 – August 19, 2003; May 21 – September 5, 2007). Fish were captured in bag nets in the Larviksfjord 3.0 km from the Numedalslågen River estuary bridge. Only undamaged fish swimming freely in the nets were selected for the study. To increase sample size, four of the salmon in 2007 were captured with drift nets in the river and transported to the estuary for tagging with the other group. Fish were held in a small net pen for 0-10 days in 2003 and up to 15 days (mean = 6 d) in 2007 before tagging and release.

For tagging, fish were placed in a 0.5 mL/L 2-phenoxy-ethanol bath (EEC No. 204 589-7) for three minutes for anaesthesia and then an external radio transmitter (model F2120 and F1970 from Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA) was attached with wire passed through the dorsal musculature below the dorsal fin. The transmitters were rectangular and measured 19 × 50 × 9 cm with a weight in air of 15 g in 2003, and 13 × 29 × 7 mm with a weight in air of 4.3 g in 2007. In consideration that external tags were smaller in 2007 than 2003, we checked whether there were differences associated with tag sizes before pooling both together and found no effects. Therefore, the size of the tag is not considered in any analyses comparing external and internal tags. In 2003, 38 of the individuals were implanted with radio transmitters (ATS model F1830, cylindrical shape, 12 x 53 mm, 11 g in air) in the coelom instead of external attachment. These transmitters were surgically implanted in anaesthetized fish by making a 2.5 cm long incision on the right side of the abdomen behind the pectoral fins 1-3 cm from the centre, inserting the transmitter, drawing the antenna through a separate hole in the skin made by a surgical cannula, and suturing the incision with non-absorbable silk (Ethicon 2/0). During the surgery, the fish were held supine with water pumped over the gills. Individual fish were identified by using radio transmitters with unique combinations of frequency (within the 142.003-142.493 MHz range) and pulse rate (40 to 60 pulses per minute). The transmitters had a guaranteed battery life of 94-129 d.

Before tagging, sex was assigned to each fish by visual assessment of secondary sexual traits, was measured, and was sampled for 2-3 scales posterior to the dorsal fin near the midline. Scale samples were visually analyzed to determine the origin of the tagged salmon (wild or cultivated from hatcheries; none were identified as escaped from commercial marine salmon farms). After tagging, fish were transferred to a recovery tank until they could swim normally and be released into the sea.

Tracking

Migration of salmon in Numedalslågen was monitored by stationary and manual radio tracking. Stationary data logging stations (ATS DCCII Datalogger, with four or nine element Yagi antennas at each site) were established at Åbyfoss, Holmfoss, and Hoggtveita (Figure 2). The Bommestad station was established to identify the entrance of fish into the river and was placed sufficiently upriver to avoid incursion of tidal water that would attenuate radio signals and reduce the probability of registering salmon. The stations at Holmfoss and Hoggtveita were established to monitor the passage of the waterfalls. Delays were defined as time spent in the pool below the waterfall. Because the Åbyfoss waterfall is below Bommestad, the delay and passage time of fish at this waterfall were calculated using manual tracking positions. Technical problems in 2007 caused the stationary data loggers at Bommestad (July 15-22), Holmfoss (August 19-22), and Hoggtveita (July 31 – August 13) to be out of operation. Positions were generated (approximate accuracy ± 150 m) by manual radio tracking of fish with an ATS R2100 radio receiver at three-day intervals (May 24 - October 1 in 2003 and May 27 – October 25 in 2007) and then weekly, until November 26 in 2003 and until December 28 in 2007. Radio tracking was also conducted in the nearby Drammen River (59.739314, 10.216454) September

17, 2007 and November 21-22, 2007. Spawning likely occurs in early November (Heggberget 1988); therefore, positions on November 2 were taken to be representative of the final spawning position of salmon in the river.

Environmental Monitoring

Recordings of water flow at Holmfoss and water temperature at Bommestad were provided by Norwegian Water Resources and Energy Directorate. Daily rainfall was registered in Larvik (59.058320, 10.121998) and Kongsberg (59.624465, 9.637968) and atmospheric barometric pressure was recorded in Kongsberg.

Analyses

Our first set of analyses focused on using radio tracking data to calculate the timing of movements by Atlantic salmon within Numedalslågen. From detection data, we calculated the timing of river entry, the spawning site (km upriver), rate of displacement in kilometres per day (log transformed to suit the assumption of normally distributed residuals), and the time required to attain the maximum position in the river (d). Each of these analyses was implemented with linear models with the *lm* function in R (R Core Team 2017) considering fish body size, sex, date first recorded in the river, origin (hatchery or wild), and tag type (externally attached or implanted) as fixed effects. To account for variance among years the data should ideally incorporate a random intercept, i.e. fit a mixed effects model with year as random factor, however, with only two levels (2003 and 2007) the model cannot effectively account for the variance so we considered year as a fixed effect. In consideration of possible effects of the timing of river entry and distance traveled, these variables were also tested as fixed effects that could explain the displacement by the migrating fish. We checked for violation of independence in case of temporal autocorrelation but found no evidence of this in the model. The final model was selected by backwards selection from the initial model by considering AIC improvement and significant fixed effects. Because there was some skewedness in the distribution of the response variables, we also considered a generalized linear model for the number of days to enter the river using rapid (< 2 d to enter) or latent (> 2 d to enter) as a binned binomial response variable using the *glm* function in R.

Our second set of analyses was to investigate the factors related to waterfall passage. The first aspect we modelled was the number of days delayed below each waterfall. The second was the daily probability of passage, which was modeled by generalized linear mixed effect model (*glmer* function from the *lme4* package in R), with fish ID as random factor to account for temporal pseudoreplication because we have repeated measurements from the same individual. Owing to poor resolution of passage data at Åbyfoss, models were only constructed for the Holmfoss and Hoggtveita waterfalls. Fixed effects hypothesized to influence the number of delay days and daily passage probability were body size, sex, origin, tag type (only for 2003 model), day of year, days since arrival, barometric pressure, precipitation at Larvik and at Kongsberg, water discharge and temperature, change in water discharge and temperature since previous day, relative mean discharge (equal to the day's discharge minus the average discharge recorded each day since arrival at waterfall), and relative minimum discharge (equal to the day's discharge minus the minimum discharge recorded on each day since arrival at waterfall). Means are presented ± standard deviation.

Results

Summary

Among the 113 salmon tagged, six were neither recorded by radio receivers nor recaptured and may have entered/ spawned in distant rivers or been recaptured without being reported or died for other reasons. Eight individuals were captured in marine fisheries and eight in river fisheries (Rivers Drammen and Glomma) and harvested without entering Numedalslågen. Ninety-one (81%) salmon (77 ± 12 cm; 30 M, 60 F, 1 unknown) were recorded in Numedalslågen on average 3.70 ± 9.38 d after tagging (range = 0.19 – 70.52 d). The majority of these (56%) entered within 1 d of tagging. We did not find any significant relationships between time from release to entry of River Numedalslågen and sex, body size, tag type, or origin using linear regression. In consideration of skewedness in the distribution of entry times by using rapid (< 2 d) or latent (> 2 d) entry as a binomial response, and when only considering rapid enterers, there were no significant effects. However, the later in the season the fish was released, the faster it entered ($t = -2.08$, $P = 0.04$).

Considering the 91 salmon that were recorded in Numedalslågen, 24 (26%) permanently exited the river, five of which were harvested or tracked by manual tracking in the nearby Drammen River. More salmon tagged in 2003 (16 of 50; 32%) than 2007 (8 of 40; 20%) exited the river. Twenty-eight of the 67 salmon that remained in Numedalslågen (42%) were harvested by fishers (17 [25%] by hook-and-line anglers, 11 [16%] in the traditional fishery). Therefore, 39 salmon were recorded in Numedalslågen during the spawning period, on average 34 ± 18 km upriver. The final model for spawning position was reduced to only include fish body size and tag type. Therefore, spawning position was not different between male and female or between cultured and wild salmon, or dependent on timing of river entry. Fish with implanted transmitters spawned farther upriver than those with externally attached tags ($t = 2.11$, $P = 0.04$). Longer salmon also spawned significantly farther upriver ($t = 3.07$, $P < 0.01$; Table 1).

The salmon that remained in the river through spawning moved at an average ground rate of displacement of 10.3 km/d from river entry to spawning grounds (Figure 3). There were no significant predictors of displacement except for year, in which fish were delayed longer in 2007 (when there was a flood event, see below). The number of days for a salmon to reach its maximum upriver position was not affected by sex, tag type, or whether the fish was cultivated or wild and these variables were excluded from the final model. However, displacement was positively influenced by fish body size ($t = 2.39$, $P = 0.02$) in a univariate model reduced based on AIC. This suggests that larger fish moved upriver more quickly than smaller fish. There was equivalent evidence to suggest that the date of first record in the river negatively influenced displacement, with later fish swimming slower (t = -2.41; $P < 0.02$). The multivariate model with both factors fit poorly because of negative collinearity.

Waterfall Passage

Åbyfoss, Holmfoss, and Hoggtveita were obstacles to upriver migration of salmon in Numedalslågen based on observations of delays below these obstacles (see below) compared to fast displacement between the waterfalls (Table 2, 3). Within three days, 64% of wild and 58% of cultivated salmon ascended Åbyfoss, but a regression model to explain the timing of ascent was not possible because of low resolution of ascent timing without the stationary loggers.

Delay Below Waterfall

Average delay of wild salmon at Holmfoss was 15 ± 9 d (range = 0 – 28 d) and was 29 ± 29 d (range = 10 – 78 d) for cultivated salmon. Six of 12 wild salmon and 2 of 5 cultivated salmon exhibited downstream and upstream searching behaviour after encountering Holmfoss and one of the cultivated salmon returned to sea. The best linear model of 2003 salmon delaying at Holmfoss excluded sex, cultivation, and environmental variables. Larger fish delayed longer under Holmfoss (t = 2.68, P = 0.02) and delays were longer later in the season (t = 8.80, $P < 0.01$). Fish with external tags also delayed longer than fish with implanted tags (t = -4.47, $P < 0.01$; Table 4).

Seven wild salmon ascended Hoggtveita in 2003 after 15 ± 16 d (range = 1 – 38 d). Whereas the delay days were predicted by body size, day of year, and tag type for salmon at Holmfoss, these variables were excluded from the final model for delay days at Hoggtveita. Because the tag type had no effect on the model, it was constructed with data from both 2003 and 2007. For both years, 15 salmon ascended after 8 ± 12 d (range = 0-38 d). The best model included only the two discharge variables, the relative mean ($t = -12.7$, $P < 0.01$) and relative minimum ($t = 3.85$, $P < 0.01$) discharges, suggesting that salmon delayed at the waterfall until days when the discharge attained values lower than they had experienced since arrival. However, because the two variables were correlated, we conclude that a univariate model with only relative mean discharge ($t = -8.46$, $P < 0.01$) as the best model for ease of interpretation.

Daily Probability of Passage

Salmon ascended Holmfoss at flows up to 235 $m^3 s^{-1}$ and as low as 57 $m^3 s^{-1}$. Average water flow at passage of Holmfoss was 107 ± 75 $m^3 s^{-1}$. Salmon ascended both when flows were rising (N = 12) and declining (N = 15), as well as when they were stable (N = 6). Various water flows were available to fish while they were resting below Holmfoss, and monitoring of the flows concurrently with radio tracking suggested that there were potential opportunities (i.e. favourable flows) for salmon to ascend that they did not capitalize on. The final model considering the daily probability to ascend Holmfoss for 2003 and 2007 combined excluded water discharge variables and was reduced to include only body size ($z = -2.19$, $P = 0.03$) and atmospheric pressure (z = -1.91, P = 0.06); although barometric pressure was not significant its inclusion improved the model by ΔAIC = 13.1. Therefore, longer fish had less daily probability to pass Holmfoss than shorter salmon on any given day, which aligns with the finding that longer fish experienced longer delay along with some evidence that probability of passage was higher on days with low barometric pressure (Table 5).

Passage of Hoggtveita was undertaken by salmon at water discharges between 59 and 140 $m^3 s^{-1}$ (mean = 86 ± 25 $m^3 s^{-1}$). Ten of the fifteen salmon that ascended Hoggtveita did so when flows were in decline. Apparently, the longer delay at Hoggtveita increased the discharge that salmon were willing to ascend at. Similar to salmon at Holmfoss, salmon experienced a range of flows while holding in the pool below Hoggtveita. There was also evidence that the individual fish's experience influenced the delay below Hoggtveita given there was a significant negative relationship between probability of passage and the water discharge (z = -3.29, P < 0.01) as well as the relative mean discharge (z = -3.16, P < 0.01). In fact, all except one salmon that ascended Hoggtveita did so at the lowest discharge measured during their stay below the fall (Figure 4). As with Holmfoss, the barometric pressure was also included in the final model but in this instance, it was a significant predictor of daily passage probability (z = 5.40, P < 0.01); however, the positive relationship suggested that passage probability was higher on days of high pressure, which was the opposite of what was observed at Holmfoss (Table 6).

Behaviour during a flood event

Between June 28 and July 6, 2007, water flows increased from 156 to 1020 m/s^3. Wild salmon (N = 7) moved downstream on average 2.1 km (range 0.6 – 3.7 km) during the flood. As above, the average rate of displacement, kilometres per day, was smaller in 2007 than in 2003, likely because of this flooding. All salmon survived the flood and moved back upriver. They were back to the site where they resided before the flood within 1-2 weeks, i.e. when the water discharge was decreasing again after the flood. One cultivated salmon exited the river during the flood and returned later in the season.

Discussion

Anadromous fishes are admired for their feats of stamina and strength in ascending complex hydraulic landscapes for spawning. Salmonids can travel long distances in high gradient rivers, beyond rapids and waterfalls and now also fish passage structures (Gowans et al. 1999). Ascent of such natural and anthropogenic migration obstacles is energetically taxing (Booth et al. 1997; Burnett et al. 2014) and fish may opt to migrate during favourable conditions to economize energy expenditure during the migration (Jensen et al. 1986; Richard et al. 2014). Here, we revealed that salmon naturally delay at waterfalls during the upriver migration; once they overcame the obstacle, they resumed rapid movement upriver towards spawning grounds or until another obstacle was encountered. This expands on the general model of Atlantic salmon upriver migration proposed by Økland et al. (2001); our findings corroborate the rapid ascent of the river by salmon towards spawning grounds but add that natural barriers impose significant natural delays on the migration that can be difficult to predict, not unlike what is sometimes observed at anthropogenic barriers equipped with fish passage facilities. Ultimately, salmon that encountered obstacles in our study still arrived early at spawning grounds and hold near the spawning site for an extended period, as in Økland et al. (2001).

Most of the salmon tagged in the estuary of Numedalslågen entered the river soon after tagging and commenced their freshwater migration. Size was consistently an important factor predicting migration behaviour of the salmon, a significant predictor of both distance traveled upriver and the number of days elapsed before reaching the spawning site. Fitness is related to size for this fish insofar as large individuals are endowed with greater reproductive capital (Heinimaa and Heinimaa 2004). The asset protection principle (Clark 1994) suggests that large fish, having higher fitness, should forego foraging opportunities at sea earlier than small individuals for the relative safety of freshwater; indeed, large fish return earliest and migrate farther (Laughton and Smith 1992). However, body size did not predict timing of river entry potentially because the fish that were captured for tagging were already on the way to enter the river and therefore not a random sample to test this on. Longer salmon are capable of faster swimming (Thorstad et al. 2008), and therefore should move more quickly than smaller counterparts (Laughton and Smith 1992); however, large body size also seems to increase susceptibility to delays associated with low flow (Jonsson et al. 1990). Precisely why the longest tagged salmon would move farther upriver is unknown (Fleming 1996). Interestingly, the finding that longer fish moved faster and farther contradicts findings from the waterfall passage (covered later), which showed longer delays and lower probability of passage of the Holmfoss waterfall of long salmon, which is consistent with findings at a waterfall in the Laxa River (Kristinsson et al. 2015).

Although most of the tagged salmon spawned in Numedalslågen, many also entered neighbouring rivers. Straying is uncommon in Atlantic salmon but some fish do migrate to non-natal rivers (Jonsson et al. 2003; Ulvan et al. 2017). The proximity of Numedalslågen to the Drammen River might increase the probability of non-native fish to intrude given that there is a hatchery in Drammen and cultivated salmon tend to have less accurate homing to natal rivers (Jonsson et al. 1991). Havn et al. (2015) also identified salmon exiting the southern Norwegian river Otra and entering nearby rivers throughout the summer and it is probably not uncommon for salmon to move between local rivers during the migration. Numedalslågen was subjected to wood pulp pollution during 2003 and a flood in 2007 that affected the movement of fish in the river. Effects of wood pulp pollution on salmon migration was detailed in Thorstad et al. (2005) and could account for why more fish exited the river in 2003 than in 2007. Increased flows may stimulate upriver migration (Taylor and Cooke 2012), but extreme flow events can be stressors (Costa et al. 2017) and floods could disturb migrating fish, as we observed in Numedalslågen. Given that this is one of the first studies to document the migration of salmon during flood events, it is particularly notable that fish remained in the river and continued migrating once flows normalized.

Salmon delayed at both the Holmfoss and Hoggtveita waterfalls for variable durations and there were considerable differences among individuals in timing of their ascent. Although we were only able to model the external variables, there is also individual decision making that creates intraspecific variation, which is likely important to the overall equation given the relatively low explanatory power of the models. Nonetheless, we were able to reveal important external determinants of delays. Delays of salmon at both Holmfoss and Hoggtveita were longer than delays recorded at waterfalls in the Icelandic River Laxa, where salmon were delayed only up to 19 d (Kristinsson et al. 2015). At Hoggtveita, delays apparently extended until the water discharge at the fall decreased to an acceptable rate, which was different depending on the individual's experience since reaching the fall. Salmon evidently benefit by delaying at waterfalls rather than ascending hastily. Interestingly, salmon passed Holmfoss at higher discharges than the discharges at which they ascended Hoggtveita, potentially because the latter is a larger, more energetically demanding fall. Salmon were active at much higher discharges than were salmon in the Scottish River Tummel (moved into entrance chamber only up to 65.6 m^3 s^{-1}) and paused migration at lower discharges than identified elsewhere. In Norwegian rivers Vefsna and Målselva, salmon ascended fish ladders at up to 300 m^3 s^{-1} (Andeson and Langeland 1971; Jensen et al. 1986). Correspondingly, catches of salmon by anglers apparently decreases beyond 250 m^3 s^{-1}, approximately the highest flow at which we recorded waterfall ascent in Numedalslågen. Although water discharge seems important to the passage of salmon, water discharge was only a significant predictor of passage probability at the larger waterfall where perhaps the physical exertion would be more significant at high flows.

Although temperature has elsewhere been correlated with salmon passage (Gowans et al. 1999; Kennedy et al. 2013; Kristinsson et al. 2015), barometric pressure was the only consistent predictor variable included in final models explaining daily passage probability at both waterfalls, yet it appeared to act in opposite ways at the two falls. Evidence that fish behaviour is manipulated by barometric pressure is equivocal (Banks 1969), although birds may use it to forecast weather (Bauer et al. 2011). In fact, significance of pressure is likely explained by correlations with other potentially relevant meteorological factors such as cloud coverage, precipitation, and water temperature (Holmsten 2015). Pressure could therefore be used in forecasting oncoming temperatures and water discharges caused by insolation and precipitation. Why there were opposite effects of barometric pressure at the two waterfalls is mysterious but is consistent with the observation that salmon behaviour was different at the two waterfalls, with different flow requirements preferred for passage. Local knowledge is that salmon cannot pass Hoggtveita beyond 150 $m^3 s^{-1}$, so low water levels and high pressure favour movement of salmon at this waterfall whereas high water levels stimulate migration in other reaches. High water discharges present a migration obstacle and salmon clearly delay their migration to pass at favourable flows. Obstacles may differ substantially in their permeability to salmon both within and among systems; each obstacle should therefore be considered independently when modeling the upriver passage of salmon.

Relative to surgically implanted tags, external tags reduced distance travelled and prolonged delays below the Holmfoss waterfall. Transmitter attachment methods are known to affect the swimming performance of fish (Bridger and Booth 2003; Jepsen et al. 2015). Lewis and Muntz (1984) found that external tagging increased both tail and opercular beat frequency of fish and Arnold and Holford (1978) quantified a decrease in swimming speed, suggesting that an increase in power output to compensate for drag caused by external transmitters. Contrastingly,

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Thorstad et al. (2000) identified no impact of external or implanted transmitters on the swimming performance of Atlantic salmon in swim flumes. However, few studies have reported on comparisons of wild fish performance between tag types or tagging methods. The effects of external transmitters may be variable depending on water velocity, with negative effects increasing with flows. If so, then ascent of waterfalls would be negatively impacted by external transmitters compared to implanted transmitters. Compromises in speed of the procedure and invasiveness of tagging are necessary when deciding how to tag salmon (Jepsen et al. 2015). We suggest that the environmental conditions that they will encounter must factor into the decision, with internal tags preferable where salmon are expected to encounter high flows (Thorstad et al. 2000), but with the warning that new surgical incisions may not heal well for salmon negotiating a river with waterfalls such as Numedalslågen (as shown by two recaptured fish in this study). Gastric tagging was not evaluated here but is a rapid method of non-surgically implanting a tag; however, gastric tags may damage the stomach of the fish (Dick et al. 2017) and the long-term effects are unknown, potentially making them unsuitable for iteroparous species.

Radio telemetry enabled us to investigate the natural behaviour and performance of Atlantic salmon past natural obstacles in a regulated river. Although our analyses lack information about individual decision making that creates variation, we were able to construct models that effectively explain some of the variation in waterfall ascent based on external, measurable variables. Wild and cultivated Atlantic salmon in Numedalslågen were capable of ascending each natural obstacle in the river under the normal flow regime of the river and make it onto spawning grounds (see also Kennedy et al. 2013). Waterfalls are natural features in some rivers and natural flow regimes are characterized by variability caused by annual differences in precipitation, temperature, and snowpack (Poff et al. 1997) and it is known that waterfalls naturally cause delays of salmon (Jensen et al. 1986), particularly during early season flood events. Although we were able to identify significant predictors of waterfall ascent, models are limited in the amount of variance that they can explain because many different factors (e.g. experience, motivation, social impacts by conspecifics, Dodson 1988) can affect migration rate and are difficult to quantify. Nonetheless, our findings are consistent with other assessments of migrating Atlantic salmon and provide an important update to the general model of the spawning migration of Atlantic salmon. Given that salmon delay at waterfalls and may become aggregated, vulnerability to angling may increase and local closures may be considered to protect salmon as they prepare to ascend these challenging areas of rivers. In rivers such as Numedalslågen where the discharge can be manipulated by hydropower generating stations, research is needed to understand how modifications to the flow regime in the river can affect the timing of migration and spawning success of salmon in the river in ways that differ from the natural flow regime.

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References

Arnold, G. P., & Holford, B. H. (1978). The physical effects of an acoustic tag on the swimming performance of plaice and cod. *ICES Journal of Marine Science*, *38*(2), 189-200.

Baisez, A., Bach, J. M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M., & Laffaille, P. (2011). Migration delays and mortality of adult Atlantic salmon Salmo salar en route to spawning grounds on the River Allier, France. *Endangered species research*, *15*(3), 265-270.

Bauer, S., Nolet, B. A., Giske, J., Chapman, J. W., Åkesson, S., Hedenström, A., & Fryxell, J. M. (2011). Cues and decision rules in animal migration. In: Milner-Gulland, E. J. et al. (eds), Animal migration: a synthesis. Oxford University Press, pp. 68–87.

Booth, R. K., McKinley, R. S., Økland, F., & Sisak, M. M. (1997). In situ measurement of swimming performance of wild Atlantic salmon (Salmo salar) using radio transmitted electromyogram signals. *Aquatic Living Resources*, *10*(4), 213-219.

Bridger, C. J., & Booth, R. K. (2003). The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Reviews in Fisheries Science*, *11*(1), 13-34.

Burnett, N. J., Hinch, S. G., Braun, D. C., Casselman, M. T., Middleton, C. T., Wilson, S. M., & Cooke, S. J. (2014). Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. *Physiological and Biochemical Zoology*, *87*(5), 587-598.

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, *5*(2), 159-170.

Costa, M. J., Lennox, R. J., Katopodis, C., & Cooke, S. J. (2017). Is there evidence for flow variability as an organism-level stressor in fluvial fish? *Journal of Ecohydraulics*, *2*(1), 68-83.

Cryan, P. M., & Brown, A. C. (2007). Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines. *Biological Conservation*, *139*(1), 1-11.

Dick, M., Eliason, E. J., Patterson, D. A., Robinson, K. A., Hinch, S. G., & Cooke, S. J. (2018). Short-term Physiological Response Profiles of Tagged Migrating Adult Sockeye Salmon: A Comparison of Gastric Insertion and External Tagging Methods. *Transactions of the American Fisheries Society*, *147*(2), 300-315.

Dingle, H. (1980) Ecology and evolution of migration. In Cauthreaux, A., eds., Animal Migration, Orientation, and Navigation. Academic Press, New York, pp. 1–101.

Dingle, H. (2014). *Migration: the biology of life on the move*. Oxford University Press, USA.

Dingle, H., & Drake, V. A. (2007). What is migration? *Bioscience*, *57*(2), 113-121.

Dodson, J. J. (1988). The nature and role of learning in the orientation and migratory behavior of fishes. *Environmental Biology of Fishes*, *23*(3), 161-182.

Erkinaro, J., Økland, F., Moen, K., & Niemelä, E. (1999). Return migration of the Atlantic salmon in the Tana River: distribution and exploitation of radiotagged multi-sea-winter salmon. *Boreal Environment Research*, *4*, 115-124.

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Erkinaro, J., Økland, F., Moen, K., & Niemelä, E. (1999). Return migration of the Atlantic salmon in the Tana River: distribution and exploitation of radiotagged multi-sea-winter salmon. *Boreal Environment Research*, *4,* 115-124.

Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M., & Mathes, M. T. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology*, *81*(6), 697-708.

Fiske, P., Lund, R. A., Østborg, G. M., & Fløystad, L. (2001). Escapees of reared salmon in coastal and riverine fisheries in the period 1989–2000. *NINA Oppdragsmelding*, *704*, 1-26.

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries*, *6*(4), 379-416.

Gowans, A. R. D., Armstrong, J. D., & Priede, I. G. (1999). Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. Journal of Fish Biology, 54(4), 713-726.

Hager, S. B., Cosentino, B. J., McKay, K. J., Monson, C., Zuurdeeg, W., & Blevins, B. (2013). Window area and development drive spatial variation in bird-window collisions in an urban landscape. *PloS one*, *8*(1), e53371.

Havn, T. B., Uglem, I., Solem, Ø., Cooke, S. J., Whoriskey, F. G., & Thorstad, E. B. (2015). The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon Salmo salar during spawning migration. *Journal of fish biology*, *87*(2), 342-359.

Heggberget, T. G. (1988). Timing of spawning in Norwegian Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *45*(5), 845-849.

Heinimaa, S., & Heinimaa, P. (2004). Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic River Teno. *Boreal Environment Research*, *9*(1), 55-62.

Holmsten, A. (2015). The impact of abiotic factors on daily spawning migration of Atlantic salmon (*Salmo salar*) in two north Swedish rivers. MSc Thesis, Swedish University of Agricultural Sciences.

ICES 2017. Report of the Working Group on North Atlantic Salmon (WGNAS). 29 Mars -7 April 2017. Copenhagen, Denmark. ICES CM 2017/ACOM:20: 1-296

Jensen, A. J., Heggberget, T. G., & Johnsen, B. O. (1986). Upstream migration of adult Atlantic salmon, *Salmo salar* L., in the River Vefsna, northern Norway. *Journal of Fish Biology*, *29*(4), 459-465.

Jepsen, N., Thorstad, E. B., Havn, T., & Lucas, M. C. (2015). The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. *Animal Biotelemetry*, *3*(1), 49.

Jonsson, B., Jonsson, N., & Hansen, L. P. (1991). Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, *98*(1-3), 69-78.

Jonsson, B., Jonsson, N., & Hansen, L. P. (2003). Atlantic salmon straying from the River Imsa. *Journal of Fish Biology*, *62*(3), 641-657.

Jonsson, N., Jonsson, B., & Hansen, L. P. (1990). Partial segregation in the timing of migration of Atlantic salmon of different ages. *Animal Behaviour*, *40*(2), 313-321.

Kareiva, P., Marvier, M., & McClure, M. (2000). Recovery and management options for spring/summer chinook salmon in the Columbia River Basin. *Science*, *290*(5493), 977-979.

Kristinsson, K. Ó., Gudbergsson, G., & Gislason, G. M. (2015). Variable migration and delay in two stock components of an Atlantic salmon population. Environmental Biology of Fishes, 98(6), 1513-1523.

Laughton, R. & Smith, G. W. (1992). The relationship between the date of river entry and the estimated spawning position of adult Atlantic salmon (Salmo salar L.) in two major Scottish east coast rivers. In Wildlife Telemetry: Remote Monitoring and Tracking of Animals (Priede, I. G. & Swift, S. M., eds.), pp. 423–433. New York: Ellis Horwood.

Lennox, R. J., Chapman, J. M., Souliere, C. M., Tudorache, C., Wikelski, M., Metcalfe, J. D., & Cooke, S. J. (2016). Conservation physiology of animal migration. *Conservation Physiology*, *4*(1), cov072.

Lennox, R. J., Uglem, I., Cooke, S. J., Næsje, T. F., Whoriskey, F. G., Havn, T. B., Ulvan, E., Solem, Ø., & Thorstad, E. B. (2015). Does catch-and-release angling alter the behavior and fate of adult Atlantic Salmon during upriver migration? *Transactions of the American Fisheries Society*, *144*(2), 400-409.

Lewis, A. E., & Muntz, W. R. A. (1984). The effects of external ultrasonic tagging on the swimming performance of rainbow trout, Salmo gairdneri Richardson. *Journal of Fish Biology*, *25*(5), 577-585.

Lund, R. A., Økland, F., & Hansen, L. P. (1991). Farmed Atlantic salmon (Salmo salar) in fisheries and rivers in Norway. *Aquaculture*, *98*(1-3), 143-150.

MacCrimmon, H. R., & Gots, B. L. (1979). World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Board of Canada*, *36*(4), 422-457.

Mäkinen, T. S., Niemelä, E., Moen, K., & Lindström, R. (2000). Behaviour of gill-net and rod-captured Atlantic salmon (Salmo salar L.) during upstream migration and following radio tagging. *Fisheries Research*, *45*(2), 117-127.

Noonan, M. J., Grant, J. W., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, *13*(4), 450-464.

Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R. S., & Thorstad, E. B. (2001). Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology*, *59*(4), 862-874.

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (Salmo salar)? *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 281-287.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., ... & Stromberg, J. C. (1997). The natural flow regime. *BioScience*, *47*(11), 769-784.

Quinn, T. P., McGinnity, P., & Reed, T. E. (2015). The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(999), 1-16.

Richard, A., Bernatchez, L., Valiquette, E., & Dionne, M. (2014). Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(11), 1730-1739.

Roscoe, D. W., & Hinch, S. G. (2010). Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries*, *11*(1), 12-33.

Smith, G. W., Smith, I. P., & Armstrong, S. M. (1994). The relationship between river flow and entry to the Aberdeenshire Dee by returning adult Atlantic salmon. *Journal of Fish Biology*, *45*(6), 953-960.

Stensland, S. (2010). Fishing Rights and Supply of Salmon Angling Tourism in Mid-Norway. *Scandinavian Journal of Hospitality and Tourism*, *10*(3), 207-230.

Taylor, M. K., & Cooke, S. J. (2012). Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews*, *20*(4), 211-219.

Tentelier, C., & Piou, C. (2011). Obstacles to migration constrain nest distribution of Atlantic salmon. *Ecology of Freshwater Fish*, *20*(3), 400-408.

Thorstad, E. B., Forseth, T., Aasestad, I., ØKland, F., & Johnsen, B. O. (2005). In situ avoidance response of adult Atlantic salmon to waste from the wood pulp industry. *Water, Air, and Soil Pollution*, *165*(1-4), 187-194.

Thorstad, E. B., Økland, F., & Finstad, B. (2000). Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *Journal of Fish Biology*, *57*(2), 531-535.

Thorstad, E. B., Økland, F., Aarestrup, K., & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, *18*(4), 345-371.

Thorstad, E. B., Økland, F., Kroglund, F., & Jepsen, N. (2003). Upstream migration of Atlantic salmon at a power station on the River Nidelva, Southern Norway. *Fisheries Management and Ecology*, *10*(3), 139-146.

Ulvan, E. M., Foldvik, A., Jensen, A. J., Finstad, B., Thorstad, E. B., Rikardsen, A. H., & Næsje, T. F. (2017). Return migration of adult Atlantic salmon (*Salmo salar* L.) to northern Norway. ICES Journal of Marine Science, 00, 00-00.

Tables

Table 1. Linear model of the spawning position of Atlantic salmon in the Numedalslågen River, Norway. Parameter estimates are given as ± the 95% confidence interval. For tag type, which is a factor, the reference level is in brackets and is relative to external attachment. Significant values are highlighted in bold.

Parameter	Estimate ± 95% CI	DF	t-value	P-value
(Intercept)	-41336 ± 47829	35	-1.69	0.10
Tag Type				
(Implant)	**14314 ± 13299**	**35**	**2.11**	**0.04**
Body size	**900 ± 576**	**35**	**3.06**	**<0.01**

Table 2. Summary of the passage of the Holmfoss waterfall in Numedalslågen for individual fish. Passage times were determined by stationary logging stations situated at the waterfall. Range in flow prior to passage covers the period when the individual was recorded in the pool below the waterfall without passing. Resulting from technical failure, the exact timing of passage and therefore the flow at passage is missing for some fish. For fish that passed quickly, the range and spread in flow were not possible to calculate and are therefore NA.

Year	Flow ($m^3 s^{-1}$) at passage	Flow trend upon passage	Days recorded below waterfall prior to passage	Average flow ($m^3 s^{-1}$) prior to passage	Range in flow ($m^3 s^{-1}$) prior to passage
2003	NA	NA	24	108 ± 27	82-160
	NA	NA	29	119 ± 27	78-170
	57	stable	53	79 ± 31	39-170
	87	stable	8	108 ± 26	78-170
	61	declining	62	96 ± 25	68-148
	119	rising	48	86 ± 17	69-139
	74	rising	23	77 ± 34	39-152
	78	declining	74	64 ± 25	39-152

	68	declining	9	108 ± 31	75-152
	119	rising	1	79 ± 0	NA
	68	declining	5	104 ± 31	75-148
	71	rising	22	95 ± 29	69-170
	69	stable	5	79 ± 9	70-88
	79	declining	5	89 ± 2	87-91
	152	rising	11	81 ± 16	69-119
	94	declining	NA	NA	NA
	69	stable	8	83 ± 9	70-91
	70	declining	21	96 ± 21	78-152
2007	101	declining	22	142 ± 61	80-283
	82	declining	8	102 ± 18	80-126
	461	declining	24	236 ± 156	82-733
	152	declining	28	219 ± 51	164-357
	122	declining	20	112 ± 25	85-184
	162	rising	13	114 ± 27	85-175

69	rising	17	79 ± 35	51-184
72	declining	6	75 ± 1	73-76
95	declining	0	NA	NA
162	rising	2	154 ± 30	133-175
61	stable	24	73 ± 8	61-89
69	rising	13	68 ± 14	51-89
133	declining	10	112 ± 28	85-175
68	rising	14	68 ± 6	61-79
68	rising	13	67 ± 6	61-79
98	stable	78	94 ± 47	51-282
235	rising	27	72 ± 11	61-121

Table 3. Summary of the passage of the Hoggtveita waterfall in Numedalslågen for individual fish. Passage times were determined by stationary logging stations situated at the waterfall. Range in flow prior to passage covers the period when the individual was recorded in the pool below the waterfall without passing. Resulting from technical failure, the exact timing of passage and therefore the flow at passage is missing for some fish. For fish that passed quickly the range and spread in flow were not possible to calculate and are therefore NA.

Year	Flow ($m^3 s^{-1}$) at passage	Flow trend upon passage	Days recorded below prior to passage	Average flow ($m^3 s^{-1}$) prior to passage	Range in flow ($m^3 s^{-1}$) prior to passage
2003	107	declining	4	130 ± 16	115-152
	70	stable	0	NA	NA
	109	declining	3	122 ± 45	56-152
	56	stable	1	56	56
	55	declining	0	NA	NA
	79	rising	3	79 ± 4	75-83
	75	stable	8	113 ± 30	75-152
	79	declining	NA	NA	NA

	140	declining	36	312 ± 191	146-963
	112	declining	38	249 ± 125	116-733
	112	declining	15	213 ± 76	116-391
2007	68	rising	4	80 ± 11	65-89
	72	declining	3	76 ± 1	75-76
	91	declining	7	188 ± 60	122-282
	64	declining	1	72	72

Table 4. Linear model of delay at Holmfoss. Factors excluded from the model were sex, cultivation, and environmental variables (see Analyses in Methods). Parameter estimates are ± the 95% confidence interval. For tag type, which is a factor, the reference level is in brackets and is relative to implanted. Significant values are highlighted in bold.

Parameter	Estimate ± 95% CI	t-value	P-value
(Intercept)	**-125.75 ± 60.52**	**-4.07**	**<0.01**
Tag Type (External)	**-20.93 ± 9.17**	**-4.47**	**<0.01**
Body size	**0.57 ± 0.41**	**2.68**	**0.02**
Julian Date	**0.77 ± 0.18**	**8.80**	**<0.01**

Table 5. Generalized linear model of the daily probability of passage at Holmfoss in 2003 and 2007. Water discharge variables were excluded from the model (see Analyses in Methods). Parameter estimates are ± the 95% confidence interval. Significant values are highlighted in bold.

Parameter	Estimate ± 95% CI	z-value	P-value
(Intercept)	51.21 ± 50.55	1.99	0.05
Body size	**-0.07 ± 0.06**	**-2.19**	**0.03**
Barometric Pressure	-0.05 ± 0.06	-1.91	0.06

Table 6. Generalized linear model of the daily probability of passage at Hoggtveita. Relative mean discharge is the water discharge on the day of passage for a given fish relative to the daily mean of the discharge on days prior to passage that the fish was tracked below the waterfall. Parameter estimates are ± the 95% confidence interval. Significant values are highlighted in bold.

Parameter	Estimate ± SE	z-value	P-value
(Intercept)	**-88.56 ± 33.77**	**-5.14**	**<0.01**
Water Discharge	**-0.07 ± 0.04**	**-3.29**	**<0.01**
Barometric Pressure	**0.09 ± 0.04**	**5.40**	**<0.01**
Relative Mean Discharge	**-0.04 ± 0.02**	**-3.16**	**<0.01**

Figures

A

B

Figure 1.

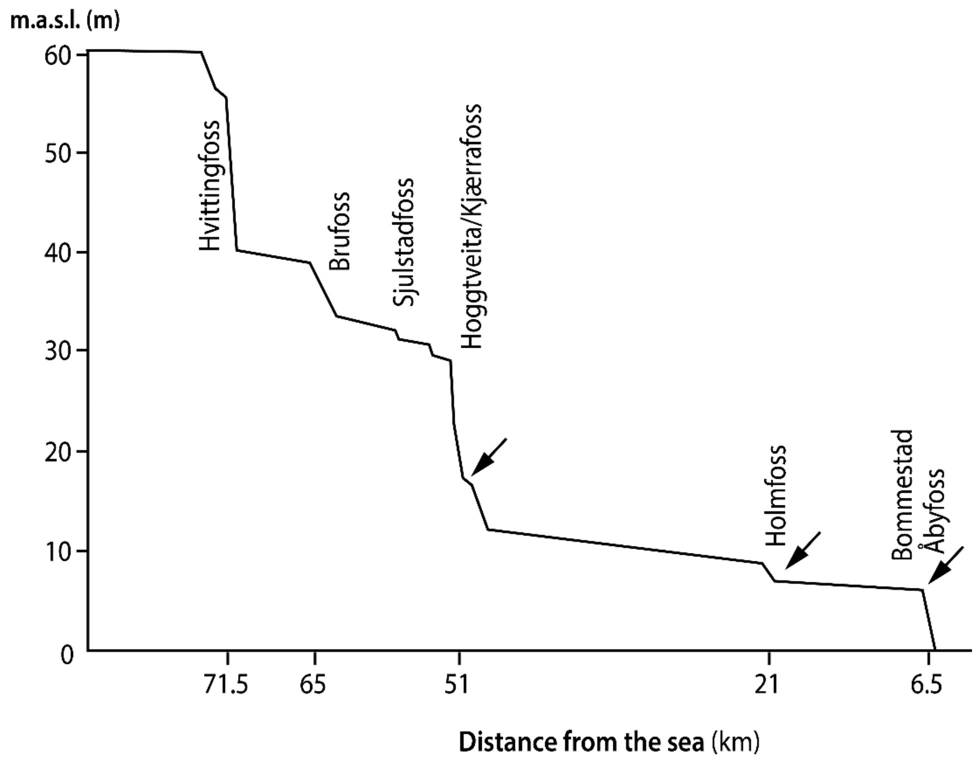
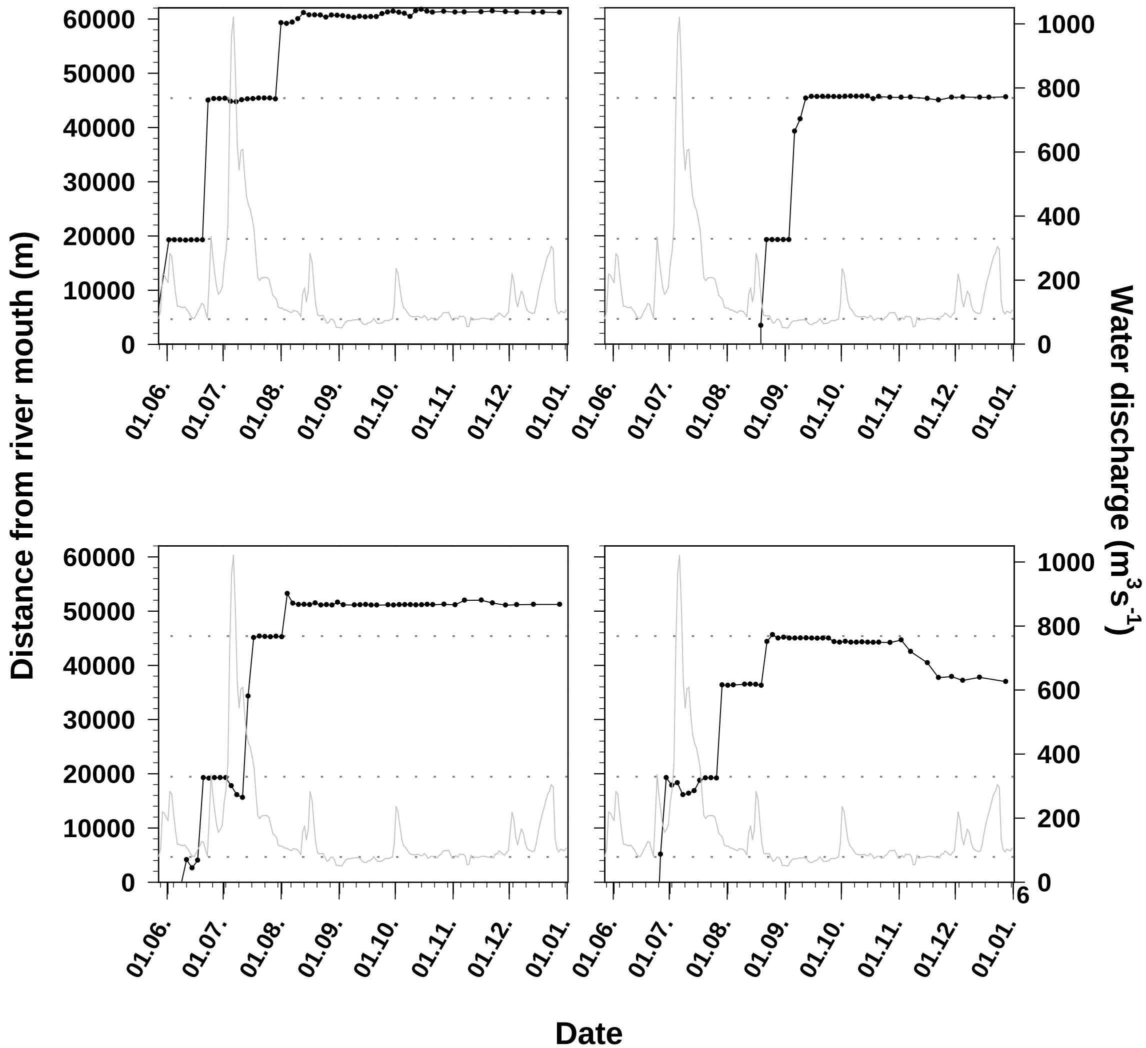

m.a.s.l. (m)
60
50
40
30
20
10
0
Hvittingfoss
Brufoss
Sjulstadfoss
Hoggtveita/Kjærrafoss
Holmfoss
Bommestad
Åbyfoss
71.5
65
51
21
6.5
Distance from the sea (km)

Figure 2.



Distance from river mouth (m)
60000
50000
40000
30000
20000
10000
0
Water discharge (m3 s-1)
1000
800
600
400
200
0
01.06.
01.07.
01.08.
01.09.
01.10.
01.11.
01.12.
01.01.
Date

Figure 3.

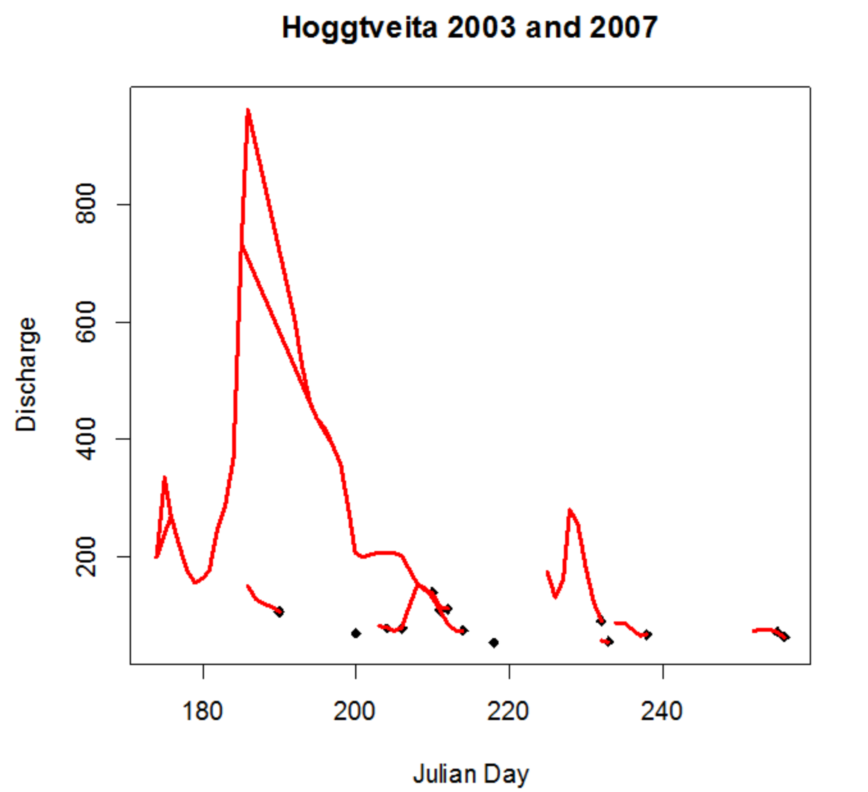

Hoggtveita 2003 and 2007
Discharge
200
400
600
800
180
200
220
240
Julian Day

Figure 4.

Figure Legends

Figure 1. Photographs of the Holmfoss (A) and Hoggtveita (B) waterfalls in Numedalslågen. Holmfoss measures 2 m high and Hoggtveita measures 3 m high; both represent natural barriers to upriver migration by Atlantic salmon.

Figure 2. Elevation map of the Numedalslågen River relative to distance from the fjord. The first waterfall, Åbyfoss, is located near Bommestad where the first stationary data logging station was located. Note that the longest delays for salmon were recorded at Holmfoss, a relatively low-elevation waterfall en route to the spawning territories upriver. Hoggtveita is the highest-elevation waterfall in the anadromous section of the system, which ends below Hvittingfoss. M.A.S.L. is the metres above sea level. Arrows point to the locations of logging stations.

Figure 3. Example migration patterns of Atlantic salmon moving from the river mouth to spawning grounds. Migration shown as distance from river mouth for four individuals (black lines, where small black dots indicate the tracking). The horizontal dashed grey lines indicate Åbyfoss, Holmfoss and Hoggtveita, and clearly shows these as migration barriers in terms of delaying migration. Water discharge is presented on the alternate y-axis and is indicated by the grey line. Dates on the x-axes are given as dd.mm.

Figure 4. Water discharge at the Hoggtveita waterfall in Numedalslågen. Black points illustrate the dates and discharges at which individual Atlantic salmon (*Salmo salar*) ascended the waterfall. Red lines indicate the discharge history for each fish: the water

discharge on days prior to passage. No red tail indicates that the fish passed on the same day as arriving (i.e. had no discharge history). Fish tracked in 2003 and 2007 are combined in the figure. Regression modelling suggested that salmon ascended on days during which the water discharge at the waterfall was lower than the average daily discharge encountered on previous days, which is illustrated in this figure insofar as the black dot (date and discharge of passage) is generally the lowest point in the discharge history (red line).