Title: Behaviour and mortality of downstream migrating Atlantic salmon smolts at a small power station with multiple migration routes

Short title: Functional fishway reduced smolt mortality

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Abstract

Salmon smolts were released upstream of a run-of-river hydropower site and recaptured downstream for inspection. Descending fish behavior through three possible migration routes (turbines, fishway, spillway) were analyzed using telemetry, fyke-nets and diving.

Tagged smolts did not follow the main water flow; over 70% used the fishway, which received only about 10% of the flow. The turbines received about 80% of the water, but less than 25% of the smolts. Smolts were not fully stopped from entering the turbines by 25 mm bar racks. Mortality of smolts passing through the Kaplan turbines was minimum 36%. No mortality was found in fish moving through the fishway or spillway.

This shows that small and fast-rotating Kaplan turbines can cause relatively high mortality. No mortality in alternative migration routes resulted in a total mortality.
Many fishes perform migrations between different habitats in order to optimize fitness (Northcote, 1978, 1984; Dingle & Drake, 2007). Human activities that obstruct migration represent potential threats to migrating animals (Lennox et al., 2016). For centuries, rivers and streams have become modified for navigation, hydropower production and water regulation purposes (Lucas & Baras, 2001). Migrating fishes are particularly impacted by hydropower dams, weirs and other migration barriers hindering or delaying their migration (Nyqvist et al., 2017; Birnie-Gauvin et al., 2018; Tambets et al., 2018). Studies of how anthropogenic activities influence fishes during migration are necessary to assess consequences for individuals and populations, and to evaluate mitigation measures.

Atlantic salmon (Salmo salar) is one of the most well-known diadromous species, important for recreational fisheries and local economies. Migration barriers in rivers may lead to reduction or the complete loss of salmon populations. In Estonia, Atlantic salmon declined severely during the second half of the 20th
century (Kangur, 1996). The most profound impact on salmonid habitat availability is due to hydropower development, and man-made migration obstacles are common in most rivers, preventing access to about 70% of the historical salmon habitat (HELCOM, 2011). Poor water quality has also severely reduced salmonid production. Historically, there were salmon in 12 rivers in Estonia, but a few years ago only five rivers still had natural reproduction without additional stocking (HELCOM, 2011). After restoration measures, salmon presently reproduce regularly in ten rivers (Kesler et al., 2017).

In the Purtse River, where this study was carried out, modest but regular wild salmon reproduction occurs in addition to regular enhancement releases of hatchery-reared fish (HELCOM, 2011; Kesler et al., 2017). Historically this was the second-best salmon river in Estonia, but since the 1930s, salmon gradually disappeared due to pollution from oil shale mining (Mikelsaar, 1984). Wastewater containing sulphates, chlorides, sulphides, oil products and phenols were discharged into the river and its tributaries and seriously affected aquatic life (Velner, 1972; Rätsep et al., 2005). Since the 1990s, wastewater discharge has decreased, leading to a considerable reduction of pollutant concentrations in the river water after 2000 and a suitable water quality for salmonids (Kesler et al., 2011; Roosimägi, 2014). Salmonids recolonised Purtse River after the water quality improvement, and in 2005, spawning of salmon and sea trout (Salmo trutta) was recorded and a restocking programme for salmon initiated. However,
the Sillaoru power station, 4.9 km from the river mouth, was opened in 2005 and prevented upstream fish migration until a functional fishway was built in 2014. With salmon and sea trout returning to the upstream areas, there is now a need to ensure safe downstream migration for both wild and hatchery produced smolts past the hydropower station. Hence, information of the factors causing smolt mortality, and the effects of mitigation measures, is needed.

The aims of this study were to examine 1) the distribution of fish and water flow between different migratory routes past the power station, testing the importance of the spillway and fishway as downstream migration routes, 2) immediate and delayed mortality at the power station, and injury inflicted on the smolts when passing, 3) migration speeds in the reservoir and at the hydropower station, and 4) possible diel activity patterns. A combination of methods was used, including tagging fish with acoustic transmitters and monitoring fyke net catches downstream of the power station.
Material and methods

Study site

The 51.1 km long Purtse River, with a catchment area of 811 km$^2$ and annual mean water discharge of 6.9 m$^3$ sec$^{-1}$, runs into the Gulf of Finland in Northeastern Estonia (Fig. 1). Main tributaries are the rivers Kohtla, Erra and Ojamaa. The Sillaoru Hydroelectric Plant complex was constructed 4.9 km from the river mouth in 2004-2005, with a 3.2 m high dam preventing upstream fish migration. A natural type fishway with a low gradient (2.1%) was built during 2014-2015. Surveys have indicated that this fishway is functional for several species, including trout and river lamprey.

Downstream migrating fish must pass the 2.1 ha reservoir. From the lower end of the reservoir, fish can move downstream 1) through the fishway, 2) into the canal towards and through the turbines, or 3) over the spillway (Fig. 1). The water discharge in the fishway is 0.6 m$^3$ sec$^{-1}$ (Anon. 2013). The river discharge determines the turbine and spillway discharge. One or two Kaplan turbines with adjustable blades are operating (307-kW and 220 kW, capacity of 0.5-4.0 m$^3$ sec$^{-1}$ and 1.5-4.0 m$^3$ sec$^{-1}$, respectively), while surplus water is released over the 3.2 m high spillway. Both turbines have four blades and a 1 m runner diameter (gaps between the runner blade tips and the hub are 3-5 mm). The rotation speed is 428 rpm for the 307-kW turbine and 385 rpm for the 220 kW-turbine. The power company implements turbine shutdowns during low water level to maintain the
required discharge in the fishway. During the first three days of the study (14-16 May), both Kaplan turbines were operating, while only the 307-kW turbine was operating during the rest of the study. The power station utilises a fall of 7.8-9.0 m.

A bar rack with 25 mm vertical openings (52 ° slope to the ground in the flow direction) is placed in the entrance of the turbine channel to prevent downstream migrating fish from entering the turbines (Fig. 1). Two additional bar racks with 45 mm vertical openings (60 ° slope to the ground) are placed at the turbine intakes. The turbine channel inflow is at an almost 90 ° angle to the river flow, to lead floating debris over the spillway.

Tagging experiment

To enhance the salmon population, 491 two-year-old Atlantic salmon smolts were released on 14 May 2015 at 17.00 (local time, UTC + 3 hrs) at a site 50 m upstream of the last rapid above the reservoir, which is 0.6 km upstream of the Sillaoru dam. The breeding stock originated from Kunda River, and the smolts were reared in the Põlula Hatchery. The mean total length (TL) of the smolts was 207 mm (range 145-256 mm, SD ± 24 mm) and mean weight 87 g (range 36-152 g, SD ± 29 g), based on a random sample of 40 individuals. All stocked smolts

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had the adipose fin removed. According to catches by electrofishing and fyke-net, no wild two-year-old salmon smolts were present in the study area.

Tags and tagging

Thirty-eight smolts were tagged with individually coded acoustic transmitters (ATID LP-7.3 or ATID LP-9, weight in water of 1.2/2.5 g; battery life of 44/174 days; random pulse intervals from 5 to 15 s; Thelma Biotel AS, Trondheim, Norway). Tagging occurred 1.5-4.0 hours before release. Two sizes of transmitters were used to ensure a low tag/fish weight ratio. The smaller 7.3 mm diameter tags were applied to 20 of the smallest fish (mean mass 70 g). The larger 9 mm diameter tags were applied to 18 of the larger fish (mean mass 106 g). The group of fish selected for tagging had the same mean TL and weight as the total group of stocked fish. The expected battery life of the tags exceeded the duration of the study period. Each smolt was anaesthetised immediately before surgery. During surgery, fish gills were supplied with flowing aerated water. The acoustic tags were implanted into the abdominal cavity through a 1.5 cm long ventral incision made about 1-3 cm anterior of the ventral fins. Two sutures (Ethicon, 5-0, monofilament, polypropylene) were used to close the incision. Fish were transported to the release site together with fin-clipped fish in a container with aerated water and a controlled oxygen level. Fish tagging and release were carried out according to the license V 1-15/15/133 (Environmental Board of Estonia).
Recording of fish tagged with acoustic transmitters

The movements of the tagged smolts were monitored by applying six stationary Vemco VR2W automatic receivers (Fig. 1) and a mobile receiver VR100 for manual tracking (Vemco Ltd., Canada). The VR2W receivers detected and saved individual signal codes of transmitters as well as the date and time when fish were within their detection range. Manual tracking was conducted in the reservoir and turbine channel at least once per day to locate smolts and detect shorter movements, and four times at the release site.

Monitoring by use of fyke nets

To determine the timing and selected route of downstream migration of fin-clipped smolts, the downstream end of all migration routes through the hydropower complex was closed with fyke nets (Fig. 1). One fyke net was mounted in the fishway outflow, one in the turbine channel 370 m downstream of the turbines and one in the spillway tailrace. Fyke net mesh size was 10 mm knot to knot and wing mesh size was 13 mm. The fyke nets entirely covered the migration route cross-sections, catching all the descending fish. The underwater part of the fyke net wings was controlled by diving to ensure correct positions.
The fyke net catches were monitored for 11 days, from 14 May 2015 at 18:00 to 25 May 2015 at 10:00. Fyke nets below the fishway and spillway were emptied, and catches recorded every second hour, and the fyke net below the turbine-channel was controlled in the morning and in the evening. All fish from the fyke nets were recorded: species, presence and type of damages, presence of incision and transmitter. Dead and injured fish were measured (TL, estimated in case of damage) and removed. Seemingly healthy fish were released into the river downstream of the fyke nets, except that some of them were used for monitoring of delayed mortality (see below).

In the tailrace of the turbine channel, diving was performed in the morning and in the evening in front of the fyke net to register and collect dead and injured fish. Smaller parts of dead fish were also found during inspection of the channel bank.

At the end of the study (25 May 2015), electric fishing by using portable D.C. fishing aggregates was done in the fishway and under the spillway to register smolts that might have descended from the reservoir without having been caught in the fishway or spillway fyke nets. On 26 May 2015, electric fishing was done twice in the turbine channel outlet to register any released fish. The water flow was reduced in the fishway and in the turbine channel to facilitate electrofishing. Electrofishing was also performed at the upstream release site on 16 June 2015 to search for any remaining fish.
Monitoring of delayed mortality

To monitor for possible delayed mortality, some of the seemingly uninjured smolts that descended through the turbines (n = 67), fishway and spillway (control group, n = 65 and n = 4 respectively) were kept after being captured in the fyke-nets. These fish were then immediately released in one of two keep net boxes (0.8 x 1 x 1.5 m), placed in a slowly running part of the river. Visual observation (without handling) of fish condition was done daily over an eight-day period.

Most of the fish (over 80%) were added during the first three days (cf. Tab. 2), and the last group of fish after four days. Dead fish were immediately removed.

Evaluation of possible underestimation of dead fish count from the turbine tailrace

To check if all the fish that were lethally injured when descending through the turbines were detected by fyke nets or diving surveys, 32 of the dead smolts previously collected in the fyke-nets were marked by removing the anal fin and released in the outflow of the turbine on 25 May 2015. These fish were searched for by diving in the evening (i.e. 7 hours after release), the next morning, and under low and slow flowing water conditions in the afternoon 26 May 2015.
Water discharge

An acoustic flow rate meter (Sontec FlowTracker, Xylem Inc., USA) was used to determine the water discharge at the fishway entrance. For calculating the water discharge in the spillway, the depth and width of the water layer flowing over the spillway was measured, and the spillway discharge was calculated based on a table from Estonian Hydraulic Engineers (designed to estimate the flow volumes in analogous free-flow conditions). The turbine channel discharge was calculated based on the Estonian Environment Agency river hydrometric station data (situated 3.2 km upstream) by subtracting fishway and spillway discharges from the Purtse River discharge.

Data analyses

Data were analyzed using the statistical program R Development Core Team Version 3.5.1 (2018). The distribution of fish and water flow between different migratory routes past the power station was tested with a Chi-squared test ($2 \times 3$ table). Fin-clipped smolts and smolts tagged with acoustic transmitters were not separated, because their distribution did not differ. This was controlled for using a Fisher’s exact test ($2 \times 3$ table), because minimum expected number was less than one and approximation for using a Chi-squared test was not met.
To test whether there were differences in mean size (TL) of smolts that descended through the turbine and smolts released in the river upstream of the hydropower complex, a Welch two sample t-test was used. Assumptions for the Welch two sample t-test were examined by using Shapiro-Wilk test and F test (for the normality of data distribution and for the equality of variance, respectively). Smolts with approximate TL were excluded (these were severely damaged fish with missing bodyparts after passing through the turbine).

A Chi-squared test (2 × 2 table) was used for testing differences in delayed mortality between the turbine group and control group. The same test was used for testing if the proportional share of smolts between the fishway and other routes differed between the first and subsequent days. For 2 × 2 tables, “n – 1” Chi-squared test was used as recommended by Campbell (2007).

Median movement speeds for fish using the different routes were based on the shortest distance through water between the upper and lower end of each route. The shortest distance through the reservoir was 310 m for fish using the fishway, and 350 m for the other fish. When passing the power station, the shortest distance for those using the fishway was 155 m, and for those moving through the turbine 115 m (two fish) or 230 m (four fish). Distances were not calculated downstream of the reservoir for the fish who fell over the spillway (two individuals).
Results

The distribution of fish and water flow between the different migration routes

Salmon smolts used all three migration routes to pass the power station. In total, 459 salmon smolts (94%) were detected descending past the power station, of which 448 (91%) were caught in fyke nets or during diving and 11 recorded by electrofishing or telemetry receivers. The distribution among the three migration routes did not differ between fin clipped smolts and smolts tagged with acoustic transmitters (Fisher’s exact test, \( p = 0.29 \)). Among smolts with acoustic transmitters, 71% descended through the fishway, 7% over the spillway and 21% through the turbines (\( n = 20, 2 \) and 6, respectively). Among the fin-clipped fish, the proportions were 74%, 3% and 24%, respectively (\( n = 317, 11 \) and 103, Fig. 2).

The water discharge through the turbine was much higher than over the spillway and the fishway (about 4/5 of total discharge, Fig. 2). The spillway and the fishway had approximately similar discharges (Fig. 2). Between 14 and 25 May 2015, the Purts River water discharge decreased from 6.5 to 3.8 m\(^3\) sec\(^{-1}\). At the same time, the discharge through the turbine and spillway decreased (from 5.4 to 3.0 m\(^3\) sec\(^{-1}\) and from 0.6 to 0.35 m\(^3\) sec\(^{-1}\), respectively). However, the proportion of the total discharge in the different routes was not greatly altered. A slight decrease in the proportion through the turbine (from 84% to 80%) and no change over the spillway (9%) implies a slight increase in the fishway (from 0.40 to 0.45

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The proportional distribution of smolts among the different migration routes was different from the proportional distribution of the water discharge ($\chi^2 = 364.8$, $n = 457$, $df = 2$, $p < 0.001$, Fig. 2). Far more fish moved downstream via the fishway and fewer through the turbines than the proportion of water flow would indicate. The mean size of smolts that descended through the turbine was smaller than the smolts that were released in the river upstream of the hydropower complex (187 mm and 207 mm, respectively, Welch two sample t-test, $t = 2.88$, $df = 27.09$, $p = 0.008$).

According to receiver data, about 90% of the fish (25 of 28) that passed the reservoir explored only one of the possible exit routes at the power station. Nineteen of the 20 fish that descended via the fishway were not recorded in the turbine channel. The two fish that descended via the spillway were never detected in the turbine channel or near the fishway entrance. Among the six smolts that descended via the turbine channel, one fish resided in the fishway for the first two days, two were recorded near the fishway a couple of times during the first days for up to 15 minutes, while the three remaining fish appeared to avoid the fishway entrance.
According to the fyke net catches and diving data, mortality appeared only among the salmon smolts that migrated through the turbine, and not among those using the other migration routes. Thirty-three salmon smolts were found dead immediately below the power station (Tab. 1), constituting 30% of the 109 salmon smolts that were recorded descending through the turbine (receiver recordings and direct catches). For 29 of these fish, the reason for mortality seemed to be linked to external physical injuries, i.e. missing (17 fish) and seriously damaged (12 fish) body parts. Only three smolts were found dead without visual injuries, and one with a minor injury (missing caudal tip). Of the dead smolts, 30 were found in front of the fyke net, on the bottom of the turbine channel or in the fyke net wings, while three were captured in the fyke net itself. No acute mortality was recorded for fish passing via the fishway (0 dead of 330 fish) (Tab. 1).

In addition to acute mortality, delayed mortality appeared among the smolts that descended through the turbine (Tab. 2). During four to eight days following descent, five of 67 smolts (7.5%) that appeared uninjured after passing the turbines were found dead. There was no delayed mortality among the 69 fish that had descended through the fishway and spillway (control group), which was significantly lower than for the turbine group ($\chi^2 = 5.31, n = 136, df = 1, p = 0.021$).
The total turbine-induced mortality was 36%, considering both the acute and delayed mortality (Tab. 1). Only seven of the 32 dead smolts that were released in the turbine outflow were later recorded, indicating that the total turbine-induced mortality was underestimated. One of the dead smolts was removed from the channel by a goosander (*Mergus merganser*) immediately after release, while six were located after seven hours by diving. The dead fish were left in the channel, and one of them disappeared during the following night (7-19 hours after release).

Migration speeds in the reservoir and at the hydropower station

Of the 38 salmon smolts tagged with acoustic transmitters, 33 were detected in the reservoir, three remained at the release site and two were lost after release. Most of the smolts started their descent immediately after release. Two thirds (n = 22) of the smolts had descended to the reservoir before sunset the same day (i.e. within six hours), 88% (n = 29) within 10 hrs and the last ones within 80 hrs. One smolt returned upstream and became stationary at the release site. Overall, the median time from release to reaching the reservoir was 4.9 hours (IQR = 7.1-2.7 hours).

After descending to the reservoir, the smolts (n = 32) spent median 31 hours (IQR = 121 – 7 hours) before being detected below the dam (median speed 0.27 km day⁻¹; Fig. 3 A). The slowest descenders did not complete descent during the
study. One of them was captured by electrofishing in the fishway in good condition at the end of the study. Median movement speeds for fish on the other distances were as follows: in the reservoir 0.45 km day\(^{-1}\), in the fishway 0.60 km day\(^{-1}\), and in the turbine channel 3.18 km day\(^{-1}\) (Fig. 3: A1, A2 and A3).

According to fyke-net catches and observations during diving, 278 (62\%) of the smolts passed the power station within the first 24 hours. During first three days, 443 (90\%) of the smolts had passed (Fig. 4). The proportional share of smolts between the fishway and other routes differed between the first and subsequent days (\(\chi^2 = 11.3, n = 448, df = 1, p = 0.001\)). A large number of smolts (220 individuals, 49\%) descended through the fishway within 24 hours.

Diel activity

The salmon smolts showed a clear diel pattern in activity in descending past the power station area (Fig. 5). According to fyke net catches, 92\% of the fish descended between 16:00 and 6:00, with the main peak between 22:00 and midnight, and a smaller peak between 18:00 and 20:00. The stationary receivers in the fishway opening and in the reservoir (Fig 1) showed movements towards and away from the fishway. The activity patterns recorded by these receivers resembled the diel activity recorded by the fyke nets (Fig. 5), with again 92\% of the movements occurring between 16:00 and 6:00. The highest activity in the
reservoir near the entrance of the fishway was recorded between 19:00 and 20:00, and between 21:00 and 23:00.

Fish with acoustic tags descended through the bar racks to the turbine during nighttime. According to receiver data (six fish, nine episodes), fish descended through the first turbine-channel bar rack between 22:06 and 02:22 and through the second bar rack (six fish, six episodes) between 22:46 and 03:20. Some fish visited the turbine-channel several times, and fish were detected also moving back from the turbine inflow channel to the reservoir. These upstream movements (two fish, four episodes) were recorded only during daytime (between 5:24 and 17:49).

Combining fyke net catches and recordings of tagged fish showed that the smolts were most active during night, starting about 4 hours before sunset and ending around sunrise (during the study, sunset occurred between 21:39 and 22:03, and sunrise between 4:42 and 4:21).
Discussion

Most of the Atlantic salmon smolts released upstream of a hydropower dam in the Purtse River used the fishway rather than the spillway or the turbine channel for their descent past the hydropower dam (74/71% of the fin-clipped/acoustically tagged smolts used the fishway, 3/7% the spillway, and 24/21% moved through the turbines). Hence, the smolts clearly did not use the three available routes according to the proportion of water discharge. They used the fishway more often than expected from the small proportion of the water discharge (7-11%) supplied to the fishway - and moved through the turbines less often than expected from the large proportion of the water discharge supplied to the turbines (80-84%).

Previous studies have indicated that the proportion of smolts passing through turbines is often in accordance with the proportion of water diverted through them (Ruggles, 1980; Hvidsten & Johnsen, 1997; Serrano et al., 2009). However, this is apparently not always true (Havn et al., 2017; Haraldstad et al., 2018; this study).

The results in this study resemble the results from a German study, where Havn et al. (2017) also found that Atlantic salmon smolts to a larger extent used fishways than was expected by their small proportion of the water discharge compared to in the turbines. Havn et al. (2017) found that the probability of smolts choosing a fishway instead of the turbine route increased with fish body length and decreased with discharge, which may indicate that smolts preferred to move through the fishway, and that larger body size and lower discharge improved their ability to...
maneuver and select the favoured migration route. Also in the present study, smolts that descended through the turbine were among the smaller smolts. This might indicate that the smolts prefer the fishway, but that the smaller smolts were less able to manoeuvre in the current and more often moved with the main flow through the turbines. However, there might also have been a size selection by the bar rack in front of the turbines in the present study, with the largest smolts being prevented or more reluctant to pass through the rack with 25 mm bar spacing (see below).

Even though most of the smolts used the fishway, a relatively large proportion of the smolts also descended through the turbines. Since a large proportion of the water discharge was supplied to the turbines, it was expected that a proportion of the smolts would move downstream through the turbines. A bar spacing of 25 mm did not fully prevent smolts from passing the double racks and entering the turbines. In the Estonian Loobu River, it was shown that 99.99% of all Atlantic salmon smolts were physically able to pass through racks with 25 mm bar spacing (Anon., 2017). Other studies have shown that a smaller bar spacing (10 and 15 mm) seems to prevent the passage of most salmon smolts (Havn et al., 2017; Thorstad et al., 2017). This is in accordance with estimates by Adam et al. (2005) and Larinier & Travade (2002) indicating that 25 mm bar racks would only physically hinder salmon smolts larger than approximately 250 mm body length. Hence, none of, or only a few of the largest smolts in this study may have been
physically prevented by the 25 mm bar rack. Bar racks may act as a behavioural or visual barrier and reduce the proportion of fish passing, despite having openings that are larger than the fish width (Adam et al., 2005). In this study, smolts descended during darkness, implying reduced potential visual effect of the bar racks. Daytime recordings of smolts passing through the rack in an upstream direction indicate that the visual impact of the 25 mm rack was insignificant. Smolts that descended via the turbine experienced 30% acute mortality, with an additional 6% delayed mortality over a four to eight day period. Hence, including delayed mortality, the minimum estimate for total mortality among fish descending via the turbine was 36%. Other studies report salmon mortality rate for Kaplan type turbines between 0-35% (Stier & Kynard 1986; Larinier, 2008; Gustafsson, 2010; Huusko et al., 2012). Thus, the mortality rate recorded in this study is one of the highest reported for Kaplan type turbines. There are two possible reasons for this. Firstly, local conditions facilitated direct observation of dead fish. A fyke net could be positioned in the fast-flowing section of the turbine outflow channel where the dead fish were carried with the swift flow, and it was also possible to detect fish laying on the bottom of the outflow channel by diving. Secondly, relatively small Kaplan turbines were operating, and smaller turbines may cause more injuries because fish have to pass closer to the walls and blading and also possibly because these turbines generally have higher rotation speeds (Larinier, 2008).
Both the acute and delayed mortality recorded in this study must be regarded as minimum estimates. The acute mortality estimates are minimum numbers because several predators, including Amerikan mink (*Neovison vison*) and goosanders, are present and able to remove dead or injured fish from the turbine tailrace. The delayed mortality estimates are minimum numbers, because fish may also get injuries that cause delayed mortality at a later stage, or injuries may reduce their physiological adaptations to saltwater and thereby induce elevated mortality when they enter the sea (McCormick *et al*., 2009; Zydlewski *et al*., 2010).

Among smolts descending via the fishway, neither acute nor delayed mortality was recorded, indicating that the fishway functioned well, despite receiving only a low proportion of the water flow. Few fish migrated over the spillway, and although no mortality was recorded among these fish, the low number of smolts using the spillway indicates that this is not an efficient alternative.

The smolts started to move downstream quickly after release. The median speed in passing the reservoir and power station was relatively fast (median 31 hours), indicating that the power station did not significantly delay the timing of smolts entering the sea. However, migration speeds were slower than usually recorded on free-flowing river stretches (Thorstad *et al*., 2012, Havn *et al*., 2018). In river systems where smolts must pass several power stations or other weirs, the cumulative delay may be substantial (Norrgård *et al*., 2013).

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Salmon smolts showed the highest movement activity during the dark hours, which is in accordance with other smolt migration studies. The riverine migration usually takes place during the night, and this is thought to be an adaptive behaviour to avoid predation by visual predators (Thorstad et al., 2012; Haraldstad et al., 2017). Hence, operating turbines during daytime and closing them during the dark hours could be a measure to reduce smolt mortality at power stations. This is perhaps more efficient early than late in the smolt migration season, because daytime activity often increases towards the end of the season (Thorstad et al., 2012; Haraldstad et al., 2017).

In conclusion, downstream migrating salmon smolts did not merely follow the main flow but used the fishway instead of the spillway and turbine route more often than expected from the proportion of the water discharge. Still, about 20% of the smolts descended through the turbines, which were supplied with about 80% of the total water discharge. Racks with 25 mm bar spacing was not fully efficient in preventing smolts from entering the turbines, likely because the bar spacing was too wide. Mortality rate of smolts passing through the turbines was minimum 36%, which is among the highest mortalities reported for Kaplan turbines in previous studies. These results show that small and fast-rotating Kaplan turbines can cause relatively high mortalities. Because a high proportion of the smolts used alternative migration routes (fishway, spillway), where they did not experience mortality, the total mortality due to this hydropower station in the

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Purtse River was only 8.5 % of all descending smolts. Without alternative migration routes at the power station, the mortality would have been minimum 36% for downstream migrating smolts passing this site. The causes of mortality seemed to be external physical injury like missing and seriously damaged body parts, but also internal damage and/or physiological stress that were not detected during visual inspection of the smolts. Smolts migrated mainly during night time, indicating that operating turbines during daytime and closing them during night time could be an efficient mitigation measure. Since the study was based on hatchery-reared smols, it is important to follow up the study later if self-sustaining populations are established, to examine whether the wild-bred salmon show a similar behaviour.
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Table 1. Acute and delayed mortality of downstream migrating Atlantic salmon smolts at the Sillaoru power station in the Purtse River. Acute mortality is given as number of smolts found dead below the power station. Delayed mortality is based on recording of mortality among fish that were held in captivity for 4-8 days after passing the power station (see Tab. 2). Both acute and delayed mortality are also given as proportion of the smolts passing the turbines (A; turbine mortality), and as proportion of the total number of smolts passing the power station area, including bypass routes outside the turbine (B). Total mortality is acute plus delayed mortality.

<table>
<thead>
<tr>
<th></th>
<th>A. Proportion (%) of</th>
<th>B. Proportion (%) of total</th>
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</thead>
<tbody>
<tr>
<td>No. of dead smolts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acute mortality</td>
<td>33</td>
<td>30.3</td>
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<tr>
<td>Delayed mortality</td>
<td>6</td>
<td>5.5</td>
</tr>
<tr>
<td>Total mortality</td>
<td>39</td>
<td>35.8</td>
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</table>
Table 2. Delayed mortality for salmon smolts that were seemingly uninjured after passing the turbine and that were subsequently held in captivity for 4-8 days (Turbine group) compared to smolts that had not passed the turbine (Control group). Number of smolts held in captivity (Sample size) and number of these found dead (Mortality) are given per date for both groups. The control group are fish that had descended through the fishway (n = 65) and spillway (n = 4).

<table>
<thead>
<tr>
<th>Date</th>
<th>Turbine group</th>
<th>Control group</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Sample size</td>
<td>Mortality</td>
</tr>
<tr>
<td>15.05.2015</td>
<td>34</td>
<td>2</td>
</tr>
<tr>
<td>16.05.2015</td>
<td>51</td>
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</tr>
<tr>
<td>17.05.2015</td>
<td>57</td>
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</tr>
<tr>
<td>18.05.2015</td>
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</tr>
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<td>19.05.2015</td>
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<td>20.05.2015</td>
<td>67</td>
<td>1</td>
</tr>
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<td>21.05.2015</td>
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<td>0</td>
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<tr>
<td>22.05.2015</td>
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</tr>
<tr>
<td>23.05.2015</td>
<td>67</td>
<td>1</td>
</tr>
<tr>
<td>Total (sp.)</td>
<td>67</td>
<td>5</td>
</tr>
</tbody>
</table>

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Figure legends

Figure 1. The location of the Purtse River and study area. Blue arrows indicate the flow direction, red circles the location of stationary receivers, yellow rings the fykenets, F the fishway, Sp the spillway, T the turbine, and Br the bar racks. The release site was 350 m upstream of the reservoir shown on the right map, i.e. approx. 350 m below the lower edge of the map. Base maps: Estonian Land Board.

Figure 2. Use of different migration routes by salmon smolts with acoustic transmitters (n = 28, orange bars) and those only finclipped (n = 431, green bars). The proportion of the total water flow through the different migration routes is also shown (blue bars).

Figure 3. Migration speeds of smolts tagged with acoustic transmitters: (A) from first detection in the reservoir until first receiver detection or being captured in a fyke net below the power station (n = 31), (A1) from first to last detection in the reservoir (n = 31), (A2) from last detection in the fishway entrance until capture in the fyke net below the fishway (n = 18), and (A3) from last detection in the reservoir until first receiver detection below the turbines (n = 6). Note the
logarithmic scale of the y axis. Circles with asterixes are maximum speed estimates, because some fish did not finish their migration during the study.

Figure 4. Number of smolts that moved through the fishway, turbines and spillway (blue, red and grey bars respectively) in day 1 to 11 after release, according to fyke net catches and diving. Days are calculated as 24 hr periods starting at 17:00.

Figure 5. The diel distribution of fyke net catches during the 11-day study period given as number of smolts captured per two-hour period (bars). Dashed line indicates diel activity of acoustically tagged salmon smolts while passing the power station area (14 May-7 June, UTC time + 3 hrs), based on movements between stationary receivers deployed in the fishway entrance and reservoir. The timing of each movement was defined as first recording when arriving at the fishway or reservoir.
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