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Impacts of a weir and power station on downstream migrating Atlantic salmon smolts in a German river

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Abstract

Weirs are barriers built across rivers for a wide range of other purposes than hydropower production. Like hydropower installations, weirs can negatively impact fish migrations. Downstream migration and mortality of Atlantic salmon smolts were studied during passage of a weir and power station by tagging 227 smolts with radio transmitters. Extra loss of smolts due to the weir and adjacent reservoir was 5.2%. Mortality was likely related to physical damage imposed to the smolts and/or increased predation risk. Extra loss of smolts did not differ between the weir and the power station (7.2%). Migration speeds were reduced at the power station but not at the weir. We conclude that mortality at one power station site may differ considerably among years, because the mortality was more than four times higher in a previous year than in this study. Increased river discharge seemed to decrease mortality and increase migration speeds at the power station.

KEYWORDS
downstream migration, migration speed, mortality, power station, radio telemetry, salmon smolt, weir

1 | INTRODUCTION

Migration is a strategy that has evolved in many animal taxa to increase individual fitness by utilizing the best suited habitat during different life stages (e.g., Dingle & Drake, 2007; Lucas & Baras, 2001). Diadromy is a migration pattern where all or some individuals perform migrations between freshwater and the sea, with spawning and juvenile phases in one habitat and feeding migrations to another habitat (Gross, Coleman, & McDowall, 1988). Diadromous fishes often have a high economic, cultural, and recreational value, such as species of the salmonid, eel, and sturgeon families (Salmonidae, Anguillidae, and Acipenseridae).

Many diadromous species have declined, and many are classified as vulnerable to critically endangered, such as the European eel (*Anguilla Anguilla*) and several species of sturgeons (IUCN Red List of threatened species). The use of multiple habitats and migrations through them imply exposure to a multitude of impacts and threats (Lucas & Baras, 2001). Fish can be easy to catch during migrations, and exploitation in several habitats can lead to high catch rates. Connectivity of habitats is crucial to maintain migrations, but during the last centuries, rivers worldwide have become increasingly modified for navigation, hydropower, and water regulation purposes, negatively impacting habitat connectivity, fish migrations, and survival (Lucas & Baras, 2001; Nilsson, Reidy, Dynesius, & Revenga, 2005). Examining how obstacles influence fish migration is necessary to assess consequences for individuals and populations and to evaluate management measures (Silva et al., 2018).

Most Atlantic salmon populations depend on individuals being able to migrate between spawning areas in rivers and feeding areas in lakes or at sea (Klemetsen et al., 2003). Atlantic salmon can therefore be severely impacted by installations interrupting their migration, and hydropower production and other barriers are among the major threats (Larinier, 2008; Forseth et al., 2017; Nyqvist, Greenberg, et al., 2017; Nyqvist, McCormick, et al., 2017). Weirs are barriers built across rivers usually for a wide range of other purposes than hydropower production, such as flood prevention, water discharge measures, boat navigation, and fish farming. Weirs can negatively impact fish migrations for instance by obstructing or delaying the fish, thereby reducing connectivity in rivers or by causing physical injuries to the fish (Birnie-Gauvin et al., 2018; Piper, Wright, Walker, & Kemp, 2013; Tambets et al., 2018), but there seem to be much fewer studies of the impacts of weirs than of hydropower installations.

In Germany, Atlantic salmon have been lost from all watersheds (Monnerjahn, 2011). The decline likely began with the expansion of watermill technology during the Middle Ages, followed by decreased water quality, habitat degradation, and river fragmentation by weirs and dams after the industrial revolution (Lenders et al., 2016; Monnerjahn, 2011). By the end of the 1950s, salmon were extinct in many rivers, including the River Rhine, which used to be among the main salmon rivers in Central Europe (Lenders et al., 2016; Molls & Nemitz, 2008; Monnerjahn, 2011). Re-introduction programmes have been initiated in the Rhine. Atlantic salmon have reproduced naturally in tributaries including in the River Sieg, where this study was performed, but self-sustaining populations are not yet re-established (Molls & Nemitz, 2008; Monnerjahn, 2011; Schneider, 2011). Hydropower production constitutes a political trade-off between sustainable energy generation and the impact on the connectivity and thus on the integrity of rivers. The government of North Rhine-Westphalia has initiated projects to examine possible negative consequences involved for fish bypassing weirs and power stations.

In this study, the downstream migration of Atlantic salmon smolts were studied during passage of the Buisdorf weir and Unkelmühle power station by tagging smolts with radio transmitters. The aims of this study were to (a) record whether the weir caused increased mortality and migration delays, (b) document migration routes used by smolts at the weir, (c) record mortality, migration routes, and delays at the power station, (d) compare the results at the power station with results from the two previous years to examine variation in survival and behaviour among years, and (e) compare mortality and migration delays between the weir and the power station.

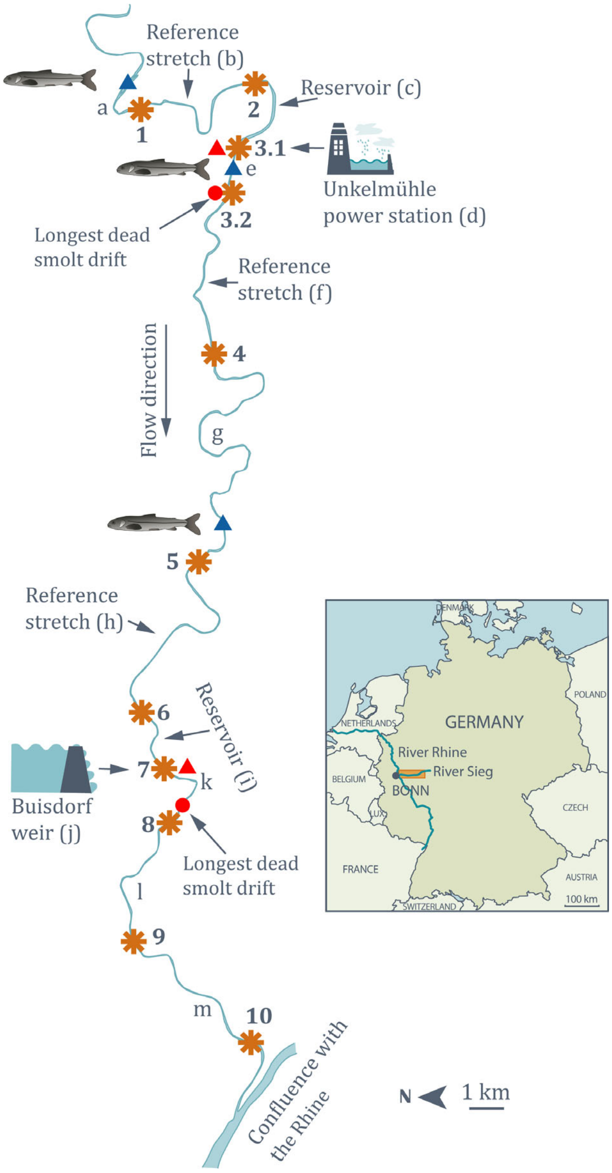

FIGURE 1 Map of the River Sieg showing the three different release sites of smolts tagged with radio transmitters (blue triangles) and sites where they were recorded by stationary receivers (orange stars). The different stretches are denoted with letters a–m. Lengths of the stretches are given in Table 1. Release sites of already dead smolt released at the power station and weir (red triangles) and the smolts longest drift downstream (red points) are also shown (longest drift downstream of the power station and weir was 1.9 and 1.8 km, respectively)

2 | MATERIALS AND METHODS

2.1 | Study area

The Rhine is 1,233 km long, most of which flows through Germany, and has a catchment area of 185,000 km^2. It originates in Switzerland and empties into the North Sea in the Netherlands. The Sieg, where this study was performed, is a 153-km-long tributary, with a catchment area of 2,862 km^2 (Figure 1). The average water discharge at the confluence with the Rhine is 53 m^3 s^{-1}, approximately 370 river kilometres from the sea.

Unkelmühle is a run-of-the-river power station 44-km upstream from the confluence with the Rhine (Figure 1). The reservoir upstream of the power station is 2.3 km long and has no water storage capacity. The power station has three Francis turbines with a total capacity of 27 m^3 s^{-1} and exploits a drop of 2.7 m. The turbine intakes are covered by a horizontally sloped rack (27° relative to the ground) with 10 mm bar spacing. The power station and migration routes are described by Havn et al. (2018). Ten migration routes can be used by downstream migrating fish at the power station (Figures 2 and S1). Bottom and side passes designed for eel were not in operation during this study. The spillway gate is opened when the water discharge exceeds the turbine capacity and was open for 6.2 days in the beginning of the study period (study period from March 31 to May 16, 2016). Thereafter, it was opened on nine occasions (median time open 0.9 hr, range 0.5–9.8 hr). Discharge in the vertical slot fishway was 0.3 m^3 s^{-1}, in the nature-like fishway 0.2 m^3 s^{-1}, and in the canoe pass 0.2 m^3 s^{-1}.

One of the possible migration routes for downstream migrating fish is through custom-made openings in the racks (14 or 24 cm deep and 70 cm wide) in front of the turbines, which enable fish to bypass the turbines via the flushing channel (termed surface bypass, water discharge 0.6 m^3 s^{-1}). From the flushing channel, fish were either guided to holding pools where they were collected for monitoring purposes or back to the river outside the turbines via a channel. Debris from the racks were flushed out in the same channel when rack cleaners were in operation. Which of these routes fish were guided to was determined by the position of a valve. The operation of

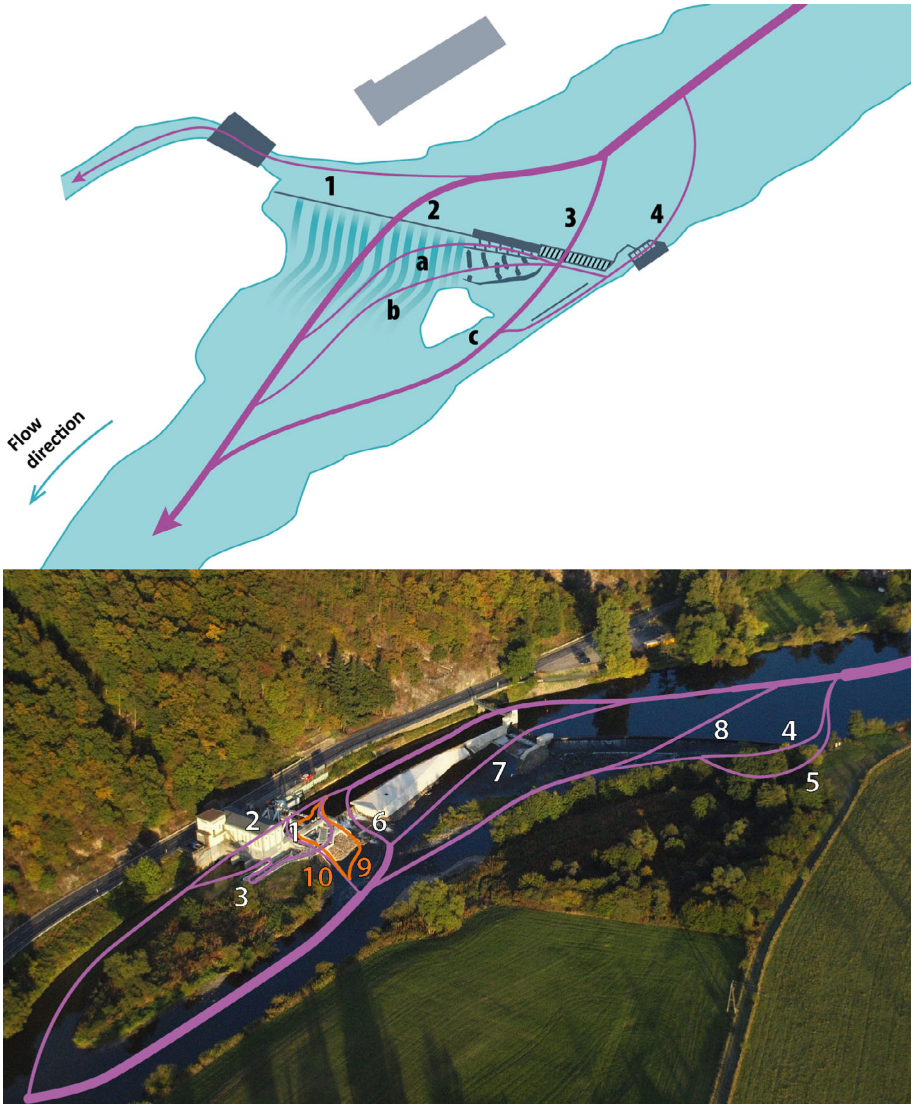

FIGURE 2 Upper panel: Migration routes available for downstream migrating fish at the weir: (1) via the side stream, (2) over the weir, (3) through the fence, or (4) through the fish trap, and then via (a) the vertical slot fishway, (b) natural fishway, or (c) ramp-like fishway or canoe pass. Lower panel: Migration routes available for downstream migrating fish at Unkelmühle power station: (1) via the surface bypass; custom-made openings in the racks that leads fish to a route outside the turbines via the flushing channel, (2) through turbines if they slip through the bar spacing of the racks, (3) through the vertical slot fishway constructed for upstream migrants, (4) through the nature-like fishway, (5) through the canoe pass, (6) via the ice gate, (7) over the spillway gate, (8) over the dam, (9) via the bottom bypass for eel, and (10) via side bypasses for eel (the two latter, indicated in orange, are only in operation during the eel run in the autumn). More detailed figures of the power station area can be found in Havn et al. (2018)

the rack cleaners depended on the amount of debris. During periods of high water and increased debris transport, they were continuously operated.

The Buisdorf weir in the Sieg, 15-km upstream of the confluence with the Rhine and 29-km downstream of the Buisdorf weir (Figures 1, 2, and S2–S4), was constructed more than 500 years ago to supply water to a monastery. Later, water mills were installed, producing power for industrial purposes. The head of the weir is 2.6 m. The weir slows down the water flow on a 1.9-km-long upstream stretch, resembling and termed a reservoir (Figure 1), but which unlike a true reservoir does not have a water storing capacity. Today, the weir is of no practical use, and there is no power production connected to the weir.

Downstream migrating fish can use eight different migration routes when they pass the weir (Figures 2, S3, and S4). Fish can pass over the weir or via a side stream (water discharge 0.5 m^3 s^{-1} during flooding; otherwise, it depends on the discharge in the Sieg) and thereafter re-enter the river 5.1 km below the weir. A monitoring station has been constructed at the south bank of the weir, enabling counting and catching of upstream migrating fish. Downstream migrating fish can also pass the weir through the monitoring station, and fish using this route or fish passing the weir via a fence (adjustable bar spacing; 40–60 mm) can thereafter migrate through a vertical slot fishway (seven pools, maximum water current at 1.9 m s^{-1}), a nature-like fishway (length: 65 m, width: 15 m, water current: 0.5 to 2.0 m s^{-1}), or via a ramp-like fishway or canoe pass.

2.2 | Capture and tagging of smolts

When studying mortality caused by power stations and other obstacles, it is important to take into consideration that dead fish may drift downstream and be mistaken for live smolts (Havn et al., 2017) and to include control groups to separate between extra mortality caused by the obstacle and mortality that might have occurred on the same stretch if this had been a free-flowing river stretch. A balanced design with different control groups was used in the present study to take this into consideration. A similar approach was used to study the behaviour and mortality of smolts passing the Unkelmühle power station in two previous years (Havn et al., 2018).

A total of 227 smolts were radio tagged and released (mean total length 158 mm, range 116–224, *SD* 18, mean mass 35 g, range 14–98, *SD* 12); 120 upstream of the power station (groups Unkelmühle 1 and 2), 60 just downstream of the power station (groups Downstream Unkelmühle 1 and 2), and 47 upstream of the weir (groups Buisdorf 1 and 2, Figure 1, Table 1). In addition, 20 already dead smolts (mean total length 158, range 125–190, *SD* 17) were tagged and released immediately downstream of the power station and weir to help distinguishing between live downstream moving fish and dead drifting fish (Table 1). All smolts were captured for tagging by guiding them from the flushing channel to holding pools during their downstream migration at the power station, except five smolts taken from the Agger hatchery. The former fish likely originated from stocking of 0+ or 1+ fry or parr by local hatcheries but could also be the result of natural spawning in the Sieg (Monnerjahn, 2011; Schneider, 2011). Groups of smolts were released at different times to increase variation in environmental variables (Table 1). Neither body length or mass differed between live smolts released upstream of the power station, downstream of the power station and at the weir, or between already dead smolts released immediately downstream of the power station and the different groups of live smolts, one-way analysis of variance body length: $F(3, 243) = 0.22$, $p = .88$, mass: $F(3, 243) = 0.72$, $p = .54$.

Prior to tagging, fish were anaesthetized in 50 mg L^{-1} benzocaine (aethylium *p*-aminobenzoicum, Caesar & Loretz GmbH, Hilden, Germany). A 1- to 3-cm incision was made by a scalpel on the ventral surface posterior to the pelvic girdle. The transmitter was inserted through the incision and pushed into the body cavity above the pelvic girdle. Two or three independent monofilament sutures were used to close the incision (3/0 Resolon). During surgery, a 25 mg L^{-1} solution of benzocaine was circulated through the gills of the fish. Radio transmitters used were individually coded Nano tags produced by Lotek Wireless Inc., Canada, model NTQ-2, frequency 150.300 MHz with trailing whip antennas (dimensions $5 \times 3 \times 10$ mm; mass in air 0.31 g, pulse rates between 2.0 and 7.2 s, expected life time 16 to 31 days dependent on pulse rates). Transmitters of this size were not expected to severely impact the tagged smolts (Brown, Cooke, Anderson, & Mckinley, 1999; Newton et al., 2016). Still, there is always a risk that catching, handling, and tagging may impact fish survival and behaviour. The risk that potential negative impacts would impact our conclusions was minimized by using a design where data from similarly tagged and handled fish were used both on the impacted river stretches and as controls on the reference stretches (see Section 2.4 below).

2.3 | Recording of tagged smolts after release

Downstream migration was recorded at 11 sites by 17 receiver stations that recorded fish id and time when the tagged fish passed a

TABLE 1 Groups of radio-tagged smolts

Group	*N*	Release date (2016)	Release site
Unkelmühle 1 and 2	60 and 60	April 1 and 7	Above Site 1 (a)
Downstream Unkelmühle 1 and 2	30 and 30	April 2 and 7	Below power station (e)
Dead Unkelmühle 1 and 2	5 and 5	April 2 and 7	Flood gate and turbines tailrace (d)
Buisdorf 1 and 2	24 and 23	April 2 and 8	Between Site 4 and Site 5 (g)
Dead Buisdorf 1 and 2	5 and 5	April 2 and 8	Weir Buisdorf (j)

Note: N is sample size. Letters denoting release site refer to Figure 1. Groups of fish already dead when released are termed “dead.”

TABLE 2 Description of the different river stretches at the power station and weir

Stretch		Start and end of stretch	Distances from release site (km)	Length of stretch (km)
a	Above the most upstream receiver site	Release site to site 1	0–1.5	1.5
b	Reference stretch	Site 1 to Site 2	1.5–7.3	5.8
c	Reservoir at power station	Site 2 to Site 3.1	7.3–9.6	2.3
d	Power station area	Within Site 3.1	9.6–9.8	0.2
e	Downstream of power station (Stretch 1)	Site 3.1 to Site 3.2	9.8–11.7	1.9
f	Downstream of power station (Stretch 2)/ reference stretch	Sites 3.2 to 4	11.7–17.3	5.6
g	Between Site 4 and Site 5	Sites 4 to 5	17.3–29.5	12.2
h	Reference stretch	Sites 5 to 6	29.5–36.8	7.3
i	Reservoir at weir	Sites 6 to 7	36.8–38.7	1.9
j	Weir area	Within Site 7	38.7–38.9	0.2
k	Downstream of weir (Stretch 1)	Sites 7 to 8	38.9–41.4	2.5
l	Downstream of weir (Stretch 2)	Sites 8 to 9	41.4–45.9	4.5
m	Between Site 9 and Site 10	Sites 9 to 10	45.9–51.2	5.3

Note: Stretches are denoted with letters referring to Figure 1. The start and end of the each stretch refer to sites where stationary receivers were installed (shown as stars in Figure 1).

station. The study area was divided into several stretches defined by a receiver site at the start and end (Figure 1, Table 2).

Detailed behaviour and choice of migration route at the weir and power station were recorded by using multiple antenna receivers (five receivers and 17 antennas at the power station and three receivers and eight antennas at the weir, Figures S1 and S4). Each receiver was connected to one to six antennas, and scan time per antenna was set to 7 s. Lotek model SRX 600 receivers were used with 3-, 4-, and 6-element Yagi antennas and underwater antennas. Antennas had reception ranges covering different areas (some overlapped, see Figures S1 and S4), and all antennas were thoroughly range tested by using a boat and submerged dummy radio tags prior to release of tagged fish. The results were used to establish criteria that enabled identification of all possible migration routes past the weir and power station. These criteria consisted of a combination of signal strengths and the logical sequential order of detections on different antennas that were expected for downstream migrating fish using each migration route. Violation of these criteria, such as missing or illogical order of detections on antennas, would prevent the determination of migration route or speed for an individual fish. However, this did not occur, and migration routes were determined for all smolts that passed the power station and weir. Migration speeds were based on the first and final detections on antennas at the different receiver sites.

Tagged fish were also positioned during 20 manual tracking surveys by boat from April 3 to May 11, 2016. The surveys alternated between covering the area upstream of the weir and the stretch from the weir to the confluence with the Rhine. Manual tracking was used to monitor tagged fish in areas of the river that were not covered by stationary receivers. The results were used to monitor movements in the river to confirm the presence of fish in the river and that data from the stationary receivers were interpreted correctly.

2.4 | Estimation of smolt loss

Estimation of smolt loss was based on fish (i.e., transmitters) that stopped moving or disappeared from the river. The reasons for loss can be predation by mammals, fish, or birds, other mortality reasons, and transmitter failure. The transmitters used are usually reliable, so significant loss due to transmitter failure was not expected. For fish eaten by fish predators or that died for other reasons, the transmitter will remain in the river. For transmitters failing, or for fish being taken by bird or mammal predators or scavengers that move the fish out of range, the transmitter signal will disappear from the river. Some smolts showed clear signs of being taken by bird predators or scavengers based on bird-like recordings, such as for instance fast upstream movements past the power station. Of the dead smolts released at the power station, two drifted 1.5- and 1.9-km downstream before becoming stationary, and eight remained stationary or were predated at the power station. At the weir, two released dead smolts drifted 1.0- to 1.8-km downstream, and eight remained stationary or were predated at the weir.

To calculate the extra loss of smolts caused by the weir and power station, we compared the loss on the impacted stretches at the weir and power station with the loss on upstream free-flowing reference stretches. Loss on a stretch downstream the power station and weir was included in the estimates of extra loss, because the release of 20 dead smolts at the power station and weir indicated that smolts that died during passage could potentially drift at least 1.9-km downstream of the power station and 1.8-km downstream of the weir before becoming stationary. Hence, for these calculations, loss of tagged fish was recorded (a) on free-flowing reference stretches (Stretches b and h), (b) in the reservoirs (Stretches c and i), (c) at the power station or weir (Stretches d and j), and (d) on a river stretch below the power station or weir (Stretches e–f and k–l, Table 2). Loss on impacted stretches exceeding the baseline mortality on the reference stretches was defined as loss caused by hydropower production or the presence of the weir. If expected loss on a developed stretch exceeded the observed loss, resulting in negative extra loss, extra loss on that stretch was set to zero.

The loss estimates assume that loss per kilometre recorded on the reference stretches is representative for the developed stretches if they had been free-flowing river stretches instead of being impounded and having the weir or power station. This may not necessarily be true, because there might have been a selective mortality with the potentially weakest individuals being lost first and the strongest individuals remaining at the time when they reached the power station and weir. If so, extra loss estimated for the impacted stretches would be underestimated. Alternatively, the opposite could be true, if smolts were stressed by passing developed stretches resulting in increased mortality with time and distance moved. Therefore, loss on impacted stretches was also compared with smolts released just below the power station (groups downstream Unkelmühle 1 and 2, Table 1), using their loss on Stretch f (Figure 1, Table 2) below the power station as an alternative reference. This enabled us to test if using a reference value derived from below versus upstream of the impacted stretches gave different estimates of extra mortality at the power station.

2.5 | Data analysis

To test if extra loss of smolts caused by the power station differed from extra loss caused by the weir, Fisher's exact tests were used to compare the proportion of extra lost fish with the number of fish entering the developed stretches between the two sites. Fisher's exact tests were used due to the low number of lost fish. Numbers of extra fish lost were estimated with decimals, but because a Fisher's exact test requires integers, and to make the test conservative, numbers of extra fish were rounded off up or down for largest difference between the power station and the weir. Extra loss at the power station for the groups Unkelmühle 1 and 2 (Table 1) was compared with the extra loss at the weir for two different samples of fish: (a) loss at the weir for groups of fish that were released upstream of the weir (Buisdorf 1 and 2, Table 1) and (b) loss at the weir for all fish entering reference Stretch h, irrespective of release site. Due to these multiple comparisons, a Bonferroni correction was applied to the Fisher's exact tests as suggested by MacDonald and Gardner (2000). Fisher's exact tests were also used to test if proportion of fish lost on reference Stretches b and f (Figure 1, Table 2) differed and to examine if there was any indication of selective morality of potentially weaker fish after release or of increased mortality with time. The latter was done by comparing mortality in groups of fish released on different sites (upstream of the power station, just downstream of the power station, and upstream of the weir, see Table 1 for groups) on the stretches (h–l) where all groups were monitored. Migration speeds on the different stretches and routes past the power station were compared by using nonparametric statistics (pairwise Wilcoxon and Mann–Whitney *U* tests) due to the data being highly skewed. Data were analysed using the software R (R Development Core Team, 2018).

3 | RESULTS

3.1 | Loss of smolts at and upstream of the power station

Of the 120 smolts that were released upstream of the power station (groups Unkelmühle 1 and 2, Table 1), six did not migrate from the release area, three were lost on the free-flowing reference stretch (Stretch b), and six were lost in the reservoir (Stretch c). The remaining 105 smolts entered the power station area. This corresponds to a loss of 2.6% of the fish entering the reference stretch (0.5% per kilometre).

3.2 | Migration routes at the power station

Of the 105 smolts that passed the power station, 63 smolts (60%) followed migration Route 1 towards the trash racks in front of the

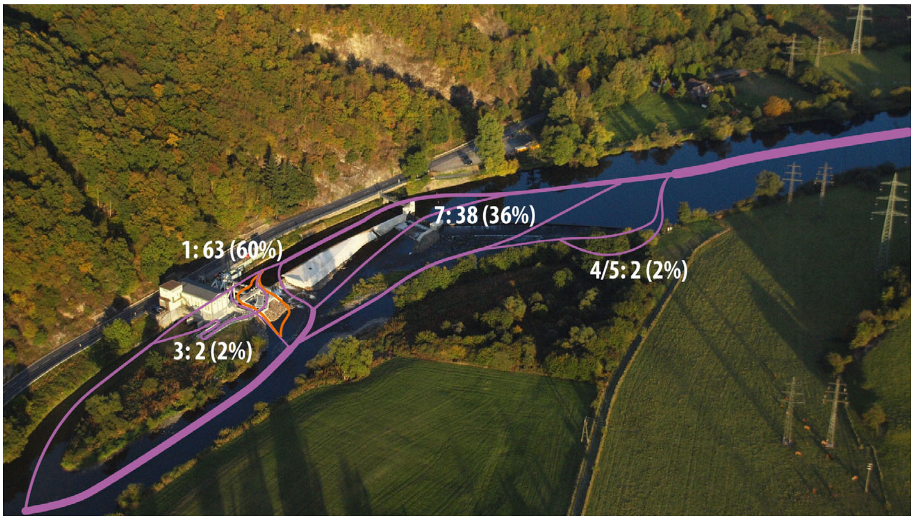

FIGURE 3 Number and proportion of smolts using the different migration routes past the power station. Route numbers refer to lower panel in Figure 2

TABLE 3 Overview of results in 2016 and two previous study years (Havn et al., 2018)

Year	Loss on reference stretch (per km)	Extra loss in reservoir	Extra loss at power station area	Extra loss due to the power station (includes loss on downstream stretch)	Total extra loss from reservoir to downstream stretch
2014	1.5%	7.2%	9.9%	Not known[a]	16.0%[b]
2015	1.6%	17.1%	3.6%	12.8%	25.1%
2016	0.5%	4.4%	2.9%	2.9%	7.2%

[a] Fish were not monitored downstream of the power station, and the loss estimates for the power station are incomplete and underestimated in 2014.
[b] For instance, fish dying at the power station and floating dead downstream are not included in this estimate.

turbines and passed through the surface bypass, 38 (36%) passed through the flood gate (Route 7), two (2%) used the vertical slot fishway (Route 3), and two smolts (2%) used the nature-like fishway or the canoe pass (Route 4 or 5; Figure 3). No smolts slipped through the bar spacing of the racks and passed through the turbines. Six smolts were captured for monitoring purposes and removed from analyses.

3.3 | Loss of smolts at and downstream of the power station

Of the 99 smolts that passed the power station and were not captured for monitoring purposes, five were lost at the power station or between the power station and Site 4. One of them passed through the surface bypass and became stationary. One was predated or scavenged after passing the power station via the spillway gate and was moved upstream to the entrance of the natural fishway where the transmitter became stationary. One passed the power station via the surface bypass and then moved upstream and downstream in the tailrace before it moved at a speed of more than 50 km hr^{-1} between two receiver sites, indicating that it was predated or scavenged by a bird. The transmitter was later recorded at a cormorant colony 34-km downstream of the power station. Two smolts disappeared from the tracked stretches between Site 3.2 and Site 4. In summary, three smolts were lost at the power station and two on the stretch from Site 3.1 to Site 4. The proportion of fish that likely survived after passing the power station did not differ between those passing via the headrace (56 of 59) and those passing over the weir (38 of 40, Fisher's exact test, $p = 1$).

3.4 | Estimates of loss related to the reservoir and power station

Based on the results given above, there was 4.4% extra loss in the reservoir compared with what would be expected if the loss was the same as on the free-flowing reference Stretch b upstream of the reservoir (i.e., 4.4% of the smolts entering the reservoir were lost due to this being a reservoir instead of a free-flowing river). Extra loss due to the power station was 2.9% (extra loss at the power station area and 7.5-km downstream combined). If the losses in the reservoir, power station area, and 7.5-km downstream are combined, the total minimum extra loss due to hydropower was 7.2% (i.e., of smolts entering the reservoir).

3.5 | Estimates of loss related to the power station based on different reference values

Loss on the reference stretch below the power station (Stretch f, Figure 1) for fish released downstream of the power station (groups Downstream Unkelmühle 1 and 2, Table 1) was slightly higher (1.0% per kilometre) than loss on the reference stretch upstream of the power station (Stretch b, 0.5% per kilometre). However, the proportion expected lost fish due to the power station was not significantly different when using Stretch b as a reference value (3.4 of 99 fish expected lost) than when using Stretch f as a reference value (7.4 of 99 fish expected lost, Fisher's exact test = 0.21). Because there was no significant difference in expected loss based on the two different reference values (and consequently no difference in extra loss), we present extra loss calculated based on the reference value from Stretch b, because this is comparable with previous study years (2014 and 2015).

3.6 | Extra loss on developed stretches at the power station compared to previous study years

Extra loss of smolts due to the power station was lower in 2016 (2.9%) compared with two previous study years (9.9% in 2014 and 12.8% in 2015, Havn et al., 2018, Table 3). Similarly, total extra loss due to hydropower (power station and reservoir combined) was lower in 2016 (7.2%) compared with 2014 (16.0%) and 2015 (25.1%, Table 3). Note that fish were not monitored downstream of the power station during the first study year, and the loss estimations for the power station are therefore incomplete and underestimated in 2014.

3.7 | Migration speeds

Median time spent by smolts from release to passing Site 4 was 25.1 hr (mean 79.4, range 3.7–465.5, *SD* 99.5, $n = 93$). Migration speed on reference Stretch b (median 4.2 km hr^{-1}) was faster than in the reservoir (median 2.5 km hr^{-1}) and in passing the power station

TABLE 4 Migration speeds and hours spent on the reference Stretch b and in the reservoir upstream of the power station, past the power station, and from the power station to Site 4

River stretch	Median (km hr^{-1}/hr)	Average (km hr^{-1}/hr)	Minimum-maximum (km hr^{-1})	Minimum-maximum (hr)	Standard deviation (km hr^{-1}/hr)
Reference Stretch b	4.2/1.4	3.4/7.3	0.04–7.9	0.7–140.5	1.8/18.1
Reservoir	2.5/0.9	2.3/3.9	0.03–4.6	0.5–66.9	1.3/9.3
Power station	0.4/0.5	0.8/6.2	0.001–4.2	0.05–137.3	0.8/17.7
Power station to Site 4	4.5/1.7	3.5/13.5	0.05–6.1	1.2–142.0	2.1/29.6

Note: Only smolts recorded on all receiver sites from release to Site 4, excluding those captured for monitoring purposes, are included (n = 93).

TABLE 5 Migration speed past the power station for fish using different migration routes

Migration route past the power station	Median (km hr^{-1})	Average (km hr^{-1})	Minimum-maximum (km hr^{-1})	Standard deviation (km hr^{-1})
Surface bypass (Route 1, n = 54)	0.1	0.29	0.001–2.4	0.5
Vertical slot fishway (Route 3, n = 2)	0.05	0.05	0.01–0.08	0.05
Canoe pass or natural fishway (Route 4, n = 2)	0.9	0.9	0.3–1.6	0.9
Spillway gate (Route 7, n = 36)	1.6	1.6	0.4–4.2	0.7

Note: Route numbers refer to the lower panel in Figure 2. All smolts that successfully passed the power station and reached Site 4 are included (n = 94).

(median 0.4 km hr^{-1}, pairwise Wilcoxon test with Bonferroni correction: both p-values <.01 Table 4) but did not differ from the speed on the stretch from the power station to Site 4 (4.5 km hr^{-1}, p = 1). The fish migrated slower past the power station than on all other stretches (pairwise Wilcoxon test with Bonferroni correction: all p-values <.01). At the power station, those passing via the headrace (surface bypass or vertical slot fishway) were slower in passing the power station (median 0.1 km hr^{-1}, range 0.001–2.4, *SD* 0.5, n = 56) than those using the spillway gate, natural fishway, or canoe pass (median 1.6 km hr^{-1}, range 0.3–4.2, *SD* 0.7, n = 38, Mann–Whitney *U* test: W = 103.5, p < .001, n = 94, Table 5).

4 | LOSS AT THE WEIR

4.1 | Loss of smolts upstream of the weir

Of the 47 smolts that were released upstream of the weir (groups Buisdorf 1 and 2 released on Stretch g, Table 1, Figure 1), seven did not migrate from the release area, one was lost on the reference stretch (Stretch h), and two were lost in the reservoir (Stretch i). The remaining 37 smolts passed the weir. This corresponds to a loss of 2.5% on the reference stretch (0.4% per kilometre).

4.2 | Migration routes at the weir

Of the 37 smolts that passed the weir, 35 smolts (95%) migrated over the weir (Route 2), and two (5%) passed through the fence and then moved down the ramp-like fishway or canoe pass (Route 3-c, Figure 4, see Figure 2 for route numbers).

4.3 | Losses of smolts at and downstream of the weir

No smolt was lost in the weir area (0.2 km). Two smolts were predated or scavenged between the weir and Site 8, and one stopped moving between Site 8 and Site 9. All the lost smolts had passed over the weir.

4.4 | Estimates of loss related to the reservoir and weir

Based on the results given above, there was 4.5% extra loss in the reservoir compared with the reference stretch h (i.e., 4.5% of the smolts entering the reservoir were lost due to this being a reservoir instead of a free-flowing river). Extra loss due to the weir was 5.7% (extra loss at the weir and 7.0-km stretch downstream combined). If the loss in the reservoir, at the weir and on the downstream stretch is combined, total minimum extra loss due to the weir and its reservoir was 9.9% (of smolts entering the reservoir).

4.5 | Migration speeds

Median time spent by smolts from release to Site 9 was 53.1 hr (mean 59.2, range 4.4–229.9, *SD* 50.6, n = 34). Migration speed did not differ

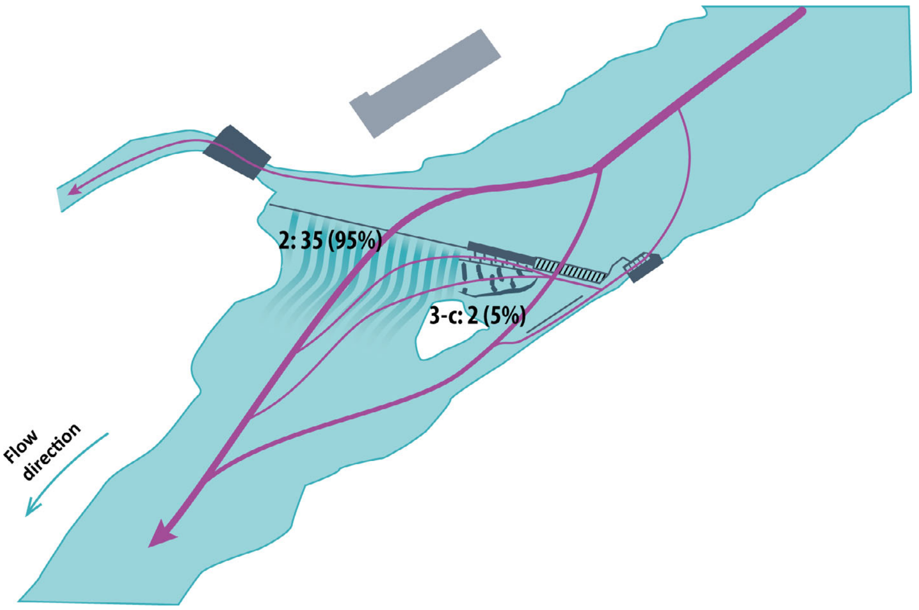

FIGURE 4 Number and proportion of smolts using the different migration routes past the weir. Route numbers refer to upper panel in Figure 2

TABLE 6 Migration speeds and hours spent on the reference stretch (Stretch h) and in the reservoir upstream of the weir, past the weir, and from the weir to Site 9

River stretch	Median (km hr^{-1}/hr)	Average (km hr^{-1}/hr)	Minimum-maximum (km hr^{-1})	Minimum-maximum (hr)	Standard deviation (km hr^{-1}/hr)
Reference Stretch h	4.3/1.7	3.9/4.1	0.3–5.9	1.2–25.0	1.8/6.4
Reservoir	2.6/0.7	2.5/1.7	0.1–3.9	0.5–15.0	0.9/3.2
Weir	4.4/0.5	4.5/2.6	0.003–12.0	0.02–68.6	3.2/11.8
Weir to Site 9	4.1/1.7	3.7/7.4	0.2–5.9	1.2–47.1	1.8/13.5

Note: Only smolts recorded on all receiver sites from release to Site 9 were included in the table (n = 34).

between the reference stretch, weir, and the stretch from the weir to Site 9 (median 4.3, 4.4, and 4.1 km hr^{-1}, respectively, pairwise Wilcoxon test with Bonferroni correction: all p-values >0.95, Table 6). Migration speed in the reservoir was slower than on other stretches (pairwise Wilcoxon test with Bonferroni correction: all p-values <.03, Table 6).

5 | COMPARISON OF LOSS AND MIGRATION SPEED AT THE POWER STATION AND WEIR

5.1 | Loss at the power station and weir

The proportion extra loss due to the weir (at the weir and on the downstream stretch) for groups Buisdorf 1 and 2 (5.7%) did not differ from extra loss due to the power station (at the power station and downstream stretch) for groups Unkelmühle 1 and 2 (2.9%, Fisher's exact test with Bonferroni correction: p = .61, Table 7). Similarly, there was no difference in the total extra loss at developed stretches at the weir (9.9%) compared with the power station (7.2%, Fisher's exact test with Bonferroni correction: p = 1, Table 7).

There was no indication of selective mortality of potentially weaker fish after release, or of increased mortality over time, because there was no difference in the proportion of fish lost between groups of fish released on different sites (groups Unkelmühle 1 and 2, Downstream Unkelmühle 1 and 2, and groups Buisdorf 1 and 2) on any of the stretches (h–l) where all groups were monitored (Fisher's exact tests: all p-values >.60). Because we did not find an indication of selective mortality, we compared the extra loss caused by the weir and power station by including all fish entering reference Stretch h, irrespective of release site, in the analysis as a basis for the loss estimate at the weir (n = 175). Like the results above, the extra loss due to the weir (at the weir and on the downstream stretch; 3.4%) did not differ from the extra loss due to the power station for groups Unkelmühle 1 and 2 (2.9%, Fisher's exact test with Bonferroni correction: p = 1, Table 7). Similarly, there was no difference in total extra loss on developed stretches including the reservoir (5.2% at the weir and 7.2% at the power station, Fisher's exact test with Bonferroni correction: p = .61, Table 7).

5.2 | Migration speed

Migration speed over the weir was higher for fish released upstream of the weir (Buisdorf 1 and 2, n = 34) than speed at the power station for fish released upstream of the power station (Unkelmühle 1 and

TABLE 7 A comparison of extra loss of smolts between Unkelmühle power station and Buisdorf weir for the different groups of fish

Site	Release group	Reference stretch	*N* entering reference stretch	Loss on reference stretch (per km)	Extra loss in reservoir	Extra loss at power station or weir	Extra loss due to power station or weir (includes loss on downstream stretch)	Total extra loss from reservoir to downstream stretch
Unkelmühle	Unkelmühle 1 and 2	b	114	0.5%	4.4%	2.9%	2.9%	7.2%
Buisdorf	Buisdorf 1 and 2	h	40	0.4%	4.5%	0.0%	5.7%	9.9%
Buisdorf	All groups[a]	h	175	0.6%	1.9%	1.2%	3.4%	5.2%

Note: Information about the groups can be found in Table 1.

[a] Results for all smolts entering Stretch h irrespective of release site (released on either Site a, e, or g).

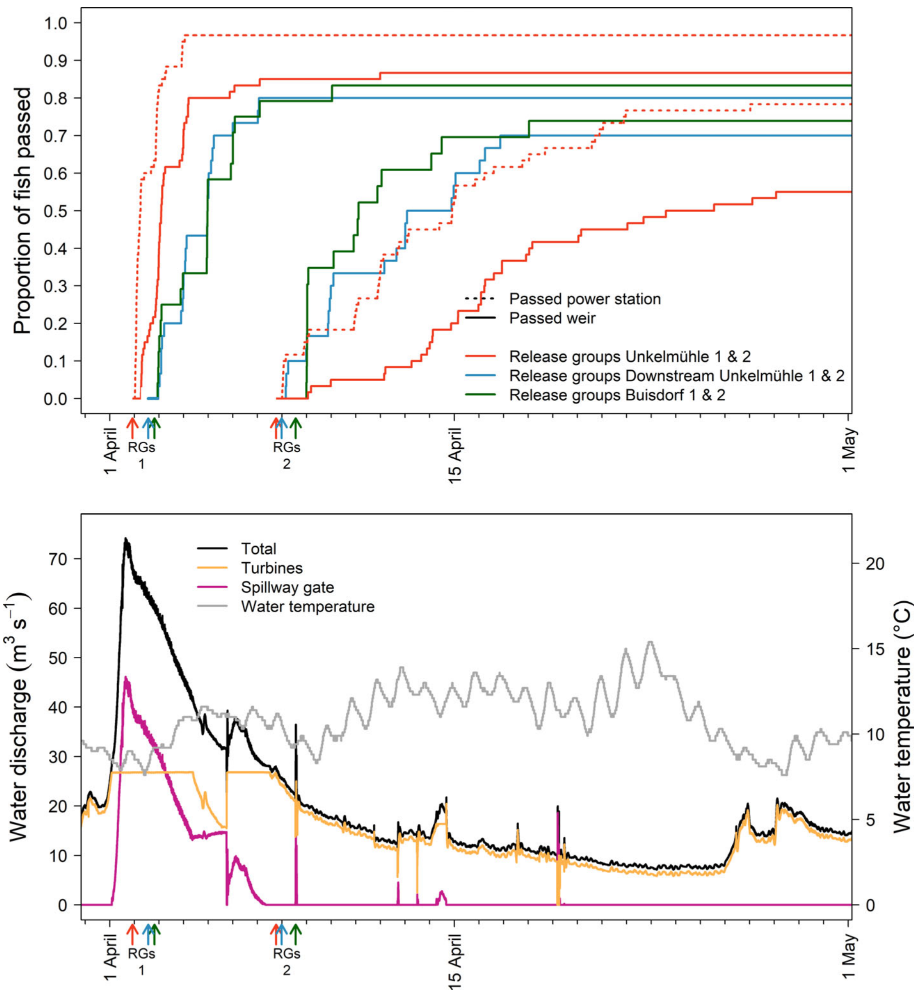

FIGURE 5 Upper panel: Cumulative proportions of tagged smolts that passed the power station (dotted lines) and weir (solid lines) are shown for the groups released upstream of the power station (red lines), just downstream of the power station (blue lines) and at the weir (green lines). The first three groups were released April 1 and 2 (indicated by arrows and "RGs 1") and the last groups were released April 7 and 8 (indicated by arrows and "RGs 2," see Table 1 for more information about the groups). Lower panel: Total water discharge (black line), turbine discharge (yellow line), spillway gate discharge (purple line), and water temperature (grey line) at the power station during the study

2, $n = 94$, Mann–Whitney *U* test: W = 430, $p < .001$), even though water discharge was higher and water temperature was lower when fish passed the power station (median 59 m^3 s^{-1} and 9.2°C) than the weir (median 35 m^3 s^{-1} and 11.0°C, Figure 5, Mann–Whitney *U* tests: both *p*-values <.02). Similarly, when considering fish that passed both the power station and the weir ($n = 62$), the speed was faster at the weir (Wilcoxon signed-rank test: V = 11, $p < .001$).

6 | DISCUSSION

The results in this study showed that the extra loss of downstream migrating smolts was low when passing a low-head weir. Only 5.2% of the smolts that entered the reservoir upstream of the weir were lost due to the presence of the reservoir and weir compared with if this had been a free-flowing river stretch. However, smolts passing the weir may be injured and experience delayed mortality downstream of the monitored stretches or when entering saltwater (McCormick et al., 2009; Zydlewski, Zydlewski, & Danner, 2010; Stich, Kinnison, et al., 2015; Stich, Zydlewski, et al., 2015). Loss estimates should therefore be regarded as conservative estimates. The exact reasons for the extra loss of smolts at the weir are not known, but there was extra mortality both in the reservoir and at or below the weir. There were no turbines at the site, and hence no turbine mortality, so mortality must have been related to physical damage imposed to the smolts when passing over the weir, or perhaps increased predation risk in case smolts were injured or confused after passing the weir, or in the slow-flowing reservoir. Fish and bird predators like great cormorant, *Phalacrocorax carbo* L., and northern pike, *Esox lucius* L., are present in this area and are known to prey on Atlantic salmon smolts (Dieperink, Pedersen, & Pedersen, 2001; Jepsen, Aarestrup, Økland, & Rasmussen, 1998; Jepsen, Pedersen, & Thorstad, 2000).

There is also a risk that obstacles delay downstream migrating smolts if they accumulate above the obstacle or if they are stunned, stressed, and disoriented after they have passed (Norrgård, Greenberg, Piccolo, Schmitz, & Bergman, 2013; Stich, Kinnison, et al., 2015). Delays in migration in reservoirs and at migration obstacles could also increase the predation risk, but this was not the case at the weir in this study because the migration of the smolts was not slowed down over the weir compared with on the free-flowing reference stretch. However, the migration speed was slowed down in the slow-flowing area upstream of the weir (reservoir), which could have contributed to an elevated mortality in the reservoir due to increased predation.

A typical situation in many watersheds is that migrating fishes must pass several weirs and power stations, and the cumulative impacts of the obstacles may be large even though the mortality at each of them is low (Larinier, 2008; Norrgård et al., 2013). For instance, if there are five obstacles in the same watershed, and the mortality at each of them is 5%, like the relatively low mortality at the Buisdorf weir, the total mortality for downstream migrating smolts that must pass all of them is 23%. This may even be a minimum cumulative mortality, because if some smolts are injured, they may have a further reduced chance of surviving passage of downstream obstacles. In Atlantic salmon, there are no compensatory mechanisms for additional mortality in the smolt phase (Einum & Nislow, 2011; Milner et al., 2003). Elevated mortality for instance at a weir during the smolt migration can therefore result in a proportional reduction in the number of spawning adults, so that 5% mortality at a weir can result in the same reduction in the number of adults returning to the river. Such mortality may not necessarily be detrimental for a healthy population with few other negative impacts, but for a population under re-establishment, such as in the River Rhine, a mortality at this level may hamper re-establishment. The long migration route of salmon smolts in this study area may additionally lead to a high natural mortality compared with smolts in shorter river systems (Lothian et al., 2018).

The majority of the smolts that passed the weir migrated over the weir instead of using the other migration routes and thereby followed the route where most of the water was flowing. These results resemble several other studies suggesting that proportion of smolts passing through, for instance, hydropower turbines is related to the proportion of water diverted through them (Hvidsten & Johnsen, 1997; Ruggles, 1980; Serrano, Rivinoja, Karlsson, & Larsson, 2009). However, there are also indications that smolts can manoeuvre and choose to use routes with less water instead of following the main flow (Havn et al., 2017).

Extra loss of smolts due to the power station was lower in 2016 (2.9%) compared with two previous study years (9.9% in 2014 and 12.8% in 2015, Havn et al., 2018). Both 2014 and 2015 were years with low river discharge during the smolt run. Therefore, few tagged smolts passed over the spillway gate. In 2016, the discharge was higher, and more smolts passed the power station via the spillway gate. However, loss of smolts passing the power station via the headrace was also low, and the high water discharge was probably an important factor for reducing loss of smolts using all migration routes in 2016. High flow resulted in smolts spending less time passing the power station compared with previous study years (Havn et al., 2018), thus reducing the exposure time for predators in the tailrace and on the downstream stretch. Furthermore, high flow also increased the turbidity and thus the visibility of the smolts to potential predators. The exact causes of mortality at the power station are unknown but might be related to injuries inflicted in the bypass routes and increased predation. No fish entered the turbines, and like previous years (Havn et al., 2018), there was consequently no turbine mortality, as expected due to racks with narrow bar spacing (10 mm) in front of the turbines.

The results in this study and Havn et al. (2018) showed that mortality could be relatively high in the power station reservoir but that the mortality also here varied among years (7.2% in 2014, 17.1% in 2015, and 4.4% in 2016). The main reason for the extra loss in the reservoir is likely the presence of more fish predators in the slow-flowing reservoir compared with the free-flowing river stretches. Water discharge was higher, and fish migrated faster through the reservoir in 2016 compared with the two previous years, possibly reducing exposure time and visibility to predators and thus reducing the loss. However, fish migrated faster through the reservoir in 2015 than in 2014, so time spent in the reservoir may not always explain variation in loss. The variation among study years may be caused by variation in the predator community in terms of number, size, and species composition. Jepsen et al. (2000) found that the temporal overlap between the smolt run and predator-spawning may be an important factor affecting smolt survival, which may also vary among years.

In all three study years, smolt loss caused by the power station was estimated as the extra loss on impacted stretches compared with what the loss would have been if this was unimpounded stretches (based on loss on a free-flowing reference stretch upstream of the reservoir). An assumption for these estimates is that the reference mortality on the free-flowing stretch was representative for the impacted stretches, which may not be true. Hypothetically, there might have been a selective mortality in the reference stretch, reservoir, and power station, with the potentially weakest individuals being lost and the strongest individuals remaining. If so, extra loss was underestimated due to overestimating baseline loss on impounded stretches. Alternatively, smolts may have been weakened by passing developed stretches resulting in increased mortality with time and distance moved. There was, however, no difference in mortality when comparing groups of tagged smolts that had migrated long stretches before entering a river stretch with those being released immediately above, and hence, no indication that selective mortality impacted the results and conclusions.

An alternative to using the loss on a stretch upstream of the reservoir as reference mortality was to release fish below the power station and record losses on the downstream stretch. Although this does not solve the potential selection problem discussed above, estimates of baseline loss would be based on reference loss on the same stretch as some of the loss caused by the power station was recorded, instead of using an upstream stretch as a proxy. On the other hand, predators may be attracted to areas downstream of power stations due to occurrence of dead and injured fish (Koed, Jepsen, Aarestrup, & Nielsen, 2002). Uninjured smolts released in this area might therefore experience an increased predation risk as an indirect effect of the power station, which makes such stretches less suitable as reference stretches. Nonetheless, although the loss of smolts was slightly higher on the reference stretch downstream of the power station compared with on the reference stretch upstream, the total extra loss did not differ when comparing estimates based on the two different reference stretches.

In conclusion, the results in this study showed that there was some extra mortality of downstream migrating smolts caused by a low-head weir but that the mortality was relatively low. The extra loss was likely related both to mortality in the reservoir upstream of the weir and caused by the weir itself. Losses of smolt did not differ between the weir and the power station, neither when passing the power station and weir, nor in the reservoirs. However, the migration speed of salmon smolts was significantly reduced at the power station but not at the weir. Further, the study showed that mortality at the same power station may differ considerably among years, and the mortality was more than four times higher in the year with the highest mortality compared with the year with the lowest mortality. Both lower mortality and faster migration in the last study year might be related to the generally higher river discharge that year.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, LH, upon reasonable request

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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