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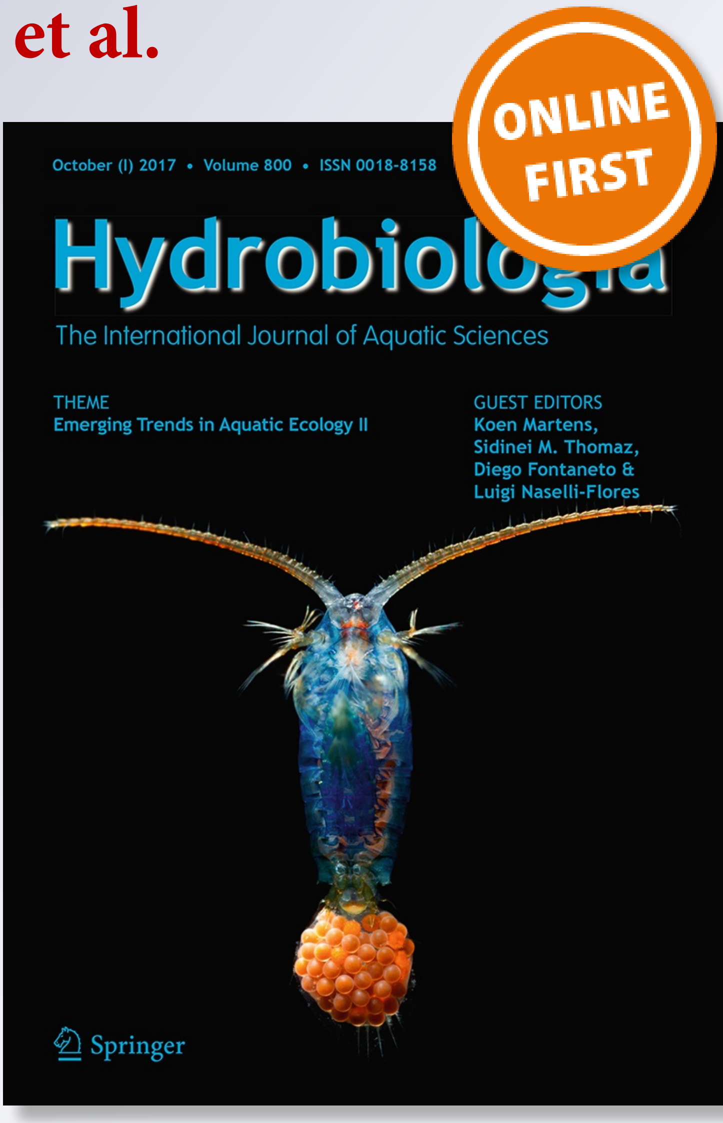

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PRIMARY RESEARCH PAPER

Hydropower-related mortality and behaviour of Atlantic salmon smolts in the River Sieg, a German tributary to the Rhine

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Abstract We studied downstream migration of 256 radio-tagged Atlantic salmon smolts passing a low-head power station where technical facilities have been improved to allow safe migration via several bypass routes. Extra mortality was 7 and 17% (two years) in the power station reservoir, and a minimum of 10 and 13% at the power station compared to in a control stretch. The majority of the smolts followed the main flow at the power station, towards the turbines. Sloped bar racks with 10 mm bar spacing hindered smolts from entering the turbines, hence there was no turbine mortality. Smolts used surface openings in the racks, which directed them to a bypass route outside the turbines. The extra mortality in the reservoir and at the power station was related to physical injuries in bypass routes and to predation. The mortality risk in the reservoir and at the power station decreased with increasing migration speed. Migration speeds increased with water discharge. Migration was slower when the smolts passed the power station than on other stretches. This study shows that hydropower regulation caused elevated mortality and delays for downstream migrating fish, even with improved technical facilities to reduce mortality.

Keywords Radio tag · Telemetry · *Salmo salar* · Downstream migration · Migration speed · Bypass

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Introduction

Atlantic salmon (*Salmo salar* Linnaeus, 1758) is a fish species of large cultural and economic importance. Salmon spawn and spend the juvenile phase in freshwater. After they reach the age and size for smoltification, they typically migrate from river to sea, and perform long-distance marine feeding migrations in the Atlantic Ocean (Thorstad et al., 2011). Atlantic salmon populations have declined in most of the distribution area (ICES, 2016), and have been lost from all German watersheds due to pollution, migration barriers and habitat destruction (Monnerjahn, 2011).

A decline of Atlantic salmon in German rivers likely began with the expansion of watermill technology

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during the Middle Ages (Lenders et al., 2016), followed by decreased water quality, habitat degradation and river fragmentation by weirs and dams after the industrial revolution (Monnerjahn, 2011). By the end of the 1950s, salmon populations were extinct in many rivers, including the River Rhine, which once was among the main Atlantic salmon rivers in Central Europe (Molls and Nemitz, 2008; Monnerjahn, 2011). Re-introduction programs have been initiated in the Rhine. Atlantic salmon have reproduced naturally in several tributaries including the River Sieg, where this study was performed, but self-sustaining populations are not yet re-established (Molls and Nemitz, 2008; Monnerjahn, 2011; Schneider, 2011).

Concurrent with attempts to re-introduce Atlantic salmon, there is a desire to produce renewable hydroelectric energy. Hydropower installations may reduce river connectivity and can cause injuries, delay and mortality for migrating fish (e.g., Rivinoja et al., 2001; Larinier, 2008; Stich et al., 2015a, b). Atlantic salmon smolts migrate downstream in rivers, mainly in the spring (Thorstad et al., 2011). After the feeding migration, salmon return to their home river to spawn. To re-establish Atlantic salmon populations, the migrating fish need to pass hydropower installations with little mortality. Increased mortality in regulated rivers may be due to fish being killed by turbines, predation in the reservoir above the power station and increased mortality in alternative passages that lead fish outside the turbines (Thorstad et al., 2012).

Many fish ladders have been built, improving upstream migration of fish at man-made migration barriers, although challenges still remain (Bunt et al., 2012; Katopodis and Williams, 2012; Noonan et al., 2012). Passage routes suitable for downstream fish migration are often missing (e.g., Calles and Greenberg, 2009; Kraabøl et al., 2009), and it is necessary to improve mitigation measures for downstream migration. At the Unkelmühle Power Station in the River Sieg, technical facilities have been modified to allow safe downstream migration. The power station has been designed with several possible bypass routes that fish can use instead of passing through the turbines. Narrowly spaced racks (10 mm opening between the racks) are installed at the turbine intakes to prevent fish from entering the turbines and to guide them to one of the bypass routes.

The aim of this study was to examine mortality and downstream migration of Atlantic salmon smolts in the River Sieg and past the Unkelmühle Power Station. The study was performed by tagging downstream migrating smolts with radio transmitters and following their movements using automatic stationary receivers and manual tracking (Thorstad et al., 2013). Migration behaviour and mortality were estimated in the reservoir upstream of the power station, when they passed the power station, and on downstream stretches. Specifically, we examined (1) extra loss of smolts in the reservoir and when passing the power station area compared to the loss in a free-flowing control stretch, (2) passage routes used at the power station and (3) migration speeds in the reservoir and past the power station compared to in the control stretch.

Materials and methods

Study area

The Rhine (catchment area 185,000 km^2) originates in Switzerland, forms part of the Swiss–German and French–German borders, flows through Germany, and empties into the North Sea in the Netherlands. It is 1,233 km long—most of which runs through Germany—and has a mean discharge of 2,280 m^3 s^{-1} at the German–Dutch border. The Sieg is a 153-km-long tributary to the Rhine, with a catchment area of 2,862 km^2. The average water discharge at the confluence with the Rhine is 53 m^3 s^{-1}.

Unkelmühle is a run-of-river power station on the Sieg, 44 km upstream from the Rhine (Figs. 1, 2), with an upstream lake-like reservoir (2.3 km in length and up to 99 m in width). The reservoir is not used to regulate river discharge, but the water level can be increased during floods. The power station has three Francis turbines with a total capacity of 27 m^3 s^{-1} and an available head of 2.7 m.

The power station has ten passage routes that can be used by downstream migrating fish (Figs. 2, 3, 4). One possible passage route is through custom-made openings in horizontally sloped racks (27° relative to the ground, 10 mm bar spacing) covering the turbine intakes, which enable fish to bypass the turbines via a flushing channel (Figs. 3, 4, discharge in flushing channel of 0.6 m^3 s^{-1}). Fish can swim from the flushing channel, where they are either collected for monitoring purposes in holding pools, or guided to the river downstream of the turbines via a channel when rack debris is flushed out during rack cleaning; the

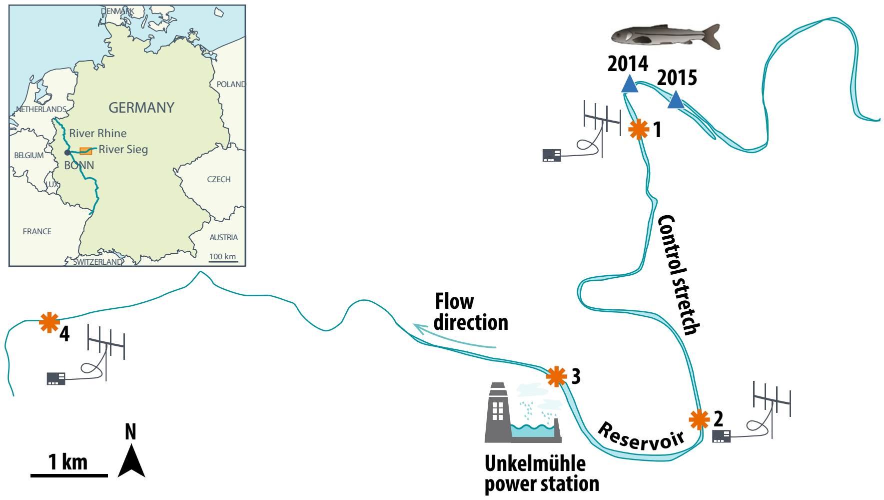


Fig. 1 Study area in the Sieg showing release sites for radio-tagged Atlantic salmon smolts (*blue triangles*), receiver sites where they were recorded when passing (*orange stars*, denoted with site numbers *1–4*) and the Unkelmühle Power Station. *Site 4* was only operating in 2015

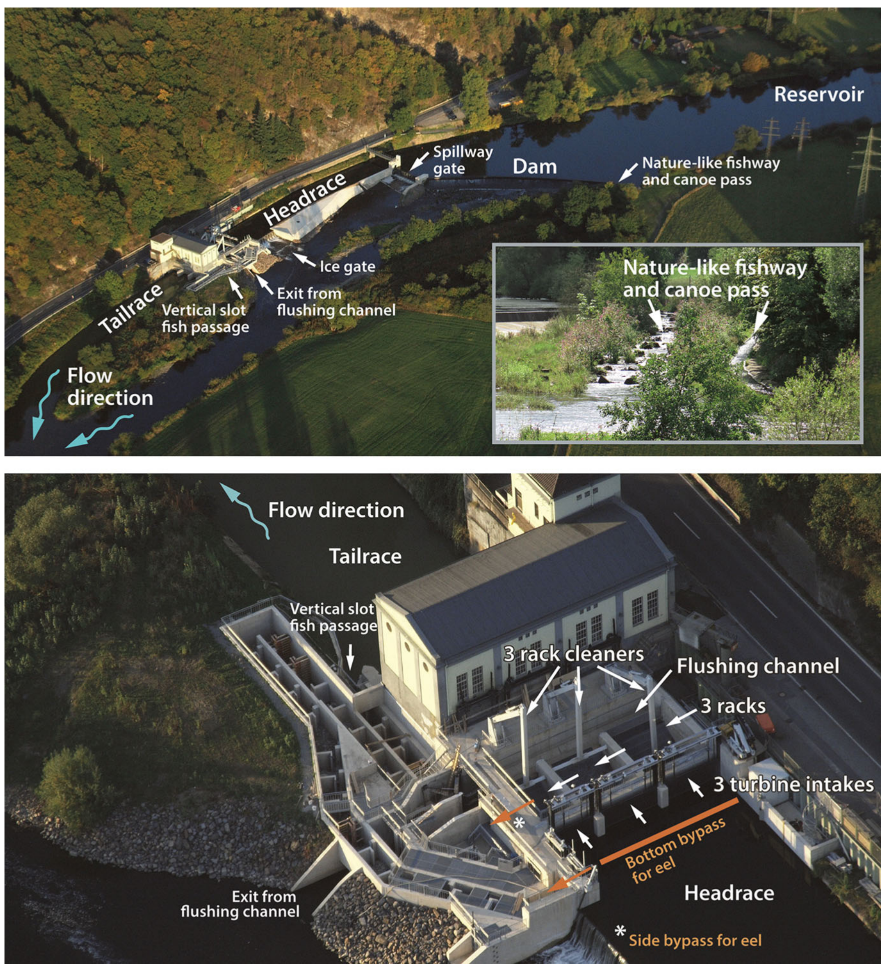


Fig. 2 Unkelmühle Power Station with the different passages where downstream migrating fish can pass. The *upper panel* shows an overview of the power station area, and the *lower panel* shows the power station in more detail. The different passage routes past the power station are further shown in Fig. 3. *Photos* Wikimedia Commons and Eva B. Thorstad

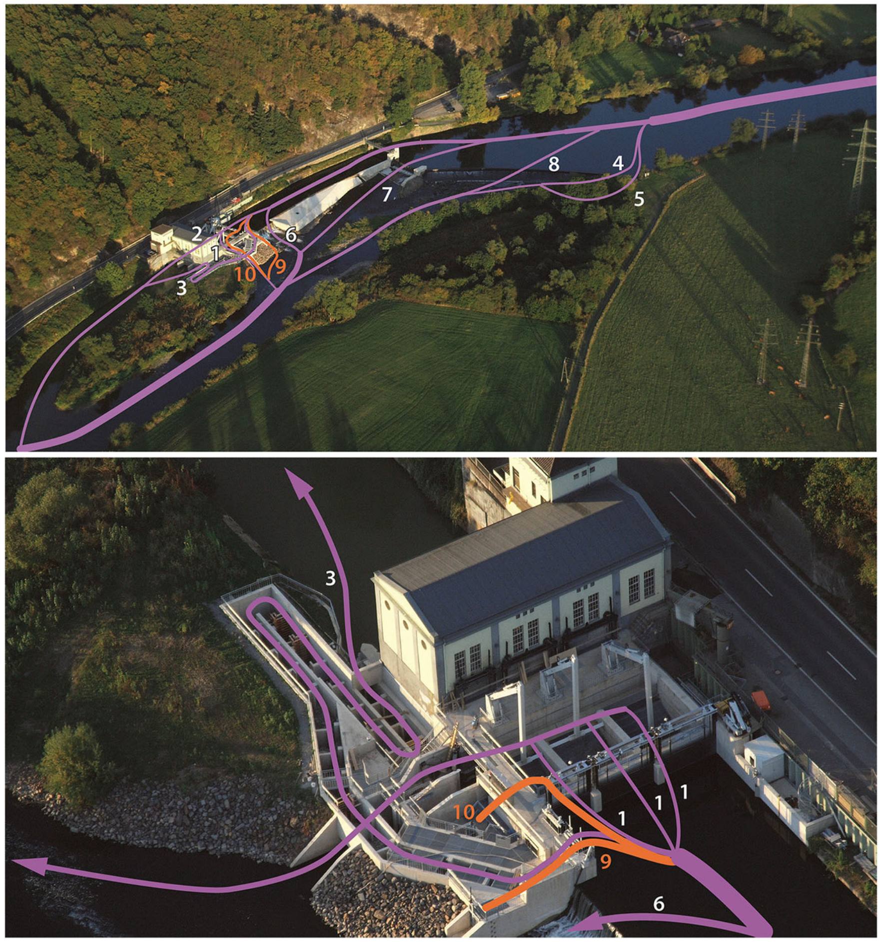


Fig. 3 The different routes downstream migrating fish can use to pass the Unkelmühle Power Station: (*1*) via custom-made openings in the racks that lead fish to a route outside the turbines via the flushing channel, (*2*) through turbines if they slip through the bar spacing of the racks, (*3*) through the vertical slot fish passage 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 (*9* and *10* are only in operation during the eel run in the autumn). *Numbers* in both *panels* refer to the different passage routes. *Photos* Wikimedia Commons

control of the route is determined by the operation of gates. The operation of the rack cleaners depends on the amount of debris. During periods of high water and increased debris transport, they are continuously operated. Fish near to the racks may be pushed over them by the rack cleaners, which could potentially facilitate passage, but also injure the fish.

Water discharge was 0.3 $m^3\ s^{-1}$ in the vertical slot fish passage, and 0.2 $m^3\ s^{-1}$ in the nature-like fishway and the canoe pass. Due to low water discharge during the study, water was not released over the ice gate and dam, so these routes were closed. The spillway gate was open on eight occasions in 2014 (median time open 60 min, range 30 min to 3 h) and five occasions in 2015 (median time open 22 min, range 16 min to 5 h). Bottom and side passes designed for eel were not in operation during the study. River discharge and temperature during the study are shown in Fig. 5.

Capture and tagging of smolts

We tagged 256 Atlantic salmon smolts in 2014 and 2015 (Table 1). Most of the smolts ($n = 206$) were captured for tagging at the power station during their downstream migration, and are termed wild in the following. These 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). They were held at the power station for up to 5 days before tagging and release. In addition, 50 smolts were hatchery-reared smolts from the Albaum Hatchery (all released 9 April 2015). Total body length did not differ between wild (mean length 159 mm) and hatchery-reared smolts in 2015 (mean length 162 mm, independent two sample t test, $t_{166.5} = -1.30$, $P = 0.20$), but hatchery-reared smolts were heavier (mean body mass 44 g) than wild

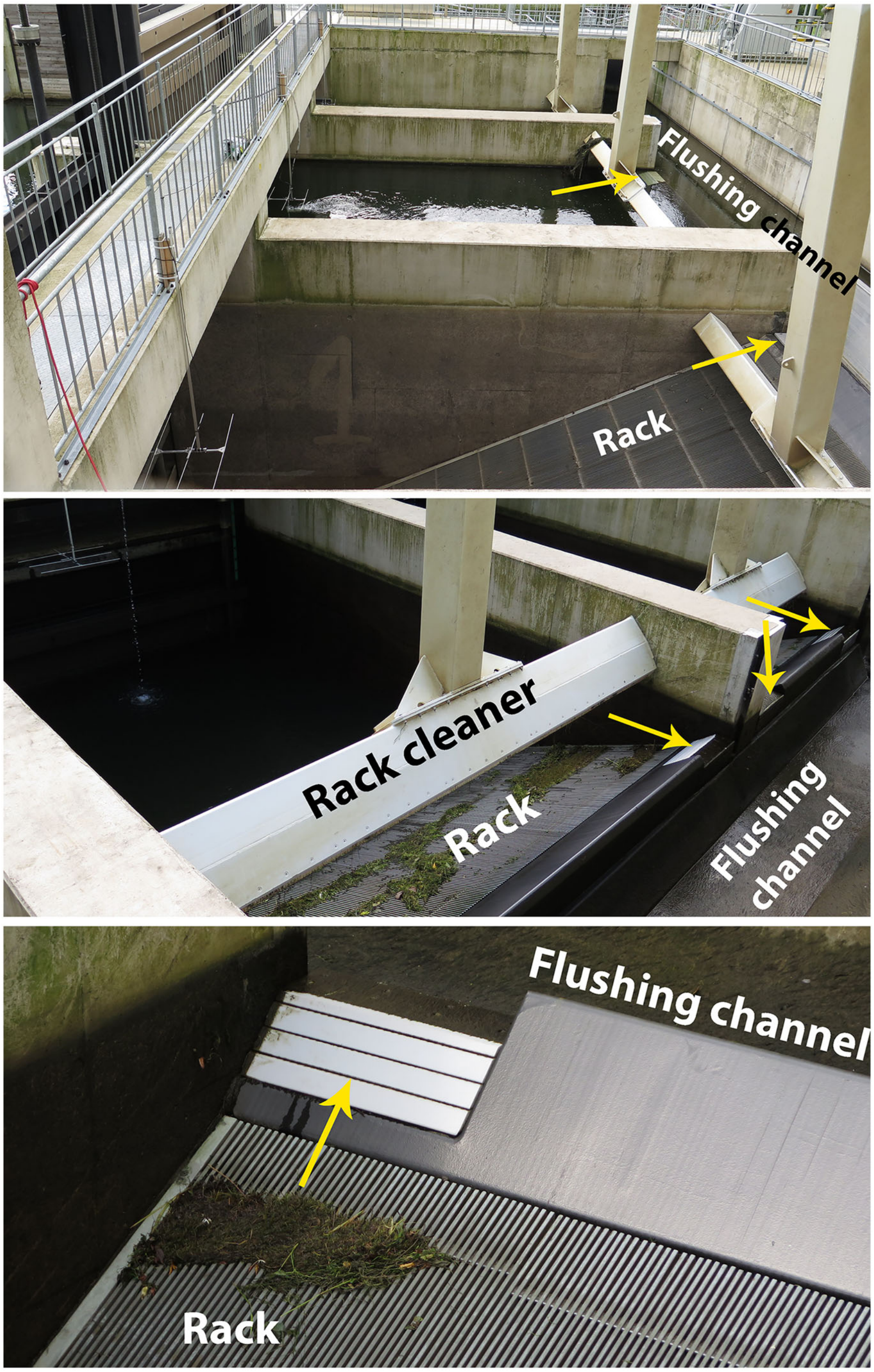


Fig. 4 Details from the turbine intake at the Unkelmühle Power Station. *Upper panel* the three turbine intakes with racks and rack cleaners. *Yellow arrows* show custom-made openings near the surface where fish approaching the rack can pass through and move into the flushing channel. There are two openings in each rack, one on each side, in total six openings. Fish that enter the flushing channel can follow a passage route past the power station outside the turbines. When turbines were operating during this study, the water level covered the racks, openings and flushing channel. When the photo was taken, only two turbines were operating and one of the racks was therefore not submerged. Yagi antennas detecting signals from tagged fish in each of the turbine intakes can also be seen. *Middle panel* two of the three turbine intakes. *Lower panel* close-up of one of the rack openings, where fish can pass (turbine not operating and therefore not submerged). *Photos* Eva B. Thorstad

smolts (mean body mass 36 g, independent samples *t* test, $t_{127.63} = -4.92$, $P < 0.001$). Some of the wild smolts (37 in 2014 and 81 in 2015) had leeches (*Piscicola respirans* Troschel, 1850) (median 3 and 2 leeches per smolt of those having leeches, range 1–25 and 1–18 in 2014 and 2015, respectively). Leech counts were made after surgery. Some leeches may have fallen off during capture and handling, although our impression was that this was rare.

A radio transmitter was surgically implanted into the body cavity of each smolt (methods described by Finstad et al., 2005). Prior to tagging, smolts were

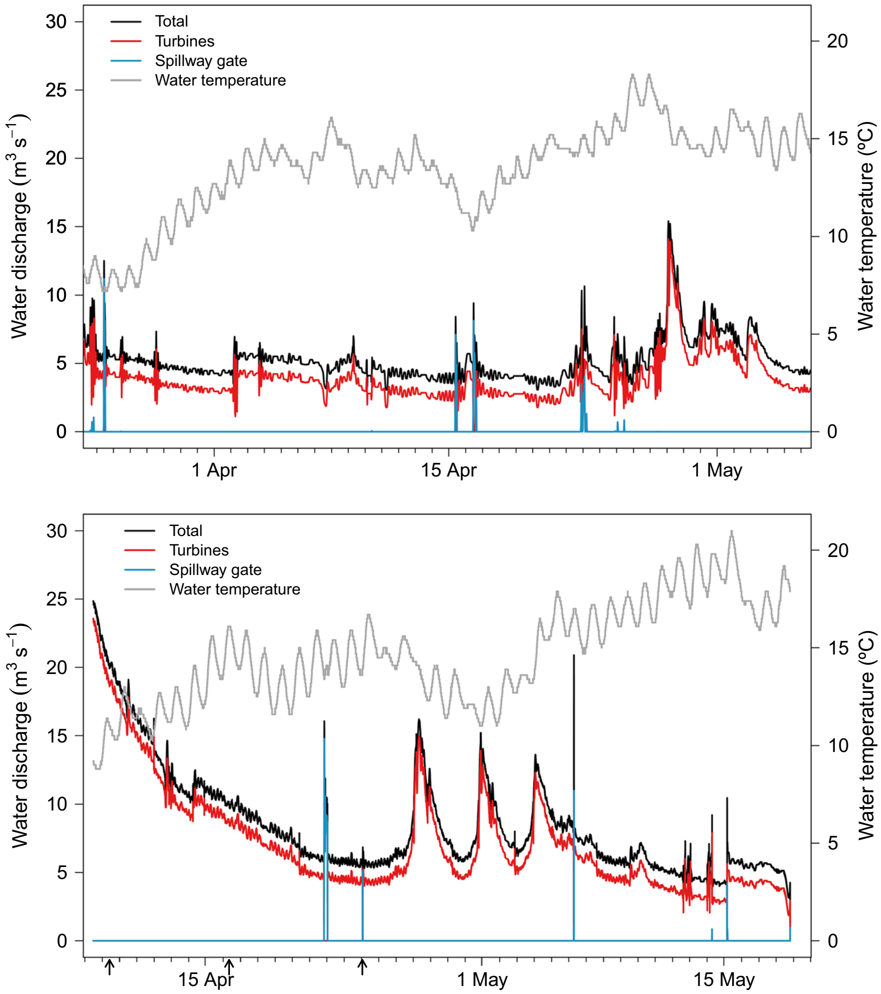


Fig. 5 Total water discharge (*black line*), turbine discharge (*red line*), flood gate discharge (*blue line*) and water temperature (*grey line*) recorded at Unkelmühle during the study period in 2014 (*upper panel*) and 2015 (*lower panel*). Water discharge in the surface bypasses (constant at 0.6 $m^3 s^{-1}$), vertical slot fish passage (constant at 0.4 $m^3 s^{-1}$) and in the nature-like fishway and canoe pass (constant at about 0.3 $m^3 s^{-1}$) are not shown in the figure, but are included in the total. *Arrows* indicate release dates for smolts

anaesthetized for approximately 3.5 min in 50 mg l^{-1} benzocaine (Aethylium *p*-aminobenzoicum, Caesar & Loretz GmbH, Hilden, Germany). During surgery, a 25 mg l^{-1} solution of benzocaine was circulated over the gills. All smolts were released on the day they were tagged. The transmitters used were individually coded NanoTags produced by Lotek Wireless, Inc., Canada, model NTQ-2 (frequency 151.500 MHz, dimensions 5 × 3 × 10 mm; mass in air 0.31 g, pulse intervals between 2.3 and 7.2 s, expected life time 18–38 days dependent on pulse interval).

Recording of tagged smolts after release

The smolts were released 8.9 km (2014) or 9.8 km (2015) upstream of the power station (Fig. 1). In 2014, the smolts were monitored from the release site to the power station, whereas in 2015 they were also monitored downstream of the power station, enabling more complete mortality estimates (see below).

The smolts were recorded when they passed automatic receiver stations installed 8.3 km upstream from the power station (site 1), when they entered the reservoir (2.5 km upstream from the power station, site 2), when they arrived at the downstream end of the reservoir (0.2 km upstream from the power station), at the power station (site 3) and 7.5 km downstream from the power station (site 4, only operating in 2015, Fig. 1). The length of the unimpounded control stretch was 5.8 km, the reservoir was 2.3 km, the power station area was 0.2 km and the stretch from the power station to site 4 was 7.5 km. Lotek model SRX 600 receivers were used with either three-, four- or six-element Yagi antennas or underwater antennas

Table 1 Overview of radio-tagged Atlantic salmon smolts released in the Sieg in 2014 and 2015. The smolts were not weighed in 2014

Years	Number of fish tagged	Fish total length (mm) mean (minimum–maximum, SD)	Fish mass (g) mean (minimum–maximum, SD)	Tagging and release dates	Water temperature (°C)/ discharge (m^3 s^{-1}) on release dates
2014	78	168 (137–212, 17)	–	25–30 March (25 March n = 20, 28 March n = 21, 30 March n = 37)	8/5, 10/5, 11/5
2015	178	116 (105–202, 18)	38 (9–64, 12)	9–24 April (9 April n = 100, 16 April n = 50, 24 April n = 28)	10/21, 15/10, 13/6

comprising stripped co-axial cable. Behaviour at the power station was recorded using multiple antenna receivers (a total of 5 data loggers, and 15 antennas in 2014 and 17 antennas in 2015, Fig. 6). Antennas had reception ranges covering different areas, enabling identification of the passage routes and speeds of individual smolts. Range tests indicated that receivers would always detect passing tagged smolts. This was confirmed by the actual recordings; no smolt recorded by automatic receivers or manual tracking had passed any upstream receiver without being recorded (manual tracking was used to document a 100% detection probability for the most downstream receiver).

Smolts were also tracked manually. In 2014, eight tracking surveys were performed between the release site and the power station from 1 April to 5 May, and in 2015, 30 surveys from 10 April to 14 July. Most surveys in 2015 covered a 38.8 km river stretch from 50 m above the release site to 29 km downstream of the power station. Tracking was performed by driving alongside the river in 2014, and by boating and cycling alongside the river in 2015. Fish were positioned using a portable receiver (SRX 600) connected to a three-element Yagi antenna. Great black cormorant (*Phalacrocorax carbo* Linnaeus, 1758) colonies were also searched for transmitters (two colonies in 2014 and three in 2015).

Experimental release of dead smolts

To distinguish between live downstream migrating smolts and drifting dead smolts below the power station, 20 dead smolts were radio-tagged and released in the turbines' tailrace (10 smolts on 9 April and 10 smolts on 16 April 2015, mean body length 163 mm, range 135–190 mm, SD 15). The longest drift recorded by any dead smolt was 2.4 km downstream from the power station (median distance 1.5 km, range 0.1–2.4, Havn et al., 2017a). Four of the 20 dead smolts (20%) disappeared from the river soon after release, which showed that dead fish can be removed from the river by scavengers.

Data analyses

Assessment of smolt losses on the different stretches was based on smolts (i.e., transmitters) that stopped moving or disappeared. For tagged smolts taken by fish predators, or that die in the river due to other reasons, the transmitter will remain in the river. For tagged smolts taken by bird or mammal predators, the tag may be removed from the river. Smolts assessed as being taken by a predator were those with transmitter signals registered on sites upstream of the preceding registration (e.g., registrations on site 2 after passing the power station), those with unlikely high migration speeds (e.g., moving from the power station to site 4 in less than 20 min) or a combination (sometimes also combined with erratic behaviour indicative of bird or fish predator movements).

A mortality estimate for the power station should not just consider smolts becoming stationary at the power station as lost (which we did for the 2014-estimate) since smolts dying at the power station can drift downstream or be removed from the river by scavengers. We, therefore, based the mortality estimate for the power station in 2015 on the total of smolts lost at the power station and within the first 7.5 km downstream of the power station (i.e., to site 4)

Fig. 6 Overview of radio antennas and their approximate detection ranges used to record signals from radio-tagged smolts at Unkelmühle Power Station in 2014 and 2015. *Upper panel* overview of the power station area. *Lower panel* power station in more detail. Detection ranges for aerial Yagi antennas are shown with *blue bubbles* and co-axial underwater antennas with *pink* or *orange bubbles*. *Orange bubbles* indicate antennas only used in 2015. *Photos* Wikimedia Commons

compared to the loss in the control stretch, standardised as loss per km river stretch.

Analyses of variables affecting smolt losses in different parts of the study area were done using generalized linear models with a binomial error structure and a logit link function. Predictors in the models were fish body length, number of leeches, origin (hatchery-reared or wild), year, water discharge and water temperature. Migration speed in the control stretch was included as a predictor in the models predicting loss in the reservoir and at and downstream of the power station. Only data for 2015 were included in the model predicting loss caused by the power station due to different methods of estimating loss in the two study years, and loss at the power station in 2014 was analysed separately with non-parametric statistics (Mann–Whitney *U* tests) due to the low sample size. Full models containing all predictor variables (without interactions) were simplified using a backwards elimination method until the best model was found (lowest AIC value). Two tagged smolts in 2014 and 12 in 2015 were collected for monitoring purposes when they passed the power station via surface openings in the bar racks (route 1, Fig. 3) instead of being guided back to the river, and were therefore removed from analyses of loss at the power station.

Migration speeds on the different river stretches were based on final detection at site 1, first detection at site 2, first detection at the dam upstream of the power station, final detection at the antennas pointing downstream below the power station and first detection at site 4. In both years, some fish stopped for periods, probably due to preference for migrating during night, causing highly positively skewed migration speeds. Corresponding migration speeds will therefore not have been informative for a model analysing stretch-specific variables affecting migration speed, and slow individuals were not included in the model (threshold for removing based on visual inspection of the data: less than 0.5 km h^{-1} in the control stretch, in the reservoir and on the stretch from the power station to site 4, and less than 0.1 km h^{-1} at the power station). Within the fast group, we analysed how different variables affected migration speed using a linear mixed-effects model fitted by maximum likelihood implemented with the *lmer* function in the R package lme4 (Bates et al., 2015), with fish body length, number of leeches, stretch, study year, water temperature and discharge as fixed effects, including an interaction between discharge and stretch. Fish-ID was used as a random effect. The model was simplified by backward elimination of non-significant terms ($P > 0.05$) based on likelihood ratio tests.

Differences in overall migration speed between stretches, including slow and fast smolts, were analysed using pairwise Wilcoxon signed-rank tests and Bonferroni correction. Only smolts that were registered at all stations were included ($n = 51$ in 2014 and $n = 78$ in 2015) to avoid the potential for bias resulting from possible speed-dependent mortalities on different stretches. Spearman's rank-order correlations coefficients among stretches in individual migration speed were compared using the standard Fisher z transformation, as implemented in the R package psych version 1.6.12. We treated the Spearman coefficients as though they were Pearson coefficients, which is robust against type I errors (Myers and Sirois, 2006).

Non-parametric tests (Fisher's exact tests and Mann–Whitney U tests) were used to test whether proportions were different between groups, or whether two samples were likely to derive from the same population, when assumptions were not met for parametric tests. All statistical analyses were conducted in R version 3.3.1 (R Core Team, 2016).

Results

Passage routes at the power station

Most of the smolts that passed the power station ($n = 59$ in 2014 and 115 in 2015, Table 2) followed the passage route towards the bar racks in front of the turbines (83% in 2014, 95% in 2015, route 1, Fig. 3), which led to a route outside the turbines via the flushing channel. Few smolts used the spillway gate (0% in 2014, 1% in 2015, route 7), vertical slot fish passage (5% in 2014, 1% in 2015, route 3) or nature-like fishway or canoe pass (12% in 2014, 3% in 2015, route 4 or 5). No smolts slipped through the bar spacing of the racks to pass through the turbines. There was no difference between wild and hatchery-reared smolts released on 9 April 2015 in terms of the

Table 2 Overview of tagged Atlantic salmon smolts and where they were lost. Extra loss of downstream migrating smolts due to hydropower development is calculated by comparing loss in the control stretch with loss in the reservoir and past the power station. Extra loss in the reservoir is given as percentage of those entering the reservoir, extra loss past the power station as percentage of those entering the power station and extra loss in the reservoir and past the power station as percentage of those entering the reservoir. All losses are minimum estimates, because injured fish can survive the monitored stretches, but experience delayed mortality later. – means data lacking because there was no receiver at site 4 in 2014

Years	Number of fish tagged	Number of fish lost at release site, before reaching site 1 (% of tagged fish)	Number of fish lost in control stretch, site 1–site 2 (% loss on stretch/% loss per km)	Number of fish lost in reservoir, site 2–site 3 (% loss on stretch/%loss per km)	Number of fish reaching the power station (site 3)	Number of fish reaching site 4	Extra loss in reservoir compared to control stretch (%)	Extra loss at power station compared to control stretch (%)	Extra loss in reservoir plus at power station compared to control stretch (%)
2014	78	6 (7.7)	6 (8.3/1.5)	7 (11/4.8)	59	–	7.2	9.9*	16.0*
2015	178	19 (11)	14 (8.8/1.6)	30 (21/9.6)	115	78	17.1	12.8	25.1

* Loss estimates for 2014 are incomplete and underestimated compared to the loss estimate in 2015, because fish were not recorded below the power station area in 2014. For 2014, the loss therefore only constitute those smolts that became stationary within the range of the antennas at the power station

proportion using the different passage routes (Fisher's exact test, $P = 1$).

Loss of smolts before the power station

Release area

Six smolts in 2014 (8%) and 19 in 2015 (11%) did not migrate downstream from the release area (Table 2). Most of these (4 of 6 in 2014 and 14 of 19 in 2015) disappeared from the river, likely removed by a bird or mammal predator (or scavenger).

Control stretch

Loss rates in the control stretch were similar between the study years (1.5 and 1.6% per km, Table 2). Of the smolts that were lost (Table 2), 2 of 6 in 2014 and 12 of 14 in 2015 disappeared and were likely removed from the river by a predator. Transmitters of the rest of the lost smolts became stationary in the river until the batteries expired.

Reservoir

The loss of smolts in the reservoir was elevated compared to the control stretch, both in 2014 and 2015 (3.2 times larger per km in 2014 and 6 times larger per km in 2015, Table 2). If the mortality per km in the reservoir had been equivalent to that in the control stretch, 2.2 of 66 smolts entering the reservoir would have been lost in 2014 (instead of the 7 that were observed lost) and 5.2 of 145 smolts in 2015 (instead of the 30 that were observed lost). Hence, the extra loss in the reservoir compared to the control stretch was 7.2% in 2014 and 17.1% in 2015 (Table 2).

In 2015, transmitters from 20 of the 30 smolts lost in the reservoir became stationary until their batteries expired, whereas 10 tagged smolts disappeared from the reservoir. Numbers for 2014 are unknown due to uncertain tracking data.

Loss of smolts at or downstream of the power station

2014

The loss of downstream migrating smolts in the power station area was 6 of 59 smolts (10.2%), or 41.5% loss per km (0.2 km stretch). This is a minimum loss estimate compared to 2015 because tagged smolts were not monitored downstream of the power station. The six lost smolts had followed the route towards the bar racks in front of the turbines (route 1, Fig. 3), and the loss seemed related to injury in the bypass route. Two smolts probably died in the bar rack area, which could be due to injury at the bar racks unrelated to operation of the rack cleaners. Four smolts were likely lost in the bypass immediately before exit to the river, in an area where smolts could become trapped in accumulated debris within the bypass, based on the location where the transmitters became stationary.

The loss of smolts on the 0.2-km-long stretch of the power station area was much higher than in the control stretch. If the loss in the power station area had been similar to the control stretch, no smolt (estimated at 0.18 smolts) would have been expected lost, instead of the 6 smolts that were lost. Hence, there was a minimum 9.9% extra loss in the power station area compared to the control stretch (Table 2). The total loss related to hydropower production (estimated from combined loss in the reservoir and at the power station) was 16.0% of smolts entering the reservoir (Table 2). Transmitters from two smolts that had passed the power station were found at a cormorant colony 2 weeks later.

2015

Of the 103 smolts that passed the power station without being captured for monitoring, 78 (76%) passed the receiver 7.5 km downstream (site 4, see Fig. 1), and 25 smolts were lost. One of the lost had a transmitter detection pattern that became stationary in the power station area at the exit of bypass route 1 (Fig. 3), and three were likely taken by bird predators after exit from this bypass. Four smolts (three that had passed via route 1 and one via route 4 or 5) had transmitters that became stationary close to the power station (within the 2.4 km stretch where dead smolts settled). Signals from 13 smolts (11 that had passed via route 1, 1 via route 4 or 5, 1 via route 7) disappeared from the river after they had passed the power station, of which 9 later had bird-like recordings. These 13 smolts could potentially have died immediately in the power station area and drifted downstream, or they could have been lost somewhere between the power station and site 4. The remaining four smolts had

Table 3 Results from logistic regression models used to identify factors predicting whether individual fish were lost or not in different parts of the study area

	Estimates	Standard errors	z values	Pr(>|z|)
Lost on the control stretch versus entered the reservoir (n = 20/211)				
(Intercept)	1.8948	2.2754	0.833	0.405
Body length	−0.0225	0.0139	−1.618	0.106
Origin (wild)	−0.8616	0.5065	−1.701	0.089
Lost in the reservoir versus passed the power station (n = 37/174)				
(Intercept)	−3.1742	0.7036	−4.511	<0.001
Origin (wild)	1.3887	0.5877	2.363	0.018
Study year (2015)	1.1496	0.4669	2.462	0.014
Migration speed on control stretch	−0.3961	0.1686	−2.349	0.0188
Lost at the power station or downstream of Unkelmühle versus passed site 4 (n = 25/78)				
(Intercept)	−0.9521	0.3130	−3.042	0.002
Leeches	0.2325	0.1181	1.969	0.049
Migration speed on control stretch	−0.4399	0.2058	−2.137	0.033

Predictors in the models were fish body length, number of leeches, origin (hatchery-reared or wild), study year, water discharge and water temperature. Migration speed on the control stretch was included as a predictor in the models predicting loss in the reservoir and at and downstream of the power station. Only data for 2015 were included in the model prediction of loss at the power station due to different methods of estimating loss in the two study years. Positive estimates indicate an increased probability of being lost, and negative estimates indicate a decreased probability of being lost (estimates are given on the logit scale). Sample sizes are given in brackets where n = lost/survived

transmitters that became stationary in the lower part of the 7.5 km stretch below the power station. Signals from four transmitters were later registered in cormorant colonies (one of these disappeared between site 3 and 4, and three had passed site 4). Tags lost at the power station and river tended to disappear from the river more (16 out of 25 lost, 64%) than those in the reservoir (10 out of 33 lost, 33%) (Fisher's exact test, $P = 0.032$).

The minimum extra loss of smolts due to the power station was 12.8% (of smolts entering the power station, Table 2), based on the recorded loss at the power station and the 7.5 km stretch below compared to the loss in the control stretch. The total loss related to hydropower production (estimated from combined loss in the reservoir, at the power station, and in the 7.5 km stretch below the power station) was 25.1% of smolts entering the reservoir (Table 2).

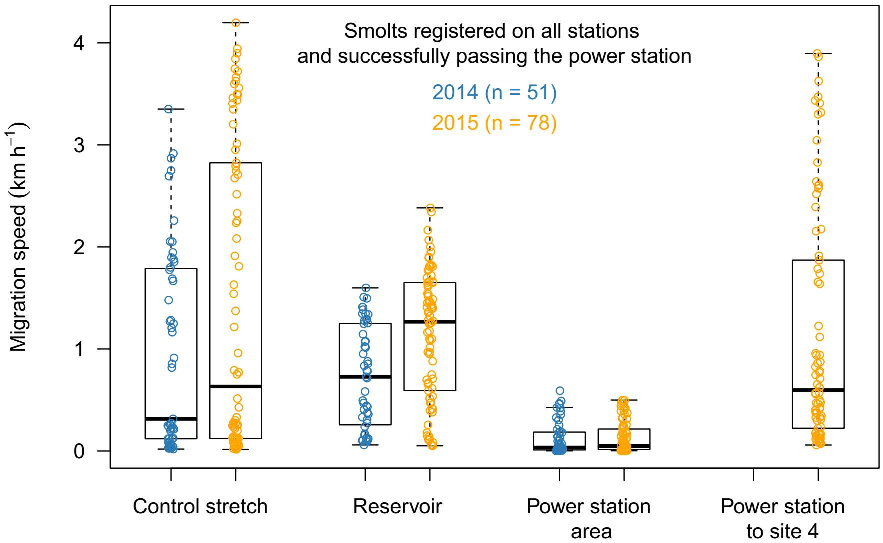
Variables affecting loss of smolts

In the control stretch, none of the variables—number of leeches, hatchery versus wild origin, water temperature or discharge, study year or body length—had any significant effect on whether the fish were lost or not, although the latter two predictors were not omitted by model simplification (logistic regression, Table 3). The probability of being lost in the reservoir was higher for wild than hatchery-reared smolts and higher for smolts tagged and released in 2015 than in 2014. Increasing migration speed in the control stretch reduced the probability of being lost in the reservoir (logistic regression, Table 3). At and downstream of the power station in 2015, the probability of being lost was positively related to number of leeches and negatively related to increasing migration speed in the control stretch (logistic regression, Table 3). The proportion of lost smolts did not differ among the passage routes used at the power station (Fisher's exact test: $P = 0.17$). In 2014, none of the predictors had any effect on whether smolts were lost or not at the power station (Mann–Whitney U tests, all P values >0.19).

Time spent passing the different stretches

The time spent by individual smolts, from release to passing the power station, lasted on average 137 h in

Fig. 7 Migration speed of smolts in 2014 (*blue*) and 2015 (*orange*) in the control stretch, reservoir, when passing the power station area and after the power station. *Open circles* show individual values (jittered horizontally), *boxes* show the median and upper and lower quartile, *whiskers* show the range within the upper/lower quartile ±1.5 IQ. Included are only those smolts registered on all sites and successfully passing the power station. Similar figure including all smolts is shown in Online Resource 2



2014 (median 125, range 15–329, SD 85, $n = 51$) and 99 h in 2015 (median 85, range 5–442, SD 79, $n = 78$). In 2015, smolts spent on average 123 h (median 99, range 6–449, SD 82, $n = 78$) from release to passing site 4.

The smolts spent a median of 18 h (average 46, range 1.7–309, SD 70) in passing the control stretch in 2014 and 10 h in 2015 (average 41, range 1.4–356, SD 69). Further, they spent 3 h in passing the reservoir in 2014 (average 8, range 1.4–39, SD 9) and 2 h in 2015 (average 5, range 1–44, SD 9). In passing the power station, they spent 6 h in 2014 (average 25, range 0.3–161, SD 42) and 4 h in 2015 (average 14, range 0.4–115, SD 24). From the power station to site 4, they spent 13 h in 2015 (average 24, range 2–128, SD 28).

Migration speed in different stretches and variables affecting migration speed

In 2014, migration speeds did not differ between the control stretch and the reservoir ($P = 0.56$), but were slower during passage of the power station than both the control stretch ($P < 0.001$) and the reservoir (pairwise Wilcoxon signed-rank tests and Bonferroni correction, $P < 0.001$, Fig. 7, see also Online Resources 1 and 2). Similarly, in 2015 there was no difference in migration speed among the control stretch, reservoir and the stretch from the power station to site 4 (all P values >0.64), but the speed was slower when passing the power station than the other stretches (pairwise Wilcoxon signed-rank tests and Bonferroni correction, all $P < 0.001$, Fig. 7). Correlations among stretches in individual migration speed were low and not significant in 2014 ($r_s = 0.03$–0.17). Correlations among the same stretches were somewhat higher, and significant in 2015 ($r_s = 0.22$–0.31, $P = 0.005$–0.05), but not significantly different from 2014 (Fisher z transformations, $P = 0.16$–0.71).

Migration speed increased with increasing water discharge in all stretches ($\chi^2 = 21.27$, DF = 1, $P < 0.001$), and wild smolts moved faster than hatchery-reared smolts ($\chi^2 = 10.09$, DF = 1, $P = 0.001$) (linear mixed-effects model, Table 4). Study year, fish body length, water temperature and number of leeches had no significant effect on migration speed.

Discussion

Smolt migration is a critical phase in the life history of Atlantic salmon, and mortality may occur due to both natural causes and anthropogenic impacts such as hydropower installations (reviewed by Thorstad et al., 2012). Even though the Unkelmühle Power Station was designed to minimise negative impacts on fish, with a bar rack to hinder entrance to turbines and several alternative bypass routes for downstream migrants, there was elevated mortality of downstream migrating smolts at the power station compared to the control stretch. Extra mortality at the power station in the two study years of 10 and 13% may be regarded as

Table 4 Results from a linear mixed-effects model used to identify factors predicting migration speeds for smolts within the fast speed group on the control stretch ($n = 96$), reservoir ($n = 113$), when passing the power station ($n = 57$) and below the power station ($n = 52$)

Fixed effects	Estimates	Standard errors
(Intercept)	0.1765	0.1118
Discharge	0.0266	0.0056
Origin (wild)	0.2590	0.0815
Stretch (reservoir)	−0.4725	0.0617
Stretch (power station)	−2.0994	0.0741
Stretch (below power station)	−0.2594	0.0826

Random effects	Variance	Standard deviation
Fish-ID	0.0410	0.2025
Residual	0.1776	0.4214

Fixed effects in the model were study year, water discharge and temperature, stretch, origin (wild or hatchery-reared), fish body length and number of leeches. Fish-ID was used as a random effect. The fast speed group comprised smolts with a migration speed higher than 0.5 km h^{-1} in the natural river stretch, reservoir and below the power station and higher than 0.1 km h^{-1} at the power station. Estimates are given on a log scale

low mortalities, considering that mortalities at power stations can be as high as 50–100% (e.g., Ruggles, 1980; Larinier, 2008; Calles and Greenberg, 2009). However, smolt mortality at some power stations can also be much lower, and for instance, Larinier (2008) reported average mortalities of smolts moving through Kaplan turbines of between 5 and 20%. The mortalities of smolts passing through Francis turbines were more variable, from below 5% to over 90% (Larinier, 2008). Considering the mortality levels reported by Larinier (2008), the mortality of 10–13% at the power station in the present study may be described as a relatively high mortality for a low-head dam where the fish did not even pass through the turbines, but through supposedly safer passage routes. However, it should be pointed out that mortality estimates are not directly comparable among studies, because different methods have been used to obtain the estimates, and some studies consider only direct turbine mortality, whereas others include mortality in bypass routes, and to a varying extent delayed mortality. Further, at many power stations, as those referred to above, a large part of the documented mortality is turbine mortality, which is also not directly comparable to the results in this study, since turbine mortality was zero. A similar method of calculating extra mortality was used at another German power station with a movable bulb turbine, where the extra mortality due to the power station was 3–6% (Thorstad et al., 2017). Hence, also compared to this power station, the mortality at the Unkelmühle Power Station was higher.

The mortality in this study was recorded over short distances, up to 7.5 km downstream of the power station in 2015. If Atlantic salmon smolts are injured and stressed by passing dams and power stations, additional delayed mortality even further downstream, and when entering saltwater, may be expected (McCormick et al., 2009; Zydlewski et al., 2010; Stich et al., 2015a, b). Hence, mortality estimates in the present and similar studies are conservative. The mortality at the power station in 2014 was likely underestimated compared to 2015, because smolts were not recorded downstream of the power station, and only those becoming stationary at the power station could be assessed as dead. Hence, fish that possibly died at the power station but floated downstream, or were removed from the river by scavengers (Calles et al., 2010; Havn et al., 2017a) were not included in the 2014-estimate.

We recorded no direct turbine mortality, because none of the smolts passed through the turbine bar racks to enter the turbines, which was as expected due to the narrow bar spacing (10 mm) of the racks (Larinier and Travade, 2002; Adam et al., 2005). Hence, the extra loss of smolts passing the power station seemed related to physical injuries in bypass routes outside the turbines, and to increased predation. Bar racks in front of turbines can increase survival by hindering fish from entering the turbines, but can cause mortality if fish impinge upon them and are injured (Adam et al., 2005; Calles et al., 2010, 2013). Overall, the bar racks at this power station seemed successful in guiding fish to bypass routes without causing injury or mortality. However, we cannot exclude that some mortality due to injuries at the racks occurred, because two smolts seemed to have died in this area.

The majority of the smolts followed the main flow of water at the power station, i.e., towards the bar racks in front of the turbines, and passed the power station via surface openings in the bar racks into the bypass route that led smolts outside the turbines. This is according to previous studies, showing that the proportion of smolts passing through turbines or other passages may be related to the proportion of water diverted through each of the routes (Hvidsten and Johnsen, 1997; Serrano et al., 2009). However, smolts may not always follow the main flow, as demonstrated in a recent study where smolts used the fishways instead of routes through turbines more often than expected from the proportion of water discharge, especially larger smolts at lower discharge (Havn et al., 2017b).

A higher mortality was recorded for smolts using the bypass route via surface openings in the bar racks in 2014 than in 2015, probably because smolts were more prone to entrapment in debris in 2014 than 2015. We observed debris in this migration route during field work in 2014 and installed video monitoring in 2015, which showed that debris did not aggregate this year (own unpublished data), likely because of different discharge conditions. Hence, our results show that mortality rates in power station bypass routes may vary between years. Further, the results emphasise the importance of constructing bypass routes that minimise the risk of physical injury to fish, and keeping bypass routes in a state such that they do not impose extra mortality.

Transmitters from six smolts that passed the power station were later found in cormorant colonies, and a relatively large number of smolts passing the power station disappeared from the river. Release of dead smolts demonstrated that these could be removed by scavengers (Havn et al., 2017a), and it is difficult to know if the reason for smolts disappearing from the river was due to predation of smolts that might have been injured and weakened by passing the power station, or to smolts being killed when passing the power station and then being removed from the river by scavengers. Another explanation is that predation downstream of power stations may increase compared to other river stretches, even for uninjured smolts, because predators may be attracted to such areas in a response to the smolt run and presence of disorientated, injured and dead fish (Koed et al., 2002). A high predation rate (70%) for smolts released immediately downstream of a power station was found in the study by Koed et al. (2002), and they suggested that this was due to fish and bird predators being attracted to the area downstream of the power station. Also Nyqvist et al. (2016) found that smolts disappeared from the power station area, likely due to predation.

This study showed that reservoirs upstream of power stations can be areas of high smolt mortality. Extra mortality in the reservoir was 7% in 2014 and 17% in 2015, and in one study year, the loss in the reservoir was even larger than at the power station. It is known that reservoirs and slack water above dams may create favourable habitats for predatory fish species that normally do not occur in faster-flowing river stretches (Jepsen et al., 1998, 2000; Aarestrup et al., 1999; Serrano et al., 2009). Jepsen et al. (1998) and Aarestrup et al. (1999) recorded 90% mortality through a reservoir, largely due to predation by northern pike (*Esox lucius* Linnaeus, 1758) (56% mortality) and birds (31% mortality) such as red-necked grebe (*Podiceps grisegena* Boddaert, 1783) and grey heron (*Ardea cinerea* Linnaeus, 1758). We therefore suggest that the extra loss recorded in the reservoir compared to the control stretch in the present study was mainly caused by predation, both due to bird predators and due to the presence of more fish predators in the slow-flowing lake-like reservoir than on the faster-flowing control stretch. Only 10 of 30 (33%) tags from lost smolts in the reservoir disappeared from the reservoir, whereas 16 of 25 (64%) tags from lost smolts at the power station and downstream disappeared, which may indicate that there was more predation by fish than birds in the reservoir, and vice versa (more predation by birds) at the power station and on the stretches downstream. However, fish predators such as northern pike have also been recorded in the tailrace area below this power station (Nemitz and Steinmann, 2001).

The results showed that the reservoir mortality can vary considerably between years, which may be due to several reasons. Smolts migrated faster through the reservoir in 2015 than in 2014, so a longer time spent in the reservoir may not explain the larger mortality in 2015. Further, a difference in smolt size does not explain the differences between years. The fact that the mortality in the control stretch was almost the same in both years also indicates that there was not a large difference in smolt quality between the years. It is possible that variation in the predator community in terms of number, size and species composition, within the study years affected the proportion of smolts lost. 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.

Environmental factors and the state and characteristics of individual smolts may impact their mortality risk, both in general, and when being exposed to extra stress such as when passing a power station. At some stretches, the mortality risk was larger for the slower migrating smolts, which is similar to results shown by Vollset et al. (2016). The slower migrants (as indicated by their migration speeds in the control stretch) had a higher likelihood of being lost in the reservoir and at and downstream of the power station than the faster migrants. This may be because the risk of being taken by predators increases with time spent in the reservoir and at the power station, or alternatively, the fish with the lowest migration speeds were the weakest fish, and therefore more likely to be taken by predators. Hence, factors impacting migration speed may also impact smolt survival.

Migration speeds increased with increasing water discharge in all stretches, which may be due to smolts being stimulated to migrate faster at higher discharge (Thorstad et al., 2012), and also simply because fish are displaced downstream faster due to a faster water velocity. Environmental impacts like water discharge and temperature did not impact greatly on the mortality rates.

The mortality in the reservoir and at the power station was estimated as extra mortality compared to mortality in the upstream control stretch. This enabled mortality estimates that were corrected for the natural mortality of the same batch of smolts during migration in an unimpounded part of the same river. Without a control group, it would be difficult to assess how large a proportion of the recorded mortality could have been caused by the impoundment and hydropower installations—relative to the natural mortality of the river and variation in smolt quality. However, the assumption was that the mortality on the affected stretch would have been the same as in the control stretch had there been no power station and reservoir, which may not necessarily be true. In particular, there might have been a selective mortality in the natural river stretch, reservoir and power station, with the weakest individuals being lost and the strongest individuals remaining. Therefore, the expected mortality for the power station and stretch below the power station in the absence of an effect from hydropower regulation might have been lower than the loss recorded on the natural river stretch that we used for comparison, and this may contribute to underestimating the reservoir and power station mortality.

At the power station, but not at other river stretches, infestation by leeches contributed to an increased mortality risk. These external parasites are known to occur in the Rhine (Molls and Borcherding, 1997; Jueg et al., 2004), but their impact on individual fish and fish populations is not well studied. If they impose physiological stress on the fish, a combined impact with other stressors may lead to increased mortality risk, which could explain the elevated mortality recorded in this study. An alternative explanation could be that fish that have a higher mortality risk due to some other reason also have a higher frequency of leeches for that same reason.

Individual fish spent on average 5 days in passing the study stretch, which is a slower migration than recorded in some other studies (Urke et al., 2013; Karppinen et al., 2014), and which is a slow migration speed considering the long distance these smolts must migrate to reach the sea in the Netherlands. However, there was large individual variation in migration speeds, indicating that the time taken to reach the sea will also vary. Migration was slower during passage of the power station than in the control stretch and the reservoir, similar to results found by Stich et al. (2015a, b). Hence, in river systems where smolts have to pass several power stations or other weirs, the cumulative delay may be substantial (Norrgård et al., 2013). Smolts seem have a preference for reaching the sea at certain ocean temperatures and use environmental cues in the rivers that may predict favourable ocean conditions to initiate downstream migration (Hvidsten et al., 1998, 2009). A preference for reaching the sea at certain ocean temperatures could be due to low salinity tolerance and low survival at lower temperatures (Sigholt and Finstad, 1990), and increased survival when prey availability is optimal (Rikardsen and Dempson, 2011), perhaps in combination with increased swimming performance that enhances predator avoidance when the water is warmer (Hvidsten et al., 2009). Hence, the timing of the smolt run may be adapted through natural selection to meet the most optimal environmental conditions in the sea (McCormick et al., 1998; Thorstad et al., 2012), and delays due to hydropower installations may therefore reduce the sea survival.

Conclusion

In conclusion, the extra mortality due to the power station, including the reservoir, was at minimum 16 and 25% of tagged smolts entering the reservoir in 2014 and 2015, respectively. This mortality occurred despite the power station being constructed with fish-friendly solutions such as bar racks in front of the turbine intakes, alongside several types of bypass routes being accessible for downstream migrating smolts. This study shows that extra mortality can be expected for smolts using bypass routes, and that mortality in reservoirs upstream of power stations may be severe. There are no compensatory mechanisms for additional mortality at the smolt stage of Atlantic salmon (Milner et al., 2003; Einum and Nislow, 2011), and mortality caused by a power station like this can result in a corresponding reduction in the return of adult spawners after ocean migration. Whether an extra loss of 16–25% of the population can threaten salmon populations depends on the state of the population. Such mortality might not be detrimental for a healthy population with few other negative impacts (although it may reduce the harvestable surplus). However, for a population under re-establishment, such as in the River Rhine, a mortality at this level may hamper re-establishment, not least in combination with other negative impacts along the long migration routes.

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References

Aarestrup, K., N. Jepsen, G. Rasmussen & F. Økland, 1999. Movements of two strains of radio tagged Atlantic salmon, *Salmo salar* L., smolts through a reservoir. Fisheries Management and Ecology 6: 97–107.

Adam, B., R. Bosse, U. Dumont, R. Hadderingh, L. Joergensen, B. Kalusa, G. Lehmann, R. Pischel & U. Schwevers, 2005. Fish Protection Technologies and Downstream Fishways. Dimensioning, Design, Effectiveness Inspection. DWA German Association for Water, Wastewater and Waste, Hennef.

Bates, D., M. Maechler, B. Bolker & S. Walker, 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Bunt, C. M., T. Castro-Santos & A. Haro, 2012. Performance of fish passage structures at upstream barriers to migration. River Research and Applications 28: 457–478.

Calles, O. & L. Greenberg, 2009. Connectivity is a two-way street – the need for a holistic approach to fish passage problems in regulated rivers. River Research and Applications 25: 1268–1286.

Calles, O., I. C. Olsson, C. Comoglio, P. S. Kemp, L. Blunden, M. Blunden, M. Schmitz, & L. Greenberg, 2010. Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. Freshwater Biology 58: 2168–2179

Calles, O., S. Karlsson, P. Vezza, C. Comoglio & J. Tielman, 2013. Success of a low-sloping rack for improving downstream passage of silver eels at a hydroelectric plant. Freshwater Biology 55: 2167–2180.

Einum, S. & K. H. Nislow, 2011. Variation in population size through time and space: theory and recent empirical advances from Atlantic salmon. In Aas, Ø., S. Einum, A. Klemetsen & J. Skurdal (eds), Atlantic Salmon Ecology. Wiley-Blackwell, Oxford: 277–298.

Finstad, B., F. Økland, E. B. Thorstad, P. A. Bjørn & R. S. McKinley, 2005. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. Journal of Fish Biology 66: 86–96.

Havn, T. B., F. Økland, M. A. K. Teichert, L. Heermann, J. Borcherding, S. A. Sæther, M. Tamberts, O. H. Diserud & E. B. Thorstad, 2017a. Movements of dead fish in rivers. Animal Biotelemetry 5: 7.

Havn, T. B., S. A. Sæther, E. B. Thorstad, M. A. K. Teichert, L. Heermann, O. H. Diserud, J. Borcherding, M. Tambets & F. Økland, 2017b. Downstream migration of Atlantic salmon smolts past a low head hydropower station equipped with an Archimedes screw and Francis turbines. Ecological Engineering 105: 262–275.

Hvidsten, N. A. & B. O. Johnsen, 1997. Screening of descending Atlantic salmon (*Salmo salar* L.) smolts from a hydropower intake in the River Orkla, Norway. Nordic Journal of Freshwater Research 73: 44–49.

Hvidsten, N. A., T. G. Heggberget & A. J. Jensen, 1998. Sea water temperature at Atlantic salmon smolt entrance. Nordic Journal of Freshwater Research 74: 79–86.

Hvidsten, N. A., A. J. Jensen, A. H. Rikardsen, B. Finstad, J. Aure, S. Stefansson, P. Fiske & B. O. Johnsen, 2009. Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway. Journal of Fish Biology 74: 1532–1548.

ICES. 2016. Report of the Working Group on North Atlantic Salmon (WGNAS), 30 March–8 April 2016, Vol. 10. ICES CM 2016/ACOM, Copenhagen: 1–321.

Jepsen, N., K. Aarestrup, F. Økland & G. Rasmussen, 1998. Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. Hydrobiologia 372: 347–353.

Jepsen, N., S. Pedersen & E. B. Thorstad, 2000. Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. Regulated Rivers: Research and Management 16: 189–198.

Jueg, U., C. Grosser & A. Bielecki, 2004. Zur Kenntnis der Fischegelfauna (Hirudinea: Piscicolidae) in Deutschland. Lauterbornia 52: 39–73. **(in German with English abstract)**.

Karppinen, P., P. Jounela, R. Huusko & J. Erkinaro, 2014. Effects of release timing on migration behaviour and survival of hatchery-reared Atlantic salmon smolts in a regulated river. Ecology of Freshwater Fish 23: 438–452.

Katopodis, C. & J. G. Williams, 2012. The development of fish passage research in a historical context. Ecological Engineering 48: 8–18.

Koed, A., N. Jepsen, K. Aarestrup & C. Nielsen, 2002. Initial mortality of radio-tagged Atlantic salmon (*Salmo salar* L.) smolts following release downstream of a hydropower station. Hydrobiologia 483: 31–37.

Kraabøl, M., S. I. Johnsen, J. Museth & O. T. Sandlund, 2009. Conserving iteroparous fish stocks in regulated rivers: the need for a broader perspective. Fisheries Management and Ecology 16: 337–340.

Larinier, M., 2008. Fish passage experience at small-scale hydro-electric power plants in France. Hydrobiologia 609: 97–108.

Larinier, M. & F. Travade, 2002. Downstream migration: problems and facilities. Bulletin Français de la Pêche et de la Pisciculture 364(Suppl. 2002-1): 181–207.

Lenders, H. J. R., T. P. M. Chamuleau, A. J. Hendriks, R. C. G. M. Lauwerier, R. S. E. W. Leuven & W. C. E. P. Verberk, 2016. Historical rise of waterpower initiated the collapse of salmon stocks. Scientific Reports 6: 29269.

McCormick, S. D., L. P. Hansen, T. P. Quinn & R. L. Saunders, 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 77–92.

McCormick, S. D., D. T. Lerner, M. Y. Monette, K. Nieves-Puigdoller, J. T. Kelly & B. T. Björnsson, 2009. Taking it with you when you go: how perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. American Fisheries Society Symposium 69: 195–214.

Milner, N. J., J. M. Elliott, J. D. Armstrong, R. Gardiner, J. S. Welton & M. Ladle, 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62: 111–125.

Molls, F. & J. Borcherding, 1997. Der Fischegel *Cystobranchus respirans* (Troschel 1850) am unteren Niederrhein mit neuen Daten zur Phänologie und zum Wirtsfischspektrum. Lauterbornia H 28: 37–44. **(in German with English abstract)**.

Molls, F. & A. Nemitz, 2008. Restoration of Atlantic salmon and other diadromous fishes in the Rhine River system. American Fisheries Society Symposium 49: 817–834.

Monnerjahn, U., 2011. Atlantic salmon (*Salmo salar* L.) re-introduction in Germany: a status report on national programmes and activities. Journal of Applied Ichthyology 27(Suppl. 3): 33–40.

Myers, L. & M. J. Sirois, 2006. Spearman correlation coefficients, differences between. Encyclopedia of Statistical Sciences. doi:10.1002/0471667196.ess5050.pub2.

Nemitz, A. & I. Steinmann, 2001. Zum Aufkommen und zur Abwanderung von Lachssmolts im Siegsystem. Unveröffentlichte Studie Im Auftrag der LÖBF/LAfAO Nordrhein-Westfalen, 46 pp.

Noonan, M. J., J. W. A. Grant & C. D. Jackson, 2012. A quantitative assessment of fish passage efficiency. Fish and Fisheries 13: 450–464.

Norrgård, J. R., L. A. Greenberg, J. J. Piccolo, M. Schmitz & E. Bergman, 2013. Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration through multiple dams. River Research and Applications 29: 1306–1317.

Nyqvist, D., L. A. Greenberg, E. Goerig, O. Calles, E. Bergman, W. R. Ardren & T. Castro-Santos, 2016. Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. Ecology of Freshwater Fish. doi:10.1111/eff.12318.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Rikardsen, A. H. & J. B. Dempson, 2011. Dietary life-support: the marine feeding of Atlantic salmon. In Aas, Ø., S. Einum, A. Klemetsen & J. Skurdal (eds), Atlantic Salmon Ecology. Wiley-Blackwell, Oxford: 115–144.

Rivinoja, P., S. McKinnell & H. Lundqvist, 2001. Hindrances to upstream migration of Atlantic salmon (*Salmo salar*) in a northern Swedish river caused by a hydroelectric power-station. Regulated Rivers: Research and Management 17: 101–115.

Ruggles, C. P., 1980. A review of the downstream migration of Atlantic salmon. Canadian Technical Report on Fisheries and Aquatic Sciences 952: 1–39.

Schneider, J., 2011. Review of reintroduction of Atlantic salmon (*Salmo salar*) in tributaries of the Rhine River in the German Federal States of Rhineland-Palatinate and Hesse. Journal of Applied Ichthyology 27(Suppl. 3): 24–32.

Serrano, I., P. Rivinoja, L. Karlsson & S. Larsson, 2009. Riverine and early marine survival of stocked salmon smolts, *Salmo salar* L., descending the Testebo River, Sweden. Fisheries Management and Ecology 16: 386–394.

Sigholt, T. & B. Finstad, 1990. Effect of low temperature on seawater tolerance in Atlantic salmon (*Salmo salar*) smolts. Aquaculture 84: 167–172.

Stich, D. S., M. T. Kinnison, J. F. Kocik & J. D. Zydlewski, 2015a. Initiation of migration and movement rates of Atlantic salmon smolts in fresh water. Canadian Journal of Fisheries and Aquatic Sciences 72: 1339–1351.

Stich, D. S., G. B. Zydlewski, J. F. Kocik & J. D. Zydlewski, 2015b. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. Marine and Coastal Fisheries 7: 68–86.

Thorstad, E. B., F. G. Whoriskey, A. H. Rikardsen & K. Aarestrup, 2011. Aquatic nomads: the life and migrations of the Atlantic salmon. In Aas, Ø., S. Einum, A. Klemetsen & J. Skurdal (eds), Atlantic Salmon Ecology. Wiley-Blackwell, Oxford: 1–32.

Thorstad, E. B., F. Whoriskey, I. Uglem, A. Moore, A. H. Rikardsen & B. Finstad, 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology 81: 500–542.

Thorstad, E. B., A. H. Rikardsen, A. Alp & F. Økland, 2013. The use of electronic tags in fish research – an overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13: 881–896.

Thorstad, E. B., T. B. Havn, S. A. Sæther, L. Heermann, M. Teichert, O. Diserud, M. Tambets, J. Borcherding & F. Økland, 2017. Survival and behaviour of Atlantic salmon smolts passing a run-of-river hydropower facility with a movable bulb turbine. Fisheries Management and Ecology. doi:10.1111/fme.12216.

Urke, H. A., T. Kristensen, J. B. Ulvund & J. A. Alfredsen, 2013. Riverine and fjord migration of wild and hatchery-reared Atlantic salmon smolts. Fisheries Management and Ecology 20: 544–552.

Vollset, K. W., S. Mahlum, J. G. Davidsen, H. Skoglund & B. Barlaup, 2016. Interaction between migration behaviour and estuarine mortality in cultivated Atlantic salmon *Salmo salar* smolts. Journal of Fish Biology 89: 1917–2218.

Zydlewski, J., G. Zydlewski & G. R. Danner, 2010. Descaling injury impairs the osmoregulatory ability of Atlantic salmon smolts entering seawater. Transactions of the American Fisheries Society 139: 129–136.