Anthropogenic and natural size-related selection act in concert during brown trout (*Salmo trutta*) smolt river descent

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Abstract By hindering migration and inducing direct turbine mortality during downstream migration, hydropower is regarded as one of the most serious threats to anadromous salmonids. Yet, little attention has been paid to long-term turbine-induced selection mechanisms effecting fish populations. This work evaluates turbine and post-turbine survival of PIT-tagged wild brown trout smolts. By estimating individual river and sea survival rates, we were able to compare survival rates of smolts that had migrated through the turbine with smolts that had bypassed the turbine, as well as investigate both natural and anthropogenic size-selective mechanisms operative on the population. Total river-descent survival probability was 0.20 for turbine migrants and 0.44 for bypass migrants. The surviving turbine migrants were significantly smaller than their bypass counterparts and more exposed to predation from Northern pike. The estimated mean-adjusted selection gradient was − 0.76 for turbine migrants and + 1.85 for the bypass migrants. The resulting disruptive selection may ultimately lead to increased phenotypic smolt size variation provided sufficient additive genetic variance associated with smolt size. Mitigation measures at hydropower plants are thus essential for preserving sustainable populations of anadromous fish and maintaining population genetic variation.

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Introduction

Humans have altered natural river ecosystems for decades imposing decline and extinction for several species (Dynesius & Nilsson, 1994). Hydropower is regarded as one of the more serious threats to anadromous salmonids, and concerns about river dams effecting free movement of migrating fish to feeding- and spawning grounds have existed for centuries (Katopodis and Williams, 2012; Noonan et al., 2012). In particular, increased mortality of fish migrating through the turbines is well documented from a variety of systems and often a major concern (Montèn, 1985; Čada, 2001; Pracheil et al., 2016). However, little is known about how hydropower may alter the adaptive landscape of migratory fish, both directly, as a form of human-induced selection, and indirectly by interacting with natural selection processes such as predation, however, see (Haugen et al., 2008; Waples et al., 2008; Schwinn et al., 2017).

In fisheries, there is an increasing body of evidence showing interaction between anthropogenic and natural selection processes, transforming the adaptive landscapes (e.g. Arlinghaus et al., 2008; Olsen and Moland, 2011; Sutter et al., 2012; Wilson et al., 2015). Natural selection and fisheries selection interact in dynamic ways, like a tug-of-war, yielding adaptive landscapes that may vary from year to year depending on other external environmental forces such as ambient temperature conditions (Carlson et al., 2007; Edeline et al., 2007). Given the lessons learned from fisheries studies, similar combined effects from natural selection (e.g. size-biased predation) and hydropower-induced selection (e.g. size-dependent turbine-passage survival) may be expected to act on fish living in hydropower regulated ecosystems.

Turbine-associated injury and mortality result from a variety of sources encountered by fish in the turbine tunnel, shear forces, turbulence, cavitation, pressure, and blade strike (Čada, 2001), with the severity of the injury varying significantly, thus resulting in harmed fish that are likely to experience a reduced survival probability than undamaged fish. To date, few studies have addressed such indirect or delayed mortality (Čada, 2001) but see Koed et al. (2002) and Ferguson et al (2006). Due to high turbine mortality for descending fish, a common practice is to safely guide fish past hydropower plants (Larinier and Travade, 1999). However, some mitigation measures are inefficient or only benefit a part of the population (Scruton et al., 2003; Haraldstad et al., 2019). Particularly strong selection can be expected in systems where fish have the potential to choose between two different migration strategies (i.e. bypass or turbine) with significantly different survival. Owing to the potentially severe fitness consequence associated with such a choice, prospects of adaptive responses are high, even under modest levels of trait heritability.

Brown trout displays a broad diversity of life history traits, ranging from resident to anadromous forms (i.e. sea trout), and is among the most flexible of the salmonids in this regard. This plasticity manifests in individual variation in the migration timing, duration of the sea sojourn, and the number of spawning returns to the river (Thorstad et al., 2016). The smolt-run of sea trout is a fine-tuned migratory event, where a fraction of a cohort leaves their natal river during spring to start their migration towards the river mouth and feeding areas in the coastal areas. When physiologically ready, downstream migration is initiated by environmental cues in the river, such as changes in temperature and/or discharge (Thorstad et al., 2016). The migration speed of sea trout smolts is reported to vary considerably from 1 to more than 60 km day^{-1} (Aarestrup et al., 2002). Often, a positive correlation between migration speed and temperature or river discharge is observed (Thorstad et al., 2016). The smolt and post-smolt stages are critical parts of the life cycle of salmonids due to both physiological sensitivity and the behavioural changes (Thorstad et al., 2012). The smolts go from being a territorial and camouflaged parr sheltering in the substratum, to actively swimming downstream in shoals exposing themselves to predators. Several studies highlight predation as a major cause of smolt mortality during migration in river, brackish water, and at sea (Jepsen et al., 1998, 2019; Dieperink et al., 2001; Koed et al., 2006).

This work investigates size-related survival of PIT-tagged wild brown trout smolts that pass a sequence of multiple PIT-antennas and traps during their river descent in a regulated Norwegian river system. By

estimating individual survival in the river and at sea, we were able to compare size-specific survival rates between smolts that migrated through a hydropower turbine with smolts that bypassed the same turbine. The following hypotheses were addressed: (1) turbine mortality is positively related to smolt size, (2) mortality is lowest for bypass migrants at any size, in the river and at sea, and (3) the combined effect from natural and human-induced selection processes yield differential mean-adjusted selection gradients on smolt size between turbine migrants and bypass migrants.

Material and methods

Study site

The river Storelva flows through the county of Agder, Norway (58° 40′ N, 8°59′ E, Fig. 1). Sea trout (*Salmo trutta* Linnaeus, 1758) use the lowermost 20 km of the river as spawning and nursery habitats. The catchment area is 409 km^2, with an annual average water discharge of 12 m^3 s^{-1}. In the upper reaches, the river flows through woodlands and fluctuates between riffles and small pools, while the lowermost 3,5 km is slow flowing, meandering through agricultural dominated landscape. Before entering Songevannet estuary, the smolts pass through the lake Lundevannet (surface area: 0.38 km^2, max depth 19 m). Northern pike (*Esox lucius* Linnaeus, 1758) were introduced to Storelva around 1750 (Kleiven & Hesthagen, 2012) and occupy lower parts of the river system and were they potentially prey on salmonid smolts during the smolt-run period.

The watercourse has been regulated for hydroelectric power production since 2008. Fosstveit hydroelectric powerplant is a run-of-the-river plant located 6.5 km upstream the river mouth. It comprises of one four bladed Kaplan turbine that operates at 14.5 m head with an outer diameter of 1.65 m that rotates at 330 rpm at a maximum capacity of 16 m^3 s^{-1}. The power-generating water is abstracted from a small river reservoir (0.018 km^2, 6 m depth) and led back into the river through a tunnel tail race. At the tunnel inlet there is a 25 m^2 conventional trash rack with 50 mm spacing mounted at a 70° angle from the vertical. At the side of the trash rack, there is installed a surface bypass to secure safe downstream migration of brown trout and Atlantic salmon (*Salmo salar* Linnaeus, 1758) smolts (Haraldstad et al., 2018a, b). The main river flow is allocated to the turbine tunnel, resulting in extensively reduced water discharge (300 l s^{-1}) in the original river between the intake dam and tunnel tail race (residual flow stretch). There are two fish ladders in this river stretch to secure migration to upstream spawning and nursery areas.

Fish sampling, tagging, and release

Wild brown trout smolts were caught in two rotary screw traps (RST) from 27 April to 31 May 2010, 337 in the RST upstream HEP and 273 in the tail-race RST (Table 1). An RST is a passive sampling gear which takes advantage of flowing water to capture and retain downstream migrating fish (Chaput & Jones, 2004). The RST was fitted with leader net (bar-mesh 10 mm) set at approximately 45° angle from the RST to the shore to increase catch efficiency. Sea trout smolts (*n* = 610) were anesthetized with benzocaine (30 mg/l) and tagged with passive integrated transponder (PIT) tags (23 mm, half duplex, Oregon RFID), with a unique eight-digit code. The tag was inserted through a small incision made ventrally between the posterior tip of the pectoral fin and the anterior point of the pelvic girdle. The tagged fish recovered in perforated cages in the river for one day before being released.

One batch of smolts were caught in an RST and released in a riffle area 350 m upstream the dam forebay (Station A, Fig. 1). This batch of smolts could migrate downstream through the turbine tunnel or the surface gate in the dam. In addition, a batch of smolts were caught in the tail-race RST (i.e. after migrating and surviving through the turbine tunnel, Station B2) and released in the junction between the tail race and the residual flow stretch.

Detecting smolt movements

The movements of smolts were monitored by multiple PIT-antennas and RSTs. The swim-through PIT-antenna loops were wired to a remote tuner board and connected to an antenna reader box (TIRIS RI-CTL MB2A; Oregon RFID, USA) and supplied with 12 V battery. When a tagged fish passed through the antenna loop, tag number, date, and time were recorded and logged by the reader box.
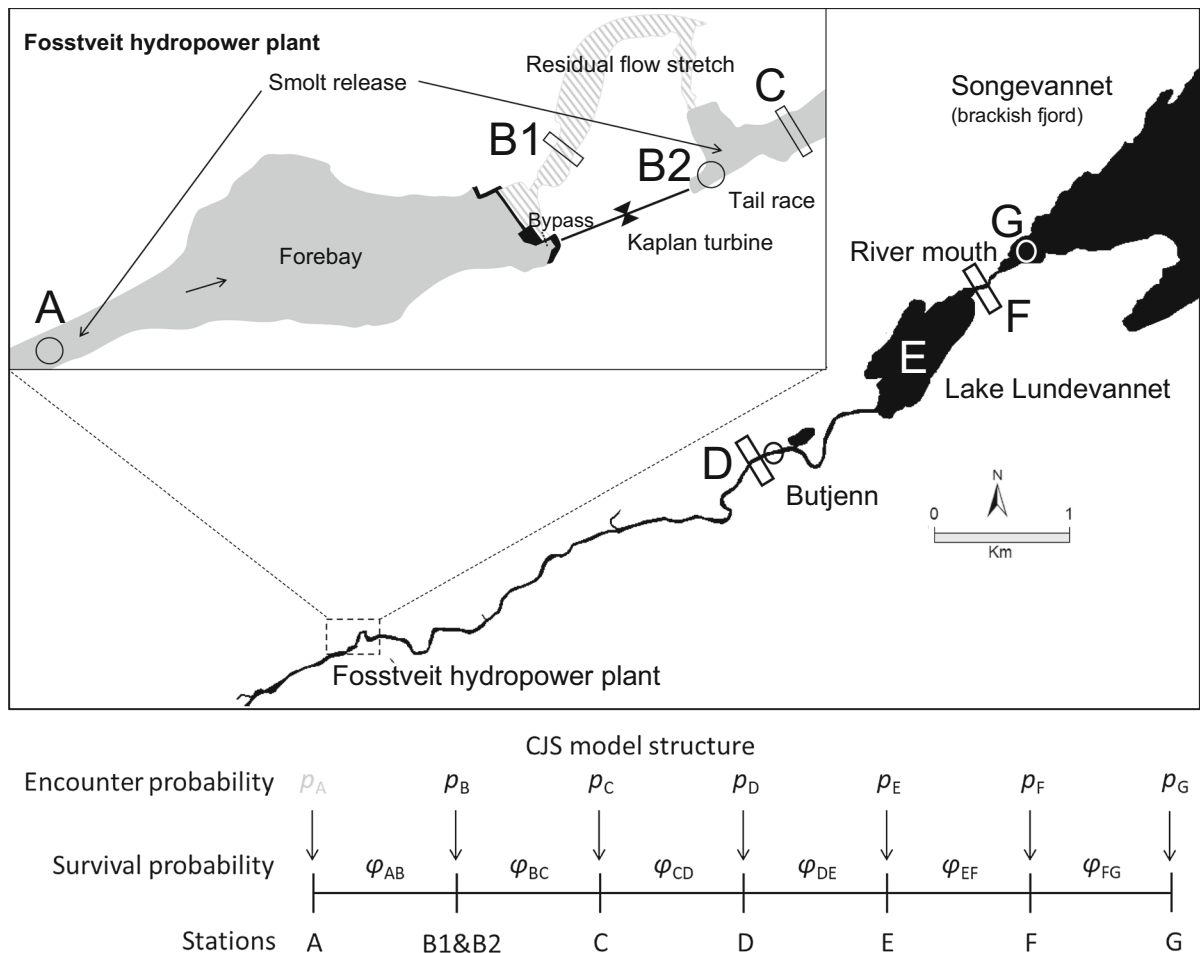
Fig. 1 Fosstveit hydropower station (expanded) and lower parts of River Storelva including catch and recapture locations (A-G, rectangles = PIT-antennas, circles = rotary screw traps) with subsequent CJS model structure. p_A is shaded as this parameter is not estimable

Smolt could move past Fosstveit HEP using either the turbine tunnel or the surface bypass in the dam. Smolts using the bypass were detected by a PIT-antenna in the residual flow stretch (Station B1) between the dam and the turbine tail race. The turbine migrants were caught in the tail-race RST (Station B2), either as dead or alive. Further downstream, both turbine and bypass migrants could be detected at five recapture stations; in the junction between the residual flow stretch and the tail race (PIT-antenna, Station C), upstream the ox-bow lake Butjenn (PIT-antenna and RST, Station D), at the outlet of lake Lundevannet (PIT-antenna, Station F) and at the river mouth (RST, Station G). To address the mortality of smolts in the lower parts of the river, Northern pike were caught with gillnets and by anglers during the smolt migration period and their stomachs were scanned for PIT-tags (Kristensen et al., 2010) (Station E). Note that these tag recoveries represent only a fraction of the potential loss of smolts to the piscivorous pike. After the sea sojourn, returning sea trout (conditional on positive detection in the river mouth pit or RST as smolts, in 2010) were registered by PIT-antennas during the 2010–2017 spawning runs to Storelva.

One possible source of error when dealing with post-turbine mortality is that dead smolts may be detected in antennas and wrongly assessed as alive (Havn et al., 2017). Median drift distance for dead Atlantic salmon smolts has been found to range from 0 to 1.5 km, downstream of three German hydropower plants (16, 23 and 53 $m^3 \, s^{-1}$) (Havn et al., 2017). However, we believe that this potential for error is

Table 1 Number of PIT-tagged sea trout smolts in Storelva 2010 including their migration route at the Fosstveit hydropower plant and recaptures in the PIT antennas and rotary screw traps downstream. Note highly variable encounter probability in recapture stations

Release date	Migration route at HEP	
	Bypass	Turbine (tagged in tail race after turbine migration)
30.04.2010	3	31
01.05.2010	2	24
03.05.2010	6	73 (13)
09.05.2010		1 (1)
11.05.2010		1 (1)
12.05.2010		2 (1)
13.05.2010	1	4 (4)
14.05.2010	2	29 (18)
16.05.2010	27	105 (73)
18.05.2010	31	185 (162)
19.05.2010	6	12
21.05.2010	26	39
	104	506
Recaptures		
Residual flow stretch PIT (B1)	104	
Tail-race RST (B2)		347
Junction PIT (C)	71	173
Butjenn PIT and RST (D)	20	114
Pike stomachs (E)	0	14
River mouth PIT (F)	36	111
River mouth RST (G)	2	15
River mouth combined[a]	37	116
Returned after sea sojourn	11	24

[a]Number of unique ids retrieved in both river mouth PIT and river mouth RST stations (some ids overlap)

accounted for. in our study, as drift distance is likely dependent on the hydromorphology and discharge of the river. During the 2010 smolt-run, River Storelva had an average discharge of 2–6 m^3 s^{-1}, significantly lower than in the study by Havn et al. (2017). In addition, a large proportion of the smolts were physically recaptured in traps downstream Fosstveit HEP (B2: 69% and D: 15%). The RST in the tail race were also fitted with leader nets and placed in the main current. Escaping this trap probably requires active swimming out of the main current. During fieldwork, we observe the tail race daily in search for dead smolts, and after years of fieldwork, we have good knowledge of backwaters where dead eels, smolts, and kelts (Haraldstad et al., 2018b) pile up. Thus, turbine migrant smolts were alive downstream of the hydropower plant and not dead, drifting with the current.

Mark–recapture analyses

Capture–mark–recapture analyses were carried out in program MARK, version 6.2 (White & Burnham, 1999), by fitting sequential Cormack–Jolly–Seber models (CJS) (Lebreton et al., 1992) to the individual recapture histories. This model structure estimates two sets of parameters: encounter probability (P) and apparent survival probability (φ). In our study, p_i constitutes the probability of detecting or recapturing a PIT-tagged smolt at station i, (an antenna, RST, or pike stomach). The parameter ϕ_{ij} constitutes the probability of surviving a river stretch between encounter stations i and j. This model structure assumes that all surviving individuals swim downstream and encounter stations in the same downstream sequence. Take note that this form of mark–recapture modelling does not consider time effects on survival or detection probability.

In this study, it was essential to have a very high detection probability at the PIT-antenna located in the residual flow stretch between the dam and the turbine tail race (Station B1). Smolts could then be correctly assigned to either bypass migration group (detected in this antenna) or turbine migration group (not detected in this antenna). To verify this assumption, 50 PIT-tagged Atlantic salmon smolts were released 40 m upstream antenna at five different occasions during the smolt-run. All 50 smolts were detected in the antenna and p_{B1} was thus fixed to 1 in the CJS-analysis. Downstream Fosstveit HEP, smolts were detected in the end of the tail race and at Butjenn [combined encounter probability Station C and D, $P_{CD} = 0.743 \pm 0.032$ (SE)], at the outlet of lake Lundevannet (Station F, $P_F = 0.515 \pm 0.062$) and in the river mouth (Station G). There are no detection opportunities beyond the last recapture location in the Storelva river mouth unless we wait for the sea trout to return after the sea sojourn. Due to this, the P_G and ϕ_{F-G} cannot be separated. To overcome this constraint, which is common for mark–recapture analyses (Lebreton et al., 1992), we fitted candidate CJS-models with ϕ_{F-G} fixed at 1, assuming all individuals to survive this 150 m river stretch. Due to the short distance, this is probably very close to reality, but the RST catchability estimates will be lower than expected (biased) if there are substantial deviations from this assumption. Using this approach, we estimated the mean RST catchability (P_G) to be 0.060 ± 0.015.

Candidate survival models were fitted under fully station variation of P according to the just mentioned estimates. For all survival stretches (i.e. φ_{ij}), five candidate models were fitted for a full consideration of the nature of eventual migration group (G) differences in length-specific (L) survival:

1. $\varphi_{ij} = 1$, constant survival, independent of migration group and body length
2. $\varphi_{ij} = G$, different between migration groups, but independent of body length
3. $\varphi_{ij} = L$, body length dependent, but not different between migration groups
4. $\varphi_{ij} = G + L$, additive effect of migration group and body length
5. $\varphi_{ij} = G * L$, differential body length effects between the two migration groups

We also fitted candidate models with a coarser spatial resolution where survival processes taking place during dam passage (i.e. Station A to B1 and A to B2, Fig. 1) were parameterized differently than the downstream dam reaches (i.e. B to G). This coarser spatial structure was subjected to the same five candidate models for survival. Model selection was based on AICc where the candidate model with lowest AICc was considered to have the highest support in the data (Anderson, 2008). However, candidate models that differed with less than 2 AICc units to the most supported one were considered in the following discussions. A global model [ϕ(group*stretch) P(group*stretch)] was subjected to goodness-of-fit tests using the built-in test 1 to test 3 in Mark. These revealed no overall lack of fit for test 2 and 3 ($P_{Test2} = 0.1337$; $P_{Test3} = 0.1877$), suggesting both detection probabilities to be independent on previous detections and survival probability to be independent on release site.

The statistical software R (R Development Core Team, 2016) was used for all data inspection and statistical analyses, except the mark–recapture analyses. Linear models (lm), with corresponding one-way anova, was fitted to test for difference in individual length between turbine and bypass migration smolts and to analyse smolt migration speed, fitting candidate models including river temperature, river discharge, and migration route at the turbine intake as model predictors. Water discharge and temperature were not used in the same model due to its significant correlation. Fish migration speed was based on individuals detected at both Fosstveit PIT-antenna (Station C) and the river mouth PIT-antenna (Station F, $n = 57$, distance C-F = 6.3 km). Fish caught in the Butjenn RST (Station D) were excluded from this analysis due to disrupted migration caused by handling time in the trap (emptied once a day). To account for the intrinsic higher swimming capacity in larger smolts compared to smaller ones, migration speeds were converted to length-specific measures (body length·second^{-1}) in the analyses.

The probability of surviving, returning to the river, and being detected after a sea sojourn was estimated using generalized linear models (GLM) fitting candidate models including smolt length and migration route at the turbine intake as predictor variables. The logit link function was used for linearization of the binomial response (0 = not resighted; 1 = resighted in

river PIT-antenna). In order to explore eventual non-linear effects from size on return probability, candidate models including total length (TL^2) effects were also fitted. The reason for including quadric effects of size is to allow for not only directional selection, but also disruptive and stabilizing selection. GLM model selection was based on Akaike's information criterion (Akaike, 1974; Anderson, 2008).

In order to assess potential evolutionary consequences imposed by mounting a hydropower plant into the river and thus changing the migratory route of brown trout smolt, we estimated the mean-standardized selection gradients (β) (Houle, 1991; Hereford et al., 2004), for both turbine migrants and bypass migrants:

$$\beta_G = \frac{\mu_P S_G}{\sigma_P^2}$$

where $S_G = \mu_P - \mu_G$, corresponding to the selection differential (Falconer and Mackay, 1996). σ_P is the population phenotypic standard deviation and μ_P is the population phenotypic mean (prior to selection) and μ_G is the post-selection group-specific phenotypic mean ($G \varepsilon$ (turbine, bypass)). This selection gradient metric entails some very useful properties including being an elasticity metric for fitness, i.e. measuring how fitness change as a response to a relative change in trait value (Caswell, 2001).

Results

The PIT-tagged wild brown trout smolts (mean length: 164 ± 26 mm ($\pm$ SD)) were released upstream the Fosstveit HEP. There was no significant difference in length between smolts that used the bypass and the smolt that migrated through the turbine ($P = 0.774$).

For predicting river survival during migration, the most supported CJS model attained AICc-values 2.3 AICc units lower than the second-most supported model (Table 2) and included migration-route group effects and length effects for most river sections (Table 3; Fig. 2). Candidate models with full spatial resolution on apparent survival between station B and G (i.e. stretch effect) attained lower AIC support than models with no stretch effects (ΔAIC > 5.13, Table 2). The selected model predicted differential survival between the two migration-route groups. All the

bypass migrants survived the 230 m long residual flow stretch between the bypass and the junction between the old riverbed and the tail race. The turbine migrants experienced higher mortality during their tunnel turbine tail-race descent, and estimated survival probability was 0.47 ± 0.05 ($\pm$ SE) for a mean-sized individual (i.e. 164.5 mm). In addition, the estimated survival probability for the turbine migrants was negatively size dependent. The selected model predicted survival probabilities > 0.6 for smolts smaller than 130 mm while the largest smolts, > 250 mm, had estimated survival probabilities close to 0.2.

In the river stretch downstream Fosstveit HEP, the survival was positively size dependent for both migration groups, and higher for bypass migrants than turbine migrants. Only turbine-migrating smolts were found in pike stomachs ($n = 14$). Furthermore, mid-sized smolts seem most vulnerable to predation (Fig. 3). Total river-descent survival from Fosstveit to the river mouth was estimated to be 0.20 ($\pm$ 0.07) for turbine migrants and 0.44 ($\pm$ 0.10) for bypass migrants (for tagging length = 164.5 mm). The surviving turbine migrants were significantly smaller than their bypass counterparts (Welsh Anova, $P_{G-} < 0.0001$) and the estimated mean-adjusted selection gradient for size at tagging was $- 0.76$ and $+ 1.85$ for the turbine migrants and bypass migrants, respectively (Fig. 4).

The smolts used on average 4.7 ± 3.9 days ($\pm$ SD) from Fosstveit to the river mouth and progressed at a rate of 2.1 ± 1.4 km d^{-1} ($\pm$ SD) or 0.14 ± 0.098 BL s^{-1} ($\pm$ SD). Model selection supported a temperature effect on migration speed (PR = $- 0.014$ ± 0.057 + 0.012 ± 0.004*Temp ($R^2 = 0,076$, $F = 7.89$, df = 83, $P = 0.006$) (Supplementary Information, Table S1). The selected model predicted an increase in migration speed from 0.11 to 0.17 BLs^{-1} when temperature increases from 10 to 15°C.

After the sea sojourn (conditional on positive detection in the river mouth pit or RST as smolts, $n = 152$), 23% of the PIT-tagged sea trout were detected in the river as return migrants. The selected model predicted return probabilities of 0.21 ± 0.038 ($\pm$ SE) for turbine migrants, while 0.31 ± 0.077 ($\pm$ SE) for bypass migrants, although not statistically significant [logit(return) = $- 0.821$ ± 0.362 + 0.523 ± 0.428 Route$_{Turbine}$ (LR-ratio test: $P_{route} = 0.222$] (Supplementary Information, Table S2).

Table 2 Model selection metrics for the 10 most supported candidate Cormack–Jolly–Seber models fitted to estimate apparent survival (φ) in brown trout smolt during their 2010 river descent in Storelva

River section		AICc	ΔAICc	AICc weights
A–B	B–G			
BP(Intercept);T(Length)	Group*Length	11,792.39	0.00	0.622
BP(Intercept);T(Length)	Group + Length	11,794.01	2.32	0.132
BP(Intercept = 1);T(Length)	Group	11,795.50	3.12	0.110
BP(Intercept);T(Length)	Intercept	11,796.84	4.45	0.056
BP(Intercept);T(Length)	Group*Length + Stretch*Length	11,797.52	5.13	0.040
BP(Intercept);T(Intercept)	Group*Stretch	11,799.73	7.35	0.013
BP(Intercept);T(Length)	Length	11,799.79	7.41	0.013
BP(Length);T(Length)	Group + Length	11,801.25	8.86	0.006
BP(Length);T(Length)	Group + Stretch + Length	11,801.64	9.26	0.005
BP(Intercept);T(Length)	Group*Stretch + Length	11,807.55	15.16	0.000

The accompanying recapture (p) model structure was p_{B-G}(station)p_E(Length + Length^2) for all models. AICc is the n-corrected version of Akaike's information criterion (Burnham & Anderson, 2002), ΔAICc is the difference between a candidate model's AICc compared to the one with the lowest AICc, AICc Weights is the relative AICc support for a given candidate. Group = migration group [bypass (BP) or turbine (T)], Stretch = part of river between two detection stations; Intercept = constant

Table 3 Logit parameter estimates for the selected Cormack–Jolly–Seber model (see Table 1) fitted to model section-wise apparent survival (φ) and station-wise encounter probability (P) along the downstream migration route of brown trout smolt in the river Storelva during the 2010 descent

Parameter type	Station/Stretch	Group	Term	Est	SE
φ	A-B	Bypass	Intercept	3.861	0.715
φ	B-F	Bypass	Intercept	2.130	0.499
φ	B-F	Bypass	Length	0.539	0.438
φ	F-G	Both	Intercept	Fixed = 1	
φ	A-B	Turbine	Intercept	− 0.090	0.155
φ	A-B	Turbine	Length	− 0.336	0.146
φ	B-F	Turbine	Intercept	1.674	0.247
φ	B-F	Turbine	Length	0.312	0.178
p	B1	Bypass	Intercept	Fixed = 1	
p	C&D	Both	Intercept	1.064	0.167
p	E	Bypass	Intercept	Fixed = 0	
p	F	Both	Intercept	0.060	0.249
p	G	Both	Intercept	− 2.752	0.274
p	B2	Turbine	Intercept	0.603	0.225
p	E	Turbine	Intercept	− 4.135	0.808
p	E	Turbine	Length	22.396	11.185
p	E	Turbine	Length^2	− 21.668	11.054

Parameter estimates are provided according to migration-route group (turbine migrants, bypass migrants or both = all individuals get the same estimate). Terms are either intercept estimators or slope estimators (for length and length^2)
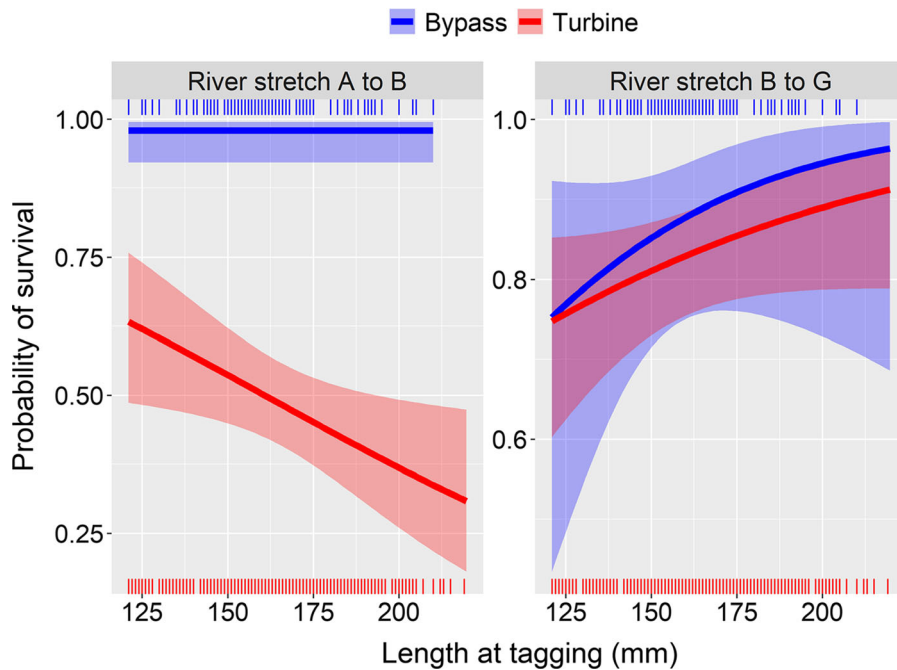
Fig. 2 Predicted migration-route- and length-specific survival probabilities of passing Fosstveit HEP (Station A-B, left panel) and total river descent (Station B-G, right panel). Predictions were made from the selected Cormack–Jolly–Seber model presented in Table 2. Shaded areas represent 95% confidence bounds and red and blue rug at bottom and top of figures represent observed individual lengths for turbine and bypass migrants, respectively
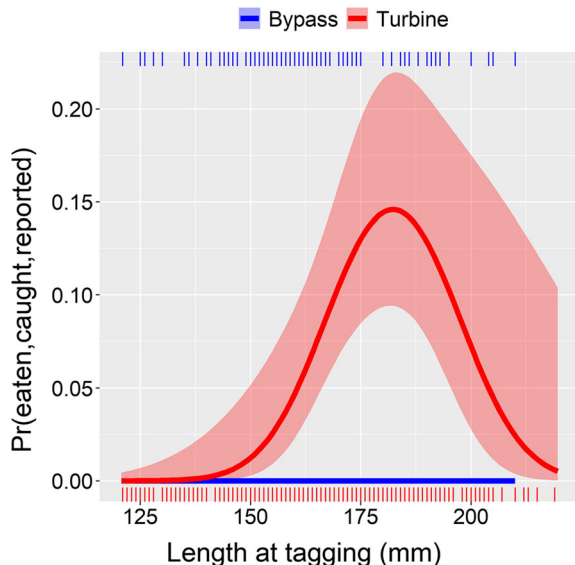

Fig. 3 Predicted probability of smolt being consumed by pike that, in turn, gets caught by an angler and reported. Predictions were made from the selected Cormack–Jolly–Seber model presented in Table 2. Shaded areas represent 95% confidence bounds and red and blue rug at bottom and top of figures represent observed individual lengths for turbine and bypass migrants, respectively

Of the returning sea trout ($n = 35$) ,17.1% returned the same summer as they left the rivers as smolts while 45.8% returned the second summer, 17.1% the third, while 20.0% returned after their fourth season at sea. The average time spent at sea were 570.0 ± 432.9 days (± SE) for bypass migrants and 597.7 ± 358.4 days (± SE) for turbine migrants. Model selection did not support any effects of migration route or fish length on the duration of the sea sojourn (Supplementary Information, Table S3). Of the returning sea trout, 37% returned to spawn in the years after their first return.

Discussion

This study revealed how hydropower dams can introduce a new selection regime for salmonid smolts during their downstream migration, and that this new selection regime also interacts with natural selection processes in the river. Specifically, we found that the hydropower turbine favoured the survival of small brown trout, while the mid-section of the river
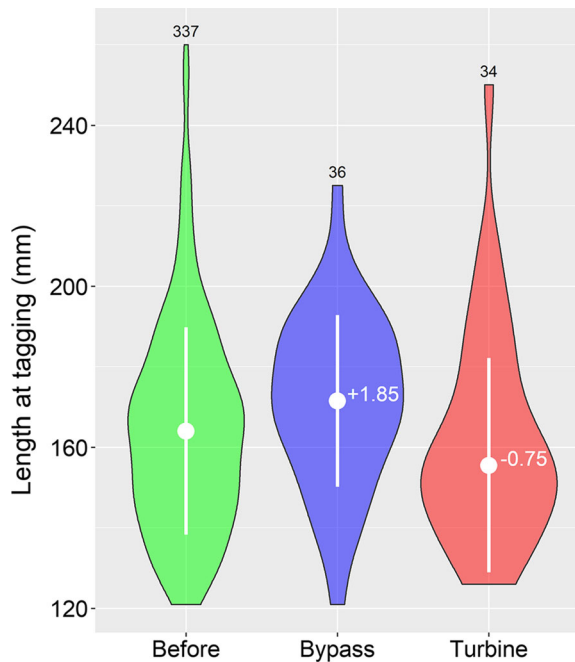
Fig. 4 Violin plots of individual lengths at tagging observations for all upstream Fosstveit HEP dam brown trout smolt individuals (i.e. before choice of migration route) along with tagging length measurements of confirmed (at PIT and/or RST in river mouth) surviving individuals of bypass migrants and turbine migrants. Numbers at top of violins represent number of observations and white numbers within violins represent mean-standardized selection gradients. Dots with error bars represent mean and ± 1 SD

favoured larger individuals. Intermediate-sized turbine migrants were more prone to Northern pike predation than smaller and larger individuals from the same group. No bypass migrants were documented eaten by Northern pike.

The shift in size-selective survival experienced by the turbine migrants yielded a negative mean-adjusted selection gradient for survivors at the river mouth. By contrast, bypass migrants were predominantly affected by natural selection during their river descent, resulting in a size-biased survival of larger individuals, culminating in a clear positive selection gradient coefficient (Hereford et al., 2004). Such opposite directions of the selection gradients will cause disruptive selection for the whole smolt population in the river, driving the population apart where extreme trait values increase in frequency. This may lead to increased phenotypic variation (Rueffler et al., 2006). Moreover, in addition to the smaller size and the lower survival to the river mouth in turbine-

migrating smolts, a generally lower sea survival often found in small-sized post-smolts (Dieperink et al., 2001) must be considered for this group of fish. Thus, turbine-migrating fish can be affected by selection processes throughout the smolt-run, including the sea migrating phase. This accentuates the importance of alternative migration routes at hydropower plants, and that this type of mitigation measures can strengthen the population not only by decreasing acute mortality but also mitigating delayed effects such as sea and river mortality. However, it is important to keep in mind that a bypass system is just a mitigation measure, and do not fully restore the river system. One important measure that can be done to increase survival of descending smolts is to prohibit all smolts from entering the turbine tunnel by changing the 50 mm trash rack to a 10 mm angled screen. It is also important to note that other hydropower plant-related factors occurring upstream the dam, potentially having negative impacts on descending smolt, are not addressed in this study.

Similar to our finding, other studies have documented negative size-selective survival for turbine migrants (Montén, 1985; Clay, 1995; Coutant and Whitney, 2000). Even though this is well known, few studies have addressed the possible selective mechanisms involved. Considering the high variation in age and length at smolt in this species, such selection agents might also affect life history strategies. According to the emerging framework of pace-of-life syndrome, linking variability in behaviour and developmental ratio to reproduction strategies (Réale et al., 2010) selection acting at size at smoltification may radically change the traits composition in a population.

Overall, there was a positive size-selection in survival of individuals in the river stretch downstream of Fosstveit HEP, with larger fish more likely to survive in both migration groups. Several studies highlight predation as one of the major mortality factors of smolts during migration in river, brackish water and at sea (Jepsen et al., 1998; Dieperink et al., 2001; Koed et al., 2006). In general, small individuals are probably at greater risk in natural river systems (Thorstad et al., 2016). Typical smolt predators in other Norwegian rivers are mainly brown trout, but also cormorants [*Phalacrocorax carbo* (Linnaeus, 1758)], red-breasted merganser (*Mergus serrator* Linnaeus, 1758), grey heron (*Ardea cinerea* Linnaeus,

1758), American mink [*Neovison vison* (Schreber, 1777)], and otter (*Lutra lutra* Linnaeus, 1758). Piscivore fish are likely to eat smaller individuals than Northern pike as Northern pike have a larger gape size. In addition, Dieperink et al. (2001) documented significantly higher predation from avian predators on small than large sea trout smolts. Under such predation conditions without hydropower plants, impose even more positive mean-adjusted selection gradient.

Only turbine-migrating smolts were found in pike stomachs. It is likely that some sublethal injuries from the turbine lead to inadequate smolts that may be more vulnerable to predation (Mesa et al., 1994). Ferguson et al. (2006) hypothesized that delayed mortality was caused by sublethal impacts to fish sensory systems, which increased vulnerability to predation in the tail race. In addition, laboratory experiments performed by Neitzel et al. (2000) demonstrated that rainbow trout [*Oncorhynchus mykiss* (Walbaum, 1792)] exposed to levels of shear stress and turbulence that do not cause obvious physical damage may nonetheless suffer significantly greater predation than controls. Dependent on the severity of the injury caused by the turbine, and the possibility that some injuries and behavioural changes may be temporary, post-mortality may vary significantly between systems with different densities of predators in the downstream river stretches and in the fjord system. This study documents delayed mortality effects which should be incorporated when estimating potential loss of turbine-migrating smolts. The lack of PIT-tagged recaptures in Northern pike stomachs of bypass migrants is not the same as claiming these individuals were not eaten by pike. The number of tagged bypass individuals was about 20% (104 vs. 506) of the tagged turbine migrants (Table 1) and on average about 47% survived the turbine passage. Hence, even if the two groups had similar pike predation probabilities the expected number of bypass migrants retrieved from Northern pike stomachs would be $\sim$ 6.1 individuals (5.88% of the turbine survivors get recaptured in Northern pike stomachs). Clearly, zero recaptures are much lower than the expected six individuals indicate that the turbine migrants are more prone to be predated on than bypass migrants, but six is a sufficiently low number to not rule out a random result completely. Most likely, a large proportion of the overarching size-dependent mortality estimated for the entire station B to station G

stretch (Fig. 2-right) can be attributed to Northern pike predation. However, contrary to what is the case for sympatric Atlantic salmon smolt (Kroglund et al., 2011), the CJS model selection did not support a differential size-dependent survival in Lundevannet (Station D to Station F) compared to other downstream Station B sections.

The smolt migration speed in River Storelva was within the lower ranges of similar studies on sea trout smolt migration (Aarestrup et al., 2002, 2014; Serrano et al., 2009). A large part of the river stretch from Fosstveit to the river mouth is slow flowing, including lake Lundevannet. Lakes and reservoirs have been shown to delay the migration speed of Atlantic salmon smolts (Thorpe et al., 1981; Hansen et al., 1984; Thorstad et al., 2012). The delay is probably due to the loss of directional moving currents and smolts therefore require more time to traverse the lake and locate the outlet. In addition, slow-flowing water expose smolts to pike predation more than in fast water (Jepsen et al., 2000) and the absence of ripples on the surface may improve vision for avian predators. Greater vulnerability of smolt may reduce the migration speed further. One anticipates that turbine migrants swam at a slower speed than bypass migrants and were therefore exposed to predation over a longer period, but there was low support for the model that included difference in migration speed between turbine and bypass migrants. In this study, analysis of migration speed was dependent on individuals being detected in the river mouth. Consequently, this analysis only includes those fish which survived the total river descent. Therefore, no information is provided on the migration speed of those individuals that die before reaching the river mouth. Telemetry approaches that allow for more detailed migration data on post-turbine smolt behaviour (Chaput et al., 2019; Patterson & Pillans, 2019) could derive appropriate data in order to investigate this further.

The migration-route choice at Fosstveit HEP appears crucial for individual fitness, with the decision of migrating route unlikely to be random. When in the hydropower forebay, the smolts are faced with a choice of two different migration alternatives with very different appearances: one being a dark fenced tunnel and the other a small surface bypass channel. Haraldstad et al. (2019) hypothesized that contrasting behavioural profiles may be an underlying factor to this migration-route decision. The significant

difference in fitness related to the migration-route choice discloses selection on behavioural traits. It has been documented that behavioural traits are often organized in suites of traits that show consistency across context and time, which represent different behavioural syndromes within a population (Sih et al., 2004). Moreover, such individual variation has been associated with life history traits. Rèale et al., (2009), and Mittelbach et al. (2014) pointed out that little attention has been paid to the ecological consequences of the varying behavioural phenotypes in wild populations. Route choice at Fosstveit HEP seems essential for individual fitness and further studies are required in order to elucidate behaviour-dependent selection at hydroelectric power plants and their potential effects at the population level.

Conclusion

Turbine migrants experienced different size-selective regimes while progressing downstream, yielding low survival and maladaptive size distribution when compared to the bypass migrants. The combination of predation from introduced Northern pike and hydropower substantially reduces the survival of descending smolts. Mitigation measures for descending smolts at hydropower plants are thus essential for preserving sustainable populations of anadromous fish and maintaining population genetic variation.

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