



Evaluation of mitigation measures for Atlantic salmon and brown trout at hydropower plants and their prospect as selective agents

Tormod Haraldstad

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Preface

I still remember that overwhelming feeling of excitement after landing my first 1 kilo sea trout at age of 10 in a small boat of the southern coast of Norway together with my father. I could not hold back the tears of joy! Such an amazing creature! Perfectly adapted to the marine environment, but still a visitor, far away from its home stream.

During the 20th century, acid rain had devastating effects on fish and other aquatic life in lakes and rivers of southern Norway. Growing up, I saw rivers gradually being brought back to life due to liming, leading to an increased abundance of trout and the re-establishment of salmon populations. I've always had a profound interest in nature and particularly salmonids. A special thanks goes to my father for encouraging that interest. Thank you for bringing me along from a very early age and for sharing your knowledge and enthusiasm. I am happy and proud to see that you now share this exciting universe with my sons, your grandchildren. Being a boy who was constantly planning were to go fishing or play in the woods I'm also truly grateful to my mother who over the years have demonstrated an endless patience in helping me with my early schoolwork.

Several people have contributed to this PhD-project, and I feel very lucky to be able to learn from you and build on your experience. First, I wish to thank my supervisors. Erik Höglund, thank you for competently managing the balance between being a supportive friend and a bossy main supervisor when needed. I really appreciate your ability to guide me in the process from discover something novel and transpose that into a story worth reading. Thronn Haugen, thank you for your enthusiasm, profound knowledge of ecology and your beyond generous support with the stats (if I bear to wait). Esben Moland Olsen and Torbjørn Forseth for sharing your knowledge and valuable inputs on article drafts. Thanks to all of you for being positive and enthusiastic whenever I contacted you for guidance.

A special thanks goes to Frode Kroglund, who decided to take me under his wing when I first started working for NIVA as a young research assistant. I learned a lot from working with you. Your eagerness to gather data has formed the basis of this thesis and I am beyond grateful for that. I would also like to extend a special thanks to Jim Güttrup. We have spent countless hours in the field over the last ten (!)

years. I have enjoyed all of them. Thank you for your flexibility and for always being positive.

I am grateful to Agder Energi and Norwegian Environmental Agency for founding the project. A special thanks goes to Svein Haugland who early on believed in me and my project. The staff at Rygene hydropower plant, for their good mood, coffee and for lending me a helping hand whenever I needed. Roy Langåker, thank you for your enthusiasm and positive feedback.

I am grateful to NIVA for allowing me to keep my permanent research position at the institute while working on my PhD-studies. Thank you Åse Åtland, Øyvind Kaste and Trine Dale for given me flexibility to focus on my PhD.

Many thanks to Steve Cooke and his lovely family for their overwhelming hospitality during my research stay in Ottawa, Canada in 2019. Your family and all the great people at the Fish Ecology and Conservation Physiology Lab at Carleton University made this a fantastic research stay for both my family and me.

I also want to thank my colleagues at NIVA Region South, where I have spent most of my time while writing my PhD. An extra thanks goes to Christopher Harman for time well spent commuting from Dvergsnes to Grimstad in your leaf, and for removing the worst typos in my research texts. Thank you, Kurt Johansen for valuable help in the field and for always bringing baked goods.

Lastly, a huge thanks to my wife Hilde Terese and our three fantastic boys Tobias, Herman and Torjus for always being there for me and helping me take my mind off work, while still expressing interest and support for my research.

A handwritten signature in black ink, appearing to read 'Svein Haugland'. The signature is fluid and cursive, with a long horizontal stroke at the beginning.

Abstract

Renewable energy contributes towards the world's growing energy demands and urgent need for mitigating climate change. However, these renewable sources of energy may have localized, detrimental environmental effects. For instance, hydropower dams have dramatically affected river ecosystems by changing habitats and hindering fish migration. Especially, in anadromous salmonid fishes, such obstacles are responsible for the decline of many populations.

Fish passages, offering a safe migration at hydropower dams, are therefore instrumental to secure populations of anadromous salmonids in regulated rivers. However, the small body size of smolts and their tendency to follow the main current downstream, impose design challenges to measures that prevent migration into turbines. Coherent with this, investigations of fish passages from a range of sites reveal a generally low overall efficiency. Considering that the fish passage and the turbine tunnel offers two migration routes with different survival, surprisingly little attention has been paid to selection regimes acting at hydropower plants.

In this doctoral thesis, I evaluated the efficiency of mitigation measures for downstream migrating Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) and their prospect as selective agents. The studies were conducted at Fosstveit hydropower plant in the River Storelva and at Rygene hydropower plant in the River Nidelva located in southern Norway. Results are based on measuring or estimation of behavior and survival from individually PIT-tagged fish and the subsequent detections and recaptures in antennas and traps.

My data show that guidance efficiency of a surface fish passage increased as more relative river discharge is allocated to the passage and tests of efficiency of several surface gates documented that it should be located as close to the intake trash rack as possible. However, temporary closing of fish passages outside Atlantic salmon smolt-run periods to increase electricity production will potentially have negative effects on other species and life stages. My data show that emigration prone post-spawners either migrate through the turbine tunnel following high mortality or are restrained upstream the dam. Safeguarding

downstream migration of these individuals might secure future repeat spawning that contribution significantly to population resilience.

My data also demonstrate differences in survival and size selection regimes between turbine and fish passage migrating smolts. For turbine migrants, survival decreased with increasing smolt size. In contrast, smolts that used the fish passage were predominately affected by natural selection during their river descent, characterized by higher survival of larger individuals. In general, survival to the river mouth were significantly lower for turbine migrants than fish passage migrants. This is probably due to turbine blade strike and increased predation from Northern pike (*Esox lucius*) experienced by turbine emigrants. These findings highlight how migration route choice at a hydropower intake effect both survival and selection pressure during smolt migration in the river. In addition, data show that migration route choice is a consistent trait and that individuals with higher activity in a behavioral assay had a higher probability of using the fish passage than the turbine tunnel. Potentially, the lower survival for turbine migrants opens for selection on behavior traits.

Taken together, the results suggest that selection on several traits is expected to act on fish living in hydropower regulated ecosystems. This may lead to an altered evolutionary pattern that might impact population viability. In anadromous salmonids, hydropower-induced selection might remove traits favorable in other part of the life cycle leading to reduced overall production. Thus, accounting for hydropower-induced selection that goes against natural selection processes is therefore important to incorporate in management strategies of anadromous salmonids in regulated rivers.

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1. List of publications

The present thesis is based on the following papers:

- I** **Haraldstad, T.**, Höglund, E., Kroglund, F., Haugen, T. O., & Forseth, T. (2018). Common mechanisms for guidance efficiency of descending Atlantic salmon smolts in small and large hydroelectric power plants. *River Research and Applications*, **34** (9), 1179-1185.
- II** **Haraldstad, T.**, Höglund, E., Kroglund, F., Lamberg, A., Olsen, E. M., & Haugen, T. O. (2018). Condition-dependent skipped spawning in anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, **75** (12), 2313-2319.
- III** **Haraldstad, T.**, Höglund, E., Kroglund, F., Olsen, E. M., Hawley, K. L., & Haugen, T. O. (2020). Anthropogenic and natural size-related selection act in concert during brown trout (*Salmo trutta*) smolt river descent. *Hydrobiologia*, 1-14.
- IV** **Haraldstad, T.**, Haugen, T. O., Kroglund, F., Olsen, E. M., & Höglund, E. (2019). Migratory passage structures at hydropower plants as potential physiological and behavioural selective agents. *Royal Society open science*, **6** (11), 190989.
- V** **Haraldstad, T.**, Haugen, T. O., Olsen, E. M., Forseth, T., & Höglund, E. Hydropower-induced selection of behavioral traits in Atlantic salmon (*Salmo salar*). (Submitted).

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2. Introduction

Evolution by natural selection has formed species and populations that are adapted to survive and successfully reproduce in a variety of environments. As we have entered the age of Anthropocene, few wild animal populations are unaffected by human activity. Accordingly, humans may well be the most powerful driver of contemporary evolution (Fugère and Hendry 2018; Hendry et al. 2017). Selection is a key mechanism in evolution. Thus, to understand the causes, strengths and directions of anthropogenic selection and how it interacts with natural selection is crucial for proper management that aim to secure sustainable wildlife populations and biodiversity in the long run.

Renewable energy sources, such as hydro-, wind- and solar power, help meet the worlds growing energy demands and at the same time the urgent need for mitigating climate change, through lower carbon emissions (Owusu and Asumadu-Sarkodie 2016). However, these renewable sources of energy may have localized, detrimental environmental effects (Gibson et al. 2017). For instance, hydropower dramatically affects river ecosystems, especially by changing and degrading habitats. Despite this, in such anthropogenically altered landscapes, certain individuals thrive. Their phenotypes might have high fitness and, given enough trait heritability, favorable traits will increase in frequency in future generations. 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. In this thesis, an evaluation of mitigation measures for migratory salmonids at hydropower plants and their potential as selective agents, is presented.

2.1 Animal migrations and the life cycle of salmonids

Migration enable animals to exploit fluctuating resources and to settle in areas where life might not have been possible year around (Lucas and Baras 2008). The migration often carries great costs that involves energy expenditures and high mortality risk but also large growth- and fitness benefits like increased fecundity. Accordingly, a migratory life history is only maintained if these costs are offset by increased benefits in the habitat accessible as a result of migration. Migration is found in all major animal groups, including fish. One of the most iconic long-

distance travelers is the Atlantic salmon (*Salmo salar*). Its anadromous life cycle involves a juvenile phase in freshwater before setting out on a sea sojourn covering large distances before they return to their home river to spawn one to several years later (Klemetsen et al. 2003).

The Atlantic salmon smolt run, an ontogenetic habitat shift, is a fine-tuned migration event, where the majority of a cohort leave their natal river during a few weeks to start their migration towards the feeding areas in the North Atlantic Ocean (Klemetsen et al. 2003). The migration is initiated by environmental cues in the river, such as changes in temperature or flow, that coincide with optimal temperature and food supply in the coastal areas (Hvidsten et al. 1998; Jonsson and Ruud-Hansen 1985). Due to the physiological sensitivity and high predation risk of smolt and post-smolt individuals, these are critical stages in the life cycle of salmonids (Thorstad et al. 2012). Entering saltwater at the right time is essential for survival and this period of optimal environmental conditions is often termed the smolt window (McCormick et al. 1998). The productive marine environment allows salmon to grow rapidly, before they return to their home river to spawn one to several years later. Following spawning, some individuals die because of predation, exhaustion or disease, but survivors may return to spawn several times during their lifetime (Fleming 1996).

Atlantic salmon occupy the northern Atlantic Ocean and rivers that drain therein. In the eastern part of their distribution range they often share spawning and nursery habitats with brown trout (*Salmo trutta*), a closely related species. The migration to sea is obligatory for most Atlantic salmon, while brown trout often display partial migration where the populations consist of both anadromous (sea trout) and resident brown trout individuals (Klemetsen et al. 2003). In addition, brown trout is known for its broad diversity and flexibility of life history strategies. 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).

Connectivity between freshwater spawning and nursery habitat and marine feeding areas is essential to maintain Atlantic salmon populations and to preserve the life history diversity observed in brown trout populations. Salmonid spawners traversing thundering waterfalls is thus a living proof of a healthy ecosystem with an open two-way corridor between the small inland spawning stream and the high

seas. Unfortunately, many of the most spectacular animal migrations of the world have either disappeared or are declining due to impact from human activities (Wilcove and Wikelski 2008). Specifically, the construction of migration obstacles is responsible for the decline of many anadromous salmonid populations (WWF 2001).

2.2 Hydropower

Hydropower is the leading source of renewable energy worldwide and the main source of energy in Norway (Graabak et al. 2017). The low carbon emission makes it a vital component of our climate change mitigation strategy. Many hydroelectric power plants utilize and store water in large reservoirs in mountain regions while others are located within rivers, called run-of-the-river hydropower plants. The latter cannot store water and are subjected to seasonal flow variations.

Hydropower and its associated infrastructures have a large impact on the local environments and especially large water reservoirs, lead to habitat loss and fragmentation for both aquatic and terrestrial animal populations (Gibson et al. 2017). The environmental impacts from run-of-the river hydropower plants to aquatic ecosystems are often assumed to be negligible due to the smaller spatial footprint compared to reservoirs (Gibeau et al. 2017). However, run-of-the-river hydropower has the potential to substantially alter the aquatic environment by altering the flow regimes and disrupting connectivity in the river (Calles and Greenberg 2009; Poff et al. 1997). The latter includes halting up- and downstream movements of fish. This is critical for anadromous fish species that require unimpeded migration routes between marine environments and inland freshwaters several times during their lifespan. Accordingly, hydropower dams are regarded one of the major causes for salmonid population declines in Europe and North America (WWF 2001).

2.2.1 Mitigation measures at run-of-the-river hydropower plants

Historically, attention has been directed towards implementing measures to assist upstream salmonid spawning migration, and mitigation measures for descending fish were scarce (Larinier and Travade 1999). The goal of the early upstream measures was to facilitate fishing, spawning and recruitment in areas upstream of

the barriers. For almost a century, descendants of individuals aided upstream had to migrate through the turbine on their way to sea as smolts. Later, mortality of fish migrating through hydropower turbines was documented in a variety of rivers and turbine types (Coutant and Whitney 2000; Montèn 1985; Pracheil et al. 2016). Following this, measures to facilitate downstream migrants has attained increased focus (Larinier and Travade 1999; Calles et al. 2013a; Silva et al. 2017).

The small body size of salmonid smolts and their tendency to follow the main current downstream, impose design challenges to measures that prevent migration into turbine intakes. The most common method to overcome these challenges is to use a narrow-spaced racks which cover the turbine tunnel intake as a behavior or physiological barrier and guide the smolts towards a fish passage, often a surface gate that allow smolts to bypass the turbine tunnel (Larinier 2008; Larinier and Travade 1999). In old hydroelectric plants, not originally optimized for fish migration, retro- fitting fish passage constructions might be extra challenging and expensive (Ovidio et al. 2017). Due to this, more knowledge is needed on how to design measures that both minimize the cost related to retrofitting and maximize fish guidance.

2.3 Selection in anthropogenically altered environments

Evolution by natural selection has formed species and populations that are adapted to survive and successfully reproduce in a variety of environments. Natural selection happens at an individual phenotypic level while evolution is changes in a genotype or allele frequency in a population. Selection can be directional, disruptive or stabilizing. For selection to lead to evolution there must be enough trait variation among individuals, fitness differences associated with the trait and finally heritability of the traits (Endler 1986). In an anthropogenically altered world, animal populations adapt to human activity (Fugère and Hendry 2018; Hendry et al. 2017; Palumbi 2001). At present, climate change and habitat alteration expose species to extreme selection pressures, that ultimately may lead to extinction. Understanding the extent and consequences of such anthropogenic selection can contribute towards safeguarding healthy populations and securing biodiversity.

In fisheries research, there is an increasing body of evidence showing interaction between anthropogenic and natural selection processes, transforming the adaptive landscapes (i.e., Arlinghaus et al. 2008; Olsen and Moland 2011; Sutter et al. 2012). 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, combined impacts of natural selection and anthropogenic-induced selection may also be expected to act on fish living in hydropower-regulated ecosystems.

2.3.1 Hydropower infrastructure and mitigation measures as selective agents

Mitigation measures at hydropower dams aid up and downstream migration of fish to secure anadromous populations in regulated rivers. However, investigations of fish passage efficiency from a range of sites reveal a generally low overall efficiency (Noonan et al. 2012). It is widely recognized that upstream fish passages can be species and size-selective (Bunt et al. 2012; Mallen-Cooper and Brand 2007; Noonan et al. 2012) (Figure 1). For instance, such a size-selective fishway, led to loss of the largest size classes of Atlantic salmon spawners in Penobscot River (Maynard et al. 2017). On the contrary, construction of a fish ladder in the River Gudbrandsdalslågen led to stabilizing body-size selection favoring mid-sized brown trout in contrast to the pristine waterfall that induced directional selection, favoring larger individuals (Haugen et al. 2008). Even within the same size-group of brown trout, upstream fishways may induce selection on particular life history phenotypes, e.g. favoring anadromous phenotypes at the expense of freshwater resident adults (Lothian et al. 2020). Similar selective regimes are expected to happen at mitigation measures for descending fish, however studies that address this issue are still largely lacking.

Ineffective measures for descending smolts may divide a population, where one component migrates through the fish passage while others migrate through the turbine tunnel (Figure 1). Turbine migrants often experience higher mortality, and turbine-associated injuries make them more vulnerable to predation in the downstream river stretch (Ferguson et al. 2006; Muir et al. 2006; Pracheil et al. 2016). In nature, predator-prey interactions are major drivers of evolution

(Berryman 1992). Owing to the potential negative impact from turbines on migratory performance, hydropower infrastructure may change the underlying foundation for this predator-prey interplay. In general, a scenario where a smolt population migrate through both turbine tunnel and fish passage has the potential to induce contrasting selection regimes between individuals choosing different migratory paths to the ocean.

Atlantic salmon smolt migrations follow a relative rigid pattern, where descendence commences in spring, as a response to environmental triggers (Jonsson and Ruud-Hansen 1985). Following this, a model based upon river temperature has been shown to predict timing and duration of future runs (Haraldstad et al. 2017). Potentially, such models may provide useful tools for altering fish passage opening days to the smolt-run and concurrently maximize water allocations to turbines outside this time period. However, it is important to consider that other life stages require a safe migration past hydropower plants. Safe downstream migration of post-spawners is needed to secure repeat spawning in the following years. Sea-ward migration of post-spawners is reported to be risky and energy-intensive for steelhead (*Oncorhynchus mykiss irideus*) in the highly regulated Columbia River system (Wertheimer and Evans 2005) and likewise for Atlantic salmon and sea trout in other regulated rivers (Baktoft et al. 2020; Östergren and Rivinoja 2008). Downstream migration patterns of post spawners is overlapping, but not as rigid as seen in salmon smolts (Jonsson and Jonsson 2011a). The consequences of restraining emigration prone post-spawners upstream the dam pending the opening of a fish passage for smolt is uncertain. These issues require further investigations since repeat spawners may contribute significant to population resilience (Halttunen 2011; Moore et al. 2014).

Most fish passage facilities depend on certain fish behavior responses in order to function properly, such as repelling response to trash racks and/or attraction towards bypass channels. However, individual differences in response to guidance structures or preferences towards migration routes may lead to limited efficiency of these measures. Often, the different migration alternatives at hydropower plants have very different appearance: one being a submerged, dark and fenced turbine tunnel and the other a small surface fish passage channel. Individual differences in migration route choice might be a consequence of differences in physiological or

behavioural traits. Ineffective measures may thus have the potential to act as selective agents on traits associated with the migration route choice.

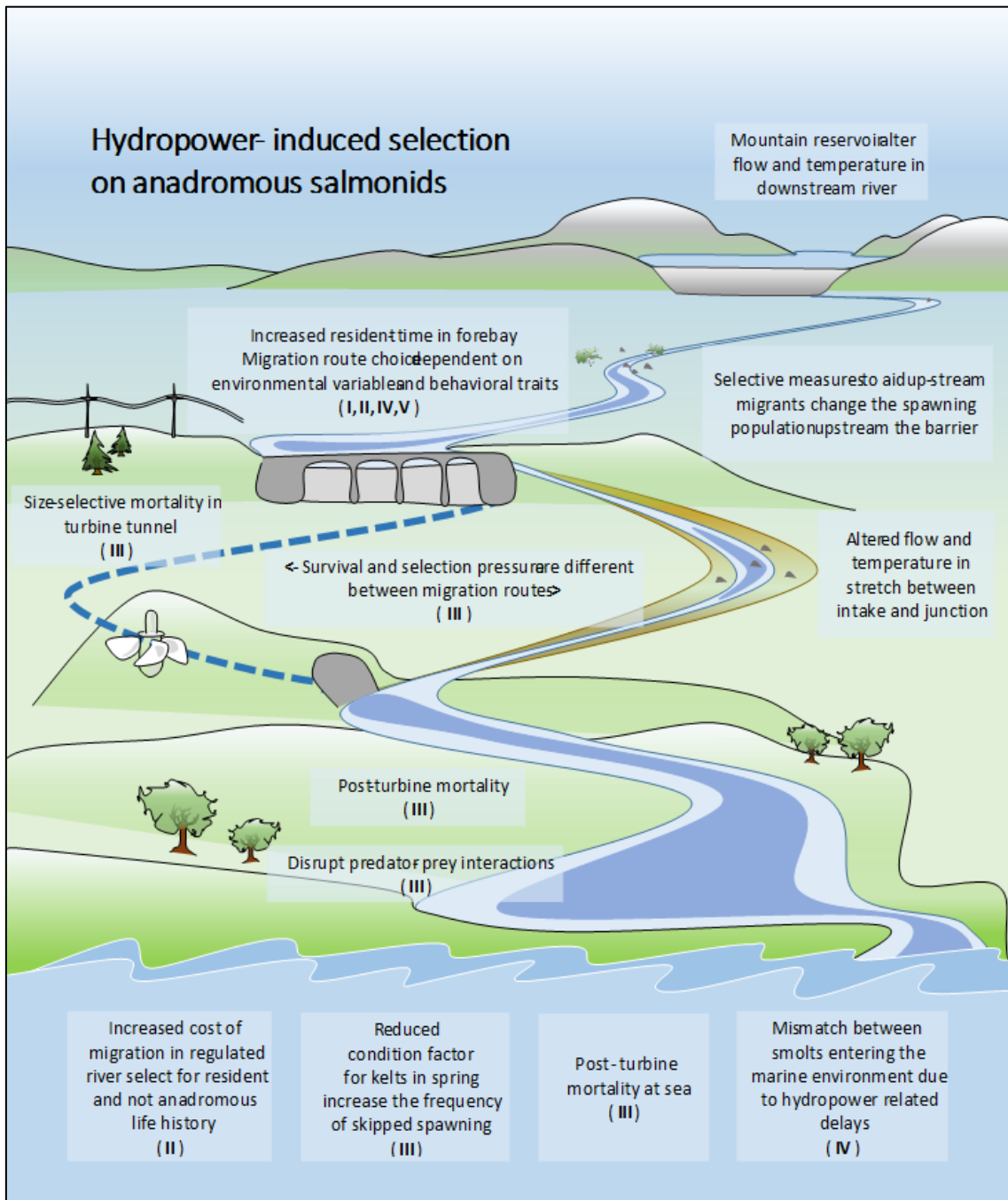


Figure 1 Graphical abstract of possible selective effects from hydropower on anadromous salmonid populations including concerns addressed in this thesis and papers (roman numbers).

3. Objectives

In this doctoral thesis, I evaluated the efficiency of mitigation measures for descending salmonids at run-of-the-river hydropower plants and studied if inefficient measures may induce selection on migratory Atlantic salmon and sea trout populations. The specific objectives were to:

- Evaluate the efficiency of retrofitted fish passages and examine common mechanisms to increase their effectiveness (**paper I and IV**).
- Study the consequences of restraining emigration prone post-spawned sea trout upstream of the dam pending the opening of a fish passage optimized for Atlantic salmon smolt run (**paper II**).
- Estimate river and sea survival for turbine and fish passage migrating smolts and study the possible difference in natural and human-induced selection processes linked to the migration route choice (**paper III**).
- Study if migratory passage structures have the potential to induce selection on behavioral traits in smolts and if individual differences in migration route choice is a consistent trait (**paper IV and V**).

4. Study sites

The studies presented in this thesis were conducted at Fosstveit hydropower plant in the River Storelva (**paper I, II, III, IV**) and at Rygene hydropower plant in the River Nidelva (**paper I, V**), both located in southern Norway and draining into coastal Skagerrak (Figure 2). The River Storelva is a small lowland river ($12 \text{ m}^3\text{s}^{-1}$), while the River Nidelva ($115 \text{ m}^3\text{s}^{-1}$) drains a catchment ten times larger, including large water reservoirs in the mountain areas. Both Rygene and Fosstveit are run-of-the-river hydropower plants located relatively close to the river mouth and downstream the natural migration barrier for Atlantic salmon. Both hydropower plants utilize water from small reservoir head races through Kaplan turbines.

At Rygene, an upstream fish ladder was constructed in the beginning of the 20th century and improved several times, while the first attempt to guide smolts away from the turbine inlet were initiated more than 100 years later in 2013 (Kroglund et al. 2013). During smolt migration, water is released through surface fish passage channels bypassing the turbine inlet. At both plants the fish passage is located perpendicular to the approaching flow on one side of the trash rack. The surface gates were originally designed to get rid of ice and debris that gathers on the rack, and not for fish migration purposes. At both facilities trash rack covers the turbine tunnel inlet, with a spacing of 80 mm between the vertical bars at Rygene and 50 mm at Fosstveit.

In Southern Norway, the majority of the hydroelectric powerplants were built in the mid-1900s, a period with heavy acidification and low Atlantic salmon abundance in many rivers (Sandøy and Langåker 2001). The River Nidelva lost their native Atlantic salmon population during this period while the River Storelva population probably survived due to sufficient water quality in tributaries draining through marine sediments. Spawners from the River Storelva were used as donors when a new salmon population was re-established in the River Nidelva following liming (Hesthagen et al. 2011). At present both rivers are limed to maintain water quality.

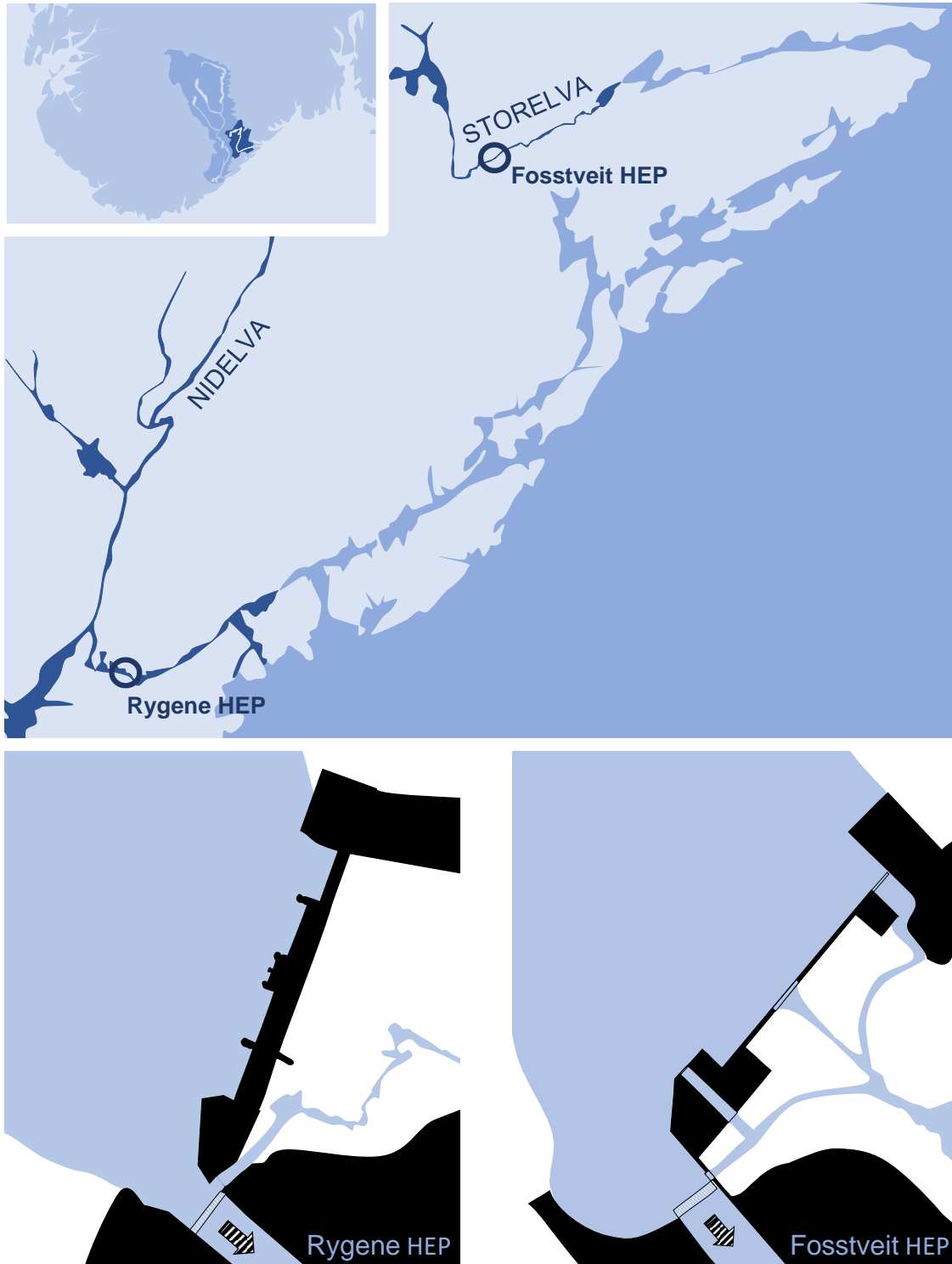


Figure 2 Catchment areas (upper left) and lower parts of the River Storelva and the River Nidelva holding anadromous brown trout and Atlantic salmon including Fosstveit and Rygene hydroelectric powerplant (HEP).

5. Methodological approach

All studies in this thesis are based on measuring or estimation of behavior and survival from individually tagged fish and the subsequent detections and recaptures in traps and antennas.

Wild Atlantic salmon and brown trout smolts were caught in rotary screw traps (**paper III, IV**), Wolf traps (**paper I, II, IV, V**) or fyke nets (**paper V**) (Chaput and Jones 2004; Wolf 1951). All of which are passive traps, that depend on fish actively moving downstream to get caught.

Fish were tagged with 23 mm passive integrated transponder (PIT) tags. The tags were implanted into anesthetized smolts (**paper I, III, IV, V**) through a small incision made ventrally between the posterior tip of the pectoral fin and the anterior point of the pelvic girdle, while in larger post-spawners, implantation was in the dorsal muscle tissue posterior to the dorsal fin (**paper II**).

The PIT-tags consists of a small microchip that is activated and emits a radio-frequency signal when it passes through an antenna-induced magnetic field transmitting a unique ID to a reader box that is connected to an antenna (Gibbons and Andrews 2004). The simple tag-construction makes it cheap compared to other telemetry tags on the market (acoustic or radio) and the lack of battery makes it possible to construct small, long-lasting tags. The tag features make them ideal for both individual and population studies of salmonids that migrate to the sea at a small body size and return to their home river to spawn several years later.

The movement pattern and survival of individual fish were recorded by multiple PIT-antennas and traps. Tagged fish that migrated through the fish passage were re-captured in a Wolf-traps and identified using a handheld PIT-reader (**paper I, V**) or in a swim through antenna loop mounted in the residual flow stretch between the dam and the turbine tail race (**paper I, III, IV**). The turbine migrants were detected in antennas and traps in the tail race (**paper I, III, IV**) or by snorkelling or observations from the riverbank (**paper II**). At Rygene hydropower plant, turbine migrants were not detected due to methodological limitation of PIT-antenna size and placement in such high-discharge / high-current tail-race area. Non-recaptured smolts were therefore assumed to be turbine migrants (**paper I,**

V). After the sea sojourn, returning spawners were registered by PIT-antennas in the river mouth (**paper II, III**).

In **paper V**, smolts caught in the Songeelva tributary represented individuals that were naive to the hydropower water intake, while smolt caught after migrating through the fish passage at Rygene hydropower plant represent fish passage experienced smolts. Smolts from the two catch-locations were PIT-tagged and released in the hydropower forebay.

To explore if behavioral characteristics affect migration route choice, as hypothesized in **paper IV**, smolts were subjected to three behavioural assays whereupon they were released in the hydropower forebay (**paper V**). Behaviour were scored in each of the following contexts: A basal locomotor activity (adapted from (Adriaenssens and Johnsson 2013; Dingemanse et al. 2007; Larsen et al. 2015)), response to net restrain (adapted from (Castanheira et al. 2013; Larsen et al. 2015)) and willingness to leave a familiar area (adapted from (Brown et al. 2007; Castanheira et al. 2013; Huntingford et al. 2010)). These assays were chosen because they have been used to characterize important aspects of behaviour in fish, such as basal activity pattern, escape response and risk-taking behavior.

6. Results and discussion

6.1 Evaluating retrofitted fish passages for descending fish at run-of-the-river hydropower plants

Paper I demonstrated that guidance efficiency increased as more relative river discharge is allocated to the fish passage irrespective of size of the hydropower plant (Figure 3). Tests of guidance efficiency of several surface gates in **paper IV** documented that it should be located as close to the intake trash rack as possible (Figure 4). Recommendations from these papers will be applicable in both large and small run-of-the-river hydropower plants and give scientific support to directions given in several national fish passage guidelines (Calles et al. 2013b; DWA 2005; Larinier and Travade 1999; Odeh and Orvis 1998; Turnpenny and O`Keeffe 2005). Moreover, the results from **paper I** show that total river discharge affected the guidance efficiency negatively, yielding low fish guidance efficiencies under flood-like events. Under such scenario smolt might have problems locating the fish passage due to changed flow patterns and decreased attraction towards the fish passage. Run-of-the-river hydropower plants cannot control river discharge due to the lack of water storage capacity. Sometimes, storage of water in upstream mountain reservoirs may be used to reduce river discharge during the smolt run period and thus improve the guidance efficiency (Fjeldstad et al. 2014). Following this, variable river discharges throughout the smolt-run period opens for a flexible water allocation on a day to day basis to increase both guidance efficiency whilst not spilling unnecessary amount of water for electricity production.

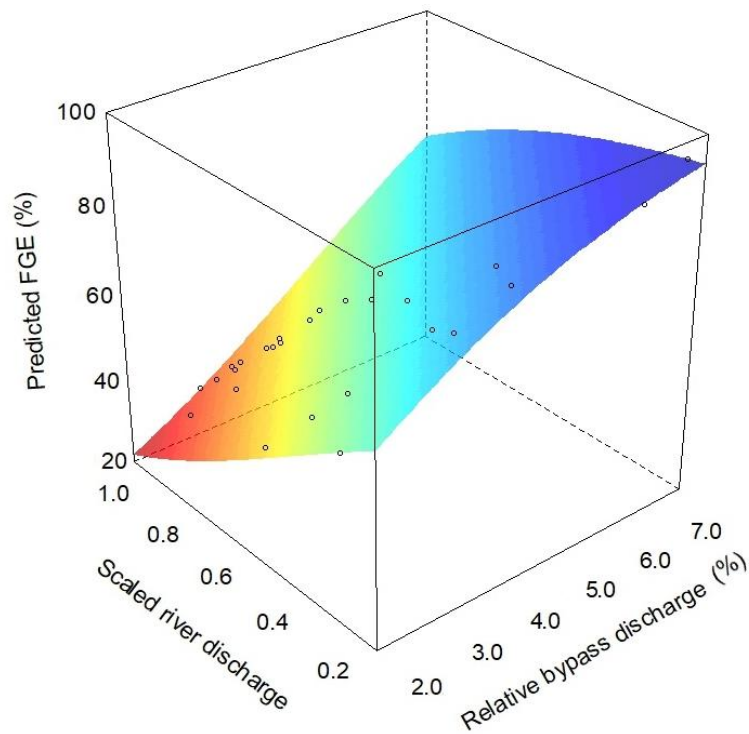


Figure 3 Predicted Fish Guidance Efficiency (FGE) for Atlantic salmon smolts at Fosstveit and Rygene hydropower plant as a function of relative river discharge (Q_{river}/Q_{HEPmax}) and relative fish passage discharge ($Q_{bypass}/Q_{turbine}$) derived from the selected binomial GLM reported in Table 3, paper I. Open circles represent different fish-release batches (**paper I**).

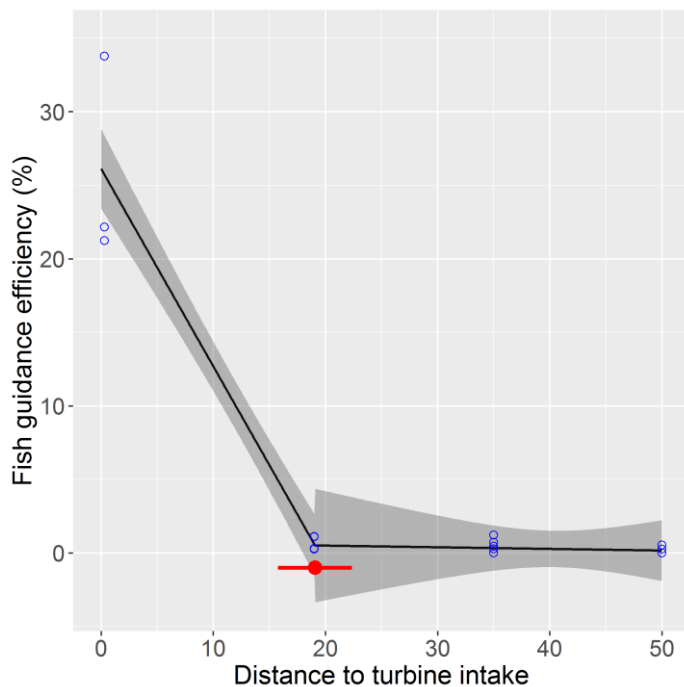


Figure 4 Predicted fish guidance efficiency for different surface gates in the hydropower dam as distance from the turbine intake (meter). Breakpoint estimate with corresponding standard error bars is shown in red. Shaded areas correspond to 95% confidence bounds (**paper IV**).

In **paper I**, it was demonstrated that smolt migration timing differed between the River Storelva and the River Nidelva even though the catchment areas are adjacent to one another. Measures that require water to be allocated away from turbines are often time-limited due to the economic costs associated with turbine water loss. Knowledge of river-specific smolt-run timing and duration is thus a valuable tool for management of measures in regulated rivers aiming at maximizing smolt descent survival and electricity production. However, it is important to consider that other species and life stages also require a safe migration past hydropower plants. This is especially true for post-spawners, because safeguarding descendance of these individuals secure future repeat spawning that contribution significantly to population resilience (Halttunen 2011). If fish passage opening days are optimized for Atlantic salmon smolt run, post spawned sea trout are faced with two options; migrating through the turbine tunnel with a following high mortality (**paper II**), or an anorectic wintering in the river with a resulting drop in condition factor (Baktoft et al. 2020). Furthermore, **paper II** demonstrated how low condition individuals have a higher probability of skip spawning because they need two growth seasons in coastal waters to regain energy for another spawning event. The increased cost of migration in regulated rivers may select towards a semelparous life history strategy or ultimately a reduction in an anadromous life history for the benefit of a resident strategy as described in whit-spotted char (*Salvelinus leucomaenis*) and steelhead (Morita et al. 2000; Waples et al. 2008). Temporary closing of fish passages, to increase electricity production, should be thoroughly assessed and based upon knowledge of migration patterns of local species and life history diversity.

Taken together, **paper I, II** and **IV** emphasize that mitigation measures need to be aligned to the specific location and to the specific behavior of the targeted species and their life stages.

6.2 Sub optimal mitigation measures at hydropower plants induce new selection regimes

For turbine migrating sea trout smolts, survival decreased with increasing smolt size (**paper III**, Figure 5). In contrast, smolts that used the fish passage and were predominately affected by natural selection during their river descent, were characterized by higher survival of larger individuals. In general, survival to the river mouth were significantly lower for turbine migrants than fish passage migrants. This is probably due to turbine blade strike and increased predation from Northern pike (*Esox lucius*) experienced by turbine emigrants. These findings highlight how migration route choice at a hydropower intake effect both survival and selection pressure during smolt migration in the river.

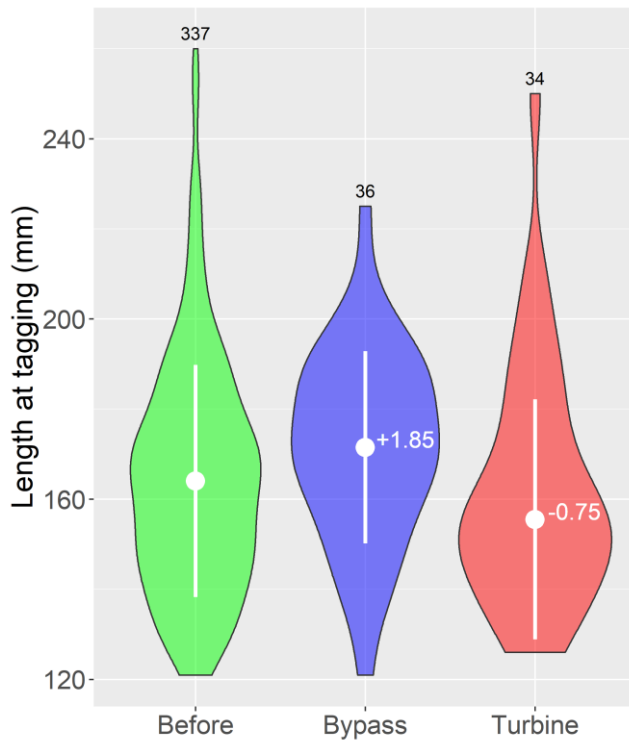


Figure 5 Individual lengths at tagging observations for all upstream Fosstveit HEP dam brown trout smolt individuals (i.e., before choice of migration route) along with tagging length measurements of confirmed (at PIT and/or RST in river mouth) surviving individuals of bypass migrants and turbine migrants. 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 (**paper III**).

The migration-route choice at hydropower water intakes appear crucial for individual survival (**paper III**). Both **paper I** and **V** documented that increased water allocation could increase the number of smolts migrating through the fish passage. Thus, in **paper V**, individuals with former fish passage experience had, under similar discharge conditions, a significantly higher probability of making the same migration route choice again compared to their naive counterparts. This finding demonstrates that the route choice is partly a consistent trait and strengthens the hypothesis that the migration route preference is partly based on individual trait variation, and not environmental aspects alone. The higher survival for fish passage migrants than turbine migrants opens for selection on traits associated with migration route choice.

Paper IV documented that some smolts migrated into the turbine tunnel almost instantly, while others hesitated and stayed in the forebay for days to weeks until a suitable alternative migration route became available. Given the appearance of the powerplant water intake, a submerged dark fenced tunnel inlet, it was hypothesized that turbine migrants and hesitating individuals represented different behavior types. Most mitigation measures depend on certain fish behavior responses to function and will thus potentially act as selective agents. Following this hypothesis, smolts were scored in behavior assays before release upstream a hydropower plant in **paper V**. Smolts with high activity pattern had a higher probability of finding the fish passage (Figure 6). This lends support to the hypothesis that differences in behavioural phenotypes effect route preferences of Atlantic salmon smolt at hydropower water intakes.

The significant difference in survival related to the migration-route choice (**paper III**) opens for selection on behavior traits associated with the choice (**paper IV, V**). Personality differences are important for maintaining stability, resilience, and persistence of populations and the genetic component makes it an important dimension of biodiversity (Cordero-Rivera 2017; Wolf and Weissing 2012).

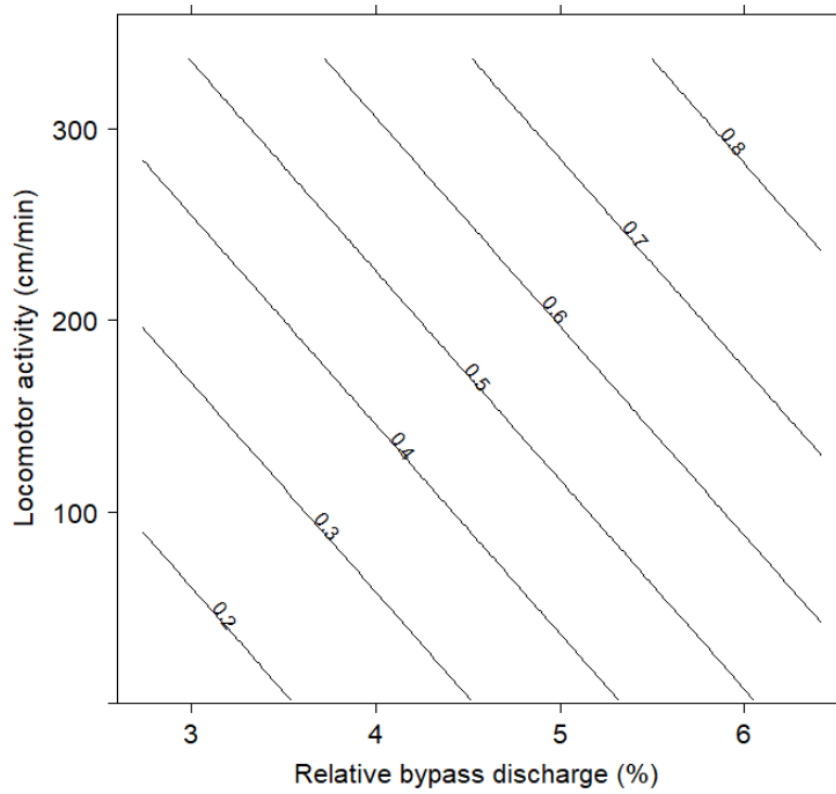


Figure 6 Predicted fish passage migration probability for Atlantic salmon smolts at Rygene hydropower plant as a function of locomotor activity (distanced swam per min during the 20 min activity assay) and percent discharge allocated to the fish passage in relation to the turbine tunnel. Probability predictions, displayed as isolines, were derived from the most supported binomial GLM, as reported in Table 2, paper V (paper V).

7. Conclusions

Guidance efficiency increased as more relative river discharge is allocated to the fish passage and tests of efficiency of several surface gates documented that it should be located as close to the intake trash rack as possible. Moreover, the results show that river discharge affected the guidance efficiency negatively, yielding low guidance under flood-like events.

Predictions of smolt-run timing and duration can be used to optimize opening days aiming at maximizing smolt descent survival and electricity production. However, temporary closing of fish passages outside smolt-run periods negatively affects other life stages like post-spawners. The high mortality and increased cost of migration in regulated rivers may select towards a semelparous life history strategy at the expense of repeat spawners. The results emphasize the need for strategies to safeguarding descendance of post spawn individuals to secure future repeat spawning that, in turn, contribute to population resilience.

The data demonstrate differences in survival and size selection regimes between turbine and fish passage migrating smolts. For turbine migrants, survival decreased with increasing smolt size. In contrast, smolts that used the fish passage were characterized by higher survival of larger individuals. In general, survival to the river mouth were significantly lower for turbine migrants than fish passage migrants. These findings highlight how migration route choice at a hydropower intake effect both survival and selection pressure during smolt migration in the river. In addition, data show that migration route choice is a partly consistent trait and that individuals with higher activity had a higher probability of using the fish passage than the turbine tunnel. Potentially, the lower survival for turbine migrants opens for selection on behavior traits.

Selection on several traits is expected to act on fish living in hydropower regulated ecosystems, leading to an altered evolutionary pattern that might impact population viability. Hydropower-induced selection might remove traits favorable in other part of the salmonid life cycle leading to reduced overall production. Thus, accounting for hydropower-induced selection that goes against natural selection processes is therefore important to incorporate in management strategy of anadromous salmonids in regulated rivers.

8. Future perspectives on hydropower-induced selection

In the present thesis, aspects of hydropower induced selection on downstream migrating salmonids were addressed. Thus, there are several parts of hydropower induced selection not covered in this thesis (Figure 1). Several studies address both species (Bunt et al. 2012; Mallen-Cooper and Brand 2007), size (Haugen et al. 2008; Maynard et al. 2017) and life-history (Lothian et al. 2020) selection posed by mitigation measures for upstream migrants. However, the probable numerous indirect selective effects from an altered flow and temperature regimes in regulated rivers are still lacking (Angilletta et al. 2008; Waples et al. 2008).

In general, hydropower systems alter the aquatic environment and therefore the selection regimes experienced by salmonids. In addition, many of the traits under selection, have been shown to have a heritable component (Waples et al. 2008). Thus, the long-term evolutionary effects on populations are still unknown. Tracing such an effect is probably further complicated by the migratory life history of many salmonids. They encounter very different environments and selective pressures during their life span and hydropower-induced selection is probably restricted in space and time. More knowledge is needed on how hydropower-induced selection affects fitness.

Evolution is not always a long-term process. Rather, it can occur on contemporary time scales, within decades. These are timeframes that are relevant to most conservation plans. Accounting for hydropower-induced selection that goes against natural selection processes should therefore be an important component of a sustainable management strategy of anadromous salmonids in regulated rivers.

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10. Papers I-V

RESEARCH ARTICLE

Common mechanisms for guidance efficiency of descending Atlantic salmon smolts in small and large hydroelectric power plants

Tormod Haraldstad^{1,2}  | Erik Höglund^{1,2} | Frode Kroglund³ | Thron Oddvar Haugen⁴ | Torbjørn Forseth⁵

¹Section for aquaculture, Norwegian Institute for Water Research – NIVA, Grimstad, Norway

²Department of environment, Centre of Coastal Research, University of Agder, Kristiansand, Norway

³County Governor of Aust- and Vest-Agder, Arendal, Norway

⁴Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

⁵Aquatic Ecology Department, Norwegian Institute for Nature Research – NINA, Trondheim, Norway

Correspondence

Tormod Haraldstad, Norwegian Institute for Water Research – NIVA, N-4879 Grimstad, Jon Lilletuns vei 3, Grimstad 4879, Norway. Email: tormod.haraldstad@niva.no

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Abstract

Dams and turbines associated with hydroelectric power plants (HEP) disrupt connectivity by affecting fish movement and survival. There has been an increasing focus on measures to facilitate downstream migration at HEPs. The fish guidance efficacy (FGE) of downstream mitigation measures largely remains suboptimal and calls for development of knowledge on factors influencing FGE. In this study, we analyse 6 years of wild Atlantic salmon smolt passive integrated transponder (PIT)-telemetry data ($N = 1,498$) from a neighbouring small- and a large-scale HEP. Timing of the smolt migration period was significantly different between the two rivers. Thus, river-specific smolt-run timing is imperative for proper measures management in regulated rivers aiming at maximizing smolt-descent survival. A generalized linear model including additive effects of relative bypass discharge and scaled river discharge on the FGE for descending smolts received highest Akaike's information criterion support in the data and explained 74.2% of the FGE variation. This model, including no river effect, predicted high FGE (up to 90%) at low river flow ($\leq 30\%$ of HEP maximum capacity) when 7% of the water is allocated through the bypass. Many run-of-the-river HEPs have highly variable river flow during the smolt-run period. Our model suggests that these HEPs could utilize their manoeuvre flexibility to obtain water allocation routines between bypass and turbines that optimize both FGE and hydroelectric production.

KEYWORDS

bypass, fish guidance efficiency, passive integrated transponders, run-of-the-river, salmonids

1 | INTRODUCTION

Atlantic salmon (*Salmo salar*) migrates between spawning and nursery habitats in rivers and feeding areas at sea. To complete an anadromous life cycle, Atlantic salmon requires unimpeded migration routes between these two environments: both as smolts descending from upper-reach nursery areas in the river towards oceanic feeding areas and as returning adults ascending from the oceanic areas towards the upper-reaches spawning areas (Jonsson & Jonsson, 2011). Dams associated with hydroelectric power disrupt connectivity by affecting fish movement and survival (Thorstad et al., 2012). In accordance,

dams are regarded one of the major causes for Atlantic salmon population declines in Europe (Forseth et al., 2017; Parrish, Behnke, Gephard, McCormick, & Reeves, 1998; WWF, 2001).

The mortality associated with passage of hydroelectric power plants (HEPs) facilities can be both direct and indirect (Kynard & O'Leary, 1993; Nyqvist et al., 2016; Östergren & Rivinoja, 2008). Mortality from turbine blade strikes is a direct effect (Montèn, 1985), whereas minor injuries and nonlethal trauma may lead to delayed mortality (Mesa, Poe, Gadowski, & Petersen, 1994; Muir, Smith, Williams, & Sandford, 2001). In addition, migratory fish may be delayed by dams and suffer elevated energetic costs, loss of migration motivation, and

reversion of physiological adaptation, and the match between completion of migration and the time of appropriate arrival conditions may be disrupted (Marschall, Mather, Parrish, Allison, & McMenemy, 2011; Nyqvist et al., 2016). Also, the upstream reservoirs created by the dam may reduce smolt survival for two reasons: They are a challenge for downstream navigation of smolt, and predation is typically higher in dam reservoirs due to provisioning of a more predator-friendly habitat (McLennan, Rush, McKelvey, & Metcalfe, 2018; Schwinn, Aarestrup, Baktoft, & Koed, 2016).

Initially, the main efforts on fish passage over dams focused on upstream migrations to facilitate upstream fishing and ensure spawning and recruitment. However, recently, there has been an increasing focus on measures to facilitate downstream migration of fish (Calles, Rivinoja, & Greenberg, 2013; Silva et al., 2017). Despite these efforts, the fish guidance efficacy of downstream mitigation measures remains suboptimal (Ovidio et al., 2017), and many downstream bypass systems have poor overall functioning (Coutant & Whitney, 2000; Johnson & Dauble, 2006).

In Southern Norway, the majority of the HEPs were built in the mid-1900s, a period with heavy acidification and low Atlantic salmon abundance in many rivers. Therefore, mitigation measure for descending smolts was typically not considered or constructed. Re-establishment or recovery of salmonid populations following liming (Hesthagen, Larsen, & Fiske, 2011) has boosted activities on retrofitting downstream migration facilities for fish in this region (e.g., Fjeldstad et al., 2012). The main objective of such measures is to safe-guide fish past dams and HEP intakes with minimum delays.

The small body size of Atlantic salmon (typically 12–17 cm) smolts and their tendency to follow the main current downstream impose design challenges to measures that prevent migration into turbine intakes. The most common method to overcome these challenges is to mount small-spacing racks at the turbine intake and provide access to an adjacent bypass (Larinier, 2008; Larinier & Travade, 1999). Typically, in such measures, there is a trade-off between water used for power production and water needed for fish bypass redirection. Moreover, retrofitting bypasses in old hydroelectric plants, not originally optimized for fish migration, might be extra challenging (Ovidio et al., 2017). It can be difficult to perforate a hole in the concrete structure of the dam to create a new bypass route, or one might be forced to use a flood gate with suboptimal location. In addition, replacement of a new small-spaced angled trash rack is complicated and often requires more space than the original rack. In general, retrofitting fish mitigation measures in old plants is challenging and expensive. Due to this, more knowledge is needed on how to design measures that both minimize the cost related to retrofitting and maximize fish guidance.

Substantial information and guidelines related to fish passages exist in the grey literature (Calles et al., 2013; DWA, 2005; Turnpenny, Struthers, Hanson, & Unit, 1998), reporting fish passages efficiency to be strongly related to the specificity, configuration and typology of the HEP site. Still, general knowledge about guidance efficiency of fish passages is needed for optimizing survival of descending smolts. In this study, we analyse passive integrated transponder (PIT)-telemetry data from a small- and a large-scale HEP to explore and quantify how river flow and bypass discharge dynamics affect fish guidance efficiency of descending Atlantic salmon smolts.

2 | MATERIALS AND METHODS

2.1 | Study area

The Rygene HEP is located in River Nidelva, whereas the Fosstveit HEP is located in River Storelva, both in the county of Aust-Agder, southern Norway (Figure 1). The two rivers differ largely in catchment size, where Nidelva catchment is 10 times larger than that of Storelva. Fosstveit HEP is the only power plant in the Storelva catchment, whereas River Nidelva has several power plants in the main river. In addition, the catchment of River Nidelva contains large water reservoirs in the mountain areas that can alter river flow and if necessary store large amounts of water. Both Rygene and Fosstveit HEPs are run of the river and use water from a small river reservoir head race through Kaplan turbines. The Kaplan turbines, however, differ largely in both size, head, and capacity (Table 1). During smolt migration, water is released through a surface bypass. At both plants, the bypass is located perpendicular to the approaching flow on one side of the trash rack. The bypass gates were originally designed to get rid of ice and debris that gather on the rack and not for fish migration purposes. At both facilities, the flow through the bypass can be manipulated quite easily. At Rygene, there is a hydraulic engine that controls the gate, whereas the bypass at Fosstveit has to be operated manually by adding or removing logs that covers the gate.

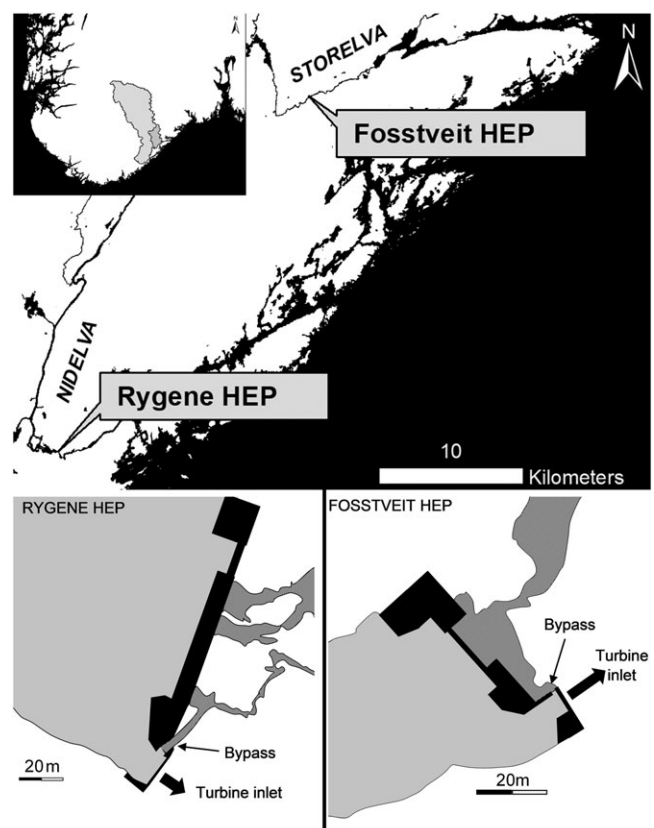


FIGURE 1 River catchment areas (upper left) and lower parts of the River Storelva and the River Nidelva with schematic diagram of the two hydroelectric plants at Rygene (down left) and Fosstveit, including locations of turbine inlet and bypass channels. HEP: hydroelectric power plant

TABLE 1 Characteristics of the hydroelectric plants at the Rygene HEP (River Nidelva) and the Fosstveit HEP (River Storelva)

		Rygene HEP	Fosstveit HEP
Discharge	Average river (Q_{river})	115 m ³ s ⁻¹	12 m ³ s ⁻¹
	Capacity (Q_{HEPmax})	170 m ³ s ⁻¹	16 m ³ s ⁻¹
Head		38 m	14.5 m
Turbine	Type	Kaplan	Kaplan
	Blades	5	4
	Rotation	167 rpm	330 rpm
	Outer diameter	4.56 m	1.65 m
Trash rack			
	Spacing	80 mm	50 mm
	Areal (LxW)	15.5 m × 9 m	4.3 m × 5.9 m

Note. HEP: hydroelectric power plant.

2.2 | Fish sampling

Downstream-migrating wild Atlantic salmon smolts were caught by a Wolf-trap in the bypass channel (Wolf, 1951). The smolts were anaesthetised with benzocaine (30 mg/L) before being tagged internally with PIT tags (23 mm, half duplex, Oregon RFID; Table 2) and released upstream the power plant after 1 day of recovery. Recycling of individuals is commonly used for these kind of studies (Calles, Karlsson, Hebrand, & Comoglio, 2012; Scruton et al., 2007). Tagged smolts that migrated in the bypasses were detected at PIT-antennas (TIRIS RI-CTL MB2A; Oregon RFid, USA) and hand held PIT-readers (smolt recaptured in Wolf-traps). The Wolf-traps covered the entire water column in the bypass channel with a spacing of 11 mm, which gives a catch efficiencies close to 1 for smolt bypass migrants. Non-recaptured fish were assumed to be turbine migrants, due to recapture difficulties of turbine migrants in the tailrace area.

2.3 | Data analyses

The statistical software R (R Core Team, 2016, version 3.2.5) was used for data inspection and statistical analyses. Linear models were used to estimate and test potential differences in smolt length and migration timing between River Storelva and River Nidelva. The probability of

TABLE 2 Number of PIT-tagged wild Atlantic salmon smolts at the Fosstveit HEP (River Storelva) and the Rygene HEP (River Nidelva) divided into release batches at different years

Year	Location	PIT-tagged Atlantic salmon smolts released upstream the hydroelectric power plants	Number of release batches
2010	Fosstveit	253	2
2011	Fosstveit	174	4
2012	Fosstveit	185	4
2013	Rygene	202	5
2014	Rygene	208	8
2016	Rygene	476	4
Sum		1,498	27

Note. HEP: hydroelectric power plant; PIT: passive integrated transponder.

bypass migration (fish guidance efficiency) for the two facilities combined was estimated by fitting candidate generalized linear models (GLMs; McCullagh & Nelder, 1989) with river temperature, bypass discharge (Q_{bypass}), relative bypass discharge ($Q_{\text{bypass}}/Q_{\text{turbine}}$), and river discharge as predictor variables. Due to the large difference in discharge between the two rivers, and also in order to get a more general model, discharge was scaled in relation to the power plant capacity ($Q_{\text{river}}/Q_{\text{HEPmax}}$). In order to explore eventual non-linear effects from discharge on guidance efficiency (exploring eventual minimum/maximum effects), candidate models including a second-degree polynomial effects were also fitted. In order to explore if the scaled discharge (i.e., $Q_{\text{river}}/Q_{\text{HEPmax}}$) was a more parsimonious (and general) way to estimate river-specific discharge effect on fish guidance efficacy, we fitted alternative models where scaled discharge was substituted with river location (as a factor effect). The logit link function was used for linearization of the binomial response (0 = not recaptured; 1 = recaptured in bypass). Model selection was based on corrected Akaike's information criterion (AICc; Akaike, 1974; Anderson, 2008), and adjusted R^2 for GLM was estimated using methods suggested in Zhang (2017).

3 | RESULTS

A total of 10,201 wild Atlantic salmon smolts were caught in the bypass Wolf-traps at Rygene and Fosstveit during the 6-year study period (2010–2014, 2016). The smolt migration period started in late April and coincided with increasing river temperatures and, in most years, decreasing river discharges for both the River Storelva and the River Nidelva (Figure 2). The mean river temperature in May was 1.5°C higher in River Storelva than in River Nidelva in the 2010–2016 period. Timing of the smolt migration period was significantly different between the two rivers ($p < 0.05$) and earlier in River Storelva. In addition, the smolt lengths differed ($p < 0.05$), with average smolt length at 142.2 ± 15.9 mm in the River Storelva and 151.4 ± 15.2 mm in the River Nidelva (Figure 3).

Of 27 batches of smolts that were released during the 6-year study period, highest guidance efficiency was achieved at Fosstveit HEP with two batches above 90%, whereas the highest at Rygene HEP was 77%. Five smolt release batches had guidance efficiency below 40%, including two from Fosstveit and three from Rygene. Lowest guidance efficiency was documented at Rygene in 2013, with one batch achieving 28%.

To look more closely at the fish guidance efficiency, all fish-release batches from the two rivers were pooled and used in a GLM with river temperature, bypass discharge (Q_{bypass}), relative bypass discharge ($Q_{\text{bypass}}/Q_{\text{turbine}}$), and scaled river discharge ($Q_{\text{river}}/Q_{\text{HEPmax}}$) as candidate predictor variables. AICc-based model selection revealed highest support of additive effects of relative bypass discharge and scaled river discharge on the guidance efficiency for Atlantic salmon smolts at the two hydroelectric plants (i.e., $\text{Pr}[\text{bypass migration}] = Q_{\text{bypass}}/Q_{\text{turbine}} + Q_{\text{river}}/Q_{\text{HEPmax}}$; Table 3). This model explained 74.2% of the guidance efficiency variation and attained an AICc-score 0.19 lower than the second ($Q_{\text{bypass}}/Q_{\text{turbine}} * Q_{\text{river}}/Q_{\text{HEPmax}}$), and 0.44 units lower than the third-most supported model

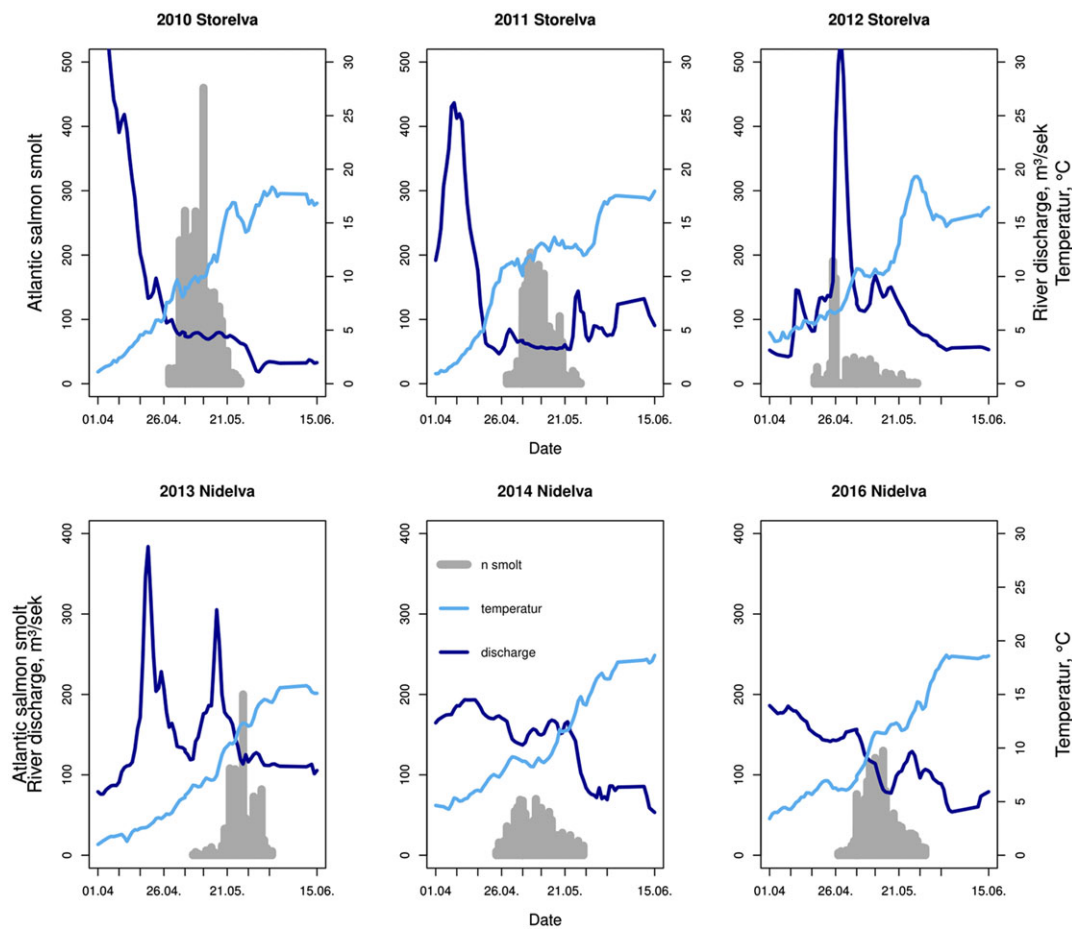


FIGURE 2 Daily catches of untagged smolts in the bypass at the Fostveit hydroelectric power plant (HEP; 2010–2012) in the River Storelva and the Rygene HEP (2013, 2014, and 2016) in the River Nidelva, as well as river flow and temperatures during the migration period [Colour figure can be viewed at wileyonlinelibrary.com]

($Q_{\text{bypass}}/Q_{\text{turbine}} + Q_{\text{bypass}}$; Table S1). The selected model predicted highest guidance efficiency when the relative discharge in the bypass was high and the total river discharge was low, and lowest at flood-like events with additional low relative bypass discharge (Figure 4). Typically, scaled river discharges would have to be $\leq 30\%$ and relative bypass discharges $>6.7\%$ in order to attain fish guidance efficiencies at 90% and beyond. When substituting the $Q_{\text{river}}/Q_{\text{HEPmax}}$ -part of the two most supported models with river location, these substituted models received little support attaining ΔAICc of 3.97 and 6.44, respectively.

4 | DISCUSSION

High bypass discharge in relation to the turbine discharge seems to be a key success factor for the fish guidance efficiency of Atlantic salmon smolt bypasses at hydropower intake both at small and large run-of-the-river plants. During optimal conditions, over 90% of the smolt used the bypass as migration route past the hydropower dam. Findings in our study indicate that 7% of the turbine discharge needs to be allocated to the bypass to secure that 90% of the Atlantic salmon smolts migrate through the bypass. Recommendations regarding relative bypass flow are available from several national fish

passage guidelines (Calles, Degerman, et al., 2013; Larinier & Travade, 1999; Turnpenny & O'Keeffe, 2005). The U.S. Fish and Wildlife Service (Odeh & Orvis, 1998) advocates for a minimum bypass attraction flow of 5% where the rack is oriented perpendicularly to the flow, like the bypasses in the present study. Due to annual variation in ice melting periods and precipitation, several Norwegian run-of-the-river HEPs have highly variable turbine discharges throughout the smolt-run period. These sites may utilize their manoeuvre flexibility to vary the bypass discharge during the smolt-run period to increase both guidance efficiency and not spilling unnecessary amount of water for electricity production.

In addition to the positive additive effect of relative bypass discharge, river flow affected the guidance efficiency negatively, yielding low fish guidance efficiencies under flood-like events. Spring floods are common in Atlantic salmon rivers throughout the distribution range, and in some areas, they coincide with the smolt-run period (Hvidsten, Jensen, Vivås, Bakke, & Heggberget, 1995). This might decrease the potential for high guidance efficiency. Run-of-the-river HEPs cannot control river discharge due to the lack of water storage capacity. Sometimes, storage of water in upstream mountain reservoirs may be used to reduced river discharge during the smolt-run period and thus improve the bypass guidance efficiency (Fjeldstad, Alfredsen, & Boissy, 2014).

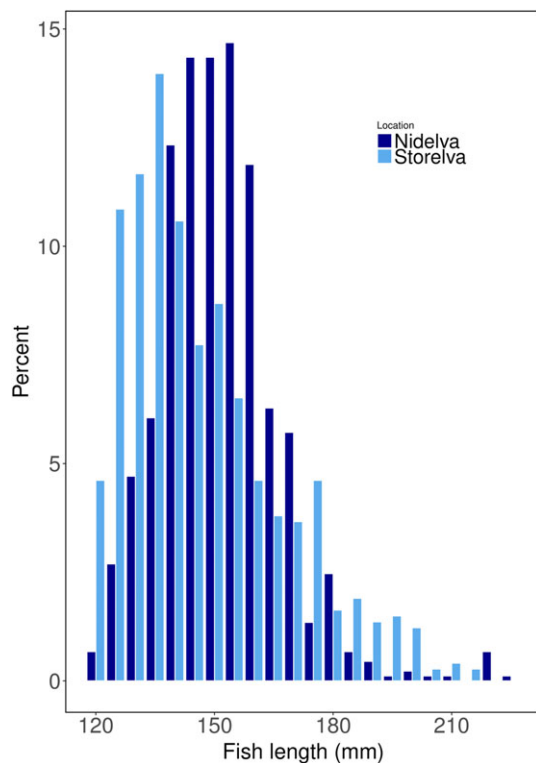


FIGURE 3 Length distribution for passive integrated transponder-tagged Atlantic salmon smolts caught at Fosstveit hydroelectric power plant (HEP), Storelva (blue), and Rygene HEP, Nidelva (dark blue) [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

Retrofitting mitigation measures for fish migration in old hydroelectric plants, not originally optimized for this, might be extra challenging (Ovidio et al., 2017). The bypass gates at Rygene and Fosstveit are good examples of this dilemma, as they originally were designed to get rid of ice and debris that accumulate on the rack, and not for fish migration purposes. The fish guidance efficiencies at these sites can probably be improved by actions proven to have positive effects of fish guidance efficiencies in other studies (Calles, Degerman, et al., 2013; Larinier & Travade, 1999). Examples of such modifications or retrofitting include reducing rack spacing so the smolts cannot pass through, angled racks, decreasing turbulence at bypass entrances, reducing acceleration of the water into the bypass, and reducing the amount of upwelling water at the bypass entrance. In general, retrofitting fish mitigation measures in old plants is challenging and expensive. Due to this, more knowledge is needed on how to design measures that both minimize costs related to retrofitting and maximize fish guidance efficiency.

TABLE 3 Logit-parameter estimates and corresponding likelihood-ratio test statistics for the most supported GLM fitted to predict bypass probabilities in PIT-tagged Atlantic salmon smolts from Storelva and Nidelva

Parameter estimates			LR-test statistics			
Term	Coeff.	SE	Effect	df	χ^2	p
Intercept	0.09602	0.292	$Q_{\text{bypass}}/Q_{\text{turbine}}$	1	101.972	<0.001
$Q_{\text{bypass}}/Q_{\text{turbine}}$	40.139	6.292	$Q_{\text{river}}/Q_{\text{HEPmax}}$	1	97.194	<0.001
$Q_{\text{river}}/Q_{\text{HEPmax}}$	-2.140	0.224				

Note. GLM: generalized linear model; PIT: passive integrated transponder. $Q_{\text{bypass}}/Q_{\text{turbine}}$ = relative bypass discharge, $Q_{\text{river}}/Q_{\text{HEPmax}}$ = Scaled river discharge. $R^2_{\text{adj}} = 0.742$ (Zhang, 2017).

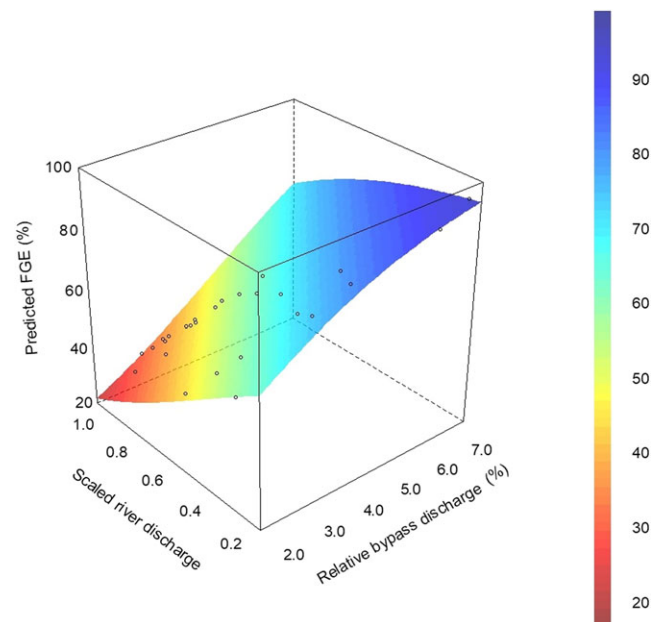


FIGURE 4 Predicted fish guidance efficiency (FGE, %) for Atlantic salmon smolts as a function of scaled river discharge ($Q_{\text{river}}/Q_{\text{HEPmax}}$) and relative bypass discharge ($Q_{\text{bypass}}/Q_{\text{turbine}} \cdot 100$) derived from the selected binomial generalized linear model reported in Table 3. Open circles represent different fish-release batches [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

Smolt migration timing differed between River Storelva and River Nidelva even though the catchment area is adjacent to each other. The difference in smolt-run timing between the two rivers studied may be related to the difference in catchment size and altitude distribution where the Nidelva catchment is 10 times larger than that of Storelva and also includes more mountain areas. Due to this, mean river temperature in May is 1.5°C higher in Storelva than in Nidelva. River temperature is found to be an initial trigger for the annual smolt-run timing in River Storelva (Haraldstad, Kroglund, Kristensen, Jonsson, & Haugen, 2016), and this might be the case in Nidelva as well. Measures that require water to be allocated away from turbines are often constrained by time restrictions due to the economic costs associated with lowered electricity production induced by water loss. By improving knowledge about smolt-run timing improvements of both timing and duration of water allocation measure may be achieved. Lack or not use of such knowledge may result in delayed smolt migration and/or smolt migration through turbine tunnels and thus high mortality rates. Knowledge of river-specific smolt-run timing is therefore instrumental for proper

management of measures in regulated rivers aiming at maximizing smolt descent survival.

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ORCID

Tormod Haraldstad  <http://orcid.org/0000-0002-9575-5144>

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SUPPORTING INFORMATION

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Condition-dependent skipped spawning in anadromous brown trout (*Salmo trutta*)

Tormod Haraldstad, Erik Höglund, Frode Kroglund, Anders Lamberg, Esben Moland Olsen, and Thronoddvar Haugen

Abstract: Repeat spawners of anadromous salmonids may contribute significantly to population resilience by providing multiple cohorts to both seawater and freshwater life stages. In this study, winter survival of sea trout (*Salmo trutta* Linnaeus, 1758) post spawners (kelts) was 89%. Sea survival increased linearly with female length with a return probability between 30% and 50%, whereas males attained a maximum return probability of 60% at 520 mm. Of the returning sea trout, 40% skipped spawning and they had significantly lower condition factor as kelts compared with those who returned after one summer. These results suggest that sex-specific differences in individual post-spawning growth–survival trade-off exist and that energetic status of descending kelts may influence the probability to skip spawning. We discuss to what extent hydropower may reduce post-spawning survival due to blocking of river descent opportunities, potentially altering the fitness landscape and favouring new life-history adaptations. From a management perspective, it is concluded that it is crucial to maintain connectivity in regulated rivers, allowing fish to complete repetitive spawning and feeding migrations, thus contributing to population productivity.

Résumé : Les salmonidés anadromes qui fraient plus d'une fois pourraient faire une contribution importante à la résilience des populations en fournissant des cohortes multiples aux stades tant marins que d'eau douce du cycle biologique. Dans l'étude, le taux de survie hivernale des truites brunes (*Salmo trutta* Linnaeus, 1758) vides était de 89 %. La survie en mer augmentait de manière linéaire avec la longueur des femelles, la probabilité de retour oscillant entre 30 % et 50 %, alors que les mâles atteignaient une probabilité de retour maximum de 60 % à 520 mm. Des truites brunes qui effectuaient un retour, 40 % ne frayaient pas et elles présentaient un facteur d'embonpoint significativement plus faible que les truites vides qui retournaient après un été. Ces résultats donnent à penser qu'il existe des différences selon le sexe sur le plan des compromis individuels entre la croissance et la survie après le frai et que l'état énergétique des truites vides en dévalaison pourrait influencer la probabilité de sauter un frai. Nous abordons l'ampleur de la réduction de la survie après le frai que pourrait causer la production hydroélectrique en bloquant des occasions de dévalaison, modifiant potentiellement le paysage adaptatif et favorisant de nouvelles adaptations du cycle biologique. Du point de vue de la gestion, nous concluons qu'il est crucial de maintenir la connectivité dans les rivières régularisées pour permettre aux poissons de terminer leurs migrations répétitives d'alimentation et de frai et ainsi contribuer à la productivité des populations. [Traduit par la Rédaction]

Introduction

In anadromous salmonids, repeat spawners may play an important role in population dynamics by increasing both total recruitment and the long-term stability of a population (Halttunen et al. 2011; Moore et al. 2014). They represent a genetic contribution of a particular year class to the stock over a number of years, thereby safeguarding against years of reproduction failure (Niemelä et al. 2000). However, their positive impacts are often neglected in management strategies of salmonid populations in regulated rivers.

The majority of salmonid species, except for the Pacific salmon (*Oncorhynchus*), are iteroparous, meaning that they can spawn several times after sexual maturity (Taylor 1991). Anadromous salmonids that survive spawning are commonly referred to as kelts. These individuals migrate to sea soon after spawning in late autumn or may overwinter in the river and return to the sea the following spring (Aarestrup and Jepsen 1998; Bendall et al. 2005).

It has been hypothesised that river size and the presence of suitable habitats such as deeper pools and lakes may favour riverine overwintering instead of brackish or seawater overwintering (L'Abée-Lund et al. 1989; Östergren and Rivinoja 2008). In addition, individual energy reserves may affect migratory timing. For example, Halttunen et al. (2013), showed a positive relationship between timing of sea emergence and condition factor in Alta River Atlantic salmon (*Salmo salar* Linnaeus, 1758) kelts. The authors hypothesised that kelts with higher condition factor can afford to stay longer in the safer but less productive river environment. Generally, the life history of anadromous brown trout (*Salmo trutta* Linnaeus, 1758), hereafter referred to as sea trout, is more flexible than in Atlantic salmon. The mechanisms underlying individual sea trout variability in the duration of the sea sojourn, migration timing, and the number of spawning returns to the river is poorly understood (Thorstad et al. 2016).

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T. Haraldstad* and E. Höglund. Norwegian Institute for Water Research (NIVA), N-4879 Grimstad, Norway; Centre for Coastal Research, University of Agder, N-4604 Kristiansand, Norway.

F. Kroglund. County Governor of Aust- and Vest-Agder, N-4809 Arendal, Norway.

A. Lamberg. Scandinavian Nature Surveillance Ltd., N-7055 Ranheim, Norway.

E.M. Olsen. Centre for Coastal Research, University of Agder, N-4604 Kristiansand, Norway; Institute of Marine Research (IMR), N-4817 His, Norway.

T.O. Haugen. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway.

Corresponding author: Tormod Haraldstad (email: tormod.haraldstad@niva.no).

*Present address: Jon Lilletuns vei 3, 4879 Grimstad, Norway.

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When iteroparous fish such as the sea trout do not use each spawning opportunity after sexual maturity, this is often referred to as skipped spawning (Rideout et al. 2005). This phenomenon has been described for several fish species including Atlantic salmon (Jonsson et al. 1991). Spawning migration and gonad development are energy-consuming processes, and animals commonly adjust their reproductive investment to maximize lifetime reproductive success (Jørgensen et al. 2006; Wootton and Smith 2014). Skipped spawning in sea trout may be common, and a proximate driver may be incomplete recovery from last year's spawning or differential energy allocation between somatic growth and gonad development (Skjæraasen et al. 2012). Skipped spawning may also reflect an adaptation resulting from the ultimate trade-off between individual growth, future reproduction, and survival (e.g., Stearns 1992; Roff 2002).

Natural selection on skipped spawning is likely determined by a trade-off between growth benefits and survival costs resulting from postponing future reproduction. By skipping spawning, the extra year of marine somatic growth may increase future reproduction potential in both males and females by increasing egg size in females and by improving fighting abilities over access to female partners (L'Abée-Lund and Hindar 1990; Labonne et al. 2009). The strength of this trade-off will change as future survival probability decreases over age, due both to natural causes and to harvesting (e.g., Aarestrup et al. 2015). In natural populations of sea trout, one may therefore expect to find non-linear size and age effects on the probability to skip spawning, as seen in other fish species (e.g., Jørgensen et al. 2006).

Dams, e.g., associated with hydropower production, affect fish movement and survival in many watercourses (Katopodis and Williams 2011). The effects can result directly from turbine blade strikes when fish migrate through the turbine tunnel or indirectly by delaying migratory fish (Coutant and Whitney 2000; Nyqvist et al. 2017). The most commonly used method to facilitate bypass of fish at small- to medium-sized European hydroelectric plants is to prevent the fish from entering turbines using trash racks and at the same time giving them access to an adjacent escape route allowing them to proceed downstream (Larinier and Travade 2002; Larinier 2008). Potentially, there might be high benefits from protecting kelts at power plant intakes because of their contribution to population productivity (Ferguson et al. 2008). Data on survival in river and sea of repeat spawning sea trout from regulated rivers are few. In addition, few studies have considered the possible change in selection regime induced by hydropower that might influence survival and migration timing of sea trout kelts.

The aims of the present study were to investigate if there is a relationship between the condition factor, size, and the probability of skipped spawning of sea trout kelts and to quantify winter survival rate of post-spawned sea trout in a regulated river and the subsequent sea sojourn survival.

Materials and methods

Study area

The River Storelva, Norway (N58°40'9.99; E8°58'48.99; Fig. 1), has been regulated for hydroelectric power production since 2008. Fosstveit hydroelectric plant (HEP) is a run-of-the-river plant located 6 km above the river mouth. It utilizes a 14.5 m high waterfall, and the power-generating water comes from a small river reservoir head pond through one Kaplan turbine (330 rpm, 16 m³s⁻¹). The Kaplan turbine is a propeller-type water turbine that has adjustable blades and is widely used for electrical power production. The water is led back into the river through a tunnel tailrace, leaving a by-passed stretch between the dam and the downstream tunnel tailrace. There is no water in this river stretch during winter, except during short-term flooding episodes when the water discharge exceeds the power plant intake capacity. Dur-

ing fish migration periods (spring, summer, and fall), approximately 0.5 m³ s⁻¹ is released in bypasses and (or) fish ladders to secure descending smolts and ascending sea trout and Atlantic salmon to feeding and spawning areas, respectively. At the tunnel inlet, there is a 25 m² trash rack with 50 mm spacing mounted at a 70° angle from the vertical. A concrete wall covers the uppermost 0.5 m to avoid icing on the rack during winter. At the tunnel inlet, there are also two bypass routes for fish migrating downstream; one surface bypass mainly for salmonid smolts and one submerged bypass (at 6 m depth) mainly for maturing European eel (*Anguilla anguilla* (Linnaeus, 1758)).

The sea trout population in River Storelva has been monitored for several years, and the smolts descend during April and May, with an average total length ranging from 150 to 190 mm (Haraldstad et al. 2017). The most common strategy is to stay two growth seasons at sea before returning to spawn for the first time (Haraldstad and Güttrup 2015). The sea trout caught in the Skagerak coastal area, which the Storelva catchment belongs to, range from 2 to 8 years with females in excess (64%) (Olsen et al. 2006). The average growth increase during the first growth season at sea is around 150 mm and decreases with increasing age of the fish.

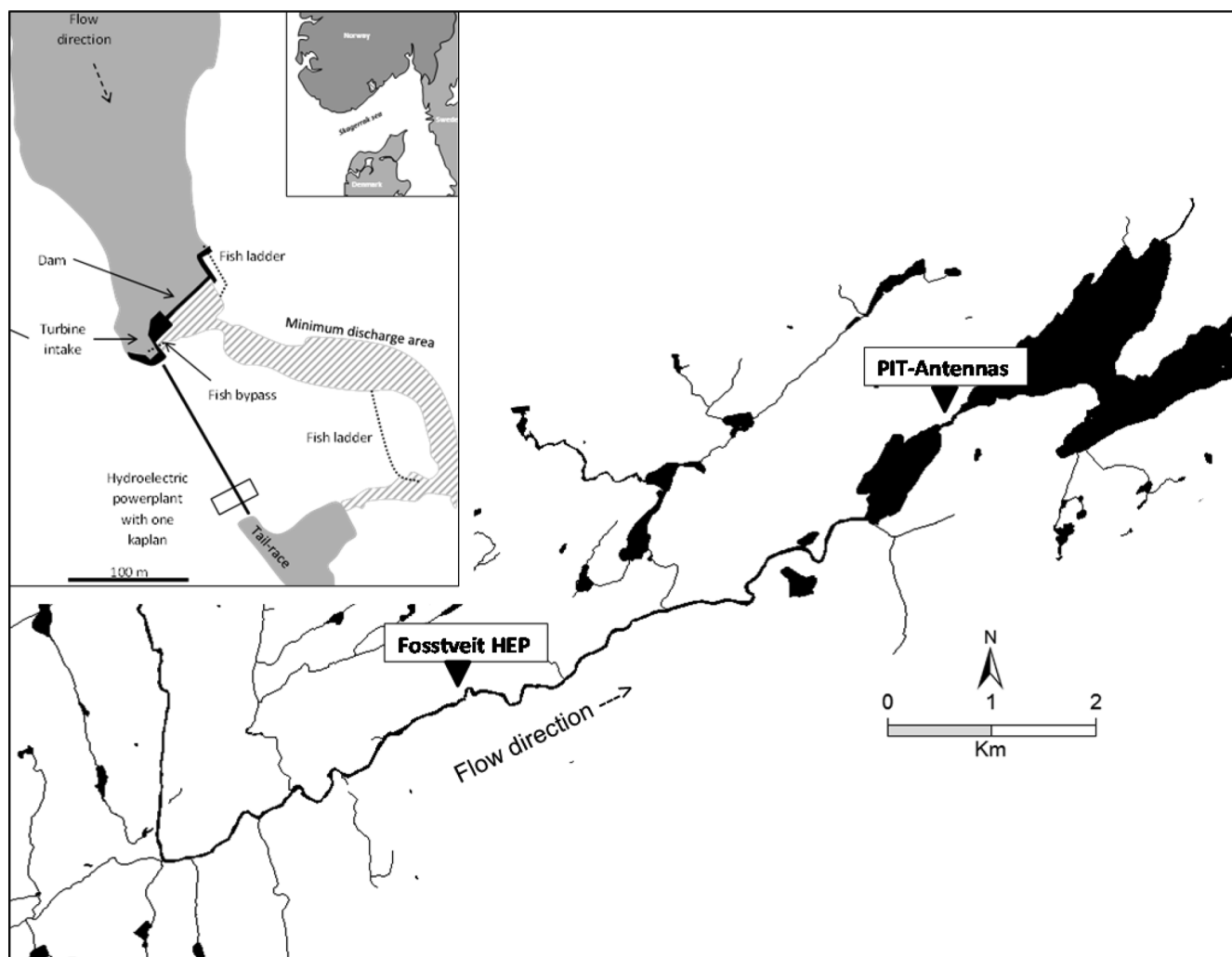
Fish sampling

Sea trout migrating upstream were counted in the fish ladders at Fosstveit in spring to autumn 2011 (1 May – 6 November). The fish counter comprised an underwater video camera, a light source, and a recorder with a trigger device mounted in the last ledge of the ladder (Svenning et al. 2017). On the hard disk of the video recorder, both video clips (approximately 2 frames per second) triggered by the counter and time lapse recording were stored. The time lapse recording was analysed manually to ensure that no fish could pass without being registered.

During the autumn, post-spawned sea trout could migrate downstream through the turbine tunnel or through the submerged bypass designed for maturing European eel. In addition, the dam crest was overflowed twice (total of 12 days) during winter. Except for these short-term flooding episodes, no water ran in the surface bypass or in the former course of the river between the power plant intake and the tailrace during winter. The surface bypass (shape: rectangular, width: 43 cm, depth: 20 cm) was opened 10 April, adjusted 20 April (depth: 33 cm) and closed 1 July in 2012. Turbine-migrating kelts that were killed were recorded in the tail-race area by snorkelling or observations from the river-bank every second day. Moribund fish observed were landed to prevent duplicate counts. Conditions for visual inspection are good due to clear water (1–2 FNU, Formazin Nephelometric Units) and small surveillance areas (10 m wide and 0.2–1.0 m depth). These count data represent a minimum estimate of turbine-induced mortality.

The descending kelts that used the surface bypass in spring 2012 were counted in a trap tank. A total of 195 post-spawners of sea trout 487 ± 69 mm (mean total length ± standard deviation (SD)) were anesthetized with benzocaine (25 mg L⁻¹), measured for total length and total mass, and ID-tagged with passive integrated transponder (PIT) tags (23 mm, half duplex, Oregon RFID, Portland, USA). The tag was implanted in the dorsal muscle tissue posterior to the dorsal fin using a PIT-tag-injector. Owing to the sexual dimorphism in sea trout (Monet et al. 2006), most individuals (*n* = 176, sex ratio: 120 females to 56 males) were also sexed based on external characteristics (mouth morphology, oviduct, shape of anal fin). Fish condition *K* was estimated from Fulton's condition factor, $K = W/TL^3 \times 10^6$, where *W* = total mass (g) and *TL* = total body length (cm). We acknowledge that Fulton's condition factor is not a perfect way of describing the actual physical state of the post-spawned fish. The Fulton's condition factor could be different between sexes at the same length. In addition, it may change with the fish length so that larger fish are favoured by the formula (expecting higher *K* for larger fish). To address this latter problem,

Fig. 1. River Storelva with the PIT antennas in the river mouth and a schematic diagram of the Fosstveit Hydroelectric power plant (HEP) located 6 km upstream from the river mouth.



we replaced K with a size-adjusted condition metric in the GLM analysis, although this gave no changes in the main results.

Fish movements were detected using two swim-through PIT-antennas located upstream the river mouth during 2012–2015. The antenna station consisted of two swim-through antennas (Haraldstad et al. 2017). The river was 9 m wide and 0.9 m deep. The two swim-through antennas were set 2.5 m apart and wired to two remote tuner boards, one for each antenna. The two tuner boards were connected to an antenna reader box (TIRIS RI-CTL MB2A; Oregon RFID, USA) and supplied with a 12V battery. When a tagged fish passed through the antenna loop tag number, antenna number, date, and time were recorded and logged by the reader box. Swimming direction was determined from consecutive detections at the two antennas. Migration speed (km day^{-1}) was calculated from release at Fosstveit HEP to detection in the river mouth PIT-antennas.

Data analyses

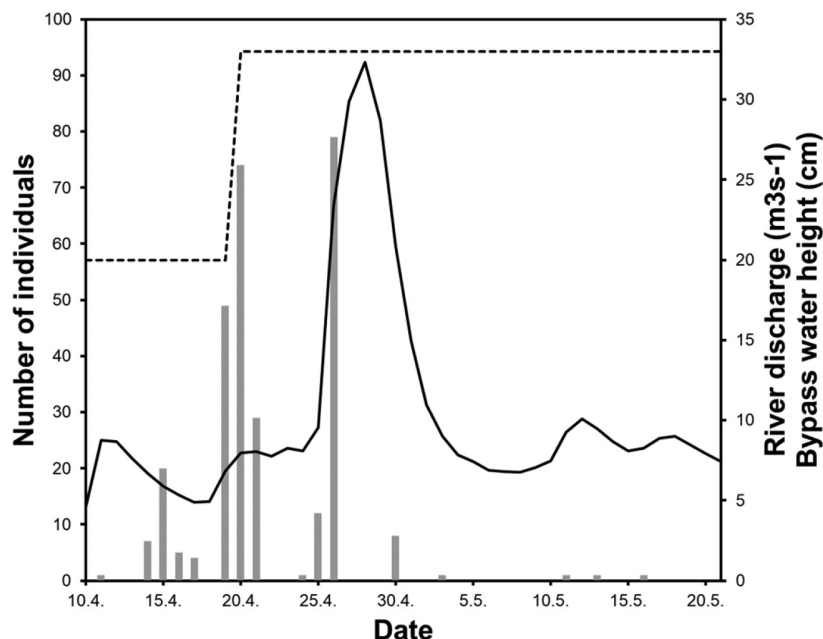
The statistical software R (R Core Team 2016) was used for data inspection and statistical analyses. Over-winter survival and turbine-passage mortality were estimated by fitting generalized linear models (GLM, binomial response with logit link function). Based on number of registered survivors (i.e., re-sighted in PIT antenna assigned as “1”) and number of non-recaptures (i.e., not

re-sighted in PIT antenna, assigned as “0”), the number of turbine-related dead recoveries and number of non-recaptures were calculated, respectively (GLM: McCullagh and Nelder 1989). The timing of downstream migration in relation to body condition, sex, and body length was estimated using linear models (LMs). The probability of surviving and returning to the stream after a sea sojourn was estimated using GLM fitting candidate models including sex, body length, and body condition as predictor variables. To explore eventual non-linear effects (e.g., due to stabilizing or disruptive selection) from size on return probability, candidate models including TL^2 effects were also fitted. The reason for including quadratic effects of size is to open for not only directional selection, but also disruptive and stabilizing selection. Model selection was based on the corrected version of Akaike’s information criterion (AICc, Akaike 1974; Anderson 2008). For the subset of fish that survived at sea and returned to the stream, a similar GLM approach was used to estimate the probability of skipped spawning. Here, individuals returning after one summer at sea were assigned the response value of “0” and those returning later were assigned the response value of “1”.

Results

During summer and autumn, at least 341 sea trout entered the fish ladder at Fosstveit whereas 305 kelts were registered descend-

Fig. 2. Number of descending sea trout kelts through the surface bypass (columns), river discharge (black line), and water height in the surface bypass (black dotted line) at Fosstveit HEP during spring 2012.



ing the following spring yielding an over-winter river survival of 89.4% (standard error (SE) = 1.7). Of these over-wintering sea trout, 26 individuals were found dead in the tailrace area. Because no dead individuals were encountered upstream the dam, turbine migration accounts for a minimum of 72.2% (SE = 7.5, 26 out of potentially 36 descendants) of the mortality during this period. The spring descent of sea trout kelts at Fosstveit occurred during 10 April to 16 May and included two distinct migration peaks. The first peak was during 19–21 April 2012 ($n = 152$) co-occurring with the day when the water depth in the bypass channel was increased from 20 to 33 cm. The second migration peak ($n = 91$) coincided with heavy rainfall on 25 April and a resulting increase in river discharge peaking the following night (Fig. 2). There was no significant relationship between the sea trout's condition factor and timing of downstream migration (LM, $P = 0.292$).

Model selection yielded highest support for an interaction effect between sex and length at tagging (including a second-degree polynomial) on the probability of surviving and return to the river after a sea sojourn (i.e., $\text{Pr}(\text{return}) = \text{sex} \times \text{TL}^2$, Supplementary Table S1¹). The most supported model (Table 1) predicted return probability to increase linearly with female kelts length at tagging, yielding predicted return probabilities between 0.3 and 0.5 (Fig. 3). For males, the model predicted a sharp increase in return probability, from 0 to 0.6, for length at tagging between 420 to 520 mm and a similarly sharp probability decrease, from 0.6 to 0, for sizes above 520 mm (Fig. 3).

The average time spent at sea was 119 ± 40 and 134 ± 32 days (\pm SD) for male and female sea trout, respectively, that returned during first summer (60%, $n_{\text{males}} = 11$, $n_{\text{females}} = 25$). For sea trout that skipped spawning and returned during the second summer (40%, $n_{\text{males}} = 6$, $n_{\text{females}} = 19$), males and females spent 472 ± 51 and 456 ± 33 days at sea, respectively. No tagged kelts skipped two consecutive spawning seasons and returned during the third summer.

Model selection yielded highest support for (lowest AICc) an interaction effect between tagging length and condition factor

Table 1. Logit-parameter estimates and corresponding likelihood ratio test statistics for the most supported GLM fitted to predict return probabilities in PIT-tagged sea trout kelts from Storelva.

Parameter estimates			Likelihood ratio test statistics			
Term	Coefficient	SE	Effect	df	χ^2	p
Intercept	-155.892	71.467	TL ²	2	2.4599	0.2923
TL	5.965	2.793	Sex	1	2.0325	0.1540
TL ²	-0.057	0.027	Sex \times TL ²	2	12.667	0.0018
Sex (female)	154.406	71.897				
TL (female)	-5.951	2.813				
TL ² (female)	0.057	0.027				

Note: df, degrees of freedom; TL, total length at tagging (mm).

(including a second-degree polynomial) on the probability of skipped spawning (Table 2; Supplementary Table S2). The selected model predicted small individuals with low condition factor to have the highest probability for skipped spawning, and the lowest probabilities were predicted for both small and large high-condition individuals (Fig. 4). Individuals between 450 and 520 mm attained probabilities around 0.5 of skipped spawning, irrespective of condition factor.

Discussion

This study found that up to 40% of the sea trout skipped spawning. These individuals had a lower condition factor as kelts during the spring migration compared with the sea trout that returned to spawn the following autumn. In Atlantic salmon, the higher energetic costs to regain reserves needed for spawning a second time could explain the increased tendency to skip spawning in large (multiple years at sea) compared with small (1 year at sea) fish (Jonsson et al. 1991). Similarly, energy-demanding spawning migration have been demonstrated to be an important factor contributing to skipped spawning in pelagic species such as Atlantic cod (*Gadus morhua*) (Jørgensen et al. 2006). Generally, in sea trout,

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0076>.

Fig. 3. Predicted return probabilities in PIT-tagged sea trout kelts from Storelva as a function of tagging length and sex. Shaded areas represent the 95% confidence bounds for the corresponding colour. Upper points represent tagging lengths of returning individuals and lower points represent the corresponding non-returning individuals (females as red, small points). Predictions derive from the most supported return-rate model provided in Table 1. [Colour online.]

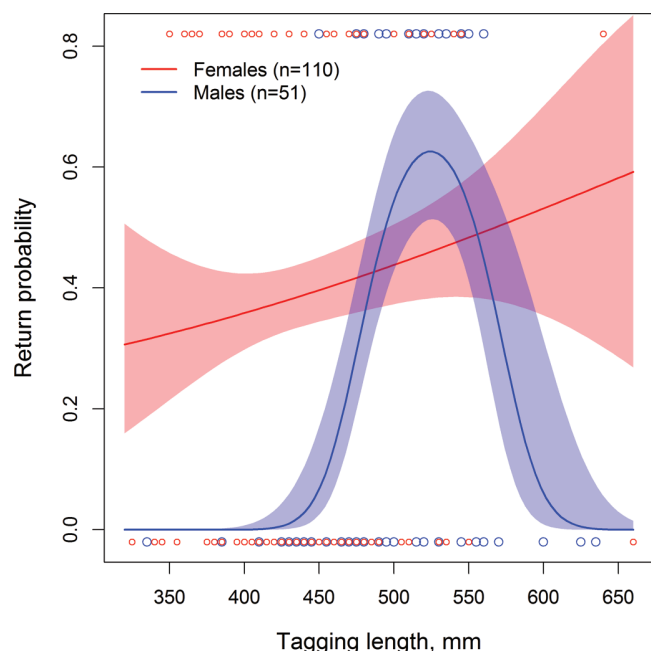


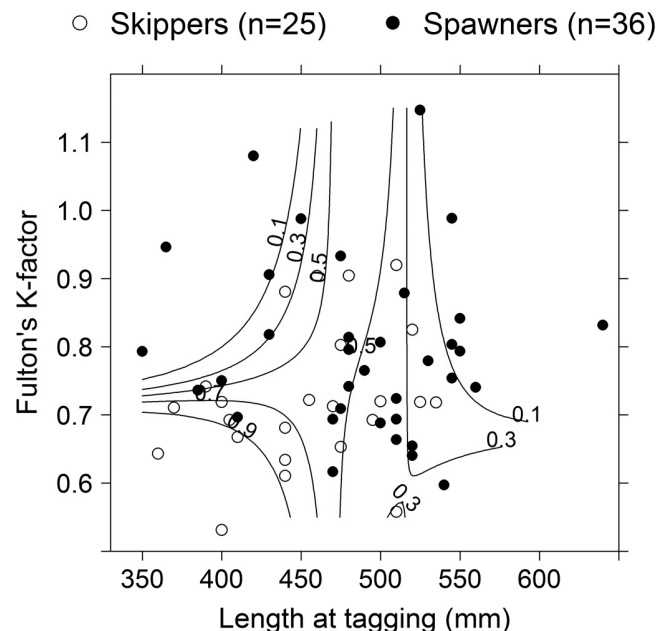
Table 2. Logit-parameter estimates and corresponding likelihood ratio test statistics for the most supported GLM fitted to predict probabilities to return after one summer at sea in PIT-tagged sea trout kelts from Storelva.

Parameter estimates			Likelihood ratio test statistics			
Term	Coefficient	SE	Effect	χ^2	df	<i>p</i>
Intercept	-804.6	483.3	TL ²	8.209	2	0.017
TL	3.245	2.002	K	5.227	1	0.022
TL ²	-0.0033	0.0021	TL ² × K	7.721	2	0.021
K	1138.0	657.7				
TL × K	-4.619	2.723				
TL ² × K	0.0047	0.0028				

Note: The probabilities are conditional on an eventual return to spawn and that the individuals are detected during the return. df, degrees of freedom; TL, length at tagging (mm); K, Fulton's condition factor.

migration to spawning grounds and development of gonads are energy consuming. Consequently, annual spawning may lead to low fecundity due to incomplete recovery from last year's spawning. The time and energy required for reproduction may be better channelled into growth and survival to increase future success rather than intensifying already low energy reserves by spawning in the current year. This is supported by observations that older and larger individuals are often caught in open sea (Knutsen et al. 2001), indicating that they use these areas for feeding throughout the year (Knutsen et al. 2004; Olsen et al. 2006), not returning until the energy reserves needed for spawning are restored. However, Eldøy et al. (2015) found that long-distance sea trout migrants had poorer body condition in spring prior to sea migration but returned earlier to freshwater than short- and medium-distance sea migrants. Our results, showing a negative relationship between condition factor and probability to skip spawning, do not support such earlier return of "poor body condition sea trout". On the

Fig. 4. Predicted Storelva sea trout kelt probability of skipped spawning as a function of tagging length and condition factor. Probability predictions, displayed as isolines, were derived from the selected binomial GLM, as reported in Table 2. Note that the probabilities are conditional on an eventual return after seaward migration. Filled points represent individuals returning after one summer at sea and open points display skipped spawners.



contrary, our results lend support to the mechanism proposed by Jørgensen et al. (2006), where it was suggested that skipped spawning was a strategy to regain energy needed for spawning, which in the long run could maximize lifetime reproductive success.

In the present study, estimated river survival of the kelts was 89.4%. These findings are in accordance with other studies that report high post-spawn survival for sea trout, though only in unregulated rivers (Berg and Jonsson 1990; Bendall et al. 2005). A 10-year study from Vardnes River in northern Norway estimated minimum survival rates in freshwater to be between 66% and 74%. In northern Sweden, Östergren and Rivinoja (2008) documented an overwintering survival of 92% in the unregulated parts of the river; although during the spring descent, passage mortality at the two power stations were 69% and 25%. The head pond that often results from regulating rivers can provide suitable overwintering habitats and high overwinter survival. However, the overall post-spawn survival of kelts may be reduced in such regulated rivers due to mortality associated with migration and dam passages.

The majority of the estimated river mortality in our study was attributed to migration through the turbine tunnel, and that turbine migration occurred in periods when the surface bypass was closed. Furthermore, in the present study, increased emigration rate coincided with time when the minimum depth in the bypass increased from 20 to 33 cm and a following increase in river discharge. This result indicates that water flow and bypass design constitute important factors for optimizing bypass efficiency of kelts, as also shown in other studies (Wertheimer and Evans 2005; Arnekleiv et al. 2007).

In sea trout populations, there is considerable diversity in life-history strategies. For example, kelts may migrate from the river just after spawning or choose to overwinter in rivers unaffected by hydroelectric power plants (Jonsson and Jonsson 2009). This raises questions about the population consequences of restrain-

ing emigration-prone fish in rivers as the inevitable drop in condition factor resulting from this practice may (Cunjak and Power 1987; Jonsson and Jonsson 2009), as we show in this study, increase the probability of skipped spawning. Life-history studies show that postponement of reproduction events is sensitive towards changes in pre- and post-reproduction survival schedules (Stearns 1992; Roff 2002). As a large fraction of the post-spawning river mortality found in our study could be attributed to turbine passage when the bypass was closed, this stresses the importance of a proper management of river power plant bypass routes. In particular, knowledge about population consequences of restraining fish by temporarily locking bypass passages is needed.

A high amount of kelts returned to River Storelva after the sea sojourn, and the estimated sea survival was in accordance with other studies that have documented survival of kelts from one spawning to another to be 30%–50% in a French river (Euzenat 1999) and 58–68% in northern Norway (Berg and Jonsson 1990). The sea survival for this life stage is higher than sea survival of virgin migrants, which is assumed to be a bottleneck in the anadromous salmonids life cycle (Klemetsen et al. 2003; Jonsson and Jonsson 2009).

Moreover, in the present study, there was a significant positive effect of body length on sea survival in females and males smaller than 520 mm, where small males had very low survival compared with similarly sized females. The male size-specific sea survival curve was curved with an optimum at 520 mm. This may be indicative of a more pronounced trade-off between individual growth, future reproduction, and survival in males than females (Stearns 1992). However, results pertinent to sizes beyond a TL of 570 mm should be interpreted with caution as they rest upon few observations ($n = 5$). In addition, the tagged kelt in our study were not aged from, for example, scale samples. It is possible that senescence could be an explanation for the observed decrease in survival probability for male sea trout with lengths greater than 520 mm. As in our study, Aarestrup et al. (2015) recently documented a positive trend in the body length and sea survival relationship of sea trout kelt. The generally higher survival of kelts than virgin migrants and the positive relationship between length and survival within kelt populations may, for instance, be attributed to size-biased predation on sea trout at sea (e.g., Wootton 1998); however, data on sea trout predation are not available from our system. Because the size-specific sea survival differs between sexes in our study system, one may suggest the two sexes to have differential behaviour and (or) habitat use during the post-spawning sea sojourn. To our knowledge, no data on sex-specific distribution or behavior of sea trout kelts at sea exist (Drenner et al. 2012). We encourage future studies on sex-specific post-spawning sea trout behaviour to be undertaken in the future.

In conclusion, this study showed that the probability for skipped spawning for post-spawned sea trout increases with decreasing condition factor in spring. Therefore, skipped spawning may be a strategy to regain energy needed for spawning, which in the end may maximize lifetime reproductive success. Altered post-spawning survival and blocking of river-descent opportunities by damming may alter both proximate and ultimate effects on the probability of repeat spawning. The generally higher survival of kelts than virgin migrants and the positive relationship between length and survival within kelt populations supports the hypothesis that there may be a size-biased predation on sea trout at sea.

Acknowledgements

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

Tormod Haraldstad · Erik Höglund · Frode Kroglund · Esben M. Olsen · Kate L. Hawley · Thron O. Haugen

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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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T. Haraldstad (✉) · E. Höglund · K. L. Hawley
Norwegian Institute for Water Research, Jon Lilletuns vei
3, 4879 Grimstad, Norway
e-mail: tormod.haraldstad@niva.no

T. Haraldstad · E. Höglund · E. M. Olsen
Centre for Coastal Research, P.O. Box 422,
4604 Kristiansand, Norway

F. Kroglund
County Governor of Agder, P.O. Box 788, 4809 Arendal,
Norway

E. M. Olsen
Institute of Marine Research, Flødevigen, 4817 His,
Norway

K. L. Hawley · T. O. Haugen
Department of Ecology and Natural Resource
Management, Norwegian University of Life Sciences,
P.O. Box 5003, 1432 Ås, Norway

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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 km², with an annual average water discharge of 12 m³ 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 km², 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 m³ s⁻¹. The power-generating water is abstracted from a small river reservoir (0.018 km², 6 m depth) and led back into the river through a tunnel tail race. At the tunnel inlet there is a 25 m² 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 RICTL 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.

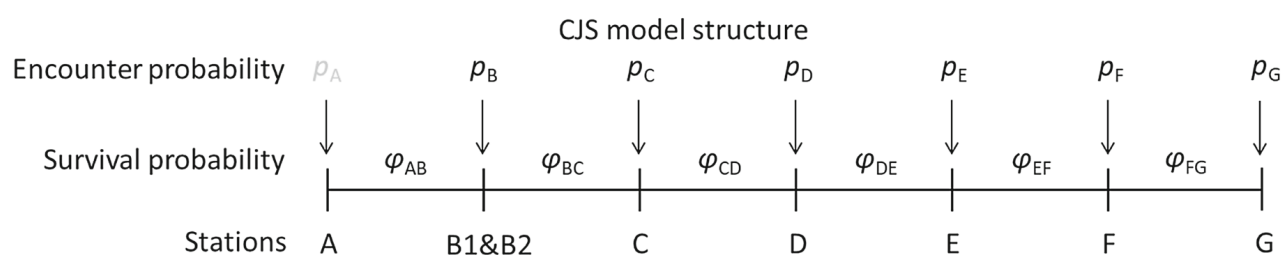
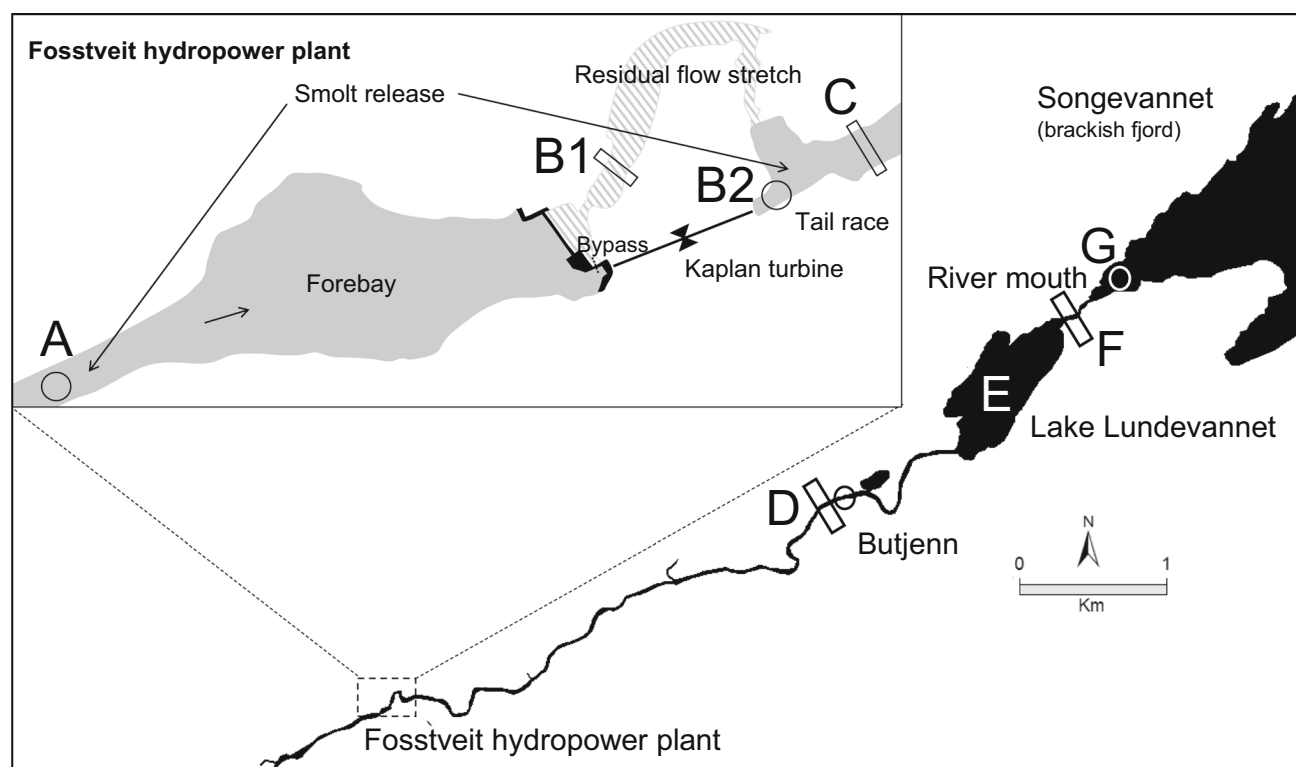


Fig. 1 Fostveit hydropower station (expanded) and lower parts of River Storelva including catch and recapture locations (A–G, rectangles = PIT-antennas, circles = rotary screw traps) with

subsequent CJS model structure. p_A is shaded as this parameter is not estimable

Smolt could move past Fostveit 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 $\text{m}^3 \text{s}^{-1}$) (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

^aNumber 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 $2\text{--}6\text{ m}^3\text{ s}^{-1}$, 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 hydro-power 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. $\phi_{ij} = 1$, constant survival, independent of migration group and body length
2. $\phi_{ij} = G$, different between migration groups, but independent of body length
3. $\phi_{ij} = L$, body length dependent, but not different between migration groups
4. $\phi_{ij} = G + L$, additive effect of migration group and body length
5. $\phi_{ij} = G * L$, 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 [$\phi(\text{group} * \text{stretch}) P(\text{-group} * \text{stretch})$] 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 ($P_{\text{Test2}} = 0.1337$; $P_{\text{Test3}} = 0.1877$), 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 (TL²) 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 ($G \in$ (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 (Δ AIC > 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 = $-0.014 \pm 0.057 + 0.012 \pm 0.004 * \text{Temp}$ ($R^2 = 0.076$, $F = 7.89$, $df = 83$, $P = 0.006$) (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) = $-0.821 \pm 0.362 + 0.523 \pm 0.428 \text{ Route}_{\text{Turbine}}$ (LR-ratio test: $P_{\text{route}} = 0.222$] (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	Δ AICc	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 $p_{B-G}(\text{station})p_E(\text{Length} + \text{Length}^2)$ for all models. AICc is the n-corrected version of Akaike's information criterion (Burnham & Anderson, 2002), Δ AICc 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 length²)

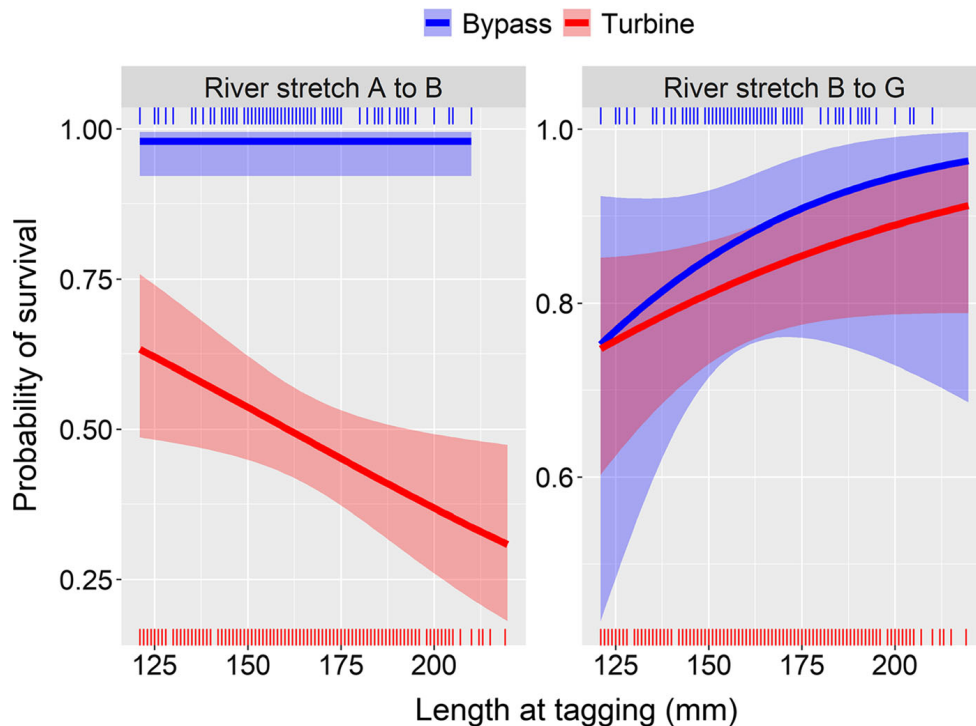


Fig. 2 Predicted migration-route- and length-specific survival probabilities of passing Fosstveit HEP (Station A-B, left panel) and total river descent (Station B-G, right panel). Predictions were made from the selected Cormack–Jolly–Seber model

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

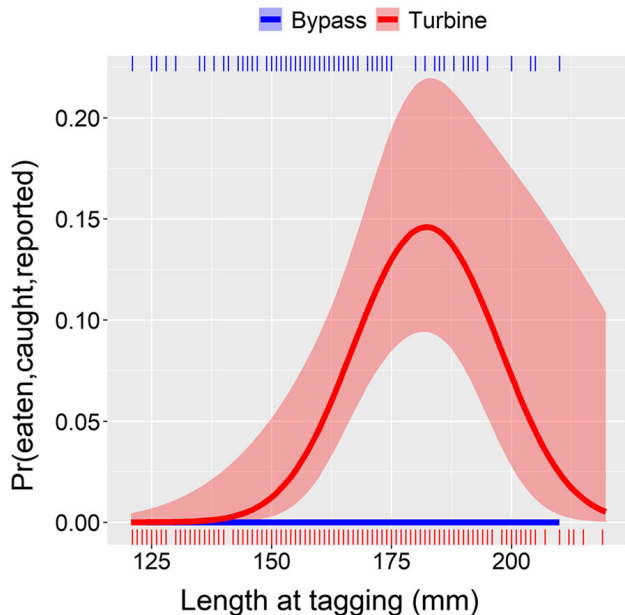


Fig. 3 Predicted probability of smolt being consumed by pike that, in turn, gets caught by an angler and reported. Predictions were made from the selected Cormack–Jolly–Seber model presented in Table 2. Shaded areas represent 95% confidence bounds and red and blue rug at bottom and top of figures represent 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 (\pm SE) for bypass migrants and 597.7 ± 358.4 days (\pm 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

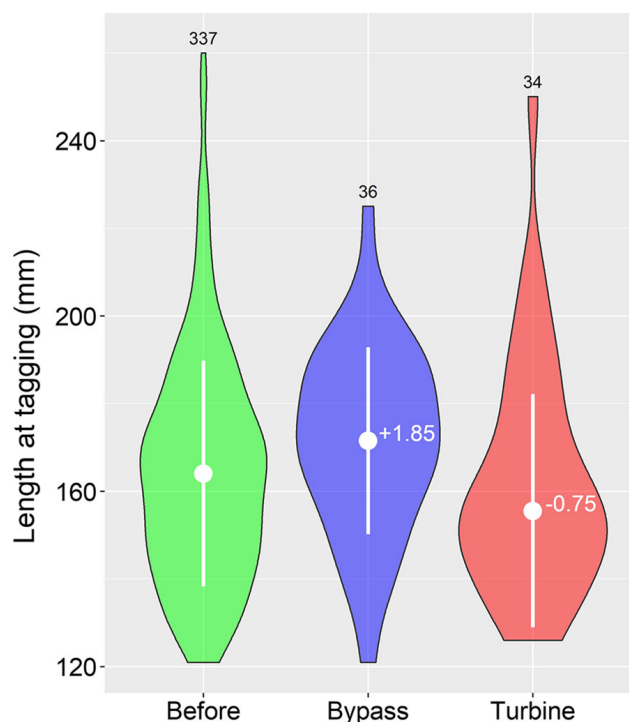


Fig. 4 Violin plots of individual lengths at tagging observations for all upstream Fosstveit HEP dam brown trout smolt individuals (i.e. before choice of migration route) along with tagging length measurements of confirmed (at PIT and/or RST in river mouth) surviving individuals of bypass migrants and 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 predominately 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 ~ 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. R eale 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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Author for correspondence:

Tormod Haraldstad

e-mail: tormod.haraldstad@niva.no

Migratory passage structures at hydropower plants as potential physiological and behavioural selective agents

Tormod Haraldstad^{1,2}, Thron Oddvar Haugen³,
Frode Kroglund⁴, Esben Moland Olsen^{2,5}
and Erik Höglund^{1,2}

¹Norwegian Institute for Water Research (NIVA), N-4879 Grimstad, Norway

²Centre for Coastal Research, University of Agder, N-4604 Kristiansand, Norway

³Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway

⁴County Governor of Aust- and Vest-Agder, N-4809 Arendal, Norway

⁵Institute of Marine Research (IMR), Flødevigen, N-4817 His, Norway

TH, 0000-0002-9575-5144; EH, 0000-0002-1350-8255

Anthropogenic activities affect fish populations worldwide. River dams have profound impacts on ecosystems by changing habitats and hindering migration. In an effort to counteract such effects, a range of mitigation measures have been installed at hydroelectric power plants. However, not all individuals in a population use these measures, potentially creating strong selection processes at hydroelectric power plants. This may be especially true during migration; fish can get heavily delayed or pass through a hydropower turbine, thus facing increased mortality compared with those using a safe bypass route. In this study, we quantify migration route choices of descending wild passive integrated transponder (PIT)-tagged Atlantic salmon smolts released upstream from a hydroelectric plant. We demonstrate how only a few metres' displacement of bypass canals can have a large impact on the fish guidance efficiency (FGE). The proportion of fish using the bypasses increased from 1% to 34% when water was released in surface gates closer to the turbine intake. During a period of low FGE, we observed two different smolt migratory strategies. While some individuals spent little time in the forebay before migrating through the turbine tunnel, others remained there. We suggest that these groups represent different behavioural types, and that suboptimal mitigation measures at hydropower intakes may, therefore, induce strong selection on salmon behavioural traits. The ultimate outcome of these selection mechanisms is

1. Introduction

By reducing river connectivity and thereby blocking or slowing down fish migration, hydropower dams are considered one of the main challenges for restoring and maintaining sustainable fish populations worldwide [1,2]. To complete an anadromous or catadromous life cycle, fish require unimpeded migration routes between freshwater and seawater, for both descending and ascending migrants [3], and a range of mitigation measures have been tried to address this problem [4].

Mitigation measures need to be appropriately aligned to the individual location and the specific behaviour of the targeted species. For instance, downstream migrating salmonid smolts are mainly surface orientated and follow the main river flow. Thus, mitigation measures for Atlantic salmon (*Salmo salar*) smolts are adjusted to this behaviour and guide fish away from the turbine inlet towards a safe bypass and further downstream [5]. The guidance structures can be mechanical barriers that prevent fish from entering hazardous areas or behavioural barriers, repelling fish from hazardous area and/or guiding fish towards a safe area. When aggregated in a safe area, mechanical fish collection systems remove and transport fish further downstream; alternatively, fish swim past the obstacle and into the tailrace via bypass channel systems. However, despite good intentions, some mitigation measures are inefficient or only benefit a part of the population [6,7]. Moreover, since the migration delay and turbine passing are both associated with mortality [4,8], there are potentially strong selection processes at hydropower intakes.

There is mounting evidence that human impacts on wild animal populations are not limited to ecological changes but may also involve strong directional selection and contemporary evolutionary changes [9]. In particular, harvest-induced selection and evolution of life-history traits, such as growth and maturation, have received much attention [10], while fewer studies have investigated human-induced selection and evolutionary change of animal behavioural traits [11]. Despite being a global threat to freshwater fish migration and therefore population viabilities, hydropower-induced selection has so far attracted minimal attention (but see [12,13]).

The smolt run of Atlantic salmon is a fine-tuned migration event, where the majority of a cohort leave their natal river during a period of a few weeks to start their migration towards the feeding areas in the North Atlantic Ocean [14]. The migration of physiologically prepared smolt is initiated by environmental cues in the river, such as changes in temperature or flow [15,16], that coincide with optimal temperature and food supply in the coastal areas [17]. Due to the physiological sensitivity and high predation risk of smolt and post-smolt individuals, these are critical stages in the life cycle of salmonids [15]. Entering saltwater at the right time is essential for survival, and this period of optimal environmental conditions is often termed the smolt window [18]. In general, heavy delay of Atlantic salmon smolt migration is likely to have highly negative impact on survival. The delayed smolt may suffer from increased predation and accumulated energetic costs [18–20].

Damming of rivers may affect both the environmental cues that initiate the smolt run and alter the timing of sea entrance [21]. Water reservoirs in the mountain areas have the capacity to withhold a large amount of water during high precipitation periods and conversely release water during droughts. The natural discharge pattern in the downstream rivers is thus flattened out and controlled by hydropower production profitability rather than natural precipitation variations and catchment run-off. In addition, retention of water from the higher altitude catchment areas may alter river temperatures downstream. By holding back meltwater in spring, these rivers are dominated by low-altitude tributary run-off with higher temperature rather than a mixture of the two. In addition, general lower river discharges cause a faster temperature impact from the external environment throughout the year. Due to hydropower-induced changes in river temperatures, cues that initiate smolt run timing are altered and smolts may not reach the coastal waters when food and temperature are optimal for survival.

Fish migrating through a hydropower turbine are associated with negatively size-dependent mortality [4,8], while using a safe bypass secures survival. Turbine intakes are typically covered by metal gratings or 'trash racks'. These are often substantially submerged, shaded and with higher water flow than the close-to-surface bypass alternatives. Therefore, individual smolt must choose between passage alternatives with very different properties potentially involving individual behaviour and physiological characteristics related to personalities and swimming capacity. Such selection

processes may be crucial in river systems where mitigation measures ought to be timed with phenological events, such as the smolting in salmonids. Thus, the knowledge about the overall efficiency and consequences of possible selection processes at fish passage facilities is needed for optimizing survival and mitigating hydropower-induced selection on behaviour traits.

In this study, we quantify the migration behaviour of wild passive integrated transponder (PIT)-tagged Atlantic salmon smolts released upstream of a newly built hydroelectric plant (HEP). We tested the hypothesis that the placement of a bypass (distance) in relation to the turbine intake (i.e. the distance between the two) is a proxy for its guidance efficiency. In addition, we examine if the trash rack (50 mm spacing) will function as a behaviour barrier, causing repellent behaviour for downstream migrating smolts. Furthermore, we discuss to what extent this repellent effect could be related to fish behaviour characteristics.

2. Methods

The River Storelva, Norway (58°40'9.99 N, 8°58'48.99 E; figure 1) has been regulated for hydroelectric power production since 2008. Fosstveit HEP is a run-of-the-river plant located 6 km above the river mouth and is the only HEP in the catchment area. It uses a 14.5 m high waterfall and the power-generating water comes from a small river forebay through one Kaplan turbine (4 blades, 330 r.p.m.) that is led back into the river through a tunnel tailrace, leaving a residual flow stretch of 230 m between the dam and the downstream tunnel tailrace. At the tunnel inlet, there is a 25 m² conventional trash rack with 50 mm spacing between the vertical bars mounted at a 70° angle from the vertical. A concrete wall covers the uppermost 0.5 m to avoid icing on the rack during winter. At the hydropower dam, there are four surface spill gates (trash gate, fish ladder and two floodgates) that may be used as safe bypasses past the hydropower facility for descending smolts. During the smolt run period, the gates were opened at different time intervals (table 1). In general, the water velocity at the trash gate in front of the tunnel inlet area varies with river discharge. If the power plant uses less than 16 m³ s⁻¹ (Q_{\max}), the water velocity never exceeds 0.64 m s⁻¹ ($Q_{\max}/\text{rack area}$).

Wild Atlantic salmon smolts were caught in the uppermost rotary screw trap (RST; figure 1) on their downstream migration [22]. The smolts were anaesthetized with benzocaine (40–50 mg l⁻¹, ACD Pharmaceuticals AS) before being tagged internally with 23 mm PIT tags (23 mm, half-duplex, Oregon RFID). The tags were inserted through a small incision made ventrally between the posterior tip of the pectoral fin and the anterior point of the pelvic girdle. Based on the previous findings, the incision closed and healed without suturing [23]. The tagged fish were held for one day before being released at the catch site 350 m upstream the hydropower dam. A total of 923 smolts were released between 30 April and 21 May 2010. Migrating smolt could move past the dam using either the turbine tunnel or one of the four surface gates. The turbine migration route was open throughout the smolt run, while the opening of the different surface gates was alternated for the purpose of the experiment. The surface gates were opened sequentially, starting with the gate farthest away from the turbine followed by the one closer to the turbine (table 1). In addition, the fish ladder was opened again from 18 to 19 May to allow upstream migration of Atlantic salmon and sea trout (*Salmo trutta*) spawners that aggregated downstream of the dam. This is in accordance with the concession to operate, which is required of a Norwegian hydropower plant and includes site-specific compensation measures to mitigate possible damage caused to the environment.

The smolts were detected at three PIT antennas (TIRIS RI-CTL MB2A; Oregon RFID) and three RSTs between release site and river mouth. Smolts, using one of the surface gates in the hydropower dam, were detected in a PIT antenna in the residual flow stretch between the dam and the turbine tailrace (figure 1). The detection probability for this PIT antenna was estimated to be 100%, and detection in this antenna was used as evidence for migration through one of the surface gates [24]. An RST with leader net caught the turbine migrants, both dead and alive, in the tailrace (catch probability: 62%). In addition, both turbine and surface gate migrants could be detected in three PIT antennas (catch probability: 45% and 79%) and two RSTs (catch probability: 32% and 21%) between Fosstveit and the river mouth [24]. Only detections in the antennas and traps at Fosstveit were used for the estimation of forebay time (time-to-event analysis) to avoid including time spent in the river stretch between Fosstveit HEP and recapture location further downstream.

The estimation of detection probability for the PIT antenna in the residual flow stretch between the dam and the turbine tailrace was based on the detections of tagged smolts released upstream of the antenna on five different occasions ($n = 50$). This antenna covered the total water column and a

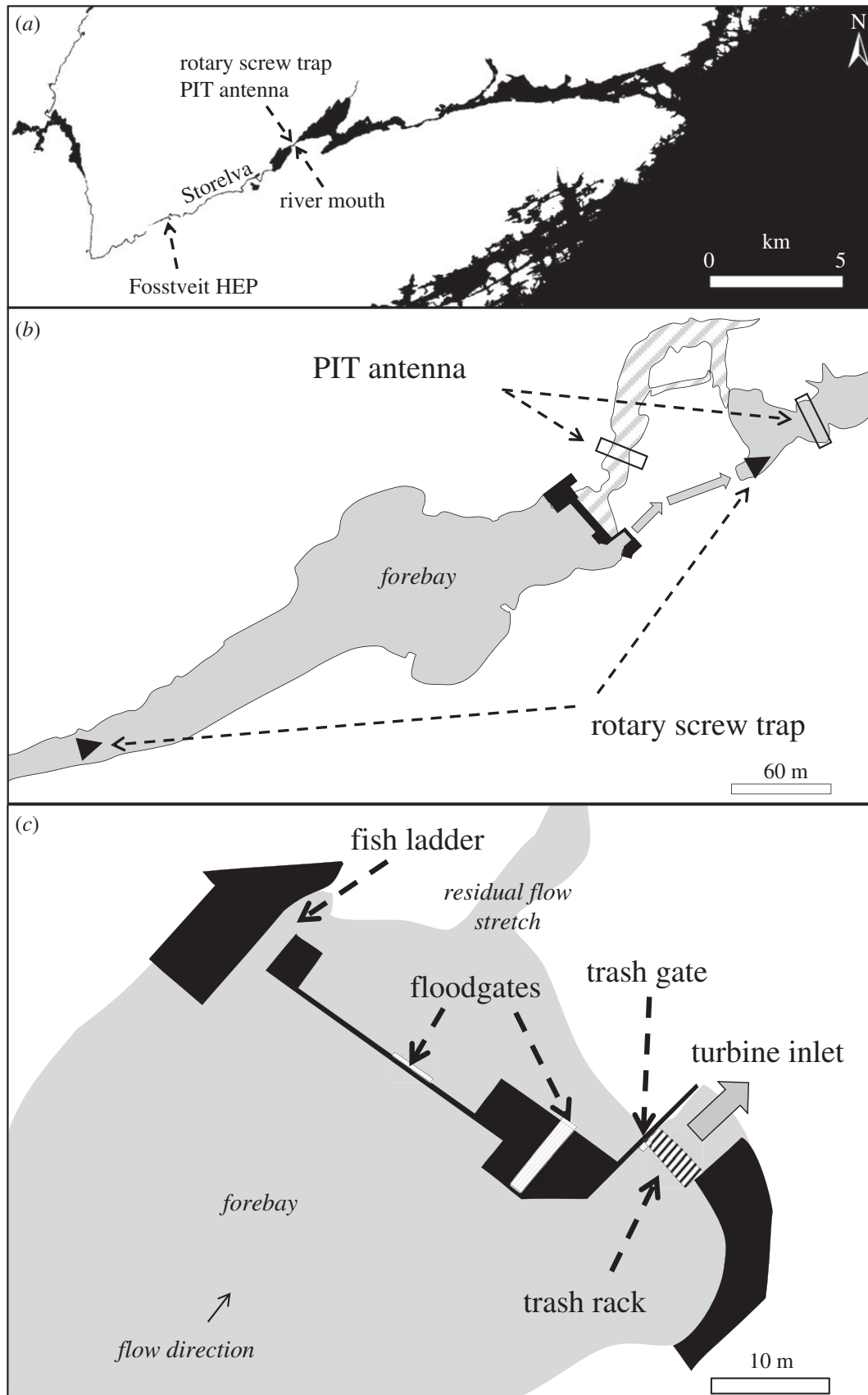


Figure 1. (a) The anadromous parts of River Storelva. (b) Fostveit hydropower station with forebay, residual flow stretch (reduced discharge) and tailrace including catch and recapture locations. (c) Schematic diagram of Fostveit dam with intake trash rack and different surface gates.

higher detection probability at this antenna, compared with the others, is expected due to the reduced discharge in this river stretch. The other PIT antenna detection probability (p_{PIT}) and catchability of RST (p_{RST}) were estimated from the mark-recapture analysis in program MARK [25], by fitting the sequential Cormack–Jolly–Seber model [26] to the individual recapture histories (see [24] for details).

Table 1. Experimental design where the different gates at Fosstveit hydropower dam with individual opening days (grey shades), size and distance to turbine inlet and associated river discharge and temperature (May 2010).

	size (m) (width × depth)	distance to turbine inlet (m)	May					
			1–3	4–7	8–12	13–17	18–19	20–31
turbine inlet	4.30 × 5.90							
fish ladder	0.60 × 0.30	50						
floodgate NW	0.43 × 0.20	35						
floodgate NW	0.43 × 0.30	35						
floodgate SE	1.00 × 0.30	19						
trash gate	0.70 × 0.40	0.3						
river temperature (°C)			8.9	8.9	9.8	11.1	13.4	15.6
river discharge (m ³ s ⁻¹)			4.7	4.5	4.6	4.4	4.7	3.7

The statistical software R [27] was used for data inspection and statistical analyses. Differences in descent trajectories between the RSTs were tested using a bootstrapping routine applied to the Kolmogorov–Smirnov test [28,29]. This routine allows for distribution ties [30]. The tests were run using the `ks.boot`-function in the `matching` library of R [28]. The calculations of daily fish guidance efficiency (FGE) were based on tagged smolts using the open surface gate, divided by the tagged smolts that were available for migration. Smolts that were available for migration were calculated based on released tagged smolts from the start of the study, subtracting the fish detected in the turbine tailrace and the surface gates the previous days. The length difference between turbine and surface gate migrants and the potential effect of distance from the turbine to the surface gates were tested using linear models both as linear predictors and as polynomials of degree 2 (to allow for possible minimum/maximum effects). In addition, a piecewise regression model was fitted to explore breakpoint values for the distance to the turbine intake effect on daily FGEs [31]. This piecewise regression was conducted using the `segmented` R library. Model selection was based on Akaike's information criterion (AIC) [32,33].

In order to quantify and compare the timing of migration between release cohorts and migration routes, candidate time-to-event models were fitted using the `survival` library in R [34]. As predictors, we used day of release (integer) and before/after opening trash gate (categorical, `BA_TG`), and migration routes were included as a group effect. Candidate models, using various additive and multiplicative combinations of these three predictors, were fitted as the Cox proportional hazards model that was subjected to model selection using AIC [35,36]. For this analysis, only individuals that were detected after release were used.

3. Results

Atlantic salmon smolts 2010 cohort in River Storelva were on average 139.0 ± 14.5 mm (s.d.) in total length, and the dominating age at smolting was 2 years. Untagged smolts were captured almost daily in RSTs along the river migration route during the 2010 smolt run, at the trap upstream the hydropower plant ($n = 4832$), in the tailrace ($n = 3487$) and in the river mouth ($n = 726$) (figure 2). The smolt run started in late April and ended at the end of May. The day with 50% cumulative smolt descent was 3 days earlier in the trap upstream the hydropower plant compared with the trap in the tailrace, and the accumulated catch trajectories at the two RSTs were significantly different (two-sample Kolmogorov–Smirnov test, $D_{\text{Fosstveit}} = 0.588$, $p < 0.001$). Furthermore, catches in the river mouth RST were 7 days later than in the tailrace RST (difference in 50% cumulative descent), and the accumulated catch trajectories at the two RSTs were significantly different (two-sample Kolmogorov–Smirnov test, $D_{\text{river mouth}} = 0.794$, $p < 0.001$).

During the smolt run, tagged smolt could move past the dam using either the turbine tunnel or one of the four surface gates. The turbine migration route was open throughout the smolt run and 451 smolts

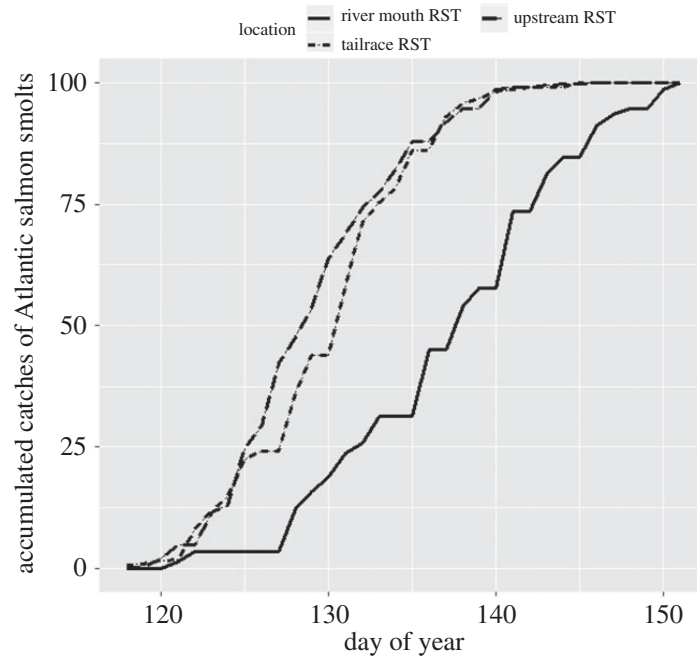


Figure 2. Accumulated daily catches of Atlantic salmon smolts in upstream, tailrace and river mouth RST.

used this as their migration route. A total of 231 smolts were never recaptured, while 239 used one of the different surface gates (table 2). The surface gates were opened sequentially during the smolt run, starting with the gate farthest away from the turbine. The FGE varied from 0% to 33.8%, and the highest guidance efficiency was achieved when the trash gate closest to the turbine inlet was opened. A linear model, including distance to the turbine inlet as explanatory variable, predicted the highest FGE for the gate closest to the turbine inlet (trash gate; figure 3). Trash gate migrants were significantly larger than the turbine migrants ($p < 0.0001$). Note that turbine migrants also include smolts that were detected while dead in the tailrace due to turbine blade strike ($n = 16$).

From the selected time-to-event model, it was estimated that turbine migrants (progression coefficient 2.178 ± 0.465) spent a shorter time in the forebay before migrating compared with the floodgate migrants (coefficient = 0.465) (table 3 and figure 4a). However, the fastest progression rate was found for trash gate migrants (5.056). Even though start day had a significant effect on migration probability, the predicted migration probability trajectories were not very different among release cohorts for the before trash gate opening migrants (figure 4). However, because route was involved in significant interactions with both before/after opening trash gate (i.e. route*BA_TG) and with start day (i.e. route*start), this resulted in a substantial cohort effect for the trash gate migrants. In particular, early release trash gate migrant cohorts had high initial migration probabilities (typically greater than 0.7) at the opening day of the trash gate but with relatively gentle response slope as time progressed (figure 4). Later release trash gate migrant cohorts had lower initial migration probabilities (approx. 0.5) that rapidly progressed to cumulated migration probability of 1. After opening the trash gate, the model predicted much higher probabilities for using the trash gate alternative than the other alternatives (figure 5).

4. Discussion

It is often assumed that the construction of a fish passage automatically restores functional river connectivity. In this study, 22 out of 921 tagged Atlantic salmon smolts used the floodgates and the fish ladder during the initial 20-day period when the trash gate near the turbine intake was closed. However, during this time a part of the population migrated through the turbine, while others waited in the forebay. In the last days of the smolt run, the trash gate, nearby the turbine inlet, was opened and considerable smolt migration occurred through this migration route. This demonstrates how just a few metres' misplacement of a surface bypass may substantially decrease the probability of succeeding with a fish bypass at a power plant intake. Moreover, since both delayed migration and migration through the turbine are associated with high mortality, this suggests potentially strong selection processes at hydropower plants.

Generally, national fish guidelines recommend that the bypass should be placed close to the trash rack or other guidance structures [37–39]. However, there are few case studies testing this recommendation.

Table 2. Number of PIT-tagged Atlantic salmon smolts released upstream of Fostveit hydropower dam and the number of smolt migrating at the different migration routes. In addition, a calculation of accumulated smolts in the forebay each day is added (fish from previous release + daily release – migration routes). Shaded areas correspond to days when the gates were closed.

	PIT-tagged smolts	accumulated in forebay	migration routes					trash gate
			turbine tunnel	fish ladder	floodgate NW (20 cm)	floodgate NW (30 cm)	floodgate SE	
30 April	9	9	0					
1 May	87	96	0	0				
2 May	0	43	53	0				
3 May	127	165	5	0				
4 May	0	128	37		0			
5 May	76	204	0		0			
6 May	51	220	34		1			
7 May	39	254	5		0			
8 May	49	247	53			3		
9 May	53	279	19			2		
10 May	60	337	2			0		
11 May	54	358	32			1		
12 May	70	369	58			1		
13 May	0	340	28				1	
14 May	33	364	5				4	
15 May	31	393	1				1	
16 May	6	360	35				4	
17 May	41	400	0				1	
18 May	2	372	28	2				
19 May	36	389	18	1				
20 May	1	316	4					70
21 May	96	325	18					69
22 May	0	231	16					78
	921	231	451	3	1	7	11	217

In the present study, we demonstrated that how just a few metres' misplacement of a surface bypass may substantially decrease the probability of succeeding with a fish bypass at a power plant intake and further highlighted the importance of assessing passage structures and their efficiency. A short distance between water intake and bypass structure is essential, and a recent study on radio-tagged Atlantic salmon demonstrated how smolts preferred the surface gate located closest to the turbine intake when several other gates further away were available for migration [40]. Downstream migrating smolts are mainly surface orientated and follow the main river flow. In forebays, the main current velocity leads to the turbine intake. We hypothesize that smolts first start their search for other alternative migration routes when facing the dark turbine intake covered with a trash rack. If the alternative migration routes are placed too far away the smolts struggle to locate them. Thus, the findings in our study and the study performed by Havn *et al.* [40] present empirical support to the general advice that the placement of surface bypasses in relation to the turbine intake is important for the FGE, and that it should be placed close to the inlet trash rack or other guiding structures like louvre deflectors or bobble screens.

The data show an up to 20-day delay for bypass migrants due to inadequate placement of the surface bypass. The delay would probably have been even longer if the trash gate close to the intake trash rack had not been opened towards the end of the smolt run. The delayed smolt may suffer high predation

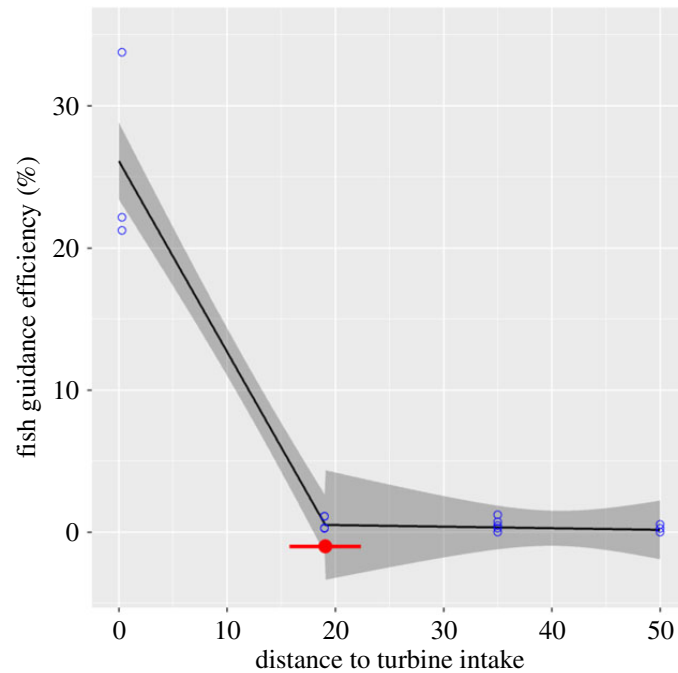


Figure 3. Predicted FGE for different surface gates in the hydropower dam as the distance from the turbine intake (m). Breakpoint estimate with corresponding standard error bars is shown in red. Shaded areas correspond to 95% confidence bounds.

Table 3. Cox proportional hazards parameter estimates for the selected time-to-event model estimation migration trajectories for salmon smolt descending the Storelva river system. BA_TG = before/after opening the trash gate (two levels). Model fit statistics: concordance = 0.771 (0.013, s.e.), $R^2 = 0.561$; likelihood ratio test: $\chi^2 = 569.1$, d.f. = 7, $p < 0.0001$.

term	coef	exp(coef)	s.e.(coef)	Z	Pr(> z)
start	0.465	1.592	0.076	6.080	<0.0001
route[Trash gate]	5.056	156.989	0.828	6.105	<0.0001
route[Turbine]	2.178	8.832	0.644	3.382	0.0007
BA_TG[Before]	6.351	572.924	0.535	11.877	<0.0001
start*route[Trash gate]	-0.300	0.741	0.076	-3.916	<0.0001
start*route[Turbine]	-0.200	0.819	0.069	-2.884	0.0039
start*BA_TG[Before]	-0.266	0.766	0.034	-7.764	<0.0001

levels, elevated energetic costs and decreased migration speed [18–20]. Normally, the smolts enter the coastal waters at a time with optimal temperature and food supply [17]. The importance of this optimal migration window is demonstrated by smolts entering the coastal waters at other times that have low survival to adults [41]. In addition, several smolts were not recaptured after release in our study, which indicates that some smolts lost motivation upstream of the dam and stopped migrating, suffered predation or died. Alternatively, they migrated through PIT antennas and traps without being registered. This last alternative is highly unlikely due to the total detection/encounter probability through the system of PIT antennas and RSTs being close to 1 [24]. If smolts are prevented from reaching seawater, a partial re-adaptation to freshwater will occur, known as de-smolting or parr-reversion [42]. Our findings indicate that a part of the smolt population might postpone migration if only turbine migration and a misplaced bypass are available as migration routes. Much effort has been made to develop fish-friendly turbines [43], thus our findings highlight another aspect of this development. Even though the turbine is fish friendly with high survival for turbine migrating fish, there could still be characteristics at the turbine intake that will prevent a part of the smolt population from migrating. A combination of both surface bypasses and fish-friendly turbines could be a provident mitigation measure that allows safe downstream migration for smolt with individual migration preferences.

The smolts that used the turbine as a migration route were smaller than the smolts that waited and migrated through the trash gate. Potentially, the trash rack could function as a strainer, only letting

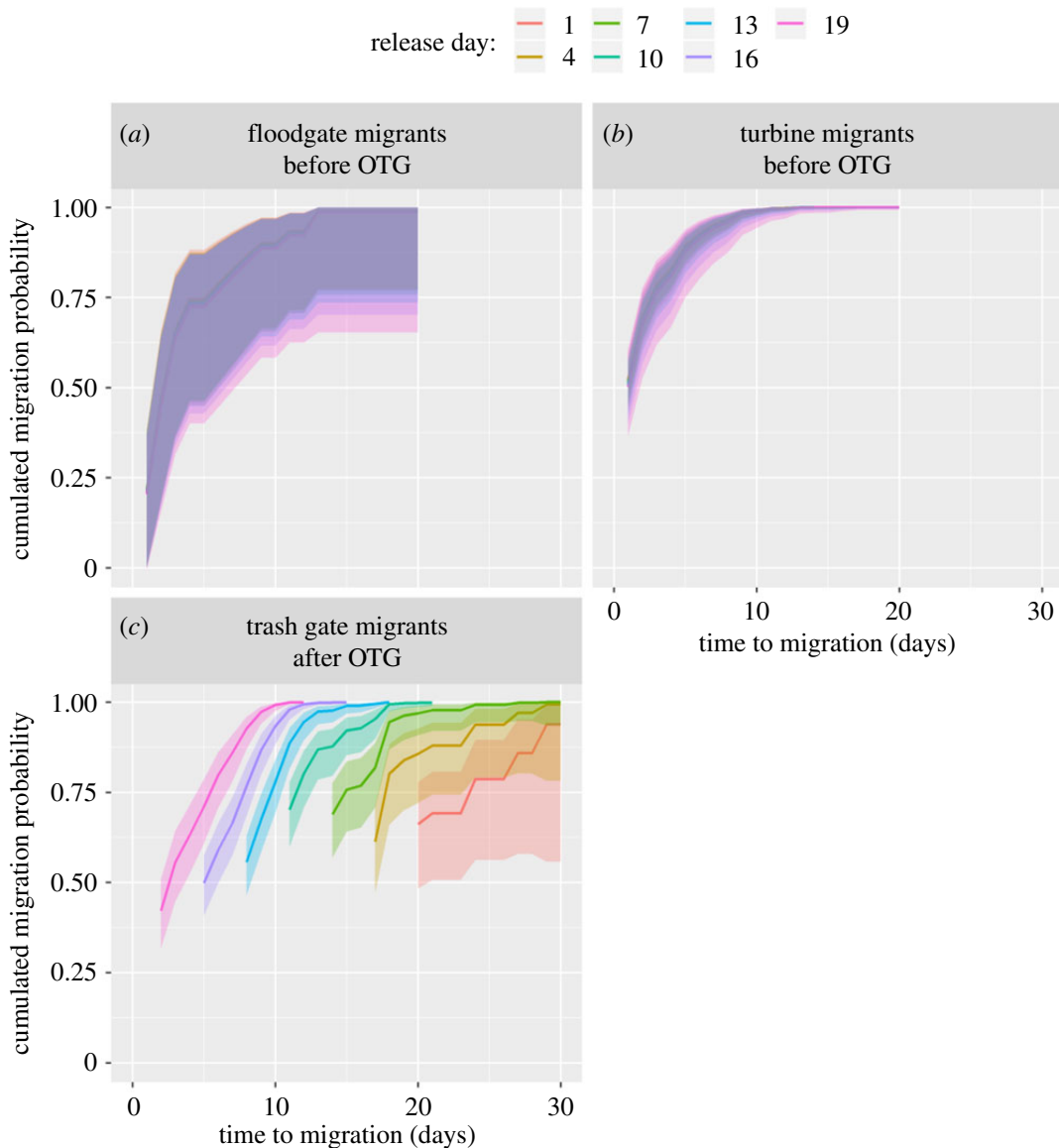


Figure 4. Prediction plot for the cumulated migration probabilities for the selected Cox proportional hazards model. For the floodgate (a) and turbine migrants (b), the before open trash gate (OTG) period is plotted only, as trash gate migrants do not have migration opportunities during this period. The different colours reflect different release cohorts, but they are hard to separate as the confidence bounds are largely overlapping. (c) The predicted trash gate migrants' cumulated migration trajectories for seven release cohorts (different colours) for the OTG period. The most recent cohorts appear from the left in the figure. Shaded areas correspond to 95% confidence bounds.

through the smallest individuals. However, the rack spacing is rather large (50 mm) and Haraldstad *et al.* [44] document that sea trout kelts (*S. trutta*) up to 450 mm migrated through this trash rack during spring descent. This lends support to the assumption that there are other mechanisms, such as behavioural traits, in addition to length that could explain smolt preference for different migration routes. It is clear that larger smolts have a greater capacity to withstand high water velocities over time compared with small fish [45]. Smolts might hold their position in front of the rack for a period and only the best swimmers (large individuals) resist the strong current. However, a study by Peake and McKinley [46] demonstrated that wild Atlantic salmon smolts of 124–211 mm in length did not show differences in swimming capacity against currents up to 1.26 m s^{-1} . Considering the large rack spacing and that the water velocity at the tunnel inlet area is low (less than 0.19 m s^{-1}) at Fosstveit HEP, then this suggests a minor contribution of size and swimming capacities to the factors underlying individual differences in migration routes in our study. Thus, contrasting behavioural profiles may be an underlying factor to the observed size differences between turbine and bypass migrating smolts in the present study.

Time spent in the forebay was fairly similar among turbine migrants and did not depend on time until the trash gate was open when the majority of the fish migrated. It is possible that this constancy in time to migrate through the turbine represents a certain behavioural profile in smoltified salmon. It

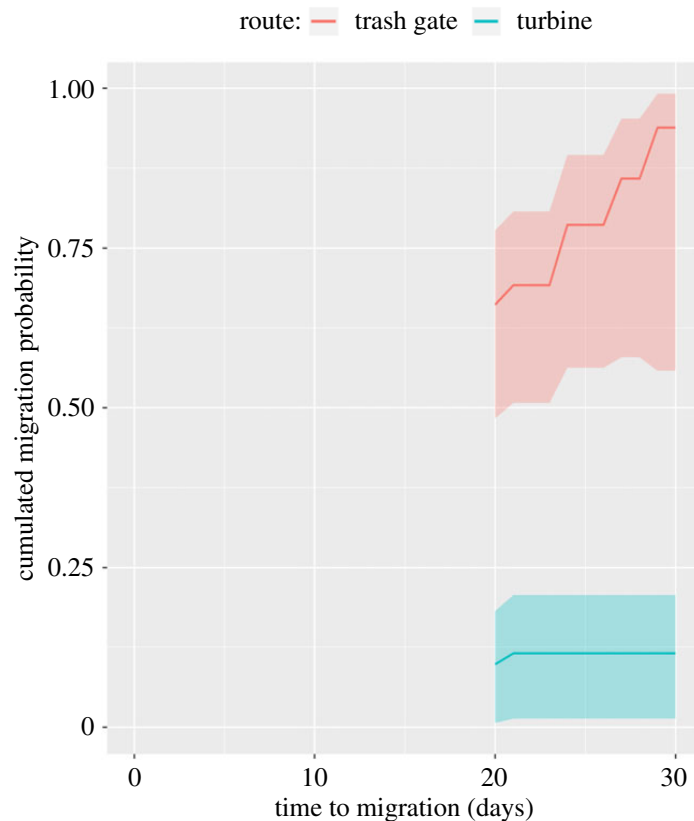


Figure 5. Prediction plot for the cumulated migration probabilities for the selected Cox proportional hazards model focusing on the ‘after trash gate opening’ period. Trash gate and turbine migrants are plotted only, as no migrants used floodgate alternatives during this period. The plotted trajectories are for individuals that were released the day before opening the trash gate. Shaded areas correspond to 95% confidence bounds.

has been documented that behavioural traits are often organized in suites of traits that show constancy across context and time, representing different behavioural syndromes within a population [47]. Moreover, such an individual variation has been associated with life-history traits [48], and in a recent review, Mittelbach *et al.* [49] pointed out that little attention has been paid to the ecological consequences of the varying behavioural phenotypes in wild populations. The results from our study point towards selection processes operating on the behavioural axis in delayed migrants versus turbine migrants. Despite the expected increase in mortality for turbine migrants due to turbine blade strikes, the surviving turbine migrants may experience higher post-smolt survival compared with smolts that experience significant delays in migration [15]. Hence, there might be complex trade-offs between acute survival costs (via turbines) for the benefit of optimal sea entrance timing versus acute survival maximization (via bypass) at the cost of suboptimal sea entrance timing. The ultimate outcome of this selection game remains to be elucidated by lifetime survival and reproduction data. Moreover, because growth rate and the behavioural profile of an individual often are linked to each other [50], contrasting behavioural profiles may be an underlying factor to the observed size differences between turbine and bypass migrating smolts in the present study. Further studies are needed to untangle the interplay between size- and behaviour-dependent selection at hydroelectric power plants and their potential population-level effects.

These results emphasize that timing and placement of mitigation measures are important for optimal management of Atlantic salmon. Moreover, it sheds light on the potential selection processes at hydropower intakes, stressing that both behaviour and size should be included as important traits under selection in wild Atlantic salmon populations in regulated rivers.

Ethics. Permission to catch Atlantic salmon smolt in River Storelva was granted by the County Governor of Aust-Agder. PIT-tagging of fish was approved by the Norwegian Animal Research Authority, NARA (Forsøksdyrutvalget, FDU, FOTS ID 2447).

Data accessibility. All data and R scripts used in the present study are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.8b876q6> [51].

Authors’ contributions. F.K. designed the study; F.K. and T.H. collected and prepared data for analysis; T.H., F.K., E.M.O., T.O.H. and E.H. analysed the data and interpreted the results; T.H. drafted the manuscript; T.H., F.K., E.M.O., T.O.H. and E.H. were involved in finalizing the manuscript. All authors gave final approval for publication.

Competing interests. The authors declare no competing interests.

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Hydropower-induced selection of behavioural traits in Atlantic salmon (*Salmo salar*)

Tormod Haraldstad^{1,2}, Thron O. Haugen³, Esben M. Olsen^{2,4}, Torbjørn

Forseth⁵, Erik Höglund^{1,2}

¹ Norwegian Institute for Water Research, Jon Lilletuns vei 3, NO-4879 Grimstad, Norway

² Centre for Coastal Research, P.O. Box 422, NO-4604 Kristiansand, Norway

³ Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

⁴ Institute of Marine Research, Flødevigen, NO-4817 His, Norway

⁵ Norwegian Institute for Natur Research, Trondheim, Norway

Correspondence: T. Haraldstad, Norwegian Institute for Water Research, Jon Lilletuns vei 3, 4879 Grimstad, Norway,

E-mail: tormod.haraldstad@niva.no

Abstract

Renewable energy contributes towards the world's growing energy demands and urgent need for mitigating climate change. However, their infrastructure has the potential to substantially alter the environment which, in turn, can induce new challenges and therefore selection regimes for affected animals. To explore selection processes operating at a river hydropower plant, we monitored Atlantic salmon smolt individuals during their seaward migration. When passing the hydropower plant, the smolts would have to choose between a surface fish passage or a submerged turbine intake. Smolts were scored for behavioural type prior to their migration choice, and we found that smolts with high basal activity had higher probability of using the fish passage than the turbine tunnel. In addition, migration route choice was a partly consistent trait, as fish passage migrants that were faced with the migration route choice twice tended to repeat their original route. Higher mortality among turbine migrants could potentially reduce behavior- and corresponding genetic diversity that is essential to cope with future environmental challenges.

Introduction

Human activities, such as intensive agriculture, forest management and urbanization have tremendous impact on the nature and have thus been changing the adaptive landscape of many organisms. Especially, industrialisation, including overfishing, release of pesticides, herbicides and release of toxic compounds, are well known examples of such human induced selection. Accordingly, humans may be the most powerful evolutionary force of the world [1], and therefore a central driving force in contemporary evolution [2].

Renewable energy is vital for meeting the worlds growing energy demands and urgent need for mitigating climate change. However, the local ecological impacts of such hydro, wind and solar technologies can be detrimental [3]. Hydropower has dramatically affected river ecosystems, partly by reducing river connectivity by blocking or slowing down fish migration. As such, hydropower is considered one of the main challenges for restoring and maintaining sustainable fish populations worldwide [4, 5]. However, surprisingly little attention has been paid to the important question of whether hydropower may also induce new selection regimes that affect fish populations.

Atlantic salmon (*Salmo salar*) is an iconic species, having high ecological and socioeconomic importance. Its anadromous life history requires unimpeded migration routes between the oceanic feeding areas and freshwater spawning and nursing habitats [6]. Thus, hydropower dams represent major obstacles for Atlantic salmon populations [7, 8]. Following this, a range of mitigation measures have been explored, often exploiting fish behaviour patterns to divert fish away from dangerous areas and guide or attract fish towards alternative migration routes [9]. However, some salmon smolt individuals do not respond to guidance structures during their river descent but instead use the turbine tunnel as a migration route [10], which may lead to high mortalities [11, 12].

It is widely recognised that fishways can be species [10, 13, 14] and size selective [15-17]. Still, even within the same size-group in a fish population there may be among-individual variation in migration route choice. Accordingly, Haraldstad [18] suggested that the migration route choice of salmonid smolts at a hydropower forebay was not random, but rather a consequence of individual differences in physiological and behavioural traits. However, it remains to be investigated whether the significant differences in mortality related to migration-route choice at hydropower dams will induce selection on individual behavioural traits.

To explore potential selection processes at a hydropower plant, we compared the migration route of previously behaviour-scored Atlantic salmon smolt individuals and their choices between a surface fish passage or a submerged turbine intake under a wide range of environmental conditions. Individually tagged fish were subjected to three behavioural assays; basal locomotor activity, net restraint and willingness to leave a familiar environment. Whereupon they were released in the hydropower forebay and the individual migration route choices were then recorded from route-specific trap recaptures. Moreover, the consistency of migration route choice was investigated by releasing two groups of smolts; one “naive” group, never confronted with the hydropower intake and one “experienced” group that had migrated through the fish passage once before.

Materials and methods

Study area

The study was carried out in the river Nidelva, southern Norway (58.41540°N, 8.74242°E).

The river has a mean annual discharge of $110 \text{ m}^3\text{s}^{-1}$ and the Atlantic salmon uses the lowermost 35 km as spawning and nursery habitat. Several tributaries are important habitats for salmonids in this river system, including the River Songeelva that intersects Nidelva at Froland, 25 km upstream the river mouth. Nidelva catchment is 4015 km^2 and extensively regulated for hydropower. The lowermost hydroelectric plant is a run-of-the river plant, situated at Rygene, 9.4 km upstream the river mouth. The experiments of the current study were undertaken at this power plant. During smolt migration in spring, water ($5 \text{ m}^3\text{s}^{-1}$) is released through a surface fish passage to aid the salmonid smolts past the turbine intake [19]. The fishway is located perpendicular to the approaching flow on the eastern side of the submerged intake trash rack. The vertical bar spacing in the trash rack is 80mm, and thus large enough for smolts to pass. When in the hydropower forebay, the smolts are thus faced with a choice of two different migration alternatives with very different appearances: one being a submerged, dark and fenced turbine tunnel and the other a small surface fish passage channel.

Fish sampling and tagging

Downstream migrating wild Atlantic salmon smolts were caught at two locations during the smolt migration period; in a Wolf-trap placed in the fishway at Rygene and in the tributary Songeelva using a modified fyke-net (Table 1). Traps were emptied every morning. Smolts captured in Songeelva were transported by car to Rygene hydropower station. The smolts were anesthetized with MS222 (Metomidate) (2 mg/l) before being tagged internally with

passive integrated transponder (PIT) tags (23 mm, half duplex, Oregon RFID). 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.

Behavioural assay

Behaviour traits were scored in each of the following contexts: A basal locomotor activity (adapted from [20-22]), response to net restraint (adapted from [22, 23]) and willingness to leave a familiar area (adapted from [23-25]). These assays were chosen because they have been used to characterize important aspects of behaviour in fish, such as basal activity pattern, escape response and risk-taking behaviour [22-24].

Basal locomotion: After 24 h of tagging recovery, four smolts were netted from the holding tank and inserted individually into each of four visually isolated observation aquariums (25, 15, 20 cm L, W, D) standing on a UV-table. Fish behaviour was recorded in total darkness by video cameras with UV-filters for 20 min, and the analysed for swimming distance by EthoVision XT (Noldus, Version 11).

Net restrain; After the locomotion assay, fish were placed in nets, held in an angle of 45° by stands and the number of escape attempts was recorded for 10 sec.

Willingness to leave a familiar area: At each day, individually behaviour-scored fish were collected in a white semi-transparent tank (1x1x1 m) at the riverside. The tank was supplied with flow-through river water. A dark tube (10 cm diameter) drained water from the surface of the tank back into the river. After one night of acclimation to the tank environment, a net was removed from the surface tube and smolts could swim back into the River Nidelva 100 m upstream the hydropower intake. Individuals

leaving the tank during the next 32 h were registered in a PIT-antenna mounted on the escape tube. Remaining individuals (after 32 h) were manually PIT-scanned for identification. The binomial response; leavers or stayers were used in further analysis. To allow assays to be conducted every day, the assay was performed in duplicate tanks.

Consistency of migration route choice

Smolts caught in the Songeelva tributary represented individuals that were naive to the hydropower water intake, while smolt caught after migrating through the fish passage at Rygene hydropower intake represent fish passage experienced smolts. Smolts from the two locations were PIT-tagged and placed in the same holding tank supplied with flow through river water. After one night, smolts were released in the hydropower forebay 100 m upstream the water intake and fish passage.

Table 1: Number of PIT-tagged Atlantic salmon smolts released upstream Rygene hydropower plant during 2018 smolt migration period. Experienced smolts were caught in the trap at Rygene fishway while naïve smolts were caught in Songeelva tributary.

Release date	Consistency test		Behavioral scored
	Experienced	Naive	Naive
04.05.2018			1
05.05.2018		2	
06.05.2018	1	1	4
07.05.2018		1	16
08.05.2018	20	55	27
09.05.2018	24	2	19
10.05.2018	85	14	20
11.05.2018	93	14	34
12.05.2018		87	5
13.05.2018			10
14.05.2018	52	166	5
15.05.2018	31	43	24
16.05.2018		5	1
17.05.2018		1	
18.05.2018		2	18
	306	393	184

Recapture of tagged smolts

PIT-tagged smolts that had been subjected to behavioural scoring and consistency test were captured in a Wolf-trap if they used the fish passage. The Wolf-trap covered the entire water column in the fish passage channel with bar spacing of 10 mm. Tagged individuals were identified using a handheld PIT-reader. Turbine migrants were not detected due to methodological limitation of PIT-antenna size and placement in such high-discharge / high-current tail-race area. Non-recaptured smolts were therefore assumed to be turbine migrants.

Statistical analysis

The statistical software R [26] was used for data inspection and statistical analyses. Linear models (lm), with corresponding one-way anova, was fitted to test for correlations between behavioural assay scores. The probability of fish passage migration was estimated by fitting candidate generalized linear models (GLM) with relative fish passage discharge to turbine intake discharge ($Q_{rel} = Q_{fish\ passage} / Q_{turbine}$, %), Q =water discharge (m^3/sec), fish length (mm), locomotor activity (distance moved in cm), net restrain assay (number of escape attempts) and willingness to leave a familiar environment (0=leavers; 1=stayers).

To test for consistency of migration route choice at the hydropower forebay we fitted candidate GLMs with catch location (Songeelva tributary: “naive” and Rygene fish passage: “experienced”), fish length and relative fish passage discharge as predictor variables. The logit link function was used for linearization of the binomial response in both GLMs (0 = not recaptured; 1 = recaptured in fish passage). Model selection was based on corrected Akaike's information criterion (AICc; [27, 28])

Results

The Atlantic salmon smolt migration period commenced on 3 May in the Songeelva tributary and ended 15 May. The median migration date were three days earlier in the Songeelva tributary than in the main river at Rygene, though there was not a statistically significant difference in catch trajectories between the two sites ($p > 0.05$ two-sample Kolmogorov-Smirnov test). Relative fish passage discharge was on average $4.2 \pm 1.23\%$ (\pm SD) during the smolt migration period. The Songeelva smolt were on average 131 ± 9.8 mm long (\pm SD).

The smolts had an average swimming speed at 52.14 ± 57.15 cm/min (\pm SD) during the basal locomotor activity assay and there was a positive relationship between the smolt activity in the first and finale 10 minutes of the assay ($p < 0.001$), but no correlation with the net restraining assay results ($p > 0.05$). Number of escape attempts during the 10 second net restraining assay were on average 13.6 ± 8.4 (\pm SD). There was no difference in the escape attempts nor locomotor activity between smolts that left or stayed in the familiar environment ($p > 0.05$). In total, 33.3 % of the smolts left the familiar environment before the assays were terminated. When back in the river, 63 smolts were recorded in the fish passage, while 127 were assumed to be turbine migrants. There was no correlation between fish length and the three behavioural essays ($p > 0.05$).

To investigate which of the above factors could explain variation in fish passage migration probability, environmental and individual variables were incorporated in a GLM. AICc-based model selection revealed highest support for an additive model including relative fish passage discharge and activity (i.e. $\text{Pr}[\text{fish passage migration}] = \text{Activity} + Q_{\text{rel}}$, Table 2, Figure 1). This model attained an AICc-score 0.66 lower than the second model ($\text{Activity} + Q_{\text{rel}} + \text{Stayers}$). The selected model predicted highest probability of fish-passage

migration when a high amount of water was released in the fish passage for individuals that had a high basal locomotor activity.

155 out of 306 experienced smolt showed consistency in migration route choice and were recaptured in the fish passage a second time, while 183 out of 393 naïve smolts used the fish passage. AICc-based model selection revealed highest support in the data for an additive effect of relative fish passage discharge and load experienced on the probability of fish passage migration at the hydropower intake (i.e., $\text{Pr} [\text{fish passage migration}] = Q_{\text{rel}} + \text{load experience}$; Table 3, Figure 2). This model attained an AICc-score 1.36 lower than the second-most supported model (load experience + Q_{rel} + fish length). The selected model predicted highest probability of fish passage migration when a high amount of water was released through the fish passage and higher for experienced than naïve smolt.

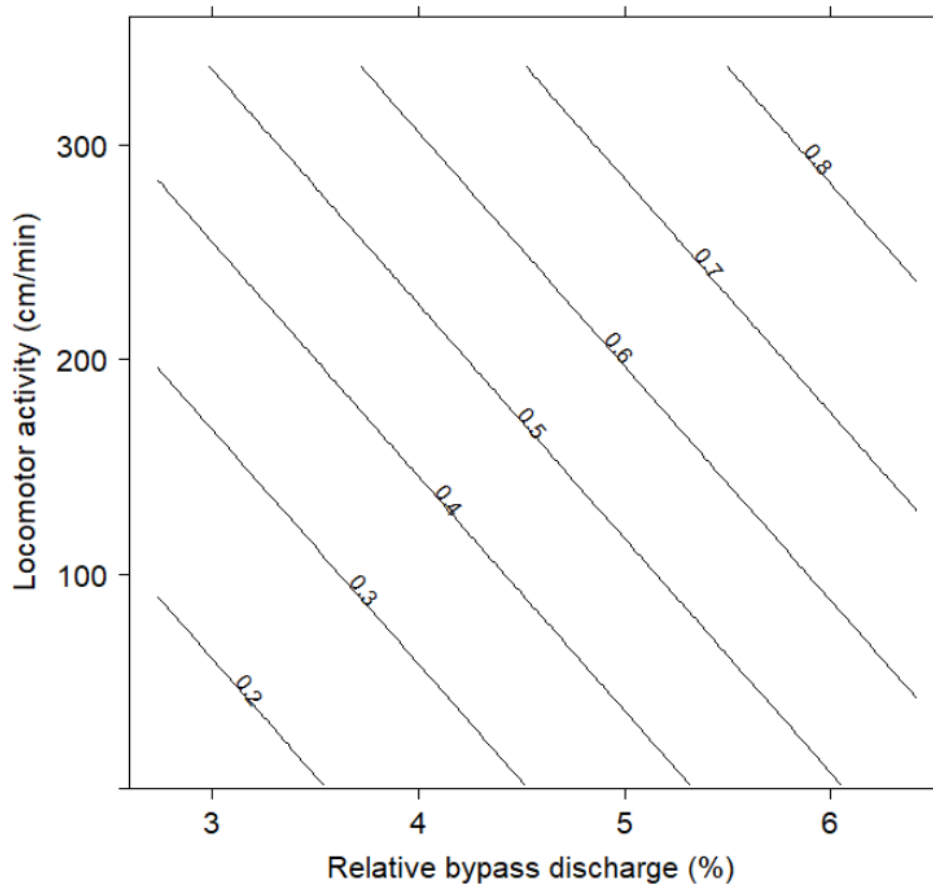


Figure 2: Predicted fish passage migration probability for Atlantic salmon smolts at Rygene hydropowerplant as a function of locomotor activity (distanced swam per min during the 20min basal locomotion activity assay) and percent discharge allocated to the fish passage in relation to the turbine tunnel. Probability predictions, displayed as isolines, were derived from the most supported binomial GLM, as reported in table 2.

Table 2 Logit-parameter estimates and corresponding likelihood-ratio test statistics for the most supported GLM fitted to predict fish passage probabilities in PIT-tagged Atlantic salmon smolts from the Nidelva tributary Songeelva. Q_{rel} (Relative fish passage discharge) = Discharge in the fish passage/discharge in the turbine tunnel, Activity = The distance smolt swam in the aquarium during the 20 min trail.

Parameter estimates			LR-test statistics			
Term	Coeff.	SE	Effect	df	χ^2	p
Intercept	-3.348	0.604	<i>Q_{rel}</i>	1	18.08	< 0.001
<i>Q_{rel}</i>	0.552	0.133	<i>Activity</i>	1	7.08	0.0967
<i>Activity</i>	0.001	0.001				

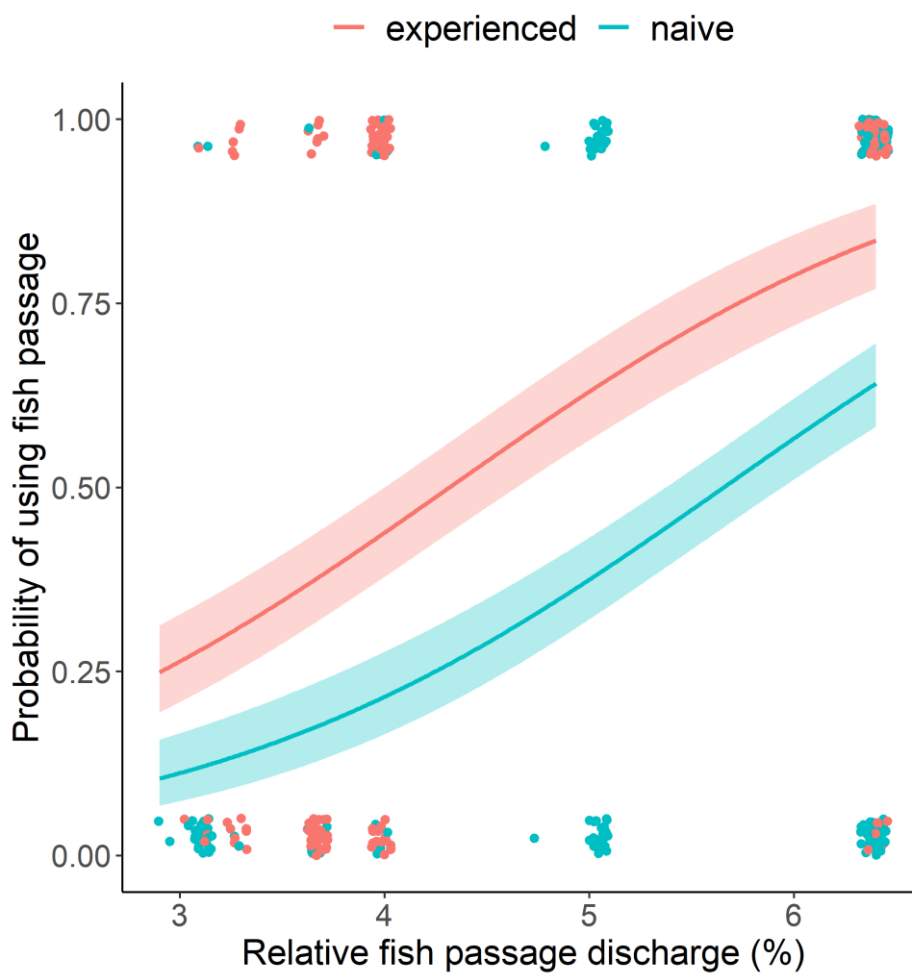


Figure 2: Predicted fish passage migration probability for experienced (red line) and naive (blue line) Atlantic salmon smolts at Rygene hydropower intake as a function of water allocation derived from the selected binomial GLM reported in Table 3. Shaded areas represent 95 % confidence bounds including the distribution of individual bypass- ($y=1$) and turbine migrants ($y=0$) at different discharge regimes (the observations have been x-y-jittered to reveal overlapping data).

Table 3 Logit-parameter estimates and corresponding likelihood-ratio test statistics for the most supported GLM fitted to predict fish passage probabilities for fish passage experienced and fish passage naïve PIT-tagged Atlantic salmon smolts at Rygene HEP. Q_{rel} (Relative fish passage discharge) = Discharge in the fish passage/discharge in the turbine tunnel, Load experience = Fish passage naïve (catch location: Songeelva) and fish passage experienced (catch location: Rygene fish passage).

Parameter estimates			LR-test statistics			
Term	Coeff.	SE	Effect	df	χ^2	p
Intercept	- 3.367	0.352	<i>Load (Naive)</i>	1	1.15	<0.001
<i>Load (Naive)</i>	- 1.045	0.201	Q_{rel}	1	126.69	<0.001
Q_{rel}	0.780	0.078				

Discussion

In this study, we show that individual differences in migration route choice in front of a hydropower intake was a consistent trait, associated with contrasting behavioural profiles in migrating Atlantic salmon smolts.

Smolt with a high basal activity pattern had higher probability of using the fish passage than smolt with lower activity in this study. Generally, activity is widely used as a personality proxy in animal behavioural research [29]. Accordingly, field studies of wild salmonid document repeatability of movement patterns over time and across different contexts [30]. In a previous study, Haraldstad [18] showed that some smolts migrated into the turbine tunnel almost instantly, while others hesitated and stayed in the forebay for days until a suitable alternative migration route became available. Moreover, it was hypothesized that the turbine migrants and hesitating individuals represented different behaviour types. In relation to this, it is important to consider that the smolts are faced with a choice of two different migration alternatives with very different appearances: One being a dark, submerged and fenced tunnel and the other a small surface bypass channel. The current study demonstrates that the route choice is linked to individual variation in basal activity. This lends support to the hypothesis that differences in behavioural phenotypes effect route preferences of Atlantic salmon smolt at hydropower plant water intakes.

Individuals with former fish passage experience had, under similar discharge conditions, a significantly higher probability of making the same migration route choice again compared to their naïve counterparts. This finding demonstrate that the route choice is a partly consistent trait and strengthens the hypothesis that the migration route preferences is partly based on individual trait variation, and not environmental aspects

alone. An alternative explanation is that experienced smolts learned from their previous choice [31], thus our set-up was not made for discriminating between learning and personalities. Furthermore, learning and personalities may be parts of the same story because cognitive abilities have been suggested to be linked to personality traits in fish [32]. Given the significant higher survival for fish passage migrants than turbine migrants [33] opens for evolutionary responses on traits associated with the migration route choice, provided both sufficient additive genetic variance for these traits and that this variance is correlated with life-time fitness [34]. Clearly, the smolt does not only face behavioural selection while descending the river and therefore may be countered by other selection situations later in life. This makes it hard to predict what the ultimate outcome of these combined selection factors will favour in the longer term. As a first step our data suggests that mitigation measures at hydropower plants aimed at contracting turbine mortality potentially will induce new selection regimes.

Generally, behaviour traits tend to disassociate during ontogenetic shifts [35]. Such a disassociation phenomenon may explain why just basal activity pattern seemed to impact emergence route choice where other behaviour traits did not. This finding indicate that previously reported relationships between responses in the different behavioural assays, as found in [22, 23, 36], have weakened in our groups of smolt. Further studies are needed to clarify how physiological and behavioural changes associated with smolting affects the individual's trait association and how these, in turn, are affected by selection in anthropogenically altered environments.

Allocating relative more flow to the fish passage increased guidance efficiency in both experiments and this is in accordance with several other studies [19, 37]. Still, smolts

with low basal activity had a lower probability of fish passage migration than the more active counterparts throughout the range of flow regimes. Most mitigation measures depend on certain fish behavior responses to function and will thus potentially act as selective agent when there is a possibility to migrate through the turbine. Personality differences is important for maintaining stability, resilience, and persistence of populations and the genetic component makes it an important dimension of biodiversity [38, 39]. In fisheries, there is an increasing body of literature showing how anthropogenic selection processes transform the adaptive landscape and induce selection on behavioral traits [40-42]. Given the lessons learned from these studies, selection on behavioral traits may be expected to act on fish living in hydropower regulated ecosystems, leading to an altered evolutionary pattern followed by a reduction in behavior and corresponding genetic diversity. The present study highlights the importance of non-selective fish passages at hydropower plants. Specifically, implementing small-spaced trash racks will prohibit descending Atlantic salmon smolts from entering the turbine tunnel and help protect the population behavioral diversity.

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